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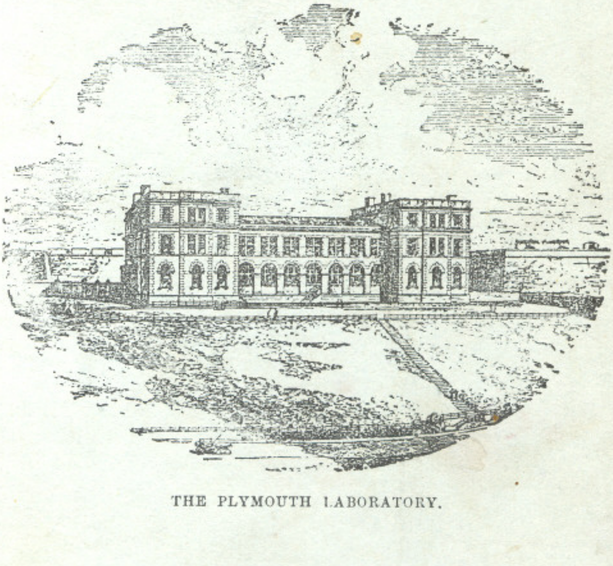

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Observations and Experiments on Sex-Change in the European Oyster (*O. edulis*). Part III. On the Fate of Unspawned Ova. Part IV. On the Change from Male to Female.

By

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With Text-Figures 1 (Part III) and 1–7 (Part IV).

CONTENTS.

PART III. ON THE FATE OF UNSPAWNED OVA.

AN analysis of the quantity and distribution of unspawned eggs in the gonad of *O. edulis* recorded in Table IV, **1**, 1927 (of oysters with young) and Table IX, **1**, 1927 (of post-spawned oysters), gives useful information regarding the occurrence and fate of unspawned ova as may be seen from the figures given in Table A.

TABLE A.

Group.	Developmental stage* of embryos or larvæ found in mantle cavity.	No. of *O. edulis* in each period.	Gonad of parent. with few relict ova. no.	%	with ∞ relict ova. no.	%	Totals with unspawned ova. no.	%
1.	Embryos (A + B + C) . .	205	122	*60*	46	**22·5**	168	*82·5*
2.	Ciliated and early shell stages (D + E)	241	113	*47*	28	**21·3**	141	*68·3*
3.	Coloured larvæ with bivalve shell (F)	256	54	*21*	8	**3·1**	62	*24·1*
	Totals . .	702	289		82		371	
	Table IX *loc. cit.*							
4.	Postsick† (G to J)	444	13	*2·9*	11	**2·5**	24	*5·4*

These figures show an important sequence correlated with the lapse of time after spawning; thus few unspent ova occur in 60% and many unspent in 22·5% of individuals in Group 1, which have recently spawned (A+B+C), as is attested by the occurrence of only embryos in the mantle cavity. Many of these oysters spawned after the act of dredging, and may be considered to have spawned prematurely. Such individuals were doubtless on the point of spawning and some might have spawned if they had been left undisturbed, but it is probable that in a fair proportion spawning was precipitated by the act of dredging and the retention afterwards out of water.

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* See I, p. 983, for definition of these stages.

† Individuals carrying embryos or larvæ are designated "sick" by oyster-cultivators.

Those individuals (D+E) which were carrying ciliated or partially shelled larvæ (aged 3 to 4 days) had clearly spawned naturally on the beds before being dredged. Nevertheless 47% of them showed a few unspawned ova, and 21·3% many. Oysters with coloured and fully shelled larvæ (F), however, show only 21% with few and only 3·1% with many relict ova. After extruding their larvæ a total of 444 oysters (G to J) showed only 2·9% with few ova with the addition of only 2·5% with many unspent ova.

The decreasing percentages of unspawned ova in the parents correlated with (*a*) the increasing age of their larvæ and (*b*) the post-sick phase, clearly show that it is normal for unspent eggs to be voided from the gonad after the main act of egg-spawning. The sudden drop in the percentage between Group 2 (D+E) and Group 3 (F) is critical, since all the individuals in these groups spawned naturally on the beds ; it indicates that the voiding of unspawned ova is effected largely at the time the parent is carrying well-developed larvæ. This process is continued after the larvæ are extruded, but appears to be still incomplete in 5·4%, of which 2·9% are negligible. The residual 2·5% of cases with numerous unspawned ova among post-sick phases are noteworthy.

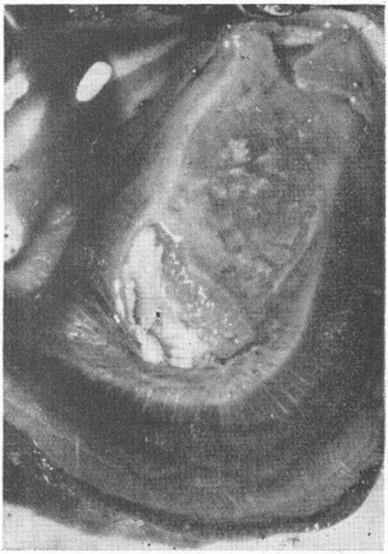

FIG. 1.—Photo of visceral mass of *O. edulis* living showing one large and several small patches of unspawned ova. The large patch is in the centre of the visceral mass. × *ca.* 2. (Photo by A. J. Smith.)

Confirmatory evidence of the extrusion of relict ova after spawning has been obtained in seasonal studies of oyster populations, but information so obtained is less easy to present and is perhaps less satisfactory than such convincing figures deduced from data already published—as are given above.

The different percentages obtained for Groups 1 and 2 in Table A are in part a measure of the differences resulting from premature and natural spawning, but since relict ova are shown to be extruded in bulk when the embryos are only a few days older (in Group 3) it is possible that this process may begin soon after the spawning act. In Table IV, *loc. cit.*, 12 instances are recorded of the occurrence of numerous to 70% unsegmented eggs occurring along with embryos in the mantle cavity, and many similar instances are recorded in **2**, 1927. It is probable that in these spawning individuals extrusion of unfertilised ova may have occurred after the main spawning act. In some cases fertilisation had occurred, so that larvæ of different ages were found together in one oyster. These facts already published confirm the deduction from Table A that relict ova may be voided from the gonad soon, i.e. within a few days, after the main spawning act.

In the event of relict ova remaining in patches in the gonad (see Fig. 1) the body of the oyster often presents an appearance to the naked eye designated as "curdley." It would appear that degeneration with absorption of these eggs usually and possibly always occurs.

Microscopic sections of a number of different types have confirmed observations on fresh material that degeneration usually occurs, but extensive exploration of preserved types is required to learn what happens in all circumstances.

In examining fresh smears of the gonad of oysters at the beginning of the breeding season when eggs are developing rapidly, the possible occurrence of new or old (i.e. last season's) relict ova is a disconcerting factor, and great care is needed in assessing the effective sexual condition of the material examined. There can be little doubt that mistakes have been made in this respect by both experienced and inexperienced workers.

The proportion of females found incompletely spawned while carrying young varies in different seasons, and is probably usually slightly higher at the beginning of the breeding season on most grounds. In Table IV, **1**, there are incompletely spent 65% (163) in June; 57·5% (256) in July; 45% (182) in August; 48·5% (95) in September; and 16·7% (12) in October. The numbers in brackets give the total examined each month, and the monthly grouping gives a close approximation to the course of the spawning season on the different beds whence material was obtained.

Abnormal incomplete spawning was found on the Fal Estuary beds in 1927 and is discussed in **2**, pp. 403–4.

SUMMARY.

An analysis is made of the records of unspent ova in the gonad of 1146 oysters (*O. edulis*) with—or recently with—young. High percentages of gonads with relict ova occur within a few days from spawning, much smaller percentages a few days later and still smaller ones one to two months after spawning. It is inferred that unspent ova are normally and mostly extruded from the gonad within a few days after spawning; confirmatory evidence for this view is adduced from published observations. It was found that masses of relict ova may be retained in the gonad for a longer period in about 2·5% of recently spawned females. It is pointed out that if these residual ova were fertilised upon extrusion they would give rise to a successful but spurious second spawning.

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1. Orton, J. H. Journ. Mar. Biol. Assoc., N.S., Vol. XIV, p. 967, 1927.
2. do. Nature, Vol. 120, p. 403, 1927.

PART IV. ON THE CHANGE FROM MALE TO FEMALE.

Review of Earlier Work.

Since the year 1920 the writer has been accumulating evidence on the problem of sex-change in the European oyster, *O. edulis*. In 1927 (**1**) the relevant literature on the subject was reviewed and an outline given of the observations and experiments being made with a view to obtaining critical information regarding sex-changes (**1**, p. 969). The first part of the projected programme consisted in the examination of the gonad of more than 1000 individuals at various periods after the extrusion of ova from the gonad. This part of the programme was accomplished by laboratory and field observations and by isolating proved and spawning females in tanks and in cages in the sea. The results of this work were published in 1927 (**1**), wherein it was demonstrated :—

(1) that among 702 individuals carrying young 97·3% were found in some phase of developing maleness ;
(2) that development of sperm-morulæ begins normally in the gonad of oysters within a few hours after the act of egg-extrusion ;
(3) that this development normally accelerates in the course of a few days, so that by the time the oyster is carrying black-coloured larvæ the gonad contains ripe sperm-morulæ (in many such individuals the gonoducts are also full of ripe sperm-morulæ ready to be discharged, see **2**, Fig. 1, p. 316.) ;

(4) that this phase of sperm-development attains a peak within one to two months after the act of egg-spawning and then wanes, *if spawning has occurred early in a normal season on a productive type of oyster bed*, e.g. West Mersea, River Blackwater, Essex; or Upper Fal Estuary; or Whitstable beds, Thames Estuary. The probability was discussed that this phase of sperm-development may be slowed down or arrested in the autumn and winter in individuals spawning as females late in the breeding season (see **3**, Table VI, category 21), and be completed in the following spring and early summer. Evidence on this aspect has since been accumulated and is presented in this paper.

(5) that a variety of intersexes (or mixed sexes) occurs, some of which can be recognised by naked-eye inspection.

In 1928 the breeding period of the oyster was discussed (**3**) in a general way in relation to spring and autumn periods of shell-growth (increase in shell area). In that paper (p. 399 and Table VI) is given an analysis of the sex-condition in October and November 1927 of some 1800 oysters from the beds in the Upper Fal Estuary. Thirty categories of individuals in different sexual or physiological conditions are recognised. A study in the seasonal variation of these categories during 1926 and 1927 has been made and will be discussed later in its bearing on sex-change in the population. In 1931 figures were published (**2**) of the gonad of the oyster at successive stages after the act of egg-spawning. Some results of experiments on the change of sex from male to female were given in the paper (**1**) (1927, lots 106 to 115B, pp. 1027 to 1033), but a discussion of the results was reserved for a separate publication. The portions of the original programmes of work dealing with the experiments on sex-change from male to female, **1**, p. 969 (*b*) and (*c*), are given in the following pages. A statistical investigation of seasonal sex condition in oyster populations from data already collected and extending over a period of three years is being undertaken along with other work, and a full discussion of the sex-physiology of the European oyster is reserved for a later publication.

INTRODUCTION.

During the period 1922–27 experiments were designed and carried out in the River Blackwater, in the River Yealm near Plymouth, and on the Fal Estuary to obtain evidence of the change of sex in individuals of *O. edulis* from male to female. These experiments have been partially successful inasmuch as this sex-change has been detected in a relatively small proportion of individuals (i.e. ranging from 10 to 50%). An ideal experiment should give sex-change in very nearly 100% of the animals. The change in sex from male to female is clearly not of the same automatic nature as that from female to male ; moreover, the recognition of a female phase will be lost if individuals spawn as females and evacuate their young in the interval between successive examinations of the experimental oysters, for such spawning individuals revert rapidly to the male condition as is now abundantly proved (**1**). The knowledge acquired in the course of these experiments would be used, it was hoped, to design more promising experiments on a larger scale, but the recent shortage of oysters on most English beds (**4**) has interfered with this project.

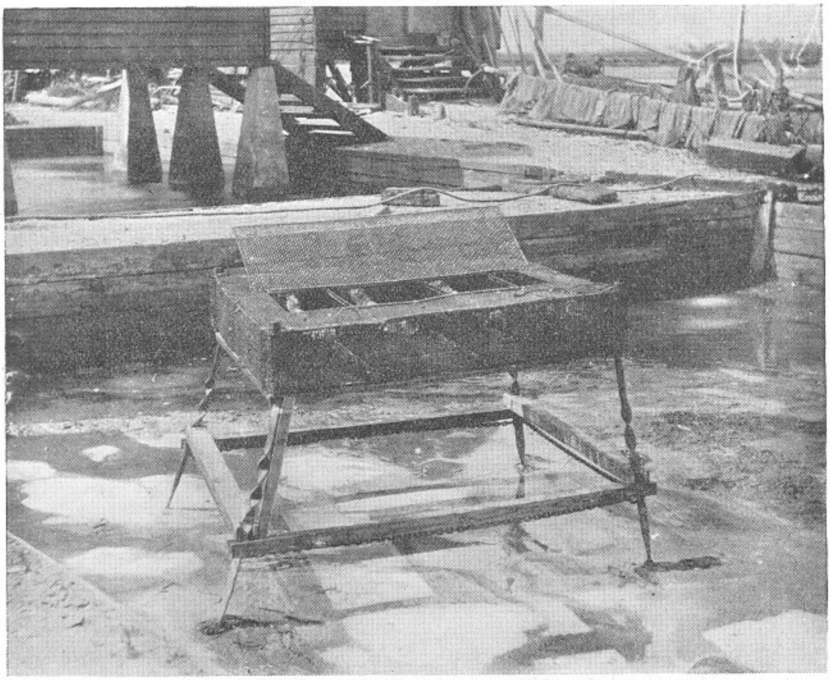

FIG. 1.—View of the experimental oyster cage used at West Mersea, showing the oyster pits at low water.

The chief difficulty in carrying out experiments on change of sex in oysters lies in keeping the experimental individuals under healthy conditions while at the same time taking precautions to isolate them unimpeachably from others. The writer holds the view that for work of this kind, the animals should live under conditions as nearly natural as possible. It was therefore decided to fix the site of the experiment *on grounds where oysters form natural beds* so that there can remain no doubt of the suitability at least of available water and food.

In order to isolate the experimental material and render recovery easy, a large cage 6 feet by 5 feet by 10 inches deep made of iron wire mesh

($\frac{3}{8}$ inch in diameter) was designed and used for the work (see Fig. 1, p. 7). This cage was divided by permanent partitions into four compartments, two large and two small, so arranged that each compartment could be recognised without the provision of a label (see Fig. 2, p. 10). This device proved extremely useful in dealing with heterogeneous material. Oysters in a known sex-condition at a known time were placed together in one compartment; individuals were mostly easily distinguished by tracing the outline of the shell and adding drawings *in situ* of barnacles and other permanently attached growths; some shells not otherwise easily recognised were marked with a distinctive file-mark. In special cases a small cage was constructed and attached inside the large cage to isolate an individual. The practical difficulties of maintaining an experimental cage of this kind on a commercial oyster bed for a number of years are very great; it was only by the hearty co-operation and good-will of the Directors and employees of the Tollesbury and Mersea Native Oyster Company that experiments in the River Blackwater were rendered possible; the difficulties of experiments on the River Yealm near Plymouth were overcome by the personal interest of Mr. J. Kingcome and the Director of the Yealm Oyster Fisheries. On the Fal Estuary where the beds are public, experiments had to be confined to the summer period, when the beds are closed for general dredging; permission for these experiments was courteously given by the Truro Oyster Beds Committee and rendered possible by the help of Mr. E. Searle and many oyster-dredgermen.

MATERIAL.

The oysters used in these researches were obtained by dredging in the breeding season chiefly at West Mersea, River Blackwater. Some were also obtained from other English grounds, namely Fal Estuary, Whitstable, River Yealm, and the River Helford. The age of the experimental oysters varied from about 3 to 7 years, but was estimated at being mostly from 4 to 6 years. In the earlier years, from 1922, the average age would probably be greater than later when the larger individuals were becoming relatively scarce. It is a difficult matter to obtain large numbers of oysters carrying young without destroying these valuable molluscs. The writer was fortunate at West Mersea in being able frequently to examine catches of many thousands dredged for the purpose of relaying, and at the same time of following the course of the breeding season. On productive beds such as occur at West Mersea, it is desirable to find out each year when a significant proportion of oysters have reached the blacksick stage, in order to make preparations for putting out clean shell at a time which will coincide as nearly as possible with the probable settling time of the oyster larvæ. The examination for spawning oysters is therefore a routine operation, of which advantage was taken to collect as many young-bearing individuals as possible. When oysters with young are kept out of water for some time a proportion will often exude a few embryos or larvæ from the edge of the shell, having opened the shell presumably in response to some stimulus, such as the need to respire, whereupon a few of the young flow out of the shell with a little of the mantle liquor. It is possible that the embryos themselves provide the stimulus for the opening of the shell merely by exerting continuous unusual pressure upon sensitive parts of the mantle. Individuals suspected of carrying young may be tested as described on p. 15.

Early in the breeding season 1% of a sample may be detected as female spawners after exposure to air on warm nights, while later in the season as high a proportion as 7% may be found in this way.

On beds where oysters are not caught in bulk in summer the experimental oysters were obtained as is described on p. 15, or in process of opening large samples.

METHODS.

The experiments on sex-change from male to female were of two kinds :—

(A) A total of 313 individuals, proved to be male at the time of examintion (usually about July), were isolated at different times and places in one compartment of the cage and returned to the oyster bed (see Fig. 4, p. 13). These oysters were taken out of the sea after various intervals of time—usually about a year later—and tested at intervals during the ensuing spawning season for individuals carrying young. In this kind of experiment only those females which were actually carrying young at the time of examination could be detected. If individuals spawned and released their young during the interval between successive examinations, their sex-change would not be known. It was considered imperative to return the oysters to the natural habitat as soon as possible after examination in order to maintain normal and healthy conditions of growth and gonad development. Although sex-change was found in experiments of this kind there can be no doubt that the actual percentage of individuals undergoing sex-change was greater than was observed.

As a variation of this experiment samples of the material were opened at various intervals after the beginning of the experiment and examined macro- and micro-scopically for stages of development of femaleness.

The detection of males for experimental purposes was effected by examining the contents of the gonad extracted by means of a fine pipette passed through a boring made in the shell of the oyster (see Fig. 3, p. 11). Only those individuals were selected as "male" which yielded only sperm-morulæ. Hermaphrodite individuals and any others from which eggs as well as sperm-morulæ were obtained were rejected.* The individuals selected were therefore essentially passing through one or other of the male phases (see p. 16). The shell boring was made in the left valve from a position varying from postero-dorsal to sub-median (see Fig. 3). From this position the gonad can be tapped near the surface of the body (see **5**, 1924, Plate XII) with relatively little risk of damage. In some instances the intestine was perforated.

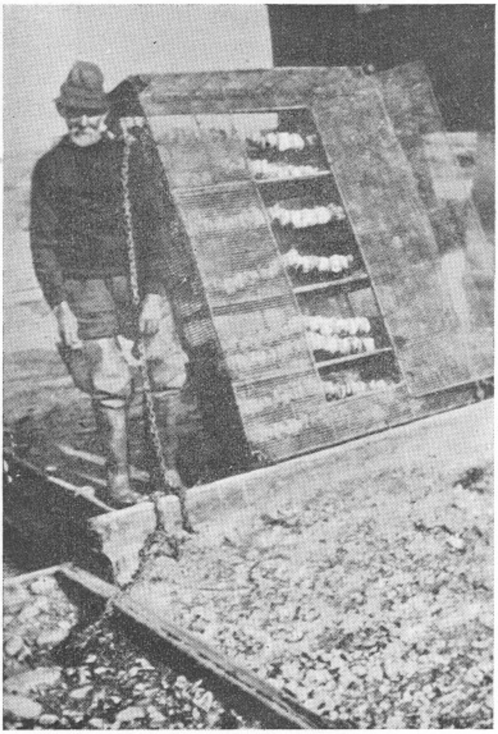

FIG. 2.—View of the experimenta oyster cage, dismantled and prepared with shells for catching oyster and Crepidula spat.

The experimental oysters mostly recovered easily and well from this operation (see pp. 18, 23), though doubtless some of the mortality which subsequently occurred was caused directly or indirectly from the operation. The boring in the shell was observed in some cases to be quickly sealed by deposition of a horny or calcareous membrane derived from the epidermis of the oyster ; the body wound also healed quickly but sometimes formed a scar. In a few cases the perforation of the shell was so well sealed

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* In Experiment 1 a few males with obviously relict ova were accepted.

internally (see Fig. 3, B, D) that a drill had to be employed to expose the body again; usually the new shell was thin and could be broken with the assistance of a small steel instrument. Sympathetic deposits sometimes occurred on the right valve (see Notes, p. 25).

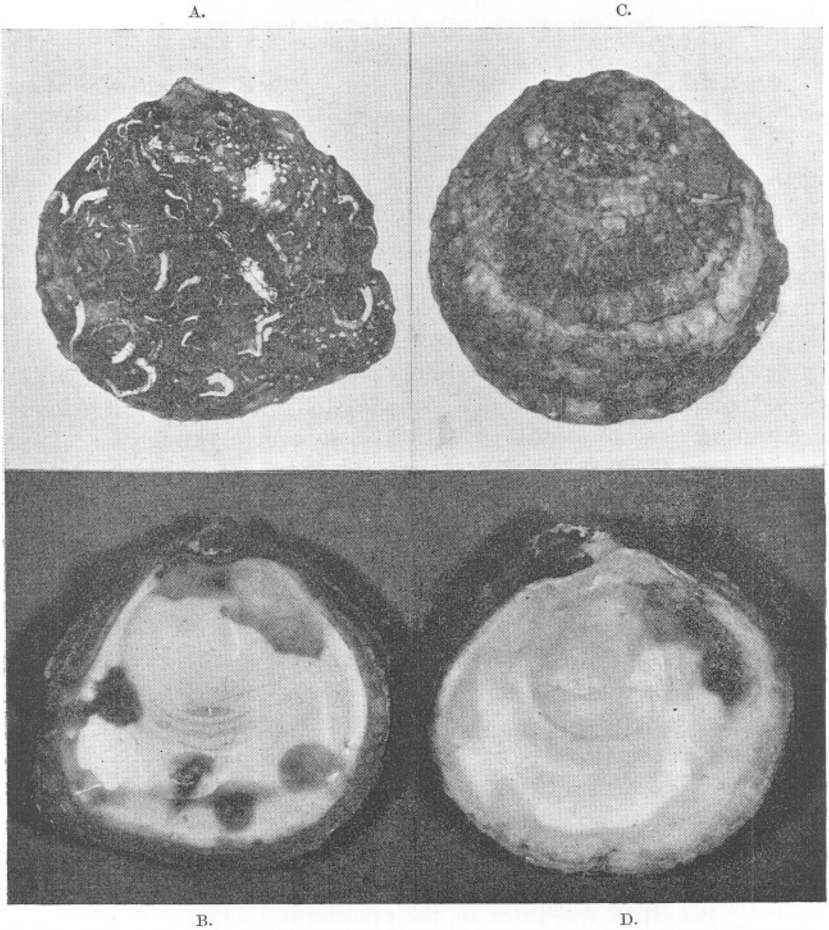

Fig. 3.—Views of external and internal faces of two bored left valves of *O. edulis* from Experiment 3. × *ca.* $\frac{5}{8}$. (Photos by P. Bond.)

A and B views of one valve. In A the boring is well shown near the umbo on the right. In B the site of the boring is near the umbo on the reader's left, and is covered with nacreous shell. The dark area extending from the boring is due to infiltration, but is little more than a stain on the shell itself.

C and D are views of another valve also showing perfect sealing of the boring internally. The site of the boring in D is near the umbo on the reader's left; the sealing is perfect.

(B) As adequate proof has been obtained that spawning females change normally—to the extent of 97%—into males immediately after the spawning act (**1**), it is sufficient to isolate individuals carrying young to obtain thereby a collection of males in the early stage of developing the male phase. Samples of oysters (amounting to a total of 663 individuals) bearing young were therefore isolated in compartments of the cage in the years 1922–25 and 1927, and kept in the sea for periods of months or years during which they were examined at intervals for the return of the female phase.

The reliability of this kind of experiment depends upon the degree of completeness of the egg-spawning act. There can be no doubt that the normal method of egg-spawning results in the extrusion of all or most of the eggs in the gonoducts and gonad at one and the same time (see **6**), although 50% of egg-spawners may retain a few to many scattered eggs in the gonad; nevertheless, the experience gained in examining more than 1000 spawning females, as well as many thousands of other specimens throughout the seasonal cycle of sex changes, indicates that *in a few cases* females incompletely spawned at the first attempt may spawn successfully again as a female within a period varying from a few days to more than a month. Successive spawnings of this kind, it will be noted, occur from one batch of eggs and do not involve two phases of egg-production. The fate of unspawned eggs is discussed in **1**, p. 976, and **6**, in this issue of this Journal; the significance of two acts of egg-spawning from one phase of egg-production will be discussed later with the results of the experiments.

ON THE CAGE AND CAGE OPERATIONS.

The experimental cage with its addition of legs is shown in Fig. 1. Legs were found to be desirable to avoid the accumulation of mud which occurs even in an open iron wire-meshed cage lying on the bottom in such silty water as occurs in the Blackwater creeks. The meshes of the cage were $\frac{3}{8}$ths of an inch square. In the earlier experiments when the cage lay on the bottom a disastrous mortality and weakening of the oysters accompanied the accumulation of mud in the structure. The cage itself could be removed from the collapsible table structure and was conveniently placed in sea-water in the pit, shown in Fig. 5, p. 14, underneath the storeroom, which was used as a laboratory. As the experimental material was prepared it was transferred direct to its appropriate compartment in the cage and maintained conveniently in sea-water. During spring tides the sea-water in these pits is well and frequently renewed (see Fig. 5).* The compartments of the cage and central lid on one face —so constructed as to prevent loss of material in the event of the lid being forced open—with the strengthening rods and tubular corner sockets for

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* During neap tides it was noticed that *Ciona intestinalis* especially seemed to find conditions intolerable in these pits. As the water and aeration appeared to be good, the lethal condition suspected was the exposure to very strong sunlight.

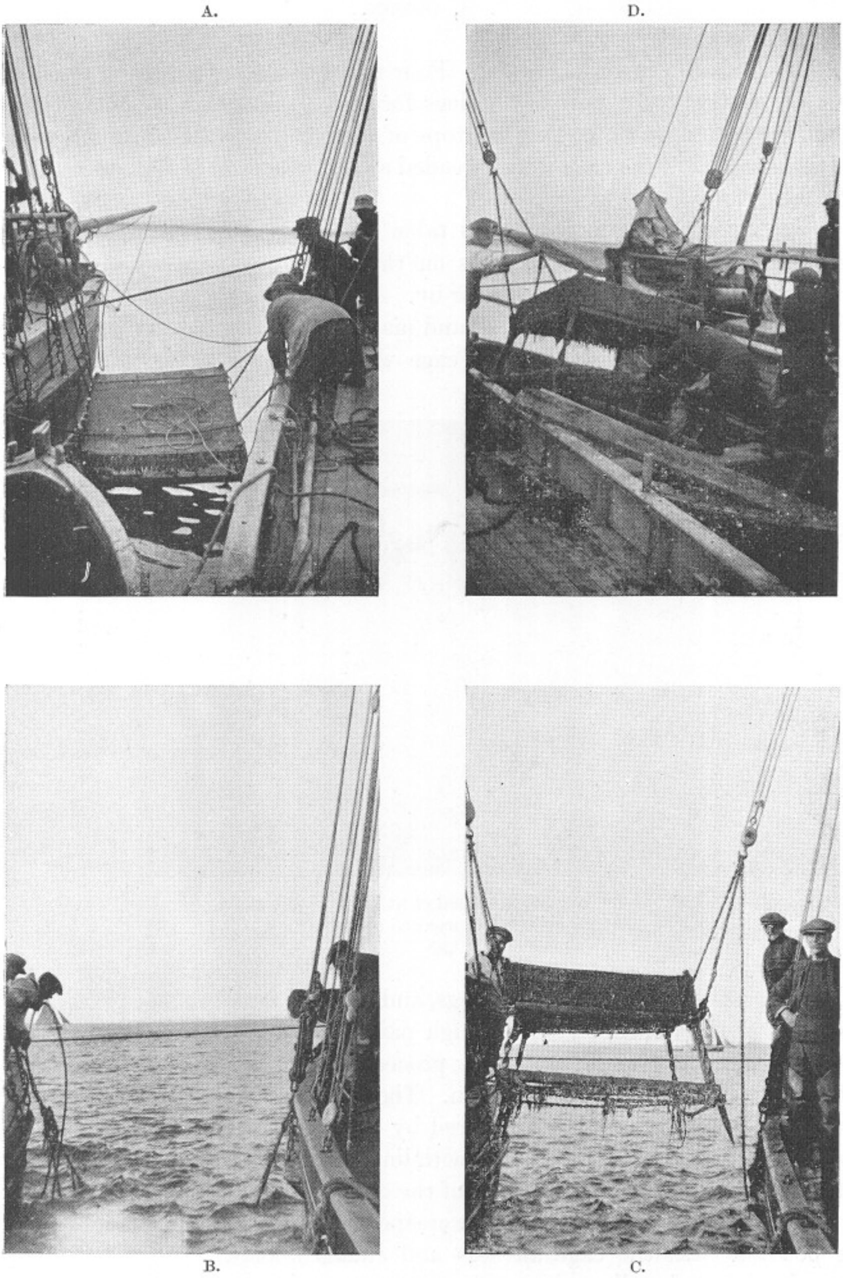

FIG. 4.—Four views of the operations in putting out and hauling the experimental cage.

A. The skiff has been withdrawn from below the cage, which is now being lowered into the water.
B. Hauling the cage after recovery of the anchors and chains.
C. Cage hauled clear of the water to permit the passage below it of the skiff.
D. Cage being lowered into skiff, preparatory to conveyance to the oyster-store.

the legs are seen in Figs. 1 and 2. Four narrow iron bars with end-holes fitting on the upper part of the legs formed a skeleton table on which the cage rested (see Fig. 1). The tops of the legs projecting through the corner sockets of the cage were threaded so that the cage could be secured by good bolts.

The cage was assembled on its table and the experimental material enclosed while the apparatus was on the foreshore, or in a large flat-bottomed boat, a skiff beached near by. At low water the skiff was towed to the Deeps (**9**, see Chart, Fig. 2) and manœuvred between two anchored and yoked dredging-boats. The cage was then hoisted by its anchor chains, which were secured to the legs, and the skiff removed (see Fig. 4, A, p. 13). Ropes were then run through pairs of handles on the top edges of the cage, and lowering gradually proceeded with until the bottom was reached. Bearings were then taken. The anchors, two in number, were run out separately, held and lowered by ropes until taut, when the rope was slipped and hauled in. A lead with line was left on the cage for testing the position of the cage at the end of the operations.

FIG. 5.—View of the oyster pits flooded at high water, showing the oyster store on the left used as a laboratory.

In hauling, the anchors were first creeped, then the two boats anchored in position with the cage anchors and chains aboard. The cage was then hauled and well washed ; the skiff was run under it while clear of the water (see Fig. 4, B, C, and D). In a clean haul the cage could be dropped snugly into the skiff and taken at once to the store for further washing and examination of its contents. When the cage had lain undisturbed on the beds during the winter an accumulation of mud was *always* found in it. On the site of the experiment there was a depth of two fathoms at low water; the same site was used in all the experiments carried out at West Mersea, River Blackwater.

ON TESTING FOR INDIVIDUALS CARRYING YOUNG.

In testing for individuals incubating embryos or larvæ in the mantle cavity at the time of examination, the adults, after being washed or scrubbed, were usually laid out with the flat valve downwards on glass plates on a temporary bench in a room serving as a laboratory. In warm weather under these conditions oysters will often soon extrude a few embryos or larvæ at the edge of the mantle. The sample was usually left under these conditions overnight, covered in hot weather with a damp cloth, the young-bearing individuals being isolated in sea-water in shallow dishes as they were detected. On transferring young-bearing forms to water in a dish a certain number of the young are usually soon extruded into the water (see Fig. 6, above), thus permitting confirmation of the first indication of the gravid condition.

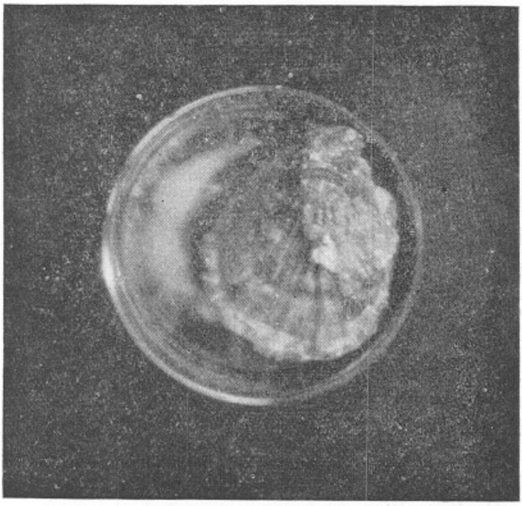

FIG. 6.—Photo of *O. edulis* found to be carrying young by the method of testing in small dishes—× ca. $\frac{1}{3}$. The white mass on the reader's left, concentric with the shell, is composed of hundreds of thousands of larvæ.

The oysters which failed to extrude larvæ on the bench were each again washed and isolated in a small dish of sea-water. The water in these dishes was renewed at intervals for one or two days, during which careful examinations were made. Usually the gravid individuals would evacuate a large portion of their young sooner or later, but sometimes the young were retained tenaciously. To detect these latter cases without injury advantage was taken of any such oyster opening its shell-valves widely to close the valves forcibly and quickly by hand-pressure. In this way a volume of water was suddenly expelled from the mantle cavity, carrying with it a number of larvæ if such were present. Widely open oysters could be examined by the naked eye.

This method of testing was efficient, but necessarily involved a constitutional strain on the material, especially when repeated after short intervals, and no doubt contributed towards delay in sex-development and the high mortality found during the experiments. A quicker method of testing, which avoids injurious effects, is desirable in future experiments.

On the Developmental Series of Male Sex-phases.

In a study of the state of the gonad at various intervals of time after egg-spawning it was convenient to establish an arbitrary series of possible conditions of the gonad (**1**, p. 981). Ten such arbitrary categories in the condition of the gonad with regard to the development of sex-cells were instituted (*loc. cit.*). Among these ten categories, numbered in succession I to X, it was found that seven (numbers III to IX) form definitely a series of sex-phases in the development and history of maleness. This series is given below in Table B and renumbered I to VII. A stage VIII is recognised, in which all the male elements have been evacuated from the gonad. This stage is neuter, but is historically related to the male-phases, and is conveniently retained as No. VIII in succession to No. VII.

For convenience the old arbitrary category numbers are given against the serial numbers of the sex-phases.

TABLE A. The Developmental Series of Male Sex-phases.

No. of male sex-phase.		Sex-cells present in gonad.			Arbitrary Category given in **1**.
		Ripe sperm-morulæ.	Developing sperm-morulæ.	Ripe unspawned ova.	
I	waxing	none	a few to ∞ young up to 40 μ.	none or a variable no.	III
II		none	f. ∞ or ∞ over 40 μ.	do.	IV
III		few or f. no.	∞	do.	V
IV	ripening, or ripe with gonoducts filling or full	f. ∞ or ∞	f. ∞ or ∞	do.	VI
V		∞	f. no. to few	do.	VII
VI	waning	f. ∞ or ∞	none	do.	VIII
VII		f. no. to few	none	do.	IX
neuter =VIII		none	none	none or a variable no.	neuter =X

Abbreviations : no.=number ; ∞ = numerous ; f.=fair or fairly.

SERIES A.

EXPERIMENTS ON OYSTERS PROVED TO BE MALE.

Experiment 1. *West Mersea, R. Blackwater*, 1922.

The details of the first experiment in investigating the change of male individuals into female are given in Table I. One hundred and fifteen males were identified from June 28 to July 7, 1922, and put in the cage in the sea on July 8. The cage was left undisturbed and could not be examined until July 14, 1923, about one month after the breeding season had begun—when it was found to have become very heavily silted with mud, following heavy rains and much stormy weather. The accumulation of mud* had smothered most of the oysters and probably interfered with the normal development of those remaining. This experiment was regarded as a failure, and a new one begun at once; nevertheless, the surviving individuals were cared for and their sex-changes investigated.

Nineteen oysters survived the experience of the first winter, and of these four died in the summer following. None of the remaining fifteen were detected in a female phase from July 15 to August 2, nor from October 17 to 22, 1923. During the latter period oysters would not normally be expected to occur in spawn on the Blackwater beds, so that these oysters were in reality examined during the period of only two weeks of the spawning season. Some of these oysters may, therefore, very well have passed undetected through a female phase during the breeding season of the second summer†—which in this year began late, about the middle of June, and extended into August and possibly into early September.

Six specimens were tested on July 15, however, and found to be males. Nine others were put in the cage to winter again. On June 7, 1924, 2 of these were found dead, and another died soon afterwards. In the 3rd summer of this experiment 6 individuals only were left; 2 of these produced either embryos or larvæ; 1 was hermaphrodite and 3 were good males accumulating food reserves. One individual, carried through a third winter, was opened on July 16, 1925, again late in the breeding season, and found to be in the male phase.

Summary of Experiment 1.

Of 115 oysters proved to be males in July 1922, none were found to have developed a female phase in the next (2nd) summer. In the

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* A large number of *Ciona intestinalis* (up to 15 cm. long living contracted) and of *Ascidiella aspersa* (up to 7 cm. long living and extended) were growing on the oyster-shells and on the cage, having survived—but no doubt assisted in—the deposition of mud.

† The summer in which an experiment is begun is designated the 1st summer of the experiment; the summer in the following year is the 2nd summer; and the next following summer the 3rd summer of the experiment, and so on.

3rd summer, 3 of the surviving 6 individuals became ovigerous or larvigerous. The larvigerous individuals were found developing a new male phase.

Heavy mortality occurred among the experimental oysters in the winter of 1922–23, and examinations for female phases were made during only a part of the breeding season in 1923 and 1924.

Female phases may have been inhibited by the bad experimental conditions in 1922–23, and some may also have escaped detection in the limiting conditions of the experiment, i.e. the possibility of examining for individuals carrying young during only a portion of the spawning period.

TABLE I.

EXPERIMENT 1.

West Mersea, River Blackwater, on O. edulis *proved to be male.*
June 28th to July 7th, 1922.

Date.	Operations.	Dead in cage.	♂	♀ with young.	Un-spawned ♀	Total dead.	Total living.
July 8, *1922*	115 ♂'s put out in the cage in the sea						115*
July 14, *1923*	Cage hauled . . .	**96***					19
,, 15	4 individuals ♂ opened and preserved : 2 individuals A. ♂ phase V B. ♂ phase VI . . .		4 (2)	?	?	100	15
15	15 individuals put again in the sea . . .						15
,, 23– Aug. 1	Oysters re-examined for ♀ spawning individuals—none found . . .	**2**	?	?	?	102	13
,, 2	13 individuals put out in cage						13
Oct. 17	Cage hauled again . .	**2**				104	11
	No ♀'s in spawn, C. opened found in ♂ phase VI ; D. opened, ♂ phase VIII		(2)	?	?	106	9
Oct. 22	9 oysters put in sea in cage						9
June 7, *1924*	Cage hauled . . .	**2**				108	7
,, 7–9	No ♀'s found in spawn .						
,, 9	Cage put in sea . .						7
,, 30	Cage hauled . . .	**1**				109	6
July 1–6	Oysters re-examined and finally opened, except one ♀	0	3*a*	2*b*	1*c*⚥	114	1
,, 9	One ♀-spawning oyster put back in sea . .						1
July 2, *1925*	Cage hauled . . .						
,, 16	Oyster opened ; ♂ phase VI	0	1*d*	0	0	115	0

* Ninety-three of these shells were examined : 54 showed good recovery from the boring operation ; 33 no recovery and 6 a bad recovery.

Notes to Table I.

(*a*) The condition of these three oysters was as follows :—

		Growth of Shell				Sex-elements. Sperm-morulæ.		
	Fish.	1923.	1924.	Length.	Recovery from Boring.	Ripe	Unripe	Ova.
1.	Good	9–10 mm.	?	64 mm.	v. good	∞	fair no.	none
2.	F.g.	?	2–5	61	a boss of nacreous material projecting into tissues which have grown well around it.	∞	v. few	none
3.	Good	nil ?	2–5	65/82	perfect	∞	f. ∞	none

All three individuals were good male oysters accumulating reserve products.

(*b*) 1. One of these oysters extruded an enormous number of heliotrope coloured and shelled larvæ on July 1. The shell boring was opened and the gonad tapped and found to be developing maleness giving ∞ ripe sp. m., ∞ unripe sp. mor., and no ova (phase IV). On July 6 the gonad was again tapped and found to be male in a later phase (VI). The shell of this oyster was then marked with a file and put back in the sea on July 9. It was taken out of the sea on July 2, 1924, opened and found on July 16 to be in the ♂ phase VI (see *d*).

2. On July 6 the other oyster extruded during the night white embryos not ciliated ; this individual was opened on July 8 after two days in the sea and found to be in ♂ phase I with f. ∞ eggs left in spots in the gonad. It was therefore incompletely spawned but changing into the ♂ phase.

(c) 1.	Good	nil ?	5–10 v. thin	77	perfect	∞	none	∞ ripe

The gonad was of the type described as curdley : the individual had developed femaleness, and spawned incompletely as a female. This oyster had retained ripe sperm-morulæ whilst acquiring ova, and had become hermaphrodite, but a functional female.

(*d*) The " d " individual found with young in 1923 had a gonad in male-phase VI.

Experiment 2. *West Mersea, River Blackwater, and River Yealm, near Plymouth,* 1923.

In the second experiment with oysters proved to be male the following improvements were made in the cage and procedure with a view to diminishing the limitations.

(1) The cage was mounted on legs (see Fig. 1, p. 7) to enable the silt to fall through the bottom of the cage, which formerly had rested on the river bed.

(2) It was decided to visit the cage twice a year to overhaul and clean the cage and its contents.

(3) After examining the experimental oysters at the beginning of the breeding season on the Blackwater beds in the 2nd summer, it was decided to transport the experimental oysters to beds near Plymouth, whence they could be hauled at intervals during the same breeding season. In this way more opportunities would occur for detecting individuals at the instant they were carrying young.

The details of Experiment 2 are shown in Table II, p. 22. During the period July 24–August 1, 1923, 101 oysters were found to be male by examination of the contents of the gonad extracted by means of a fine pipette from the living animal through a boring made in the shell. These oysters were put in the cage in Deeps on August 2, 1923. On October 17, 1923, the cage was hauled for the purpose of cleaning away accumulations of mud and growths* and for examination of the oysters. It was found that the cage had overturned.

The oysters were, however, in good condition and had grown remarkably fine shell-shoots, as indeed had most of the oysters on the dredging grounds. Tests were made for spawning individuals, although the spawning season was considered to be finished ; no individuals were, however, found in spawn. A sample consisting of 18 of the experimental oysters was opened and examined (see note *a*, Table II). It was found that good recovery from the operations of boring and tapping had mostly been made : new shell-material had been laid down on the inside of the shell-perforation and effectively sealed the body from the external medium. Some individuals had made a poor recovery, but such might be expected to recuperate in the future. The mortality was low, amounting to 5%. The sample consisted of 10 neuter individuals, some of which were in poor condition, but others were accumulating food reserves normally, and 8 still in the male phase, but mostly in a waning male phase. None was found certainly in a female phase, though No. 11 may have had a few young ova in the gonad.

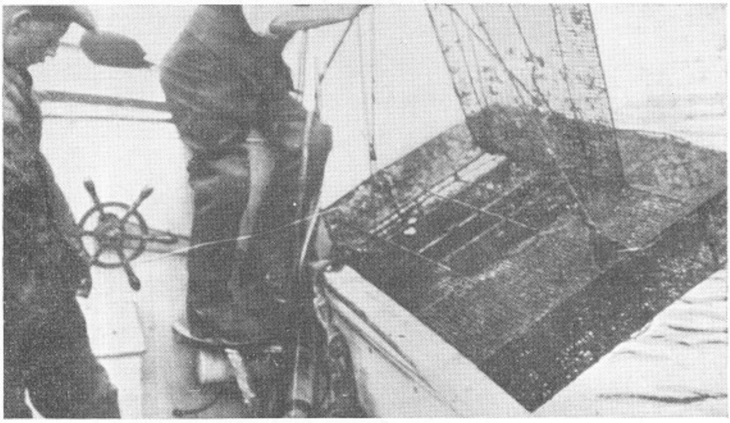

FIG. 7.—View of the smaller experimental oyster cage used in the R. Yealm being hauled from a motor-boat.

The remaining experimental material was returned to the sea on the Deeps bed on October 22, and hauled the following summer on June 7,

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* *Ciona intestinalis* up to 4·3 cm. long extended, *Ascidia conchilega* up to 2·5 cm. long extended and *medium Ascidiella aspersa* were found in numbers and removed. These animals are an important factor in the accumulation of mud in a cage.

when the cage was found upright, containing very little mud, and with a low mortality amongst the oysters. A very fine growth of colonies of *Alcyonidium gelatinosum* (commonly 10 cm. long) covered the top of the cage and served on this occasion—and on others—to show how the cage had been lying on the sea-bottom.

At this time cold weather set in, and as none of the oysters were found in spawn on the day after hauling the cage, it was decided to put the cage back in the sea in Thornfleet Creek and examine it after a period of warmer weather. The cage was again hauled on June 30, and the oysters tested for females carrying young. Two such were found from July 1 to 6, and as it was thought that no others were in spawn, the whole sample was returned to the sea, pending its removal to Plymouth. Quick transport was arranged and the experimental oysters were put out in another cage in the oyster beds in the River Yealm on July 15. This cage was hauled on August 6 and the oysters tested August 6–8 for those carrying young. Two of such were found and the remainder put back in the sea on August 8. Again the cage was hauled on August 26 and, after testing, three more young-bearing females were detected. The remainder were again returned to the sea, but unfortunately a site could not be obtained on the proper oyster bed, and the most promising site near the dredging grounds had to be adopted. This site proved quite unsuitable (see note *h*, Table V); nearly all the oysters died during the following winter and the experiment was concluded.

Summary of Experiment 2.

One hundred and one oysters proved to be male on July 24 to August 1, 1923, were isolated in a cage in the sea in the River Blackwater on August 2, 1923. These were tested for individuals carrying young during October 17–22, 1923, and June 7–9, 1924; two oysters carrying larvæ were found in June. The experimental oysters were then transferred to a cage in the sea on the River Yealm near Plymouth. Further testing on August 6–8 yielded two more larva-bearing oysters; after another short period in the sea another test, made August 26–28, 1924, yielded three more larvigerous oysters, so that during 1924 7 individuals which were in a male phase in July 1923 had passed into a female phase and produced larvæ. Heavy mortality occurred in the remaining individuals in the winter of 1924–25 and the experiment was closed.

TABLE II.

Experiment 2.

On the Change from Male to Female: West Mersea, R. Blackwater, and R. Yealm near Plymouth.

Date cage put out. 1923	Cage hauled.	Remarks.	Dead in cage or opened.	♀ with young.	Total dead and opened.	Total living.
Aug. 2		In the Deeps oyster bed with 101 proved ♂ oysters				101
	Oct. 17		**5**			96
	Oct. 17–22	Sample examined; all tested	18*a*	0	23	78
Oct. 22		In Deeps			23	78
	1924 June 7		**5**		28	73*b*
	,, 7–9	Oysters tested		0	28	73
June 9		Cage put in Thornfleet				
	June 30	Cage hauled	**4***c*	–	32	69
	July 1–6	Oysters tested	**2***e*	2*d*	36	65
July		Oysters in sea temporarily	–	–	36	65
July 15		Oysters removed to Plymouth and put in cage in R. Yealm	**4**	–	40	61
	Aug. 6				40	61
	,, 6–8	Oysters tested at R. Yealm		2*f*		
Aug. 8					42	59
	,, 26		**1**		43	58
	,, 26–28	Oysters tested at R. Yealm		3*g*	46	55
Aug. 28					46	55
	1925 June 26	Experiment concluded	**46***h*	0	92	9

Notes on Table II.

(*a*) A very good growth of shell (increase in area) was found in all the oysters except 19 on hauling the cage on Oct. 17. The new growth increased the height of the shell from 10 to 18 mm. and is described in **3**, p. 382.

The 18 individuals opened to obtain information on sex-change were found to show the following features on Oct. 18 to 21.

	No.	Length 1923 in mm. Aug. 3	Length 1923 in mm. Oct. 17	Recovery[1] of shell.	Fish.[2]	Gonad.	Ripe sp. m.	Unripe sp. m.	Ova.	Sex phase.[3]
	1	66	81	good	f.g.	undifferentiated	none	none	none	neuter
	2	50	67	do.	fair	not recorded	∞	do.	do.	♂ VI
	3	52	52	do.	f.g.	undiff.	none	do.	do.	neuter
gaping	4	51	59	poor	poor	do.	do.	do.	do.	do.
	5	48	48	do.	v.g.	n.r.	∞	a few	do.	♂ V
	6	53	53	perfect	v. poor	undiff.	none	none	do.	neuter
	7	62	69	good	do.	do.	do.	do.	do.	do.
	8	53	68	perfect	v.g.	do.	do.	do.	do.	do.
	9	60	68	good	do.	well dev.	∞	f. no.	fair no. relict	♂ IV
	10	58	68	perfect	fair	undiff.	none	none	none	neuter
	11	65	81	do.	f.g.	n.r.	∞	do.	few young ?	♂ VI
	12	69	87	do.	do.	do.	∞	few	none	♂ V
	13	76	86	do.	g.	do.	occ.	none	do.	♂ VII
	14	55	62	do.	fair	undiff.	none	do.	do.	neuter
	15	63	63	good	do.	n.r.	few	do.	do.	♂ VII
	16	70	76	do.	n. 0	do.	∞	do.	do.	♂ VI
	17	46	46	bad	poor	undiff.	none	do.	do.	neuter
	18	52	52	v.g.	do.	do.	do.	do.	do.	do.

(1) In 15 cases good to perfect recovery from the boring of the shell had been effected by sealing the boring from the inside with a nacreous deposit. In some of these shells, however, infiltration of foreign material had occurred, but this had been isolated on the shell and covered with a deposit of horny or calcareous material. When a poor recovery had been made these infiltrations were often extensive and had resulted in a great strain on the oyster in its effort to recover. In many cases the body showed a distinct scar opposite the boring where the gonad had been tapped.

(2) Under the term "fish" is given the relative condition of nourishment of the body as a whole; it is to be noted that a very good fish may occur in a neuter individual, e.g. No. 8.

(3) In these individuals in early male phases the gonoducts were full of ripe sperm-morulæ, in the older phases these were either empty or had few contents. In the neuter cases the ducts were often filled with a milky fluid which contained no sex-elements.

(*b*) On hauling the cage on June 7, 1924, 15 oysters had a new rim of shell-growth 3 to 8 mm., a slight growth only showed in 41, while no growth had occurred in 17.

(*c*) Of the four oysters found dead three had a slight recent growth of shell, 5 to 7 mm. in width, around the edge of the left valve.

(*d*) One oyster extruded into a dish ciliated larvæ on July 1; the next day the larvæ showed a trace of the larval shell and a tapping of the gonad showed the gonad to be in the ♂ phase I with a fair number of unspawned ripe ova. This individual was put in the sea and opened on July 8 when all the larvæ had been extruded. The gonad was found to be in ♂ phase III with relict ova in spots. Shell-recovery from the original boring had been perfect. Another individual extruded early embryo on July 6 at 7 p.m.; the next day the embryos at 11 a.m. were in the early heart-shaped stage and the gonad found in ♂ phase II with large sperm-morulæ ca. 110 by 30 μ. Recovery from shell-boring had been perfect.

(*e*) Two gaping individuals were opened; one was neuter with muscle spindles (see **5**, p. 48) in the tissues, and the other in ♂ phase V with relict ova suggestive of recent female-spawning.

(*f*) Aug. 8. Black and shelled larvæ were extruded from two individuals whose gonads were in ♂ phase IV.

(*g*) On Aug. 27 one more oyster extruded black-shelled larvæ, and two similar cases were found the next day; all these oysters had passed into ♂ phase IV, as was found by retapping the gonad through the old boring.

(*h*) After the summer of 1924 the cage had to be moved off the dredging ground, and was placed in what was regarded as the most favourable place outside these grounds. The resulting mortality proved that the ground was entirely unsuitable. Periodical freshets and muddy water it is considered accentuated that weakening of the oysters which was no doubt caused by their removal in summer from West Mersea to Plymouth.

Experiment 3. *R. Yealm near Plymouth*, 1922.

Ninety-seven oysters proved to be male—from an examination of the gonad made through a boring in the shell—were put in the sea in a cage (see Fig. 7) on the oyster beds in the River Yealm on July 23, 1922. The experimental material consisted of 69 Yealm oysters (which are mostly relaid from Falmouth or Saltash), 20 from the River Blackwater (1922) and 8 Whitstables (1922). The cage was hauled on July 28 and 13 dead were found. A sample of the oysters was brought in for examination and found to be in good condition in good male phases (see note *a*, Table III). The rest were returned to the sea without delay. No further examination was made during the summer. In the spring the cage was visited for the purpose of cleaning and an unexpected accumulation of sticks and mud found in the cage with a concomitant very high mortality among the experimental animals. After a further examination on May 10 the cage was hauled and the oysters brought in on July 7 to be tested for female spawners. Only 19 individuals remained at the beginning of the spawning season of 1923. From July 7 to 10 two individuals were found with young embryos ; one of these yielded but few embryos, it is interesting to note. On July 9, 4 oysters were re-tapped and found to be in male phases ; their shells were marked with a distinctive file-mark ; 2 others were opened and found to be male and neuter respectively. The cage was hauled again seven weeks later (on August 30), when 4 more dead were found ; the remaining living were again tested for females with young. One such individual extruded numerous black-shelled larvæ and was found to have a filework on its shell. This oyster had therefore passed into a female phase since July 9 ! (See, however, pp. 26 and 42.) On September 4 the gonad of this specimen was again tapped and found to be in male phase V. The survivors, now reduced to 10, were again tested unsuccessfully for larvigerous individuals on September 11 and October 1.

On overhauling the cage on December 8 seven more dead were found and the remaining 3 failed to survive to the breeding season of 1924.

Summary of Experiment 3.

Of 97 oysters proved to be male in May–June 1922, 6 were found to be still in male phases in July 1922. No observations were made on the remainder for young-bearing individuals during the breeding season of 1922. Only 19 oysters survived to the winter and 4 more died during the following summer. Tests were made four times during the breeding season of 1923 for young-bearing females and 3 such individuals found. None survived the winter of 1923–24. One oyster carrying larvæ on August 30 had been proved to be male seven weeks earlier, on July 9.

Summary of Three Experiments on Sex-change in samples of Male Oysters.

It is advisable to consider the results from these experiments apart from those obtained in a second series which is described later.

When the results of these experiments are brought together as in Table IV below, it is seen that in the second summer of Experiments 2 and 3, 10% to 16% of the male oysters *were detected* in the act of carrying young. When it is considered that the breeding season may extend over about three months, and that oysters normally carry their young only from 6 to 14 days, it is highly probable that many of the experimental oysters passed through a female phase undetected. In Experiment 1 it is probable that female phases had just been experienced when the first test was made, and only one other test was made in the second summer. In the third summer of this experiment out of the remaining 6 individuals 3 (50%) were in a female phase.

The evidence obtained from these experiments offers definite proof

TABLE III.

EXPERIMENT 3.

On the Change from Male to Female, R. Yealm near Plymouth.

Cage put out.	Cage hauled.	Remarks.	Dead in cage or opened.	Female with young.	Total dead & opened.	Total living.
1922						
June 23		97 oysters proved ♂				97
July 28	July 28	Sample of 6 brought in and opened July 31	13 6*a*	 –	 19	84 78
	1923					
March 12	March 12	Cage examined and put out again	55*b*	–	74	23
May 10	May 10	do.	1	–	75	22
	July 7	Oysters tested; 4 rebored; 2 opened	3 2*d*	 2*c*	78 82	19 15
July 10		Oysters returned to sea				
	Aug. 10	Oysters tested	4	1*e*	87	10
Sept. 4		Returned to sea	–	–	87	10
Sept. 11	Sept. 11	Tested oysters	0	0	87	10
	Oct. 1	Tested oysters	0	0	87	10
Oct. 16		Returned to the sea	–	–	87	10
Dec. 8	Dec. 8	Examined cage	7	–	94	3
	1924					
	June 24	Experiment finished. The 3 survivors died later	3	–	97	0

NOTES ON TABLE III.

(*a*) Six individuals showed the following features on July 31, 1922.

No.	Boring.	Fish.	Ripe sp. mor.	Unripe sp. mor.	Relict ova.	Sex-phase.
1	Covered; partly calcified	v. good	∞	f. ∞	none	♂ IV
2	Covered; beautifully calcified	do.	∞	none	rare	♂ VI
3	Covered; partly calcified	do.	∞	rare	none	♂ V
4	Covered; horny	good	∞	f. no.	do.	♂ V
5	Covered; partly calcified	f. good	∞	∞	do.	♂ IV
6	Two borings both covered; partly calcified	v. good	∞	f. ∞	few	♂ IV

It was noted that sympathetic deposits were present in all cases on the right valve in a position corresponding to that called forth to cover the boring on the left valve: in one case the deposit was noted to be partly calcified.

(*b*) Heavy mortality had occurred from a great accumulation of sticks and mud.

(*c*) On July 8 one oyster extruded numerous eggs in late segmentation stages. On July 9 another individual extruded a few eggs also in late segmentation stages; upon opening this oyster the gonad was found empty: it is presumed that most of the larvæ had been extruded during the hauling process.

(*d*) The gonad in 4 individuals was re-examined on July 9 by breaking through the old boring; one was in the male phase IV, two in V, and one in VI. The shells of these rebored individuals were marked with a cross by means of a file. Two weakly individuals were opened; one was neuter and the other feebly ♂ V.

(*e*) One oyster marked with a cross extruded on August 31, 1923, numerous black-shelled larvæ; this oyster had been proved to be male as recently as July 9, 1923. On September 4 the boring of this oyster was again opened and the gonad tapped, yielding a few ripe sp. mor. and numerous unripe; it had thus attained again the male phase No. III.

that oysters pass from the male phase into the female phase in significant numbers. As the male oysters were taken at random from a population, it is not known how long such individuals had already existed in the male phase.

Evidence of sex-change from male to female in one summer was obtained in one instance, but such a rapid change was unexpected, and these experiments were not conducted with a view to detecting such a rapid development of the female phase. Evidence of the occurrence of successive male and female phases in successive summers is given by 10% to 16% of such changes in Experiments 1 and 2. Fifty per cent of the few survivors (6) in the third summer of Experiment 1 showed passage into the female phase in that summer, but the experimental conditions in this case were such as might be expected to cause delay in egg development.

The severity of the experimental conditions is clearly shown by an average total mortality of 65% before the advent of the second summer. It is therefore reasonable to suppose that more rapid changes are likely to occur in oysters lying free and naturally on the oyster grounds. The sex-changes observed experimentally are factual, but do not necessarily represent all the changes undergone; neither does the period intervening between successive sex-phases necessarily represent the minimum period; it is highly probable that the normal may be shorter than the observed period. Finally, the absence of records in sex-change in individuals in the second summer may be due either (1) to the detrimental effect of the whole of the experimental conditions (e.g. boring, tapping, muddy environment, repeated exposure in testing) or (2) to the passing of female phases during periods when the oysters were in the sea between successive periods of testing, or (3) to the intervening period being too short to permit the completion of those phases occurring between one egg-bearing phase and the next. The close analysis of young-bearing individuals with regard to the fate of their unspawned ova, given in **6** in this Journal, has an important bearing on these experiments. The effect of that analysis is to reveal the possibility that an oyster, presumably proved to be male by a tapping of the gonad, may nevertheless give spurious spawning as a female, if masses of relict ova occur in some other part of the gonad, and if these ova are extruded and fertilised. The possibility of this chance—i.e. a second spawning from one batch of eggs—occurring in females which spawned the previous summer is on the evidence available remote; the possibility of the chance occurring in the same season is, however, on the evidence available 2·5 in 100, but it is advisable to double this number and regard 5 in 100 as possible in the discussion of results. Thus isolated cases of sex-change from male to female *in one season*—as in the instance noted above—must be regarded as non-significant if female-spawning could have occurred in the same breeding season. In the three experiments described above sex-change was rarely investigated in the first summer (see Table IV, below).

CONCLUSIONS.

Under such environmental conditions as occur on English oyster beds, it is found by experiment that oysters proved to be male in a given breeding season change to functional females in significant numbers (10 to 16%) in the next breeding season. Under wholly natural conditions it is highly probable that the percentage of males changing into functional females within a period of one year is much greater than that found under experimental conditions.

TABLE IV.

SUMMARY OF THREE EXPERIMENTS WITH SAMPLES OF MALE OYSTERS.

	1st Summer.			2nd Summer.			3rd Summer.		
	No. of oysters.	No. of tests for ♀'s	No. of ♀'s found	No. of survivors.	No. of tests for ♀'s.	♀'s found.	No. of survivors.	No. of tests for ♀'s.	♀'s found.
Expt. 1	115	*0*	0	19	*2*	0	7 (1 died)	*2*	3 (50%)
,, 2	101	*0*	0	73	*4*	7 (ca 10%)	9	*0*	—
,, 3	97	*1/14**	0	19	*4*	3 (ca 16%)	nil	—	—

TABLE IV*a*.

NUMBERS OF ORIGINAL MALE-PHASES IN EXPERIMENTS 1, 2 AND 3.

Sex-phase	II	III	IV	V	VI	VII	Totals.
Expt. 1	–	3	36	62	17	–	118 (3 died)
,, 2	–	2	44	34	18	3	101
,, 3	1	1	26	54	12	1	95 + 2 n.r.†
Totals	1	6	106	150	47	4	314

SERIES B.

EXPERIMENTS WITH OYSTERS BEARING YOUNG.

In the following series of experiments individuals found carrying either embryos or larvæ (see p. 15) were isolated in compartments of the cage and returned to the oyster beds to permit normal development of the succeeding sex-phases. It is known that the male phase is assumed immediately after egg-spawning, so that the samples dealt with here would all (but see discussion on p. 26) be males after extruding their

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* 6 individuals opened July 31.

† n.r. = not recorded.

larvæ. The precaution was, however, observed in the later experiments of isolating whitesick individuals (i.e. those carrying young embryos or trochophore larvæ) separately from the blacksick ones (i.e. carrying coloured and shelled larvæ) even when both categories of oysters were found with young at the same time. Observations on this material were made as follows :—

(1) At various intervals after immersion in the sea samples were *opened* and the condition and sex-phases recorded.

(2) At intervals in the breeding season following that in which the experiment was begun, the oysters were taken out of the sea and *tested* for individuals carrying young at that time. After the test the remaining oysters were returned to the sea and again submitted to the same test after a short interval. Tests and immersions of this kind were repeated as frequently as desirable and possible during the breeding season of successive years. A preliminary account of the earlier experiments was given in 1922 (**8**).

Experiment 4. *On Females Bearing Young* (1922), *West Mersea, R. Blackwater.*

The first experiment with oysters carrying young was begun on July 8, 1922 ; details are given in Table V. Seventy-eight individuals found with embryos or larvæ between June 28 and July 7, 1922, were put in the sea in the cage on the Deeps oyster bed (**9**). The cage was hauled late in the breeding season of 1923, i.e. on July 14, when out of 32 living oysters 1 individual was found carrying young. Two other tests for gravid females were made in July without positive result, before the cage was returned to the sea on August 2. The cage was hauled on October 17 for cleaning and returning on October 22. In June 1924 19 oysters remained to be tested and 3 of these died in June. Of the 16 remaining specimens (see note *c*, Table V) 1 was found carrying embryos on July 6 ; 2 were fully ripe females ready to spawn ; 1 other was a ripe female dying, while 3 showed evidence of a recent female phase by the presence of relict ova in the gonad ; 8 others were good males and the 1 remaining was neuter.

Summary of Experiment 4.

Of 78 individuals found to be carrying young in July 1922, only 32 survived until July 1923. Tests for gravid oysters were not made at the beginning of the breeding season in 1923, and only 1 oyster with young was found in three tests made in July 1923. No other tests were made until June–July 1924 ; the remaining 16 oysters were opened on July 5–6, 1924, when 1 more gravid and 3 ripe females were found : 3 other individuals bore evidence of a recent female phase. In this experiment with individuals which all bore young in 1922, 1 again carried young in 1923, 1 was found with young in 1924, and 2 or possibly 3 were ready to spawn ova in July 1924. Three others in July 1924 showed evidence of having recently passed through a female phase.

TABLE V.

Experiment 4.

On Females Bearing Young (1922), *West Mersea, R. Blackwater.*

Cage put out. 1922	Cage hauled.	Remarks.	Dead in cage or opened.	♀ with young.	Total dead & opened.	Total living.
July 8		Bearing young, June 28 to July 8, 1922	–	–	–	
		Cage put out in Deeps				78
	1923					
	July 14		**46**			32
	July 14–15	Tested; 6 opened	5*b*	1*a*	52	26
July 15		In sea in creek	–	–	52	26
	July 23	Tested		0	52	26
	July 31	Tested again	**1**	0	53	25
Aug. 2		In Deeps	–	–	53	25
	Oct. 17		**3**	0	56	22
Oct. 22			–	–	56	22
	1924					
	June 7		**3**	–	59	19
	June 7–9	Tested; 2 opened	2*c*	0	61	17
June 11	June	In sea in creek	–	–	61	17
	June 30	Tested	–	0	61	17
July 2		In cage in pit		–	64	14
	July 5–6	Tested and opened all; found 4 ripe females and 3 in recent ♀ phases	**3** 13*c*	1*c*	78	0
		Experiment finished.				

Notes on Table V.

(*a*) One other found greysick July 14, 1923: opened July 15/23 and found in ♂ phase V with patches of unspawned ova. The shell showed a growth of 12 mm. new shell at the ventral edge.

(*b*) Five oysters were opened and found as follows:—

			New shell growth ventrally.	♂ phase.	Length of shell.
1.	ripe ♂	ducts full	6 mm.	V	
2.	do.		6 mm.	IV	
3.	waning ♂ fair fish		nil	VII	70 mm.
4.	waning ♂	poor fish	8 mm.	VI	65 mm.
5.	waning ♂	good fish	7 to 9 mm.	V	65 mm.

(*c*) Two oysters found gaping on June 8, 1924, were opened and the 14 remaining opened on July 5–6, 1924. Their condition and sex-characters are as follows: 9 showed slight new shell growth from a trace at the exhalant aperture to a rim of 8 mm. of very thin shell at the ventral edge.

	Length in mm.	Fish.	Gonoducts.	Ripe sp. m.	Unripe sp. m.	Ova.	Sex-phase.
1.	80	f. good	full	none	none	∞ deg.	♀→ϕ
2.	60	v. poor	empty	do.	do.	small patches relict	♀→ϕ
	5.7.24						
3.	64*	poor	do.	do.	do.	none	ϕ
4.	60	good	f. full	v. ∞	do.	do.	♂ V
5.	67*	do.	empty	∞	a few	f. no.	♂(♀)A
6.	71*	v. good	do.	fair no.	none	∞ ripe	⚥
7.	49	do.	do.	none	do.	do.	♀
8.	79*	do.	do.	∞	∞	none	♂ IV
9.	73*	fair	f. full	∞	∞	do.	♂ IV
10.	62*	v. good	do.	∞	f. ∞	do.	♂ IV
11.	64*	good	empty	f. ∞	f. ∞	do.	♂ IV
12.	58–72	poor artery	do.	v. few	occ.	do.	♂ V
13.	57	good	do.	∞	do.	∞ deg.	♂(♀) B
14.	62*	do.	do.	∞	∞	none	♂ IV
15.	58	v. good	n.r.	∞	f. ∞	do.	♂ IV
16.	58*	good	full on left	none	occ. v. young	∞	♀–♂ I

No. 16 extruded embryos in late segmentation stages; when opened it was found to have spawned the eggs from the right side of the body only, the left remaining full of ripe ova. The gonad on the right had a curdled appearance due to many small patches of unspent ova. The individual had spawned incompletely some 12 to 18 hours before examination.

Experiment 5. *On Females Bearing Young* (1922). *Relaid R. Yealm.*

During June 16–22, 1922, 27 oysters recently forwarded to Plymouth from Whitstable, Port Navas, and the River Yealm, were found to be carrying embryos (whitesick). These were kept in the tanks at Plymouth until put out in the Yealm cage on June 23. Details of the experiment are given in Table VI, p. 31. The cage was hauled five weeks later when 2 oysters were found dead: 10 were brought back to the Laboratory and opened for information regarding development of gonad; 1 of these was found blacksick, carrying a large number of larvæ.

On March 12, 1923, the cage was hauled for cleaning; 10 individuals were found dead. The remainder were tested four times during the breeding season of 1923, but none found with either embryos or larvæ. None of these survived to the following breeding season.

Summary of Experiment 5.

Ten of the orginal 27 oysters used in the experiment were opened after being in the sea five weeks. One of these was found blacksick and had either retained its larvæ or spawned a second time from the eggs matured

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* Nine individuals showed a slight new growth of shell, June 7–9, consisting of very thin shoot varying from a trace at the exhalant aperture to a rim of about 3 to 8 mm. at the ventral edge. The gaper, No. 1, and several others had grown good shell-shoots in the autumn of 1923.

in June. Ten of the 15 remaining oysters died during the following winter and none of the survivors was found in spawn during four tests made in the succeeding breeding season.

TABLE VI.

EXPERIMENT 5.

On Females Bearing Young (1922), *R. Yealm near Plymouth.*

Cage put out.	Cage hauled.	Remarks.	Dead in cage or opened.	♀ with young.	Total dead & opened.	Total living.
	1922					
June 23						27
	July 28	Tests made	**2**	–	–	25
		10 opened and examined	10*a*	1	12	15
	1923					
March 12	March 12		**10**	–	22	5
May 10	May 10		0	–	–	5
	July 7	Tests made	0	0	–	5
July 10			0	–	–	5
	Aug. 30	do.	**1**	0	23	4
Sept. 4			0	–	–	4
	Sept. 11	do.	0	0	–	4
Sept. 15						
	Oct. 1	do.	0	0	–	4
Oct. 16			0	–	–	4
	Dec. 8		**2**	–	25	2
1924	June 24	Experiment ended	**2**	0	27	0

(*a*) All these individuals were in either No. V or No. VI male phases.
See **1**, Table IX, lots 92 and 93, for details of 8 of these oysters.

Experiment 6. *On Females Bearing Young* (1923), *W. Mersea, R. Blackwater.*

In this experiment 29 *O. edulis* carrying either embryos or young were detected between July 14 and August 2, 1923, at West Mersea and returned to the sea in Deeps in the cage on August 2, 1923. Details of the experiment are given in Table VII, p. 32. After a cleaning inspection in October 1923 the cage was hauled again on June 7, 1924, when 23 living oysters remained. A test made in June revealed no individuals bearing young, but early in July 2 such individuals were found. The survivors were opened on July 8, eleven months after the experiment began, when 1 more individual was found with embryos, 1 ripe female was ready to spawn, and 3 contained ova which were regarded as unspent from a previous female phase.

Summary of Experiment 6.

In 1924 3 oysters which bore young in 1923 were again found in good female phases (2 with young and 1 full of ripe ova) in July. This experiment was begun with 29 individuals, of which 20 survived to be examined in the following breeding season.

TABLE VII.

Experiment 6.

On Females Bearing Young (1923), *West Mersea, R. Blackwater.*

Cage put out.	Cage hauled.	Remarks.	Dead in cage and opened.	Ripe ♀.	♀ with young.	Total dead & opened.	Total living.
1923							
Aug. 2		In Deeps					29
	Oct. 17		**1**		0	1	28
	Oct. 20	Opened 2	2*a*		–	3	26
	Oct. 22		–		–	3	26
1924							
	June 7		**3**			6	23
	June 8	2 gaping ; opened	2*b*		0	8	21
June 9		In Thornfleet	–	–	–	8	21
	June 30		**3**	–	–	11	18*c*
	July 1	1 gaping ; opened	1	–	–	12	17
	July 1–2	Tests made	–	–	0	12	17
July 2		In cage in pit					
	July 5	Tests made	0	–	2*d*	14	15
	July 8	Remainder opened	15	1	1	29	0

Experiment ended.

(*a*), (*b*), and (*c*) are described in **1**, pp. 1027–8, Table IX, lots 107, 108, and 110.

(*c*) Amongst the 18 oysters opened and examined from July 1 to 8, 13 were in good male phases, two were found with numerous embryos or larvæ, one was a ripe female, and three others retained in their gonad ova which appeared to be degenerating and may be regarded as relict from the last female spawning.

(*d*) One of these individuals was a doubtful spawner : a few black larvæ were discovered on the glass plate below the oyster, but none were found in the mantle cavity.

Experiment 7. *On Females Bearing Young* (1923), *R. Yealm, near Plymouth.*

Experiment 7 was begun with 21 oysters received at Plymouth from various oyster grounds during June, July, and August 1923, and proved to be carrying young. Most of them were in the whitesick stage on arrival, but a few of the later ones were blacksick or bore shelled larvæ. Eighteen were sent from Whitstable, 2 from Port Navas, and 1 from West Mersea ; whitesick individuals were received from the three localities between June 18 and 21. After being proved these oysters were kept in the tanks in the Plymouth Laboratory until put out in the experimental cage on August 30.

The cage was hauled on October 2 and a sample of 8 brought back to the Laboratory for the purpose of photographing the new good shell-growth made by the experimental oysters (see note *a*, Table VIII). When the oysters were again examined on June 24, 1924, 19 survivors were found and 1 extruded numerous embryos. Two more were carrying abundant young at another test made July 15–16, and 1 more was found at the fourth test made on August 8. Although these oysters had been relaid from various parts of England, 17 out of 21 survived a winter and the following summer. Only 1, however, survived the second winter.

Summary of Experiment 7.

Of 21 oysters carrying young in 1923 and relaid in the River Yealm on August 30, 1923, 4 were found again with young during the summer of 1924.

TABLE VIII.

EXPERIMENT 7.

On Females Bearing Young (1923), *R. Yealm near Plymouth.*

Cage put out.	Cage hauled.	Remarks.	Dead.	♀ with young.	Total dead or opened.	Total living.
	1923					
Aug. 30		On the Yealm oyster beds	–			21
	Sept. 15	Tests made	0	0	0	21
Oct. 16	Oct. 2–16	Sample of 8 brought in. Tests made; shell-growth good (*a*)	0	0	0	21
Dec. 8	Dec. 8	Cage overhauled	0	–	0	21
	1924					
	June 23	Tests made	**2**	1*b*	2	18+1*
June 26						18+1
	July 15–16	Tests made	0	2*c*	2	16+3
July 18			1	–	3	15+3
Aug. 8	Aug. 6–8	Tests made	0	1*d*	3	15+3
	Aug. 26		0	0	3	15+3
Aug. 28		Tests made	**1**	0	4	14+3*
	1925					
	June 26	Experiment ended	**13+3**	0	20	1

NOTES ON TABLE VIII.

(*a*) A photograph of these 8 oysters is given in **3**, p. 381, with a description on p. 382. The new shell-growth varied from a few to 8 mm. in extent.

(*b*) This oyster extruded numerous embryos on June 24, in late segmentation stages, and was traced and put back in the cage. On July 16 the gonad was tapped and found to be in male phase V.

(*c*) One individual extruded numerous embryos at the instant of developing cilia and acquired a good ring of cilia by July 18. The gonad was retapped on July 17, and found to be in male phase I.

The other extruded numerous embryos in a similar stage; these also developed cilia and could swim on July 17. The gonad was in male phase I on July 18 and contained some unspent ova. Both oysters were traced and put back in the cage in the sea. On August 28 both borings were found to have been repaired. These oysters died during the following winter.

(*d*) One extruded numerous slate-coloured larvæ with shells 180 to 190 μ: on opening it was found to have a gonad in male phase III and to be completely spent (as a female).

* Individuals which spawned again in 1924.

Experiment 8. *On Females Blacksick, July* 1924, *West Mersea, R. Blackwater.*

From July 1 to 9, 1924, 60 blacksick oysters were proved and put out in the cage in Deeps on July 9. On July 2, 1925, the cage was hauled and 21 dead individuals found. The 39 living were tested unsuccessfully, July 2–5, for sick individuals and were put back in the sea from July 5 to July 13. On the latter date they were taken out of the sea and all opened during the following two days. The characters of these oysters at this time are given in detail in **1**, p. 1028, lot III, and are summarised as follows :—

TABLE IX.

1925	No.	Sex-condition.	Fish.
July 13–15	4	Carrying embryos or larvæ	poor to fair*
	1	Ripe female ready to spawn	very good
	12	Male phase IV	fair to good
	10	,, ,, V	poor to good
	8	,, ,, VI	poor to good
	3	,, ,, VII	poor to good
	1	macerating	
	—		
	39		

Experiment 9. *On Females Whitesick, June–July* 1924, *West Mersea, R. Blackwater.*

From July 10–13, 1924, 72 oysters were proved to be whitesick and stored in a pit. On July 8–9, 3 more whitesick individuals were found and all were put in the cage in the sea in Deeps on July 9, 1924, at the same time as those used in Experiment 8.

On hauling the cage on July 2, 1925, 49 living oysters were found. These were tested July 2–3 and 1 found blacksick ; 4 found gaping were opened and examined. From July 5–13 the sample was re-examined, when one was found dead ; the remainder were tested and opened July 13–16. The details of the examination are given in **1**, p. 1029, lot 112, and may be summarised as follows :—

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* Two had retained a few unspent eggs in the gonad. Only one individual among the 33 male phases had eggs in the gonad ; this individual had a gonad of curdley appearance, and the eggs were regarded as relict from a previous female phase. The cage was hauled after the beginning of the breeding season, it is to be noted, when early female spawners may already have extruded their larvæ.

TABLE X.

No.	Sex-condition.	With unspent ova.	Fish.
3	Carrying embryos or larvæ	1	poor to fair
0	Ripe females	0	
3	Male phase IV	0	poor to fair
13	,, ,, V	0	poor to v. good
21	,, ,, VI	2	poor to v. good (mostly fair to good)
3	,, ,, VII	1	fair to good
5	,, ,, VIII=neuter	3	poor to good
48		7	

In this experiment six individuals in non-functional female phases had retained few or many eggs from a previous female phase. As in the case of Experiment 8 some individuals may have spawned and evacuated their young in the early part of the breeding season of 1925, before the cage was hauled.

Experiment 10. *On Females* (*West Mersea and Fal Estuary*) *Blacksick, July* 1925, *West Mersea, R. Blackwater.*

A. During July 1925 a collection was made of 38 blacksick oysters from dredgings from the West Mersea beds. These were put out in the cage in Deeps on July 21, and hauled July 3, 1926. Twenty-eight individuals were found alive. The sample was opened at once and examined for sex-condition. Particulars are given in **1**, p. 1030, lot 113A. Two were functional females, 1 of these being hermaphrodite but full of ripe eggs; the remaining individuals were mostly good males in good condition.

B. Sixteen blacksick oysters sent on from the Fal Estuary beds in July 1925 were treated in the same way as the preceding sample A. When the 7 survivors were examined on July 3, 1926, 1 individual was found to be hermaphrodite with abundant ripe ova. This type of individual is regarded as a functional female. Five others were in good condition as ripe or ripening males and 1 was neuter in poor condition.

Experiment 11. *On Females* (*West Mersea and Fal Estuary*) *Whitesick, July* 1925, *West Mersea, R. Blackwater.*

A. During July 1925, 48 whitesick oysters were found amongst samples dredged at West Mersea, and put in the cage in Deeps on July 21, 1925. When the cage was hauled on July 3, 1926, 41 oysters were found alive and tested July 3–5. None were then found in spawn. On July 7 the whole sample was opened and the sex-condition noted as is given in **1**, p. 1030, lot 113B. Three individuals were found carrying young, 3 were ripe or ripening females, and 1 was a ripe female with sperm in the gonad ; the remainder of the sample were males in various phases except for 3 weakly and neuter individuals.

B. Twenty-one whitesick oysters sent to West Mersea from the Fal Estuary in July 1925 were treated in the same way as the sample A described above. When examined on July 3, 1925, of the surviving 6 oysters 1 was a ripe female ready to spawn, 4 were ripe males in good or very good condition, and 1 was a weakly neuter.

Experiment 12. *On Females Bearing Young* 1926, *Truro Beds, Fal Estuary.*

A. In this experiment 61 Fal Estuary oysters found with black or grey-shelled larvæ in July 1926 were put out in a new cage in Trelissick Reach on July 29, 1926. This sample was hauled and examined on September 29, 1926, to obtain information on gonad changes in the same breeding season as the oysters were found in spawn. The details of this sample are given in **1**, pp. 1031–2, lot 114A, and may be summarised as follows :—

The sample consisted of 43 with normal shells, of which 2 died, and 18 with dumpy shells (for definition see **7**, p. 200), of which 1 died.

TABLE XI.

Category.		Normal.		Dumpy.	
		No.	With relict ova.	No.	With relict ova.
♀ with young		1 Bl.	0	1	0
ripe female		0	0	0	0
♂ phase IV		0	0	0	0
,, V	waning or arrested	2	0	1	0
,, VI		17*	1	11	0
,, VII		9	0	2	0
,, VIII=neuter		10	1	2	0
not observed		2	0	0	0
		41	2	17	0

B. Three whitesick oysters were put out and hauled with sample A noted above. One died ; the two remaining were in male phases IV

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* One of these might have had very young ova, but microscopic sections are required for certainty in identification.

and V respectively on September 29, 1926, and neither had unspent ova in the gonad (see *loc. cit.*, lot 114B).

C. A sample of 28 blacksick individuals was also put out in another cage moored to the Poles Rocks, Fal Estuary. These were put out on July 21, 1926, and examined for general gonad condition on September 30, 1926. Three died. The details of the living ones are given in **1**, p. 1032, lot 115A, and may be summarised as follows :—

TABLE XII.

Category.	Normal. No.		Dumpy. No.	
	C.	D	C	D
♀'s with young	2§ (1 sl ; 1 Wh)		0	
ripe females	0		0	
♂ phase IV	1		0	
,, V	2		1	1
,, VI	8§	7§	1	1
,, VII	5*	2	4†	1
,, VIII	1	3‡	0	
	—	—	–	–
Sample C totals	19		6	
Sample D ,,		12		3

D. In the cage moored to Poles Rocks on July 21, 1926, were also isolated 15 oysters found whitesick during July 1926. These all survived and were examined on September 30, 1926. Details of their general condition are given in **1**, p. 1033, lot 115B, and are summarised under D in the table given above.

Experiment 13. *On Females Bearing Young*, 1926, *West Mersea, R. Blackwater.*

In earlier experiments females carrying spawn have been examined after isolation in the sea for twelve months or more, or in the case of the last experiment after about two months. In this experiment 45 blacksick and 66 whitesick oysters were collected and put out in the sea at West Mersea on July 14, 1926, and examined just before the beginning of the breeding season in 1927, namely on May 27, the cage having been hauled

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* One with numerous young ova.

† Two with doubtful young ova.

‡ One with doubtful young ova.

§ One with unspent ova, probably many young relict ova in the ♀ with larvæ.

on May 26. The details are given in Tables XIV and XV, pp. 39 and 40, and may be summarised as follows :—

TABLE XIII.

Category.	A. Blacksick, 1926.	B. Whitesick, 1926.
♀'s with young	0	0
ripening and ripe ♀ phases	8	5
young ♀'s	1	1
♂ (♀) B	2	1
neuter	3	0
ripening and ripe ♂'s	21	39
young and developing ♂'s	3	18
died	7	2
	—	—
	45	66

SERIES C. EXPERIMENTS ON RIPE FEMALES AND RIPE FEMALE INTERSEXES.

Experiment 14. *On the Isolation in the Sea of Ripe Females, West Mersea, R. Blackwater*, 1923.

When boring oysters for the purpose of finding males in July 1923, 12 ripe female individuals were discovered. These were returned to the sea in a whelk-pot hung over the stern of a vessel in Thornfleet until October 1923, when they were hauled and opened and examined on October 29. Eight of them were found to have made good shell-growth, of which a photograph is shown in **3**, Fig. 6, p. 379. The sex-phases were as follows :—

TABLE XVI.

Male Phases.	V	VI	VII	VIII
Total 12	2	5	1	4
,, 8 with relict ova	2	1	1	4

All the individuals had spawned, but eight showed indications of a recent female phase in the presence of relict ova in the gonad.

Experiment 15. *On the Isolation in the Sea of Hermaphrodites, West Mersea, R. Blackwater*, 1923.

Four hermaphroditic oysters were found at the same time and in the same way as the females mentioned in Experiment 14. These were also isolated in Thornfleet and examined on October 29, 1923. Three had

TABLE XIV.

EXPERIMENT 13, A.

On Females Blacksick, West Mersea, July 1926, *examined May* 27, 1927.

					Sex-elements. Sperm-morulæ.			Shell.[3] Length in mm.		Shell.[3] Shoots in mm.	
No.	Condition of Fish.	Appearance[1] of gonad.	Gonoducts.	Sex-phase.[2]	Ripe.	Unripe.	Ova.	1926	1927	1926	1927
1	f.	sq. & trs. retic.	½ full	ca. ripe ♂	∞	∞	none	74	83	13	0
2.	f.	—	full	ripe ♂	N.O.			60	60	4	0
3.	f.g.	ram. A trs. retic.	empty	♂ IV	∞	∞	none	70	84	13	3
4.	g.	white nf. (♂) ⚥ ♀	filling	♂ (♀) A	few	∞	∞	49	70	22	0
5.	f. to p.[4]	trs. retic. ; st. B	empty	neuter	none	none	none	58	65[3]	13	0
6.	f.[4] [5]	sq. & trs.	do.	♂ V	fair no.	occ.	none	48	56[3]	8	0
7.	v.g.[6]	ram. A op. retic.	do.	♂ (♀) A	v. ∞	f. ∞	f. ∞	57	64	18	0
8.	f.g.	—	full	ripe ♂	N.O.			50	61	10	tr.
9.	f. to p.	—	filling	ca. ripe ♂	N.O.			50	16	15	0
10.	f.g.[6]	ram. A trs. retic. wh.	empty	♂ (♀) A	∞	∞	f. no.	49	64	15	0
11.	g.	—	full ; long	ripe ♂	N.O.			47	63	20	0
12.	g.	—	do.	do.	N.O.			52	61	16	0
13.	g.	—	do.	do.	N.O.			48	48	0	0
14.	g.	—	do.	do.	N.O.			41	55	13	0
15.	g.	—	do.	do.	N.O.			53	62	12	3
16.	g.	sq. & trs. st.	empty	♂ III	few	v. ∞	occ. rel.	55	60	5	4
17.	v.g.	white nf. (♂) ⚥ ♀	filling	♂ (♀) A	∞	few	∞	46	59	12	3
18.	g.	—	full ; long	ripe ♂	N.O.			62	76	20	tr.
19.	f.g.	—	filling	ca. ripe ♂	N.O.			55	63	10	tr.
20.	g.	—	full ; long	ripe ♂	N.O.			65	69	10	0
21.	f. to p.[7]	G.D. st. A–ram. A	empty	young ♀ ?	none	none	∞	43	55	16	0
22.	g.[4]	sq. & trs., honeyc. & retic.	do.	neuter	none	none	none	52	54	5	tr.
23.	v.p.[7]	watery	do.	do.	N.O.			49	56	15	0
24.	f.	sq. & trs. honeyc. retic.	do.	♂ I	none	few	none	53	63	10	2
25.	f.g.	—	full ; long	ripe ♂	N.O.			54	61	11	0
26.	g.	—	do.	do.	N.O.			50	65	15	0
27.	f.	—	do.	do.	N.O.			62	78	15	5
28.	v.g.	white ff. (♂) ⚥ ♀	full of ova	ripe ♀	occ.	none	∞ ripe	57	65	9	0
29.	g.[6]	white nf. (♂) ⚥ ♀	filling	ca. ripe ⚥	v. ∞	none	f. ∞	55	70	15	0
30.	f.[6]	sq. & trs. retic. honeyc.	empty	♂ III	few	v. ∞	occ. rel.	47	58	10	0
31.	g.[6]	ram. A wh. retic. ♂ ?	empty	♂ (♀) B	∞	∞	f. ∞	67	81	17	0
32.	f.g.	—	filling ; long	ca. ripe ♂		N.O.		46	67	22	0
33.	v.g.	—	do.	do.		N.O.		54	60	9	0
34.	g.[6]	wh. retic. nf. (♂) ⚥ ♀	empty	♂ (♀) B	∞	∞	few	50	73	22	0
35.	v.g.	rather sq.	filling ; long	ca. ripe ♂		N.O.		65	66	13	0
36.	v.g.	ram. A opaque	empty	♂ (♀) A	v. ∞	none	f. no.	47	59	9	0
37.	g.[6]	ram. A wh. & trs. retic.	do.	♂ (♀) A	∞	∞	f. no.	48	70	23	0
38.	g.	—	full ; long	ripe ♂		N.O.		58	70	15	0

NOTES ON TABLE XIV.

[1] The abbreviations used to denote the naked eye appearance of the gonad will be amplified and discussed in a later communication on a seasonal study of an oyster population.

[2] For a description of sex-phases, see **1**, pp. 975 and 981.

[3] The comparison in this sample and that noted in Table XV between the growth of large shell-shoots in the autumn of 1926 and the slight, or absence of such growth in the spring of 1927, is especially interesting (see **3**, p. 377). The length of the shell is measured antero-posteriorly and is on the average about the same as the height measured dorso-ventrally ; the shoot is measured in the mid-ventral line, where it is usually largest, tapering off anteriorly and posteriorly.

[4] Shells chambered indicating constitutional trouble of some kind, at some unknown period.

[5] Muscle spindles (see **5**, p. 48) present in the visceral mass.

[6] An appearance of abundant food reserve material is noted in correlation with the presence of degenerating and/or developing ova (see **1**, p. 976).

[7] Mantle cavity choked with mud ; this fact in correlation with the poor condition of the fish indicates permanent weakness.

Abbreviations :

f. = fair or fairly.
∞ = numerous.
g. = good.
no. = number.
v. = very.
tr. = trace.
p. = poor.
G.D. = Gonad developing.
G.L.D. = Gonad little or slightly developed.
G.M.D. = Gonad mediumly developed.
G.W.D. = Gonad well developed.

N.O. = not observed, as experience taught that microscopic examination is not necessary in such cases.

General.

The gills in this sample were mostly coloured slightly green and were thus on the point of the seasonal change from the winter state of being coloured a ferrous-sulphate green to the summer state of white gill. Some gills were brown, i.e. nos. 3, 4, 9, 17, 19, 22, 23, 25, and 38.

TABLE XV.*

EXPERIMENT 13, B.

On Females Whitesick, West Mersea, July 1926, *examined May* 27–28, 1927.

					Sex-elements.			Shell.[3]			
					Sperm-morulæ.			Length in mm.		Shoots in mm.	
No.	Condition of Fish.	Appearance[1] of gonad.	Gonoducts.	Sex-phase.[2]	Ripe.	Unripe.	Ova.	1926	1927	1926	1927
1.	f.g.	f. trs. honeyc. retic.	full ; long	ripe ♂		N.O.		53	80	24	0
2.	f.g.	do.	do.	do.		N.O.		48	69	18	2
3.	f.g.	ram. A. trs. retic. G.L.D.	—	♂ I	none	few	none	58	66	10	0
4.	f.g.	ram. A. wh. & trs. retic. G.M.D.	—	♂ (♀) A	few	v. ∞	f. no.	70	78	10	0
5.	f.	ram. A, trs. retic .G.L.D.	—	♂ I		N.O.		50	73	16	0
6.	f.	G.L.D.	full ; long	ripe ♂		N.O.		53	73	10	3
7.	f.	trs. retic. G.L.D.		♂ I	none	∞	occ. rel.	47	67	19	0
8.	f.	sl. ram., wh. trs. retic.		♂		N.O.		55	74	18	tr.
9.	f.	do.		♂		N.O.		50	80	21	tr.
10.	f.	G.L.D.	full ; long	ripe ♂				56	67	17	?
11.	f.g.	do. sq., & trs. retic.	—	♂ IV	∞	∞	none	57	60	0	3
12.	v.g.	ram. A. op. G.n.f.D. (♂) ⚥ ♀	—	♂ (♀) A	∞	f. ∞	∞	44	59	13	2
13.	f.g.		full ; long	ripe ♂		N.O.		38	56	14	0
14.	f.	trs. retic. G.L.D.	—	♂ I	none	∞ young	none	41	48	7	4
15.	f.g.	G.M.D.	filling	ca. ripe ♂		N.O.		49	65	11	tr.
16.	f.	G.L.D.	do.	do.		N.O.		47	62	13	3
17.	f.g.	sq. & trs. retic.	—	♂ I		N.O.		63	75	10	tr.
18.	f.g.	do.	filling	♂ IV		N.O.		56	68	16	0
19.	f.	f. trs. G.L.D.	full	ripe ♂		N.O.		49	76	19	0
20.	g.	sq. & trs. retic.	—	♂		N.O.		55	63	7	0
21.	g.	do.	—	♂		N.O.		61	63	7	0
22.	v.g.	ram. A trs. G.W.D.	filling	ca. ripe ♂		N.O.		56	63	8	tr.
23.	g.	do	do.	do.		N.O.		63	81	16	0
24.	v.g.	G.W.D.	do. long	do.		N.O.		56	72	14	3
25.	f.	G.L.D.	full	ripe ♂		N.O.		46	60	17	0
26.	g.[6]	ram. A. wh. retic.	—	♂ (♀) B	v. ∞	∞	some	58	66	8	0
27.	f.	sq. & trs. retic.	—	♂		N.O.		58	68	7	0
28.	g.	G.M.D.	full	ripe ♂		N.O.		56	61	7	0
29.	v.g.	G.W.D.	do. long	do.		N.O.		50	69	19	0
30.	f. to p.	sq. & trs. sl. retic.	—	neuter or ♂ I		N.O.		68	80	9	0
31.	f.	sq. & trs. sl. retic. G.L.D.	—	♂		N.O.		56	76	17	0
32.	f.	do.	little in ducts	♂ IV		N.O.		50	58	7	0
33.	g.	G.M.D.	full	ripe ♂		N.O.		49	60	10	0
34.	g.[6]	G.v.W.D. white nf. (♂) ⚥ ♀	filling	♂ (♀) A	few	f. ∞	∞	55	65	13	0
35.	g.	trs. retic. G.W.D.	do.	ca. ripe ♂		N.O.		61	75	16	tr.
36.	f.	sq. & trs. retic.	—	♂		N.O.		55	70	20	0
37.	f.	ram. trs. retic. G.L.D.	filling	♂ IV		N.O.		50	69	10	0
38.	g.	G.W.D.	full	ripe ♂		N.O.		50	64	20	0
39.	f.g.	G.M.D.	do. long	do.		N.O.		60	73	11	0
40.	f.g.	sq. & trs. retic.	filling	♂ IV		N.O.		55	63	6	0
41.	f.	do.	do.	♂ IV		N.O.		45	62	17	0
42.	f.g.	sq. & trs. st. B		♂ III	few	∞	none	58	69	12	0
43.	g.	G.M.D.	full	ripe ♂		N.O.		53	62	13	tr.
44.	g.	G.v.W.D.	do. long	do.		N.O.		50	61	12	tr.?
45.	g.	G.M.D.	do.	do.		N.O.		54	66	16	0
46.	g.	G.M.D.	filling	ca. ripe ♂		N.O.		58	70	12	0
47.	f.	G.L.D.	full	ripe ♂		N.O.		45	50	9	0
48.	f.g.	do.	do.	do.		N.O.		44	51	9	0
49	f.	st. ram. trs. retic.	little	♂ IV		N.O.		46	53	6	tr.
50.	f.	do.	do.	♂ IV		N.O.		53	62	8	0
51.	v.g.	white (♂) ⚥ ♀ G.F.D.	filling	⚥ (♀)	f. ∞	none	∞ ripe	62	79	13	6
52.	g.	G.M.D.	do.	ca. ripe ♂		N.O.		63	73	14	0
53.	f.g.	do.	do.	do.		N.O.		53	68	17	0
54.	f.	do.	do.	do.		N.O.		50	65	21	tr.?
55.	g.[6]	ram. A wh. retic. G.M.D.	—	♂ (♀) A	∞	∞	f. ∞	53	63	11	tr.?
56.	f.g.	sq. & trs. retic. G.L.D.	—	♂ III	rare	∞	none	68	74	10	tr
57.	f.	f. trs. dendritic ducts	filling	ca. ripe ♂		N.O.		45	63	16	0
58.	f.	st. A—ram. A wh. retic. G.L.D.	—	young ♀	none	none	∞ ripening	64	81	13	0
59.	f.	G.L.D. ram. retic.	—	♂		N.O.		56	70	17	0
60.	f. to p.	sq. & trs.	—	♂ V	fair no.	few	none	47	63	16	0
61.	f.	sq. & trs. st. B	little	♂		N.O.		75	87	6	0
62.	f.g.	do.	do.	♂		N.O.		62	70	7	0
63.	f. to p.	trs. retic. G.L.D.	—	♂ I	none	∞ young	none	46	67	21	3
64.	v.g.	ram. honeyc. G.W.D.	filling	ca. ripe ♂		N.O.		68	73	8	0

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* See notes to Table XIV for explanatory remarks. In this sample the gills were mostly slightly green : in 11 individuals they were brown.

spawned all or nearly all the ova, but 1 had spawned its ova only partially. The latter was in sex-phase VII with relict ova, and with two others, which were in sex-phases VI and VII, had made a perfect recovery from the boring. The fourth had made a very bad recovery from the operation and its gonad had no sex-elements.

SUMMARY AND DISCUSSION OF EXPERIMENTS ON ISOLATING OYSTERS CARRYING YOUNG (SERIES B) AND ON THOSE WITH RIPE EGGS (SERIES C).

The results obtained in the set of experiments with oysters bearing young are summarised in Tables XVII A and B, p. 44, and XVIII, pp. 46–47.

From Table XVII B it is seen that at the end of the same breeding season as that in which the experimental individuals were found, i.e. the 1st summer, a proportion as high as 3·4% were again detected bearing young. In the second summer about 5% were found again with young and an additional 7% were ready to spawn as females. Among the small number of individuals surviving to the third summer of the experiments about 5% were again found with young and at least an additional 15% ready to spawn as females. Among all the experimental oysters about 11% were discovered again in ripe female functioning stages.

It may be presumed that *all* female-functioning oysters revert again to the female phase at some time after passing through an intermediate male (and possibly a neuter) phase. Hence the gross percentage of reversion to the ripe female phase found is small except in the experiment which ran into the third summer. There can be no doubt that the actual reversions occurring were much greater in number than found from the following considerations :—

(1) In several experiments (e.g. 10 and 11) only one test was made during the breeding season, so that only those females existing as such at that time of the season were detectable. It is known that female phases may develop throughout the extent of the breeding season, although on the beds in the River Blackwater a maximum of spawning usually occurs about July.

(2) In some experiments tests were not made until some weeks after the opening of the spawning season, hence early spawners may have extruded larvæ before examination.

(3) In experiments 7, 5, and 4, tests were made only for detecting females with young in the second summer of the experiments. In these cases only those females actually carrying young at the time of examination could be detected.

(4) When tests were made frequently, as in experiments 7, 5, and 4, young-bearing phases may nevertheless have passed undetected in the sea in the intervals of testing.

(5) The presence of ova—recognisable in most cases as relict from a recent spawning—in the gonad of eleven individuals either male or neuter examined in the *second* summer of the experiments, and of two other such individuals amongst the few surviving into the third summer, affords evidence of the occurrence of the undetected production of larvæ among the experimental oysters.

Thus the reversions found by experiment in all cases can certainly be regarded as smaller than actual.

On the oyster beds it may reasonably be expected that the reversions to the young-bearing stage would be greater than those actually occurring under experimental conditions, the detrimental effect of which is demonstrated by the known heavy mortality. The attainment of the functional female phase may be postulated to be dependent upon a period of anabolic metabolism, and the building up of good reserves would undoubtedly be delayed or depressed by those detrimental conditions ancillary to the experiments already referred to on p. 26. Thus reversion to the female phase on the oyster grounds may reasonably be expected to be not only greater than that found in the experiments, but also greater than that actually occurring in them.

Although a greater percentage of reversions to the young-bearing phase may occur naturally on the beds than in the experiments, there are indications that a small proportion of the spawning taking place under experimental conditions may be a result of these conditions. It is clear that a correct estimation of any error introduced by the conditions of the experiment is of the greatest importance in assessing the results.

During the course of these experiments the importance of incomplete spawning in females has become gradually recognised. A discussion on the fate of unspawned ova is given in **1**, p. 974, and **6**, where it is regarded as probable that in a few cases out of the large number of observations made a given female may as a result of incomplete spawning in the first instance have spawned successfully a second time in one season from one batch of ova matured for the first spawning.

Experiment 12 was designed to obtain information on this matter. It was found that among 98 surviving oysters examined in September 1926 (see Table XVII), 4 were carrying young, although all had been found previously in July with either embryos or larvæ. The condition of the young in two of these four cases indicated that spawning had occurred recently; it is possible, but not probable (owing to the small size of the larvæ), that in the two others the larvæ may have been retained in the mantle cavity from July. In Experiment 5, when 10 individuals were examined five weeks after detection with young, 1 had larvæ which had in all probability been retained during the five weeks. Thus retention of larvæ and incomplete spawning may give an appearance of the assumption of a second female phase in one and the same breeding season. Whether unspawned ova can be successfully spawned after remaining in the gonad during the winter is a moot point, though improbable. Eggs remaining in the gonad at the approach of winter are *usually* evacuated or begin to degenerate *in situ* in the gonad. Relict eggs may, however, contribute to hastening the next female phase by adding to the food reserves in the body by their absorption.

Apart from this, it may be considered that female spawning in the second summer due to incomplete egg-spawning in the previous summer is a rare event, if indeed it occurs at all. An individual which retains ova in the winter is usually of the type designated as "curdley" (see **1**, Tables IV and IX).

In **1**, Table IV, p. 999, a record is made of the occurrence or absence of unspawned ova in about 700 recently spawning females. On analysis (see **6**) it is found that about 54% retain few or more eggs after spawning; 43% of these containing a few scattered eggs, while 11% may have many in scattered or large patches. Among this large sample as many as 22 individuals are recorded with the gonad from $\frac{1}{3}$ to $\frac{7}{8}$ spent. If it were possible for these individuals to spawn successfully again in the same season the percentage would attain the figure 3, very nearly that found in Experiments 12, 7 and 5, namely 3·4. (See Tables XVII A and B.)

Thus the oysters bearing young again in September in Experiment 12 must be regarded as having almost certainly spawned a second time from eggs matured earlier in the season; it is also possible that others undergoing such a second spawning may have occurred undetected during the course of this experiment.

Among the experiments where the samples were opened in the second summer, the results obtained in Experiment 11A are especially interesting (see Table XVIII, sample 18). In this case there was little mortality during the winter, 41 surviving out of 48. Correlated with these beneficent conditions is the occurrence of 3 oysters with young and 4 ripe female phases in the following July, a total of about 17% mature female-functioning reversions. In this set of experiments 11·7% of reversions occurred. Twenty per cent of reversion is also shown in Experiment 5, where the mortality in the preceding winter was low. Even if 5% of these be attributed to the influence of incomplete spawning in the preceding breeding season, there is still a significant margin left to prove reversion in the second summer, especially when it is remembered that the figure obtained is a minimum in comparison with that likely to occur in wholly natural animals.

In the small number of individuals surviving into the third summer, as in Experiment 4, one quarter of the sample were in mature female phases at the time of examination.

Conclusions from Experiments on Oysters with Young.

The experiments therefore prove that oysters which have borne young in one summer do attain a new female phase and bear young again in significant (but small) numbers in the next summer; a rather larger proportion attained new female phases two years later. There is good reason to believe that the percentage of reversion to female phases will be very much higher in wholly natural than in the experimental oysters, and that more reversions occurred in the experimental oysters than were discovered.

TABLE XVII A.

Summary of Experiments on Isolating Oysters with Young.

	1st Summer.			2nd Summer.				3rd Summer.			
No. of Expt.	No. of oysters.	No. of tests.	No. of ♀'s with young.	No. of survivors.	No. of tests.	No. of ripe ♀'s and ⚥.	No. of ♀'s with young.	No. of survivors.	No. of tests.	No. of ripe ♀'s. and ⚥.	No. ♀' wit you
12 A	82 (56)*	*1*	**2** :								
B	3 (2)	*1*	0 :								
C	28 (25)	*1*	**2** :								
D	15 (15)	*1*	0 :								
13 A	45	–	–	38	–	8+2	– :				
B	66	–	–	64	–	5+1	– :				
8	60	–	–	38	*2*	1	**4** :				
9	75	–	–	48	*2*	0	**2** :				
10 A	38	–	–	28	*1*	2	0 :				
B	16	–	–	7	*1*	1	0 :				
11 A	48	–	–	41	*1*	4	**3** :				
B	21	–	–	6	*1*	1	0 :				
6	29	–	–	20	*2*	1	**2**+**1**?				
7	21 (21)	*1*	0	19–3†	*4*	–	**4**	1 died			
5	27 (27)	*1*	**1**	5–1†	*4*	–	0	2 died			
4	78	–	–	32–4†	*3*	–	**1**	19 (3 died)	*3*	3+1	
Totals	146		**5**	346		23+3‡	**16**+**1**?	19		3+1§	

TABLE XVII B.

	No. of oysters tested.	No. of functioning. ripe ♀'s	No. of ♀'s with young.	Total functioning ♀.	Total % functioning ♀.
1st Summer	146‖	—	5	5	3·4
2nd do.	346¶	23(+3)**	16(+1?)	39(+4)	11·3 to 12·4
3rd do.	19	3(+1)	1	4(+1)	21·0 to 26·3
Totals	511 67‖¶ 444	26(+4)	22(+1?)	48(+5)	10·8 to 11·9

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* The numbers in brackets in Table XVII A give those surviving to be tested in the first summer.

† Died during the second summer. ‡ Intersexes with ova nearly ripe.

§ With numerous doubtfully healthy ova.

‖ Includes 48 from Experiments 7 and 5 carried forward or died at end of first summer.

¶ Includes 19 from Experiment 4 carried forward at end of second summer.

** The figures bracketed in Table XVII B are derived from the totals given in Table XVII A.

SEX-PHASES INTERVENING BETWEEN SUCCESSIVE FEMALE PHASES.

It has been shown (**1**, Table IV) that among 702 oysters carrying young 97% of such individuals *immediately* pass into an active male phase after the act of egg-spawning. Many hundreds of similar cases have since been recorded. Additional evidence is afforded by the sex-phases recorded in Table XVIII from the B series of experiments. Thus, there can remain no doubt that the translation from a female to an active male phase occurs normally in *O. edulis* after the egg-spawning act. The small percentage of abnormalities—which consisted mostly of no assumption of the male phase—occurred at the end of the breeding season, when the gonad is passing into a passive condition. This fact is quickly seen from a glance at Table XVIII, pp. 46–47. Among individuals examined in July (Sections 1, 4, and 6) the male-phases are predominant, and are mainly IV, V, and VI, indicating that the gonads are still producing sperm-morulæ. On the other hand samples examined in September (Section 2) contain a high proportion of waning and neuter phases (e.g. VI, VII, and VIII). At the beginning of the second summer male phases still occur in high proportion, but are predominantly active, and it is interesting to note contain some quite young phases, namely I to III. It is thus shown that at the end of the breeding season sperm-production wanes or ceases but becomes active again in a high proportion of comparable individuals (80%) in the following early summer. During the early summer a proportion of individuals varying in the experimental material from 10% to 15% pass over into a functional female phase. A comparison of the totals in Sections 2 and 3 in the Table gives the suggestion that a proportion of the neuter individuals in September become female in the following spring. Further evidence is required, however, before this sequence can be acclaimed as a fact. No data are available from these experiments for discovering what proportion of individuals would pass from 2nd summer male phases into a 2nd summer female phase, but it is hoped to obtain the required information from an intensive study of seasonal changes in sex-phases in an oyster population. Such a study was made in 1926–27, and the results are being worked out.

In the 3rd summer the female phase was assumed in a larger proportion of the experimental oysters; 50% in Series A (see Table IV, p. 27) and 21% to 26% in Series B (see Table XVII B, p. 44), *excluding* the individuals showing signs of having recently passed through the female phase by the presence of recently relict ova in the gonad. Under wholly natural conditions there can be little doubt that the percentage of these transitions to the female phase would be much higher than in the experimental. The experiments nevertheless afford a valuable basis for more enlightening field studies. For example, it is relevant to record that in

TABLE

SEX-PHASES OF O. EDULIS, *occurring in samples examined at*

(Data derived from material

No. of Section.	No. of Sample.	Site of Expt.	No. of Expt.	Expt. begun.	No. isolated and condition of young. Bl.	Wh.	Mixed.	Origin of oysters.	Month of examination.	No. surviving to be tested or examined.
1.		Sex-phases found five weeks later (July). (In the same breeding season.)								
	1	R.Y.	5a	June			10	various	July	**10**
2.		Sex-phases found two to three months later in the 1st summer (Sept.–Oct.), (within								
	2	Fal R.	12A	July	63			F.E.	Sept.	39
	3	do.		do.	18			do.	do.	17
	4	do.	12B	do.		3		do.	do.	2
	5	Fal E.	12C	do.	22			do.	do.	19
	6	do.		do.	6			do.	do.	6
	7	do.	12D	do.		12		do.	do.	12
	8	do.		do.		3		do.	do.	3
	9	W.M.	6a	do.			2	W.M.	Oct.	2
	10	do.	14	do.			12*♀	do.	do.	12
	11	do.	15	do.			4†⚥	do.	do	4
								Totals of Section 2		**116**
3.		Sex-phases found at the approach of the next breeding season (2nd summer; May).								
	12	W.M.	13A	July	45			W.M.	May	38
	13	do.	13B			66		do.	do.	64
								Totals of Section 3		**102**
4.		Sex-phases found during the next breeding season (2nd summer; July).								
	14	W.M.	8	July	60			W.M.	July	38
	15	do.	9	June		75		do.	do.	48
	16	do.	10A	July	38			do.	do.	28
	17	do.	10B	do.	16			F.E.	do.	7
	18	do.	11A	do.		48		W.M.	do.	41
	19	do.	11B	do.		21		F.E.	do.	6
	20	do.	6	Aug.			29	W.M.	do.	20
								Totals of Section 4		**188**
5.		Tested only for young-bearing in the next breeding season (2nd summer; ca. July).								
	21	W.M.	4	July			78	W.M.	July	32–4
	22	R.Y.	5	June			27	various	do.	5–1
	23	R.Y.	7	June–Aug.			21	do.	June–Aug.	19–3
								Totals of Section 5		**56**
6.		Sex-phases found two years later (3rd summer; July).								
	24	W.M.	4c	—			(78)	W.M.	June–July	**16**
				Sum Totals	**268**	**228**	**261**			*488*
				Adjustments			78‖			44‡
				Adjusted Totals	**679**					**444**

* 12 found as ripe female by boring the shell.

† 4 found as ripe ⚥ by boring the shell.

‡ Comprises some samples not shown in Table XVII (i.e.

1. 2. 3. The small figures give the number of individuals in the

ϕ The numbers in brackets are included in one or other of the

‖ 78 individuals used for Sample 21, Experiment 4, are recorded

XVIII.

various intervals of time after being detected with young.

isolated in cages in the sea).

Male phases.							Neuter.	Female phases.							
										Ripe phases.				No. of	
I	II	III	IV	V	VI	VII	VIII	♂(♀) B	Juv. ϕ Dev.	♂(♀) A	⚥	♀	♀ with young.	Sample.	Section.
–	–	–	**3**	**3**	**3**	–	–	–	–	–	–	–	**1**	1	**1.**
but at the end of one and the same breeding season).															**2.**
–	–	–	–	2	17[1]	9	10[1]	–	(1?)	–	–	–	1	2	
–	–	–	–	1	11	2	2	–	–	–	–	–	1	3	
–	–	–	1	1	–	–	–	–	–	–	–	–	–	4	
–	–	–	1	2	8[1]	5[1]	1	–	(1)	–	–	–	2	5	
–	–	–	–	1	1	4[2]	–	–	(2?)	–	–	–	–	6	
–	–	–	–	–	7[1]	2	3[1]	–	(1?)	–	–	–	–	7	
–	–	–	–	1	1	1	–	–	–	–	–	–	–	8	
–	–	–	–	–	1	–	1	–	–	–	–	–	–	9	
–	–	–	–	2[2]	5[1]	1[1]	4[4]	–	–	–	–	–	–	10	
–	–	–	–	–	1	2[2]	1	–	–	–	–	–	–	11	
–	–	–	**2**	**10**	**52**	**26**	**22**	–	**(1+4?)**	–	–	–	**4**		
1	–	2	–	21	–	–	3	2	1	6	1	1	–	12	**3.**
18			39			–	–	1	1	4	1	–	–	13	
21			**60**				**3**	**3**	**2**	**10**	**2**	**1**	**0**		
–	–	–	12	10	8[1]	3		–	–	–	–	1	4	14	**4.**
–	–	–	3	13	21[2]	3[1]	5[3]	–	–	–	–	–	3	15	
–	–	–	24			–	2	–	–	–	1	1	–	16	
–	–	–	5			–	1	–	–	–	1	–	–	17	
–	–	–	31[1]			–	3	–	–	–	1	3	3	18	
–	–	–	4			–	1	–	–	–	–	1	–	19	
–	–	–	7	4[2]	3[1]	–	2	–	–	–	–	1	2+1?	20	
			145			**6**	**14**				**3**	**7**	**12+1?**		
													1	21	**5.**
													0	22	
													4	23	
													5		
–	–	–	**6**	**2**	–	–	**3[2]**	**1**	–	**1**	**1**	**1**	**1**	24	**6.**
								4		*26*			*22+1?*		

samples 1, 9, 10, 11) and sample 24 counted twice.
respective phases with either small patches of unspent or—rarely—developing ova in the gonad.
male phases and are not to be counted in the sample total.
again in Sample 24, Experiment 4 c.

three successive seasons on the Fal Estuary beds (Truro Rights) about 50% of the oyster population have been found to be ripe as functional females at about the beginning of each breeding season (see also **7**, p. 27). These facts alone show that on these beds there is on the average a reversion to the female phase at least every other summer.

A comparison of the male phases of the oysters in the experiments of Series A (see Table IV A, p. 27) with the male phases of individuals which were females in the preceding summer (see Table XVIII, Section 4, pp. 46–47) brings out a close similarity. Hence the males used in the Series A may have been mostly female in the summer before that in which they were identified. Some of these might very well have been female two summers ago, and therefore the rapid change to female observed in one instance (see p. 24) is—in the light of the results of these experiments and if the individual were normal—not outside expectation.

The young female stage was observed in two individuals in Experiment 13 when the whole sample was opened at the approach of the breeding season in May.* Seasonal studies have proved that the bulk of the females in an oyster population develop rapidly in the spring and early summer, hence examinations made about April–July would be the most favourable for discovering young females on most English beds. The relatively small proportion of all the different types of female phases found *in the experiments* is important in indicating :—

(1) that there is no *automatic* return to the female phase in the 2nd or the 3rd summer after that (counted as the 1st summer) in which young are borne.

(2) A return to the female phase may occur in the following breeding season (2nd summer) in a small but significant proportion of individuals.

(3) A higher proportion may revert to the female phase in the 3rd than in the 2nd summer.

(4) The male phase following egg-spawning may persist throughout the 2nd summer and possibly in the 3rd summer.

It is emphasized that these are *experimental* results, and that there is virtual certainty that the sexual processes follow each other more rapidly and more regularly on the oyster grounds than is apparent from these experiments.

Intersexes, or various hermaphrodite conditions, occur in most of the experimental samples which were examined after the 1st summer, and are especially abundant in Experiments 12 and 13 (see Section 3, Table XVIII). This result in a sample examined in May is in accordance with

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* Great caution is required in assessing young ova in recently-spawned individuals; in these cases young ova are not infrequently retained in the gonad (see Section 2, Table XVIII).

the findings from seasonal studies, in which it has been proved (unpublished) that the female phase may be assumed very rapidly and superimposed upon a variety of the male phases.

Thus the experiments show that after an oyster has spawned as a female a sperm-producing phase is assumed automatically (with rare exceptions at the end of the breeding season). Sperm-production is active for about one month and then wanes. At the approach of autumn when food-reserves are usually being accumulated, the gonad assumes a quiescent condition in a large proportion of individuals, but in some remains still active. In the first winter the gonad remains apparently in either a neuter condition or in arrested and mostly late male phases. In the following spring a new phase of male activity may begin, or the arrested male phase be continued. In some cases an active female phase is superimposed upon neuter individuals to give pure females, or upon a variety of male phases to give various types of hermaphrodites. These intersexes with ripe newly formed ova are with little doubt mostly, if not all, female-functioning, but are not all definitely proved to be of this nature by the experiments herein described (see p. 19 (c), and Experiment 15, p. 38); the rarity of purity found (unpublished researches) amongst apparently pure ripe females enhances the probability that these types of intersex produce larvæ.

DISCUSSION AND CONCLUSIONS.

The experiments herein described prove definitely for the first time that male individuals of *O. edulis* pass into the female condition *in significant proportion* within twelve months and that greater proportions attain the female condition in two years. The experimental conditions render it probable :—

(1) that only a proportion of the actual change over to the egg-producing stage in the experimental material has been observed, and

(2) that the actual changes in the experiments into female phases are less than would occur naturally when the molluscs lie free on the grounds.

For these reasons it is considered advisable to obtain further information on the rate and proportion of the change from the male to the female phase from studies in seasonal changes in sex-condition throughout an oyster population. Data for such a study have already been obtained, and will be discussed in the near future.

It would appear to emerge from the experiments—in accordance with expectation—that the change from male to female is not automatic as is the change from female to male. The age of the experimental oysters was not known definitely, although it could be stated with certainty that the bulk of the individuals ranged between 4 and 6 years. It is conceivable that the period elapsing between successive female phases may vary with age, but the fact that *O. edulis* may under *optimum* conditions become female at an age of one year (**8**) on English oyster beds indicates that age is not an all-important factor. The predominant factor in the change from the male to the female phase would seem to be the experience of a period of anabolic metabolism; for this, abundant food and healthy conditions in general are required. In some of the experiments these conditions were certainly not fulfilled during the whole period of the experiments.

The small proportion of reversions to the female phase in about twelve months and the larger proportion after two years indicates that the normal period intervening between successive female phases may be two years on English beds. Many of the experiments were not, however, designed to run for two years, and in those maintained for that period the conditions (e.g. continual testing) were admittedly bad. In new experiments in the future it would be advisable to leave some of the experimental oysters in the sea undisturbed, except for cleaning, for two years, in order to maintain the best possible conditions for determining the percentage of reversion to the female phase for this period of time.

SUMMARY.

Under such environmental conditions as occur on English oyster grounds, it has been found by the use of experimental cages that oysters proved to be male in a given breeding season change to functional females in significant numbers (a minimum of 10% to 16%) in the next breeding season: among a small number of survivors 50% became functional females within about two years.

Experiments on isolating in the sea oysters which have been found with young prove also that a significant number of individuals (ca. 11%) revert to mature female phases within about twelve months; in experiments extending over two years a higher proportion (a minimum of 21%) among a small number of survivors reverted to mature female phases under conditions which are known to have been and were necessarily unfavourable.

Owing to experimental difficulties, which are discussed, it is considered highly probable that the proportion of changes or reversions to the female phase detected is smaller than that actually occurring in the experiments and evidence is advanced that it is much smaller than occurs when the oysters are lying free and undisturbed on the oyster-bed.

On the other hand it is also shown that a small proportion of individuals

(about 3%) may spawn twice in *one* breeding season from one batch of eggs if a high degree of incomplete spawning occurs at the first attempt. The bearing of this phenomenon on the experimental results is discussed.

The experiments indicate that two years may be the more usual period intervening between successive normal female phases on English oyster beds, but new experiments conducted on different lines are required to obtain further direct information on this problem. This result is in harmony with statistical investigations, which show that females revert to the female phase at least every other breeding season.

The sex-phases found by experiment to intervene between successive female phases are recorded and discussed.

While providing important facts it is regarded that the experiments are inadequate to give a representation of the natural phenomena, and that a clearer picture of the natural changes is more likely to be obtained from a comprehensive population study, for which the experimental results herein described will provide a solid basis.

On Experiments with Oysters in Cages.

It is an interesting and somewhat surprising fact that the isolation of oysters in a cage on the natural oyster bed introduces in itself an important modification of the natural habitat. In the cages utilised in the later experiments herein described a large mesh ($1\frac{1}{2}$ inches in diameter) was utilised, as it was soon realised that the $\frac{3}{8}$-inch mesh of the cage used at West Mersea too readily permitted an accumulation of mud. There are, however, limits to the size of mesh which can be used with safety, for any of the bivalves may slip or project partially through a mesh and in that way be prevented from opening or growing shell-shoots properly. The mesh prevents so free a flow of water over the isolated oysters as occurs on the neighbouring ground. As a consequence an accumulation of silt occurs in the cage, especially if large numbers of the larger simple Ascidians, e.g. Ciona, *Ascidiella aspersa* and *Ascidia conchilega* settle on the oysters or cage and grow; their excreta add to the accumulation of silt in the cage. Silt settling in this way may either choke the oysters or interfere very seriously with normal nutrition by necessitating a large intake of silt in feeding with the consequent loss of energy in voiding it. To obviate some of these disadvantages the cage was raised off the bottom on a table structure; this arrangement gave better results than a cage lying directly on the bed. The disadvantages of a table-cage are that it is more difficult to put out and is more easily upset while lying at the bottom. On a commercial bed it is inadvisable to buoy a cage since the buoy-ropes may inadvertently be fouled by ships passing in the dark.

To prevent the accumulations of growth and silt in the cage it is advisable to raise it as frequently as possible. With a table-cage moored on the bottom frequent cleansing in this way is a laborious and expensive process, unless the experimenter be working continuously near the site of the experiment. A cage lying directly on the bottom can be relatively easily raised and cleaned on frequent occasions. Attachment of the anchors to the legless cage can be made upon the strong iron framework around which the iron mesh-work is secured. Pairs of handles along each edge of the cage at the top as well as the bottom were found extremely useful for one or other of the operations.

It is important to have the cage constructed so that every compartment can be recognised without a label, and the provision of iron-wire mesh shelves in each compartment is an additional advantage for isolating special oysters of different classes easily and quickly. If a permanent shelf be provided it is easy to construct a cover to make a new cagelet within any compartment. In a later design permanent but short legs were obtained by simply allowing the strong vertical corner rods of the framework to project beyond the bottom of the cage. A design of this kind is useful in certain kinds of experiments, though the legs may require strengthening in other ways if much weight is carried. In making the centrally placed lid regard must be paid to the accessibility of the recesses of the different compartments, but the safety accruing from the central lid is a compensation for a little trouble in handling the experimental material.

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All the experiments herein described were carried out as a part of the programme of research work of the Marine Biological Association, Plymouth, with the approval of the Council and the unfailing help of the Director, Dr. E. J. Allen.

Reference has been made to the valuable help in this work given especially by the Tollesbury and Mersea Native Oyster Company, without whose co-operation and good-will most of the experiments could not have been done. Similar valuable assistance was given also by the Yealm Oyster Fisheries and the Oyster Committee of the Truro Corporation. All these bodies, as well as the Seasalter and Ham Oyster Co., and the Duchy Native Oyster Co., helped to provide the experimental oysters by—in some cases unusual—dredging in the breeding season.

In the operations in the field I am especially indebted to Mr. Louis French, Mr. Bert French, Mr. W. M. Mole, Mr. J. Kingcome, Mr. E. Searle, and Mr. W. Searle for suggestions and assistance in handling the experimental apparatus.

Mr. J. Metherell, of Plymouth, had no difficulty in making the experimental cages; the late Mr. O. Anstey constructed the table apparatus.

I am indebted to Misses D. E. Coleman and H. M. Lewis for assistance with the manuscript and proofs, to Mr. P. Bond for the photos for Fig. 3, and enlargements of field photos, and to Mr. A. J. Smith for the photo for Fig. 1, Part III.

For a number of years small grants in aid of the expenses were received from the Royal Society and were utilised on some occasions for making highly desirable additional visits to West Mersea from Plymouth. It is a pleasure to acknowledge the usefulness of these grants.

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Chemical Constituents of Biological Importance in the English Channel. Part III. June–December, 1932. Phosphate, Silicate, Nitrate, Hydrogen Ion Concentration, with a Comparison with Wind Records.

By

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With 3 Figures in the Text.

WHEN considering wind records, the Beaufort number, B, may with advantage be replaced by its cube, B^3. According to the Observer's Handbook of the Meteorological Office (1921), this is a measure of wind force :—

$$P=0{\cdot}0105B^3, \text{ where}$$

P=Force in lb., registered by a circular disc one square foot in area facing the wind as in the plate anemometer when the density of the air is normal, and

B=Beaufort number.

The relation between B and B^3 is :—

B	1	2	3	4	5	6	7	8	9
B^3	1	8	27	64	125	216	343	512	729

At Mount Batten Air Station, Plymouth, wind records are made three times daily. These values have been cubed and the mean taken as the daily, mean cube Beaufort number, to give a mean value of the amount of wind disturbance each day. They are plotted for three periods in Fig. 1. The directions *from* which the wind blew are shown by arrows on the graph. The mean cube Beaufort number may afford a more useful index of the capacity of the wind to cause mixing and turbulence in the sea than the Beaufort number itself.

The conditions found on August 16th, 1932, were directly related with the wind in the preceding month (Figs. 1B and 2). On June 16th and July 13th, at E1, the thermocline was found at 25 metres, above which the temperature gradients were practically uniform. But on July 27th, 28th, and 29th, mean cube Beaufort numbers, 165, 105, and 115 were registered. These winds mixed the water thoroughly down to 10 metres, to give a uniform temperature of about 17·4°–17·5°. Subsequently with quiet sunny weather, the surface layers warmed to about 18·7°. The layer between 10 and 20 metres, sandwiched between two thermoclines, was of exceptional stability and its chemical composition was very unusual.

Conditions in August, 1931, were very different (Fig. 1A). The ten days prior to August 26th, when a cruise was made, showed intermittent strong winds reaching up to a mean cube Beaufort number, 320, on the 20th. These caused very marked vertical mixing right to the bottom by the 26th, although complete uniformity was not attained until some days later (Part I, p. 681).

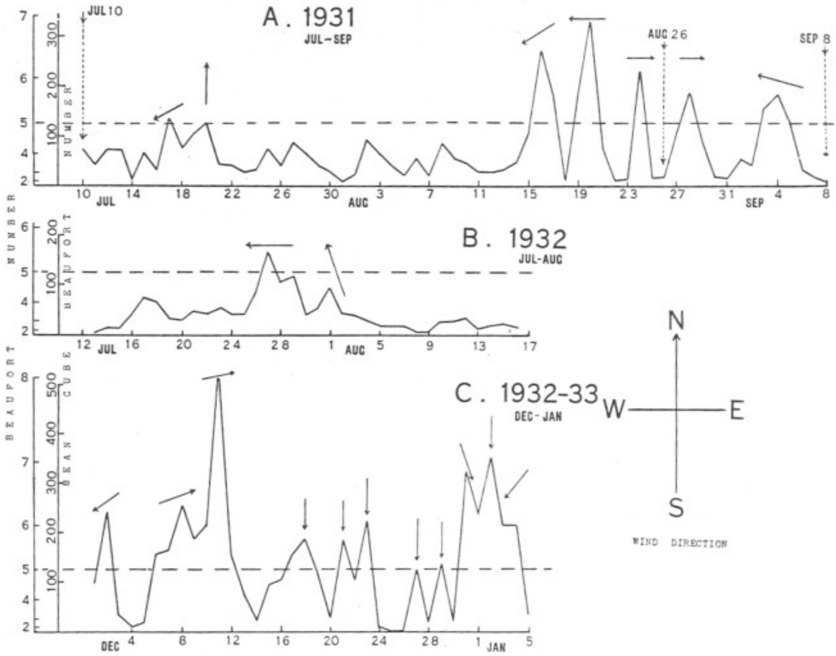

FIG. 1.—Daily Mean Cube Beaufort Numbers (Plymouth, Mount Batten). A. Between cruises on July 10th, August 26th, and September 8th, 1931, including stormy weather at end of period. B. Between cruises on July 13th and August 16th, 1932. C. December 1st, 1932, to January 5th, 1933. In each case a horizontal pecked line is drawn at mean cube Beaufort number, 125, equivalent to Beaufort number, 5. In each stormy period the direction *from* which the wind blew is shown by arrows.

Thus in July, 1932, three days of wind with mean cube Beaufort numbers around 125 were able to break down the stable layering down to 10 metres, but had little effect further down. In August, 1931, strong winds, around B^3, 200–300, acting for a longer period, were able to break down the thermocline completely. The mean cube Beaufort number brings out this factor much more clearly than the Beaufort number itself.

THE DISTRIBUTION OF NUTRIENT SALTS ON AUGUST 16TH, 1932.

The effect of the stratification of the water in mid-August on the distribution of silicate, nitrite, and pH is shown in Fig. 3, in which the scale relative to depth is the same as in Figs. 2, 3, and 5 in Part I and Fig. 1 in Part II.

High concentrations of silicate were found in the stable intermediate layer (Table I); 270 and 300 mg. SiO_2 per cubic metre were found at 15 and 20 metres respectively, compared with 110 mg. at 10 metres and 175 mg. at 25 metres. Between 10 and 20 metres there was a difference in density, σ_t, of 1·15 units, so that it would seem that dead diatoms were trapped on the thermocline and their skeletons re-dissolved. This occurrence thus provides yet further evidence for the rapid re-solution of silica in the summer months, suggested in Part I, p. 695. On August 16th, 1932, the average silicate content of the water column was 190 mg. per cubic metre. This fell, to give the usual September minimum, on September 12th (120 mg.), followed by a rise to 180 mg. on October 4th.

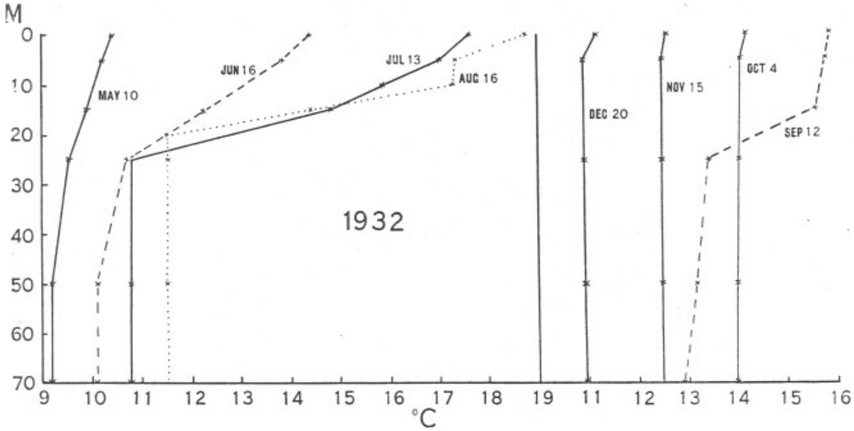

FIG. 2.—Temperature (°C.) at Station E1, Summer and Autumn, 1932.

On August 16th also, extremely high values for pH were found at E1 at 15 metres. There can be no doubt as to the accuracy of these figures since they were found with cresol red, xylenol blue, and thymol blue, in each case with duplicate samples from different bottles. It should be stated that the samples had not been preserved since determinations of pH were not part of the programme. The determinations were made just twenty-four hours after collection with the buffers used in the previous year's work. These were still in good condition. Any error due to bacterial action in the samples or to absorption of carbon dioxide from the atmosphere would tend towards low values for pH and not high ones.

TABLE I.

STATION E1.

Depth in metres.	PHOSPHATE. P_2O_5, mg./m^3.						SILICATE.‡ SiO_2, mg./m^3.						NITRITE. N, mg./m^3.			
	1932 15/6	16/8	12/9	27/10	15/11	20/12	15/6	13/7	16/8	12/9	4/10	15/11	16/8	12/9	27/10	15/11
0	13	0	0*	24*	21*	22*	75	98*	175†	230	210	175	1·0	0·32	13·5	4·32
5	1	0	4	–	22	23	55	55	100	105	200*	180	0·0	0·20	–	4·27
10	–	–	–	–	–	–	–	60	110	–	–	–	0·0	–	–	–
15	5	0	5	–	–	–	75	110	270*	105	–	–	0·0	0·58	–	–
20	–	–	–	–	–	–	–	–	300	–	–	–	2·1	–	–	–
25	5	3	11·5*	–	22	25	65	110	175	105	160	–	1·1	14·6	–	4·27
50	–	2	11·5	–	21	27	80	140	190	140	190	190	2·2	19·5	–	4·11
68–70	13	–	15	–	20	30*	70	120	220	105	170*	150*	3·0	25·0	–	4·00
A	16/6	18/8	14/9	29/10	17/11	21/12	17/6	14/7	17/8	13/9	6/10	16/11	17/8	13/9	29/10	16/11

STATION E1.

CARBON DIOXIDE SYSTEM ON AUGUST 16TH, 1932.

Depth in metres.	pH_w	$pH_{12°}$	pCO_2§ (Atm. × 10^{-4})	ΣCO_2§ (c.c./l.).
0	8·24	8·30	2·3	43·9
5	8·29	8·35	2·0	42·9
10	8·30	8·36	1·9	42·8
15	8·45	8·48	1·2	41·0
20	8·27	8·27	2·1	44·6
25	8·27	8·27	2·1	44·6
50	8·27	8·27	2·1	44·6
69	8·27	8·27	2·1	44·6

STATION E2.

Depth in metres.	P_2O_5 1932 15/11	SiO_2 13/7	SiO_2 15/11	Nitrite-N. 15/11
0	26	110*	135	2·04
5	26	75	110	1·95
10	–	75	–	–
15	–	175	–	–
25	27	175	140	1·98
50	27	155	140	1·96
75	27	–	–	1·95
87 or 91	26	155	110	2·13

L SURFACE STATIONS

NITRITE—N.

Station.	mg./m^3. 1932 12/9	15/11
L1	6·7	10·0
L2	4·25	9·8
L3	3·65	10·6
L4	1·86	13·3
L5	1·44	11·8
L6	0·42	12·2
E1	0·32	4·32
Mid E1–E2	–	4·08
E2	–	2·04

A. Date of analysis.
* Mean of duplicate analyses.
† Sample very cloudy. Reading after standing one hour in comparison tube; approximate only.
‡ Samples from waxed bottles.
§ Derived from pH, temperature and salinity.

The 20-metre samples were indistinguishable from those drawn from 25, 50, and 69 metres (bottom).

The partial pressure and total volume of carbon dioxide, found from pH, salinity and temperature, by means of the tables of Buch *et al.* (1932), are given in Table I. The partial pressure at 15 metres was about half that at the surface. It would seem that photosynthesis was proceeding in the 15-metre layer which was not mixing with the layers above and below it. In this layer phosphate was undetectable and only 5 mg. P_2O_5 per cubic metre had been found a month previously. It is quite probable that the intense regeneration of silicate was accompanied by simultaneous phosphate formation and that this never accumulated sufficiently to become detectable, being used up as it was formed. A similar consumption of carbon dioxide during a period when nutrient salts appeared scarce was noted in Part II (p. 738), a rapid fall in carbon dioxide occurring in June, 1931, when nutrient salts remained very low. This was especially the case above the thermocline.

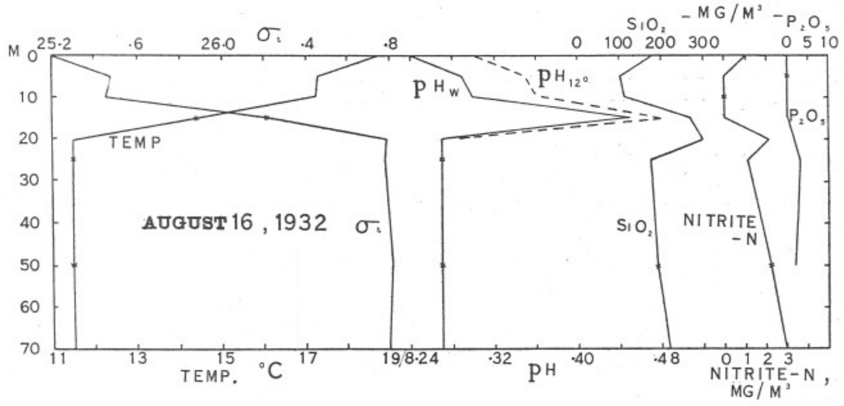

FIG. 3.—Conditions at Station E1 on August 16th, 1932. Temperature (°C.); density (σ_t); pH_W and $pH_{12}°$; SiO_2, nitrite-nitrogen and P_2O_5 (each mg./m^3).

Nitrite also showed a somewhat irregular distribution between the thermoclines on August 16th. By September the very stable stratification had begun to break down although a marked thermocline remained at 15–25 metres, above which the amount of nitrite was small. Beneath it conditions were similar to those found there by Atkins (1930) in August and September, 1928. The maximum amount (25·0 mg. N per cubic metre) was found at the bottom, suggesting that nitrification was then most active there.

On October 27th, the surface figure (13·5 mg. N per cubic metre) was probably typical of the whole water column and lies close to the figures found on October 2nd, 1928 (13·3 mg.), and October 20th, 1931 (11·5 mg.).

Later the amount of nitrite at E1 fell away, again in agreement with former years. But in or about December in each of the four years for which data are available, the inshore water has shown a notably higher nitrite content than the water at E1 (Table II). In 1930 and 1931, no clear relation could be seen between the distribution of ammonia and nitrite. The cause of these high, mid-winter, inshore nitrite figures is not very evident.

TABLE II.

Early Winter Values for Surface Nitrite-Nitrogen (mg./m^3) for Four Different Years.

Station	30/11/28	2/1/29	11/11/30	4/12/30	13/1/31	30/11/31	31/12/31	15/11/32
L1	6·0	9·5	—	—	—	10·1	5·3	10·0
L2	3·9	9·5	—	—	—	10·9	5·0	9·8
L3	3·3	9·2	—	—	—	11·8	4·7	10·6
L4	3·3	7·7	13·5	5·8	8·2	12·0	2·6	13·3
L5	—	5·6	—	—	—	13·9	1·6	11·8
L6	1·3	3·5	—	—	—	2·5	1·1	12·2
E1	1·4	3·1	2·1	2·05	0·37	0·87	1·13	4·32
Mid E1–E2	—	—	—	—	—	≦1·5	—	4·08
E2	—	—	—	—	—	0·54	—	2·04

It should be remembered that, when seasonal changes of nutrient salts in the English Channel are under consideration, exactly the same body of water cannot be examined on each cruise, so that it is not permissible to treat of events as occurring in a completely closed cycle (cf. Part I, pp. 678, § 3, and 708, § 4).

Midwinter Plankton Outbursts, Sunshine and Wind.

A "normal" figure for the daily mean cube Beaufort number, B^3, in December, calculated from the records for the nine years, 1924–32, is 102, equivalent to a "normal" Beaufort number of 4·7.

In 1925, between the cruises of November 11th and December 11th, phosphate at E1 fell by 13 mg. P_2O_5 per cubic metre at the surface, by 7 mg. at 10 metres, and by 6·5 mg. as an average of the whole column. For the ten days preceding the cruise of December 11th, sunshine averaged 3·6 hours a day (the normal for Plymouth for December is 1·58 hours) and the average value of B^3 was 55 (B=3·8). The weather was thus favourable to a surface outbreak.

In 1926, between the cruises of December 13th and 31st, phosphate fell by 5 mg. P_2O_5 (surface), 7 mg. (5 metres), and 7 mg. (average content). For the sixteen days preceding the 31st, sunshine averaged 3·2 hours and B^3 averaged 80 (B=4·3). On December 23rd, 24th, and 25th, the values of B^3 were 165, 125, and 165, thus putting up the average. During most of the period conditions were favourable to a surface outbreak. The strong northerly winds at Christmas account for the depletion extending right to the bottom.

In 1930–31, between the cruises of December 4th and January 13th, phosphate fell by 10 mg. (surface) and 3·1 mg. (average). The surface fall was, in large part, due to the mixing in of the enriched surface layer found on December 4th, but the fall in the average content would seem to indicate a definite outbreak. Over the whole intervening period of 39 days, sunshine averaged 2·1 hours per day and B^3 averaged 51. For the nine days immediately preceding January 13th, sunshine averaged 4·3 hours and B^3, 14. But for this period the parallel between quiet sunny weather and a plankton outburst may not be as close as this summarised picture suggests.

On November 30th, 1931, at four stations across the Channel, L4, E1, Midway, and E2, surface values for phosphate as P_2O_5 were 5·5–7 mg. lower than at 5 metres, suggesting a preceding, quiet, sunny spell. This was far from being the case. Between November 22nd and 29th daily mean cube Beaufort numbers were: 63, 301, 53, 259, 215, 105, 3, 23. Such a period of wind must have led to thorough mixing of the surface waters. Two days only were sunny and the last two days, which were quiet, had only 0·7 hours of sunshine between them. The weather was thus decidedly unfavourable for a plankton outburst.

We see that on three occasions, midwinter outbursts, inferred from a fall in the phosphate content of the water, followed on periods of sunny weather with light winds. On a fourth occasion there was no relation whatever between outburst and weather.

THE EFFECT OF WIND ON THE BOTTOM FAUNA AND ON THE HERRING FISHERY.

On January 5th, 1933, s.s. *Salpa* caught large numbers of *Upogebia deltaura* and *Thyone raphanus* with the otter trawl in 18–21 fathoms in Bigbury Bay. Examination of the gut of fishes has shown Upogebia to be one of the commonest fish foods in the Plymouth area, but it is seldom caught in numbers in either trawl or dredge (Steven, 1930). It is an agile burrowing animal beyond the reach of the ordinary fishing-gear. The habitat of Thyone is similar. Therefore only intense disturbance of the bottom could have put them in a position to be caught by the trawl. Probably Upogebia had been so buffeted by the storm as to be insensible to the approaching trawl. December was characterised by very stormy weather and between December 31st and January 4th, the daily mean cube Beaufort number reached 350 and never fell below 216. In other words the wind blew continuously with force 6 or greater, causing heavy seas and consequent disturbance of the bottom fauna (Fig. 1, C.).

Periods of stormy weather have been found to be followed by improved catches of herring (Ford, 1933). For this investigation, wind records on the Beaufort scale proved very useful, but it is felt that the mean cube Beaufort number, studied in conjunction with the direction of the wind, may prove yet more convenient as it emphasizes the periods of really rough weather. When dealing with large quantities of weather data, the possibility which it gives of grouping or averaging records may prove of value.

SUMMARY.

In August, 1932, marked stratification of the water in the English Channel led to an unusual distribution of minor chemical constituents. Two thermoclines were present, between which high silicate values were found, indicating rapid re-solution of silica as found in former summers; pH was also very high at 15 metres.

In or about December in four years, nitrite in inshore waters has been found much in excess of that present in the open Channel.

The " mean cube Beaufort number " is suggested as a useful practical measure of sea disturbance. Three out of four midwinter plankton outbursts, inferred from a fall in the phosphate content of the water, have followed periods of sunny weather with little wind.

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The Rapid Estimation of the Copper Content of Sea-water.

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The recent recognition of the importance of copper in nutritional anæmia and the work of Prytherch (1931) on its unique action in stimulating oyster larvæ to become attached have rendered the analytical determination of minute amounts of copper a matter of some interest.

In a former paper (1932) it was shown that the copper present in sea-water could be concentrated by electro-deposition and subsequently redissolved and estimated colorimetrically using sodium diethyl-dithiocarbamate according to the method of Callan and Henderson (1929).

In this the deposition required three hours at 90°–100° C., though but little attention was necessary during that period.

Another method of concentration has since been tried, in which, after adding the 0·1 per cent aqueous solution of the reagent and allowing a few minutes for the colour to develop, the coloured compound is extracted with an organic solvent. For this purpose the chemists of the British Drug Houses Ltd., who introduced the method, recommend chloroform, carbon tetrachloride, or other immiscible solvent.

This method is useful in testing coloured solutions containing copper and obviously increases the delicacy; it has been found to do so to an extent which renders the method suitable for direct use with sea or river water, though unlike sea-water, river water can be concentrated greatly by evaporation if necessary. Furthermore, it has been found that only a trace of the yellowish or brownish colouring matter present in the fresh or brackish waters examined is imparted to chloroform when shaken up with the sample. Iron salts give with the reagent a colour rather like that produced by copper. The presence of much iron would accordingly render the results erroneous, though it requires 1·32 mg. per litre of ferric iron to give as much colour as 0·01 mg. per litre of copper. Only in fresh water would there be any risk of error from iron.

The analysis is made by adding 10 ml. of reagent to 100 or 200 ml. of sample and after about ten minutes the process of extraction is carried out by adding 10·0 ml. of chloroform to 100 or preferably 200 ml. of the sample in a separating funnel. The mixture is shaken violently by hand for exactly two minutes and allowed to stand. The chloroform extract is then drawn off into one of the colorimeter cups and suffices to fill it to a depth of about 52 mm. The other cup receives a similar extract, but made from a standard solution containing 0·01 mg. of copper in 100 ml., or twice that amount in 200 ml. The same volume of sample and standard should always be extracted.

It is advisable also to make a blank extraction of the sample, without reagent, as traces of the brown or yellowish substances which colour fresh waters are taken up, also the pigment may be partly extracted from plankton present. It has been found that a colorimeter setting of 2·0 mm. of the standard can just be distinguished from 50·0 mm. of pure chloroform. The blank given with pure sea-water is the same, 2 mm., whereas the water of the River Yealm, a moorland river of brownish colour, gave as blank 5·2 mm. and the clear yellowish water of the Conway River, at low tide (sp. gr. 1·001), gave only 5·5 mm. On the other hand apparently colourless water from an oyster tank gave 6·5 mm. blank, equivalent to 0·0013 mg. copper in 100 ml., or 13 mg. per cubic metre.

Larger volumes, up to 1 litre, may be extracted if necessary. Even with only 200 ml. and 10 ml. of solvent, the removal of the coloured copper compound is by no means complete; further extraction will remove colour not only from the liquid, but from the droplets of the organic solvent which adhere to the walls, so it is not easy to ascertain the percentage left behind after one extraction. This does not however vitiate the results provided the extractions are carried out in an identical manner for sample and standard.

Determinations carried out as described, using 100 ml. or 200 ml. samples, gave the following results, expressed in milligrams of copper per cubic metre:

Conway River, high water 16, low water 36. River Exe, at Lympstone, Exmouth, high water 8, low water 14. River Yealm, not tidal, 0. A non-moorland tributary stream of River Yealm, 5. The oyster tanks at Lympstone and Conway varied from 0–15. None of the figures here given are of significance in bringing about the attachment of oyster larvæ, which, according to Prytherch, settle down when the copper content of the water lies between 150 and 500 mg. per cubic metre. This range contained 97·5 per cent of the larvæ he observed, with *Ostrea virginica*. The British species is *O. edulis* and may behave differently. I am indebted to Mr. H. P. Sherwood of the Conway Fisheries Experiment Station for kindly providing me with a number of water samples.

As regards the solvent used for extraction, McFarlane (1932) states that chloroform and carbon tetrachloride are unsatisfactory, but he gives no reason. He recommends the purest amyl alcohol as the colour of the extract fades with the "technical" variety. In chloroform solution fading has never been suspected to occur within the usual duration of a day's work, nor has the solvent proved unsatisfactory, save as regards the incompleteness of a single extraction. Evaporation of the solvent must be guarded against.

In order to compare the solvents chloroform, carbon tetrachloride, and amyl alcohol, 10·0 ml. of each was added to 100 ml. of Plymouth tap water, using ordinary methylated chloroform, carbon tetrachloride " purified," and amyl alcohol " analytical reagent, pyridine and nitrogen free." The soft tap water has a brownish tint of which amyl alcohol extracted between four and five times as much as did either of the others, this of course is a disadvantage. Of the 10 ml., the amounts recovered were, respectively, 8·7, 9·8, and 6·9 ml. after standing overnight.

With 200 ml. of sea-water and 10·0 ml. of solvent the volumes recovered were respectively 7·4, 9·7, and 4·0 ml. The alcohol floats, which is a disadvantage, as the large volume of sea-water has to be drawn off from the separating funnel before it, whereas the other two sink and time is saved in drawing them off. The concentration of copper compound in the alcohol is about 1·5 times, and in the tetrachloride 0·66 times that in chloroform ; but taking into account the volumes recovered, that in the tetrachloride is almost exactly the same as in chloroform, whereas only 0·8 times as much is obtained with the alcohol. The comparisons were made after standing overnight. The alcohol does not separate as readily as do the others, but separates from sea-water better than from fresh.

SUMMARY.

1. The copper content of sea and river waters can be rapidly determined using the sodium diethyl-dithiocarbamate method followed by extraction with chloroform.

2. This solvent takes up only traces of the natural colouring matters found in waters, but blank estimations should be made with some river waters and occasionally with sea-waters on account of the presence of plankton.

3. Carbon tetrachloride can be used instead of chloroform as solvent, it extracts less per unit volume, but the volume recovered is larger, the resultant yield being identical. Amyl alcohol extracts more than chloroform, but the volume recovered is smaller, the resultant yield being about 0·8 times that of the others. The alcohol takes up more colouring matter from river water, does not separate as readily as the others, and floats, whereas they, more conveniently, sink. For work in hot climates its higher boiling-point may be an advantage.

4. In fresh water iron salts in large excess might cause error ; this can be checked by the electro-deposition method.

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The Use of Cuprous Oxide and other Rectifier Photo Cells in Submarine Photometry.

By

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With 1 Figure in the Text.

THE cuprous oxide cell introduced by Lange (1930) differs greatly from the photo-electric cells heretofore in general use. The sensitivity is high and no high-tension battery is needed in the circuit. There are, however, certain limitations to the use of such rectifier cells for daylight photometry; these we have considered elsewhere (1933). The types dealt with include cuprous oxide cells of both French and German origin and a selenium rectifier cell, introduced by Bergmann (1931) and made by the Süddeutschen Apparate-Fabrik, Nürnberg, and under license by the Weston Electrical Company, from which our cell was obtained. The latter arrived too late for use in submarine measurements in the summer of 1932, but is to be preferred to the cuprous oxide type. There is another type of rectifier, the Bernheim cell, which is made in Paris. This we have not examined as yet, but from data supplied by the makers its spectral sensitivity is similar to that of the Bergmann cell, which it also resembles in its high sensitivity and improved stability.

THE SUBMARINE PHOTOMETER.

This was intended for shore work, so that it could be carried about in a diver's hand. It consists of a circular gun-metal box, 9·6 cm. diameter, flanged at the top and fitted with a ring; between ring and flange a 0·6 cm. disc of plate glass was fitted and secured. Above this the usual disc of opal flashed glass could be placed, with a colour filter in between if so desired. Two of the flange screws had projections with holes for attaching a light rope.

A "Serpidox" photo-electric cell, Sx80, obtained from the Société de Recherches et de Perfectionnements Industriels, Puteaux (Seine), was mounted immediately below the window, and beside it a small amount of calcium chloride was held in a bag.

The cable entered through a side tube with slightly bulbous nozzle, a water-tight joint being effected by means of thick pressure tubing. Six hundred megohm " cab-tyre " twin cable was used; a length of 45 m. sufficed for the coastal work and weighed 4·5 kg. The photometer weighed 3·2 kg., as against 22 kg. the weight of that formerly in use at sea. It was reported as convenient to hold and not too heavy under water.

THE AIR PHOTOMETER, GALVANOMETER, SHUNT, AND CONNECTIONS.

A similar " Serpidox " cell, No. Sx81, was used to measure the illumination in air. It was placed on a level rock, unmounted, but covered with the usual opalized glass and a water filter to lessen temperature errors. Both photometers were connected to a throw-over switch and to the special shunt. When received the two Serpidox cells were closely the same in sensitivity, but when mounted in the submarine photometer the greater distance of the cell from the opal resulted in the ratio of the readings in air, when both were under water screens, being on the average 0·75.

For measuring the current we found a Cambridge Instrument Co. " Versatile Galvanometer," weighing 1·8 kg., to be suitable. Its resistance is 10 ohms, and each scale division corresponds to $2\mu a$; the scale (upper) reads to 120, viz. $240\mu a$. With this instrument we made use of a shunt, specially designed to keep the resistance 10 ohms always; this permitted the ranges 1, 5, 10, and 50 to be used, and is figured in our previously mentioned paper.

THE STANDARDIZATION OF THE PHOTOMETERS.

In view of the lack of strict proportionality between current and intensity and of the change of sensitivity with time and exposure, it is necessary to standardize each cell against a vacuum photo-electric cell of the usual type. This was done on the Laboratory roof, over an extended range, using the potentiometer method. Low intensities were measured in a north window, using a galvanometer instead of a potentiometer. The Serpidox cell was connected to the 10-ohm galvanometer throughout. The results are shown in Figure 1, curves A and B.

As the change of sensitivity with time may depend on the intensity, the sensitivity of the cell should be checked at two or three different sensitivities from time to time.

From the form of the voltage curve, C, obtained with the rectifier cell connected directly to the No. 2 circuit of the potentiometer outfit, but with the vacuum cell connected as usual, it may be seen that this cell could be used at sea with the potentiometer outfit, viz. under conditions precluding the use of ordinary galvanometers. Illuminations can be read off from the curve, though indeed for low illuminations up to 10,000 metre candles, the deviation from a straight line is but slight in the case of a Serpidox cell. Those of other types give marked curvature in bright light on open circuit.

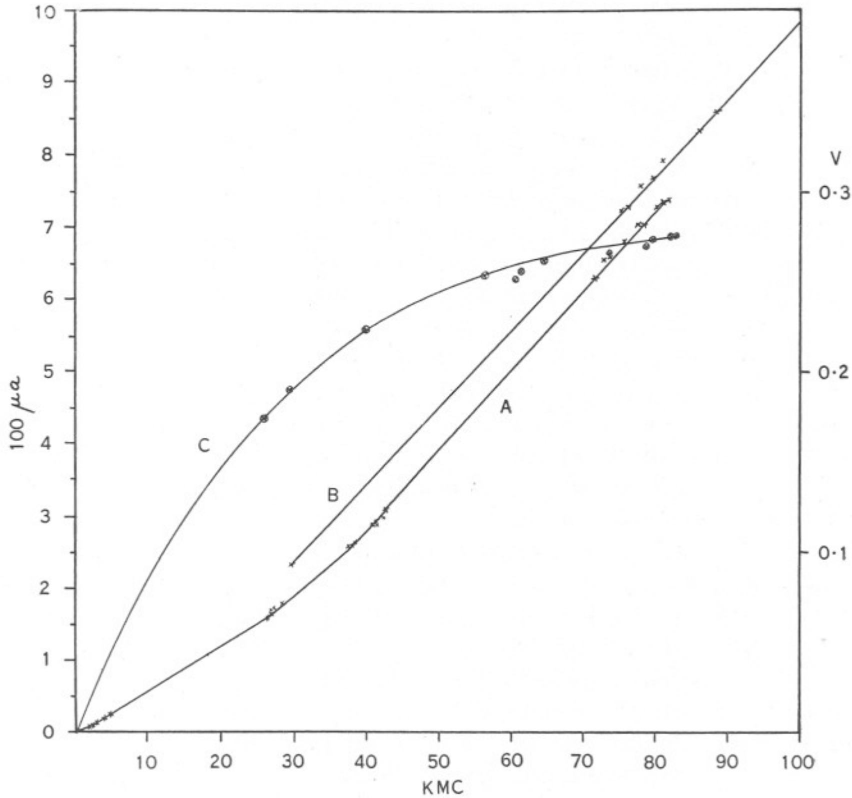

FIG. 1.—The abscissæ show vertical illuminations in thousands of metre candles (k.m.c.). The left-hand ordinates show current in 100μa units. The right-hand ordinates show E.M.F. in volts on open circuit.

Curve A gives the behaviour of a cuprous oxide cell (Sx81) when cold, curve B when the sun had warmed it up, though under a water heat filter. Curve C shows the voltage relation, as determined with the submarine potentiometer outfit, measuring illumination with vacuum cell and taking the voltage of the cuprous oxide cell directly connected to the No. 2 circuit.

The sensitivity with the voltage measurement is about the same as with the low resistance galvanometer, for approximately 10,000 m.c. gives 200μa or 0·0800 volts. The former can be read to 0·2μa or 10 m.c., the latter to 0·05 m.v. or 6·2 m.c. Voltage readings with "open circuit" or high resistance instruments are, however, more affected by temperature errors than current measurements with a low resistance galvanometer.

In carrying out such open-air standardizations one is faced with the problem of the variation of the light, which is rarely constant from one minute to another. The steadiest light is obtained with a clear sun and a clear blue sky at noon, or with a clear sun and clouds moving slowly. A hazy sky is liable to considerable variation in the degree to which the sun is obscured and a grey sky is normally very variable. Good results can be obtained, as at sea, by taking the average of a series of potentiometer readings for each photometer, or on land by two observers reading galvanometers simultaneously. In the standardizations shown in curve C, series of potentiometer readings were made, but for curves A and B one observer made absolutely simultaneous observations by sound and sight; as the galvanometer was read the potentiometer dial was adjusted to minimum sound in the telephone, then after dictating the reading the potentiometer scale was read. Owing to the difference in the colour sensitivity of the potassium and the copper oxide rectifier cells the ratio of the sensitivities will depend on the relative amount of sunlight, much as when the CMV6 type of cell is being standardized.

We cannot, however, use the readings of the submarine photometer, after standardization against the air photometer (both under water screens), to measure the illumination at various depths in the sea without introducing a factor to correct for reflection losses at the surface of the opal and internal reflection effects in the opal and between it and the surface of the sea. These we have considered fully elsewhere (1933, a). The illuminations recorded have to be multiplied by a factor 1·09 in order to give the true under-water values. Thus, since the submarine photometer was less sensitive than the air photometer, even in air, its readings must be multiplied by 1·33 to make the two agree. When the submarine photometer is in water a further factor 1·09 must be used to correct for surface effects. The procedure is to read off the illumination, on the figure, for the current given by the submarine photometer and *then* to divide this reading by 0·75 and to multiply it by 1·09, or in one operation to multiply by 1·45. For example, a reading of $200\mu a$ corresponds for the air photometer to 31·0 thousand metre candles (k.m.c.), but for the submarine photometer, when submerged below about 10 cm. or any greater depth, $200\mu a$ corresponds to $31{\cdot}0 \times 1{\cdot}45 = 44{\cdot}9$ k.m.c. Were we, however, to multiply the current ($200 \times 1{\cdot}45 = 290\mu a$), and then to read off from the figure, the result would, incorrectly, be 41·0 k.m.c. The difference is due to the curvature in the current illumination relation. In a similar manner submarine illuminations may be obtained from the voltage-illumination curve, but in this case the departure from a rectilinear relationship is very marked. For use under damp conditions, such as would arise where a cabin was not available on a ship or in northern latitudes, the fact that high insulation is no longer necessary and " dark currents " are negligible, since no high-tension battery is required, must be regarded as greatly favouring the use of this type of cell. Under normal conditions on a ship the ordinary vacuum cells have so much to recommend them in the way of greater accuracy that it would seem wise, for the present at any rate, to continue to use them. For approximate work on the coast, where the illumination is of necessity very variable, the cuprous oxide or other rectifier type of cell has the great advantage of portability in the measuring apparatus required, and the cell itself is quite accurate enough, if its limitations are remembered ; it requires, of course, to be standardized against a vacuum cell.

We are indebted to Mr. J. A. Kitching and to Mr. G. Gilson for descending with a diving helmet on the coast near Wembury, Devon, and holding the photometer in positions of ecological interest. The results will be presented by them in their survey which includes the percentage of the diffuse light in air, as determined at a given tidal level, found where various algæ, Himanthalia, Laminaria, etc., were growing. From measurements of the coefficient of absorption of the water, the illumination in the different zones could be calculated for other states of the tide. The absorption coefficient would increase greatly in rough weather and decrease in very calm weather, but during the diving operations on August 3rd, 1932, it was about 0·5, for vertical absorption. The figure is unduly high owing to diminution of light, not only by absorption, but by shading from the sides of the rocky gully investigated. We have, however, found water close to shore in rough weather to have $\mu_v=0{\cdot}8$ and even in very calm weather one could hardly expect it to be lower than 0·3, a value occasionally reached several miles out at sea. The date mentioned was the first that was possible for diving on such an exposed coast, after a period of stormy weather.

SUMMARY.

1. Photo-electric cells of the rectifier type are useful for approximate measurements of light intensity, in air or under water, using a low-resistance galvanometer, the current through which may be reduced by a special shunt keeping the circuit resistance constant.

2. Such an arrangement has proved serviceable for shore work, a light gun-metal photometer, housing a cuprous oxide cell, having been carried about by a diver.

3. These rectifier cells can also be used at sea, but instead of the current, the E.M.F. is determined by means of the potentiometer outfit as used at sea in previous years.

4. The current-illumination relation is not rectilinear over a wide range of intensity; the current–voltage relationship shows very marked curvature.

5. The cuprous oxide cells have a considerable temperature coefficient and must be used with a water screen. The coefficient is smaller in the case of the selenium cell. Under prolonged exposure to light the sensitivity of the cuprous oxide cell decreases very considerably, but the selenium rectifier cell is far more stable.

6. Further laboratory and sunlight tests carried out with the Bergmann selenium cell while this paper was in the press, give great promise as to its suitability and convenience for daylight measurements in the field and under water, when due allowance is made for the curvature of its illumination: current characteristic.

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The Seasonal Distribution of Macroplankton as shown by Catches in the 2-metre Stramin Ring-trawl in Off-shore Waters off Plymouth.

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In past years during the study of the vertical distribution of macroplankton much information has been obtained on the abundance of the different animals in the catches at different times of the year. Results have already been published to show the seasonal distribution of pelagic young fish (**4**), and also on the abundance and composition of the Sagitta population (**5**, p. 565). In this latter study the change over from the predominance of *Sagitta elegans* to that of *S. setosa* during the years 1930 to 1932 is striking. During the examination of catches it has been noticed that each year has been characterised at some time by the abundance of a species which may occur only in small numbers, if at all, in other years. This has been especially noticeable in the composition of the medusa population. It is necessary to follow these changes through a number of years to see if the presence of certain plankton organisms cannot be used as an index of conditions that may lead to other fluctuations such as those of the fisheries.

During 1930 and part of 1931 weekly catches of the 2-metre stramin ring-trawl were counted in order to obtain precise information on the seasonal abundance of the different animals throughout a whole year. The collections were made by oblique hauls of half an hour duration at the station 2 miles east of the Eddystone (**4**). Counts were made as on previous occasions by picking out directly distinctive and unusual animals and counting every animal in a $\frac{1}{10}$th sample of the remainder (**2**, p. 776).

The full results are given in the attached table which gives instructive information on the seasonal variation in abundance of the different animals, and their relative importance in numbers one to another. It seems unnecessary to analyse the tables further since any worker can abstract from it the data he may desire. One or two points must, however, be borne in mind.

1. The animals are all of a size that is normally retained in good condition by the stramin net. For instance, the medusæ are generally well-grown individuals ; the earliest stages, while perhaps not small enough to pass through the meshes, are generally too badly damaged to allow of

definite identification. A useful indication of the size of disregarded medusæ is given by the absence of *Rathkea octopunctata* in Table I, which is common in tow-nettings in the earlier months of the year. This applies also to all other animal groups ; the earliest stages of decapod larvæ do not appear in numbers in the catches as many will pass through the meshes.

In considering the seasonal distribution of any animal it must therefore be remembered that its first appearance in the catches does not imply the actual beginning of its abundance in the plankton. A period of two or three weeks should be allowed for the growth of the earliest stages to a size sufficient to appear in the catches.

2. The table does not contain any data on the abundance of young fishes which has been dealt with in another report (**4**).

3. In examining the data the vertical distribution of the various animals must be considered. The figures for *Tomopteris helgolandica* show, for instance, a great increase in July and August. This must only be regarded as an increase in abundance in the plankton ; at other times the Tomopteris may actually be present in the area, but in the unsampled layers very near the bottom (see **3**, from which data can be obtained for most of the animals).

4. The names given in the table are those used in the Plymouth Marine Fauna (1931). Phialidium sp. will be mostly *Phialidium hemisphæricum : Phialella cymbaloides* will also occur though not so commonly, as also a few *Mitrocomella brownei*. It was not possible in the time to analyse all the Decapod larvæ into species : the species that comprise each group can be found in the Plymouth Marine Fauna, where also in many cases is given the time of year at which the larval stages are most prevalent. Pandalid larvæ must be taken to include all species contained under Pandalidæ, Hippolytidæ, and Processidæ. Mysid sp. in summer consist chiefly of young specimens.

5. Examination of catches over a number of years has shown that there are species which can normally be expected to appear regularly each year. It is felt that these results are a fairly reliable picture of the average ring-trawl plankton catches to be found throughout any year. The following species, however, appeared in exceptional numbers and cannot be regarded as characteristic, but only for the year in question at the times they appeared :—

Aglantha rosea, *Liriope exigua*, and *Stephanomia bijuga* : *Clione limacina* and adult *Meganyctiphanes norvegica* also appeared in unusual numbers at the beginning of the year, although the larvæ of the latter are usually present then.

The results are to form a basis with which future years can be compared. Marked differences have been noticed in other years and it is hoped to publish these results in a separate report when sufficient data have been gathered. It should then be possible to decide on certain species whose appearance in the plankton should be watched for in future years. It is especially desirable to see whether any correlation can be found between the appearance of one characteristic species and that of another. The desirability of such observations was already stressed many years ago when Allen (**1**) prepared a list of species for special observation. Now that regular collections of these larger plankton animals are obtainable throughout the year an opportunity is afforded to attempt this study over a period of a number of years.

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TABLE I.

NUMBERS OF ANIMALS IN HALF-HOUR OBLIQUE HAULS WITH THE 2-METRE STRAMIN RING-TRAWL TAKEN 2 MILES EAST OF THE EDDYSTONE.

1930.	Dipurena (Slabberia) halterata.	Steenstrupia nutans.	Bougainvillia sp.	Amphinema dinema.	Leuckartiara octona.	Laodicea undulata.	Cosmetira pilosella.	Obelia sp.	Phialidium sp.	Saphenia gracilis.	Aequorea forskalia	Aglantha rosea.	Liriope exigua.	Muggiaea atlantica.	Stephanomia bijuga.	Chrysaora isosceles.	Cyanea lamarcki.	Aurelia aurita.	Pleurobrachia pileus.	Beroe cucumis.	Peachia arvæ.	Arachnactis larvæ.
Feb. 4th	–	–	–	–	–	–	–	–	–	–	–	52	–	–	–	–	–	–	40	–	–	–
,, 12th	–	–	–	–	–	–	–	–	–	–	–	2	–	–	880*	–	–	–	80	–	–	–
,, 19th	–	–	–	–	–	–	–	–	–	–	–	7	–	–	–	–	–	–	3	–	–	–
,, 26th	–	–	–	–	–	–	–	–	–	–	–	8	–	–	1	–	–	–	3	–	–	–
Mar. 5th	–	–	–	–	–	–	–	–	–	–	–	5	–	–	–	–	–	–	6	2	–	–
,, 12th	–	–	–	–	–	–	–	–	–	–	–	2	–	–	800*	–	–	1†	10	2	–	–
,, 19th	–	–	–	–	–	–	–	–	–	–	–	–	–	–	210*	–	–	–	8	–	–	–
,, 27th	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	6	–	–	–
April 2nd	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
,, 11th	–	–	–	–	–	–	–	–	40	–	–	7	–	–	632*	–	1	–	7	–	–	–
,, 16th	–	–	–	–	–	–	–	–	20	–	–	20	–	–	190*	–	–	–	1	–	–	–
,, 24th	–	–	–	–	1	–	–	–	140	–	–	7	–	–	450*	–	6	–	–	–	–	10
,, 29th	10	–	–	–	3	10	330	–	140	40	–	10	–	–	370*	1	1	–	10	–	–	–
May 7th	1	–	–	–	8	24	10	–	386	–	–	–	–	–	–	–	2	–	193	–	3	4
,, 15th	–	–	320	–	40	–	140	1,680	760	100	–	40	–	–	2,460*	–	1	–	520	–	–	41
,, 22nd	–	–	150	–	93	5	5	40	100	10	–	90	2	–	760*	–	1	–	520	–	1	–
June 10th	–	–	60	10	430	–	–	80	50	11	–	850	–	–	–	–	–	–	100	–	–	5
,, 19th	–	1	–	10	179	10	–	260	140	1	–	1,000	1	–	–	–	3	–	68	–	20	1
,, 26th	–	60	261	–	280	20	250	1,025	1,340	1	–	5,736	–	–	1,640*	–	1	–	180	–	2	2

July 4th	–	–	161	–	129	–	180	800	920	–	–	1,932	–	–	–	–	–	–	80	20	4	–
,, 9th	–	120	–	–	270	–	600	43,800	3,780	90	–	6,150	1	–	30	–	–	–	–	120	15	–
,, 14th	–	–	–	1,110	180	–	180	24,540	2,970	90	–	11,040	–	–	–	–	–	–	–	30	94	–
,, 23rd	–	–	–	330	180	–	1,530	1,080	5,790	150	1	28,440	–	–	–	–	2	–	–	21	127	–
,, 29th	–	–	–	990	60	–	870	810	3,750	–	–	23,040	–	–	–	–	3	–	–	39	35	–
Aug. 7th	–	–	–	–	150	300	–	330	1,620	–	1	40,020	–	–	–	–	–	–	–	26	–	–
,, 14th	–	–	–	1	44	120	60	160	4,020	40	–	33,220	446	–	–	–	–	1	–	137	–	–
,, 21st	–	6	–	–	9	500	–	–	3,240	28	–	8,360	17,442	20	641*	–	–	–	–	33	–	–
,, 28th	–	–	–	–	120	3,240	–	–	2,540	20	–	3,540	7,440	20	2*	–	–	–	–	32	–	–
Sept. 3rd	–	1	–	–	92	9,800	–	80	180	80	–	1,080	11,600	20	40*	–	–	–	1	8	17	–
,, 11th	20	–	–	–	21	4,160	–	100	4,300	–	–	340	4,280	–	–	1	–	–	161	33	55	–
,, 16th	–	–	–	–	53	2,310	10	30	100	–	–	51	2,800	30	–	–	–	–	220	6	20	–
,, 24th	–	–	–	–	77	10	–	–	640	–	–	180	3,760	20	–	–	–	–	800	4	–	–
Oct. 1st	–	–	–	–	18	–	–	–	60	–	–	50	180	–	–	–	–	–	1,370	3	–	–
,, 7th	–	–	–	–	3	–	–	–	340	–	–	20	660	–	–	–	1	–	500	4	–	–
,, 14th	–	–	–	–	–	–	–	20	510	–	–	–	4,100	20	–	–	–	–	–	–	–	–
,, 16th	–	–	–	–	–	–	–	10	330	–	–	–	1,680	–	–	–	–	–	–	–	–	–
Nov. 6th	–	–	–	–	–	–	–	–	20	–	–	–	1,650	–	–	–	–	–	–	–	–	–
,, 13th	–	–	–	–	10	–	–	–	20	–	–	–	980	50	–	–	–	–	20	–	–	–
,, 20th	–	–	–	–	–	–	–	–	10	–	–	10	1,390	10	–	–	–	–	–	–	–	–
,, 26th	–	–	–	–	–	–	–	–	10	–	–	–	710	10	–	–	–	–	–	–	–	–
Dec. 3rd	–	–	–	–	–	–	–	–	100	–	–	–	1,115	–	–	–	–	–	10	–	–	–
,, 10th	–	–	–	–	–	–	–	–	20	–	–	–	1,020	20	–	–	–	–	1	–	–	–
,, 17th	–	–	–	–	–	–	–	–	–	–	–	–	690	50	–	–	–	–	–	–	–	–
,, 22nd	–	–	–	–	–	–	–	–	–	–	–	–	140	10	–	–	–	–	–	–	–	–
1931.																						
Jan. 1st	–	–	–	–	–	–	–	–	–	–	–	–	310	130	–	–	–	–	–	–	–	–
,, 5th	–	–	–	–	–	–	–	–	–	–	–	–	230	170	–	–	–	–	–	–	–	–
,, 15th	–	–	–	–	–	–	–	–	70	–	–	–	970	1,166	–	–	–	–	–	–	–	–
,, 22nd	–	–	–	–	–	–	–	–	30	–	–	–	104	130	–	–	–	–	–	–	–	–
,, 26th	–	–	–	–	–	–	–	–	–	–	–	–	10	10	–	–	–	–	–	–	–	–
Feb. 6th	–	–	–	–	–	–	–	–	–	–	–	–	–	30	–	–	–	–	–	–	–	–
,, 12th	–	–	–	–	–	–	–	–	30	–	–	–	–	–	–	–	–	1†	–	–	–	–
,, 20th	–	–	–	–	1	–	–	–	10	–	–	–	–	30	–	–	–	–	–	–	–	–
,, 23rd	–	–	–	–	20	–	–	–	80	–	–	–	2	–	–	–	–	–	–	–	–	–
‡Mar. 17th	–	–	–	–	2	–	–	–	1,820	–	–	–	–	–	–	–	20	–	–	–	–	–
,, 26th	–	–	–	–	10	30	–	70	4,520	–	–	–	–	180	–	–	16	–	–	–	–	–
April 1st	–	–	–	–	2	–	20	–	220	–	–	–	–	20	–	–	3	–	20	–	–	–
,, 16th	–	–	–	–	–	–	660	–	12,120	–	–	–	–	–	–	–	23	–	40	–	–	1,480

° Possibly a few *A. rugosa*. ‡ Medusæ only counted. * Nectophores. † Ephyra.

TABLE I—*continued*.

1930.	Tomopteris helgolandica.	Terebellid larvæ.	Pœcilochætus serpens larvæ.	Sagitta elegans.	Sagitta setosa.	Calanus finmarchicus.	Euchæta hebes.	Metridia lucens.	Candacia armata.	Anomalocera patersoni.	Labidocera wollastoni.	Caligus sp.	Mysid sp.	Nyctiphanes couchii adult.	Euphausiid larvæ.	Meganyctiphanes norvegica.	Apherusa sp.	Hyperia galba.	Themisto gracilipes.	Idotea sp.	Cumacea.
Feb. 4th .	140	2	–	11,360	–	1,200	–	–	20	–	–	–	100	4,218	–	150	–	–	112	–	–
,, 12th .	770	–	–	16,270	130	540	–	–	–	–	–	1	–	–	380	–	–	–	–	–	–
,, 19th .	251	–	–	10,411	389	1,280	–	–	60	–	–	1	–	20	–	–	–	–	1	–	–
,, 26th .	3	–	–	452	110	580	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Mar. 5th .	165	–	–	1,517	93	450	–	–	–	–	–	–	–	4	–	–	–	–	1	–	–
,, 12th .	33	–	–	455	5	260	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
,, 19th .	–	–	–	8	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–
,, 27th .	3	–	–	1,860	–	420	–	–	–	–	–	2	–	2	–	–	–	–	–	–	–
April 2nd .	–	–	–	24	1	10	–	–	–	38	–	1	–	–	–	–	–	–	1	–	–
,, 11th .	3	–	–	240	–	440	–	60	–	–	–	1	–	2	–	–	–	–	–	–	–
,, 16th .	–	–	–	21	–	16,890	–	70	60	30	–	1	–	1	310	1	–	–	–	–	–
,, 24th .	–	–	10	860	–	7,630	–	–	510	–	–	1	–	–	1,140	–	–	–	130	–	–
,, 29th .	–	–	–	39	1	960	–	60	80	–	–	–	–	1	540	–	–	–	2	–	–
May 7th .	7	386	–	77	2	318,450	–	193	772	–	–	–	–	2	2,702	–	–	–	–	3	–
,, 15th .	10	60	–	243	7	24,720	–	80	260	–	–	–	–	–	580	–	–	–	–	–	–
,, 22nd .	10	–	–	101	–	11,210	–	–	50	20	–	1	–	–	450	–	–	–	–	–	–
June 10th .	63	–	110	1,324	–	1,968	–	–	200	4	–	1	1	4	40	–	–	–	–	–	–
,, 19th .	25	–	–	637	6	6,592	–	–	220	22	–	2	–	–	20	–	–	5	–	–	–
,, 26th .	95	–	–	760	–	3,560	–	40	320	13	–	2	2	–	40	–	20	–	20	–	–
July 4th .	10	–	–	2,218	–	2,023	–	–	200	62	–	2	2	–	–	–	20	–	1	–	–
,, 9th .	664	–	–	4,377	8	6,132	–	–	2,160	60	–	2	360	–	–	–	60	–	1	–	–
,, 14th .	741	–	–	3,942	4	8,370	–	–	930	†	–	–	152	–	30	–	–	–	–	–	–
,, 23rd .	759	–	30	2,142	10	2,910	–	30	1,860	10	–	2	60	8	30	–	750	–	–	–	–
,, 29th .	376	–	–	1,423	12	1,007	–	30	270	–	–	4	6	–	–	–	240	–	1	–	–

Aug. 7th	1,602	–	–	7,800	36	2,730	–	–	450	–	–	5	94	102	–	–	30	–	1	–	–
,, 14th	222	1*	–	5,210	5	1,041	–	–	220	1	–	8	17	–	140	–	200	–	1	–	–
,, 21st	42	1†	–	2,038	–	803	–	–	200	–	–	4	–	–	20	–	240	–	21	–	20‡
,, 28th	4	–	–	1,018	–	402	–	–	80	–	–	1	–	–	–	–	140	–	22	–	–
Sept. 3rd	179	–	–	1,222	47‖	363	–	–	140	1	–	–	20	–	–	–	360	–	1	–	–
,, 11th	–	–	–	4,398	760	612	–	–	560	3	–	7	–	1	20	–	100	–	25	–	–
,, 16th	26	1°	–	558	46	233	–	–	40	1	10	–	–	–	–	–	–	–	3	–	–
,, 24th	4	–	–	270	87	35	–	–	–	53	–	–	–	–	7	–	–	–	2	1	–
Oct. 1st	8	–	–	102	45	70	–	–	20	–	–	1	–		–	–	–	–	2	–	–
,, 7th	–	–	–	74	369	263	–	–	30	–	–	1	–	–	–	–	–	1	–	–	–
,, 14th	3	–	–	303	683	–	–	–	150	–	–	2	1	–	–	–	–	–	–	–	–
,, 16th	1	–	–	229	258	118	–	–	10	10	–	–	–	–	–	–	–	–	–	–	–
Nov. 6th	–	–	–	441	300	–	–	–	10	–	–	1	1	–	–	–	–	–	–	–	5
,, 13th	–	–	10	159	120	99	–	–	40	–	–	–	–	1	10	–	–	–	–	–	–
,, 20th	–	1**	–	32	73	7	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–
,, 26th	1	–	–	61	84	14	–	–	20	–	–	–	–	–	–	–	–	–	–	–	–
Dec. 3rd	–	–	–	730	1,080	107	–	–	40	–	–	1	–	–	–	–	–	–	–	–	–
,, 10th	–	–	–	360	162	129	–	–	100	–	–	1	–	–	121	–	–	–	1	–	–
,, 17th	–	–	–	262	372	169	–	–	70	–	–	–	–	–	30	–	–	–	1	–	–
,, 22nd	–	–	–	72	78	98	–	–	90	–	–	–	–	–	10	–	–	–	–	–	–
1931.																					
Jan. 1st	1	–	–	210	249	20	–	–	60	–	–	2	–	–	–	–	–	–	–	–	–
,, 5th	–	–	–	109	59	80	10	–	120	–	–	1	–	–	10	–	–	–	–	–	–
,, 15th	1	–	–	1,765	339	190	–	–	150	–	–	–	10	3	–	–	–	–	–	–	–
,, 22nd	–	–	–	172	270	56	–	–	20	–	–	1	–	–	8	–	–	–	–	–	–
,, 26th	–	–	–	117	101	19	10	–	20	–	–	–	–	–	7	–	–	–	–	–	–
Feb. 6th	–	–	–	51	2	–	–	–	20	–	–	–	–	–	–	–	–	–	–	–	–
,, 12th	–	–	–	83	17	40	–	–	10	–	–	1	–	–	–	–	–	–	–	–	–
,, 20th	–	–	–	816	239	446	–	–	220	–	–	1	–	–	–	–	–	–	–	–	–
,, 23rd	–	–	–	474	134	343	–	–	420	–	–	1	–	–	20	–	–	–	–	–	–
Mar. 17th	7			7,502	221									36			Rest of sample not counted				
,, 26th	25	321††	–	491	333	110	–	–	50	–	–	3	–	–	–	–	–	–	–	–	–
April 1st	–	60	–	935	1,048	320	–	–	220	–	–	–	–	–	–	–	–	–	–	–	–
,, 16th	30	200	–	764	385	1,260	–	–	180	–	–	1	–	–	–	–	40	–	–	–	–

* Young Syllid. † Glycera. ‡ Gravel in catch, near bottom. ‖ 1 *S. serratodendata.* ° 1 large polychæte, fair amount of gravel. ** 1 Autolytus. †† 1 Autolytus.

TABLE I—*continued.*

1930.	Leander sp. larvæ.	Pandalid larvæ.	Alphæid larvæ.	Crangonid larvæ.	Pontophilus spinosus larvæ.	Homarus vulgaris larvæ.	Phyllosoma larvæ.	Galatheid larvæ.	Galatheid post-larvæ.	Upogebia sp. larvæ.	Upogebia sp. post-larvæ.	Callianassa subterranea larvæ.	Axius styrhinchus larvæ.	Pagurid larvæ.	Pagurid glaucothoë larvæ.	Porcellana sp. zoea.	Porcellana sp. post-larvæ.	Ebalia sp. zoea.	Ebalia sp. megalopa.	Crab zoea.	Crab megalopa.	Squilla sp. larvæ.	Larval gastropods.	Echinospira larvæ.	Limacina retroversa.	Clione limacina.	Cephalopod young.	Young starfish.	Oikopleura.	Tornaria larvæ.	Fish eggs.	Total.
Feb. 4th	–	–	–	–	–	–	–	20	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	–	–	–	–	20	**17,787**
,, 12th	–	–	–	–	–	–	–	–	–	–	–	–	–	20	–	–	–	–	–	30	–	–	–	–	–	17	–	–	–	–	160	**19,280**
,, 19th	–	10	–	–	–	–	–	40	–	–	–	10	–	40	–	–	–	–	–	1,150	–	–	–	–	–	10	–	–	–	–	110	**13,792**
,, 26th	–	–	–	–	–	–	1	100	–	–	–	–	–	40	–	–	–	–	–	2,540	–	–	–	–	–	5	–	–	–	–	–	**3,844**
Mar. 5th	–	–	–	200	–	–	2	90	–	–	–	–	–	470	–	–	–	–	–	4,850	–	–	–	–	–	2	1	–	10	–	4,020	**11,888**
,, 12th	–	–	–	40	–	–	–	10	–	–	–	–	–	20	–	–	–	–	–	910	–	–	–	–	–	1	–	–	–	–	2,500	**4,041**
,, 19th	–	20	–	20	–	–	–	140	–	–	–	–	–	580	–	–	–	–	–	16,780	–	–	–	–	–	–	–	–	–	–	5,620	**23,177**
,, 27th	–	–	–	–	–	–	1	–	–	–	–	–	–	270	–	–	–	–	–	8,270	–	–	–	–	–	5	–	–	–	–	2,750	**13,799**
April 2nd	–	–	–	50	–	–	2	160	–	–	–	–	–	40	–	–	–	–	–	930	–	–	–	–	–	–	–	–	140	–	4,590	**5,987**
,, 11th	–	30	–	–	1	–	1	10	–	–	–	–	–	10	–	–	–	–	–	130	–	–	–	–	–	–	–	–	90	–	740	**2,445**
,, 16th	–	170	–	60	90	–	10	870	–	–	–	–	–	480	–	40	–	–	–	3,650	110	–	–	–	–	–	–	–	–	–	3,850	**26,945**
,, 24th	–	30	–	390	30	–	4	300	–	–	–	–	–	260	–	50	–	–	–	12,810	650	–	–	–	70	–	–	–	–	–	800	**26,419**
,, 29th	–	40	–	90	40	–	–	330	–	–	–	–	–	110	–	190	–	–	–	1,420	61*	–	–	–	–	–	–	–	100	–	900	**5,888**
May 7th	–	386	–	–	–	–	9	1,737	–	–	–	–	–	–	3	386	–	–	–	7,334	386	–	–	–	–	–	–	–	579	–	1,737	**335,784**
,, 15th	–	200	–	40	120	–	–	3,540	–	–	–	–	–	440	–	960	–	–	–	14,640	280	–	+	–	140	–	–	–	20	–	860	**53,302**
,, 22nd	–	390	–	80	30	–	32	2,890	–	10	–	–	–	540	–	810	–	–	–	8,430	550	–	+	10	90	–	–	–	–	–	190	**27,671**
June 10th	–	660	–	250	7	–	24	1,140	–	60	–	–	–	150	–	1,120	–	–	–	9,530	400	–	+	–	280	–	–	–	10	–	350	**19,291**
,, 19th	–	300	–	100	8	–	5	780	–	180	–	–	–	80	–	220	–	20	–	4,580	520	–	80	20	280	–	–	–	–	–	300	**16,696**
,, 26th	–	480	–	320	21	–	41	3,020	–	440	–	–	–	860	–	880	–	940	–	8,440	140	–	80	–	4,320	–	–	–	–	440	960	**37,052**
July 4th	2	80	–	20	–	–	3	380	–	–	–	–	–	140	40	800	–	–	–	1,540	180	–	40	–	600	–	1	–	–	120	1,120	**13,830**
,, 9th	31	300	–	120	1	–	–	2,130	–	1,170	–	90	–	1,560	60	300	–	420	–	13,410	900	–	300	–	1,710	–	1	–	–	4,890	120	**96,342**
,, 14th	35	510	–	240	–	–	78	2,730	–	1,980	30	60	–	360	–	3,060	120	780	–	12,900	1,230	–	+	–	23,310	–	1	–	–	3,030	180	**105,037**
,, 23rd	3	1,020	–	390	–	–	70	3,390	30	360	–	60	–	1,710	60	1,740	120	360	570	17,220	2,280	–	+	–	8,790	–	1	–	–	720	30	**85,176**
,, 29th	–	780	–	90	–	–	1	540	30	930	1	120	12	750	–	2,550	–	30	90	4,920	1,500	–	+	–	2,250	–	4	–	30	930	30	**48,554**

Aug.	7th	11	330	–	120	–	–	5	2,160	30	3,210	–	1,740	–	1,230	–	810	–	180	30	8,880	1,650	–	+	–	660	–	3	60	–	210	120	**76,736**
,,	14th	1	600	–	80	–	1	1	980	–	1,180	5	360	3	1,080	1	2,840	100	20	40	2,620	980	–	1	–	480	–	9	42	–	–	60	**56,799**
,,	21st	1	160	–	80	–	–	–	80	–	140	5	300	–	80	21	440	–	–	–	580	400	–	40	–	–	–	4	11	–	–	–	**36,010**
,,	28th	1	100	12	60	–	–	5	140	–	1,160	–	860	–	360	–	940	120	–	40	3,220	680	30	–	–	–	–	3	45	–	–	–	**26,397**
Sept.	3rd	2	320	23	160	–	1	2	60	20	80	–	1,380	–	380	2	120	60	80	100	1,840	540	5	40	–	–	–	–	90	–	20	–	**30,658**
,,	11th	–	40	–	–	–	–	–	60	–	40	–	280	–	160	41	140	–	–	20	360	100	–	–	–	–	–	1	51	–	–	20	**21,279**
,,	16th	10	30	2	10	–	–	–	20	–	30	–	160	–	60	–	–	–	–	–	470	40	10	–	–	–	–	–	167	20	–	10	**7,587**
,,	24th	1	–	–	–	–	–	–	–	–	50	–	20	–	10	–	300	–	–	–	900	80	2	–	–	–	–	2	2	20	–	10	**7,369**
Oct.	1st	1	–	2	–	–	–	–	–	–	–	–	–	–	50	–	60	–	–	–	20	30	1	–	–	–	–	–	3	100	–	–	**2,196**
,,	7th	–	10	1	–	–	–	–	10	–	20	–	–	–	20	–	170	–	–	–	250	40	–	–	–	–	–	1	62	80	–	–	**2,930**
,,	14th	–	–	2	–	–	–	–	–	–	50	–	–	1	10	–	210	–	–	–	210	20	–	–	–	–	–	1	–	10	–	10	**6,316**
,,	16th	–	1	7	–	–	–	–	–	–	190	–	–	–	60	–	440	–	–	–	440	20	–	–	–	–	–	–	–	240	–	–	**4,044**
Nov.	6th	–	–	–	–	–	–	–	–	–	–	–	–	–	10	–	10	–	–	–	60	10	–	–	–	–	–	–	10	–	–		**2,528**
,,	13th	–	–	3	30	–	–	–	–	–	–	–	10	–	30	–	–	–	–	–	30	10	–	–	–	–	–	–	–	190	–	10	**1,832**
,,	20th	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	10	–	–	–	–	–	–	–	–	40	–	492†	**2,070**
,,	26th	–	–	–	–	–	–	–	–	–	–	–	–	–	30	–	–	–	–	–	70	10	–	–	–	–	–	–	–	–	–	160†	**1,180**
Dec.	3rd	–	–	–	–	–	–	–	10	–	–	–	–	–	–	–	–	1	–	–	40	–	–	–	–	–	–	–	–	20	–	20	**3,274**
,,	10th	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	20	–	–	–	–	–	–	–	–	40	–	190	**2,185**
,,	17th	–	–	–	10	–	–	–	–	–	–	–	–	–	120	–	–	–	–	–	40	20	–	–	–	–	–	–	–	100	–	20	**1,958**
,,	22nd	–	–	–	10	–	–	–	–	–	–	–	–	–	20	–	–	–	–	–	40	–	–	–	–	–	–	–	–	70	–	70	**708**
1931.																																	
Jan.	1st	–	–	–	–	–	–	–	10	–	–	–	–	–	90	–	–	–	–	–	90	20	–	–	–	–	–	–	–	60	–	90	**1,342**
,,	5th	–	–	–	1	–	–	–	–	–	–	–	–	–	70	–	–	–	–	–	210	10	–	–	–	–	–	–	–	40	–	100	**1,220**
,,	15th	–	10	–	–	–	–	–	–	–	–	–	–	–	80	–	–	–	–	–	80	10	–	–	–	–	–	–	–	590	–	1,270	**6,704**
,,	22nd	–	10	–	–	–	–	–	50	–	–	–	–	–	30	–	–	–	–	–	140	–	–	–	–	–	–	–	–	110	–	1,300	**2,431**
,,	26th	–	–	–	–	–	–	–	–	–	–	–	–	–	50	–	–	–	–	–	80	–	–	–	–	–	–	–	–	70	–	640	**1,134**
Feb.	6th	–	–	–	10	–	–	–	90	–	10	–	–	–	20	–	–	–	–	–	370	–	–	–	–	–	–	–	–	50	–	910	**1,563**
,,	12th	–	–	–	–	–	–	–	90	–	–	–	–	–	90	–	–	–	–	–	240	–	–	–	–	–	–	–	–	50	–	530	**1,182**
,,	20th	–	–	–	–	20	–	–	810	–	–	–	–	–	260	–	–	–	–	–	6,840	30	–	–	–	–	–	–	–	110	–	7,140	**16,973**
,,	23rd	–	30	–	10	10	–	–	750	–	–	–	–	–	710	–	–	–	–	–	7,170	90	–	–	–	–	–	–	–	–	–	7,090	**17,354**
,,	26th	–	–	–	20	10	–	–	90	–	–	–	–	–	40	–	–	–	–	–	4,840	10	–	–	–	–	–	–	–	–	–	780	**11,949**
April	1st	–	80	–	20	–	–	–	80	–	–	–	–	–	600	–	–	–	–	–	14,480	20	–	–	–	–	–	–	140	–	–	80	**18,368**
,,	16th	–	140	–	60	–	–	–	200	–	20	–	20	–	1,460	–	360	–	–	–	11,060	140	–	–	–	–	–	–	–	–	–	1,040	**31,683**

* 1 small ♂ pea crab. † Pilchard.

On the Biology of *Calanus finmarchicus.* I. Reproduction and Seasonal Distribution in the Clyde Sea-Area during 1932.

By

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With 4 Figures in the Text and Plates I and II.

CONTENTS.

INTRODUCTION.

THE problems concerned with the breeding of *Calanus finmarchicus* have been dealt with by numerous workers, mainly during the last twenty years. Taken as a whole the results show remarkable uniformity if the differences in methods of sampling and in the geographical regions over which the work has been spread, are taken into account.

The two points which stand out on reviewing this work are firstly, that breeding occurs in spring and summer and secondly, that during the winter the species is represented by its fourth and fifth copepodite stages, chiefly the latter (Farran, 1927, p. 142).

Work in the Clyde Sea-Area was undertaken to discover to what extent this area was in agreement with other regions of northern temperate waters and to obtain more detailed information on the number of breeding periods, the time taken for development, and other related facts. This work was an extension of the programme carried out by Marshall and Orr in 1931 (Ann. Rep. Scot. Mar. Biol. Assoc., 1930–31).

This area with its semi-enclosed lochs appears to be particularly suitable for such work since it is separated from the waters of the Irish Sea and the Atlantic by a comparatively shallow platform. Unfortunately, little is known about the currents entering the Clyde Sea-Area, but those drift-bottle experiments which have been carried out by Cunningham (1907) of the Irish Fisheries Board lend support to the view that no deep-water currents enter the area. (Other drift-bottle experiments affecting this area have dealt only with surface drift.) The lochs of this area are, in most cases, still more completely cut off from outside waters by bars (Mill, 1889–91 ; Marshall and Orr, 1927) of shallow depth across their mouths.

It is felt that movements of surface waters will not affect the population to any great extent and will in any case be dependent upon weather conditions.

It seems certain then, especially in the lochs, that any changes in the numbers of Calanus will be due to factors operating within the locality.

STATIONS AND METHODS.

Four stations were selected within the area for investigation and comparison (see Map, Text-Figure 1). Station I was situated over the deepest part of the channel between the south end of Bute (Garroch Head) and the Little Cumbrae. This station had an average depth of 113 metres, and was taken as typical of the open waters of the Clyde Sea-Area. Station II was in the channel which runs in a north-westerly direction between Arran and Bute, ending in a " deep " of about 200 metres at the mouth of Loch Fyne. The average depth of this station, which was midway between the north of Arran (The Cock of Arran) and Inchmarnock, was 151 metres. Station II, also, was assumed to be typical of the open waters of this region and acted as a check upon Station I.

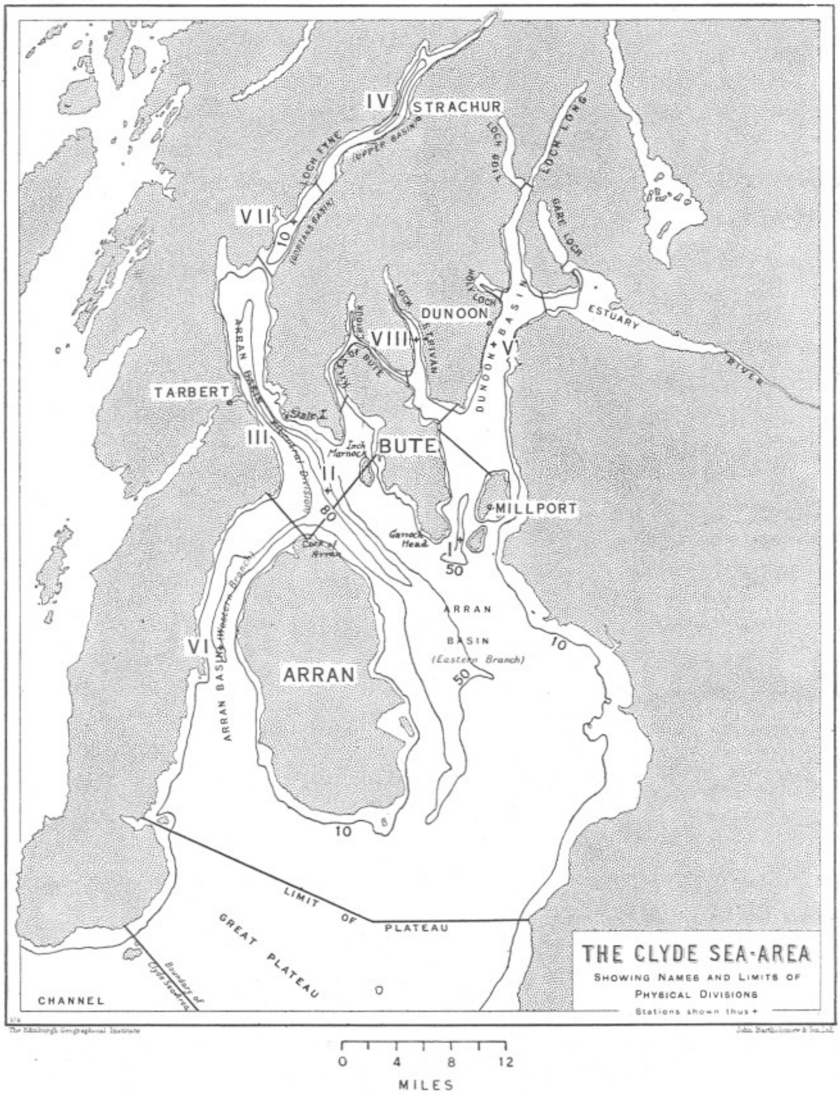
Station III was situated in the vicinity of the " deep " at the mouth of Loch Fyne, off Skate Island. The catches from this station were not counted, but rough observations were made to check the possibility of the loch forming a breeding ground whence Calanus might spread to the rest of the area, since it was known from previous work in this area that Calanus was abundant there at times when it was very scarce elsewhere.

Station IV was nine or ten miles from the head of Loch Fyne, in the deepest part of the loch, off Strachur. Upper Loch Fyne is separated from the rest of the area by two bars which divide the loch into three basins, Strachur being in the innermost. The average depth of the hauls was 130 metres.

It was hoped that these stations would give a comparison between the loch and the open waters, and that some light might be thrown on the reason for the large numbers of Calanus present here when they were scarce elsewhere.

Three other stations were selected, one off Dunoon (Station V), a second in the Kilbrennan Sound (Station VI), and the third about half-way up Loch Fyne in the middle, or Gortan's Basin (Station VII), and these were visited and hauls taken at quarterly intervals to provide a further check upon the validity of the regular stations.

Vertical hauls were taken at each of the stations with a modified form of the Standard Net described by Ostenfeld and Jespersen (1924). The



TEXT-FIG. 1.—Map of the Clyde Sea-Area showing positions of Stations. Depth contours are shown for 10, 50, and 80 fathoms.

cylindrical part of the net was made of canvas instead of netting and the conical part of fine-meshed bolting-silk (77 strands in 1 cm.). An ordinary townet bucket was used. A hand winch was used for hauling the net, the rate at first being kept as nearly as possible to half a metre per second, which approximates to that given by Ostenfeld and Jespersen. Later, as the meshes of the net became smaller with use, allowance was made for the reduced filtration and more time was taken for hauling.

The first hauls were taken on September 3rd, 1931, and continued at approximately fortnightly intervals until September 5th, 1932, a final haul being made on October 30th. At Station I extra hauls were taken when possible from March to June, making the intervals between hauls approximately a week. At the time of taking each haul notes were made of the depth of the haul, time of day, and of the time taken to haul the net from the bottom to the surface (Table I). The condition of sea and sky, and approximate force and direction of the wind were also noted.

Each station was visited at approximately the same time of day throughout the year. In a few cases, owing to weather conditions or other factors, this was not possible.

The catches were preserved in 5% formalin at the time of taking and later sorted and counted in the laboratory. For counting, Russell's modification of Bogorov's counting tray was used and found very satisfactory. A description of this tray will be found in the Scientific Reports of the Great Barrier Reef Expedition, Vol. II, 2, 1931, p. 24. My thanks are due to Mr. F. S. Russell for procuring this tray for me.

All stages from ovum to adult were counted. It was considered that a count of 1,000 would give a representative sample of the number of different stages present in the catch. In some cases this necessitated taking an aliquot sample of the catch for counting. When this was done the method described by Russell (1925, p. 776) was used. Since the apparatus in use was not identical with that described by him, the method was checked by dividing a catch into ten parts and counting each. The error in sampling was found to be similar to that obtained by Russell (p. 775).

Before examining the results of this work there are one or two points to be borne in mind.

Allowance must be made for the error incurred in using single vertical hauls as the means of obtaining the catches. It has been shown by Gardiner (1931, p. 457) that in 145 hauls, two may be taken which will deviate from the mean by as much as 90% and that occasionally even greater deviation may be expected. He states, however, that variation in the speed of hauling and in the time of day at which the hauls are made does not cause appreciable errors and the conclusion is reached that " the main cause of variation in the size of the catch " is probably due to " lack of uniformity in the distribution of the organisms themselves " (p. 467).

In the course of this investigation over 130 hauls were made of which over 100 were counted and the possibility of "freak" hauls occurring must be taken into consideration. To safeguard as far as possible against the occurrence of such "freak" hauls Gardiner suggests that 5 hauls as a minimum should be taken at each station, since 4 out of 5 will probably confine the deviation to under 40% and "give a value which for all practical purposes may be considered the true one." As he points out this requires much time.

Another factor to be considered is the difficulty of identifying the different nauplius stages and of separating these and the ova from those of other copepods without taking too much time. In most cases this separation could only be done by means of measurements, which must always be approximate owing to the variation in size of the individuals of each particular stage. The ova and nauplii of Pseudocalanus closely resemble those of Calanus and even the difference in size is not marked thus early in the life history. The figures for the nauplii, therefore, must not be regarded as being as accurate as those for the copepodites.

The initial difficulty of identification of the nauplii of Calanus was overcome with the assistance of Dr. M. V. Lebour, to whom I am indebted for sending me specimens of such nauplii from the English Channel.

Variations in the depth from time to time at different stations has not been regarded as important and no allowance has been made for such variation.

It is with pleasure that I take this opportunity of expressing my thanks to my colleagues, Miss S. M. Marshall and Mr. A. P. Orr, for much practical assistance from time to time.

Results.

In the charts, Plates I and II, will be seen the variation in the population of Calanus in this area from September, 1931, to September, 1932. The results obtained from each of the three stations counted are shown, expressed as total numbers in Plate I and as percentage composition in Plate II. Details of catches at all stations will be found in Tables II, III, IV, and V.

Owing to the considerable variation in total numbers it was impossible in Plate I to represent the individual stages separately throughout, so the Calanus were divided into four groups, ova, nauplii, copepodite stages, and adults. In the case of the percentage chart it was found necessary to group only the nauplii (I–VI) and the copepodite Stages I–III, each of the others being given individual representation.

On examining the total numbers curve for Station I (Garroch Head) it will be seen that numbers were low in September and decreased further through the autumn and early winter and it was not until the end of March that an increase occurred. This was of short duration. Numbers then increased suddenly at the end of April and through May, thereafter falling away steadily to reach a constant level in August. A final haul taken at the end of October showed little change.

Turning now to the percentage chart (Plate II) for this station it will be seen that Stage V copepodites formed the bulk of the catch through the autumn and early winter. During October and November ova, nauplii, and young copepodites formed a large percentage, but were very small in actual numbers and not sufficient to make any marked increase in total numbers. At the end of December the Stage V copepodites began to moult into adults, the maximum percentage of males being attained at the beginning of February, the largest actual number having occurred a fortnight earlier. Females attained their maximum number and percentage on February 22nd.

As will be seen from Table II the ova and nauplii found in January were relatively unimportant though representing a fair proportion on the percentage chart. There were no ova or nauplii on February 8th, but on 22nd 84 ova were found, representing 57% of the catch, females amounting to 37%. From this time onwards there followed a regular sequence of ova, nauplii, copepodites, and adults.

The adults which had moulted from the autumn-winter stock of Stage V copepodites died out early in March to be replaced shortly after by their own offspring which, liberated as ova soon after February 8th, appeared as adults soon after March 7th. Through April and May these in turn produced ova which began to reach maturity in May and June. From the middle of May until the end of June this second brood liberated eggs which grew to maturity, the later ones remaining as Stage V copepodites. Further successive small broods of ova in July and August added to the number of Stages IV and V copepodites which were to carry the stock over the autumn and early winter.

Total numbers at Station II (Cock of Arran) in September, 1931, were over 2,000, i.e. higher than those of Station I, and maintained a fairly high average (over 3,000) until the end of November, by which time a considerable and real fall off in numbers was observable, 1,000 being reached on only one occasion after that time until breeding had started in the spring.

On May 2nd numbers increased to over 40,000 from having been under 500 on April 18th, to be followed by as sudden a fall to below 4,000 a fortnight later. From this date numbers showed a gradual fall to the end of June, followed by a gradual rise to the end of September, maintaining an average of just over 2,000 for the period. The average had fallen to under 1,000 by the end of October.

It will be seen from Plate II that, as at Station I, through the autumn and early winter nearly 90% of the Calanus present were Stage V copepodites with a small percentage of Stage IV and a very few adults. Moulting of these Stage V copepodites started at the same time as at Station I, both males and females attaining their greatest numbers on February 8th.

Ova appeared shortly after January 25th and from February 8th until 22nd increased rapidly in number, falling off again to March 7th. These ova appeared as adults from March 7th until early in May. On April 18th an increase in the number of ova was again noticeable which was followed by the extraordinary increase of May 2nd, when over 34,000 ova and about 5,000 nauplii were estimated to be present. These as quickly disappeared, leaving only about 900 ova, 1,300 nauplii, and 1,500 copepodites.

For the next two months the number of ova was fairly constant, but the number of nauplii and copepodites fell off so that in the latter half of June a third noticeable increase is represented in the percentage chart for this station. Through July and August the number of Stage V copepodites moulting into adults decreased, resulting in an increase in the number of copepodites to form, as at Station I, the autumn-winter stock.

At Station IV (Strachur) the numbers of Calanus (mainly Stage V copepodites) averaged 10,000 for the first six weeks of this investigation. They then fell away steadily from November to March, by which time the survivors had all become adults, which as at Stations I and II first appeared at the end of December and attained maximum numbers on February 8th; the males far outnumbered the females all the time (see Table IV).

It is impossible to follow the sequence of events at Stations V, VI, and VII, where hauls were taken only quarterly. The figures for these stations, however (Table V), show no striking disagreement with those for other stations at the times when these hauls were taken, except that in winter numbers were usually much lower.

DISCUSSION.

The most striking features in the chart showing total numbers (Plate I) are: firstly, a fairly high number of Calanus present at the beginning of the autumn, gradually falling away to a minimal value, well under 500 in every case, at the time when reproduction is starting in the spring; secondly, the coincidence of large catches from the two stations in open waters (I and II) on May 2nd; thirdly, the disappearance of this sudden increase; and fourthly, the smaller number of Calanus present in September, 1932, compared with the same time in the previous year.

Noticeable features of the percentage chart (Plate II) are the homogeneity of the Calanus population during the autumn and winter at two stations in particular (II and IV); the appearance of three successive and well marked breeding periods at all three stations, coincident at I and II and the first slightly delayed and overlapping the second at Station IV; and the accumulation of copepodites of Stages IV and V, particularly the latter, at all stations after the middle of July.

This minimum, occurring towards the end of winter, seems to be of general occurrence and has been found by several investigators working on Calanus. Farran (1927, p. 142) investigating the same problem off the south-west coast of Ireland found a minimum in March. Ruud (1929, p. 78) studying the copepod population off the coast of Norway also found the number of Calanus to be at a minimal value in March and the recent work of Sömme (1933, p. 32) confirms this. At Station I in this area Calanus were very scarce from November to the beginning of March. At Station II low numbers were recorded from January until March, the actual minimum falling early in the latter month; but at Station IV numbers did not reach low values until the beginning of March and the minimum was delayed until April, by which time numbers were increasing at the other stations.

The low numbers found by Sömme at the end of March are ascribed to a definite migration of Calanus towards the surface early in March, after which they were carried away by surface currents. This can scarcely be the cause in the Clyde Sea-Area since it has been shown that currents can play little part in such an enclosed area. Moreover, any outward migration from Loch Fyne would have been detected at Stations II and III as explained below.

Natural mortality, possibly directly connected with food supply, will account for the steady decrease in numbers through the course of the winter leaving comparatively few females to produce the first brood which is, consequently, small in numbers compared with later broods.

Farran (1927, p. 137) found that in January males were more abundant than females and that in the following month females were in excess. This was apparent at Stations I and II though numbers were low; at Station IV males were more numerous than females right through this period, and it was not until April 18th, when the new brood had developed, that females noticeably outnumbered males.

The result, then, of this gradual moulting of the autumn-winter stock of Stage V copepodites was the production of a brood of ova, small in numbers compared with later broods, which gave rise to a new brood of adults, mainly females. These appeared through March and April (see Plate II). It was these adults which produced the extraordinary increase at Stations I and II at the beginning of May, to which reference will be made later.

We must here take into consideration the probable life of a single

Calanus ; the time taken for the development of the ovum to the adult ; and the probable number of ova produced by one female.

From an inspection of the percentage chart (Plate II) and Table III showing numbers throughout the year at Station II, it will be seen that by March 7th males, females, and Stage V copepodites of the autumn-winter stock have disappeared completely from the catch, their places being taken by younger stages which they have themselves produced. This clearly indicates that all the fifth copepodites of the autumn-winter stock moult or die at this time and that those which reach maturity, having spawned, die also. Gran (Paulsen, 1906) and Damas (1905) concluded that the individuals normally died after breeding.

This limits the life of a Calanus to one year, but in all probability it is much less. On examining the column of numbers for females for Station I (Table II) it will be seen that from December 29th to February 22nd they increase from 1 to 55, falling away rapidly to 1 at March 7th. This is followed by a sudden increase to 62 by March 21st, rising gradually to 99 on April 18th and falling away again a fortnight later to 47. This is, in turn, followed by a sudden increase to 104, rising to 757 on May 23rd and falling with fluctuations to 15 on June 13th. Once more this is followed by a sudden rise to 205 on June 27th with a fall to the end of July and a sudden drop thence to August 8th, after which the numbers remain steadily low. A similar state of affairs is observable at the two other stations.

The conclusion is that though the adult life of the females from the autumn-winter stock may be nine weeks, for succeeding broods it is not more than 6 or 7 weeks.

The results from Station I (Plate II) show that from March 7th until 21st females increased rapidly (1 on 7th to 62 on 21st), corresponding with the increase in the number of ova from February 8th to 22nd (0 on 8th to 84 on 22nd). This indicates a maximum period of 28 days for the development of the ova to adults at this time of year. The ova and nauplii present before February 8th were insignificant in number and may be neglected.

Subsequent experimental work carried out in the laboratory (jointly with Miss S. M. Marshall) confirmed the view that four weeks was the maximum time required for the ova to reach maturity.

Calanus of different stages were kept each in a separate beaker, the sea-water of which was changed daily and the Calanus examined. The temperature was kept as close as possible to that of the sea at the time (June, July, and August), by standing the beakers in shallow tanks through which sea-water was circulating. It was assumed that each Calanus would find sufficient food for its daily requirements in 250 c.c. of sea-water. Each specimen was kept until it had moulted at least twice so that the interval between each successive stage in its development could be fixed. Females were kept and the time noted from the shedding of the ova to the appearance of nauplii. It was difficult to distinguish the different nauplii while living, so the time taken to pass through the nauplius stages was taken from the shedding of the ova to the appearance of the first copepodite. The minimum time was eleven days. Each of the successive moults up to Stage V occurred at minimal intervals of 3 days, and the shortest interval between the Stage V copepodite and the adult was 4 days. It will be seen that when the shortest intervals are added together 27 days are required for the complete development from the egg to the adult.

Ruud (1929) found that in the Norwegian Sea Calanus took about 3 months for its entire development. Lebour (1916) states: "Nauplii first appeared between the 17th and 24th of April, and on May 19th Stage V was taken from the jar, having taken certainly less than two months to grow from the egg to this stage." This shows close agreement with the results obtained in this region, and it must be remembered that the slower development in the Norwegian Sea is probably correlated with a lower temperature.

We have now two and a half months as the probable life of a single Calanus during the active breeding periods of spring and summer; one month in which to reach maturity and six weeks of adult life. But the Calanus produced towards the end of the breeding season will live through the autumn and winter until early the next spring, with a life of 5 or 6 months.

There seems to be no record of the number of ova produced by one female Calanus, neither has it been possible to obtain this information experimentally. Referring to the figures in Tables II, III, and IV and correlating the number of females on any particular date with the number of eggs on the same date we find a variation of from 1 to 120 eggs per female. It is probable that the number of eggs liberated by any one female is from 60 to 70, with larger numbers occurring occasionally. It seems possible, also, from observations on the copepod *Euchæta norvegica* (as yet unpublished) that each female can produce more than one brood of ova.

Reference has been made to the striking increase in the number of Calanus which was found on May 2nd. On this date at both outside stations (I and II) extraordinarily large catches of Calanus were obtained,

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EXPLANATION OF PLATES.

PLATE I.—Chart showing the changes in total numbers and composition of the population of *Calanus finmarchicus* at three positions in the Clyde Sea-Area for one year.

PLATE II.—Chart showing the changes in the percentage composition of the population of *Calanus finmarchicus* at three positions in the Clyde Sea-Area for one year.

PLATE I.

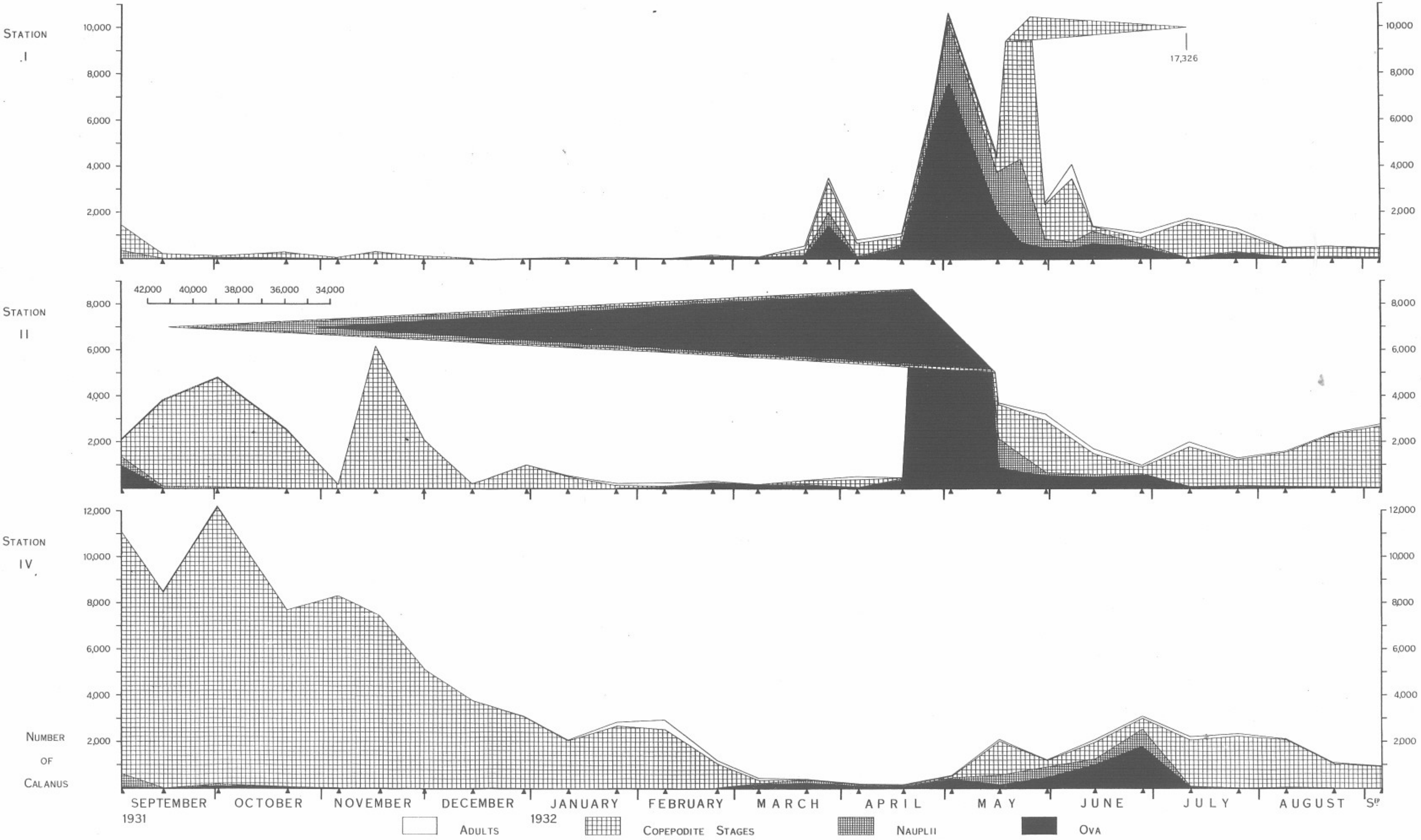
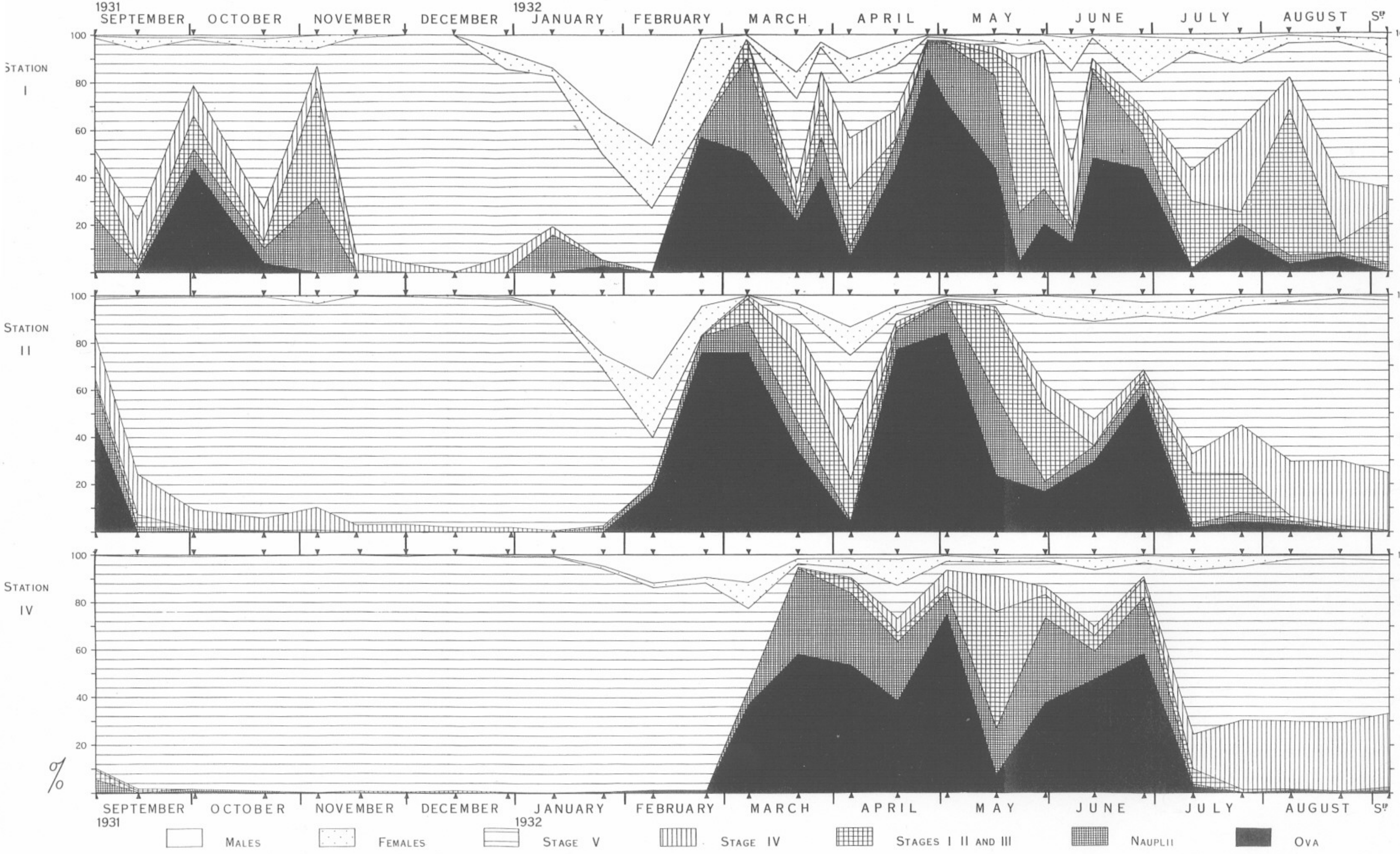

STATION I
10,000
8,000
6,000
4,000
2,000
17,326
STATION II
42,000
40,000
38,000
36,000
34,000
8,000
6,000
4,000
2,000
STATION IV
12,000
10,000
8,000
6,000
4,000
2,000
NUMBER OF CALANUS
SEPTEMBER
1931
OCTOBER
NOVEMBER
DECEMBER
JANUARY
1932
FEBRUARY
MARCH
APRIL
MAY
JUNE
JULY
AUGUST
SEP
ADULTS
COPEPODITE STAGES
NAUPLII
OVA

PLATE II.


1931
SEPTEMBER
OCTOBER
NOVEMBER
DECEMBER
1932
JANUARY
FEBRUARY
MARCH
APRIL
MAY
JUNE
JULY
AUGUST
S^r
STATION I
STATION II
STATION IV
100
80
60
40
20
%
SEPTEMBER
1931
OCTOBER
NOVEMBER
DECEMBER
JANUARY
1932
FEBRUARY
MARCH
APRIL
MAY
JUNE
JULY
AUGUST
S^r
MALES
FEMALES
STAGE V
STAGE IV
STAGES I II AND III
NAUPLII
OVA

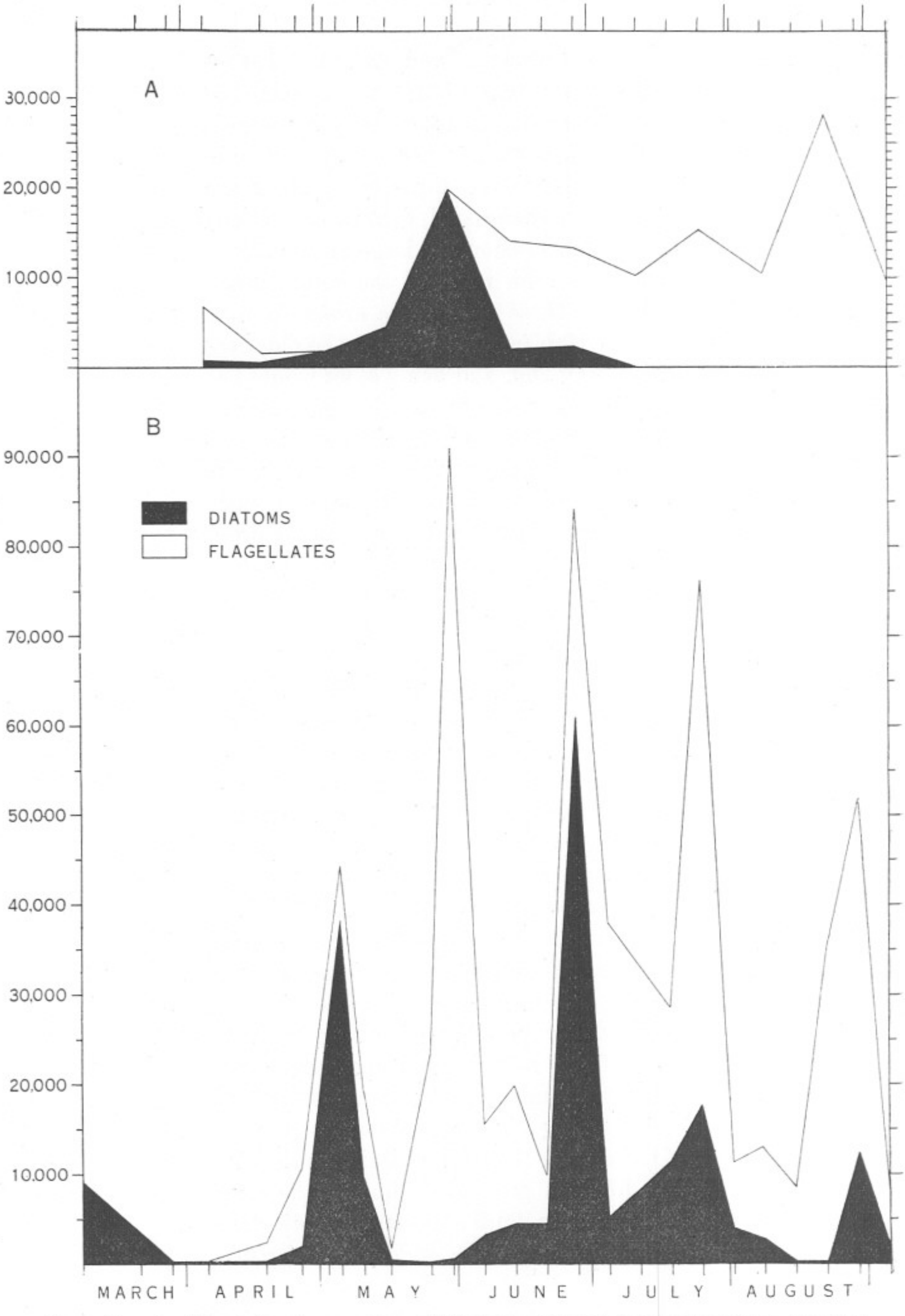
numbering over 10,000 at Station I and over 41,000 at Station II. Three weeks later another large catch (17,326) was obtained at Station I. In the first two cases this was due to a very large increase in the number of ova (with a ratio of not more than 70 per female) and an increased number of nauplii derived from these ova. Copepodite stages and adults, though present in numbers larger than usual, formed only a small percentage of the catch. On the second occasion of a large catch (May 23rd at Station I) copepodite stages formed the mass of the catch, Stages I, II and III being most abundant. These must have arisen from the ova liberated between May 2nd and 16th (about 9th) and the older copepodites would have been ova about May 2nd, and being older would have suffered more from natural mortality, the rate of which is high (p. 89).

Taking into account the length of life of the ovum as such and the time passed by Calanus in its nauplius stages, it is possible to say that, with one exception, at no time in the year were more copepodites found than could have been produced from the ova or nauplii present the requisite length of time before. The following hypothetical case may make this clear. If 10,000 ova were present on a certain date and 20,000 Stage II copepodites were found a fortnight later it might be argued that so many copepodites could not arise from so few ova and that, therefore, immigration must have occurred from some other locality where reproduction was in progress. It must be remembered, however, that whereas the ova remain as such for not more than 24 hours (Grobben, 1881) the copepodites remain in each stage for 3 days, and the effect will be an accumulation of copepodites. These will, of course, be subject to mortality.

The one exception referred to above occurred at Station I on May 16th when too few nauplii were present to produce the copepodites of May 23rd. This catch will have to be accepted as a "freak," since the number of ova present early in May was ample to produce the copepodites of 23rd.

At both stations the enormous increase found on May 2nd was of a temporary nature and died away as quickly as it had risen. This points to a very large mortality possibly correlated with the food supply. Farran (1927, p. 139) found reproduction was occurring generally in April and May, at which time numbers rose to ten times what they had been a few months before. Bigelow (1926, p. 168) records similar sudden increases in the number of Calanus in the Gulf of Maine during May.

Whereas Farran found a gradual decline in the numbers of Calanus subsequent to the increase in April and May, at both stations at which the decline occurred in this area it was sudden. Reference to the work of Marshall and Orr (1927, 1930) will show that the number of diatoms present during the spring increase of 1928 was over 5,000 cells per c.c. for some time and was over 12,500 cells per c.c. for a few days. Similar numbers were found in 1926 and 1927.



TEXT-FIG. 2.—Chart showing numbers of diatoms and of flagellates in 20 c.c. samples from the surface, A at Strachur and B at Keppel, from March until September, 1932. Other micro-organisms were negligible.

Text-Figure 2 shows the variation in the number of diatoms and in other microplankton at Keppel and at Strachur from March to September, 1932. I am indebted to Miss S. M. Marshall for the information expressed in this figure. It will be seen that though diatoms were spasmodically abundant during the spring and summer, on the whole numbers did not once reach those attained by the phytoplankton in the course of an ordinary spring increase and were, on the average, low for the whole season. The highest value reached at Keppel in 1932 was 3,000 cells per c.c. in June, and the spring increase figures were only 2,000 cells per c.c. It is possible, therefore, that under normal conditions the decline would have been as gradual as that found by Farran, and that the number present in the autumn of 1932 would have been similar to that of 1931.

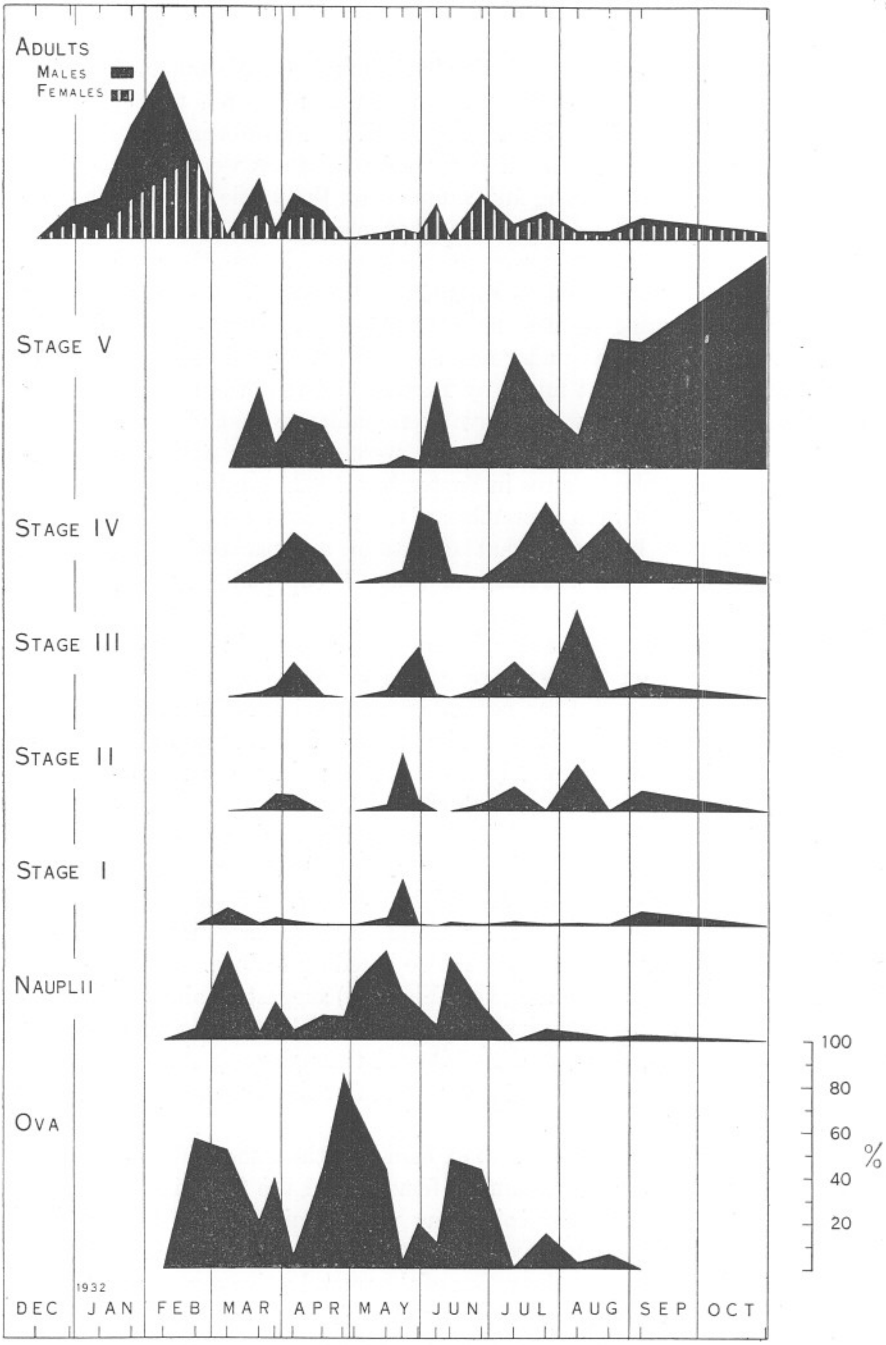
At Strachur (Station IV) diatoms were even less abundant (Text-Figure 2, A) and the Calanus in September, 1932, numbered about 1,000 compared with 10,000 in September of the previous year.

It has already been seen that as autumn approaches development is arrested and the Calanus remain as Stage V copepodites, mixed with a number of Stage IV and a very few adults.

The next point which arises is the appearance of three well defined breeding periods on the percentage composition chart (Plate II). This becomes more marked if the percentage composition of the catch during the reproductive season is separated into different stages and each is graphed individually (Text-Figures 3 and 4; in these figures certain details present in the chart, Plate II, which would only tend to confuse the issue, have been left out.) Here is plainly marked the succession of stages from ovum to adult in three successive breeding periods followed by the subsidiary ones at the end of the summer. This is not so obvious at Station IV where the results are confused by the large initial lag and a subsequent overlapping of the first two breeding periods.

The results from Station II (Text-Figure 4) suggest an almost diagrammatic accuracy. Each maximum of females is followed by a maximum of ova, and this maximum can be followed through each stage to adults, which attain their maximum at a month after the maximum of ova, and so on through the summer.

The difficulty which arises is to explain why there should be such a long interval between any maximum of females and the following maximum of ova, the latter actually coinciding with a minimum of females. It appears that the Calanus, having moulted into adults, require from three weeks to one month for maturation of the reproductive organs and for the transference of the spermatophores to the females, and that meanwhile they are subject to a high rate of mortality so that by the time that sexual maturity is reached comparatively few females remain. Thus the egg peak would coincide with the female minimum. The number of



TEXT-FIG. 3.—Diagram illustrating the succession of breeding periods at Station I (Garroch Head). Copepodite Stages IV and V occurring prior to February 22nd and ova and nauplii prior to February 8th have been omitted.

females then rises again a month later when these ova have completed their development.

This explanation appears satisfactory in its general application. If, however, we examine the curve for Station I (Plate II and Text-Figure 3) we find a number of inconsistencies with this hypothesis. Firstly, a secondary peak of ova is present at the end of the first breeding period. If this were the result of an almost immediate liberation of ova from these females which reached maturity on March 21st, it would leave only one week for the maturation of the reproductive organs and fertilisation of the females. This would appear to be too short, and, moreover, would result in continuous breeding throughout the reproductive season and a more or less constant representation of all stages throughout this period.

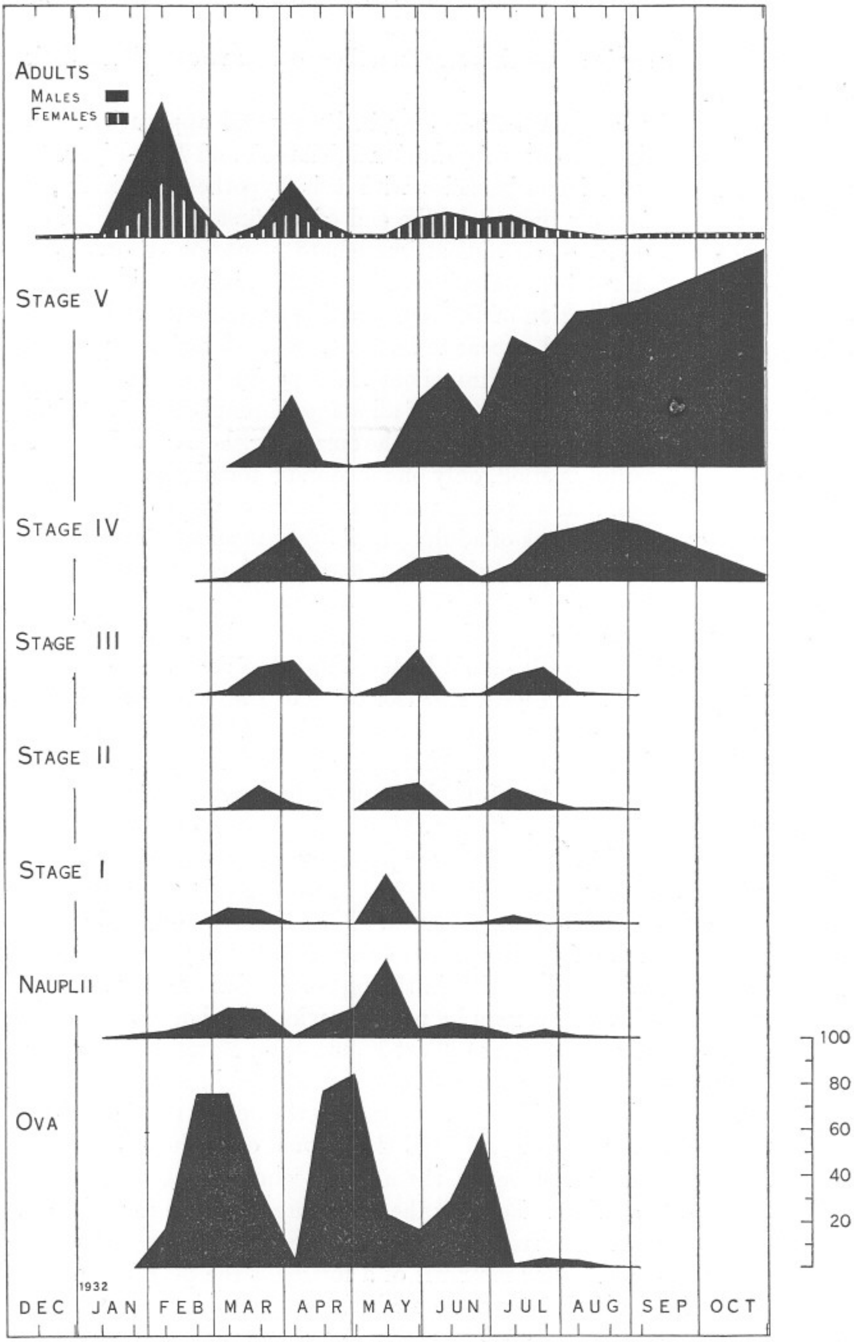
Though two peaks are thus present in the curves for the ova and nauplii during the first breeding period, only one is found a fortnight later in the Stage II copepodites, and a second reappears in the Stage V copepodites and adults. The second peak of adults (April 5th) has undoubtedly arisen from the ova of March 7th, and the ova of March 28th receive no distinct representation on these curves after Stage I copepodites ; neither do they appear to affect the curve for adults at all, these being at a minimum when the eggs of March 28th should be reaching adult stage.

From Table II it would appear that this catch of March 28th was in the nature of a " freak "—owing to the net passing through a swarm of Calanus—since, from March 7th until April 18th (neglecting March 28th), total numbers rose from 52 to 1,086 by more or less regular intervals of a few hundred each fortnight. This catch on March 28th contained 3,488 specimens and may be regarded as exceptionally and unexpectedly large.

A similar effect was produced at the end of the second breeding period (May 30th) when a minor peak occurred. It is, however, of less importance since it does not affect the curves of any of the other stages and may be regarded as a minor fluctuation in the representation of the ova.

A further question which may be raised is why ova should be present to so large an extent at Station II (Text-Figure 4) on March 21st if adults had died out by 7th and the new brood did not begin spawning until April 5th. From Table III it will be seen that the actual number of ova present on this date was only 117, and these could easily have been produced by two or three females of the autumn-winter stock which were still surviving at this time. Possibly they were producing a second brood.

It will have been seen from the Text-Figures and Plates that when catches are taken at regular intervals of a fortnight the period of reproduction can be divided into three main breeding periods, February–March, April–May, and June–July with a fourth subsidiary one early in August and that this can be applied in general to all stations. The main variations are in the number of subsidiary late summer broods at each



TEXT-FIG. 4.—Diagram illustrating the succession of breeding periods at Station II (Cock of Arran). Copepodite Stages IV and V occurring prior to March 7th, and ova and nauplii prior to February 8th have been omitted.

station (more numerous at Station I and of less importance at Station IV), and an overlapping of the first two breeding periods at Station IV owing to a lag in the starting of reproduction at this station. The cause of this has not yet been determined.

Comparison of the station inside the loch with those of the open waters showed that Calanus was still quite abundant in the early winter at Strachur when numbers outside had fallen to minimal values. This, however, was only a lag in the dying off of this population, since numbers in the loch were reduced to similar low values at a later date. Although Calanus at Station I was scarce by the middle of December it was not until late in March that it became scarce at Station IV. This lag was followed by a delay in the starting of reproduction, the first brood of eggs not appearing until the end of February, a fortnight after reproduction had begun at the stations in open waters.

Furthermore it can be stated that the enclosed waters of the loch do not form a breeding ground whence Calanus spreads to outside waters. If this had been the case evidence of such migration would have been found in the quarterly catches from Station VII and in the fortnightly catches from Station III. Those from the latter obviously followed those of Station II, and it has already been pointed out that both these stations are geographically similar.

Without more knowledge of the factors which control the development of the autumn-winter Calanus it is difficult to say why this lag occurred. That temperature is not directly concerned is fairly certain. It remains for future work to discover the actual cause.

It will have been seen that the results from this area confirm and elaborate the suggestions made by Farran (1911, p. 85) and Russell (1928, p. 444) on the course of the life cycle in Calanus.

It has been pointed out by Russell (1928, p. 434) that at certain times of the year Calanus may be found swarming at the surface during the day, even though it be a clear day with bright sunshine. This has been observed on several occasions in the Clyde Sea-Area. From March until June, and again later on, hauls at Stations I and II were divided at the 30-metre line, the object being to simplify counting by confining the diatoms to one part of the catch.

As it happened in this year diatoms were seldom rich enough to cause any difficulty of this nature. It will be noticed, however, from Tables II and III that at Station I on May 16th and at Station II on June 13th, more males, females, Stages V and IV copepodites were found in the upper 30 metres than below, a reversal of the usual condition. On both these occasions young stages and ova remained more abundant above the 30-metre line.

This will be discussed in a paper dealing with the vertical distribution of Calanus in this area.

SUMMARY.

1. Fortnightly samples were taken with a fine-meshed net in single vertical hauls at different positions in the Clyde Sea-Area.

2. Each stage of Calanus present, from ovum to adult, was counted, and charts were constructed expressing these results for one year as total numbers and as percentage composition.

3. Calanus passes the autumn and early winter mainly in its Stage V copepodite form.

4. In general, total numbers were high in September, 1931, and fell steadily to a minimum in March; in Loch Fyne the minimum occurred in April.

5. A sudden increase was observed in May and numbers rose to maximal values; the decline also was sudden.

6. Reproduction began in February and three plainly marked breeding periods were observed between February and July.

7. The time taken by the egg in developing into the adult was four weeks.

8. The total life of a Calanus during the summer was estimated to be about two and a half months; in winter it is five to six months.

9. In Loch Fyne a noticeable lag occurred during the winter and early spring.

10. The number of Calanus present in the autumn of 1932 was considerably less than at the same time in 1931. This may have been due to a shortage of food.

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TABLE I.

	STATION I.				STATION II.				STATION IV.			
Date.	Time of Day. a.m.	Depth in Metres.	Time of Haul. m.	s.	Time of Day. a.m.	Depth in Metres.	Time of Haul. m.	s.	Time of Day. p.m.	Depth in Metres.	Time of Haul. m.	s.
3/9/31	10.00	120	—		11.30	100	—		5.20	138	—	
15/9/31	9.45	105	3	20	11.25	140	4	00	5.15	130	4	30
1/10/31	9.45	110	3	35	11.30	140	3	50	4.30	150	3	50
21/10/31	9.45	120	*4	15	11.15	135	4	15	5.00	130	4	30
5/11/31	10.35	115	3	45	noon	112	3	35	4.50	132	4	20
16/11/31	10.30	109	3	40	11.40	165	4	50				
17/11/31									8.27 (a.m.)	136	4	15
30/11/31	9.15	110	3	45	10.50	155	4	50	4.15	130	4	50
14/12/31	9.26	110	4	05	11.15	154	4	20	4.32	131	5	ca.
30/12/31	9.05	113	3	45	10.10	160	5	30	5.10	128	3	40
11/1/32	9.50	120	4	00	11.30	155	3	50	4.15	129	4	15
25/1/32	9.10	120	4	00	10.30	165	5	30	3.50	134	4	05
8/2/32	9.50	110	*3	50	11.10	170	5	45	4.45	130	4	15
22/2/32	9.05	109	3	45	10.15	153	5	30				
23/2/32									8.00 (a.m.)	—	4	40
7/3/32	9.15	110	(a)3 (b)1	05 00	10.55	154	(a)4 (b)1	50 00	4.20	128	4	10
21/3/32	10.20	115	(a)3 (b)1	00 00	11.00	161	(a)6 (b)1	45 27	4.30	126	4	45
28/3/32	9.30	110	(a)4 (b)1	03 00								
5/4/32	9.15	109	(a)3 (b)1	20 00	11.15	162	(a)5 (b)1	10 00	5.00	131	4	45
18/4/32	8.20	110	(a)3 (b)1	05 00	9.55	116	(a)3 (b)1	15 00	3.10	131	4	35
27/4/32	8.50	115	(a)3 (b)1	40 25								
2/5/32	9.29	114	(a)3 (b)0	05 56	11.00	157	(a)4 (b)0	25 55	4.42	130	4	15
16/5/32	8.15	113	(a)3 (b)1	45 05	9.50	145	(a)4 (b)1	35 05	3.05	130	5	05
23/5/32	11.00	119	(a)3 (b)1	45 03								
30/5/32	8.20	110	(a)3 (b)1	00 00	9.45	166	(a)5 (b)1	35 00	6.30	130	5	15
7/6/32	9.00	118	(a)3 (b)1	40 05								
13/6/32	8.25	115	†4	30	9.55	159	(a)4 (b)1	30 00	3.15	131	5	25
27/6/32	10.20	112	4	55	12.10 (p.m.)	158	7	40	5.25	124	4	30
11/7/32	8.20	113	4	15	10.15	152	5	35	3.50	130	4	45
25/7/32	8.20	115	(a)3 (b)1	15 02	10.10	165	(a)4 (b)1	55 00	3.05	130	4	40
8/8/32	8.20	115	(a)3 (b)1	10 00	10.15	163	(a)4 (b)1	15 00	3.30	135	4	30
22/8/32	8.25	112	3	55	9.55	158	5	45	7.15	130	4	30
5/9/32	8.50	110	4	20	10.15	165	6	50	4.05	130	4	45
30/10/32	9.15	117	3	25	11.00	144	4	50	4.15	122	3	55

APPENDIX.

	STATION V.				STATION VI.				STATION VII.			
					p.m.				a.m.			
13/11/31	11.05 (a.m.)	92	2	50								
16/11/31					2.00	145	3	40				
17/11/31									10.25	60	1	45
22/2/32					12.20	125	3	35				
23/2/32									10.05	51	1	40
25/2/32	3.35 (p.m.)	89	3	30								
30/5/32					noon	117	(a)3 (b)1	25 00	p.m. 4.50	59	2	00
3/6/32	9.40 (a.m.)	90	(a)2 (b)1	25 00								
22/8/32					12.30	128	4	58	5.30	62	2	30
29/8/32	3.00 (p.m.)	88	3	20								

* Indicates that the haul was not vertical owing to state of the weather.

† Indicates that the closing apparatus failed to work and haul was not divided.

TAB

					Nauplii.			STAT
Date.		Ova.	I.	II.	III.	IV.	V.	VI.
3-9-31	No.	10	30	110	60	30	20	80
	%	*·7*	*2·1*	*7·6*	*4·2*	*2·1*	*1·4*	*5·5*
15-9-31	No.	1	–	–	1	2	–	–
	%	*·5*	–	–	*·5*	*1·0*	–	–
1-10-31	No.	50	2	1	3	3	–	–
	%	*44·2*	*1·8*	*·9*	*2·7*	*2·7*	–	–
21-10-31	No.	12	11	2	6	–	–	–
	%	*4·0*	*3·7*	*·7*	*2·0*	–	–	–
5-11-31	No.	–	1	–	5	6	2	3
	%	–	*1·9*	–	*9·3*	*11·1*	*3·7*	*5·6*
16-11-31	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–
30-11-31	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–
14-12-31	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–
29-12-31	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–
11-1-32	No.	–	2	–	7	–	–	–
	%	–	*3·5*	–	*12·1*	–	–	–
25-1-32	No.	1	–	–	1	–	–	–
	%	*2·5*	–	–	*2·5*	–	–	–
8-2-32	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–
22-2-32	No.	84	4	–	2	1	–	–
	%	*56·8*	*2·7*	–	*1·4*	*·7*	–	–
7-3-32	No. (1) (2)	$\left.\begin{matrix}8\\19\end{matrix}\right\}27$	$\left.\begin{matrix}-\\3\end{matrix}\right\}3$	– –	$\left.\begin{matrix}-\\5\end{matrix}\right\}5$	$\left.\begin{matrix}2\\3\end{matrix}\right\}5$	$\left.\begin{matrix}-\\2\end{matrix}\right\}2$	$\left.\begin{matrix}2\\3\end{matrix}\right\}5$
	%	*51·9*	*5·8*	–	*9·6*	*9·6*	*3·8*	*9·6*
21-3-32	No. (1) (2)	$\left.\begin{matrix}70\\46\end{matrix}\right\}116$	$\left.\begin{matrix}10\\1\end{matrix}\right\}11$	– –	$\left.\begin{matrix}-\\2\end{matrix}\right\}2$	$\left.\begin{matrix}-\\2\end{matrix}\right\}2$	$\left.\begin{matrix}-\\1\end{matrix}\right\}1$	$\left.\begin{matrix}-\\4\end{matrix}\right\}4$
	%	*21·0*	*2·0*	–	*·4*	*·4*	*·2*	*·7*
28-3-32	No. (1) (2)	$\left.\begin{matrix}250\\1150\end{matrix}\right\}1400$	$\left.\begin{matrix}30\\130\end{matrix}\right\}160$	$\left.\begin{matrix}-\\185\end{matrix}\right\}185$	$\left.\begin{matrix}10\\130\end{matrix}\right\}140$	$\left.\begin{matrix}5\\35\end{matrix}\right\}40$	$\left.\begin{matrix}-\\25\end{matrix}\right\}25$	$\left.\begin{matrix}5\\30\end{matrix}\right\}35$
	%	*40·1*	*4·6*	*5·3*	*4·0*	*1·1*	*·7*	*1·0*
5-4-32	No. (1) (2)	$\left.\begin{matrix}30\\19\end{matrix}\right\}49$	$\left.\begin{matrix}15\\2\end{matrix}\right\}17$	$\left.\begin{matrix}-\\1\end{matrix}\right\}1$	$\left.\begin{matrix}-\\5\end{matrix}\right\}5$	$\left.\begin{matrix}5\\3\end{matrix}\right\}8$	$\left.\begin{matrix}-\\2\end{matrix}\right\}2$	$\left.\begin{matrix}-\\3\end{matrix}\right\}3$
	%	*6·0*	*2·1*	*·1*	*·6*	*1·0*	*·2*	*·4*
18-4-32	No. (1) (2)	$\left.\begin{matrix}60\\420\end{matrix}\right\}480$	$\left.\begin{matrix}5\\25\end{matrix}\right\}30$	$\left.\begin{matrix}-\\35\end{matrix}\right\}35$	$\left.\begin{matrix}-\\45\end{matrix}\right\}45$	$\left.\begin{matrix}-\\5\end{matrix}\right\}5$	$\left.\begin{matrix}-\\5\end{matrix}\right\}5$	– –
	%	*44·1*	*2·8*	*3·2*	*4·1*	*·5*	*·5*	–
27-4-32	No. (1) (2)	$\left.\begin{matrix}138\\5570\end{matrix}\right\}5708$	$\left.\begin{matrix}90\\360\end{matrix}\right\}450$	$\left.\begin{matrix}-\\200\end{matrix}\right\}200$	$\left.\begin{matrix}-\\20\end{matrix}\right\}20$	$\left.\begin{matrix}-\\20\end{matrix}\right\}20$	$\left.\begin{matrix}-\\10\end{matrix}\right\}10$	$\left.\begin{matrix}1\\20\end{matrix}\right\}21$
	%	*85·3*	*6·7*	*3·0*	*·3*	*·3*	*·1*	*·3*
2-5-32	No. (1) (2)	$\left.\begin{matrix}14\\7635\end{matrix}\right\}7649$	$\left.\begin{matrix}15\\1785\end{matrix}\right\}1800$	$\left.\begin{matrix}-\\475\end{matrix}\right\}475$	$\left.\begin{matrix}-\\215\end{matrix}\right\}215$	$\left.\begin{matrix}1\\100\end{matrix}\right\}101$	$\left.\begin{matrix}-\\30\end{matrix}\right\}30$	$\left.\begin{matrix}-\\55\end{matrix}\right\}55$
	%	*71·8*	*16·9*	*4·5*	*2·0*	*·9*	*·3*	*·5*
16-5-32	No. (1) (2)	$\left.\begin{matrix}64\\1920\end{matrix}\right\}1984$	$\left.\begin{matrix}4\\420\end{matrix}\right\}424$	$\left.\begin{matrix}10\\630\end{matrix}\right\}640$	$\left.\begin{matrix}7\\370\end{matrix}\right\}377$	$\left.\begin{matrix}3\\200\end{matrix}\right\}203$	$\left.\begin{matrix}1\\40\end{matrix}\right\}41$	$\left.\begin{matrix}2\\90\end{matrix}\right\}92$
	%	*43·7*	*9·3*	*14·1*	*8·3*	*4·5*	*·9*	*2·0*
23-5-32	No. (1) (2)	$\left.\begin{matrix}340\\360\end{matrix}\right\}700$	$\left.\begin{matrix}150\\60\end{matrix}\right\}210$	$\left.\begin{matrix}90\\40\end{matrix}\right\}130$	$\left.\begin{matrix}960\\210\end{matrix}\right\}1170$	$\left.\begin{matrix}790\\140\end{matrix}\right\}930$	$\left.\begin{matrix}560\\110\end{matrix}\right\}670$	$\left.\begin{matrix}450\\70\end{matrix}\right\}520$
	%	*4·0*	*1·2*	*·7*	*6·8*	*5·4*	*3·9*	*3·0*
30-5-32	No. (1) (2)	$\left.\begin{matrix}370\\118\end{matrix}\right\}488$	$\left.\begin{matrix}324\\13\end{matrix}\right\}337$	$\left.\begin{matrix}2\\9\end{matrix}\right\}11$	$\left.\begin{matrix}4\\1\end{matrix}\right\}5$	– –	– –	– –
	%	*20·2*	*13·9*	*·5*	*·2*	–	–	–
7-6-32	No. (1) (2)	$\left.\begin{matrix}95\\370\end{matrix}\right\}465$	$\left.\begin{matrix}75\\100\end{matrix}\right\}175$	$\left.\begin{matrix}-\\25\end{matrix}\right\}25$	$\left.\begin{matrix}-\\30\end{matrix}\right\}30$	$\left.\begin{matrix}-\\20\end{matrix}\right\}20$	$\left.\begin{matrix}-\\5\end{matrix}\right\}5$	– –
	%	*11·4*	*4·3*	*·6*	*·7*	*·5*	*·1*	–
13-6-32	No.	670	270	60	90	70	20	–
	%	*47·9*	*19·3*	*4·3*	*6·4*	*5·0*	*1·4*	–
27-6-32	No.	475	80	20	15	20	15	15
	%	*43·4*	*7·3*	*1·8*	*1·4*	*1·8*	*1·4*	*1·4*
11-7-32	No.	20	–	–	–	–	–	–
	%	*1·2*	–	–	–	–	–	–
25-7-32	No. (1) (2)	$\left.\begin{matrix}10\\185\end{matrix}\right\}195$	$\left.\begin{matrix}-\\15\end{matrix}\right\}15$	$\left.\begin{matrix}-\\10\end{matrix}\right\}10$	$\left.\begin{matrix}5\\30\end{matrix}\right\}35$	– –	– –	– –
	%	*15·4*	*1·2*	*·8*	*2·8*	–	–	–
8-8-32	No. (1) (2)	$\left.\begin{matrix}9\\6\end{matrix}\right\}15$	$\left.\begin{matrix}-\\1\end{matrix}\right\}1$	$\left.\begin{matrix}-\\2\end{matrix}\right\}2$	$\left.\begin{matrix}-\\7\end{matrix}\right\}7$	$\left.\begin{matrix}-\\2\end{matrix}\right\}2$	$\left.\begin{matrix}-\\2\end{matrix}\right\}2$	$\left.\begin{matrix}-\\3\end{matrix}\right\}3$
	%	*3·2*	*·2*	*·4*	*1·5*	*·4*	*·4*	*·6*
22-8-32	No.	33	2	1	–	–	1	3
	%	*6·5*	*·4*	*·2*	–	–	*·2*	*·6*
5-9-32	No.	–	–	–	–		–	11
	%	–	–	–	–	–	–	*2·7*
30-10-32	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–

LE II.

ION I.

Copepodites.					Adults.		
I.	II.	III.	IV.	V	♀	♂	Total.
95 *6·6*	127 *8 8*	79 *5·5*	103 *7·0*	677 *47·0*	13 *·9*	7 *·5*	1441 *99·9*
– –	1 *·5*	5 *2·5*	35 *17·2*	147 *72·1*	10 *4·9*	2 *1·0*	204 *100·2*
1 *·9*	11 *9·7*	4 *3·5*	14 *12·4*	22 *19·5*	1 *·9*	1 *·9*	113 *100·1*
– –	1 *·3*	7 *2·4*	41 *13·8*	203 *68·1*	11 *3·7*	4 *1·3*	298 *100·0*
5 *9·3*	4 *7·4*	16 *29·7*	5 *9·3*	4 *7·4*	3 *5·6*	– –	54 *100·3*
– –	– –	2 *·7*	22 *7·4*	272 *91·0*	3 *1·0*	– –	299 *100·1*
– –	– –	– –	3 *3·7*	77 *96·3*	– –	– –	80 *100·0*
– –	– –	– –	– –	4 *100·0*	– –	– –	4 *100·0*
– –	– –	– –	1 *7·1*	11 *78·6*	1 *7·1*	1 *7·1*	14 *99·9*
– –	– –	– –	2 *3·5*	37 *63·6*	2 *3·5*	8 *13·8*	58 *100·0*
– –	– –	– –	– –	18 *45·0*	7 *17·5*	13 *32·5*	40 *100·0*
– –	– –	– –	– –	4 *26·7*	4 *26·7*	7 *46·7*	15 *100·1*
– –	– –	– –	– –	– –	55 *37·2*	2 *1·4*	148 *100·2*
$\left.\begin{matrix}2\\2\end{matrix}\right\}4$ *7·7*	– – –	– – –	– – –	– – –	$\left.\begin{matrix}1\\-\end{matrix}\right\}1$ *1·9*	– – –	$\left.\begin{matrix}15\\37\end{matrix}\right\}52$ *99·9*
$\left.\begin{matrix}-\\5\end{matrix}\right\}5$ *·9*	$\left.\begin{matrix}6\\2\end{matrix}\right\}8$ *1·5*	$\left.\begin{matrix}9\\2\end{matrix}\right\}11$ *2·0*	$\left.\begin{matrix}44\\1\end{matrix}\right\}45$ *8·2*	$\left.\begin{matrix}192\\2\end{matrix}\right\}194$ *35·5*	$\left.\begin{matrix}59\\3\end{matrix}\right\}62$ *11·4*	$\left.\begin{matrix}82\\3\end{matrix}\right\}85$ *15·6*	$\left.\begin{matrix}472\\74\end{matrix}\right\}546$ *99·8*
$\left.\begin{matrix}-\\121\end{matrix}\right\}121$ *3·5*	$\left.\begin{matrix}3\\254\end{matrix}\right\}257$ *7·4*	$\left.\begin{matrix}73\\95\end{matrix}\right\}168$ *4·8*	$\left.\begin{matrix}393\\25\end{matrix}\right\}418$ *12·0*	$\left.\begin{matrix}352\\12\end{matrix}\right\}364$ *10·4*	$\left.\begin{matrix}74\\1\end{matrix}\right\}75$ *2·2*	$\left.\begin{matrix}98\\2\end{matrix}\right\}100$ *2·9*	$\left.\begin{matrix}1293\\2195\end{matrix}\right\}3488$ *100·0*
$\left.\begin{matrix}1\\14\end{matrix}\right\}15$ *1·9*	$\left.\begin{matrix}1\\54\end{matrix}\right\}55$ *6·8*	$\left.\begin{matrix}5\\123\end{matrix}\right\}128$ *15·7*	$\left.\begin{matrix}60\\117\end{matrix}\right\}177$ *21·8*	$\left.\begin{matrix}135\\56\end{matrix}\right\}191$ *23·5*	$\left.\begin{matrix}75\\6\end{matrix}\right\}81$ *10·0*	$\left.\begin{matrix}57\\24\end{matrix}\right\}81$ *10·0*	$\left.\begin{matrix}384\\429\end{matrix}\right\}813$ *100·1*
$\left.\begin{matrix}-\\3\end{matrix}\right\}3$ *·3*	– – –	$\left.\begin{matrix}6\\3\end{matrix}\right\}9$ *·8*	$\left.\begin{matrix}120\\11\end{matrix}\right\}131$ *12·0*	$\left.\begin{matrix}185\\21\end{matrix}\right\}206$ *19·0*	$\left.\begin{matrix}95\\4\end{matrix}\right\}99$ *9·1*	$\left.\begin{matrix}37\\2\end{matrix}\right\}39$ *3·6*	$\left.\begin{matrix}508\\579\end{matrix}\right\}1087$ *100·0*
$\left.\begin{matrix}4\\30\end{matrix}\right\}34$ *·5*	$\left.\begin{matrix}2\\10\end{matrix}\right\}12$ *·2*	– – –	$\left.\begin{matrix}16\\-\end{matrix}\right\}16$ *·2*	$\left.\begin{matrix}95\\8\end{matrix}\right\}103$ *1·5*	$\left.\begin{matrix}46\\1\end{matrix}\right\}47$ *·7*	$\left.\begin{matrix}16\\-\end{matrix}\right\}16$ *·2*	$\left.\begin{matrix}408\\6249\end{matrix}\right\}6657$ *99·3*
$\left.\begin{matrix}-\\55\end{matrix}\right\}55$ *·5*	$\left.\begin{matrix}1\\15\end{matrix}\right\}16$ *·2*	$\left.\begin{matrix}-\\1\end{matrix}\right\}1$ –	$\left.\begin{matrix}6\\1\end{matrix}\right\}7$ *·1*	$\left.\begin{matrix}112\\17\end{matrix}\right\}129$ *1·2*	$\left.\begin{matrix}92\\12\end{matrix}\right\}104$ *1·0*	$\left.\begin{matrix}19\\5\end{matrix}\right\}24$ *·2*	$\left.\begin{matrix}260\\10401\end{matrix}\right\}10661$ *100·1*
$\left.\begin{matrix}3\\146\end{matrix}\right\}149$ *3·3*	$\left.\begin{matrix}-\\125\end{matrix}\right\}125$ *2·8*	$\left.\begin{matrix}2\\125\end{matrix}\right\}127$ *2·8*	$\left.\begin{matrix}11\\126\end{matrix}\right\}137$ *3·0*	$\left.\begin{matrix}22\\68\end{matrix}\right\}90$ *2·0*	$\left.\begin{matrix}36\\105\end{matrix}\right\}141$ *3·1*	$\left.\begin{matrix}4\\7\end{matrix}\right\}11$ *·2*	$\left.\begin{matrix}169\\4372\end{matrix}\right\}4541$ *100·0*
$\left.\begin{matrix}2490\\1040\end{matrix}\right\}3530$ *20·4*	$\left.\begin{matrix}3360\\1060\end{matrix}\right\}4420$ *25·5*	$\left.\begin{matrix}1840\\520\end{matrix}\right\}2360$ *13·6*	$\left.\begin{matrix}770\\143\end{matrix}\right\}913$ *5·3*	$\left.\begin{matrix}890\\86\end{matrix}\right\}976$ *5·6*	$\left.\begin{matrix}730\\27\end{matrix}\right\}757$ *4·4*	$\left.\begin{matrix}40\\-\end{matrix}\right\}40$ *·2*	$\left.\begin{matrix}13460\\3866\end{matrix}\right\}17326$ *100·0*
$\left.\begin{matrix}2\\5\end{matrix}\right\}7$ *·3*	$\left.\begin{matrix}32\\94\end{matrix}\right\}126$ *5·2*	$\left.\begin{matrix}332\\200\end{matrix}\right\}532$ *22·0*	$\left.\begin{matrix}634\\118\end{matrix}\right\}752$ *31·1*	$\left.\begin{matrix}58\\30\end{matrix}\right\}88$ *3·6*	$\left.\begin{matrix}42\\22\end{matrix}\right\}64$ *2·6*	$\left.\begin{matrix}8\\-\end{matrix}\right\}8$ *·3*	$\left.\begin{matrix}1808\\610\end{matrix}\right\}2418$ *99·9*
$\left.\begin{matrix}-\\5\end{matrix}\right\}5$ *·1*	$\left.\begin{matrix}5\\5\end{matrix}\right\}10$ *·2*	$\left.\begin{matrix}40\\15\end{matrix}\right\}55$ *1·3*	$\left.\begin{matrix}1035\\89\end{matrix}\right\}1124$ *26·9*	$\left.\begin{matrix}1515\\37\end{matrix}\right\}1552$ *38·0*	$\left.\begin{matrix}560\\3\end{matrix}\right\}563$ *13·8*	$\left.\begin{matrix}65\\-\end{matrix}\right\}65$ *1·6*	$\left.\begin{matrix}3390\\704\end{matrix}\right\}4094$ *99·5*
20 *1·4*	– –	– –	53 *3·8*	125 *8·9*	15 *1·1*	5 *·4*	1398 *99·9*
8 *·7*	39 *3·6*	43 *3·9*	28 *2·6*	120 *11·0*	205 *18·7*	12 *1·1*	1095 *100·1*
32 *1·9*	183 *10·8*	264 *15·6*	219 *13·0*	852 *50·4*	92 *5·4*	28 *1·7*	1690 *100·0*
$\left.\begin{matrix}10\\-\end{matrix}\right\}10$ *·8*	$\left.\begin{matrix}15\\-\end{matrix}\right\}15$ *1·2*	$\left.\begin{matrix}37\\1\end{matrix}\right\}38$ *3·0*	$\left.\begin{matrix}430\\11\end{matrix}\right\}441$ *34·8*	$\left.\begin{matrix}342\\9\end{matrix}\right\}351$ *27·7*	$\left.\begin{matrix}129\\5\end{matrix}\right\}134$ *10·6*	$\left.\begin{matrix}24\\-\end{matrix}\right\}24$ *1·9*	$\left.\begin{matrix}1002\\266\end{matrix}\right\}1268$ *100·2*
$\left.\begin{matrix}1\\6\end{matrix}\right\}7$ *1·5*	$\left.\begin{matrix}76\\23\end{matrix}\right\}99$ *21·2*	$\left.\begin{matrix}171\\9\end{matrix}\right\}180$ *38·4*	$\left.\begin{matrix}59\\5\end{matrix}\right\}64$ *13·7*	$\left.\begin{matrix}63\\4\end{matrix}\right\}67$ *14·3*	$\left.\begin{matrix}13\\2\end{matrix}\right\}15$ *3·2*	$\left.\begin{matrix}4\\-\end{matrix}\right\}4$ *·9*	$\left.\begin{matrix}396\\72\end{matrix}\right\}468$ *99·9*
6 *1·2*	2 *·4*	15 *3·0*	135 *26·8*	287 *56·9*	10 *2·0*	9 *1·8*	504 *100·0*
26 *6·3*	38 *9·2*	27 *6·6*	42 *10·2*	228 *55·5*	29 *7·0*	10 *2·4*	411 *99·9*
– –	– –	– –	11 *3·1*	329 *93·5*	12 *3·4*	– –	352 *100·0*

TAB

STAT

Date.		Ova.	I.	II.	Nauplii. III.	IV.	V.	VI.
3-9-31	No.	970	–	–	380	–	–	–
	%	*45·5*	–	–	*17·8*	–	–	–
15-9-31	No.	–	–	–	79	2	–	1
	%	–	–	–	*2·1*	*·1*	–	–
1-10-31	No.	25	–	–	25	–	–	–
	%	*·5*	–	–	*·5*	–	–	–
21-10-31	No.	3	–	3	3	–	–	–
	%	*·1*	–	*·1*	*·1*	–	–	–
5-11-31	No.	–	–	–	–	–	–	–
		–	–	–	–	–	–	–
16-11-31	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–
30-11-31	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–
14-12-31	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–
30-12-31	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–
11-1-32	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–
25-1-32	No.	–	1	–	2	–	–	–
	%	–	*·5*	–	*1·0*	–	–	–
8-2-32	No.	41	6	–	1	–	–	–
	%	*17·6*	*2·6*	–	*·4*	–	–	–
22-2-32	No.	231	8	–	8	1	1	2
	%	*76·0*	*2·6*	–	*2·6*	*·4*	*·4*	*·7*
7-3-32	No. (1)	–	–	–	–	–	–	–
	(2)	119 } 119	4 } 4	4 } 4	4 } 4	5 } 5	1 } 1	·3 } 3
	%	*75·8*	*2·6*	*2·6*	*2·6*	*3·2*	*·6*	*1·9*
21-3-32	No. (1)	–	–	–	–	–	–	–
	(2)	117 } 117	10 } 10	9 } 9	11 } 11	4 } 4	4 } 4	5 } 5
	%	*34·0*	*2·9*	*2·6*	*3·2*	*1·2*	*1·2*	*1·5*
5-4-32	No. (1)	4	–	–		–		
	(2)	13 } 17	3 } 3	1 } 1	–	1 } 1	–	–
	%	*3·4*	*·6*	*·2*	–	*·2*	–	–
18-4-32	No. (1)	33	3	–	–	–	–	–
	(2)	313 } 346	15 } 18	12 } 12	3 } 3	2 } 2	1 } 1	–
	%	*77·2*	*4·0*	*2·7*	*·7*	*·5*	*·2*	–
2-5-32	No. (1)	22	13	1	–	–	–	–
	(2)	34600 } 34622	3920 } 3933	1240 } 1241	190 } 190	70 } 70	50 } 50	50 } 50
	%	*84·3*	*9·6*	*3·0*	*·5*	*·2*	*·1*	*·1*
16-5-32	No. (1)	506	148	76	92	44	20	28
	(2)	370 } 876	90 } 238	250 } 326	180 } 272	90 } 134	130 } 150	140 } 168
	%	*23·6*	*6·4*	*8·8*	*7·3*	*3·6*	*4·0*	*4·5*
30-5-32	No. (1)	370	57	–	–			
	(2)	177 } 547	33 } 90	30 } 30	13 } 13	–	–	–
	%	*16·9*	*2·8*	*·9*	*·4*	–	–	–
13-6-32	No. (1)	178	66	2	–	–	–	–
	(2)	320 } 498	22 } 88	10 } 12	6 } 6	1 } 1	1 } 1	–
	%	*29·5*	*5·2*	*·7*	*·4*	*·1*	*·1*	–
27-6-32	No.	582	32	6	4	–	–	8
	%	*58·4*	*3·2*	*·6*	*·4*	–	–	*·8*
11-7-32	No.	31	1	1	7	6	6	6
	%	*1·6*	–	–	*·4*	*·3*	*·3*	*·3*
25-7-32	No. (1)	13	3	–	1			
	(2)	40 } 53	16 } 19	12 } 12	16 } 17	–	–	–
	%	*4·1*	*1·5*	*·9*	*1·3*	–	–	–
8-8-32	No. (1)	19	2	–	–	–		–
	(2)	27 } 46	6 } 8	3 } 3	8 } 8	1 } 1	–	2 } 2
	%	*2·9*	*·5*	*·2*	*·5*	–	–	*·1*
22-8-32	No.	14	2	2	2	–	–	–
	%	*·6*	*·1*	*·1*	*·1*	–	–	–
5-9-32	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–
30-10-32	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–

LE III

ION II

Copepodites.					Adults.		
I.	II.	III.	IV.	V.	♀	♂	Total.
–	3	32	387	334	19	10	2135
–	*·1*	*1·6*	*18·1*	*15·6*	*·9*	*·5*	*100·1*
–	19	179	660	2876	19	8	3843
–	*·5*	*4·7*	*17·2*	*74·9*	*·5*	*·2*	*100·2*
–	–	20	395	4320	20	5	4810
–	–	*·4*	*8·2*	*89·9*	*·4*	*·1*	*100·1*
–	–	–	135	2398	10	–	2552
–	–	–	*5·3*	*94·0*	*·4*	–	*100·0*
–	–	1	15	134	5	–	155
–	–	*·7*	*9·7*	*86·5*	*3·2*	–	*100·1*
–	–	–	190	5975	10	–	6175
–	–	–	*3·1*	*96·8*	*·2*	–	*100·1*
–	–	–	64	2038	4	2	2108
–	–	–	*3·0*	*96·7*	*·2*	*·1*	*100·0*
–	–	–	3	176	2	–	181
–	–	–	*1·7*	*97·2*	*1·1*	–	*100·0*
–	–	–	18	968	6	9	1001
–	–	–	*1·8*	*96·8*	*·6*	*·9*	*100·1*
–	–	–	3	506	8	25	542
–	–	–	*·5*	*93·5*	*1·5*	*4·6*	*100·1*
–	–	–	2	137	13	51	206
–	–	–	*1·0*	*66·5*	*6·3*	*24·8*	*100·1*
–	–	–	–	45	58	82	233
–	–	–	–	*19·3*	*24·9*	*35·2*	*100·0*
–	–	–	–	2	39	12	304
–	–	–	–	*·7*	*12·8*	*3·9*	*100·1*
–	–	3	2	–	–	–	5
11 } 11	1 } 1	– } 3	– } 2	–	–	–	152 } 157
7·0	*·6*	*1·9*	*1·3*	–	–	–	*100·1*
–	–	6	24	27	9	12	78
20 } 20	36 } 36	35 } 41	13 } 37	2 } 29	– } 9	– } 12	266 } 344
5·8	*10·5*	*11·9*	*10·8*	*8·4*	*2·6*	*3·5*	*100·1*
	–	1	19	102	55	59	240
–	14 } 14	75 } 76	87 } 106	55 } 157	6 } 61	7 } 66	262 } 502
–	*2·8*	*15·1*	*21·1*	*31·3*	*12·1*	*13·1*	*99·9*
–		–	3	4	11	11	65
2 } 2	–	4 } 4	8 } 11	10 } 14	4 } 15	9 } 20	383 } 448
·5	–	*·9*	*2·5*	*3·1*	*3·3*	*4·5*	*100·1*
–	–	–	3	219	520	98	876
17 } 17	17 } 17	15 } 15	1 } 4	7 } 226	32 } 552	20 } 118	40229 } 41105
–	–	–	–	*·6*	*1·3*	*·3*	*100·0*
54	90	52	30	96	41	23	1400
750 } 804	240 } 330	119 } 171	33 } 63	3 } 99	8 } 49	6 } 29	2309 } 3709
21·7	*8·9*	*4·6*	*1·7*	*2·7*	*1·3*	*·8*	*99·9*
–	–	10	97	897	280	3	1714
10 } 10	380 } 380	617 } 627	223 } 320	33 } 930	3 } 283	– } 3	1519 } 3233
·3	*11·7*	*19·4*	*9·9*	*28·8*	*8·8*	*·1*	*100·0*
–		–	19	251	17	1	534
1 } 1	–	3 } 3	176 } 195	446 } 697	153 } 170	18 } 19	1157 } 1691
·1	–	*·2*	*11·5*	*41·2*	*10·6*	*1·1*	*100·7*
7	18	6	20	226	59	28	996
·7	*1·8*	*·6*	*2·0*	*22·7*	*5·9*	*2·8*	*99·9*
74	186	174	163	1138	149	51	1993
3·7	*9·3*	*8·7*	*8·2*	*57·1*	*7·5*	*2·6*	*100·0*
–	–	14	161	617	51	7	867
3 } 3	59 } 59	141 } 155	107 } 268	36 } 653	– } 51	4 } 11	434 } 1301
·2	*4·5*	*11·9*	*20·6*	*50·2*	*3·9*	*·8*	*99·9*
–	–	6	351	1039	35	11	1463
6 } 6	5 } 5	15 } 21	21 } 372	33 } 1072	3 } 38	– } 11	130 } 1593
·4	*·3*	*1·3*	*23·4*	*67·3*	*2·4*	*·7*	*100·0*
14	18	6	650	1638	26	6	2378
·6	*·8*	*·3*	*27·3*	*68·9*	*1·1*	*·3*	*100·2*
–	–	5	675	2015	50	15	2760
–	–	*·2*	*24·5*	*73·0*	*1·8*	*·5*	*100·0*
–	–	–	22	755	18	–	795
–	–		*2·8*	*94·9*	*2·3*	–	*100·0*

TAB

STAT

Date.		Ova.	Nauplii. I.	II.	III.	IV.	V.	VI
3-9-31	No.	40	30	20	150	170	100	80
	%	*·4*	*·3*	*·2*	*1·4*	*1·5*	*·9*	*·7*
15-9-31	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–
1-10-31	No.	100	–	–	50	10	–	–
	%	*·8*	–	–	*·4*	*·1*	–	–
21-10-31	No.	14	21	–	7	–	–	–
	%	*·2*	*·3*	–	*·1*	–	–	–
5-11-31	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–
17-11-31	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–
30-11-31	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–
14-12-31	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–
29-12-31	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–
11-1-32	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–
25-1-32	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–
8-2-32	No.	20	–	–	–	–	–	–
	%	*·7*	–	–	–	–	–	–
23-2-32	No.	9	–	–	–	–	–	–
	%	*·7*	–	–	–	–	–	–
7-3-32	No.	156	19	4	3	2	–	–
	%	*37·0*	*4·5*	*1·0*	*·7*	*·5*	–	–
21-3-32	No.	226	54	66	16	1	–	–
	%	*58·7*	*14·0*	*17·1*	*4·2*	*·3*	–	–
5-4-32	No.	103	5	27	20	3	2	2
	%	*53·4*	*2·6*	*14·0*	*10·4*	*1·6*	*1·0*	*1·0*
18-4-32	No.	59	22	9	4	2	1	1
	%	*38·1*	*14·2*	*5·8*	*2·6*	*1·3*	*·6*	*·6*
2-5-32	No.	406	25	8	3	2	4	8
	%	*74·9*	*4·6*	*1·5*	*·6*	*·4*	*·7*	*1·5*
16-5-32	No.	150	50	70	80	100	60	50
	%	*7·1*	*2·4*	*3·3*	*3·8*	*4·8*	*2·9*	*2·4*
30-5-32	No.	455	295	65	20	25	15	15
	%	*37·5*	*24·4*	*5·4*	*1·7*	*2·1*	*1·2*	*1·2*
13-6-32	No.	990	115	40	25	20	15	30
	%	*47·6*	*5·5*	*1·9*	*1·2*	*·9*	*·7*	*1·4*
27-6-32	No.	1800	350	165	90	30	40	55
	%	*58·2*	*11·3*	*5·3*	*2·9*	*1·0*	*1·3*	*1·8*
11-7-32	No.	49	9	6	4	3	2	1
	%	*2·2*	*·4*	*·3*	*·2*	*·1*	*·1*	–
25-7-32	No.	3	–	–	–	–	–	–
	%	*·1*	–	–	–	–	–	–
8-8-32	No.	15	8	3	–	–	–	–
	%	*·7*	*·4*	*·1*	–	–	–	–
22-8-32	No.	3	–	–	–	–	–	–
	%	*·3*	–	–	–	–	–	–
5-9-32	No.	9	3	2	1	–	–	–
	%	*1·0*	*·3*	*·2*	*·1*	–	–	–
30-10-32	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–

TAB

STAT

Date.		Ova.	Nauplii. I.	II.	III.	IV.	V.	VI.
13-11-31	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–
25-2-32	No.	2	1	–	3	–	–	1
	%	*25·0*	*12·5*	–	*37·5*	–	–	*12·5*
3-6-32	No.	921	303	120	4	–	–	2
	%	*60·7*	*20·0*	*7·9*	*·3*	–	–	*·1*
29-8-32	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–

STAT

16-11-31	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–
22-2-32	No.	155	24	–	34	29	20	56
	%	*43·6*	*6·8*	–	*9·6*	*8·2*	*5·6*	*15·8*
30-5-32	No.	288	74	15	–	–	–	–
	%	*13·4*	*3·4*	*·7*	–	–	–	–
22-8-32	No.	–	1	1	2	–	2	5
	%	–	*·2*	*·2*	*·3*	–	*·3*	*·9*

STAT

17-11-31	No.	–	–	–	1		–	–
	%	–	–	–	*10·0*	–	–	–
23-2-32	No.	2	–	–	–	–	1	1
	%	*20·0*	–	–	–	–	*10·0*	*10·0*
30-5-32	No	5	5	–	15	15	20	25
	%	*·1*	*·1*	–	*·4*	*·4*	*·6*	*·7*
22-8-32	No	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–

LE IV.

ION IV.

Copepodites.					Adults.		
I.	II.	III.	IV.	V.	♀	♂	Total.
120	140	170	90	9960	–	–	11070
1·1	*1·3*	*1·5*	*·8*	*90·0*	–	–	*100·1*
20	10	30	90	8310	30	–	8490
·2	*·1*	*·4*	*1·1*	*97·9*	*·4*	–	*100·1*
–	–	–	10	11970	50	10	12200
–	–	–	*·1*	*98·1*	*·4*	*·1*	*100·0*
–	7	–	7	7650	7	–	7713
–	*·1*	–	*·1*	*99·2*	*·1*	–	*100·1*
–	–	–	10	8290	10	–	8310
–	–	–	*·1*	*99·8*	*·1*	–	*100·0*
–	–	–	30	7420	–	–	7450
–	–	–	*·4*	*99·6*	–	–	*100·0*
–	–	–	15	5120	5	–	5140
–	–	–	*·3*	*99·6*	*·1*	–	*100·0*
–	–	–	30	3750	–	–	3780
–	–	–	*·8*	*99·2*	–	–	*100·0*
–	–	–	7	3087	10	10	3114
–	–	–	*·2*	*99·1*	*·3*	*·3*	*99·9*
–	–	–	2	2070	4	10	2086
–	–	–	*·1*	*99·3*	*·2*	*·5*	*100·1*
–	–	–	8	2685	37	128	2858
–	–	–	*·3*	*93·9*	*1·3*	*4·5*	*100·0*
–	–	–	10	2515	58	348	2951
–	–	–	*·3*	*85·3*	*1·9*	*11·8*	*100·0*
–	–	–	2	1056	28	113	1208
–	–	–	*·2*	*87·4*	*2·3*	*9·4*	*100·0*
1	–	–	–	142	46	48	421
·2	–	–	–	*33·8*	*10·9*	*11·4*	*100·0*
–	–	–	1	7	8	6	385
–	–	–	*·3*	*1·8*	*2·1*	*1·6*	*100·1*
10	1	–	1	8	8	3	193
5·2	*·5*	–	*·5*	*4·1*	*4·1*	*1·6*	*100·0*
–	3	2	10	22	17	3	155
–	*1·9*	*1·3*	*6·5*	*14·2*	*11·0*	*1·9*	*100·0*
6	1	5	38	21	13	2	542
1·1	*·2*	*·9*	*7·0*	*3·9*	*2·4*	*·4*	*100·1*
56	187	796	314	122	38	28	2101
2·7	*8·9*	*37·9*	*14·9*	*5·8*	*1·8*	*1·3*	*100·0*
22	53	44	39	132	16	13	1209
1·8	*4·4*	*3·6*	*3·2*	*10·9*	*1·3*	*1·1*	*99·8*
70	40	30	80	501	102	17	2075
3·4	*1·9*	*1·4*	*3·8*	*24·1*	*4·9*	*·8*	*99·5*
60	93	93	36	177	102	3	3094
1·9	*3·0*	*3·0*	*1·2*	*5·7*	*3·3*	*·1*	*100·0*
13	21	104	326	1537	127	13	2218
·6	*·9*	*4·7*	*14·7*	*69·4*	*5·7*	*·6*	*99·9*
–	3	27	682	1520	111	4	2350
–	*·1*	*1·1*	*29·0*	*64·7*	*4·7*	*·2*	*99·9*
–	1	–	610	1442	36	3	2115
–	–	–	*28·8*	*68·1*	*1·7*	*·1*	*99·9*
–	–	2	311	743	16	2	1077
–	–	*·2*	*28·9*	*69·0*	*1·5*	*·2*	*100·1*
–	4	2	290	609	19	2	941
–	*·5*	*·2*	*30·8*	*64·7*	*2·0*	*·2*	*100·0*
–	–	–	96	1110	5	1	1212
–	–	–	*7·9*	*91·6*	*·4*	*·1*	*100·0*

LE V.

ION V.

Copepodites.					Adults		
I.	II.	III.	IV.	V.	♀	♂	Total.
–	–	2	4	22	1	–	29
–	–	*6·9*	*13·8*	*75·9*	*3·5*	–	*100·1*
–	–	–	–	–	1	–	8
–	–	–	–	–	*12·5*	–	*100·0*
2	16	59	53	15	18	1	1514
·1	*1·1*	*3·9*	*3·5*	*1·0*	*1·2*	*·1*	*99·9*
–	–	12	64	90	11	2	179
–	–	*6·7*	*35·8*	*50·3*	*6·1*	*1·1*	*100·0*
ION VI.							
–	–	1	20	625	2	–	648
–	–	*·1*	*3·1*	*96·5*	*·3*	–	*100·0*
12	–	–	–	3	8	14	355
3·4	–	–	–	*·8*	*2·3*	*3·9*	*100·0*
5	81	412	607	418	247	8	2155
·2	*3·8*	*19·1*	*28·2*	*19·4*	*11·5*	*·4*	*100·1*
10	31	27	89	389	16	6	579
1·7	*5·4*	*4·7*	*15·4*	*67·2*	*2·8*	*1·0*	*100·1*
ION VII							
1	–	–	–	8	–	–	10
10·0	–	–	–	*80·0*	–	–	*100·0*
–	–	–	–	5	–	1	10
–	–	–	–	*50·0*	–	*10·0*	*100·0*
165	485	1610	930	74	2	1	3352
4·9	*14·5*	*48·0*	*27·8*	*2·2*	*·1*	–	*99·8*
–	6	10	12	72		2	103
–	*5·8*	*9·7*	*11·7*	*69·9*	*1·0*	*1·9*	*100·0*

On the Biology of *Calanus finmarchicus*. II. Seasonal Variations in the Size of *Calanus finmarchicus* in the Clyde Sea-Area.

By

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With Eight Figures in the Text.

CONTENTS.

Introduction.

The size of copepods varies considerably both from place to place and also during the course of the year. Several hypotheses have been put forward to explain this fact.

The variations in size of the same species from different localities or depths are sometimes correlated with slight morphological differences, and this has led Steuer (1925, 1931, 1932) to suppose that the differences indicate geographical or habitat races and that the species may be in process of splitting up into several. The larger varieties are commonly found in the colder part of the range and the smaller in the warmer part, but this does not invariably hold. On the other hand, a single catch of copepods sometimes shows animals of such a great range of size that some observers (Sewell, 1912; Gurney, 1929) think that they cannot have been produced from the previous developmental stage by one moult only and have supposed that an extra moult must take place to account for the larger specimens or a moult be missed to account for the smaller.

It was therefore thought of interest to measure samples of *Calanus finmarchicus* from several stations in the Clyde Sea-Area over the course of a year to find out what amount of size variation occurred.

The Calanus used for the purpose were those taken by Dr. A. G. Nicholls in his fortnightly hauls from three different stations in the Clyde

Sea-Area and the preceding paper must be referred to for the details about the stations worked and hauls taken. The Calanus had already been picked out from the catches and the developmental stages separated and I am much indebted to him for the use of this prepared material.

Only adults (male and female), Stage V, and Stage IV Calanus were measured since it was thought that this would be enough to show variations clearly. The length measured was that of the cephalothorax and in the curves of Figures 2, 4, and 6 it is the median length which is graphed. None of the stages chosen was present in sufficiently large numbers for measurement during the whole year and it is unfortunate that at two of the stations adults were lacking during one of the most interesting times of the year. The number aimed at for measurement was in most cases about a hundred and when the catch was a large one it was sub-sampled. The adults often fell short of this number however, and, during the summer, vertical hauls with a one metre stramin net were also made at each station and the adults picked out and measured. Such hauls were not used for Stage V because it was thought that a few of the smaller specimens might escape through the meshes of the net and so give a false impression of the size. Towards the end of the summer when female Calanus were small in size a few of these too may have been lost in this way, but the number would be too small to affect the results appreciably.

In general, the sizes of the Calanus measured were greatest in spring (March–April) and smallest towards the end of the summer and the beginning of autumn, which is in accordance with results obtained elsewhere (Adler and Jespersen, 1920). There are, however, numerous variations in size throughout the summer both between different stages at the same station, and between different stations. The maximum size is not found for all stages on the same date nor on the same date at all stations. It will therefore be advisable to take each station separately.

Station I (Figs. 1 and 2).

Only Stage V Calanus were present to any extent during the autumn, and even these were not always present in numbers sufficient for measurement. The size appears to fluctuate considerably, being least in September and rising in December and January. This autumn brood of Calanus began to moult into adults in January, after which Stage V disappeared until the middle of March when the offspring of these adults had developed. After that, most stages were usually present.

The adult females found on February 22nd were those which had survived the autumn as Stage V, and were of medium size. The next occasion on which there were enough to measure was March 21st (Nicholls' first brood, see p. 88) and there was a great increase in size. These

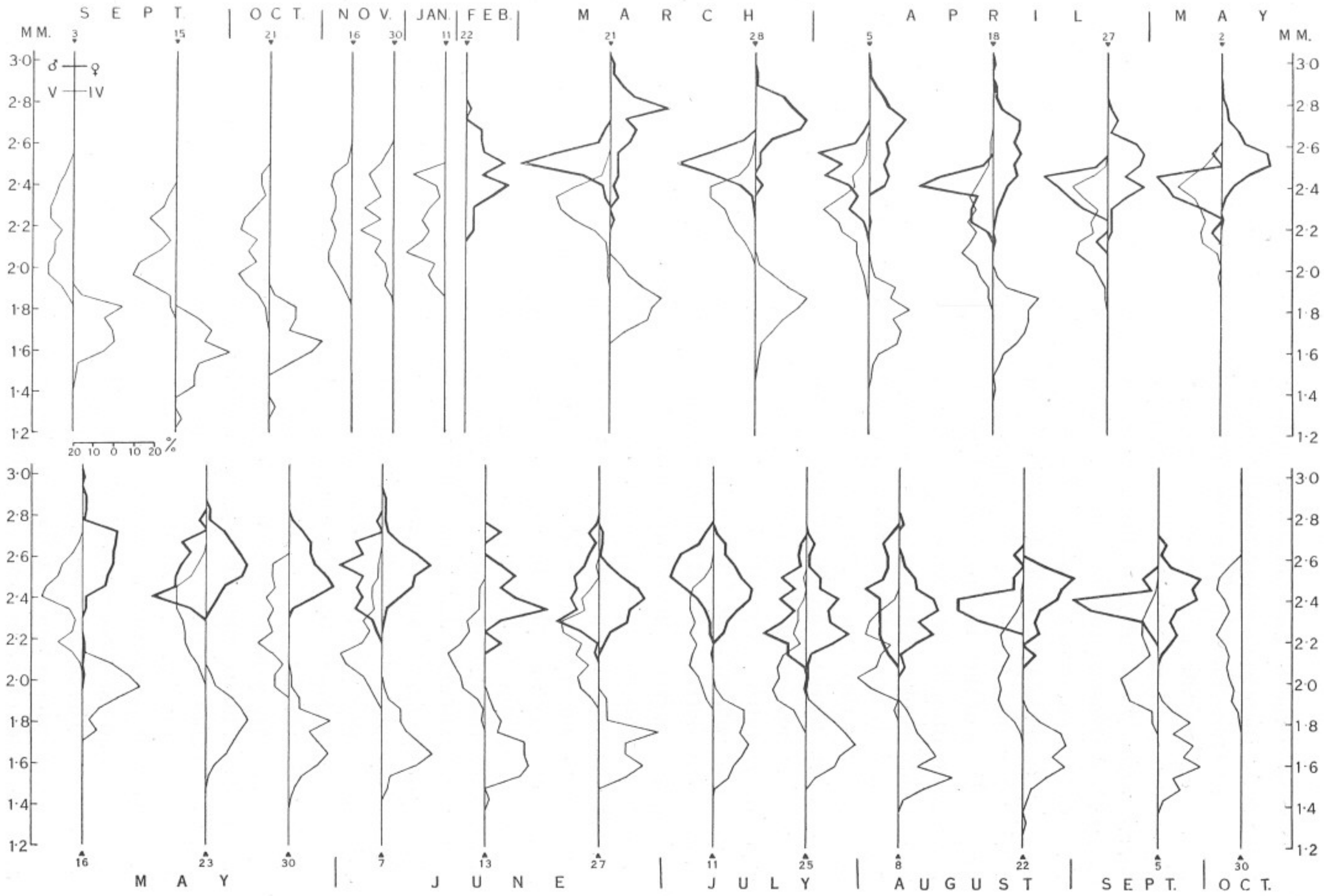

FIG. 1.—The percentage size distribution of Calanus at Station I from September, 1931, to October, 1932. Left-hand side: thick line males, thin line Stage V; right-hand side: thick line females, thin line Stage IV.

females were the biggest found during the whole year (median length 2·76 mm.); there was a wide range of sizes, but the mode was well towards the upper limit (Fig. 1). This was four weeks after the appearance of a large egg maximum, the product of the medium sized females, and these large specimens were therefore the offspring of the autumn-winter brood which had survived from 1931. Succeeding weeks showed gradually decreasing sizes until on April 27th they were not much larger than the autumn-winter brood. These smaller females laid a great quantity of eggs (April 18th–May 2nd) which appeared as adults in the catches from May 16th–June 7th and were again larger, although not so large as those of the first brood. On June 13th there was a very sudden and marked drop in size (median length 2·40 mm.) and at the same time a great number of eggs was laid. A month later these eggs had produced females slightly larger than those of June 13th, but the size had so much decreased that they were slightly smaller than the autumn-winter brood. On July 25th there was another drop in size to the minimum found during the whole year, and at the same time there was a large proportion of eggs in the catch. A month later, on August 22nd, these developed into larger females, almost the same size as the autumn-winter brood. The size curves (Fig. 1) for this date and for July 11th are more compact and have a better defined mode than those for intermediate weeks, indicating a more homogeneous population. The size remained very much the same on September 5th, but after this females became very scarce and were no longer present in quantities sufficient to measure.

It is obvious that the largest females developed during the end of February and the beginning of March when the sea-water was at its coldest, and that the smallest females, those of July 27th, developed in water which was at its maximum temperature for the year. But between these extremes there was a series of increases and decreases in size which cannot be explained on the basis of temperature alone, but which were connected rather with the breeding periods. The largest proportion of eggs in the catches was found when the females were at a size minimum and usually when they were few in number (cf. the preceding paper, p. 95). Exactly a month later than this females of a maximal size were found. Thus, for example, there was an egg maximum on February 22nd and the females on March 21st were large; this held for the periods June 13th–July 11th, July 25th–August 22nd, and probably also for the April to May period, but this was a larger and more spread out egg maximum and the females produced from these eggs were not so clearly marked off. The period from the maximum of size to the production of eggs varied, being a month in the first case (March 21st–April 18th), but much less later on in the year, e.g. July 11th–25th.

The curve of median sizes for males does not follow quite the same course. Males were scarce after the end of March and could not be measured for every station worked. Their first appearance in numbers sufficient for measurement was on March 21st when they were of large size and must have belonged to the large first brood. After this they, like the females, decreased in size till the end of April. Their increase to a secondary maximum again was delayed until May 23rd and 30th, but there followed a sharp drop in size which is not apparent till June 27th since there were not enough to measure on June 13th. The actual minimum would in all probability have been found on June 13th since it occurred on that date for all other stages. The rise to maximal size again on July 11th was well marked and on this date the males were the largest found during the year (median length 2·53 mm.). There was again, as with females, a drop in size to July 25th and a subsequent rise.

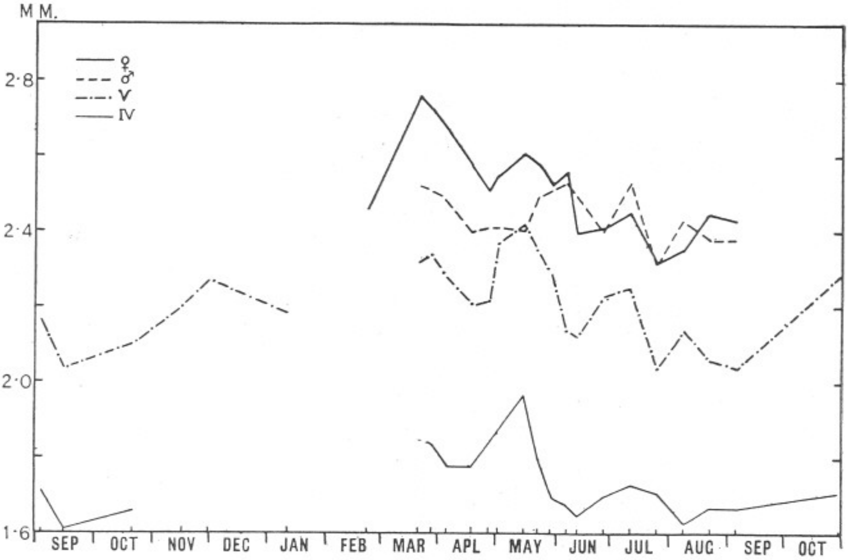

Fig. 2.—The median length of the Calanus measured at Station I (male, female, Stage V and Stage IV) during 1931 and 1932.

The curve for Stage V Calanus corresponded much more closely with the curve for females than did that for males. There were the four well defined maxima on March 21st–28th, May 16th, July 11th, and August 8th and the intermediate minima on April 18th–27th, June 13th, and July 25th. The maximum size for the year was found on May 16th (median length 2·42 mm.) and the minimum on July 25th (median length 2·04 mm.) and in the beginning of September (both in 1931 and 1932). After September, 1932, there was another increase in size and, as mentioned already, sizes fluctuated a good deal during the autumn.

Since the time usually spent as Stage V is probably only four or five days and Stations were taken only once a fortnight, it is not surprising that Stage V and adults should agree closely. Stage IV, being eight to ten days behind in development, might be expected to show peaks sometimes on the same date as adults, sometimes a week or a fortnight before. Accordingly there is only a rough agreement between the respective curves. There was a well defined maximum (when Stage IV reached its largest size of 1·97 mm. for the year) on May 16th and a subsequent marked fall to a minimum on June 13th. The smallest sizes were found on this date and in September, 1931, and August, 1932 (median length 1·62–1·65 mm.).

The size curves (Fig. 1) as a whole show a great range and no well marked mode. This is especially so with females and Stage V. On March 21st, however, the curves for all stages were more compact and had a definite mode. This is probably because the first brood appearing then develops from eggs laid within a comparatively short space of time and forms a more homogeneous population than during the rest of the year. The appearance of a new brood of maximal size had the same effect on a few other occasions (e.g. males and females on July 11th; Stage IV on May 16th). Later in the year several hundred Stage V and Stage IV were measured to see if inadequate numbers were the cause of the irregular curves, but this was not the case.

STATION II (Figs. 3 and 4).

Station II was worked only once a fortnight and, in addition, adult Calanus were too few to measure on several occasions during the March to May period, so that the size curves do not give the same picture as those of Station I. The autumn-winter brood of adults appeared, the males in January and the beginning of February and the females in February. After this they became scarce and on March 21st, the date when at Station I the largest females were found, there were not enough to measure, so that the period of maximum size, on the first appearance of the first brood, has probably been missed. On April 5th the first brood was larger than the autumn-winter brood, but not markedly so. In the females there was a subsequent decrease to May 2nd when there was a great production of eggs. At Station I the females appearing a month later than the eggs were much larger, but this was not so at Station II; the size remained constant or rose only slightly and the striking feature is the sudden drop in size which occurred on June 13th (as at Station I) and on August 8th (a fortnight later than at Station I). In the end of August and September the females found were the smallest for the year.

The curve for male sizes does not much resemble that for females. The largest males found were those of the autumn-winter brood found on January 11th; the first-brood males may have been larger on their first

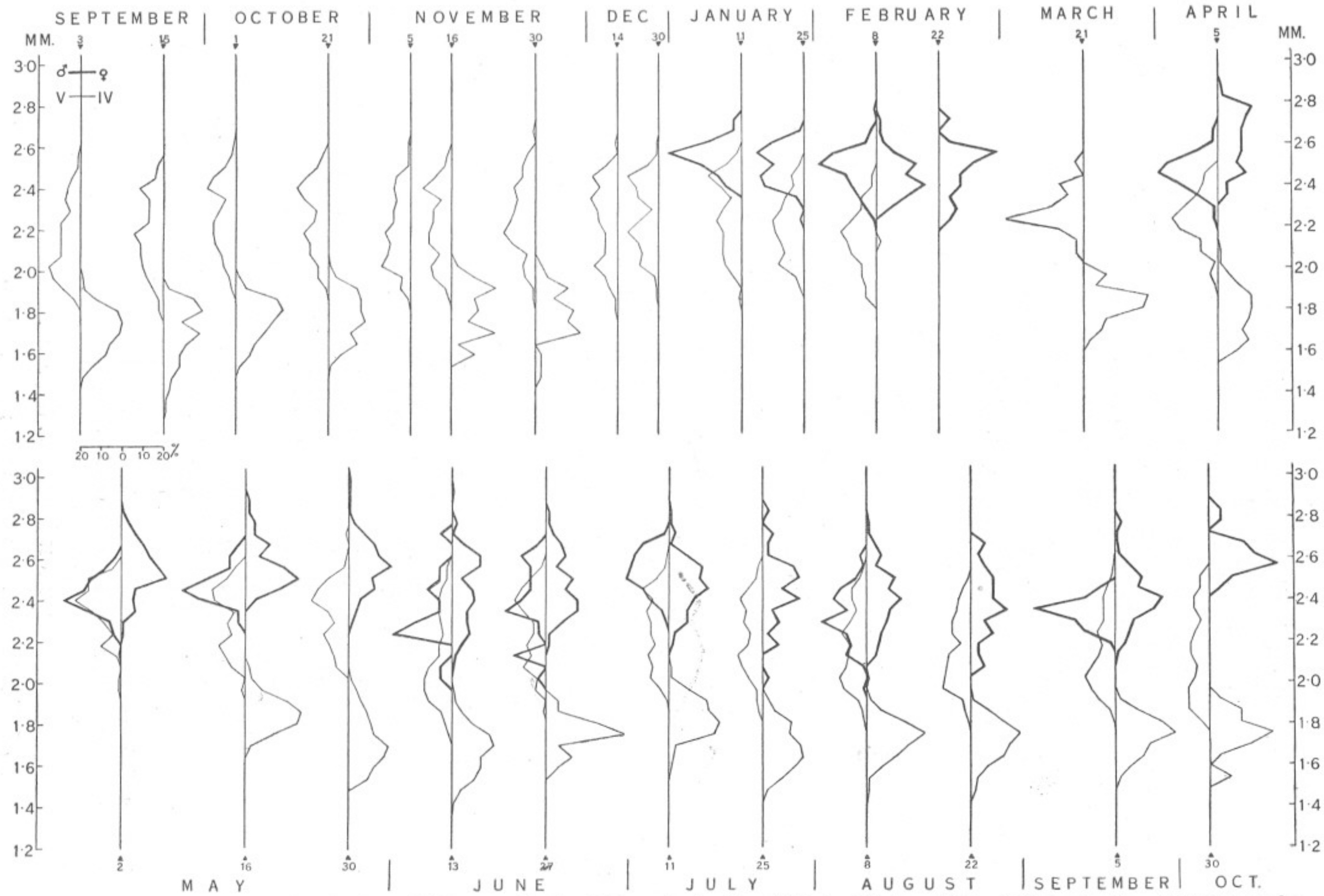

FIG. 3.—The percentage size distribution of Calanus at Station II from September, 1931, to October, 1932. Left-hand side: thick line males, thin line Stage V; right-hand side: thick line females, thin line Stage IV.

appearance, but on April 5th they were slightly smaller and decreased in size further till April 30th. There was a slight rise on May 16th, the usual fall on June 13th, when the smallest males for the year were found, and a subsequent rise to a maximum on July 11th (found also at Station I) when they were nearly as large as the autumn-winter brood. Like the females they decreased in size again at the end of August.

The Stage V curve shows as little agreement with the female as does the male. The size during the autumn varied considerably, and those of the first brood measured on March 21st were no larger than the majority of the autumn-winter stock. The size curve (Fig. 3) for that date, however, is very different; instead of having a wide range of sizes and no definite mode, it is shorter and has a well marked mode. There is no definite increase in size till May 2nd (not a date which corresponds with any of the other stages), but there was the usual marked fall on June 13th to a size smaller than that found during the rest of the year. June 27th showed a marked rise and there was a gradual fall thereafter until September.

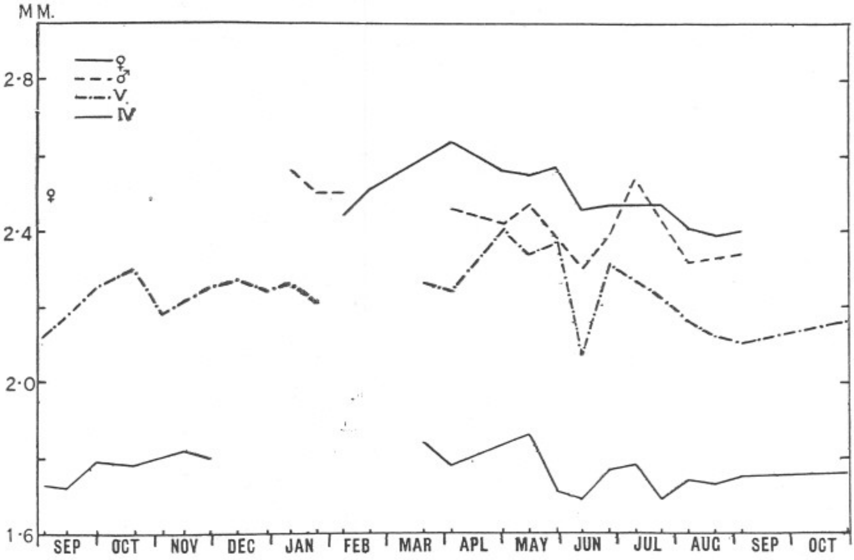

FIG. 4.—The median length of the Calanus measured at Station II (male, female, Stage V, and Stage IV) during 1931 and 1932.

The curve for Stage IV shows only a rough agreement. There was a maximum on May 16th (with a well marked mode on the size curve), a fall to June 13th, a rise and then a further fall on July 25th.

STATION IV (Figs. 5 and 6).

Station IV differed in several respects from the other two stations. During the autumn the Stage V Calanus were considerably larger than

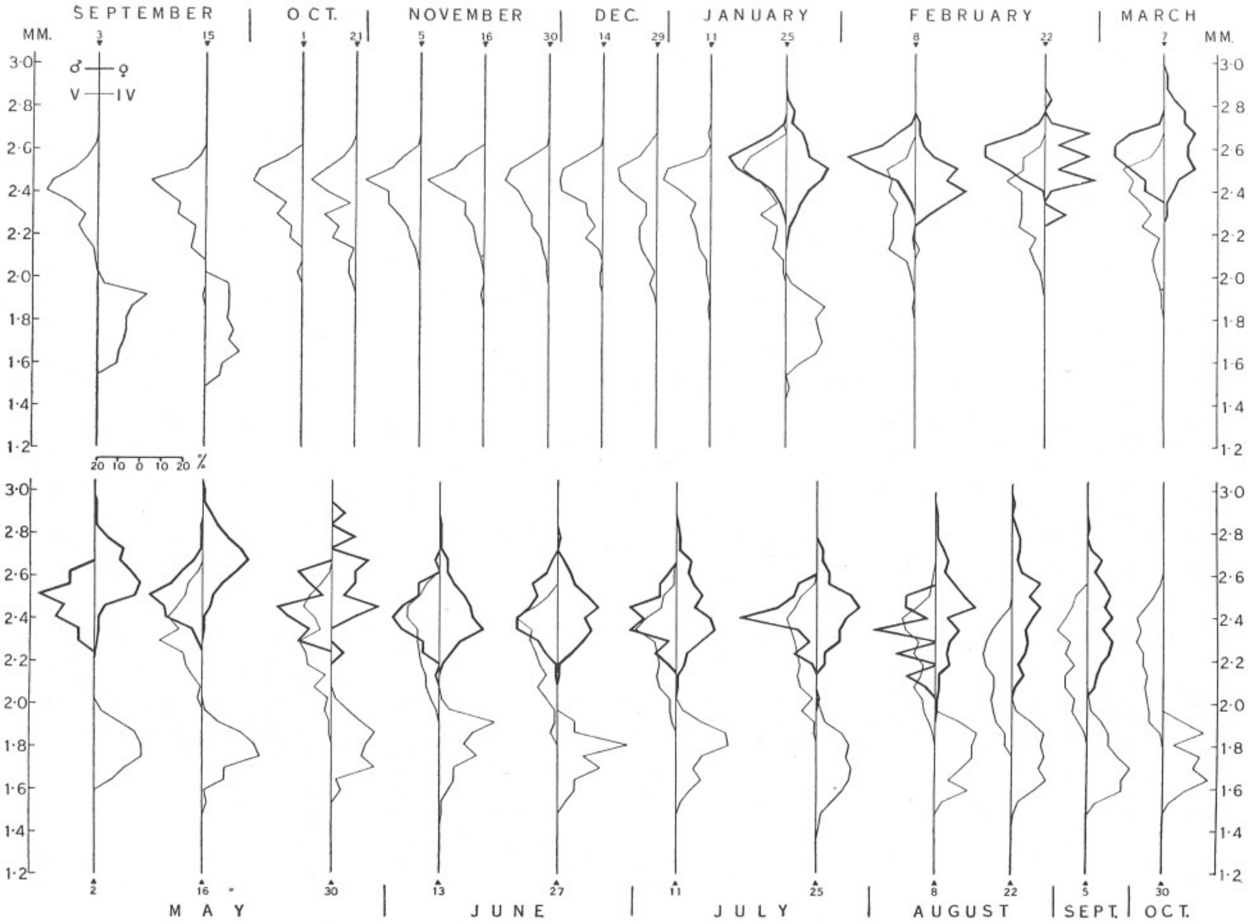

FIG. 5.—The ercentage size distribution of Calanus at Station IV from September, 1931, to October, 1932. Left-hand side: thick line males, thin line Stage V; right-hand side: thick line females, thin line Stage IV.

those from elsewhere, and the size curves (Fig. 5), although showing, like the other stations, a wide range of sizes, usually had a well defined mode near the upper limit. The size also remained much more constant throughout the autumn, owing probably to geographical conditions. The deep water of upper Loch Fyne is separated from the rest of the area by two shallow bars enclosing a basin not more than 65 metres in depth, where there is, according to Mill (1889–91), much less movement of the water by tides and winds than outside. The Calanus must therefore form a more constant and homogeneous population than at the other stations.

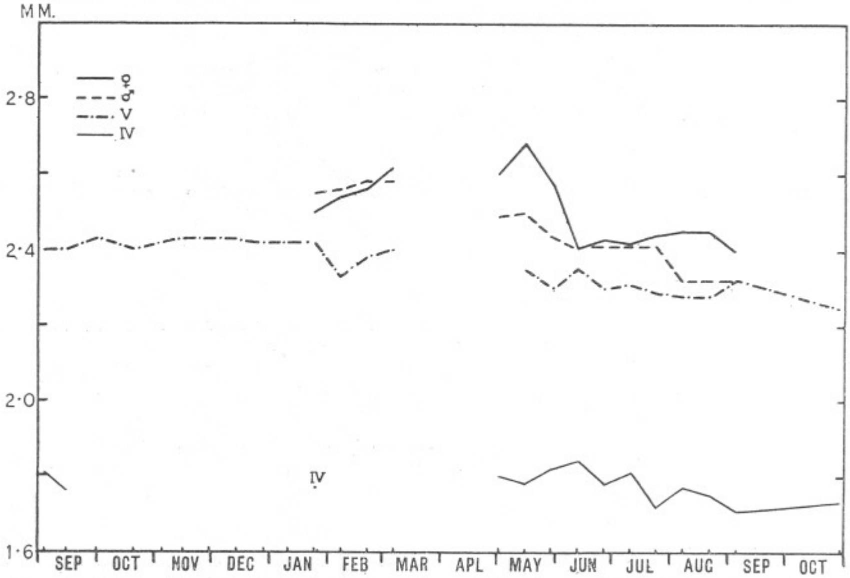

Fig. 6.—The median length of the Calanus measured at Station IV (male, female, Stage V, and Stage IV) during 1931 and 1932.

Adults first appeared on January 25th, males being then more numerous than females, and at the same time there was a distinct drop in the size of Stage V Calanus (Fig. 6) which indicates that the larger specimens moulted first. However, there was a subsequent recovery in the size of Stage V and at the same time the size of both male and female increased slightly. At first the male was a little the larger, but by March 7th the female had surpassed it. After this Calanus became too scarce to measure until May 2nd, so that measurements for the first brood have here been missed completely. The females present on May 2nd were much the same size as those of March 7th, and there was a large proportion of eggs in the catch, as indeed there had been throughout March and April. There was a sharp rise on May 16th to the maximum size recorded (although possibly not the real maximum) for the year, followed by a sharp fall to June 13th as at other stations. After this the size altered little, only rising slightly in the end of July and beginning of August. The male follows the female curve fairly closely except that there was a marked decrease in size on August 8th. There was no maximum of size for males on July 11th as there was at the other stations.

The curves for Stage V show none of the variations characteristic of the other stations. The maximum size was found during the autumn and early winter when, as mentioned above, it remained very constant. The first brood was missed completely and after this there were only minor fluctuations which included a slight rise instead of a fall on June 13th. The size in September and October, 1932, was considerably less than in 1931. The Stage IV were measured only during the summer (May–October) and on the whole decreased from the beginning to the end of that period with no very marked variations.

At Station IV it is not so easy to connect periods of maximum size with the different broods. This is in the first place because measurements for the first brood have been missed entirely and, in the second, because there was a continuous production of eggs during March, April, and the beginning of May and it is difficult to be sure from which part of this breeding period any particular adults are derived. In the case of males and Stages V and IV there was no marked maximum or minimum of size at the coldest or warmest part of the year, but a gradual decline in size throughout the summer so that conditions in September, 1932, are quite different from those in 1931.

DISCUSSION.

If we consider the results as a whole we see that none of the three stations agrees exactly with any other although certain features are common to all. The median size curves of Stations I and II (Figs. 2 and 4), and to a less extent those of Station IV (Fig. 6), can be divided into three parts, each corresponding to one of the three breeding periods described in the preceding paper. At Station I the first appearance of the new brood a month after the egg maximum was marked by Calanus of large size, and the end of the brood, which was the time when most eggs were laid, was marked by Calanus of small size. This shows well for males, females, and Stage V and less clearly for Stage IV. At Station II the three groups can still be observed, but the beginning of the new brood was not marked by an increase in size although the end of the brood, and the egg laying period, were marked by a definite decrease. Although the three groups are not equally well defined in all stages, they are quite clear in females, and two of the groups are clear in males and Stage V. At Station IV the first group has been missed completely, the second is distinct, but the third, although probably present, is marked by no distinctive features.

The same changes are often found on the same date at different stations. Thus May 16th is a date when most of the Calanus at all stations were of large size, while on June 13th all stages of Calanus were of small size at all stations (except Stages V and IV at Station IV). A possible explanation of this might be that the population of Calanus as a whole had changed by migration. This is, however, negatived by several facts. Upper Loch Fyne (Station IV) shows in general the same size changes as the other stations, but cannot be subject to immigration since it is cut off from the rest of the area by two shallow bars. That it can develop and retain a plankton different from the rest of the area has already been shown (Marshall and Orr, 1927). Text-Figures 3 and 4 in the preceding paper indicate clearly that the Calanus population at Stations I and II also was stationary and that its development could be followed from month to month.

If then, as seems most probable, the Calanus of maximal and minimal size belong to the same brood (e.g. those of March 21st to April 18th ; and of May 16th to June 13th, etc.), it follows that the Calanus developed from eggs laid early in the breeding period are large and that those from eggs laid towards the end of it are small. The former holds good throughout the year only at Station I, but the latter is true in most cases. From the size measurements and times of egg production it would appear that the main mass of eggs is produced by Calanus of small size and that the large Calanus take little part in reproduction. This is probably not altogether true. The large females develop first, but since they wait for several weeks before laying eggs there is an accumulation of females and the smaller, later developed, females outnumber the early developed large ones, especially since these are all the time subject to processes of natural mortality. That large specimens are still present is seen in the size curves (Figs. 1, 3, and 5) where the increase and decrease of the median is shown to be caused more by the shifting of the mode than by alterations in the total range.

It might be supposed that the variations in size are caused by variations in the food supply, but observations on the microplankton do not bear this out (Fig. 2 in the preceding paper). Although at Station I the small Calanus of June 13th must have developed during a period of diatom poverty and the large specimens of May 16th and July 11th during a diatom-rich period, yet there are also many exceptions. The largest Calanus of all, those of March 21st, developed while diatoms were very scarce and the small specimens of July 25th developed while diatoms were comparatively abundant. At Station IV also the small Calanus of June 13th must have developed during that time of year when diatoms were richest in Loch Fyne and the largest, those of May 16th, when diatoms, although increasing, were not very numerous. Neither does the microplankton, apart from diatoms, show any relation to size.

Water temperatures were not taken regularly but can certainly not have been responsible for the size variations during the summer. The cause of the difference between Stage V Calanus at Station IV and those of the other stations may be the slightly lower temperature of the deep waters off Strachur during the summer and autumn. Mill (1891) has shown that this deep water is, owing to the contour of the bottom and the shallow bars cutting it off from lower Loch Fyne, so much isolated that the temperature lags behind that of the more open water of the area. From about June to December it is one or two degrees colder, and from February to April one or two degrees warmer than the deep water outside. No temperature measurements are available to explain the uniformity of sizes in the autumn of 1932.

During 1930–31 catches of Calanus were taken at Station I at irregular intervals with a stramin net, and samples were measured. It is interesting to note that the Stage V Calanus during the period April to September showed four distinct groups with maxima and minima at very much the same times as in 1932. There were maximal sizes at the beginning of April (when observations began), May 30th, July 12th, and August 15th, and minimal sizes on April 10th, June 10th, August 2nd, and September 16th. The resemblance is perhaps significant.

It seems as if the size variations were caused by some factor inherent in the method of reproduction of Calanus.

During most of the summer the catches were taken in two parts, one from the bottom to 30 m., the other from 30 m. to the surface. The adults, with one exception at each station, were never present in significantly large numbers above 30 m. On three occasions Stage V and on six occasions Stage IV were numerous enough to measure separately in the two catches. In every case with Stage V the Calanus from deep water were distinctly larger than those from the surface layers, the medians being respectively: May 30th, Station VI, 2.31 mm., 2·16 mm.; June 7th, Station I, 2·15 mm., 2·08 mm.; June 13th, Station II, (Fig. 7) (when there were more above than below 30 m.), 2·34 mm., 2·01 mm. Stage IV was also usually more abundant in water below 30 m., but on May 30th at Stations II and VI they were more numerous in the upper layers. On one occasion only, May 23rd at Station I, the larger specimens were found above 30 m. and the smaller below (median lengths 1·85 mm., 1·80 mm.), but as a rule the opposite was true, e.g. the median lengths of surface and deep water specimens respectively were: May 30th, Station I, 1·65 mm., 1·71 mm.; Station II (Fig. 7), 1·67 mm., 1·85 mm.; Station IV, 1·68 mm., 1·69 mm.; June 7th, Station I, 1·64 mm., 1·68 mm.; July 25th, Station II (Fig. 7), 1·63 mm., 1·73 mm.

As has been mentioned the Calanus from different stations also varied in size. During the autumn those from Station IV were larger (median length about 2·42 mm.) than those from Station II, and the latter (median length 2·12–2·27 mm.) were slightly larger than those from Station I (2·03–2·27 mm.). This distinction had been lost by the autumn of 1932. Several extra stations were worked quarterly and as a rule the sizes of Calanus at these stations differed little from those of the fortnightly stations nearest them. In August, however, Stage V and Stage IV Calanus from Station V, which is situated further up the main channel than Station I, were much smaller than any of the rest and were, in fact, the smallest found throughout the year.

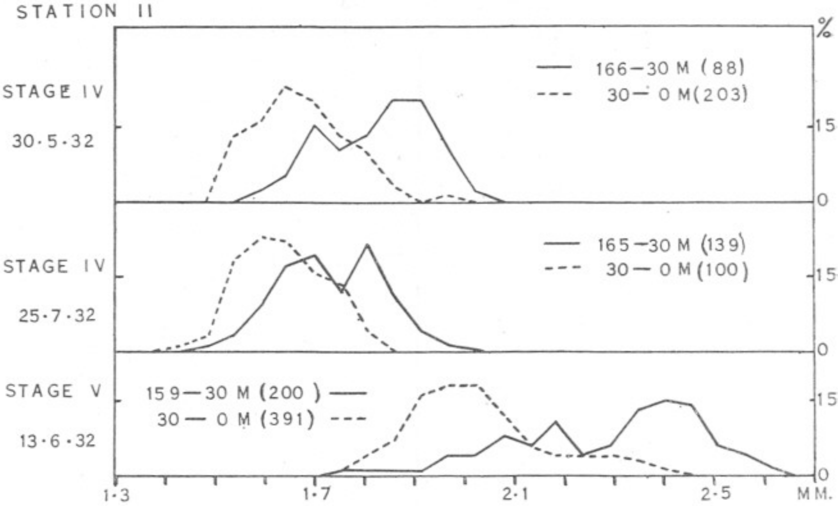

FIG. 7.—A comparison of the percentage size distribution of Stage IV and Stage V Calanus caught above and below 30 m. at Station II. The numbers for each haul are given in brackets.

One of the most striking features of the curves is the long range of sizes in almost every sample, a range almost as great as the whole yearly variation. Even when a large number of specimens is measured the curve does not lose its characteristic irregularity (Stage V: Station I, 30–10–32; Station II, 3-9-31, 22-8-32; Station IV, 13-6-32, 11-7-32). Although there is rarely any suggestion of two separate modes, yet such an irregular curve might be caused by the presence of two or more distinct forms or varieties whose sizes overlap.

Gurney (1929) and Sewell (1912, 1929, 1932) have both investigated numerous species of copepods in which the adult has a large size range, and have come to the conclusion that in many cases there are two forms of adult. Gurney assumes that there may be a second moult in the adult stage, while Sewell has put forward a more complicated scheme, in which the two adult forms, the " low " and the " high," are derived from Stages III, IV or V by moulting with appropriate growth factors. He comes to these conclusions mainly from a calculation of the growth factor (i.e. the proportion by which the length increases from one moult to the next), although there are also morphological differences between the " low " and " high " forms.

Now an examination of the curves in Figures 1, 3, and 5 would at first sight seem to support this. The curve for females always overlaps a large part of the curve for Stage V and occasionally (Station I, May 16th ; Station IV, August 8th) overlaps that for Stage IV too. The curve for males is also largely overlapped by that for Stage V and indeed the latter sometimes extends beyond it at the upper limit (Station I, April 18th ; Station II, September 5th ; Station IV, August 8th). It would therefore be quite possible for there to be two moults in either Stage V or Stage VI female, or for some Stage IV to moult directly into small females, the growth factor in these cases being one perfectly normal for copepods. Against this is the fact that the curves are never clearly bimodal and vary much from week to week. Also, if this kind of moult is as frequent as the curves suggest one would expect to find it in a fairly large percentage of cases, whereas although a large number of moulting Calanus have been observed, no abnormal moult has yet been seen.

Bogorov (1933) measured a number of all copepodite stages of *Calanus finmarchicus* from a tow netting taken in July, 1924, in the Barents Sea. He found that the size curves for Stages I, II, and III were unimodal, whereas those for Stages IV and V were bimodal, and he attributes this to the sex differentiation taking place in Stage IV. Males were not obtained but the curve for female sizes is very irregular and overlaps that for Stage V almost completely. The average size for females is actually smaller than that of Stage V and he attributes this to their belonging to a different brood. Another possibility is therefore that the small Stage V moult into males and the large into females. To test this a number of Stage V Calanus of different sizes was kept in separate beakers for about a fortnight (in autumn). Eight survived and moulted into adults. Of the large specimens (over 2·40 mm.) two became male and two female, and of the small (under 2·16 mm.) all four became female. It does not therefore appear that there is a sex differentiation in size in Stage V.

Gurney, however, has pointed out that the growth factor may change from moult to moult and is subject besides to much individual variation, facts which are borne out by the present investigation. If we consider all the adults as produced from the Stage V by a single moult (e.g. Station IV on June 13th, 1932, Fig. 5), it is obvious that they cannot all moult with even approximately the same growth factor. This, however, seems easier to believe than that there has been an abnormal moult in a large number of cases, since for that there is as yet no experimental evidence.

Some Calanus were kept separately in beakers to watch their growth, and measurements were made of the different stages (see the preceding paper, p. 91). When the growth factors are calculated it is found that there is a great deal of variation both from moult to moult in the same individual and also between individuals. Measurements made on living and active animals can of course be only approximate, but, for the moult from Stage V–Stage VI female, the factor varied from 1·06–1·21. The average factor was : Stage I–II (one case) 1·22, Stage II–III (seven cases) 1·22, Stage III–IV (thirteen cases) 1·19, Stage IV–V (thirteen cases) 1·17, Stage V–VI female (eleven cases) 1·12. Besides these specimens, which were examined especially for their development, a large number has been kept for other purposes and in no case has any but a normal moult been observed. Until some experimental evidence has been obtained the suggestions of Gurney and Seymour Sewell must remain only possibilities.

Sewell's copepods were mostly taken from brackish water at river mouths and these peculiar conditions may have affected their development, but Gurney worked on freshwater copepods from lakes in different parts of the world.

A long and irregular range of sizes may be caused, not by dimorphism in one stage or another, but by a mixture of races or varieties. Such a curve (with a range of only 0·55 mm.) has been shown by Steuer (1925) for *Pleuromamma gracilis* to be composed of three different races, characterised by slight morphological differences as well as by varying size. In his cases, however, the different varieties were usually found in different parts of the geographical range, or, if caught at the same station, could be assumed to inhabit different depths. Such an explanation would not hold with Calanus in the present case.

Calanus of varying sizes in the same catch have already been described by Leif Störmer (1929) from the west coast of Greenland, and by Ottestad (1932) from Antarctic seas. In the latter case the water mass being sampled was composed of water of several origins and the irregularities in the size curves of the Calanus (*C. acutus* and *C. propinquus*) are explained as having been caused by the Calanus belonging to these different water masses and having different developmental histories. Off the west coast of Greenland there are two distinct sizes of Calanus, a large and a small, and Störmer finds that whereas the small form is the product of the same year's growth, the large form has survived a winter and is really more than one year old. There is no evidence that in the Clyde we are dealing with anything but a homogeneous mass of water, and the Calanus in it are certainly never more than a few months old, so that neither of these explanations can hold good here.

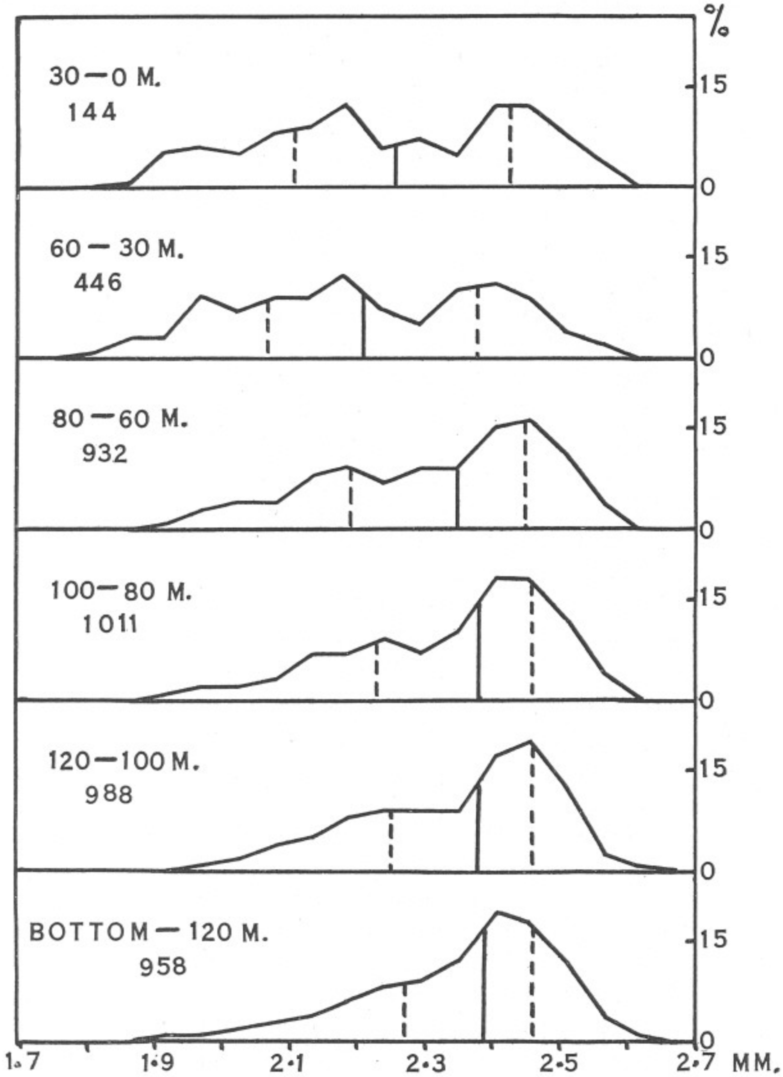

FIG. 8.—The percentage size distribution of Calanus from different depths at Station IV on January 25th–26th, 1932. The position of the first and third quartiles is marked with vertical broken lines and that of the second quartile (median) with a continuous vertical line. The numbers measured for each depth are given below the depth.

Russell (1928) has suggested that there may be a segregation of broods in different water layers, the small summer brood living nearer the surface than the large winter brood. As we have seen, during the summer (May–July) the Calanus near the surface (above 30 m.) were distinctly smaller than those from deep water. During at least the early part of this period there may have been a mixture of broods present and an examination was therefore made of the sizes of Stage V at different depths in Loch Fyne in January. At this time the population of Calanus is homogeneous, breeding has not yet begun, and all the Stage V present have survived the winter as such and are the product of the late summer broods.

On January 25–26th, a vertical distribution station was worked by Dr. A. G. Nicholls and samples are available at 20-metre depths from the bottom up to 60 m., as well as from 60–30 m. and 30 m. to the surface. Samples from all these depths were measured and it was found (Fig. 8) that in every case the samples above 60 m. contained a larger proportion of small specimens than those from below. Below 60 m. there was little difference between any of the samples. These results indicate that even in a homogeneous population the small specimens of Calanus tend to be found nearer the surface than the large. This confirms Gardiner's (1933) recent observations on Calanus in the North Sea. An examination and comparison of a small and a large Calanus showed no significant morphological differences, and the tendency can perhaps be regarded as the first step in the process which Steuer has studied, the process by which a small, surface-living variety becomes separated off from a larger deep water species.

SUMMARY.

The size of the cephalothorax in Stage IV, Stage V, and Stage VI Calanus has been measured during the year 1931–1932 at three stations in the Clyde Sea-Area.

In general the size was greatest when the water temperature was low, and least when it was high, but besides this there was a series of increases and decreases in size which were apparently connected with the breeding periods. The Calanus produced at the beginning of a breeding period were large (at Station I) and those produced at the end were small (at Stations I and II). The greatest production of eggs usually occurred when the female Calanus were of small size.

During the autumn of 1931 the Stage V Calanus from Station IV (upper Loch Fyne) were considerably larger than those from the rest of the area, but this distinction had been lost by the autumn of 1931.

Stages IV and V Calanus taken in the top 30 m. were almost invariably smaller than those from deeper water.

The Calanus show a very wide range of sizes, the range for Stage V overlapping those for both male and female. Possible causes of this are discussed.

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TABLES I–IV.

MEASUREMENTS OF CARAPACE-LENGTH IN MM. The measurements were made with an eye-piece micrometer of which one division = 0·054 mm. The figures in ordinary type are the actual numbers found; the figures in italics are percentages.

TABLE I.

MALES. LENGTH OF CARAPACE IN MM.

Station.	Date.	1·944–1·998	1·998–2·052	2·052–2·106	2·106–2·160	2·160–2·214	2·214–2·268	2·268–2·322	2·322–2·376	2·376–2·430	2·430–2·484	2·484–2·538	2·538–2·592	2·592–2·646	2·646–2·700	2·700–2·754	2·754–2·808	2·808–2·862	Number measured.	Median length.
I	21-3-32								2 *3*	3 *4*	11 *14*	34 *44*	21 *27*	5 *6*	2 *3*				78	2·522
,,	28-3-32							1 *1*	2 *2*	8 *8*	20 *21*	36 *38*	22 *23*	6 *6*					95	2·510
,,	5-4-32					1 *1*	2 *3*	7 *10*	5 *7*	7 *10*	16 *22*	10 *14*	18 *25*	5 *7*	2 *3*				73	2·481
,,	18-4-32					1 *3*	4 *11*	4 *11*	3 *8*	13 *36*	9 *25*	2 *5*							36	2·403
,,	27-4-32				1 *6*	– *–*	– *–*	2 *12*	3 *19*	4 *25*	5 *31*	1 *6*							16	2·410
,,	2-5-32					1 *5*	– *–*	2 *9*	5 *23*	6 *27*	7 *32*	– *–*	1 *5*						22	2·408
,,	16-5-32					1	–	–	4	2	2	–	2						11	2·403
,,	23-5-32								2 *8*	7 *27*	4 *15*	4 *15*	3 *12*	2 *8*	3 *12*	– *–*	1 *4*		26	2·491
,,	7-6-32						1 *3*	2 *5*	5 *13*	4 *10*	5 *13*	4 *10*	8 *21*	4 *10*	5 *13*	– *–*	1 *3*		39	2·525
,,	27-6-32				2 *2*	1 *1*	9 *9*	21 *21*	11 *11*	14 *14*	11 *11*	12 *12*	7 *7*	5 *5*	2 *2*	5 *5*	1 *1*		101	2·403
,,	11-7-32				1 *1*	– *–*	2 *2*	2 *2*	4 *4*	8 *8*	14 *14*	21 *21*	19 *19*	16 *16*	7 *7*	4 *4*			98	2·532
,,	25-7-32	1 *1*	– *–*	1 *1*	6 *9*	6 *9*	14 *21*	8 *12*	4 *6*	9 *13*	4 *6*	8 *12*	2 *3*	3 *4*	2 *3*				68	2·312
,,	8-8-32				3 *6*	4 *8*	5 *10*	5 *10*	5 *10*	5 *10*	9 *17*	4 *8*	3 *6*	3 *6*	4 *8*	2 *4*			52	2·425
,,	22-8-32							4 *21*	6 *32*	6 *32*	1 *5*	1 *5*	– *–*	1 *5*					19	2·376
,,	5-9-32						1 *4*	2 *8*	8 *33*	10 *42*	1 *4*	2 *8*							24	2·384
II	11-1-32									2 *8*	3 *12*	5 *20*	9 *36*	4 *16*	1 *4*	1 *4*			25	2·556
,,	25-1-32						1 *2*	– *–*	2 *4*	9 *19*	10 *21*	7 *15*	11 *23*	7 *15*	1 *2*				48	2·503
,,	8-2-32						1 *1*	4 *5*	6 *8*	9 *12*	11 *15*	21 *28*	16 *21*	4 *5*	2 *3*	– *–*	1 *1*		75	2·502

..	5-4-32						1 *2*	1 *2*	6 *10*	12 *20*	17 *29*	14 *24*	6 *10*	1 *2*	1 *2*				59	2·462
..	2-5-32				1 *1*	– –	5 *4*	7 *6*	20 *17*	33 *28*	21 *18*	18 *15*	9 *8*	3 *3*					117	2·419
..	16-5-32							1 *4*	1 *4*	6 *23*	8 *31*	5 *19*	2 *8*	2 *8*	1 *4*				26	2·467
..	13-6-32	1 *6*	– –	1 *6*	– –	– –	5 *29*	3 *18*	1 *6*	1 *6*	2 *12*	1 *6*	1 *6*	– –	– –	1 *6*			17	2·304
..	27-6-32		1 *4*	– –	4 *16*	– –	1 *4*	1 *4*	5 *20*	3 *12*	2 *8*	2 *8*	2 *8*	3 *12*	1 *4*				25	2·394
..	11-7-32							1 *2*	2 *4*	5 *10*	6 *13*	10 *21*	9 *19*	8 *17*	6 *13*	1 *2*			48	2·541
..	8-8-32	1 *2*	– –	1 *2*	6 *10*	5 *8*	6 *10*	14 *22*	6 *10*	10 *16*	8 *13*	3 *5*	1 *2*	2 *3*					63	2·318
..	5-9-32					1 *3*	6 *15*	8 *20*	16 *40*	6 *15*	3 *8*								40	2·341
IV	25-1-32									3 *6*	6 *12*	13 *25*	15 *29*	9 *18*	4 *8*	1 *2*			51	2·552
..	25-26-1-32						5 –	8 *1*	37 *3*	85 *7*	180 *14*	299 *23*	354 *27*	217 *17*	95 *7*	16 *1*	2 –		1298	2·543
..	8-2-32					1 *1*	– –	– –	3 *2*	8 *6*	12 *9*	28 *22*	41 *32*	21 *16*	11 *9*	3 *2*			128	2·555
..	22-2-32									1 *1*	11 *11*	18 *18*	29 *28*	29 *28*	11 *11*	3 *3*			102	2·578
..	7-3-32									4 *9*	4 *9*	7 *16*	10 *23*	10 *23*	7 *16*	1 *2*			43	2·576
..	2-5-32							2 *8*	2 *8*	5 *19*	4 *15*	7 *27*	3 *12*	3 *12*					26	2·488
..	16-5-32							4 *3*	7 *5*	22 *17*	24 *18*	33 *25*	19 *15*	13 *10*	5 *4*	1 *1*	1 *1*	1 *1*	130	2·498
..	30-5-32							3 *16*	2 *11*	4 *21*	5 *26*	1 *5*	2 *11*	3 *16*					19	2·441
..	13-6-32				1 *2*	– –	4 *8*	4 *8*	9 *18*	11 *22*	9 *18*	5 *10*	5 *10*	– –	1 *2*				49	2·410
..	27-6-32				2 *1*	2 *1*	9 *6*	13 *9*	29 *19*	29 *19*	19 *13*	15 *10*	18 *12*	8 *5*	5 *3*				149	2·413
..	11-7-32					2 *4*	5 *10*	2 *4*	11 *22*	8 *16*	11 *22*	4 *8*	4 *8*	2 *4*					49	2·410
..	5-7-32					1 *2*	5 *11*	2 *4*	4 *9*	16 *36*	8 *18*	5 *11*	4 *9*						45	2·413
..	8-8-32			1 *5*	3 *14*	– –	4 *19*	– –	6 *29*	1 *5*	3 *14*	3 *14*							21	2·349
..	5·9-32					2	3	1	3										9	2·322

TABLE II.

FEMALES. LENGTH OF CARAPACE IN MM.

Station	Date.	1·944–1·998	1·998–2·052	2·052–2·106	2·106–2·160	2·160–2·214	2·214–2·268	2·268–2·322	2·322–2·376	2·376–2·430	2·430–2·484	2·484–2·538	2·538–2·592	2·592–2·646	2·646–2·700	2·700–2·754	2·754–2·808	2·808–2·862	2·862–2·916	2·916–2·970	2·970–3·024	Number measured.	Median length
I	22-2-32					2 *4*	2 *4*	2 *4*	7 *13*	11 *21*	5 *9*	10 *19*	5 *9*	4 *8*	4 *8*	– *–*	1 *2*					53	2·462
,,	21-3-32						1 *2*	– *–*	2 *4*	1 *2*	2 *4*	2 *4*	2 *4*	5 *10*	7 *13*	4 *8*	15 *29*	6 *12*	3 *6*	1 *2*	1 *2*	52	2·756
,,	28-3-32									3 *4*	– *–*	2 *3*	2 *3*	6 *8*	16 *22*	18 *25*	14 *19*	1 *14*	*1*	1 *1*		73	2·724
,,	5-4-32						1 *1*	– *–*	– *–*	6 *8*	8 *10*	6 *8*	8 *10*	7 *9*	10 *13*	14 *18*	9 *11*		*4*	1 *1*	1 *1*	80	2·670
,,	18-4-32				1 *1*	– *–*	1 *1*	2 *2*	4 *5*	6 *7*	10 *12*	9 *11*	12 *14*	9 *11*	11 *13*	11 *13*	4 *5*	2 *2*	2 *2*	– *–*	1 *1*	85	2·583
,,	27-4-32					1 *2*	1 *2*	1 *2*	4 *9*	8 *18*	4 *9*	7 *16*	8 *18*	6 *14*	1 *2*	2 *5*	1 *2*					44	2·511
,,	2-5-32						1 *1*	– *–*	2 *2*	6 *6*	13 *13*	24 *24*	23 *23*	12 *12*	9 *9*	4 *4*	3 *3*	1 *1*	1 *1*			99	2·547
,,	16-5-32		1 *1*	– *–*	1 *1*	1 *1*	– *–*	– *–*	3 *2*	3 *2*	14 *11*	15 *12*	19 *15*	19 *15*	20 *16*	21 *17*	1 *1*	3 *2*	2 *2*	– *–*	1 *1*	124	2·608
,,	23-5-32								5 *3*	11 *6*	16 *9*	31 *18*	34 *20*	31 *18*	23 *13*	15 *9*	4 *2*	3 *2*				173	2·576
,,	30-5-32								1 *2*	7 *13*	12 *22*	10 *19*	7 *13*	6 *11*	6 *11*	4 *7*	1 *2*					54	2·525
,,	7-6-32							1 *1*	2 *2*	10 *9*	16 *15*	17 *16*	26 *24*	18 *17*	10 *9*	3 *3*	2	2 *2*	2 *2*			109	2·557
,,	13-6-32					1 *8*	– *–*	1 *8*	4 *31*	2 *15*	1 *8*	2 *15*	1 *8*	– *–*	– *–*	1 *8*						13	2·403
,,	27-6-32					5 *3*	11 *6*	26 *14*	27 *15*	41 *22*	34 *19*	20 *11*	10 *5*	2 *1*	3 *2*	4 *2*						183	2·406
,,	11-7-32						14 *5*	20 *7*	33 *12*	51 *18*	52 *19*	38 *14*	32 *11*	16 *6*	17 *6*	7 *2*	1 *–*					281	2·450
,,	25-7-32		1 *1*	1 *1*	3 *3*	14 *13*	22 *21*	13 *12*	12 *11*	17 *16*	8 *7*	7 *7*	2 *2*	2 *2*	4 *4*	1 *1*						107	2·322
,,	8-8-32			3 *3*	1 *1*	8 *8*	17 *17*	10 *10*	19 *19*	17 *17*	9 *9*	8 *8*	3 *3*	2 *2*	– *–*	– *–*	2 *2*					99	2·353
,,	22-8-32				2 *6*	– *–*	3 *8*	2 *6*	3 *8*	6 *17*	7 *19*	9 *25*	4 *11*									36	2·449
,,	5-9-32				1 *2*	3 *6*	5 *9*	3 *6*	5 *9*	10 *19*	9 *17*	11 *21*	3 *6*	1 *2*	2 *4*							53	2·430
,,	30-10-32								1	1	–	–	1	3	2	3						11	2·646
II	3-9-31					1 *5*	1 *5*	2 *10*	1 *5*	4 *20*	1 *5*	4 *20*	3 *15*	3 *15*								20	2·491
,,	8-2-32				1 *2*	– *–*	– *–*	4 *7*	8 *15*	13 *24*	8 *15*	11 *20*	5 *9*	2 *4*	1 *2*	1 *2*						54	2·440
,,	22-2-32						2 *6*	3 *9*	2 *6*	4 *11*	4 *11*	6 *17*	10 *29*	2 *6*	– *–*	2 *6*						35	2·511
,,	5-4-32								3 *5*	3 *5*	8 *14*	3 *5*	7 *12*	7 *12*	7 *12*	8 *14*	10 *17*	2 *3*	1 *2*			59	2·638

,,	2-5-32						1 *1*	2 *1*	10 *7*	8 *6*	10 *7*	31 *22*	26 *18*	20 *14*	15 *11*	10 *7*	6 *4*	2 *1*				141	2·556
,,	16-5-32									2 *5*	7 *17*	11 *26*	8 *19*	3 *7*	5 *12*	2 *5*	2 *5*	1 *2*	1 *2*			42	2·548
,,	30-5-32							3 *2*	7 *4*	10 *6*	20 *13*	19 *12*	33 *21*	24 *15*	21 *13*	13 *8*	5 *3*	1 *1*	1 *1*	1 *1*	1 *1*	159	2·572
,,	13-6-32			1 *1*	3 *2*	8 *5*	14 *9*	12 *8*	13 *8*	17 *11*	16 *10*	8 *5*	21 *14*	22 *14*	10 *6*	1 *1*	5 *3*	2 *1*	– *–*	1 *1*		154	2·462
,,	27-6-32					1 *2*	1 *2*	4 *8*	8 *16*	8 *16*	5 *10*	7 *14*	3 *6*	5 *10*	4 *8*	2 *4*	1 *2*	1 *2*				50	2·468
,,	11-7-32					3 *2*	4 *3*	13 *9*	12 *9*	16 *12*	27 *19*	21 *15*	22 *16*	13 *9*	2 *1*	4 *3*	1 *1*	1 *1*				139	2·474
,,	25-7-32		1 *3*	– *–*	– *–*	3 *8*	1 *3*	3 *8*	2 *5*	7 *18*	4 *10*	7 *18*	6 *15*	1 *3*	1 *3*	2 *5*	– *–*	1 *3*				39	2·471
,,	8-8-32		2 *1*	1 *–*	10 *5*	12 *6*	14 *7*	21 *10*	23 *11*	35 *17*	23 *11*	29 *14*	11 *5*	15 *7*	8 *4*	2 *1*	2 *1*					208	2·409
,,	22-8-32			2 *7*	1 *4*	1 *4*	3 *11*	2 *7*	5 *18*	3 *11*	3 *11*	*3* *11*	*2* *7*	*1* *4*	*2* *7*							28	2·385
,,	5-9-32				1 *1*	5 *5*	7 *7*	9 *9*	19 *19*	23 *23*	11 *11*	13 *13*	7 *7*	2 *2*	1 *1*	1 *1*	3 *3*					102	2·401
,,	30-10-32										1 *6*	2 *11*	6 *33*	4 *22*	3 *17*	– *–*	1 *6*	1 *6*				18	2·599
IV	25-26-1-32				1 *–*	2 *1*	4 *2*	10 *5*	16 *7*	23 *11*	36 *17*	43 *20*	24 *11*	22 *10*	18 *8*	6 *3*	8 *4*	2 *1*				215	2·504
,,	8-2-32					2 *2*	4 *3*	4 *3*	8 *7*	8 *7*	16 *14*	18 *15*	12 *10*	17 *14*	13 *11*	9 *8*	5 *4*	2 *2*				118	2·536
,,	22-2-32							3 *10*	– *–*	1 *3*	7 *24*	2 *7*	6 *21*	2 *7*	6 *21*	1 *3*	– *–*	1 *3*				29	2·556
,,	7-3-32							1 *2*	1 *2*	2 *5*	3 *7*	6 *15*	5 *12*	5 *12*	6 *15*	4 *10*	4 *10*	2 *5*	1 *2*	1 *2*		41	2·624
,,	2-5-32							1 *1*	3 *2*	3 *2*	9 *5*	32 *19*	36 *21*	30 *17*	20 *12*	23 *13*	11 *6*	2 *1*	1 *1*	1 *1*		172	2·597
,,	16-5-32								1 *1*	2 *1*	6 *4*	8 *5*	17 *10*	27 *16*	35 *21*	29 *18*	19 *12*	12 *7*	6 *4*	1 *1*	2 *1*	165	2·680
,,	30-5-32						1 *6*	– *–*	– *–*	2 *11*	4 *22*	1 *6*	2 *11*	2 *11*	3 *17*	– *–*	2 *11*	– *–*	1 *6*			18	2·579
,,	13-6-32					3 *2*	10 *6*	16 *10*	34 *21*	26 *16*	24 *15*	19 *12*	11 *7*	7 *4*	6 *4*	2 *1*	1 *1*	1 *1*				161	2·413
,,	27-6-32				2 *1*	2 *1*	19 *7*	31 *12*	43 *16*	35 *13*	50 *19*	36 *14*	20 *8*	15 *6*	7 *3*	1 *–*	3 *1*	1 *–*				265	2·431
,,	11-7-32			1 *1*	2 *1*	7 *4*	9 *5*	21 *11*	35 *18*	31 *16*	19 *9*	23 *12*	15 *8*	11 *6*	13 *7*	3 *2*	3 *2*	1 *1*				194	2·415
,,	11-12-7-32			2 *1*	1 *–*	10 *4*	16 *6*	38 *14*	49 *18*	43 *16*	46 *17*	27 *10*	20 *7*	9 *3*	8 *3*	3 *1*	1 *–*					273	2·402
,,	25-7-32		1 *1*	– *–*	– *–*	4 *4*	4 *4*	11 *11*	11 *11*	13 *14*	19 *20*	15 *16*	6 *6*	6 *6*	3 *3*	3 *3*						96	2·443
,,	8-8-32	1 *1*	1 *1*	4 *2*	4 *2*	12 *7*	11 *6*	13 *7*	19 *11*	10 *6*	33 *19*	23 *13*	15 *9*	8 *5*	10 *6*	7 *4*	1 *1*	1 *1*	2 *1*			175	2·451
,,	22-8-32			2 *2*	7 *6*	5 *4*	8 *7*	9 *8*	8 *7*	11 *10*	16 *14*	10 *9*	16 *14*	6 *5*	3 *3*	4 *4*	4 *4*	2 *2*	– *–*	1 *1*		112	2·452
,,	5-9-32			3 *4*	4 *5*	6 *7*	9 *11*	10 *12*	7 *8*	10 *12*	8 *9*	9 *11*	7 *8*	3 *4*	6 *7*	2 *2*	– *–*	1 *1*				85	2·398

TABLE III.

STAGE V. LENGTH OF CARAPACE IN MM.

Station.	Date.	1·674– 1·728	1·728– 1·782	1·782 1·836	1·836– 1·890	1·890– 1·944	1·944– 1·998	1·998– 2·052	2·052– 2·106	2·106– 2·160	2·160– 2·214	2·214– 2 268	2·268– 2·322	2·322– 2·376	2·376– 2·430	2·430– 2·484	2·484– 2·538	2·538– 2·592	2·592– 2·646	2·646– 2·700	2·700– 2·754	Number measured.	Median length.
I	3-9-31				7 *3*	14 *6*	27 *12*	26 *12*	20 *9*	19 *9*	14 *6*	24 *11*	25 *11*	19 *9*	15 *7*	9 *4*	4 *2*					223	2·157
,,	15-9-31			2 *3*	2 *3*	8 *12*	14 *21*	12 *18*	6 *9*	2 *3*	5 *7*	9 *13*	4 *6*	3 *4*	– *–*	– *–*	– *–*	– *–*	1 *1*			68	2·036
,,	21-10-31		1 *1*	2 *2*	6 *5*	14 *11*	19 *15*	8 *6*	13 *10*	7 *6*	17 *14*	15 *12*	9 *7*	3 *2*	5 *4*	5 *4*						124	2·104
,,	16-11-31				3 *2*	5 *4*	8 *7*	14 *11*	13 *11*	11 *9*	10 *8*	12 *10*	10 *8*	10 *8*	12 *10*	11 *9*	3 *2*	1 *1*				123	2·203
,,	30-11-31				1 *1*	3 *4*	2 *3*	3 *4*	7 *9*	5 *6*	12 *16*	5 *6*	11 *14*	5 *6*	7 *9*	9 *12*	5 *6*	2 *3*				77	2·273
,,	11-1-32					2 *5*	3 *8*	2 *5*	7 *19*	4 *11*	3 *8*	4 *11*	3 *8*	1 *3*	2 *5*	6 *16*						37	2·178
,,	21-3-32						2 *1*	2 *1*	1 *1*	3 *2*	12 *7*	30 *17*	41 *24*	45 *26*	28 *16*	7 *4*	3 *2*					174	2·318
,,	28-3-32							1 *–*	7 *2*	16 *5*	33 *10*	45 *13*	50 *15*	74 *22*	74 *22*	28 *8*	11 *3*	4 *1*	*1* *–*			344	2·337
,,	5-4-32					1 *1*	4 *2*	8 *4*	10 *6*	11 *6*	23 *13*	28 *15*	39 *22*	24 *13*	12 *7*	14 *8*	5 *3*	1 *1*	1 *1*			181	2·276
,,	18-4-32				3 *2*	3 *2*	10 *6*	15 *8*	27 *15*	20 *11*	14 *8*	22 *12*	15 *8*	20 *11*	15 *8*	9 *5*	4 *2*	2 *1*	1 *1*			180	2·208
,,	27-4-32				1 *1*	1 *1*	4 *4*	7 *7*	14 *15*	13 *14*	7 *7*	8 *8*	5 *5*	11 *12*	16 *17*	7 *7*	1 *1*					95	2·221
,,	2-5-32						1 *1*	– *–*	2 *2*	11 *9*	12 *10*	9 *8*	12 *10*	15 *13*	25 *21*	18 *15*	9 *8*	4 *3*				118	2·367
,,	16-5-32								1 *1*	4 *5*	10 *12*	4 *5*	3 *4*	6 *7*	17 *20*	15 *18*	10 *12*	8 *10*	4 *5*	2 *2*		84	2·422
,,	23-5-32							6 *2*	10 *4*	20 *8*	25 *10*	25 *10*	28 *11*	35 *14*	34 *14*	34 *14*	17 *7*	11 *4*	3 *1*			248	2·338
,,	30-5-32						4 *7*	4 *7*	2 *3*	5 *8*	9 *15*	5 *8*	6 *10*	5 *8*	7 *11*	4 *7*	5 *8*	5 *8*				61	2·286
,,	7-6-32		3 *1*	– *–*	*–*	8 *3*	17 *6*	29 *10*	50 *17*	60 *20*	36 *12*	19 *6*	27 *9*	11 *4*	15 *5*	14 *5*	5 *2*	5 *2*	2 *1*			118–30 m. 301 (⅕)	2·146
,,	,,					3 *10*	7 *23*	3 *10*	5 *17*	8 *27*	1 *3*	– *–*	1 *3*	1 *3*	– *–*	1 *3*						30–0 m. 30	2·079
,,	,,		15 *1*	– *–*	– *–*	43 *3*	92 *6*	143 *9*	255 *17*	308 *20*	161 *10*	95 *6*	136 *9*	56 *4*	75 *5*	71 *5*	25 *2*	25 *2*	10 *1*			118–0 m. (calc.) 1536	2·144
,,	13-6-32			2 *2*	1 *1*	5 *4*	12 *11*	13 *12*	17 *15*	20 *18*	13 *12*	9 *8*	10 *9*	3 *3*	3 *3*	3 *3*	– *–*	– *–*	– *–*	1 *1*		112	2·124
,,	27-6-32					3 *3*	10 *9*	11 *10*	5 *5*	12 *11*	9 *8*	18 *17*	19 *18*	7 *7*	9 *8*	4 *4*	– *–*	1 *1*				107	2·226
,,	11-7-32					6 *3*	11 *5*	17 *7*	27 *11*	25 *10*	18 *8*	26 *11*	22 *9*	26 *11*	26 *11*	23 *10*	10 *4*	2 *1*	1 *–*			240	2·248
,,	25-7-32		1 *–*	9 *3*	18 *6*	40 *14*	44 *16*	37 *13*	40 *14*	30 *11*	10 *3*	17 *6*	12 *4*	12 *4*	4 *1*	1 *–*	3 *1*					278	2·038
,,	8-8-32				1 *2*	– *–*	7 *13*	11 *20*	6 *11*	5 *9*	2 *4*	9 *16*	8 *15*	5 *9*	1 *2*							55	2·138

,,	22-8-32		3 *1*	8 *4*	22 *10*	28 *12*	24 *11*	26 *12*	24 *11*	15 *7*	23 *10*	25 *11*	16 *7*	7 *3*	3 *1*	2 *1*						225	2·057
,,	5-9-32			7 *3*	7 *3*	32 *14*	35 *16*	39 *18*	24 *11*	9 *4*	13 *6*	17 *8*	17 *8*	13 *6*	6 *3*	2 *1*						221	2·040
,,	30-10-32			2 *1*	5 *2*	15 *5*	11 *4*	17 *6*	20 *7*	18 *6*	24 *8*	35 *12*	26 *9*	17 *6*	24 *8*	38 *12*	33 *11*	17 *6*	1 *–*	1 *–*		304	2·279
II	3-9-31			1 *–*	10 *3*	25 *8*	44 *13*	50 *15*	29 *9*	31 *9*	31 *9*	29 *9*	18 *5*	22 *7*	20 *6*	14 *4*	2 *1*	2 *1*				328	2·116
,,	15-9-31			2 *2*	2 *2*	6 *5*	10 *8*	12 *10*	14 *11*	13 *11*	17 *14*	8 *7*	8 *7*	9 *7*	13 *11*	5 *4*	4 *3*					123	2·170
,,	1-10-31					3 *2*	10 *8*	8 *6*	9 *7*	13 *10*	14 *11*	15 *11*	10 *8*	7 *5*	19 *14*	15 *11*	6 *5*	2 *2*	1 *1*			132	2·248
,,	21-10-31					1 *1*	6 *5*	6 *5*	11 *9*	11 *9*	14 *12*	8 *7*	7 *6*	15 *12*	18 *15*	13 *11*	6 *5*	4 *3*				120	2·295
,,	5-11-31				2 *1*	7 *5*	5 *4*	19 *14*	15 *11*	13 *10*	16 *12*	11 *8*	11 *8*	9 *7*	11 *8*	10 *7*	2 *1*	1 *1*	2 *1*			134	2·182
,,	16-11-31				1 *1*	3 *3*	9 *9*	10 *10*	6 *6*	12 *11*	11 *11*	9 *9*	9 *9*	5 *5*	15 *14*	8 *8*	3 *3*	2 *2*				103	2·214
,,	30-11-31				1 *1*	1 *1*	7 *5*	8 *6*	6 *4*	15 *11*	20 *15*	16 *12*	14 *10*	12 *9*	13 *10*	8 *6*	8 *6*	5 *4*	– *–*	1 *1*		135	2·248
,,	14-12-31			1 *1*	1 *1*	5 *4*	8 *6*	14 *11*	8 *6*	8 *6*	8 *6*	11 *9*	13 *10*	17 *13*	11 *9*	16 *12*	7 *5*	– *–*	1 *1*			129	2·272
,,	30-12-31				1 *1*	1 *1*	3 *2*	13 *9*	12 *8*	14 *10*	21 *15*	13 *9*	4 *3*	14 *10*	16 *11*	21 *15*	7 *5*	2 *1*	1 *1*			143	2·243
,,	11-1-32				1 *1*	– *–*	5 *4*	10 *8*	12 *9*	12 *9*	12 *9*	15 *12*	12 *9*	6 *5*	13 *10*	20 *16*	9 *7*	2 *2*				129	2·261
,,	25-1-32					2 *2*	5 *4*	16 *12*	12 *9*	14 *11*	19 *14*	20 *15*	15 *11*	12 *9*	6 *5*	8 *6*	3 *2*					132	2·210
,,	8-2-32				2 *5*	2 *5*	3 *7*	3 *7*	5 *12*	6 *14*	7 *17*	5 *12*	3 *7*	3 *7*	1 *2*	1 *2*	– *–*	– *–*	– *–*	1 *2*		42	2·164
,,	21-3-32								1 *4*	1 *4*	3 *12*	10 *40*	4 *16*	2 *8*	3 *12*	– *–*	1 *4*					25	2·257
,,	5-4-32					2 *1*	4 *3*	1 *1*	12 *8*	12 *8*	26 *18*	31 *22*	23 *16*	15 *10*	10 *7*	8 *6*						144	2·240
,,	2-5-32					1 *–*	3 *1*	2 *1*	1 *–*	5 *2*	22 *10*	10 *4*	18 *8*	32 *14*	48 *22*	36 *16*	35 *16*	8 *4*	1 *–*	1 *–*		223	2·396
,,	16-5-32						2 *2*	– *–*	6 *7*	9 *10*	11 *13*	6 *7*	8 *9*	5 *6*	13 *15*	14 *16*	8 *9*	4 *5*				86	2·338
,,	30-5-32								10 *6*	12 *7*	15 *9*	20 *12*	11 *7*	17 *10*	30 *18*	25 *15*	17 *10*	4 *2*	1 *1*	– *–*	1 *1*	163	2 366
,,	13-6-32		1 *1*	2 *1*	2 *1*	2 *1*	8 *4*	8 *4*	17 *8*	12 *6*	21 *11*	8 *4*	13 *6*	26 *13*	29 *15*	28 *14*	12 *6*	9 *4*	2 *1*			159–30 m. 200	2·336
,,	,,	1 *–*	5 *1*	14 *4*	29 *7*	63 *16*	71 *18*	71 *18*	47 *12*	25 *6*	15 *4*	16 *4*	17 *4*	10 *3*	4 *1*	2 *–*	1 *–*					30–0 m. 391	2·008
,,	,,	1 *–*	6 *1*	16 *3*	31 *5*	65 *11*	79 *13*	79 *13*	64 *11*	37 *6*	36 *6*	24 *4*	30 *5*	36 *6*	33 *6*	30 *5*	13 *2*	9 *2*	2 *–*			159–0 m. 591	2·068
,,	27-6-32				2 *1*	1 *–*	11 *5*	9 *4*	23 *11*	14 *7*	19 *9*	12 *6*	13 *6*	23 *11*	31 *15*	24 *12*	16 *8*	4 *2*				202	2·312
,,	11-7-32					3 *1*	10 *4*	25 *9*	20 *8*	27 *10*	19 *7*	26 *9*	26 *9*	29 *11*	21 *8*	35 *13*	16 *6*	5 *2*	2 *1*	1 *–*		265	2·274
,,	25-7-32		1 *–*	1 *–*	6 *2*	10 *3*	10 *3*	24 *7*	33 *10*	38 *12*	24 *7*	18 *6*	30 *9*	26 *8*	34 *11*	23 *7*	9 *3*	8 *2*	1 *–*	– *–*	1 *–*	297	2·216
,,	8-8-32			3 *1*	5 *2*	13 *4*	31 *11*	37 *13*	30 *10*	26 *9*	23 *8*	35 *12*	22 *8*	15 *5*	21 *7*	19 *7*	9 *3*	2 *1*				291	2·162
,,	22-8-32		1 *–*	2 *1*	10 *3*	13 *4*	43 *14*	41 *13*	37 *12*	33 *11*	16 *5*	29 *9*	28 *9*	23 *7*	19 *6*	12 *4*	3 *1*	– *–*	1 *–*			311	2·121

TABLE III—(*continued*).

Station.	Date.	1·674–1·728	1·728–1·782	1·782–1·836	1·836–1·890	1·890–1·944	1·944–1·998	1·998–2·052	2·052–2·106	2·106–2·160	2·160 2·214	2·214–2·268	2·268–2·322	2·322–2·376	2·376–2·430	2·430–2·484	2·484–2·538	2·538–2·592	2·592–2·646	2·646–2·700	2·700–2·754	Number measured.	Median length.
II	5-9-32			2 *1*	8 *3*	21 *8*	34 *13*	39 *15*	31 *12*	20 *8*	19 *7*	23 *9*	17 *6*	16 *6*	16 *6*	10 *4*	5 *2*	2 *1*				263	2·101
,,	30-10-32		1 –	7 *3*	11 *4*	24 *10*	25 *10*	24 *10*	17 *7*	15 *6*	22 *9*	21 *9*	16 *7*	11 *4*	17 *7*	16 *7*	9 *4*	9 *4*	1 –			246	2·158
IV	3-9-31							1 –	3 *1*	5 *2*	15 *6*	22 *9*	14 *6*	32 *13*	58 *24*	52 *21*	26 *11*	12 *5*	2 *1*	1 –		243	2·403
,,	15-9-31					1 *1*	– –	– –	– –	8 *7*	7 *6*	6 *5*	15 *13*	14 *12*	23 *20*	29 *25*	11 *9*	3 *3*				117	2·395
,,	1-10-31							2 *2*	– –	– –	7 *6*	6 *5*	13 *12*	9 *8*	18 *16*	26 *23*	23 *20*	9 *8*				113	2·434
,,	21-10-31						1 *1*	3 *3*	4 *3*	1 *1*	13 *11*	9 *8*	18 *15*	3 *3*	17 *14*	25 *21*	15 *13*	7 *6*	2 *2*			118	2·400
,,	5-11-31								1 *1*	2 *2*	6 *5*	7 *6*	12 *10*	18 *15*	18 *15*	31 *26*	15 *13*	9 *8*	1 *1*			120	2·419
,,	16-11-31					1 *1*	– –	– –	1 *1*	3 *3*	5 *4*	6 *5*	10 *9*	10 *9*	22 *19*	31 *27*	16 *14*	10 *9*				115	2·430
,,	30-11-31							2 *1*	2 *1*	4 *3*	6 *4*	11 *8*	12 *8*	16 *11*	20 *14*	29 *20*	25 *18*	13 *9*	2 *1*			142	2·426
,,	14-12-31						1 *1*	1 *1*	– –	2 *2*	9 *8*	4 *4*	8 *7*	9 *8*	20 *19*	22 *20*	21 *19*	10 *9*	1 *1*			108	2·431
,,	29-12-31					1 *1*	3 *3*	1 *1*	5 *4*	8 *7*	10 *8*	10 *8*	6 *5*	6 *5*	14 *12*	20 *17*	21 *18*	10 *8*	5 *4*			120	2·417
,,	11-1-32				1 *1*	– –	1 *1*	2 *2*	2 *2*	5 *5*	6 *6*	8 *7*	10 *9*	8 *7*	15 *14*	24 *22*	21 *20*	3 *3*	– –	1 *1*		107	2·416
,,	25-1-32						1 *1*	1 *1*	6 *6*	5 *5*	4 *4*	12 *12*	4 *4*	8 *8*	13 *13*	21 *20*	17 *17*	9 *9*	– –	1 *1*		102	2·420
,,	8-2-32				1 *1*	–	1 *1*	3 *2*	5 *4*	15 *12*	13 *10*	12 *10*	12 *10*	10 *8*	15 *12*	14 *11*	16 *13*	5 *4*	2 *2*			124	2·325
,,	22-2-32						1 *1*	2 *2*	5 *5*	7 *7*	4 *4*	12 *12*	11 *11*	11 *11*	11 *11*	19 *18*	10 *10*	10 *10*	2 *2*			105	2·376
,,	7-3-32				1 *1*	1 *1*	2 *2*	5 *4*	6 *5*	5 *4*	3 *2*	12 *10*	7 *6*	12 *10*	20 *16*	17 *14*	23 *19*	7 *6*	2 *2*			123	2·398
,,	16-5-32							2 *2*	1 *1*	5 *5*	8 *8*	9 *9*	21 *20*	11 *11*	17 *16*	12 *12*	8 *8*	7 *7*	2 *2*			103	2·351
,,	30-5-32				1 *1*	2 *1*	5 *3*	4 *2*	14 *8*	5 *3*	18 *11*	20 *12*	25 *15*	9 *5*	14 *8*	21 *13*	17 *10*	9 *5*	2 *1*			166	2·299
,,	13-6-32		1 –	– –	– –	2 –	6 *1*	15 *4*	24 *6*	27 *6*	35 *8*	39 *9*	43 *10*	41 *10*	62 *15*	65 *15*	38 *9*	25 *6*	– –	1 –		424	2·349
,,	27-6-32				5 *3*	2 *1*	2 *1*	7 *5*	13 *9*	7 *5*	11 *8*	15 *10*	19 *13*	17 *12*	27 *19*	15 *10*	6 *4*					146	2·301
,,	11-7-32					5 *2*	8 *3*	11 *3*	25 *8*	29 *9*	26 *8*	30 *9*	32 *10*	62 *19*	45 *14*	23 *7*	19 *6*	2 *1*	2 *1*			319	2·312
,,	25-7-32				3 *1*	3 *1*	18 *7*	6 *2*	23 *8*	24 *9*	23 *8*	26 *9*	29 *10*	32 *12*	38 *14*	29 *10*	19 *7*	3 *1*	1 –			277	2·292
,,	8-8-32			1 –	2 *1*	7 *3*	11 *5*	15 *6*	25 *10*	16 *7*	14 *6*	25 *10*	20 *8*	34 *14*	36 *15*	19 *8*	8 *3*	4 *2*	2 *1*			239	2·279
,,	22-8-32				1 –	8 *3*	8 *3*	18 *7*	19 *8*	23 *9*	21 *8*	21 *8*	30 *12*	32 *13*	29 *12*	23 *9*	12 *5*	3 *1*				248	2·277
,,	5-9-32				3 *1*	8 *4*	16 *7*	14 *6*	23 *10*	22 *10*	13 *6*	22 *10*	18 *8*	30 *14*	23 *10*	16 *7*	12 *5*	1 –				221	2·322
,,	30-10-32				2 *1*	14 *6*	14 *6*	18 *7*	19 *8*	18 *7*	21 *9*	22 *9*	28 *12*	24 *10*	28 *12*	20 *8*	9 *4*	2 *1*	1			240	2·250

TABLE IV. STAGE IV. LENGTH OF CARAPACE IN MM.

Station.	Date.	1·188–1·242	1·242–1·296	1·296–1·350	1·350–1·404	1·404–1·458	1·458–1·512	1·512–1·566	1·566–1·620	1·620–1·674	1·674–1·728	1·728–1·782	1·782–1·836	1·836–1·890	1·890–1·944	1·944–1·998	1·998–2·052	2·052–2·106	Number measured.	Median length.
I	3-9-31						1 *1*	2 *2*	13 *15*	18 *20*	17 *19*	13 *15*	21 *24*	4 *4*					89	1·709
..	15-9-31		1 *3*	– –	– –	3 *9*	3 *9*	4 *11*	9 *26*	5 *14*	6 *17*	4 *11*							35	1·608
..	21-10-31			1 *3*	–	– –	– –	4 *10*	8 *21*	10 *26*	4 *10*	5 *13*	5 *13*	1 *3*					38	1·655
..	21-3-32										3 *7*	8 *18*	9 *20*	11 *25*	7 *16*	4 *9*	2 *5*		44	1·848
..	28-3-32							1 *1*	3 *2*	5 *3*	13 *8*	22 *13*	34 *21*	41 *25*	27 *16*	14 *9*	4 *2*		164	1·842
..	5-4-32						1 *1*	3 *2*	8 *5*	21 *14*	24 *16*	18 *12*	29 *20*	16 *11*	19 *13*	5 *3*	2 *1*		146	1·777
..	18-4-32					1 *1*	– –	4 *3*	6 *5*	13 *11*	18 *15*	20 *17*	20 *17*	27 *22*	9 *7*	3 *2*			121	1·779
..	16-5-32											8 *7*	4 *3*	9 *8*	20 *17*	32 *28*	26 *22*	17 *15*	116	1·973
..	23-5-32							1 *1*	6 *4*	14 *10*	19 *14*	23 *17*	29 *21*	21 *15*	17 *12*	6 *4*	3 *2*		119–30 m. (⅕) 139	1·795
..	,,							1 *1*	2 *1*	9 *7*	12 *9*	14 *10*	25 *18*	34 *25*	22 *16*	11 *8*	6 *4*	1 *1*	30–0 m. 137	1·845
..	,,							6 *1*	32 *4*	79 *10*	107 *13*	129 *16*	170 *20*	139 *17*	107 *13*	41 *5*	21 *3*	1 –	119–0 m. calc. 832	1·802
..	30-5-32					1 *1*	3 *3*	6 *6*	14 *13*	20 *19*	15 *14*	11 *10*	24 *22*	6 *6*	6 *6*	1 *1*	1 *1*		110–30 m. (⅙) 108	1·712
..	,,				3 *3*	2 *2*	4 *4*	9 *9*	21 *20*	21 *20*	15 *15*	9 *9*	9 *9*	4 *4*	2 *2*	2 *2*	– –	1 *1*	30–0 m. 102	1·652
..	,,				3 –	8 *1*	22 *3*	45 *6*	105 *14*	141 *19*	105 *14*	75 *10*	153 *20*	40 *5*	38 *5*	8 *1*	6 *1*	1 –	110–0 m. calc. 750	1·700
..	7-6-32						5 *2*	7 *3*	35 *17*	50 *24*	37 *18*	26 *13*	18 *9*	19 *9*	7 *3*	3 *1*			118–30 m. (⅕) 207	1·684
..	,,				1 *1*	2 *2*	6 *7*	11 *13*	18 *21*	21 *24*	15 *17*	5 *6*	7 *8*	1 *1*					30–0 m. 87	1·635
..	,,				1 –	2 –	31 *3*	46 *4*	193 *17*	271 *24*	200 *18*	135 *12*	97 *9*	96 *9*	35 *3*	15 *1*			118–0 m. calc. 1122	1·679
..	13-6-32					1 *2*	– –	8 *17*	10 *21*	9 *19*	9 *19*	3 *6*	4 *8*	2 *4*	1 *2*				47	1·650
..	27-6-32							3 *13*	5 *21*	3 *13*	3 *13*	7 *29*	1 *4*	1 *4*	1 *4*				24	1·701
..	11-7-32						2 *1*	14 *8*	19 *10*	26 *14*	32 *17*	23 *13*	28 *15*	28 *15*	10 *5*	1 *1*			183	1·726
..	25-7-32							10 *5*	30 *14*	34 *16*	51 *24*	40 *19*	30 *14*	14 *7*	2 *1*				211	1·708
..	8-8-32					1 *2*	7 *12*	15 *26*	5 *9*	10 *18*	8 *14*	5 *9*	4 *7*	2 *4*					57	1·625
..	22-8-32			1 *1*	– –	2 *2*	5 *4*	15 *11*	27 *20*	19 *14*	26 *20*	24 *18*	11 *8*	2 *2*					132	1·667
..	5-9-32					1 *2*	4 *10*	3 *7*	8 *20*	5 *12*	7 *17*	3 *7*	6 *15*	3 *7*	1 *2*				41	1·674
..	30-10-32					1	1	–	–	1	5	–	2	–	1				11	1·706
II	3-9-31						2 *1*	21 *6*	44 *12*	54 *14*	70 *19*	76 *20*	69 *18*	31 *8*	9 *2*	2 *1*			378	1·727
..	15-9-31			1 *1*	1 *1*	3 *3*	5 *4*	9 *8*	10 *8*	13 *11*	22 *18*	11 *9*	23 *19*	18 *15*	3 *3*				119	1·718
..	1-10-31							2 *2*	7 *7*	9 *9*	14 *14*	18 *18*	24 *23*	21 *20*	5 *5*	2 *2*			102	1·785
..	21-10-31							2 *1*	8 *6*	20 *14*	16 *11*	25 *18*	22 *16*	22 *16*	20 *14*	5 *4*	1 *1*		141	1·782
..	16-11-31								4 *11*	1 *3*	8 *21*	3 *8*	5 *13*	4 *11*	8 *21*	4 *11*	1 *3*		38	1·820

TABLE IV—(*continued*).

Station.	Date.	1·188–1·242	1·242–1·296	1·296–1·350	1·350–1·404	1·404–1·458	1·458–1·512	1·512–1·566	1·566–1·620	1·620–1·674	1·674–1·728	1·728–1·782	1·782–1·836	1·836–1·890	1·890–1·944	1·944–1·998	1·998–2·052	2·052–2·106	Number measured.	Median length.
II	30-11-31						1 *3*	1 *3*	1 *3*	– *–*	7 *22*	5 *16*	6 *19*	3 *9*	5 *16*	2 *6*	1 *3*		32	1·796
,,	21-3-32									1 *3*	3 *9*	4 *11*	10 *29*	11 *31*	2 *6*	4 *11*			35	1·836
,,	5-4-32								9 *9*	15 *15*	12 *12*	15 *15*	16 *16*	16 *16*	10 *10*	5 *5*	1 *1*	1 *1*	100	1·780
,,	16-5-32										1 *2*	8 *13*	15 *25*	16 *27*	12 *20*	5 *8*	2 *3*	1 *2*	60	1·858
,,	30-5-32								2 *2*	4 *5*	14 *16*	9 *10*	11 *13*	18 *20*	18 *20*	10 *11*	2 *2*		166–30 m. 88	1·850
,,	,,							8 *13*	10 *16*	14 *23*	12 *20*	8 *13*	6 *10*	2 *3*	– *–*	1 *2*			30–0 m. ($\frac{3}{10}$) 61	1·670
,,	,,							27 *9*	35 *12*	51 *17*	54 *18*	36 *12*	31 *11*	25 *9*	18 *6*	13 *4*	2 *1*		166–0 m. calc. 292	1·708
,,	13-6-32					1 *1*	6 *4*	18 *11*	23 *14*	22 *14*	32 *20*	28 *18*	16 *10*	8 *5*	3 *2*	2 *1*			159	1·691
,,	27-6-32								1 *6*	2 *12*	1 *6*	6 *37*	4 *25*	1 *6*	1 *6*				16	1·769
,,	11-7-32							2 *1*	3 *2*	4 *3*	33 *22*	36 *24*	29 *19*	27 *18*	14 *9*	2 *1*	1 *1*		151	1·779
,,	25-7-32						2 *1*	4 *3*	12 *9*	24 *17*	27 *19*	17 *12*	30 *21*	15 *11*	6 *4*	1 *1*			165–30 m. 139	1·731
,,	,,					1 *1*	3 *3*	18 *18*	23 *23*	22 *22*	16 *16*	13 *13*	4 *4*						30 -0 m. 100	1·634
,,	,,					1 *–*	5 *2*	22 *9*	35 *15*	46 *19*	43 *18*	30 *13*	34 *14*	15 *6*	6 *3*	1 *–*			165–0 m. 239	1·688
,,	8-8-32						3 *1*	4 *1*	23 *7*	44 *14*	63 *20*	86 *28*	58 *19*	22 *7*	6 *2*	– *–*	1 *–*		310	1·739
,,	22-8-32				–	1 *–*	6 *2*	9 *3*	22 *8*	41 *16*	51 *19*	63 *24*	43 *16*	23 *9*	3 *1*	1 *–*			264	1·729
,,	5-9-32					1 *–*	– *–*	4 *2*	18 *7*	34 *13*	40 *16*	71 *28*	56 *22*	24 *10*	5 *2*				253	1·751
,,	30-10-32							2 *10*	– *–*	1 *5*	4 *20*	6 *30*	3 *15*	3 *15*	1 *5*				20	1·760
IV	3-9-31								7 *9*	8 *10*	10 *12*	11 *13*	11 *13*	13 *16*	19 *23*	3 *4*			82	1·809
,,	15-9-31							4 *7*	5 *8*	10 *16*	7 *11*	8 *13*	6 *10*	7 *11*	7 *11*	7 *11*			61	1·762
,,	25-26-1-32						1 *2*	– *–*	4 *6*	9 *14*	11 *17*	10 *15*	9 *14*	12 *18*	7 *11*	2 *3*			65	1·771
,,	2-5-32									3 *8*	5 *14*	8 *22*	8 *22*	7 *19*	4 *11*	1 *3*			36	1·799
,,	16-5-32							3 *2*	2 *1*	14 *10*	14 *10*	36 *26*	34 *24*	25 *18*	10 *7*	2 *1*			140	1·784
,,	30-5-32								2 *4*	1 *2*	10 *20*	7 *14*	8 *16*	10 *20*	7 *14*	4 *8*	1 *2*		50	1·819
,,	13-6-32						1 *1*	1 *1*	3 *4*	5 *7*	5 *7*	13 *18*	9 *12*	12 *16*	19 *26*	4 *5*	1 *1*		73	1·836
,,	27-6-32							1 *4*	2 *8*	2 *8*	5 *20*	3 *12*	8 *32*	2 *8*	2 *8*				25	1·782
,,	11-7-32						1 *–*	6 *2*	16 *6*	28 *11*	19 *8*	30 *12*	60 *24*	57 *23*	28 *11*	7 *3*			252	1·806
,,	25-7-32					2 *1*	4 *2*	15 *7*	25 *12*	30 *15*	32 *16*	29 *14*	31 *15*	25 *12*	8 *4*	3 *2*			204	1·719
,,	8-8-32							5 *3*	25 *15*	10 *6*	20 *12*	28 *17*	29 *17*	31 *19*	19 *11*				167	1·774
,,	22-8-32					1 *–*	4 *1*	9 *3*	29 *10*	45 *16*	36 *13*	42 *15*	40 *14*	43 *15*	24 *9*	5 *2*			278	1·748
,,	5-9-32					1 *–*	1 *–*	9 *4*	37 *16*	39 *16*	48 *20*	33 *14*	23 *10*	23 *10*	16 *7*	5 *2*	2 *1*		237	1·710
,,	30-10-32							3 *3*	10 *12*	18 *21*	12 *14*	15 *17*	4 *5*	16 *19*	8 *9*				86	1·730

On the Biology of *Calanus finmarchicus*. III. Vertical Distribution and Diurnal Migration in the Clyde Sea-Area.

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With 4 Figures in the Text.

CONTENTS.

INTRODUCTION.

Of recent years the attention of a number of workers has been directed towards the problem of vertical distribution of plankton organisms, and in particular to the diurnal migrations made by many of these animals.

Russell (1926) and others have considered that variation in the intensity of light throughout every 24 hours was the main cause of such changes in vertical distribution.

Despite one or two facts which, at first sight, fail to support it, this hypothesis taken as a whole seems to explain the vertical movements of the plankton and, until the full explanation is found, it may be taken as a good working hypothesis. It appears probable from the evidence that change in light intensity, while playing a large part in controlling diurnal migrations, is not the sole factor concerned.

The results of the work on Calanus up to the present may be summed up as follows. The young stages and nauplii are found in the upper layers of water; the older stages live deeper and the males usually live deeper than the females. In the words of With (1915, p. 28), and neglecting the difference between the sexes, "the younger the stage of development the nearer the surface do the specimens live."

These general conclusions on the vertical distribution of Calanus arrived at by different workers are based on hauls taken in the open waters of the oceans and to depths down to 1500 metres. The hauls were made with closing nets hauled through distances varying from 50 to 700 metres at one step.

Most of the work on the diurnal migrations of Calanus, on the other hand, has been done by Russell in the English Channel, in water where the depth is only 50–70 metres. Hauls were taken for the most part with non-closing nets hauled horizontally through the water, the depth of fishing being recorded by a special instrument. Esterly (1911, 1912) investigated the diurnal migrations of Calanus and other copepods from hauls taken with a number of different nets and spread over a period of years. Hauls were taken from a maximum depth of 550 fathoms.

More recently Gardiner (1933) has studied the vertical distribution and diurnal migration of Calanus in the North Sea, using the improved form of the "Hardy" plankton indicator for collecting. The depth here is about 35 fathoms.

In all these cases the waters investigated are subject to considerable movement either tidal or due to currents.

The Clyde Sea-Area is peculiarly suitable for work on vertical distribution of such an animal as Calanus, owing to the presence of large bodies of water practically cut off from the rest of the sea, and subject to only small tidal movements. This has been discussed in an earlier paper (Part I, p. 83) and it has been shown that the population of Calanus within an area such as Loch Fyne may be regarded as having no communication with the population outside.

INVESTIGATIONS IN THE CLYDE SEA-AREA.

On two occasions during the year 1932 the vertical migrations of *Calanus finmarchicus* were studied over a period of 24 hours, at Station IV (Strachur) in Loch Fyne. It is a pleasure to express here my thanks to R. Kerr, Skipper, and D. Burnie, Boat-Hand, for their willing assistance on both occasions.

Hauls were taken with the same vertical closing net used for the work on seasonal distribution (Part I, p. 85). The depth which here averages 130 metres was divided into six sections, the first from the bottom to 120 metres, then every 20 metres up to 60 metres, with two hauls of 30 metres from that level to the surface.

The first occasion on which the diurnal migration was studied was on January 25th–26th, 1932. Weather conditions were perfect throughout the early part of the investigation. There was no wind and the surface of the water was glass calm until daylight, when a light north-easterly wind rose and caused a slight rippling of the surface. The sky was clear and a bright moon (full moon 23rd) shone from 7 p.m. on 25th until 7 a.m. on 26th when light clouds passed, occasionally diminishing the light of the moon. During the remainder of 26th conditions were not so good; the sky was overcast with misty clouds and the wind went round to the south-west, causing a slightly greater disturbance of the surface.

When a second investigation of the diurnal migration of Calanus was made on July 11th–12th, conditions were very similar. The sky was less clear during the night and the moon was in its first quarter (1st quarter 11th).

Hauls were made every three hours starting at 4 p.m.; the time occupied in taking the six hauls averaged about 45 minutes. Time has been reduced to G.M.T. throughout.

For convenience, in the Figures the time to the nearest hour at which each series of hauls was begun is indicated as being the time of that series. The actual time of beginning and ending will be found in Tables I and II. The series labelled 7 a.m. on January 26th was not begun until 7.30 a.m. owing to large sheets of ice on the surface of the loch which made it difficult to obtain a position where a suitable depth would be found.

The catches were preserved by the addition of sufficient formalin to make a 5% solution in sea-water, and the counting was done in the laboratory in Russell's modification of the Bogorov tray (see Part I, p. 86). Total counts were made in every case and all the copepodite stages of Calanus were counted in each haul.

In January, Stage V copepodites formed the bulk of the catches with a small percentage of Stage IV. The time was chosen, however, with a view to obtaining data on the migrations of the adults, which were appearing in the catches about this time (see Part I, Plate II).

Unfortunately at Strachur (where the work was carried out) the number of adults present was never very high, the majority of the Stage V copepodites dying without reaching the adult state. No copepodites of Stages I, II, or III were present at this time though one or two ova and nauplii appeared in the catches.

The number of each stage present varied considerably throughout the nine series of hauls. Stage IV copepodites were consistently scarce; so few were present that they are not worth recording graphically. The Stage V copepodites formed so large a bulk that diagrams of this stage might be taken to represent the total Calanus. Males considerably outnumbered females in the proportion of 13 : 2, and were sufficiently numerous throughout to give results in which some confidence can be placed. On one occasion only were there less than 100 (98 at 10 a.m. on 26th). Females on the other hand were present in comparatively low numbers.

The repetition of this work in July was intended to give a comparison between the winter and summer broods of Calanus. Unfortunately it was not until the work on seasonal distribution had been completed that it was realised that at Strachur the majority of Calanus present at that time were essentially of a brood directly comparable with those present during the winter, since by July reproduction was practically over and the autumn–winter stock was formed. This must, therefore, be regarded rather as a comparison of the diurnal migrations of comparable broods of Calanus under winter and summer conditions of environment.

In July total numbers were much lower than they had been in January and every stage was represented. Adults were comparatively scarce. So few males were found that nothing can be said about their diurnal migrations in summer; and though the number of females was low they were more abundant than they had been during January and some, at least, of the diagrams probably represent their diurnal migrations as accurately as the methods will allow.

Diagrams have been prepared for males, females, and Stage V copepodites in January, and for females, Stages V, IV, and III, II and I copepodites in July, showing approximately the water layers occupied by each stage at 3-hourly intervals over a period of 24 hours.

These will be seen in Figures 1–4, where they have been arranged as far as possible to compare January and July conditions. The vertical distribution of the young copepodites (Stages I, II, and III) has been expressed in one series of diagrams since their distribution was essentially the same, the slight differences being shown clearly in Table II.

In preparing these figures a base line was drawn at 135 metres for the January hauls and at 130 metres for the July hauls as these were the average depths of the mouth of the net in the nine series of hauls at each of these times. The true bottom was 3 metres below these levels.

Hauls were taken from these levels to 120 metres, from 120 to 100 metres, from 100 to 80 metres, from 80 to 60 metres, from 60 to 30 metres, and from 30 metres to the surface. The number of Calanus in each section is recorded as the percentage of Calanus at the mean depth for each 20- or 30-metre section.

This method introduces a probable inaccuracy for the 30 metre to surface and bottom to 120 metre hauls and suggests, when the Calanus were more abundant in these layers, that they were mostly right at the surface or bottom. In any case it exaggerates the importance of the numbers in these layers. This effect could have been minimized in the case of the top

30-metre haul by taking an additional haul through the top 5 or 10 metres, but at the time it was thought to be unnecessary.

Gardiner (1933, p. 597) draws attention to the difference in total numbers between day and night catches and is of the opinion that the former are usually the larger, the reverse of the condition found by Russell. Results obtained in this area suggest that there is in reality little difference. There was considerable variation throughout both periods of investigation. In January the largest and smallest catches were taken during the night while daylight catches were by no means small. If the results are averaged the night catches are slightly the larger. In July the largest and smallest catches were taken during daylight and but little difference is to be observed in the average of day and night catches.

The times of astronomical sunrise and sunset at Strachur were :—

January	25th	Sunset	4.27 p.m.	G.M.T.
	26th	Sunrise	8.37 a.m.	,,
July	11th	Sunset	8.27 p.m.	,,
	12th	Sunrise	3.58 a.m.	,,

I am indebted to Captain C. H. Brown for the correct times.

RESULTS AND DISCUSSION.

Introduction.

As far as can be ascertained statements on the vertical distribution of the different stages of Calanus are based on hauls taken during the course of a cruise for the purpose of investigating plankton in general. Results obtained by this method indicate that the first and second copepodites inhabit water above 50 metres and that third copepodites live from 100 to 50 metres. The fourth copepodites are generally distributed, but are more numerous from 100 to 50 metres than from 50 metres to the surface ; and the fifth copepodites are generally distributed. Females appear to live from 100 to 50 metres and males from 300 to 50 metres. (Störmer, 1929.)

This is, of course, in general agreement with the statement of With (1915, p. 28) that the younger the stage the nearer the surface will it be found.

Bogorov (1932) found all the copepodite stages inhabiting the upper layers (25 metres) in the Barents and White Seas. (It has not been possible to determine at what time of the day or in what month of the year these results were obtained.)

Farran (1927, p. 142) records the presence of the young stages in the surface layers of the water off the south coast of Ireland.

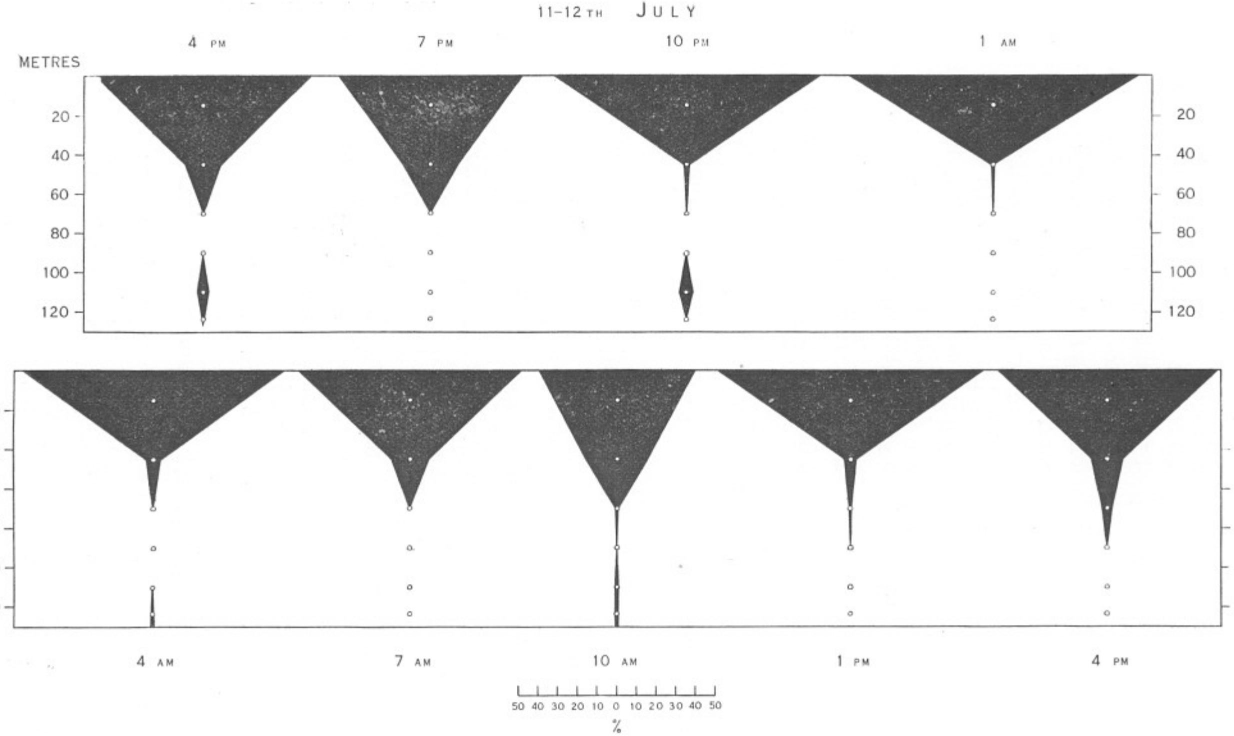

FIG. 1.—Diagram showing vertical distribution of copepodite Stages I, II, and III, at 3-hourly intervals during 24 hours on July 11th–12th. Sunset July 11th at 8.27 p.m., sunrise July 12th at 3.58 a.m.

Gran also (Paulsen, 1906) states that the young especially live at the surface in the Norwegian Sea. Gardiner (1933) using three 'Hardy' plankton indicators towed at different depths in the North Sea concluded that Calanus Stages III and IV were always to be found in the upper layers, whereas Stages V and VI lived deeper, the adults most frequently being found below the fifth copepodites.

Worthington (1931), on the other hand, working on the diurnal migration of the freshwater plankton of Lakes Lucerne and Victoria Nyanza, found (p. 432) that "in the case of nearly every species, the adults migrate less far than the young." He concludes that "the young is more susceptible to changing light intensity than the adult, or in other words, as it grows up it becomes adapted to resist intense light."

OVA AND NAUPLII.

Though the ova and nauplii present in the hauls made at Strachur on July 11th and 12th were not counted, it was observed that in every case they were most abundant in the 30-metre to surface hauls. A few were found in the 60- to 30-metre hauls, but not in sufficient numbers to indicate that they were performing a vertical migration.

During the course of the work on seasonal distribution in the Clyde Sea-Area at Stations I and II hauls were taken in two sections (from the bottom to 30 metres and from 30 metres to the surface) from March 7th until June 13th (June 7th at Station I) and again on July 25th and August 8th. The purpose of this, as explained elsewhere, was to simplify counting during the time when diatoms might be expected to be abundant. It has, however, thrown additional light on the vertical distribution of all stages of Calanus during this time.

Reference to Tables II and III (Part I, pp. 104–107) will show that ova and nauplii were always more abundant above 30 metres than below if we neglect the occasions when the numbers were relatively small. The only exception was at Station I on May 23rd when the numbers of all nauplii and copepodites below 30 metres were greater than those above, and the ova were about equally divided. As a rule the numbers found below 30 metres were small and indicated that the centre of distribution lay above 30 metres.

YOUNG COPEPODITES (STAGES I, II, AND III).

Figure 1 shows the vertical distribution of the young copepodites at 3-hourly intervals during 24 hours beginning at 4 p.m. on July 11th. At 4 p.m. and at 7 p.m. most of the young stages were above 45 metres. The two series of hauls taken between sunset and sunrise, namely, at

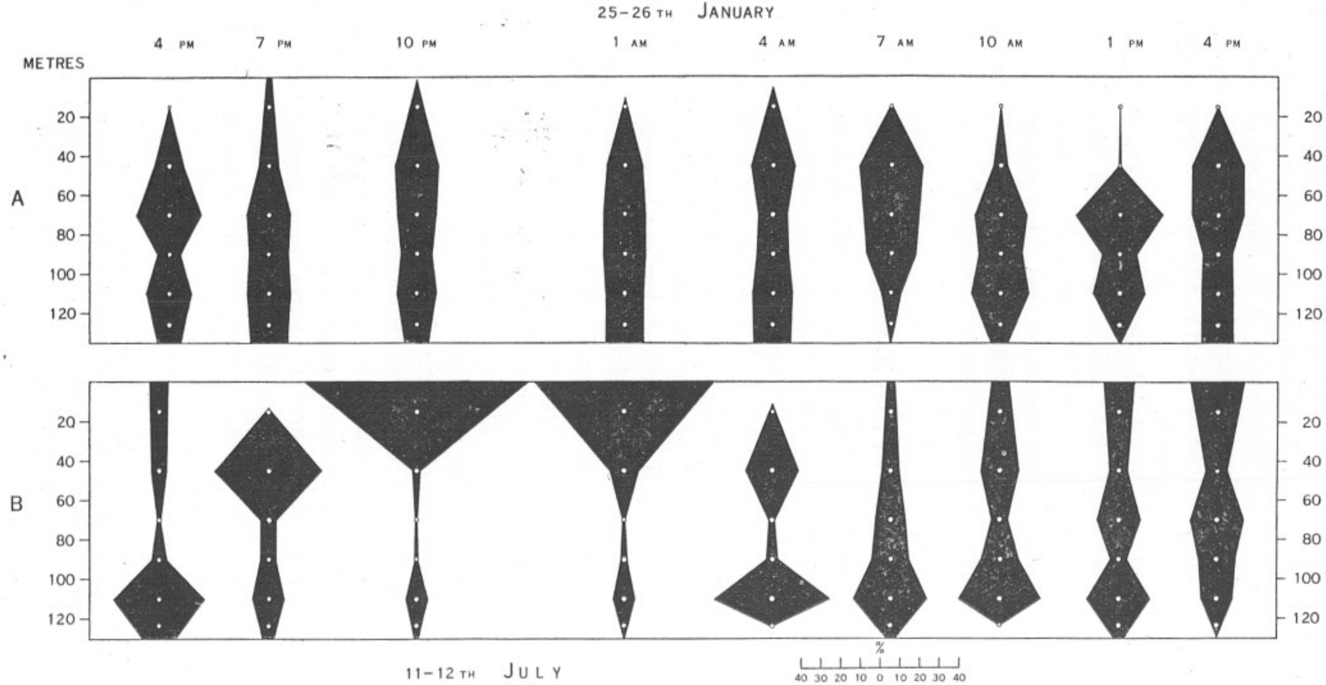

FIG. 2.—Diagram showing vertical distribution at 3-hourly intervals during 24 hours, A, of male Calanus on January 25th–26th; B, of Stage IV copepodites on July 11th–12th.

10 p.m. and 1 a.m., were very much alike and show a movement towards the surface of most of those Calanus which had been between 45 and 70 metres before sunset. The sun rose at 3.58 a.m. and the hauls taken at 4 a.m. show a tendency to return to the conditions found in daylight on the 11th. These conditions were re-established by 7 a.m. By 10 a.m. a greater proportion had left the surface layers and a very few had descended into water as deep as 90 metres. The numbers found in the 80- to 60-metre haul were, however, relatively insignificant.

The two series taken in the afternoon of 12th (1 p.m. and 4 p.m.) show an upward movement of those Calanus which had been below 45 metres at 10 a.m. On reference to the figures in Table II for the first three copepodite stages it will be seen that this slight vertical movement is practically restricted to the third copepodites. A very few of the Stage II copepodites were found below 30 metres and the first copepodites remained above 30 metres throughout.

Reference to Tables II and III in Part I (pp. 104–107), however, shows that this was not always the case at those stations situated in open water. On one occasion at Station II (May 16th), and on several occasions at Station I, a number of first copepodites was found below 30 metres. In every case where the numbers were large enough to be reliable there were many more above 30 metres than below, with the exception of the haul made on May 23rd at Station I, when the reverse was the case. Most of the evidence obtained in this region during 1932 points to the first copepodites being concentrated above 30 metres.

This in general applies also to the second copepodites which were not found below 30 metres in daylight during the investigation of July 11th–12th.

The third copepodites, on the other hand, do show a slight diurnal migration. They descended below 30 metres, a few even below 60 metres, during the day (July 11th–12th). The vertical movements of the young copepodites may be correlated with the time of day. There was an upward movement after the sun set which was maintained during the period of darkness. At 4 a.m. as the sun was rising, a slight downward movement occurred which was more marked as the sun rose in the sky. The afternoon hauls, however, do not show any close relationship to the movement of the sun. As has already been pointed out, it is the third copepodites which are chiefly responsible for changes in the diagrams for the young stages.

From Table II (Part I, p. 104) it will be seen that the third copepodites of the first breeding period (March 21st to April 18th) were more numerous above 30 metres than below, whereas those of the two later breeding periods were (with one exception) more numerous below 30 metres.

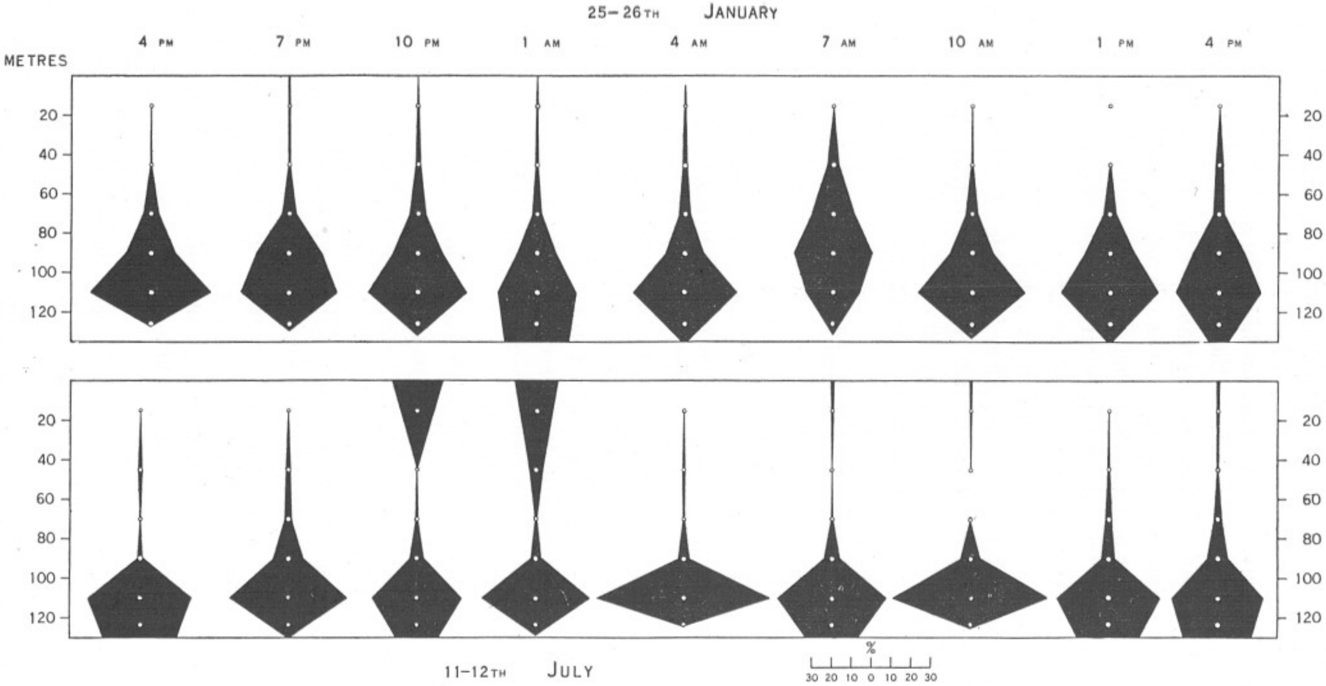

FIG. 3.—Diagram showing vertical distribution of Stage V copepodites at 3-hourly intervals during 24 hours on January 25th–26th and July 11th–12th. Sunset January 25th at 4.27 p.m., sunrise January 26th at 8.37 a.m. Sunset July 11th at 8.27 p.m., sunrise July 12th at 3.58 a.m.

Though this was so at Station I there is no indication of it at Station II. It is probable that the region usually inhabited by Stage III copepodites lies between 60 metres and the surface.

STAGE IV COPEPODITES.

Figure 2, B, shows the changes in the vertical distribution of this stage during the period from 4 p.m. on July 11th to 4 p.m. on 12th.

At 4 p.m. on 11th they were concentrated below 90 metres and were otherwise generally distributed in small numbers. Three hours later the bulk was found between 30 and 60 metres with a few in the lower levels. By 10 p.m. (sunset 8.27 p.m.) the water above 45 metres contained most of these Calanus, but, as at 7 p.m., a certain number remained in the deep water. At 1 a.m. (12th) the descent had begun though it was not very marked and most of the Calanus were still above 45 metres. The secondary maximum in the deep water was unchanged. Sunrise occurred at 3·58 a.m. and by 4 a.m. many of Stage IV were found between 30 and 60 metres, but still more had descended to the deep layer between 100 and 120 metres. By 7 a.m. only one maximum was observed and that in the deep water. The rest were distributed above this layer in diminishing numbers towards the surface. Thereafter the distribution showed little change and this stage was found at all depths.

Störmer (1929) found the fourth copepodite stage generally distributed from the bottom to the surface but more abundant between 50 and 100 metres than above that level. The deepest hauls made were from 1500 to 800 metres.

The study of the diurnal migrations of this stage made at Strachur in July suggests that they are generally distributed but tend to inhabit the deeper water and to move upwards at night to the surface layers.

There was a distinct movement towards the surface before the sun had set and by 10 p.m. they were distributed in the upper layers. By 1 a.m., however, they were leaving the surface and at 4 a.m., by which time the sun had risen, very few were found in the 30-metre to surface haul.

It is difficult to correlate the distribution found during the rest of the day with the movement of the sun. It was a bright and fairly clear day yet the general distribution showed little change from top to bottom.

The Calanus of Stage IV must be a mixture of (*a*) recently moulted third copepodites; (*b*) a proportion of those intermediate between (*a*) and (*c*) which may be regarded as true Stage IV; and (*c*) those Stage IV approaching the moult into Stage V. Since each stage can be passed in three days (see Part I, p. 92) the proportion of " transitional " Calanus may be fairly high. The vertical distribution of the third and fifth

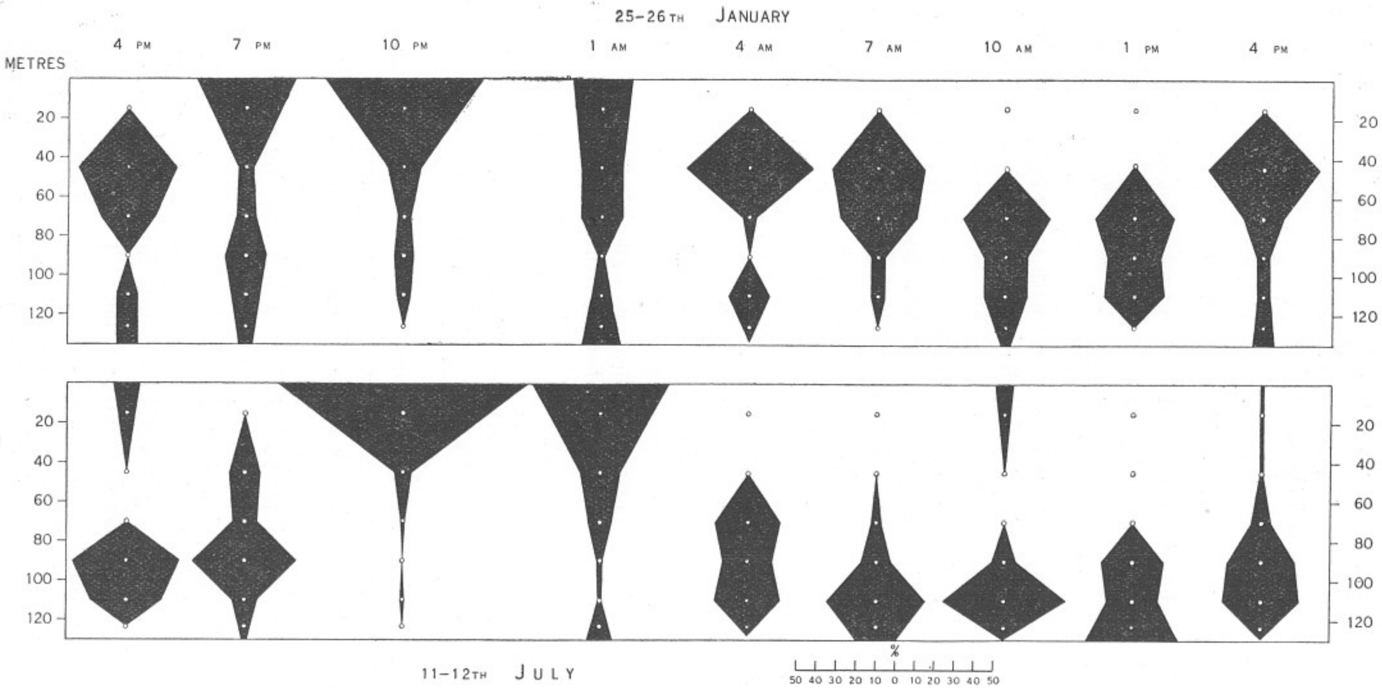

FIG. 4.—Diagram showing vertical distribution of female Calanus at 3-hourly intervals during 24 hours on January 25th–26th and July 11th–12th. Sunset January 25th at 4.27 p.m., sunrise January 26th at 8.37 a.m. Sunset July 11th at 8.27 p.m., sunrise July 12th at 3.58 a.m.

copepodites is so diametrically opposed that the distribution of those which are included under the morphological heading " Stage IV " will tend to be composite.

Physiologically, every stage will be in gradation from that immediately preceding it to the stage later. But in none will this be more apparent than in Stage IV which is transitional between those which inhabit the upper layers and those which inhabit the deep water.

It will be seen that throughout the 24 hours a certain proportion continuously inhabited that region which it seems the fifth copepodites prefer, and the numbers of such Calanus were sufficiently constant to enable the deduction to be made that these were probably soon to moult into Stage V.

Reference to Tables II and III (Part I, pp. 104–107) for Stations I and II shows more of this stage below 30 metres twice as often as above that level.

STAGE V COPEPODITES.

For this stage results were obtained in both January and July and are to be found expressed graphically in Figure 3. In January the greatest number in each series of hauls, with one exception, was found between 100 and 120 metres. Hauls taken from 100 to 80 metres contained a fair proportion but above this level Calanus was scarce. The exception occurred at 7 a.m. on 26th when the greatest number was found in the haul from 100 to 80 metres and in this series the 20-metre sections immediately above and below the 100- to 80-metre section contained about equal numbers.

The sun set at 4.27 p.m. on 25th and rose at 8.37 a.m. on 26th. A movement towards the surface in very small numbers was observed by 7 p.m. and this was maintained until 1 a.m., after which a slight descent occurred.

During the day the water above 45 metres was practically deserted by Calanus and as dusk approached a small number returned to the upper layers.

In July the majority of Stage V lived below 90 metres, and very few were found throughout the water above this level. After sunset at 8.27 p.m. a fair proportion rose to the surface layers. The descent had begun by 1 a.m., though it was not very marked. At 4 a.m., just after sunrise, the greatest concentration for this stage at any one depth was observed between 100 and 120 metres.

It is noteworthy that during January the fifth copepodites were higher in the water than during July.

The distribution of the fifth copepodite stage was remarkable and did not vary appreciably between winter and summer. They were always to be found massed in the deep water of the loch, and as a whole in January showed no movement that could be correlated with light.

In July, however, a small proportion came to the surface at night. It is suggested that those which moved up at night were the older specimens which were about to moult into adults.

Russell (1926, p. 427, and Fig. 4; 1928, p. 431, and Fig. 1) and Bigelow (1926, p. 202) have shown that there is a seasonal variation in the vertical distribution of Calanus.

The most striking feature shown in Figure 3 is this descent to a deeper level in July, when the sun was higher than it was in January. In the latter month the maximum angle of elevation of the sun is not much more than eleven degrees in this latitude, and much of the light incident on the surface of the water on a calm day must be reflected. In July when the sun is just past its zenith light will penetrate to a much greater depth.

The distribution as seen in Figure 3 suggests that the optimum light intensity for this stage is relatively low, since the majority are always massed together in the deep water. This is supported by the descent to a deeper level in July. Yet there is, apparently, no diurnal migration. Reference will be made to this below.

ADULTS—*Females.*

Females were found at both times in sufficient numbers to enable a comparison to be made. Figure 4 illustrates the diurnal changes in their vertical distribution in January and in July.

It will be seen that at 4 p.m. on January 25th the females were massed between 30 and 80 metres. The sun set at 4.27 p.m. and by 7 p.m. most of these females had moved into the upper 30 metres of water. Throughout the investigation a small proportion remained in the deeper water irrespective of the migration of the bulk. By 10 p.m. the accumulation in the upper layers was more marked, but by 1 a.m. the descent had begun and females were evenly distributed from the surface down to 80 metres.

At 4 a.m. they were concentrated between 30 and 60 metres with none at the surface. By 7 a.m. they were found between 30 and 80 metres. The sun rose at 8.37 a.m. and by 10 a.m. the upper layers were quite deserted; most were found between 60 and 80 metres, but a large proportion was distributed below 80 metres. At 1 p.m. they were fairly evenly distributed below 50 metres, and 4 p.m. on 26th saw a return to the condition in which they were found at that time on 25th.

In July, generally speaking, numbers were smaller, but three large catches brought the total numbers considerably above the January total.

At 4 p.m. on 11th the females were massed between 80 and 120 metres (one specimen was found above 30 metres). By 7 p.m. they were moving towards the surface but had not yet reached it. The sun set at 8.27 p.m., and by 10 p.m. the females were congregated in the upper 40 metres. The descent had begun by 1 a.m. The sun rose at 3.58 a.m., and at 4 a.m. all were found evenly distributed below 45 metres. By 7 a.m. few remained above 90 metres. This was more marked at 10 a.m. (one specimen found above 30 metres), and by 1 p.m. distribution was fairly even below 80 metres.

The hauls taken at 4 p.m. on 12th showed a distinct upward movement on the part of a few Calanus.

Of all the different stages of Calanus none exhibits diurnal migration so well as the females in spite of the small numbers present. In January numbers varied from 9 to 39 and averaged 25, and from the diagrams it may be assumed that these numbers are sufficient to give a true indication of their migrations.

In July numbers varied from 11 to 95 and averaged 39. The effect of such low numbers as 11 and 16 can be seen when one specimen in the top 30 metres in each case produced an apparently large discrepancy (at 4 p.m. on 11th and 10 a.m. on 12th). The largest numbers, 32, 95, 60, and 86, were found at 7 p.m., 10 p.m. on 11th and 1 a.m. and 4 p.m. on 12th. Although the bottom three metres were not sampled, on only one occasion (1 p.m.) is there any suggestion that Calanus were in this unfiltered section in relative abundance.

The results of the investigations in both January and July show that females live in the deep water during the day and move towards the surface as the sun descends, arriving at the surface after sunset.

As Russell (1925, p. 793) and Esterly (1911, p. 150) have remarked they appear to leave the surface shortly after midnight. The diagrams for January 25th–26th show a general distribution at all depths at 1 a.m., followed by an accumulation at what may be taken as the optimum, which is followed down as the sun rises. This agrees with the findings of Russell (1927, p. 237).

In July the departure from the surface appears to have been delayed and yet the descent to the deeper water was accomplished by 4 a.m., by which time distribution was general below 45 metres.

This more sudden movement is probably to be correlated with the shortness of the night in July compared with January. The sun set at about half-past eight and rose about four the next morning. This gives $7\frac{1}{2}$ hours of night (compared with 16 hours in January), but twilight at dusk and at dawn was of long duration. A light glow was visible on the northern horizon throughout the whole of the night and light began to increase after 2.30 a.m. (G.M.T.).

The general distribution throughout the 24 hours of both investigations agrees well with Russell's hypothetical diurnal migrations (1927, p. 237) when the differences in time of sunset and sunrise are taken into account.

A noticeable feature of the distribution of females (as with the fifth copepodites) is the greater depth to which they descend during the day in July, compared with January. It would not appear from Figure 4 that the moon, which rose after 7 p.m. on January 25th, had any decisive effect on the movements of the females towards the surface. Its light may have restricted their upward movement within the upper 30 metres, but for this there is no evidence.

Males.

Males were present in reliable numbers only in January (averaging 160 in each series of hauls). Their diurnal migration is illustrated in Figure 2, A. At 4 p.m. (25th) more were found between 60 and 80 metres than elsewhere and below this level distribution was fairly even. The sun set at 4.27 p.m. and by 7 p.m. a few were found above 30 metres, but below 60 metres their distribution was even. From 10 p.m. until 4 a.m. distribution was practically unchanged and differed only slightly from that found at 7 p.m. By 7 a.m., however, a slight downward movement from the surface was observed, accompanied by a distinct upward movement from the bottom. The sun rose at 8.37 a.m. and at 10 a.m. the descent was more marked and the majority were evenly distributed below 60 metres. By 1 p.m. a distinct massing was observed between 60 and 80 metres while still fewer were found above this level. At 4 p.m. on 26th distribution was very similar to that found at 4 p.m. on 25th.

Males appear to be much less susceptible to the influence of light than the females. Very little change took place in their distribution below 60 metres during the course of the investigation. There was a slight movement towards the surface at night and withdrawal therefrom as light increased during the day, which agrees with the results obtained by Russell (1931, b, Fig. 3). The main difference lies in the relative amounts of movement which were between 5 and 10 metres from the surface in his case whereas few were found in the top 30 metres at any time in Loch Fyne.

The more or less general distribution throughout the 24 hours, so markedly different from that of the females, is noticeable in the results from both the English Channel and Loch Fyne. Russell's material was, however, collected in June and too close a comparison is not perhaps allowable. Unfortunately the numbers present in July were so low that no reliable conclusions can be drawn as to their distribution at that time. It is probable that the slight amount of movement in the upper layers in January is to be correlated with the conditions of light at that time of year.

The remarkable feature of their distribution is the evenness below 60 metres. It suggests that the threshold of light for the males is higher than for the females, though this is not in agreement with the statements of others that males are usually found deeper than females (Paulsen, 1906, p. 16; Russell, 1928, p. 443; Störmer, 1929, p. 25).

GENERAL DISCUSSION.

The occurrence of Calanus in large quantities at the surface during the day, often under conditions of brilliant sunshine, has been recorded on several occasions in different regions.

One of the earliest records is that made by Brook (1886, p. 48) who observed Calanus in large quantities at the surface at Tarbert (in Loch Fyne) in May and June of 1885. They appear to have been obtainable with a surface net at all times, however, though in variable numbers. Later records are those of Herdman (1919, p. 115) who observed large numbers of Calanus on the surface at Tobermory in July, 1913; Willey (Russell, 1928, p. 444) who found them swarming on the surface in September; Bigelow (1926, p. 203) who found a similar occurrence in the Gulf of Maine in July and August; Marshall and Orr (1927, p. 860) who found Calanus abundant in the surface waters in May and June and sometimes in April in the Clyde Sea-Area; and Russell (1928, p. 443) who observed a greater abundance at the surface than below in July, August, and September. Gardiner's results (1933, p. 598) show more adults near the surface than below during the early part of the day; a more general distribution thereafter; and an accumulation in deeper water during the hours of darkness. This is, in fact, a reversal of the diurnal migration found elsewhere. His results were obtained in May, at which time Calanus has been found to be abundant at the surface during the day in this area also. Sömme (1933) shows Calanus abundant at the surface during April in the Lofoten area, but this appears to be a definite migration from the deeper water preparatory to spawning.

During 1932 this phenomenon was observed here only in May and June (see Part I, Tables II and III, pp. 104–107). On May 16th all stages of Calanus were more abundant above 30 metres than below at Station I, but not at Station II. At the latter station this happened on June 13th, but on that date the closing apparatus failed to work at Station I and the haul was not divided. Routine hauls in Loch Fyne were never divided since the expected diatom increase did not appear.

At Keppel, early in May, Calanus were present at the surface but not abundant.

Russell (1926, p. 422) also shows Calanus abundant at the surface in April, but correlates this with weather conditions since a week later on a bright day no such surface swarms were observed. The impression formed from such observations as have been made in the Clyde Sea-Area is that swarming at the surface is local and of a temporary nature. It would not be surprising, therefore, if different distributions were found in samples taken 6 days apart, but it may be observed that on the two later occasions in April (8th and 29th) on which catches were made Calanus were higher in the water than might be expected if light intensity alone controlled their distribution.

Observations in the Clyde Sea-Area in 1932 confirm observations made by Marshall and Orr (1927, p. 860) in earlier years. The explanation is not apparent.

It is doubtful if it is connected with spawning since that occurs at three different periods, and moreover, Stage V copepodites are found at the surface as well as adults. This is the more surprising in view of the usual vertical distribution of this stage.

Abundant food might be the cause, but for this there was no evidence in May and June.

The marked abundance of food in the upper 30 metres is possibly the reason why the nauplii and young copepodites inhabit this section. The stimulus to withdraw from bright light does not affect the nauplii, but becomes increasingly effective as development proceeds, the reverse of the condition described by Worthington (1931), so that there is a tendency for the third copepodites to move downwards during the day. Russell (1931, a, p. 394) has shown for *Sagitta elegans* that the younger stages are able to withstand higher light intensities than are the older stages. The fourth copepodites are still more affected and, as has been suggested above, these are probably intermediate, physiologically as well as morphologically, between the young copepodites and the fifth stage. The latter, as has been shown, generally remain in deep water.

It will be necessary, then, that during the winter they should find other food than diatoms and Marshall (1924) has shown that while these bulk largely in the food other organisms, notably Crustacea, Radiolaria, and other microplankton, are used extensively at certain times of the year. If the fifth copepodites depend upon such food during the winter there will be no necessity for them to seek the upper layers at any time of the year, since diatoms will probably be sufficiently numerous in the deep water during the summer and as these become scarce other organisms suitable for food will take their place.

In adults, particularly the females, negative heliotropism in Calanus is developed to its fullest extent. It follows that spawning must occur at night when the females are able to visit the surface, since ova are found largely in the upper 30 metres, and exist as such for so short a period (24 hours, Grobben, 1881).

Worthington (1931, p. 433) suggests that the reason freshwater Crustacea perform their diurnal migrations is that they have not become adapted to withstand intense light and so must descend during the day, but return as light diminishes to those layers of water wherein abound the organisms they require for food.

The idea that food is a factor which plays an important part in controlling diurnal migration seems well founded and it would appear that a balance is struck between this and light intensity. Spawning is probably a third factor and will affect adults alone.

The peculiar vertical distribution of Calanus at a certain time of the year, which varies in different regions but always lies between April and September, is possibly due to yet another factor more potent than any of those mentioned above.

Russell (1928, 1932) has suggested that differences in the vertical distribution of Calanus at different times of the year may possibly be correlated with physiological differences between broods. It seems probable that only one brood in each region so far investigated is subject to the stimulus which induces them to reverse their normal vertical distribution, though if the swarming at the surface in April shown by Russell (1926, p. 422) was due to this stimulus then, apparently, more than one brood may be affected. It appears that it is not necessarily the same brood in each region which is thus affected, but this is not yet clear.

SUMMARY.

1. Previous work on vertical distribution and diurnal migration is described.

2. The diurnal migration of Calanus was studied on two occasions in Loch Fyne (January and July, 1932).

3. Vertical hauls were taken every three hours with a closing net dividing the total depth into six sections.

4. The results for each copepodite stage of Calanus are discussed, and January and July conditions are compared where possible.

5. Ova and nauplii were observed to be most abundant in the top 30 metres.

6. Copepodite Stages I, II, and III were most abundant above 30 metres and only the third copepodites showed any tendency to descend as the light increased.

7. Stage IV showed a migration towards the surface at night, but were generally distributed during the next day.

8. It is suggested that the results for this stage are probably confused owing to its transitional nature between the young stages living at the surface and Stage V Calanus living in deep water.

9. Stage V was found always in deep water, slight diurnal changes being ascribed to the presence of such Calanus as were about to moult into adults.

10. Females showed definite diurnal migration in both January and July.

11. Males showed a general distribution and migrated in small numbers towards the surface at night and away from it during daylight.

12. Stage V copepodites and females both lived nearer the surface in January than in July, correlated with seasonal changes in the intensity of the sunlight.

13. The presence of swarms of Calanus at the surface under conditions of bright sunlight is discussed.

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TABLE I.

Numbers of Calanus, January 25th–26th.

Depth in metres Stage		0–30	30–60	60–80	80–100	100–120	120– Bottom	Totals
4 p.m. (4.05–4.50 p.m.) Depth 135 m.								
VI ♂	No.	–	26	57	21	40	28	172
	%	–	15	33	12	23	16	99
VI ♀	No.	–	9	5	–	2	2	18
	%	–	50	28	–	11	11	100
V	No.	4	54	428	1291	3110	239	5126
	%	–	1	8	25	61	5	100
IV	No.	–	1	5	2	1	1	10
Totals	No.	4	90	295	1314	3153	270	5326
	%	–	2	9	25	59	5	100
7 p.m. (7.00–7.55 p.m.) Depth 134 m.								
VI ♂	No.	14	25	57	52	57	51	256
	%	5	10	22	20	22	20	99
VI ♀	No.	14	3	4	8	6	4	39
	%	36	8	10	21	15	10	100
V	No.	77	71	476	2196	3254	598	6672
	%	1	1	7	33	49	9	100
IV	No.	5	2	2	5	1	–	15
Totals	No.	110	101	539	2261	3318	653	6982
	%	1·5	1·5	8	32	48	9	100
10 p.m. (10.00–10.45 p.m.) Depth 135 m.								
VI ♂	No.	15	46	43	34	43	32	213
	%	7	22	20	16	20	15	100
VI ♀	No.	17	5	2	3	2	–	29
	%	59	17	7	10	7	–	100
V	No.	56	115	364	1184	2312	636	4667
	%	1	2·5	8	25	49·5	14	100
IV	No.	1	2	1	1	1	–	6
Totals	No.	89	168	410	1222	2358	668	4915
	%	2	3	8	25	48	14	100
1 a.m. (1.00–1.50 a.m.) Depth 138 m.								
VI ♂	No.	5	33	40	39	36	36	189
	%	2·5	17·5	21	21	19	19	100
VI ♀	No.	8	6	6	1	3	5	29
	%	27·5	21	21	3·5	10	17	100
V	No.	25	41	231	1002	2017	1783	5099
	%	0·5	1	4·5	19·5	39·5	35	100
IV	No.	–	2	1	–	–	2	5
Totals	No.	38	82	278	1042	2056	1826	5322
	%	1	1·5	5	19·5	39	34	100

4 A.M.
(4.00–4.50 a.m.)
Depth 134 m.

VI ♂	No.	6	23	15	17	21	20	102
	%	6	22·5	15	16·5	20·5	19·5	100
VI ♀	No.	–	9	1	–	3	1	14
	%	–	65	7	–	21	7	100
V	No.	12	65	171	554	1568	617	2987
	%	0·5	2	5·5	19	52·5	20·5	100
IV	No.	–	1	2	1	1	1	6
Totals	No.	18	98	*189	572	1593	639	3109
	%	1	3	6	18	51	21	100

7 A.M.
(7.30–8.25 a.m.)
Depth 133 m.

VI ♂	No.	1	39	35	31	12	5	123
	%	1	32	28	25	10	4	100
VI ♀	No.	–	13	11	2	2	–	28
	%	–	47	39	7	7	–	100
V	No.	5	123	421	802	557	144	2052
	%	–	6	21	39	27	7	100
IV	No.	–	2	1	–	1	–	4
Totals	No.	6	177	468	835	572	149	2207
	%	–	8	21	38	26	7	100

10 A.M.
(10.10–11.00 a.m.)
Depth 134 m.

VI ♂	No.	–	7	25	22	28	16	98
	%	–	7	26	22	29	16	100
VI ♀	No.	–	–	4	2	2	1	9
	%	–	–	44	22	22	11	99
V	No.	7	39	261	894	2192	679	4072
	%	–	1	6	22	54	17	100
IV	No.	–	4	1	3	–	–	8
Totals	No.	7	50	291	921	2222	696	4187
	%	–	1	7	22	53	17	100

1 P.M.
(1.00–1.40 p.m.)
Depth 135 m.

VI ♂	No.	–	2	68	28	41	16	155
	%	–	1	44	18	26·5	10·5	100
VI ♀	No.	–	1	12	8	9	–	30
	%	–	3	40	27	30	–	100
V	No.	3	21	233	900	1753	680	3590
	%	–	0·5	6·5	25	49	19	100
IV	No.	–	–	1	3	4	1	9
Totals	No.	3	24	314	939	1807	697	3784
	%	–	0·5	8	25	48	18·5	100

4 P.M.
(4.00–4.40 p.m.)
Depth 135 m.

VI ♂	No.	–	34	34	19	21	21	129
	%	–	26·5	26·5	15	16	16	100
VI ♀	No.	–	17	6	2	2	3	30
	%	–	57	20	6·5	6·5	10	100
V	No.	1	132	185	851	1436	716	3321
	%	–	4	5·5	26	43	21·5	100
IV	No.	–	3	1	1	–	1	6
Totals	No.	1	186	226	873	1459	741	3486
	%	–	5	6	25	42	21	99

* *N.B.*—This figure should be increased by not more than 30% owing to a loss during sampling.

TABLE II.

NUMBERS OF CALANUS, JULY 11TH–12TH.

4 P.M.
(4.00–4.30 p.m.)
Depth 132 m.

Depth in metres Stage		0–30	30–60	60–80	80–100	100–120	120–Bottom	Totals
VI ♂	No.	–	–	–	–	–	1	1
VI ♀	No.	1	–	–	6	4	–	11
	%	9·0	–	–	54·5	36·5	–	100
V	No.	1	7	2	9	184	149	352
	%	0·3	2·0	0·6	2·5	52·3	42·3	100
IV	No.	8	7	2	7	40	23	87
	%	9·2	8·05	2·3	8·05	46·0	26·4	100
III	No.	83	29	–	–	–	2	114
II	No.	36	–	–	–	1	1	38
I	No.	7	–	–	–	–	–	7
III+ II	No.	126	29	–	–	1	3	159
+ I	%	79·4	18·0	–	–	0·6	2·0	100
Totals	No.	136	43	4	22	229	176	610
	%	22·3	7·0	0·7	3·6	37·5	28·9	100
7 P.M. (7.00–7.38 p.m.) Depth 125 m.								
VI ♂	No.	–	–	–	2	2	–	4
VI ♀	No.	–	5	4	17	4	2	32
	%	–	15·6	12·5	53·1	12·5	6·3	100
V	No.	–	10	15	62	250	82	419
	%	–	2·4	3·6	14·8	59·6	19·6	100
IV	No.	10	125	19	18	37	22	231
	%	4·3	54·1	8·2	7·8	16·2	9·5	100·1
III	No.	258	239	1	–	–	1	499
II	No.	243	8	–	–	–	–	251
I	No.	118	–	–	–	–	–	118
III+ II	No.	619	247	1	–	–	1	868
+ I	%	71·3	28·4	0·15	–	–	0·15	100
Totals	No.	629	387	39	99	293	107	1554
	%	40·5	24·9	2·5	6·4	18·8	6·9	100
10 P.M. (10.00–10.38 p.m.) Depth 130 m.								
VI ♂	No.	1	–	1	–	2	–	4
VI ♀	No.	83	8	2	–	2	–	95
	%	87·4	8·4	2·1	–	2·1	–	100
V	No.	61	2	3	24	161	105	356
	%	17·1	0·6	0·9	6·7	45·2	29·5	100
IV	No.	213	12	3	4	31	14	277
	%	76·9	4·3	1·1	1·4	11·2	5·1	100
III	No.	216	6	–	–	12	–	234
II	No.	52	2	–	–	4	–	58
I	No.	6	–	–	–	4	–	10
III+ II	No.	274	8	–	–	20	–	302
+ I	%	90·7	2·6	–	–	6·6	–	99·9
Totals	No.	632	30	9	28	216	119	1034
	%	61·1	2·9	0·9	2·7	20·9	11·5	100

1 A.M.
(1.00–1.45 a.m.)
Depth 129 m.

VI ♂	No.	–	–	1	–	–	–	1
VI ♀	No.	32	12	7	2	1	6	60
	%	53·3	20·0	11·7	3·3	1·7	10·0	100
V	No.	39	17	2	11	127	37	233
	%	16·7	7·3	0·9	4·7	54·5	15·9	100
IV	No.	136	30	3	7	22	9	207
	%	65·7	14·5	1·5	3·4	10·6	4·3	100
III	No.	337	6	–	1	–	1	345
II	No.	109	–	–	–	–	–	109
I	No.	18	1	1	2	–	–	22
III + II	No.	464	7	1	3	–	1	476
+ I	%	97·5	1·5	0·2	0·6	–	0·2	100
Totals	No.	671	66	14	23	150	53	977
	%	68·7	6·8	1·4	2·4	15·3	5·4	100

4 A.M.
(4.00–4.45 a.m.)
Depth 131 m.

VI ♂	No.	–	2	–	–	2	–	4
VI ♀	No.	–	–	4	3	4	1	12
	%	–	–	33·3	25·0	33·3	8·3	99·9
V	No.	–	6	4	32	481	23	546
	%	–	1·1	0·7	5·9	88·1	4·2	100
IV	No.	5	39	4	9	85	3	145
	%	3·4	26·9	2·8	6·2	58·6	2·1	100
III	No.	65	16	1	1	–	3	86
II	No.	95	–	–	–	–	–	95
I	No.	42	–	–	–	–	–	42
III + II	No.	202	16	1	1	–	3	223
+ I	%	90·6	7·2	0·4	0·4	–	1·3	99·9
Totals	No.	207	63	13	45	572	30	930
	%	22·3	6·8	1·4	4·8	61·5	3·2	100

7 A.M.
(7.00–7.45 a.m.)
Depth 133 m.

VI ♂	No.	1	–	–	–	–	–	1
VI ♀	No.	–	–	1	3	10	6	20
	%	–	–	5·0	15·0	50·0	30·0	100
V	No.	3	–	2	21	151	98	275
	%	1·1	–	0·7	7·6	54·9	35·6	99·9
IV	No.	5	7	12	15	30	12	81
	%	6·2	8·6	14·8	18·5	37·0	14·8	99·9
III	No.	81	64	1	–	–	–	146
II	No.	125	3	–	–	–	–	128
I	No.	84	1	–	–	–	–	85
III + II	No.	290	68	1	–	–	–	359
+ I	%	80·8	19·0	0·3	–	–	–	100·1
Totals	No.	299	75	16	39	191	116	736
	%	40·6	10·2	2·2	5·3	25·9	15·8	100

10 A.M.
(10.00–10.50 a.m.)
Depth 130 m.

VI ♂	No.	–	1	–	–	–	–	1
VI ♀	No.	1	–	–	2	10	3	16
	%	6·2	–	–	12·5	62·5	18·7	99·9
V	No.	1	–	–	21	172	23	217
	%	0·5	–	–	9·7	79·2	10·6	100
IV	No.	9	14	6	14	30	–	73
	%	12·3	19·2	8·2	19·2	41·1	–	100
III	No.	74	73	3	–	1	3	154
II	No.	45	1	–	–	3	1	50
I	No.	28	–	1	–	–	–	29
III+II	No.	147	74	4	–	4	4	233
+I	%	63·1	31·8	1·7	–	1·7	1·7	100
Totals	No.	158	89	10	37	216	30	540
	%	29·2	16·5	1·9	6·8	40·0	5·6	100

1 P.M.
(1.00–1.40 p.m.)
Depth 129 m.

VI ♂	No.	1	–	1	–	1	–	3
VI ♀	No.	–	–	–	6	5	8	19
	%	–	–	–	31·6	26·3	42·1	100
V	No.	–	3	8	18	144	104	277
	%	–	1·1	2·9	6·5	52·0	37·5	100
IV	No.	14	10	23	9	33	14	103
	%	13·6	9·7	22·3	8·7	32·0	13·6	99·9
III	No.	145	16	3	–	–	1	165
II	No.	59	1	–	1	–	–	61
I	No.	45	–	–	–	1	–	46
III+II	No.	249	17	3	1	1	1	272
+I	%	91·5	6·2	1·1	0·4	0·4	0·4	100
Totals	No.	264	30	35	34	184	127	674
	%	39·2	4·5	5·2	5·0	27·3	18·8	100

4 P.M.
(4.00–4.40 p.m.)
Depth 134 m.

VI ♂	No.	–	–	1	2	1	–	4
VI ♀	No.	2	2	9	30	33	10	86
	%	2·3	2·3	10·5	34·9	38·4	11·6	100
V	No.	7	5	29	77	348	288	754
	%	0·9	0·7	3·8	10·2	46·1	38·2	99·9
IV	No.	124	61	150	105	89	28	557
	%	22·2	11·0	26·9	18·8	16·0	5·0	99·9
III	No.	495	119	36	–	–	3	653
II	No.	48	–	–	–	–	–	48
I	No.	44	–	–	–	–	–	44
III+II	No.	587	119	36	–	–	3	745
+I	%	78·8	16·0	4·8	–	–	0·4	100
Totals	No.	720	187	225	214	471	329	2146
	%	33·5	8·7	10·5	10·0	22·0	15·3	100

The Littoral Diatoms of the Liverpool and Port Erin Shores.

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CONTENTS.

INTRODUCTION.

CERTAIN diatoms seem to live predominantly on the foreshore. While the pelagic diatoms have received very much study, relatively little attention has been given to the shore forms. There is no satisfactory account of these organisms as they occur on the coasts of Lancashire and Isle of Man, and one may expect that they have much importance as the food of many animals. In a further paper I will deal with this question. For this reason I deal here only with those littoral diatoms found along the Mersey Beach, in the vicinity of Liverpool, and with those collected from the sandy and rocky shore of Port Erin (Isle of Man). Masses of these organisms can easily be recognised with the naked eye, discolouration of the sand and mud being due mainly to them, together with some species of desmids and dinoflagellates.

On a sandy beach like that of Port Erin, it appears as if the diatoms attain maxima of abundance during the spring and summer. They do not totally disappear from those localities during the cold months, though they become relatively scarce. During the very cold months of winter I have found diatoms on the rather muddy beach of part of the Mersey

Estuary known as the "Dingle." Apparently there are optimum conditions of sunlight and temperature for the growth and multiplication of these organisms.

General Ecology.

In their living state, littoral diatoms are seen to be attached to the coarse surface of the sand grains. A minute sand grain under the microscope seems to be a substratum for not less than 20 or 30 diatoms, of various genera and species. They may also be seen gliding between the sand grains. It is in these littoral forms that the free motion of diatoms is easily recognisable. This movement is sometimes said to be due entirely to the protoplasmic action of the part of the coleoderm in the position of the raphe. It is relatively considerable, for a minute naviculoid diatom (20μ) is able to strike an obstacle in its way, that is far larger than itself, with such force as to push it aside ! A naviculoid diatom seems to move along the side of the frustule where the median line—or raphe—extends, for when this boat-like Navicula is turned on its side by just pressing delicately with a needle on the cover slip, it turns over again immediately and proceeds to move as before. The motion is more particularly noticed in those littoral diatoms which are almost free. In particular, it is in those forms that have a true conspicuous raphe, that the free motion in diatoms is best seen. In *Surirella gemma*, for example, where the raphe is less defined the motion is languid though still perceptible. The movement is a sort of backward and forward one, but it can also be a vertical or oblique one in response to the light. Phototropism is indeed marked among these forms, for on leaving the diatoms with sand in a fairly shallow enamel dish, surrounded (or even not) by a black paper, the organisms are found after a short time to be seeking the surface of the sand, so that they form, in due time, a thick yellowish green or brown layer, obviously in response to the incident light : this is the result of their motion. Most of the diatoms found on the shore exist in the free state, particularly those possessing a true raphe, but in addition, many are found connected by their valve surfaces in filaments, such as *Melosira nummuloides* and *Acnanthes longipes*, which are attached to other Algæ by more or less long stipes. Others again, such as Schizonema, are enclosed in gelatinous tubes.

Methods of Collection.

It has been suggested, as one of the best methods (**8**), that pieces of well-washed cotton cloth, of the size of a pocket-handkerchief, should be laid on the sand surface, when they will pick up, by their fibres, the diatoms, excluding the sand grains. This, however, proved to be of no use at all, since it was found that a great number of diatoms are left behind and are not attached to the cloth, while large amounts of small particles of sand are always picked up. Scraping the sand surface is by far the best way. The sand, with the diatoms, is placed in a fairly wide shallow glass dish, all the outside of which is covered with black paper. The sample of mud is then covered with water (taken from the shore where they were collected) to the height of, say, half an inch. This is then left for at least six hours, when practically all the diatoms form a thick yellowish green coating on the sand surface. It has been stated that the diatoms will be found floating in the layer of water above the sand surface, from which they can be pipetted or siphoned, but this is not the case, for the shore diatoms show a vigorous tendency to remain attached to the surface of sand grains and *do not* float in the water. Therefore, the best method I have found is to give the dish a slight gentle rotatory motion, when part of the diatoms float up in this water. I filter this, re-scrape the layer of diatoms from the sand surface, and filter this again through Number 16 to 20 bolting silk. This silk is sand-proof, to a sandy beach like that of Port Erin. It allows practically all the diatoms to pass through the silk as an intense yellowish green filtrate. If minute thread-like organic impurities pass through they can be easily got rid of during treatment with acids, and even these do not interfere with the diatoms mounted on a slip as do the objectionable sand grains. This silk filter even allows certain true planktonic species, thrown down by the tide from the open sea, to pass through. Thus in my filtrate such species as *Coscinodiscus radiatus*, *C. excentricus*, *Actinoptychus undulatus*, and *Biddulphia aurita*, were found. This filtration method is by far the best I have tried, and it is recommended to anyone for collecting and cleaning shore diatoms.

For studying them in the living state, the diatoms are kept in either their natural water or in Miquel solution sea-water (modified by Allen and Nelson, **1**). Before treatment with acids, for the purpose of studying the frustules, it is necessary to centrifuge them and thus get rid of the bulk of the water.

FIXING AND CLEARING.

Gran and Angst (**5**) state that "for the determination of the species, 95% alcohol or 4% formaldehyde in sea-water is a sufficient preservative. A solution made of 5 c.c. of 40% formaldehyde, 5 c.c. glacial acetic acid, 40 c.c. sea-water and diluted to 100 c.c. by the addition of water containing diatoms, serves for cytological studies." It is not, however, sufficient to study the diatoms when alive, though that would help in the identification of species to a certain extent, and it is necessary to see the diatom shells, depleted of their delicate organic cell-contents, so as to render the striation clear and distinct. It is always necessary to centrifuge the diatoms. They are then treated with a corrosive material. For this purpose

I have used fuming nitric acid to the extent of 1–2 c.c. to every ½ c.c. of centrifuged diatoms, and have boiled the mixture for a few seconds until the red-brown fumes of acid disappear. To this liquid distilled water is added to fill the test-tube and the mixture is cooled. A white precipitate is found in the course of an hour. The liquid is drained off and the precipitate washed repeatedly with distilled water until there is no trace of acid. The above operation takes from one to two hours, when one is left with perfect clean frustules ready for examination. The diatoms have to be mounted dry. To dehydrate the frustules, a few drops of the acid-free precipitate are taken up in a pipette and spread over a clean slide or cover slip, which is then put in an electric oven (temp. 100° C.), when all the water evaporates completely in a few minutes, and the diatom skeletons are left dry and ready for mounting.

MOUNTING.

The diatoms have to be mounted in a suitable medium. The visibility of markings such as the striation of diatoms is proportional to the difference between the refractive indices of the object and the medium in which it is mounted. The refractive index of the diatom silex is about 1·43, hence the diatom is not seen in concentrated sulphuric acid, as this has nearly the same refractive index. Canada balsam (n=1·54), monobromide of naphthaline (n=1·658), and styrax are among the media that have higher refractive indices than that of silex. I find Canada balsam and styrax unsuitable owing to their low coefficient of visibility. Monobromide of naphthaline is a liquid and is therefore unsuitable. A good mounting medium is a simple one that I have come across by mere chance and I think it is stable. A slide was found in the Liverpool Oceanography Laboratory, and on examination I found it to contain *Gyrosigma balticum*, *Pleurosigma angulatum*, and *Surirella gemma*, all mounted in a yellowish solid medium. On the slide is written "Piperine and antimony bromide," obviously indicating that this is the mounting medium. The striations of both Pleurosigma and Surirella are clear and distinct in every detail even under the ⅛-inch high-power objective. It is also very astonishing that, though the mounting was dated March 22nd, 1891, it is still as perfect as if it had been prepared to-day, despite its forty years of age, a fact which is evidence of the stability of the medium. This then must be a very good medium of high refractive index, which is not recorded in any of the references to Diatomaceæ in the Journal of the Royal Microscopical Society from 1860. I was supplied with both piperine and antimony bromide, and with the help of Dr. Daniel, I started to utilise it, with, I believe, considerable success.

Piperine is an inexpensive alkaloid of the formula $C_{17}H_{14}NO_3$. It is almost insoluble in water. It is only a very weak base and on hydrolysis gives piperidine and piperic acid. It can be obtained in a very pure state as straw-coloured crystals, with a melting point of 128° C. (262·4° F.). When it is melted it dissolves the tribromide of antimony very freely. Piperine, if heated alone directly on a bunsen flame, melts quickly into a colourless liquid which chars (blackens) with continued heat. All this may take place in the course of one minute. Bromide of antimony ($Sb\ Br_3$) melts at a lower temperature and also into a transparent liquid. Both solidify again immediately they are removed from the source of heat. In their liquid state while still hot, if they are allowed to mix, an orange or yellowish colour is produced, the intensity of the colour being dependent upon the proportion of both substances. Piperine must be used in excess of the bromide of antimony, for if the latter is in excess it crystallises out on cooling, with the result that a turbid, useless medium is formed. Different proportions of piperine and antimony bromide have been prepared and sent to the Geological Department here to find out the refractive indices. Unfortunately, I have been informed that they were unable to find these, as the medium is insoluble in their oils. It seems, however, from the examination of the various slides prepared with this mounting medium in different proportions that the best proportion is 2 parts of piperine : 1 part of $Sb\ Br_3$. Here the diatoms with their striation are so very distinct and clear that nothing more in this direction can be desired. Two parts by weight of piperine are taken with one part by weight of antimony bromide, and both are finely ground together in a mortar in their solid state, when a yellow colour immediately develops. I do not know whether this yellow material is a new chemical compound, or not. A small portion of this solid medium is put on a slide, or a cover slip, with dry diatoms. The slide or cover slip is now put on a hot plate the temperature of which must not greatly exceed 128° C. (which is the melting-point of piperine). *Under no circumstances should this medium be heated directly on the flame.* As soon as the mounting medium melts completely either lower a cover glass, or a slip, on it and take it away immediately from the source of heat, when it solidifies. A $\frac{1}{8}$-inch high-power objective gives highly satisfactory results, and the 1/12th (oil immersion) objective still better results, the striation being distinct in every detail, particularly in Pleurosigmæ which are exceedingly delicate and fine.

GENERAL REMARKS.

The diatoms recorded in this paper are true littoral forms, but among them the reader will notice certain species as Coscinodiscus, Actinoptychus, Biddulphia and the like, which are true pelagic forms. The writer believes that such forms are thrown out on the shore by the rising tide, and left there. The shore seems to be an unfavourable medium for their life, for in no instance were any of these forms found alive. The littoral diatoms here recorded include those living freely on the sand or mud, as well as those found attached to Algæ, rocks, shells, and other supports. The latter diatoms are particularly the filamentous forms. It seems also that there are no specific Algæ or water plants that are most favourable for particular diatoms; some of the filamentous forms even attach themselves to other diatoms. They are found healthy, and of different species attached to red, brown, and green Algæ.

Three main spots have been examined, namely, the "Jetty" (Pier Head, Liverpool), "Dingle shore" along the Merseyside, and the sandy beach of Port Erin (Isle of Man). It is curious to find a few freshwater forms living along the shore of the River Mersey where the water is brackish, but still covered periodically by flood tides. It seems as if the diatoms of the shore can stand water of different salinities. Common forms—particularly the Nitzschiates and some filamentous forms—are found both along the brackish Merseyside and on the highly saline beach of Port Erin. It may be the light—which is important in the process of assimilation—that is the main factor controlling the abundance of shore diatoms. It may be that these organisms get their food substances from the water that covers them at high tide, but I think it probable that drainage from the land, to the shore, is the condition that matters most. So there is still much to be done by comparing other beaches, where there is very much less land drainage carrying resolved sewage constituents, with the Dingle and Port Erin Bay.

CLASSIFICATION.

The classification adopted here is based on those of West and Fritsch (1927), and Lebour (1930).

DIATOMALES or BACILLARIALES.

Centricæ

- *Discoidæ*
  - Families Coscinodiscaceæ
    Melosiraceæ.
- *Solenoidæ*
  - Family Rhizosoleniaceæ.
- *Biddulphioidæ*
  - Family Biddulphiaceæ.

PENNATÆ

Fragilarioideæ

Families Fragilariaceæ
Tabellariaceæ
Meridionaceæ.

Achnanthoideæ

Family Achnanthaceæ.

Naviculoideæ

Families Naviculaceæ
Cymbellaceæ.

Nitzschioideæ

Family Nitzschiaceæ.

Surirelloideæ

Family Surirellaceæ.

LIST OF SPECIES IDENTIFIED.

Group **Centricæ.**

Family *Coscinodiscaceæ.*

Genus Coscinodiscus.

1. *Coscinodiscus excentricus* Ehr. Dingle, Port Erin, rare.
2. *C. lineatus* Ehr. Dingle, rare.
3. *C. nitidus* Greg. Port Erin, rare.
4. *C. radiatus* Ehr. Dingle, Port Erin, rare.

Genus Actinoptychus.

1. *Actinoptychus undulatus* (Bailey). Dingle, Port Erin, rare.

Family *Melosiraceæ.*

Genus Melosira.

1. *Melosira sulcata* (Ehr.).
   Orthothira marina W. Sm. Dingle shore, rare.
2. *M. nummuloides* (Lyngb.). Dingle shore, Jetty, Port Erin, abundant.

Family *Rhizosoleniaceæ.*

Genus Rhizosolenia.

1. *Rhizosolenia Shrubsolii* Cleve. Dingle, very rare.

Family *Biddulphiaceæ.*

Genus Biddulphia.

1. *Biddulphia aurita* (Lyngb.). Port Erin, few.
2. *B. granulata* Roper. Dingle, rare.
3. *B. rhombus* (Ehr.). Dingle, rare.

Genus Attheya.

1. *Attheya decora* West (?). Port Erin, very scarce.

Group **Pennatæ.**

Family *Fragilariaceæ.*

Genus Fragilaria.

1. *Fragilaria oceanica* Cleve. Jetty (Pier Head), rare.
2. *F. striatula* Lyngb. Jetty, few.

Genus Synedra.

1. *Synedra affinis* Kutz. Dingle, Port Erin, abundant.
2. *S. tabulata* (Ag.). Dingle, abundant.
3. *S. suberpa* Kutz. Port Erin, abundant.
4. *S. gracilis* Kutz. Dingle, abundant.

Family *Tabellariaceæ.*

Genus Rhabdonema.

1. *Rhabdonema arcuatum* (Lyngb.). Port Erin, abundant.
2. *R. minutum* Kutz. Dingle, abundant.

Genus Grammatophora.

1. *Grammatophora marina* (Lyngb.). Port Erin, abundant.
2. *G. serpentina* W. Sm. Port Erin, abundant.
3. *G. islandica* Ehr. Port Erin, Dingle, rare.
4. *G. angulosa* Ehr. Port Erin, Dingle, common.

Family *Meridionaceæ.*

Genus Licmophora.

1. *Licmophora flabellata* Ag. Port Erin, abundant.
2. *L. juergensii* Ag. Dingle, few. Port Erin, abundant.
3. *L. gracilis* (Ehr.). Port Erin, abundant.
4. *L. dalmatica* (Kutz.). Port Erin, abundant.
5. *L. lyngbyei* (Kutz.). Port Erin, abundant.

Family *Achnanthesaceæ.*

Genus Achnanthes.

1. *Achnanthes longipes* Ag. Port Erin, abundant.
2. *A. brevipes* Ag. Dingle Shore, Port Erin, abundant.
3. *A. subsessilis* Kutz. Dingle, Port Erin, common.

Genus Cocconeis.

1. *Cocconeis placentula* Ehr. Port Erin, abundant.
2. *C. scutellum* Ehr. Dingle, Port Erin, few.
3. *C. dirputa* Greg. Port Erin, very rare.

Family *Cymbellaceæ*.

Genus Amphora.

1. *Amphora complexa* Greg. Port Erin, abundant.
2. *A. coffæiformis* (Ag.). Port Erin, abundant.
3. *A. cymbifera* Greg. Dingle, not common.
4. *A. lævis* Greg. Port Erin, common.
5. *A. pellucida* Greg. Port Erin, common.
6. *A. pusilla* Greg. Dingle, Port Erin, rare.

Family *Naviculaceæ*.

Genus Caloneis.

1. *Caloneis liber* (W. Sm.). Dingle, Port Erin, common.
2. *C. æmula* (A. Schmidt). Port Erin, few.

Genus Diploneis.

1. *Diploneis smithii* (Breb.). Port Erin, abundant.
2. *D. elliptica* (Kutz.). Port Erin, Dingle, few.
3. *D. litoralis* (Donkin). Port Erin, common.

Genus Navicula.

1. *Navicula crucigera* (W. Sm.). Dingle, abundant.
2. *N. tumida* W. Sm. Dingle, few.
3. *N. grevillei* (Ag.). Dingle, abundant.
4. *N. bottnica* Grun. Dingle, rare.
5. *N. pusilla* W. Sm. Dingle, Port Erin, common.
6. *N. punctulata* W. Sm. Dingle, common.
7. *N. lyra* Ehr. Port Erin, rare.
8. *N. humerosa* Breb. Port Erin, Dingle, very abundant.
9. *N. pygmæa* Kutz. Port Erin, fairly abundant.
10. *N. tumens* W. Sm. Dingle, abundant.
11. *N. distans* (W. Sm.). Dingle, common.

Genus Gyrosigma.

1. *Gyrosigma attenuatum* (Kutz.). Dingle, abundant.
2. *G. hippocampus* (Ehr.). Dingle, Jetty, fairly common.
3. *G. balticum* (Ehr.). Dingle, Jetty, common.
4. *G. spencerii* (Quekett). Dingle, not common.
5. *G. distortum* (W. Sm.). Dingle, abundant.
6. *G. fasciola* (Ehr.). Dingle, common.

Genus Pleurosigma.

1. *Pleurosigma obscurum* W. Sm. Port Erin, rare. Dingle, common.
2. *P. angulatum* (Quekett). Dingle, common.

3. *P. angulatum quadratum* (W. Sm.). Dingle, very abundant in summer.
4. *P. nubecula* W. Sm. Port Erin, few.

Genus Amphiprora.

1. *Amphiprora paludosa* W. Sm. Port Erin, common.
2. *A. plicata* Greg. Port Erin, few.

Genus Tropidoneis.

1. *Tropidoneis maxima* (Greg.). Port Erin, common.
2. *T. pusilla* (Greg.). Port Erin, common.

Genus Amphipleura.

1. *Amphipleura pellucida* Kutz. Jetty, rare.
2. *A. sigmoidea* W. Sm. Jetty, rare.
3. *A. rutilans* (Trent). Dingle, Port Erin, abundant.

Family *Nitzschiaceæ*.

Genus Nitzschia.

1. *Nitzschia panduriformis* Greg. Dingle, not common.
2. *N. bilobata* W. Sm. Port Erin shore, abundant.
3. *N. vivax* W. Sm. Port Erin, abundant.
4. *N. spathulata* Breb. Port Erin, common.
5. *N. angularis* W. Sm. Dingle, common.
6. *N. closterium* W. Sm. Dingle, Port Erin, common.
7. *N. reversa* W. Sm. Dingle, Port Erin, rare.
8. *N. acicularis* (Kutz.). Dingle, abundant.
9. *N. linearis* (Ag.). Jetty, Dingle, not common.
10. *N. sigma* (Kutz.). Port Erin, very rare.
11. *N. valida* Cleve & Grun. Dingle, rare.
12. *N. tænia* W. Sm. Dingle, Port Erin, common.
13. *N. parvula* W. Sm. Jetty, very rare.
14. *N. sigmoidea* W. Sm. Dingle, few.
15. *N. litoralis* Grun. Port Erin, not common.

Genus Hantzschia.

1. *Hantzschia virgata* (Roper). Port Erin, common.
2. *N. amphioxys* (Ehr.). Dingle, rare.

Family *Surirellaceæ*.

Genus Surirella.

1. *Surirella gemma* Ehr. Dingle, very abundant in summer.
2. *S. ovata* Kutz. Jetty, Dingle, rare.
3. *S. lata* W. Sm. Dingle, very rare.

List of Abbreviations.

Ag. = C. A. Agardh.
Breb. = De Brebisson.
Ehr. = D. C. G. Ehrenberg.
Hass. = A. H. Hassall.
Kutz. = F. T. Kutzing.
Lyngb. = H. C. Lyngbye.
W. Sm. = W. Smith.
Thw. = G. H. K. Thwaites.
Greg. = W. Gregory.

Notes on Species.

The species of Coscinodiscus were never found alive on the shore. *Melosira nummuloides* seems to be a true littoral form, and was always healthy, had living chloroplasts and was reproducing, while *M. sulcata* was never found alive. The species *Attheya decora* West resembles that described by Boyer, except that the figure he gives is different from the actual specimens I examined, in that two spines are directed to opposite directions and the others are nearly straight. The length of each spine is half that of the frustule. The length of the valve is 30μ in one species and 14μ in another with varying breadth. *Synedra affinis* Kutz and *Licmophora flabellata* Ag. were attached to other green Algæ and even to other diatoms, particularly those enclosed in gelatinous tubes (Schizonema). *Rhabdonema arcuatum* (Lyngb.) was scraped from molluscan shells. The Licmophora species live more or less together among other flora on the rocky shore and not on the sands. It seems that such stipitate, as well as other filamentous forms, prefer a rocky substratum, perhaps on account of its stability; the sand grains being subject to the tidal movements. Moreover, such forms find, in the vicinity of rocks, small areas of water left behind by the tide. Such small ditches of water seem to be indispensable for the life of these diatoms, unlike the free forms, such as Navicula, which can live attached to sand grains, which are only covered by tidal water twice every twenty-four hours, but which nevertheless are able to continue living under these conditions.

ACKNOWLEDGMENTS.

I am indebted to the late Professor Johnstone for his valuable aid and advice, to Dr. Daniel for his continued interest and help in this work, to Mr. J. H. Fraser for his kind assistance, and to the Mersey Docks and Harbour Board for permission to work on the beach.

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On the Marine Cladocera from the Northumbrian Plankton.

By

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Armstrong College, University of Durham.

With 36 Figures in the Text and Diagrams A, B and C.

CONTENTS.

PART I. DISTRIBUTION AND SEASONAL CHANGES OF POPULATION.

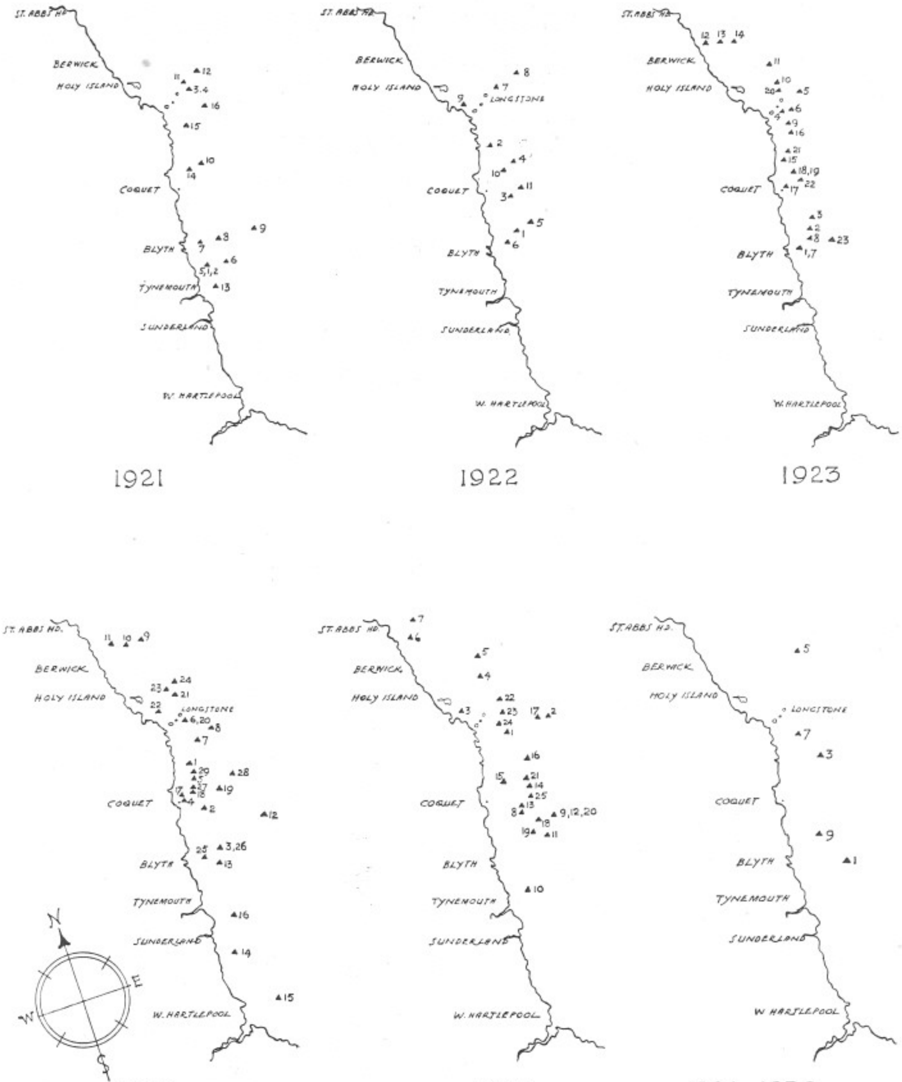
PART II. THE LIFE-CYCLE OF *EVADNE NORDMANNI*

PART I. DISTRIBUTION AND SEASONAL CHANGES OF POPULATION.

INTRODUCTION.

THE material which forms the subject of this paper has been collected over a period of ten years. The samples are divisible into two groups, each including five years' catches. During the first half of the time, 1921–1925 inclusive, the stations varied from voyage to voyage but the hauls are comparable with one another as regards the nets used and the time of fishing in each case. An account of the method of sampling is given in the Dove Marine Laboratory Report for 1923, pp. 68–69 (**45**).

In 1926 a change was made in the number and kind of nets used and in the time of fishing, in order to bring the work into line with that of the Ministry of Agriculture and Fisheries. Since that year the new method has continued, and the samples have been taken each time from the same series of stations (Fig. 1). Thus, during this period the results of different years' sampling can be correlated more satisfactorily. The new method



1921 1922 1923

1924 1925 1926 - 1930

FIG. 1.

of sampling is described in the Dove Marine Laboratory Report for 1926, p. 43 (**46**).

A preliminary statement as to the occurrence of the two genera of Cladocera which are found in the area sampled, during the period 1921–1923, is given in the above-mentioned Reports for 1923 and 1924 in " Plankton Investigations, No. 4 Crustacea " (**30** and **31**). In the analysis of these catches an attempt was made to indicate actual numbers of individuals, as is shown in the tables there presented. In the analyses of the subsequent years' samples only presence or absence and relative abundance is indicated, and for purposes of comparison the 1921–1923 records are here included in the same form.

Of the series of samples taken at every ten metres from surface to bottom at each station in the 1926 and subsequent catches, only three—surface, mid-water, and bottom—are here considered, in order to deal with the material on the same basis as in the earlier years when only three nets were used.

The data given in Figure 2 show the genera Evadne and Podon to be represented in the plankton. Of the former genus, only one species, *E. nordmanni*, is apparent in the samples. It is possible that a few *E. spinifera* may have been present on occasions amongst large quantities of *E. nordmanni*, but, if so, they were not distinguished. Norman and Brady include only *E. nordmanni* in their list of the Crustacea of Northumberland and Durham (**51**).

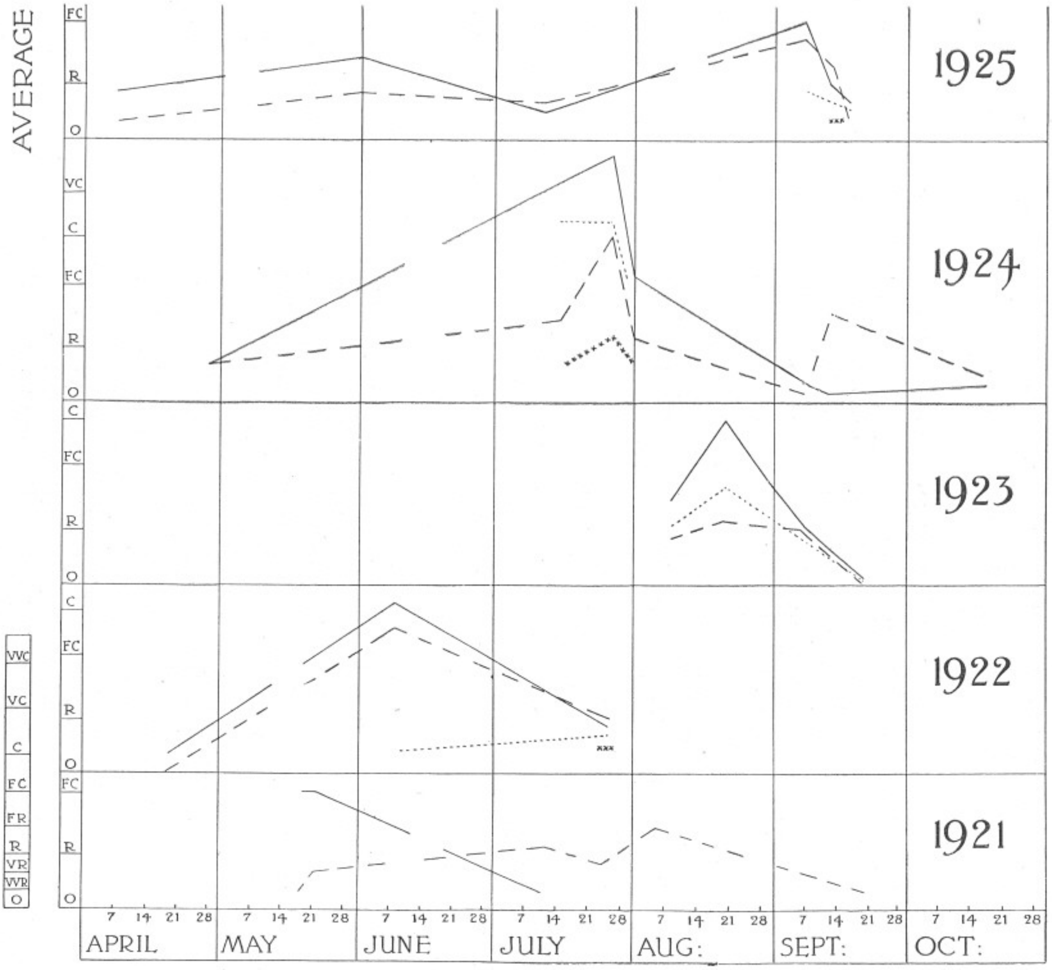
With regard to Podon, the two species, *P. polyphemoides* and *P. intermedius*, have been recorded for the district, the former being described as " not rare," and the latter as " taken occasionally." As the species are not easily identified in the course of general analyses of plankton samples, it is not proposed to discuss the distribution of the individual species of Podon in this paper. Only a general consideration of the occurrence of the two genera in the district will be undertaken. Problems of distribution and fluctuations in population will be discussed only in relation to our commonest Cladoceran, *E. nordmanni*.

ANNUAL RECORDS.

Reference to Fig. 2 and Diagrams A, B and C on pp. 186–188 will show the main facts relating to the individual years' samples as regards the occurrence of Evadne and Podon to be as indicated below.

1921.

During 1920 and 1921 abnormal conditions prevailed in the North Sea, due to a great influx of surface water from the Atlantic Ocean, as shown by the presence of *Salpa fusiformis*, *Limacina retroversa*, and other Atlantic forms in the plankton (**26**).


AVERAGE
FC
R
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VC
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R
O
C
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O
VVC
VC
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FC
FR
R
VR
VVR
O
1925
1924
1923
1922
1921
7 14 21 28
APRIL
MAY
JUNE
JULY
AUG:
SEPT:
OCT:

FIG. 2.

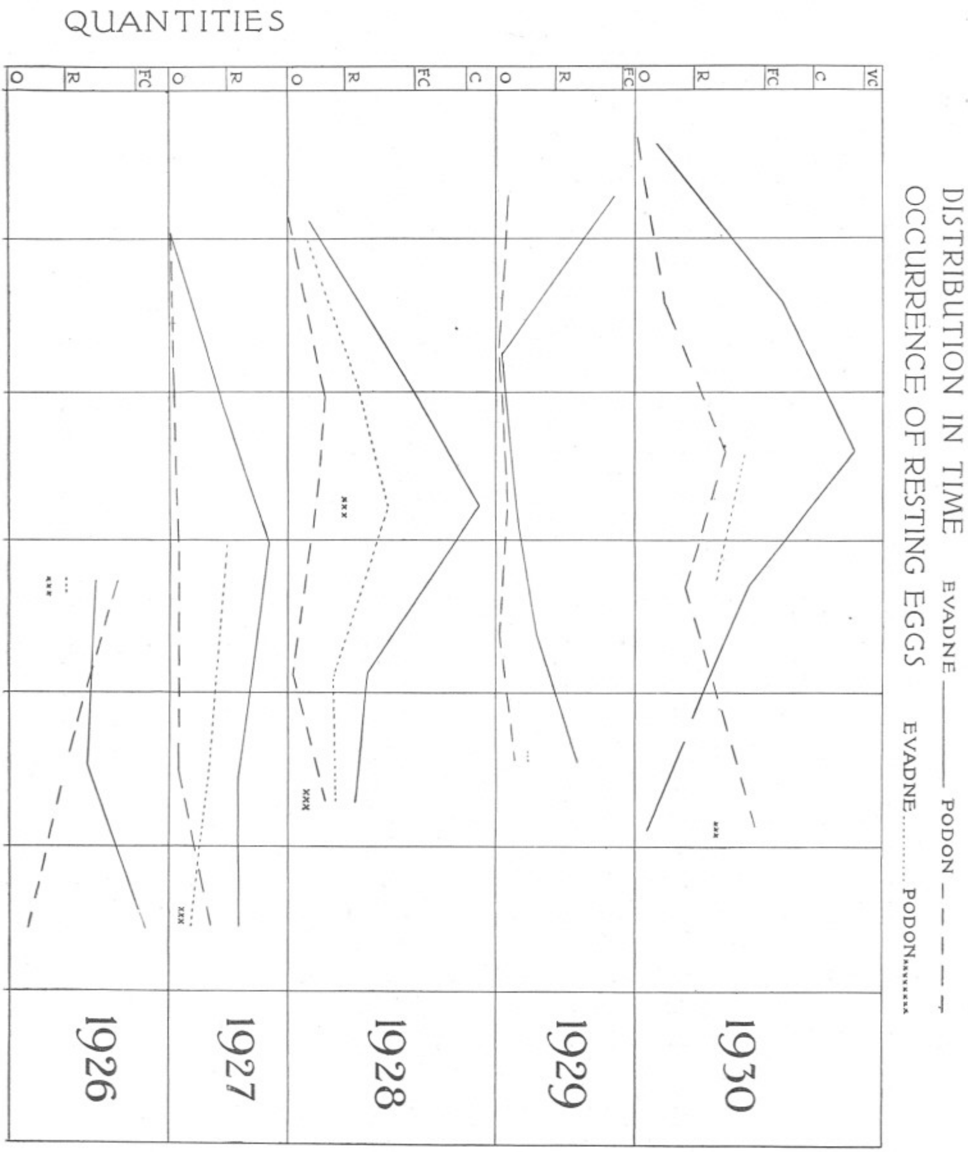
QUANTITIES
DISTRIBUTION IN TIME
EVADNE —— PODON — — —
OCCURRENCE OF RESTING EGGS
EVADNE ...... PODON xxxx
O
R
FC
C
VC
1926
1927
1928
1929
1930

FIG. 2.

When the first of our series of plankton samples was taken, between May 4th and September 20th, 1921, Cladocera were present at all but two stations, namely, at 12 miles from the shore in July and inshore near Boulmer in September.

Evadne was very abundant in May at both ends of the district, after which time it was recorded only twice—in July. Podon, on the other hand, already present in May, attained a maximum early in August and persisted in decreasing numbers until the end of the sampling for that year.

No " winter eggs " or resting-eggs of either form were observed, although the catches were specially searched for them after they had been found to occur in subsequent years.

1922.

In 1922, when the Atlantic influence was abating, sampling began on April 20th when Evadne was found to be present already in the southern part of the district. Its numbers reached a maximum early in June, when it was specially abundant in the inshore region between Coquet Island and Newbiggin. On July 25th–27th, it was again taken fairly plentifully in the same region but was very sparsely represented to the north—no specimens were taken at Station 8, i.e. 7½ miles east of the Longstone.

A few resting-eggs were noted in June and rather more in July, mainly from inshore stations.

Podon appeared first in the catches in June, its numbers increasing with distance from the shore. It was present throughout the district in July, but occurred then in greatest quantity at the inshore stations. Resting-eggs were taken only once, in July (Fig. 31, p. 208).

The analysis of a series of samples taken off the Tyne on July 13th and 14th by Savage (**61**), shows that *P. leuckarti* was fairly plentiful at 11 out of 20 stations and that *E. nordmanni* was nearly three times as abundant but rather more restricted in range. Both forms were decidedly more plentiful at Station 16, i.e. 10 miles from the coast, the farthest inshore of his stations which extended to 50 miles out (Station 30). Both forms were taken also in fair quantity, even at this last station.

We have no later records for the district in this year. A single haul was made off Spurn Head in September, but no Cladocera were present.

1923.

The more normal conditions of the previous year gave place in 1923 to an exceptional flow of Arctic water into the North Sea, bringing the large variety of *Sagitta elegans* to replace *S. setosa* which had been the predominant species since 1921 (**47**).

Unfortunately, no plankton samples were undertaken before August 7th, when Evadne was present in fair numbers over the whole district. In the third week of August it was found to have become very abundant, particularly in catches from the northerly stations. In September, the only records are of small numbers at the stations near Dunstanburgh.

Developing and fully formed resting-eggs were recorded in late August and early September in much greater quantity than in the previous year—again chiefly from inshore stations.

Podon was present throughout the period, but was taken only in small numbers except in the extreme north of the district towards the end of August when it was more plentiful, especially near the shore. No resting-eggs were recorded.

1924.

Except for three hauls in the middle region of the district at the end of April, when Evadne was taken in very small numbers, no catches were made until July 13th. From that time until August 1st this form was present in abundance at all stations. Developing and fully formed resting-eggs were obtained in considerable numbers during the whole period of maximum occurrence.

Podon was present with Evadne in most of the July–August samples, but in much smaller numbers, and it was commonest inshore. During September and October it was observed in most of the catches and usually occurred in greater quantity than Evadne. Resting-eggs were recorded from three of the July–August stations, being most frequent at the end of the period.

1925.

In 1925 the first samples were taken between April 8th and 14th from ten stations covering the whole district from north to south, and extending nine miles eastward from the coast.

Evadne was present at every station and tended to be more abundant at some distance from the shore. Unfortunately, a period of six weeks elapsed before further catches were taken, when only two stations were sampled, on June 1st. Evadne was again recorded in fair numbers. In July the numbers showed a marked decline and specimens were obtained from only four of six stations. On September 7th a decided increase in abundance was noted at the more southerly stations, especially inshore, when, also, resting-eggs in an early stage of development were taken. A week later, numbers had again decreased and resting-eggs appeared only once, at Station 25.

The records for Podon show similar, but less strongly marked fluctuations, and a tendency for numbers to decrease with nearness to the coast. Podon was always the more scarce form except in July and late September. Resting-eggs were recorded only once, from Station 22.

1926.

In this year, the change in the method of sampling took place, and only three voyages were made. In July and August Evadne was taken in fair quantity throughout the district. Increased numbers reported for September were due chiefly to the catches from the most southerly stations. Resting-eggs were taken only in July, at Stations 1 and 3.

Podon was plentifully represented in July, becoming scarcer thereafter, as regards both range and numbers of individuals. Resting-eggs occurred in July at the northern station, No. 5.

1927.

Abnormal activity of the Gulf Stream, noticeable in north-eastern European waters as an increased mid-water current running through the Faroe–Shetland Channel in 1926, now produced its maximum effect, as is indicated, e.g. by the quantities of Ray's Bream taken in the North Sea from 1926 to 1928 (**77**).

Evadne, absent from all stations at the end of April, was present in small quantities throughout the district about a month later. It reached a maximum at the beginning of July, showed a slight decrease in August and was still fairly plentiful in September at the four stations fished. It is impossible, however, to give average quantities for September as the contents of three nets were lost, due to bad-weather conditions. Resting-eggs were taken in the July and subsequent samples, decreasing, in numbers and in proportion of developing to fully formed eggs, as time went on.

Podon was present from the May–June voyage onwards, but always occurred sporadically as to range, and was scarce. Resting-eggs were observed in September, at one station only.

1928.

In this year's catches Evadne appeared in April and increased in quantity up to the latter part of June, after which it decreased progressively until sampling ceased in the latter part of August. The records for resting-eggs are remarkable, in that they show these to have appeared as early as May 1st. They were taken in every month thereafter (i.e until August). The graphic representation of their distribution takes almost identically the same form as that of the average quantities of the species, over the entire period of their occurrence.

Podon made its appearance in June, touched a very low minimum in July, and increased in quantity in August. Resting-eggs were taken in both June and August.

1929.

Following upon the diminution in amount of Gulf Stream water in

1928, the North Sea again suffered an influx of surface Atlantic water in 1929, as evidenced by the occurrence of quantities of Pteropods in the plankton. The effect, however, on this occasion was less far-reaching than was the case in 1921 and 1922.

Our first samples, collected in April, showed Evadne to be already abundant in the district. After this, its numbers fell to practically nothing in May when it was present at a single offshore station only. This was followed by successive small increases in quantity from June to August. Except for a single record at Station 5 in the latter month, no resting-eggs were observed.

Podon was scarce throughout the period, with a feebly marked maximum in April. There were no resting-eggs in the samples.

1930.

Sampling began early in April of this year, and catches were made in each month until the end of August. Evadne, present sparingly in April, had reached a considerable maximum in June, after which the amounts recorded declined greatly until August when sampling ceased. Resting-eggs occurred plentifully in June, especially at offshore stations where early stages predominated, and more sparingly in July, nearer to the coast.

Podon appeared first in May, reached moderate numbers in June, decreased again in July, and finally rose to a marked maximum in August, when it was by far the commoner Cladoceran genus present. Stages in the development of resting-eggs were obtained from four stations on the last voyage.

Summary of Records.

Figure 2 indicates graphically the average quantities of Evadne and Podon present in all nets at all stations sampled during each voyage.

During 1921 to 1925 inclusive, these averages represent numbers of stations—and therefore also of nets—which vary considerably from time to time; and there are, in some cases, long intervals of time between voyages. From 1926 onwards the quantities indicated are more uniform as regards the number of nets they represent, and the time intervals between voyages are more nearly equal.

As, however, series of samples taken over a fairly extensive area and generally at rather infrequent intervals can be used to acquire a general idea only as to the movements and phases of metabolic activity of planktonic forms, the two groups of data are regarded as being sufficiently comparable with one another to make it possible to use them to indicate the general trend of the fluctuations in numbers and distribution of the two genera of Cladocera under consideration, as they occur in our district.

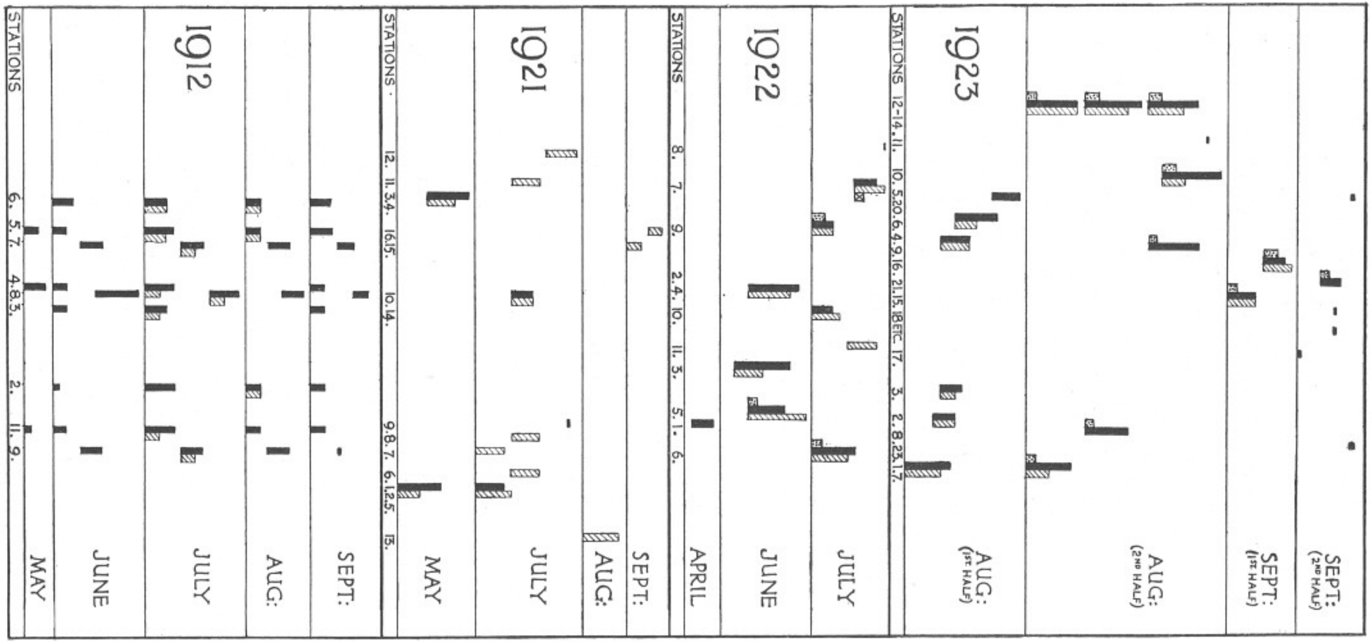

Diagram A.

AVERAGE QUANTITIES OF EVADNE, ▮
DO. DO. PODON, ▨

THE COLUMNS RESTING ON THE BASE LINE FOR EACH MONTHS RECORDS REPRESENT SAMPLES FROM INSHORE STATIONS. THE POSITION OF COLUMNS ABOVE THIS INDICATES RELATIVE DISTANCE OF OTHER STATIONS FROM THE COAST.

RESTING-EGGS OF EVADNE, ▩ RESTING-EGGS OF PODON, ⊠

THE SIZES OF THE COLUMNS REPRESENTING NUMBERS OF RESTING-EGGS ARE COMPARABLE WITH ONE ANOTHER BUT NOT WITH THOSE SHOWING AVERAGE QUANTITIES OF INDIVIDUALS. LEFT AND RIGHT SIDES OF THE DIAGRAMS REPRESENT RESPECTIVELY NORTHERN AND SOUTHERN ENDS OF THE REGION.

REFERENCE TO THE MAPS WILL SHOW THE ACTUAL POSITION OF THE STATIONS INDICATED HERE BY NUMBERS (EXCEPT FOR 1912).

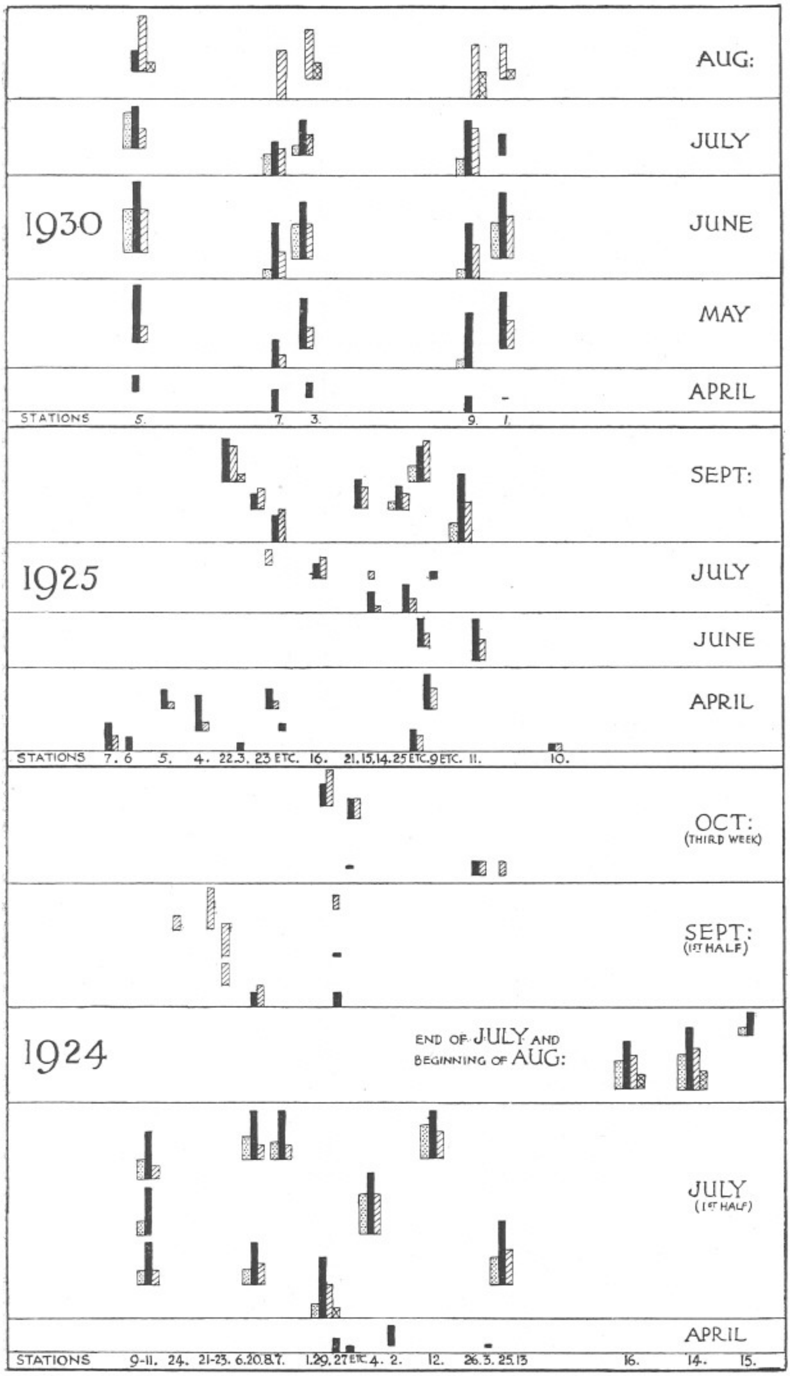
AUG:
JULY
1930
JUNE
MAY
APRIL
STATIONS 5. 7. 3. 9. 1.
SEPT:
1925
JULY
JUNE
APRIL
STATIONS 7. 6 5. 4. 22.3. 23 ETC. 16. 21.15.14.25 ETC. 9 ETC. 11. 10.
OCT: (THIRD WEEK)
SEPT: (1ST HALF)
1924
END OF JULY AND BEGINNING OF AUG:
JULY (1ST HALF)
APRIL
STATIONS 9-11. 24. 21-23. 6.20.8.7. 1.29.27 ETC. 4. 2. 12. 26.3.25.13 16. 14. 15.

DIAGRAM B.

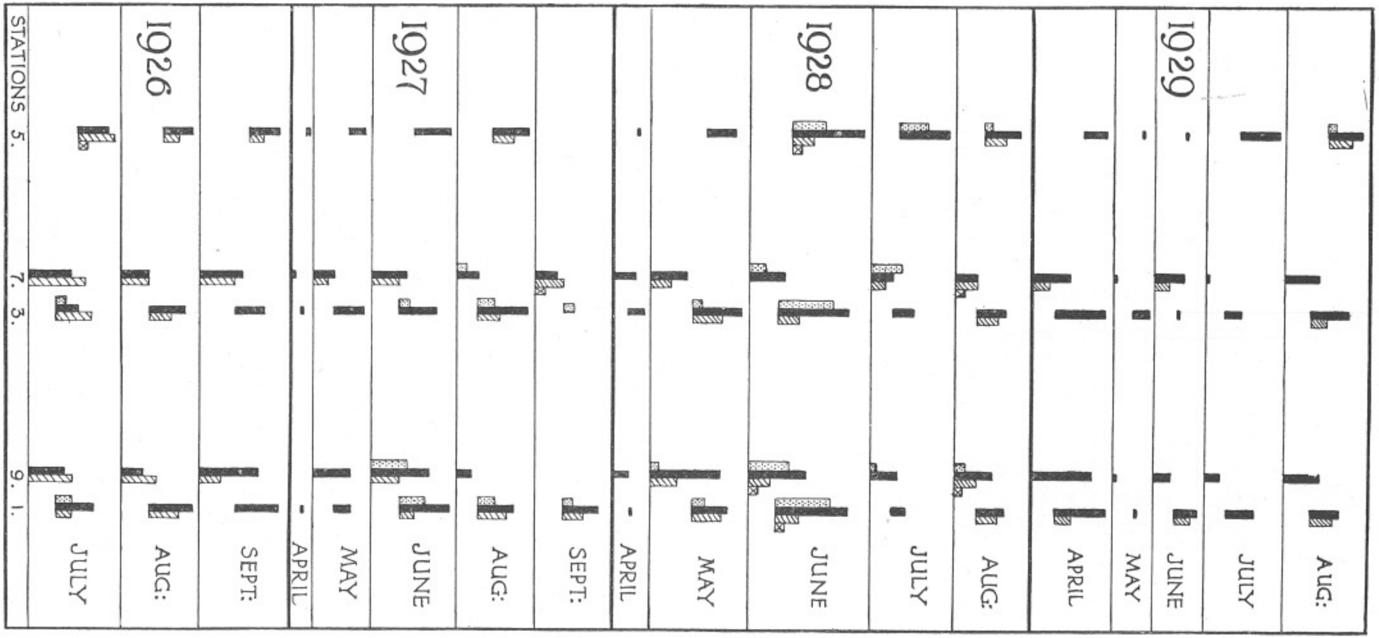

DIAGRAM C.

AVERAGE QUANTITIES OF EVADNE, ■
DO. DO. PODON, ▨
THE COLUMNS RESTING ON THE BASE LINE FOR EACH MONTHS RECORDS REPRESENT SAMPLES FROM INSHORE STATIONS. THE POSITION OF COLUMNS ABOVE THIS INDICATES RELATIVE DISTANCE OF OTHER STATIONS FROM THE COAST.

RESTING-EGGS OF EVADNE, ⊡ RESTING-EGGS OF PODON, ⊠
THE SIZES OF THE COLUMNS REPRESENTING NUMBERS OF RESTING-EGGS ARE COMPARABLE WITH ONE ANOTHER BUT NOT WITH THOSE SHOWING AVERAGE QUANTITIES OF INDIVIDUALS. LEFT AND RIGHT SIDES OF THE DIAGRAMS REPRESENT RESPECTIVELY NORTHERN AND SOUTHERN ENDS OF THE REGION.

REFERENCE TO THE MAPS WILL SHOW THE ACTUAL POSITION OF THE STATIONS INDICATED HERE BY NUMBERS (EXCEPT FOR 1912).

As the years 1921, 1923, 1927, and 1929 must be considered exceptional with regard to conditions in the North Sea, the other years' catches will be discussed first, as showing—in so far as the incompleteness of our sampling will permit—a more normal sequence of events in the life-cycles of these two genera generally, and of *Evadne nordmanni* in particular.

1. *E. nordmanni*—THE "NORMAL" YEARS.

Evadne is the first Cladoceran to make its appearance in quantity near the Northumbrian coast, being present in fair numbers in April. It is by far the commoner genus on the whole, Podon, as a rule, being markedly more plentiful only from September onwards. Diagrams A—C show, as is to be expected, that Evadne is much more widely distributed throughout the area sampled under both sets of experimental conditions. The graphs indicate, furthermore, that there is a well-marked early summer maximum apparently in June (or earlier) and, for those years of which we have records, a second, but less extensive maximum in September or later is evident.

In 1924 the first maximum appears to be in July, but it must be noted that there are no records for May or June. Also, in 1925, the smallness of the first maximum, as here recorded, is probably due to the long intervals between successive samplings at this period.

It is noteworthy that the great increase in the numbers of individuals present in the samples at these times is due, not to the sudden appearance of large numbers of young, but is produced entirely, so far as our samples are concerned, by a temporary influx of adults. Although immense numbers of young forms are, no doubt, present at these times, no very small specimens are ever taken in our nets.

The population, at the times of maximal occurrence, consists principally of females with brood-pouches containing eggs and embryos in all stages of development. Males also are noted during these periods and the so-called "winter"-eggs are associated with the early maximum as well as with the later one. Indeed, our records go to show that the numbers of "winter"-eggs produced are roughly proportional to the numbers of individuals present, and that they are therefore more plentiful in summer than at the onset of winter when the physical conditions have been supposed to be most unfavourable for the continued production of parthenogenetic generations. It will be seen on reference to the graphs that the resting-eggs appear at or about the period of maximum development and continue to be observed during the subsequent decline in numbers. These findings require a consideration of the factors involved in the change from parthenogenetic to sexual reproduction. This will be dealt with later (Part II).

Occasional observations of resting-eggs as early as June have been recorded, e.g. by Hansen (**25**), and are looked upon as being unusual. Apstein, however, notes a marked occurrence of these in June on the Dutch coast and at Kiel (**2** and **3**). For our region the only record looked upon as being exceptionally early is that of both developing and fully formed resting-eggs at three stations on May 1st, 1928. Apstein gives a similar early record for Station 4 (100 miles E. of Hartlepool) in May, 1908 (**2**).

It would appear that the explanation of the frequency of resting-eggs in early summer, which is brought to light by these investigations, is to be sought in the comparative nearness of the stations to the coast, and the large number of samples taken in a restricted area, as compared with the stations used by the International Council and other investigators.

The appearance of resting-eggs in quantity at stations comparatively near the coast, such as ours are, is associated with movements of the population of *E. nordmanni* as a whole.

It is impossible to use the 1921–1925 samples to indicate movements within the district, as stations sampled on different voyages cannot be compared with one another satisfactorily ; but, from 1926 onwards, the three years 1926, 1928, and 1930 do give some suggestion of " transnatant " movements.

In 1926 the population, represented over the whole area, was rather more abundant inshore in July, i.e. at the end of the first sexual period as indicated by the presence of a few resting-eggs. Diagram C shows a slight offshore movement in August, while in September there is evidence of a return to the inshore stations which was coincident with the onset of the decidedly early autumn maximum.

After April, 1928, in which month the small numbers present occurred mainly inshore, resting-eggs were being produced in all the months for which we have records, and the population was spread widely over the district.

The records for 1930 show a similar sequence of events up to the end of the summer sexual period, which ended in July, and the August records show the population to have disappeared from the district almost entirely.

It is suggested, therefore, that *E. nordmanni* seeks shallower coastal waters during the actively growing period when parthenogenetic broods are being produced ; that it remains in these regions until pairing has taken place and resting-eggs have been formed, and that it subsequently makes a migration or transnatation into deeper water. This is probably extensive after the autumn maximum and comparatively slight between the summer and autumn maxima—a difference associated with the length of time between these and with changes in physical conditions at different seasons of the year.

2. *E. nordmanni*—THE "EXCEPTIONAL" YEARS.

It is now necessary to consider the effect of the influence of surface Atlantic water in the North Sea in 1921 and again in 1929. In both years the changed conditions had the effect of speeding up the spring maximum, which occurred in April, 1929, and in May, if not earlier, in 1921. After this the numbers of Evadne decreased rapidly, the population evidently being swept away from our inshore waters.

The fact that no resting-eggs were associated with the first maximum in either year is regarded as significant, and will be discussed in relation to the general distribution of the species.

In 1921 there was no return of the population in autumn, but in 1929 numbers rose steadily from June onwards to produce an autumn maximum as is indicated by the taking of a few resting-eggs on the last voyage.

It is difficult to say what was the effect of the increased amount of Gulf Stream water in the North Sea in 1927, as the records show only one maximum, in early July, and this is capable of two interpretations. There is nothing to indicate whether it represents a much delayed early summer maximum or a greatly accelerated autumn one. The records are sufficient, nevertheless, to show that conditions were abnormal.

As the short sampling season in 1923—the year in which the influence of Arctic water was strongly marked—gives us records for August and September only, it is again impossible to do more than speculate as to its general effect on the species. From the fact that there was a distinct maximum in August, it would seem reasonable to assume that the autumn maximum had been produced unusually early. The phytoplankton of our samples has not yet been analysed, but when this is done it may be expected to throw some light on the problem.

One other point of interest, in this connection, remains to be mentioned, i.e. the occasional appearance of small numbers of individuals distinctly larger than the typical form. These were noticed first from the surface-net of Station 9 in 1925, and again on several occasions in the May–June records for 1927. A few occurred also at the beginning of July of that year. They were not noted again until 1930, when they appeared in both May and June. In the three years they were taken chiefly in the surface and mid-water nets.

These forms were remarkable also for the unusually large number of embryos contained in their brood pouches. The smallest number noted was 7, the majority had 9–11, and a few were observed with as many as 12 or 13. In May–June, and July, 1927, some were seen to be carrying resting-eggs.

Occurrence of Large Form of E. nordmanni.

Year.	Date.	Stat.	Net.	Record.
1925	April 14	9	S	9 or 10 embryos in brood pouch.
1926				
1927	May 30–June 1	1	S	early stages; some with resting-eggs.
		3	B	,, ,, ,, ,, ,,
		5	S	,, ,, ,, ,, ,,
		7	S	,, ,, ,, ,, ,,
		9	S	9–11 embryos in brood pouch.
		,,	M	10 embryos in brood pouch.
		,,	B	early stages.
	June 30–July 3	1	S	,, ,,
		9	S	,, ,, some with resting-eggs.
1928				
1929				
1930	May 13	1	S	quite common.
		5	S	many; one with 13 embryos.
		,,	M	11 and 12 embryos in brood pouch.
		9	M	scarce.
		,,	B	,,
	June 10	3	S	one specimen seen.
		,,	M	,, ,, ,,
		,,	B	,, ,, ,,
		5	S	several
		,,	M	one specimen seen, 7 embryos in brood pouch.

So far as 1927 and 1930 are concerned, the presence of the large form of *E. nordmanni* might possibly be considered to be associated with the influx of Atlantic water into the North Sea. The 1925 record, however, cannot be similarly explained and much remains to be discovered about the distribution of this form before it is possible to explain its presence in our coastal waters.

The only reference it has been possible to discover relating to marked variations in body-size of marine Cladocera, is that of Rammner who mentions de Lint's records for *P. polyphemoides* in the Zuider Zee where specimens taken from water of low salinity measured 500μ as against Lilljeborg's measurements of forms from more saline waters (600μ–660μ).

In relation to *E. nordmanni*, Rammner states only that individuals are bigger and have broader brood pouches at the beginning of the year than those produced towards the end of summer. If he means this as the rule rather than the exception he cannot have been referring to very large forms such as have been mentioned above. Also, if it is to be supposed that these larger, broader females are the direct products of the sexually formed resting-eggs, they ought to have been noticed in autumn also.

According to Lilljeborg, differences in shape correspond to local variations in populations, North Sea forms being ovoid or elliptical-oval and rounded posteriorly whilst the Baltic variety has a narrower body, due to the brood pouch being narrower and more pointed. He adds, furthermore, that the usual number of embryos produced by North Sea forms is 7 or 8, whereas the Baltic ones have only 3 to 5.

Our investigations show that it is necessary to have records covering a considerable period and to be sure that the forms compared occur in similar stages of the life-cycle before general statements such as the above can be made with safety.

The Northumberland population of *E. nordmanni* includes both of Lilljeborg's varieties (**35**), the proportions in which they are represented depending on the phase of activity of the species at the time. In so far as Rammner (**58**) may be understood to mean that rather larger, broader females occur at the beginning of the period of rapid increase in numbers by the production of successive parthenogenetic broods, his observations are in accord with ours. The proportion of these forms diminishes as the asexual stage of the life-cycle proceeds, until, at the time when developing resting-eggs first make their appearance in the samples, the population consists to a great extent of less bulky, more triangular forms.* These produce from 1 to 6 embryos, the majority having 2, 3, or 4. This change in body-bulk and shape, and the reduction in reproductive activity are regarded as indicating a depression in metabolic activity which is synchronous with the onset of the sexual phase. The relation of these observations to the life-cycle of marine Cladocera generally, will be considered separately below.

In this connection it may be mentioned also that the very few previous records of twin resting-eggs (Lilljeborg) have been considerably increased by these investigations. Whereas Lilljeborg observed them only in September, there are in our samples ten records for June and July as against a single one for September, indicating that not only as regards numbers of individuals present and of resting-eggs produced, but in reproductive power also, the early summer maximum is to be regarded as the chief period of activity in the annual cycle of *E. nordmanni.*

OCCURRENCE OF TWIN RESTING-EGGS.

Year.	Date.	Stat.	Net.	Record.
1924	July 13	5	S	One specimen seen.
		8	S	A few.
		9	S	,,
1925	Sept. 7	20	M	One specimen seen.
1926	July 8	1	S	A few.
1927				
1928	June 1	3	S	One specimen seen.
		9	B	,, ,, ,,
	June 24	1	S	,, ,, ,,
		1	M	A few.
		3	S	One specimen seen.
1929				
1930	June 9	1	B	,, ,, ,,

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* Sharpe (**72**) states that the brood sac may contain from 3 to 8 embryos, this causing its outline to be quite variable.

3. Podon—Occurrence from 1921 to 1930.

Until the species (or varieties) of Podon present at various times in the samples have been identified, it is impossible to make definite statements as to the precise activities of members of the genus, but one or two general facts may be mentioned.

As already noted, Podon makes its appearance in our district later than Evadne and is comparatively rare during the early summer. Nevertheless, it shows a maximum, generally feebly marked and more or less coincident with that of Evadne. This is followed by a decrease in numbers which, however, soon gives way to a considerable increase in population producing an autumn maximum which may involve the presence of vastly greater numbers.

It has been noted from time to time that, while individuals of Podon are indistinguishable from one another in the earlier part of the year, there is evidence of the presence of two distinct species (or varieties) in the later months. Resting-eggs were never taken in quantity, but the graphs (Fig. 2) indicate that they may appear in association with both periods of greatest population. The two maxima appear to be little affected by abnormal conditions, except for a general speeding up of activity in relation to time in 1921.

The above-mentioned data indicate that, in addition to being generally a less abundant North Sea genus than Evadne, it is also less strongly attracted to shallow coastal waters as a breeding place.

Previous Records of Cladocera from Northern European Seas.

1. *Northumberland.*

The only previous records of Cladocera for the Northumbrian coast are from surface and, to a less extent, bottom tow-nettings taken at long intervals in various parts of the district, between 1889 (**44**) and 1912 (**76**). Only the last of these series of samples is sufficiently complete to be comparable with the present records, and these are included in Diagram A. The distribution of the two genera in time and space may be seen to take what is regarded as the normal course. Evadne arrived from the north of the district in May, spread along the coast in June and July—being more abundant inshore in the latter month, when maximum numbers were present. It was scarce, particularly inshore, in August, and in September showed a slight tendency to return to the coast, especially towards the north. There is a decided similarity between these and the 1924 records.

Podon (identified as *P. polyphemoides*) did not make its appearance so early as Evadne. It was recorded for July and August and showed a maximum coincident with that of Evadne.

In 1899 it is evident that large numbers of both forms were present in June. The remaining records are too vague to be of value in this connection.

2. *Firth of Forth.*

T. Scott's records (**65**) for this region give no details and show only that *E. nordmanni* is more abundant than *P.* (*?*) *polyphemoides* and has a wider distribution.

3. *Clyde Sea Area.*

Marshall's records (**42**) for *E. nordmanni*, "Common in May and June, fairly common till September and frequent in October," again indicate the occurrence of two periods of maximal occurrence near the coast.

4. *English Channel.*

A consideration of Bygrave's records (**9**) of Cladocera in 1905 and 1906 shows some interesting features. He, however, made no attempt at an analysis, merely noting occurrences and making a general statement to the effect that these forms are more frequent in the western than the eastern part of the Channel, that they always appear in spring and form an important part of the plankton in summer, disappearing again in autumn, "when they form their winter-eggs and thus are able to survive the winter." (This from a record of samples taken during a period of exceptional activity of the North Atlantic Drift: Salps were present in the North Sea in 1905 and Pteropods plentiful in 1906.)

The lightship records from the western and eastern ends of the Channel (Sevenstones and Varne) show Evadne to be the commoner form in the west in 1906, while only Podon occurred at the eastern end. In 1905 Evadne was scarce to the west also.

Quarterly records from other stations (E1 and E17—10 to 20 miles offshore on the northern side) in 1906 show Evadne to be present in February, fairly common in May and abundant in August. The Plymouth records for 1906 also indicate maxima in May–June and in August–September, the latter being the greater.

Bygrave connects the general scarcity of Evadne in 1905 with a patch of water of high salinity at the western end of the Channel (near Station E1).

It is evident from the summary of records given below, that the Cladoceran population enters the Channel with the Atlantic current and normally begins to breed as soon as it reaches coastal waters. In 1905 it was evidently swept away from its usual local centre of distribution, and the fact that in 1906 the early maximum was relatively small indicates that there had not then been a complete return to normal conditions. The taking of resting-eggs only in the late summer of 1906 further accentuates the similarity between these records and ours for later years in which similar conditions prevailed in the North Sea.

SUMMARY OF BYGRAVE'S RECORDS OF EVADNE.

Year.	Month.	Stations arranged in order from W. to E.			
		Sevenstones.	E1–E17.	Plymouth.	Varne.
1905	Jan.–June	None	–	–	None.
	July	Rare	–	–	,,
	Aug.	,,	–	–	,,
	Sept.	Very rare	–	–	,,
	Oct.–Dec.	None	–	–	,,
1906	Jan.	,,	–	None	,,
	Feb.	,,	Very rare	,,	,,
	March	,,	–	Very rare	,,
	April	Rare	–	Rare	,,
	May	Rare to f. common	Common	F. rare	,,
	June	Rare to f. common	–	Rare to f. common	,,
	July	Common to rare	–	F. rare	,,
	Aug.	F. common to rare*	Common	Common	,,
	Sept.	Common	–	F. common to rare	,,
	Oct.	F. common	–	None	,,
	Nov.–Dec.	None	None	,,	,,

– indicates no samples taken. * indicates resting-eggs taken.

5. *The Irish Sea.*

The summaries of records of Cladocera given in the annual plankton reports of the Lancashire Sea-Fisheries Laboratory from 1907 to 1919 show them to refer to two species only, *Podon intermedius* and *Evadne nordmanni*. Considered together, they show the latter species to appear in the district in March or April, to increase in numbers to May or June and thereafter to fall off until September when a second maximum occurs. None are recorded later than October.

In the years 1908, 1913 and 1914, Evadne did not appear until April and, in the last two years, was always scarcer than usual. In 1912 it was not taken later than August.

Podon is shown to have a time range very similar to that of Evadne except that it generally appears rather later and persists longer.

The records are too scanty to show clearly variations in time of appearance and abundance of population from year to year, and indeed the reports frequently lay stress (perhaps rather more than would seem to be warranted) on the great constancy of occurrence of these forms.

A. Scott's records (**64**) of Cladocera from the spawning ponds at Port Erin in 1922 and 1923 indicate the presence of abnormal conditions in the earlier year, as also do our records for Northumberland. In 1923 Evadne first occurred at Port Erin in April and continued to be taken until September, while in the previous year it did not make its first appearance until June and disappeared again in August. Podon was present in 1923 from April till December excepting only August. In 1922 its range was restricted to May–July.

Gough's records (**21**) of samples taken at four lightships on the south and east coasts of Ireland in 1904 are insufficient to form a satisfactory picture of the general distribution of Cladocera in St. George's Channel and the Irish Sea although they serve to show that the population in these waters is distributed by the current entering from the south, and there is some indication of two periods of maximal abundance in inshore waters.

The fact that no Cladocera were taken at the South Arklow Lightship and their extreme scarcity at Skulmartin suggest that in this region there occurs a phenomenon similar to that noted by Bygrave and Apstein regarding the distribution of Cladocera at the eastern end of the English Channel and in the southern part of the North Sea. Apstein remarked that Cladocera were scarce in these regions, "although the physical conditions were suitable," and failed to account for this.

This matter will be discussed separately below.

6. *North Sea, Baltic Sea, etc.*

Plankton samples taken by several investigators and expeditions show *E. nordmanni* to be the commonest Cladoceran in the North Sea, on the western shores of Great Britain, in Danish waters, and in the Baltic. It is noted as being present in varying degrees of abundance at different stations, almost throughout the entire year, but always rare during the winter months. It has been mentioned as having been taken along the Norwegian coast up to 72 deg. N. lat., and, in the Atlantic, 13 deg. West of Scotland. Also, there are isolated records of its occurrence in the Barents Sea near the Murman coast and in the Irminger Current up to the south coast of Iceland.

Apstein regards the species as being abundant throughout the seas of North-West Europe during all the summer months. This conclusion is evidently based on the fact that the times of maximal abundance vary slightly from place to place and from year to year, and that the many different stations sampled were far from being equally distant from the shore. Although he quotes Hansen's records of resting-eggs taken in Dutch coastal waters in June, he does not appear to attach any significance to their production at so early a period.

Rammner, summing up records of the distribution of *E. nordmanni*, refers to its abundance in the North Sea and the Baltic and to its occurrence farther afield, but regards the Baltic as its real home. Apstein, on the other hand, considers the northern part of the North Sea to be its centre of distribution.

Rammner remarks also on its great variation in numbers from place to place, due to causes other than seasonal ones, and points out the necessity for more systematic sampling before it is possible to make a definite statement as to its distribution in a large area (such as the North Sea). He considers that currents are responsible for its distribution and notes its tendency to inhabit inshore waters.

With reference to his statement that *E. nordmanni* is not found within a distance of 100 or 200 metres from the shore, it may be noted incidentally that specimens were taken in August, 1922, in the Estuary of the River Coquet. Also, the species has been recorded by T. Scott (**67**) as being abundant at the head of Loch Fyne.

Lohmann's quantitative analyses of organisms taken in a measured volume of water, show the occurrence of two maxima in the numbers of *E. nordmanni* obtained, i.e. in June and August (1884) with a minimum between these, in July.

Investigators have remarked on apparent peculiarities in the distribution of the species, and, assuming it to be truly neritic, have had to account for its occurrence in certain places by its being carried by currents away from its normal area of distribution in coastal waters.

Rammner emphasises the effect of currents on its distribution and thinks that there may be some reason for considering the species to be a deep-sea form. Steuer goes farther and thinks that it is ridiculous not to regard *E. nordmanni* as an oceanic species since it has been shown to occur in the open ocean.

Ostenfeld explains the presence of occasional specimens along the Norwegian coast and in the Barents Sea as being due to the Gulf Stream carrying them away from the coast (of the western side of Scotland, presumably). He is unable, however, to explain the occurrence of *E. nordmanni* in the Irminger Current.

Apstein, referring to the distribution of this species, does not analyse his data, but his statements relating to that of *E. spinifera* are interesting. He regards isolated specimens taken near the Faroes as having been brought there through the influence of the Atlantic Drift. Also, while making no special reference to the exceptional conditions prevailing in 1905, he thinks that examples found in the English Channel in November, 1904, and in the south-west corner of the North Sea in the following May, might well have originated in the Atlantic Ocean. He mentions, furthermore, that the only specimens taken in any year near the Belgian Coast were obtained in May, 1905.

As 1905 is comparable with 1921, and to a less extent with 1929 as regards the cause of unusual conditions in the North Sea, the foregoing statements are of importance as emphasising the influence of an increased influx of Atlantic drift water into our coastal regions. The effect of such is evidently to interfere with the normal distribution and breeding times of the Cladoceran population, and to introduce other forms, e.g. *E. spinifera.* Its effect in 1921 and 1929 was to sweep away *E. nordmanni* from the Northumbrian coast after an early maximum in May, and to prevent the development of resting-eggs there at these times. Also, the records for 1929 show no indication of depression as regards body-shape and numbers of embryos formed, during the early part of the year. (The 1921 samples need re-examination for verification of this point.) It would thus appear that the increased amount of Atlantic drift water present produced a change in the physical conditions which are responsible, at least indirectly, for this effect. Bygrave's records for the English Channel show similar results to have been brought about there in 1905, as also do Lohmann's for the relative proportions of Podon and Evadne present at Kiel during the same period.*

From a consideration of the above data it is suggested that normally *E. nordmanni* is capable of migrating across current during the course of its denatant drift along the coast, so that it is brought into inshore waters where the environment is at first suitable for the rapid production of successive parthenogenetic broods, but which later has the effect of slowing down activity and bringing the asexual period to an end. An unusually strongly running body of water or one differently constituted from the normal coastal current may interfere very markedly with this series of events.

GEOGRAPHICAL DISTRIBUTION OF *E. NORDMANNI.*

In addition to the distribution of the species in the regions already discussed, *E. nordmanni* is also known to inhabit the Labrador Current (Hansen) and to be common off the coasts of Nova Scotia (Wright, **89**) and Massachusetts (Sharpe, **72**).

The importance of the part played by current systems as indicated

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* That similar conditions supervened in 1896 is shown by T. Scott's records for the Faroe-Shetland Channel in July and August of that year. Salps and Arachnactis larvæ were present, indicating an abnormal flow of Atlantic water. While *Podon intermedius* (or *polyphemoides*) was taken in 14 out of 19 catches, *E. nordmanni* was present in only 6 and was always rare.

above needs further consideration, and it is suggested that it is necessary to take a wider view of the geographical distribution of the species than has been done previously.

It is evident from the position of the stations from which *E. nordmanni* has been observed that one cannot regard it as a neritic species except in the sense that it " prefers " coastal waters as a breeding-place. That such regions are absolutely necessary for the purpose remains to be proved.

Ostenfeld, assuming that the species was indigenous to the coasts of North-Eastern Europe, was at a loss to explain its presence near Iceland, in the open Atlantic and in the Labrador Current.

If, however, these regions of occurrence are considered in relation to Wright's and Sharpe's records for the east coast of North America, its presence can be explained. *E. nordmanni* occurring in quantity off the coasts of Massachusetts and Nova Scotia must be picked up by the Gulf Stream and carried across the Atlantic to be distributed to the English Channel and the Bay of Biscay (**75**) on the one hand, and to the west coast of Scotland, northern North Sea, Danish waters, and Baltic Sea on the other hand. Furthermore, it may be carried likewise along the Norwegian coast even so far as the Barents Sea when conditions are favourable. Since the Irminger Current branches off from the Atlantic Drift farther to the west, this assumption provides the only explanation of the occurrence of *E. nordmanni* along its course. Since it is present in the Labrador Current also, it may be said to occur in every part of the North Atlantic circulation. Thus, the species may be regarded as having two main centres of distribution, the one on the west coast of North America, the other in the coastal waters of North-Eastern Europe. That it is a regular inhabitant of the North Atlantic Ocean is evident, though to what extent it breeds under other than coastal conditions is as yet unknown.

Records of the species from the Bay of Biscay, the Mediterranean, the coast of California, and various places along the west coast of Africa indicate that it has other centres of distribution, but the records are too scattered to make it possible to discuss this point.

Scarcity of *E. nordmanni* in Certain Coastal Areas.

A consideration of the horizontal distribution of Cladocera in the Irish Sea, North Sea, and English Channel in relation to the Admiralty chart (Fig. 3) showing the general drift of surface water in these regions, reveals the fact that the main spread of the population is along the course of the principal coastal surface currents in the regions concerned.

In the North Sea, Cladocera have been recorded as being generally scarce to the southward of a line drawn between the Tyne (55 deg. N. lat.) and Texel (53 deg. N. lat.), that is beyond the region in which the southerly flowing coastal current crosses over from the English to the Freisian coast. That a fraction of the population is retained in the offshoots of the current which continue south to about the region of Orford Ness is shown from the analysis of Savage's samples. In these the numbers of Cladocera decrease with distance southward as far as Lowestoft, the most southerly station fished.

Distribution in the Irish Sea is explainable along similar lines. The main population enters via the south coast of Ireland in the current which passes through St. George's Channel and, on reaching the Irish Sea, is deflected with it to the east, as seen from the Liverpool and Port Erin records. That it scarcely enters the region to the west of this, in which only temporary drifts approach the Irish coast, is indicated by the lightship records of that region (South Arklow and Skulmartin). Thus, in both the above cases, major movements of population depend on the circulation of the main surface currents, and only relatively small numbers are present in those parts not directly under the influence of these.

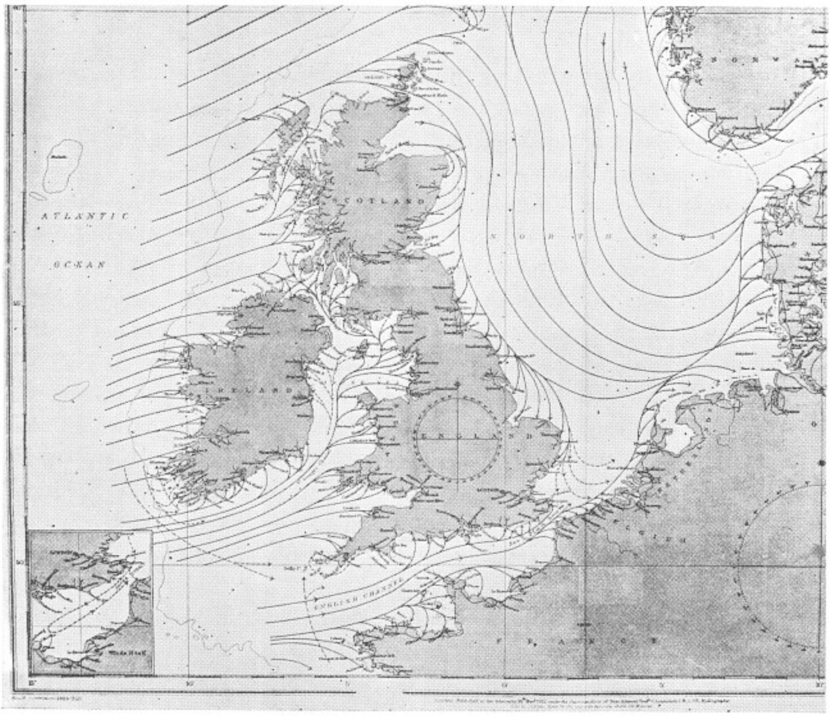


Fig. 3.—Admiralty Chart, showing direction of surface currents around the British Isles.

In the case of the English Channel, the scarcity of Cladocera in the eastern region is more difficult to account for. In consideration of the fact that the main current in which Cladocera are abundant at the western end of the Channel normally passes through the Dover Strait, would lead one to assume their presence in quantity both in the eastern part of the Channel and in the south-western region of the North Sea. Their general scarcity in these waters is probably to be accounted for in part by the effect on the current of the narrowing of the Channel eastwards, and partly to temporary conditions to be referred to shortly. On both sides of the main Channel current there are coastwise offshoots whose general tendency is to be deflected backwards. (Tidal movements here also tend in the same direction.)

If it is generally true that agamic reproduction is favoured by inshore conditions, the greater part of the Cladoceran population should be found in these parts—as it is, so far as our incomplete records including only the northern shore are able to show.

The Admiralty chart (Fig. 3) referred to includes an inset showing the temporary effect of northerly to easterly winds on the current of the Dover Strait. This illustrates that, in these circumstances, the direction of the current on the English side may be reversed and travel in the direction of C. Barfleur as far as about 1 deg. W. long. Also, the direction of the tidal streams on either side of the Dover Strait during the ebb will act in conjunction with this in its effect of further mitigating against the passage of quantities of Cladocera into this part of the Channel and through the Dover Strait into the southern North Sea. That an abnormally strong influx of surface Atlantic water into the North Sea may also accentuate this condition at times, is suggested by the entire absence of Cladocera from the Varne Lightship Station throughout the years 1905 and 1906.

Records of quantities of Cladocera in Dutch coastal waters on certain occasions—other than off the northern part of the Freisian coast—can however be accounted for only on the assumption that at times large numbers *are* able to pass through the Dover Strait, or that the temporary currents indicated as traversing the region between Lowestoft and the Hook, take part in their distribution, or that both may be contributory factors.

THE VERTICAL DISTRIBUTION OF *EVADNE NORDMANNI*.

The only material as yet available for the study of the vertical distribution of *E. nordmanni* in Northumbrian coastal waters is that taken in 1928, when all the samples were examined, i.e. the catches from the whole series of nets used at ten-fathom intervals at all stations.

The relative numbers of Evadne taken at the different depths are indicated in Fig. 4. F. S. Russell's (**59**) method of representation has been used. The narrow black lines indicate depth where no specimens were obtained.

Except in April and in a few of the later catches, when Evadne was scarce, it is shown to be present at all depths fished, i.e. down to 60 fathoms at the offshore stations with a decided tendency to be most abundant in the first 10 to 20 fathoms below the surface. If, as stated by Russell, light intensity is the main deciding factor of the depth at which a species normally lives, then the optimum intensity for *E. nordmanni* is evidently very high. Not only was it found abundantly near the surface during the summer months at times when visibility was comparatively poor, as in the early June and the August voyages, but its general distribution suffered no appreciable change when visibility was good in the later June cruise and exceptionally good in July. (A special note in the yacht's log has reference to the unusually clear conditions prevailing on July 24th to 27th.) See Table I, page 204.

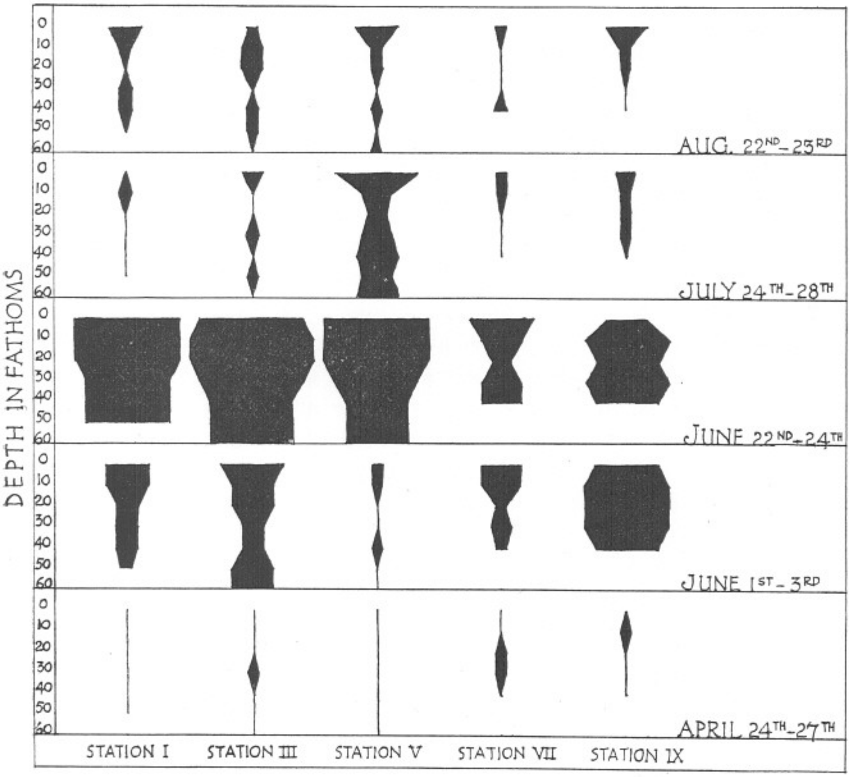


FIG. 4.—Vertical distribution of *E. nordmanni*, 1928.

Our records, therefore, bear out the general statements of other workers as to *E. nordmanni* being essentially an epiplanktonic form. Rammner however states that the species is not found actually at the surface except in dead calm weather, as it makes its way to deeper layers of water at the first sign of roughness of the sea. This does not hold good so far as our records are concerned, for the samples taken on the August voyage show a distinct aggregation of individuals at and near the surface on an occasion when the sea was moderating after a rough period. Sampling was to have begun on August 21st, but the sea was too rough for the work to be undertaken until the following day. The weather conditions prevailing during the several cruises, as recorded in the ship's log, are summarised in Table I.

The records of Stebbing and Fowler (**75**) of Cladocera in the Biscayan plankton further stress the fact of *E. nordmanni* being essentially a surface-water form. They record it from the surface on several occasions and give its lower limit as about 100 fathoms. Only a few isolated specimens were taken from greater depths (500 and 750 fathoms).

It is not expected that normal variations in temperature and salinity will be shown to have any appreciable effect on the vertical distribution of this species, as it has been observed to live under a wide range of conditions as regards both these factors (range of salinity $2\text{–}35^{\circ}/_{\circ\circ}$, limits $1{\cdot}53\text{–}35{\cdot}4^{\circ}/_{\circ\circ}$: range of temperature 6–18 deg. C., limits 1–22·6 deg. C), but until more data are available it is impossible to discuss this point or to consider differences between its diurnal and nocturnal distribution in relation to depth.

TABLE I

WEATHER CONDITIONS DURING 1928 PLANKTON CRUISES.

Date.	Wind.	Sea.	Visibility.	Remarks.
Aug. 20th	N.E.	E. ; strong	Poor ; rain	Too rough for work.
,, 21st	,,	,,	,,	,, ,,
,, 22nd	N.	N.E. moderating	Poor	
,, 23rd	S.S.E. ; light	Moderate	,,	
,, 24th	Increased	" Hashy "	Poor ; rain	
July 25th	W. ; light	Smooth	Very good	Visibility exceptionally good throughout trip — coast seen from off-shore stations.
,, 26th	,,	,,	,,	
,, 27th	Light ; variable	Light N. swell	Good	
,, 28th	Light ; N.-N.W.	,,	Cloudy, rain	
June 22nd	Fresh, W.		Moderate.	
,, 23rd	Strong, W.		Better.	
,, 24th	Fresh-strong		Good.	
June 1st	Light, S.E.	E. swell.		
,, 2nd	Light, N.	Haze, clearing later.		
April 24th	Fresh, S.		Moderate.	
,, 25th	,,	S.E.	,,	
,, 26th	Light, N.E.	Calm	,,	

PART II. THE LIFE-CYCLE OF *EVADNE NORDMANNI.*

1. THE PARTHENOGENETIC PHASE.

The paired ovaries of *E. nordmanni* are small, spindle-shaped structures lying at the sides of the intestine. The posteriorly directed end of the ovary is rounded while the opposite end may be drawn out to a fine point.

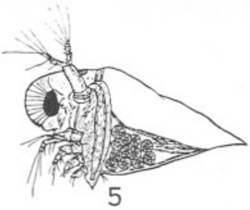
After the eggs have been shed into the brood pouch, the ovary is invisible in stained preparations (Figs. 5 and 11), but, as the embryos develop, the organ is again discernible, its contents developing meanwhile so that by the time the embryos are ready to be freed, a second generation of eggs has been formed and may be extruded even before the previous batch of embryos has been set free. (Figs. 6–9 and 14.)

As the preparations examined were made from material not specially preserved for the purpose, it has not been possible to make out the details of the early development of the ovarian cells—the nuclei not being visible. In the earliest phase in which the ovary can be seen, it is filled with a mass of tissue not shown to be definitely marked off into cells. Later a number of irregularly shaped cells are closely pressed together in all but the narrow anterior end of the ovarian sac, and finally the same space is occupied by a string of large cells varying in number from four to six or rarely eight. The last of these is placed at the extreme posterior end of the organ, while the anterior part is now filled with a group of very small cells (Figs. 15 to 18). The anterior part of the ovary thus evidently constitutes the germarium described by W. F. R. Weldon (**84**) as occupying this position. The posterior end of the ovary is turned towards the dorsal side of the body and, at the time of egg extrusion, no doubt forms a short oviduct which becomes continuous with the wall of the brood sac as suggested, though not actually seen, by Claus (**12**).

In certain preparations only four large ovarian cells are present and there is no germarium. As this condition occurs in specimens bearing only very few embryos, indicating the condition of depression already mentioned as preceding the sexual phase, it would appear to be an early stage in the formation of the resting-egg (Fig. 34). This will be discussed below.

The process of development of the parthenogenetic eggs of Polyphemidæ was described originally by Claus who stated that the tetrad-formation of ovarian cells, which undoubtedly occurs in the production of the gamic egg, occurs also in the development of the agamic generations—one cell from each tetrad giving rise to an ovum, the others serving as "nurse-cells" or feeding cells for its nourishment.

Kuttner (**33**), on the other hand, states that never was the tetrad formation observed, that no "nurse-cells" are present and that each



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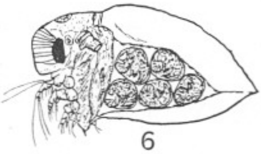

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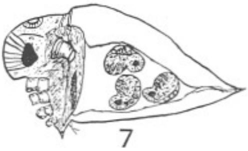

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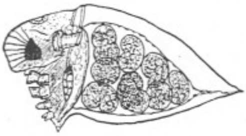

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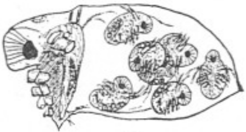

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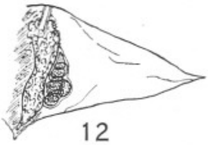

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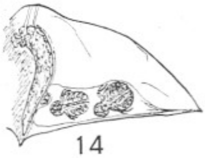

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FIG. 5.—Parthenogenetic female of *E. nordmanni* with embryos in blastula stage. Shows thickening of anterior wall of brood pouch and cells suspended in cavity towards apical end.

FIG. 6.—Developing embryos in brood pouch; ovary again becoming visible.

FIG. 7.—Brood pouch containing well-advanced embryos bearing eggs. Maternal ovary further developed than in preceding figures.

FIG. 8.—Female showing conditions during height of parthenogenetic activity; nine embryos in brood pouch. Ovary with seven egg cells and germarium.

FIG. 9.—Fertile embryos in shell cavity ready for freeing. Shows torn walls of brood pouch.

FIGS. 10 and 11.—Brood pouch with eggs; shows its relatively small size at this stage and the glandular cells of its wall, as in Fig. 5.

FIG. 12.—Newly extruded eggs in very small brood pouch with glandular cells not yet visible.

FIG. 13.—Cast cuticle containing one embryo and what appear to be cuticles of two others in shell cavity.

FIG. 14.—Brood pouch containing two fully-formed embryos and enclosing second very small brood pouch with two newly extruded eggs. Here, as in Figures 9 and 13, the embryos are free from the egg membrane.

FIGS. 15, 16, and 18.—Ovaries with varying numbers of egg cells in posterior portion; anterior end occupied by germarium.

FIGS. 19 and 20.—Ovaries including egg cells and large germaria with cellular contents.

FIGS. 17 and 21.—Most advanced stage in development of ovaries, i.e. with two generations of germ cells. (Taken from preparations of specimens with several embryos in brood pouch.)

germ cell develops independently and produces an egg. This is evidently a fact in regard to the large cells which come to occupy the more posterior part of the ovary towards the end of the period of embryonic development of the previous batch of eggs, but it may well be that each of these is the product of one of a group of four small cells produced by the germarium as stated by Weldon. He described proliferation in the germarium as giving rise to quadri-nucleate masses which form four cells, one of which becomes an ovum and is nourished by the others, which then die. As already stated, the preparations do not show the details of these earlier stages at all clearly, but are good enough to indicate that the ovary contains more protoplasmic masses or cells at the earlier stages than there are large egg cells present when these are fully grown (Figs. 19 and 20). During the active period, when many embryos are produced, the germarium may occupy more space than the remainder of the ovary and its contents are definitely cellular. This is shown in Figure 21.

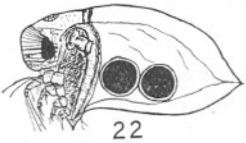
The failure of Kuttner to observe the germarium may be due to the examination of specimens nearing the end of the parthenogenetic period, or to mistaking it for the anterior end of one of the chain of egg cells from which it is sometimes difficult to distinguish it.

The presence of young germ cells and fully-formed eggs in the ovary, together with advanced embryos in the brood pouch, is interesting in that four generations of individuals may thus be seen together in different stages of development. This, taken along with the fact that the embryos also become fertile before leaving the brood sac, furnishes an adequate explanation of the rapid and enormous increase in numbers of individuals which takes place under conditions favourable to parthenogenetic reproduction.

Kuttner mentions the fact of the embryos being fertile as significant in regard to the recording of no females with empty brood sacs, but the two stages of cells in the ovary is equally important in this connection. Nevertheless, females with empty brood sacs have been observed. This occurs at the end of the agamic period and appears to be a necessary preliminary to the preparations for the nourishment of the sexually formed " winter-egg."

Claus has described the brood pouch as a closed feeding-chamber or " uterus " in which the embryos are nourished from the maternal circulation through the medium of the glandular cells of its wall and states that the feeding area is further increased by an infolding of the anterior wall by means of which glandular cells are suspended within the cavity of the brood chamber.

Kuttner's crudely figured " Blasenförmiges Organ " is shown as a band of large square-sided cells passing across the middle of the brood chamber. Nothing like this has been seen in the Northumberland material, which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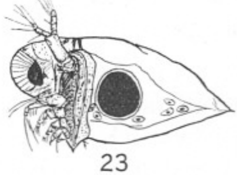
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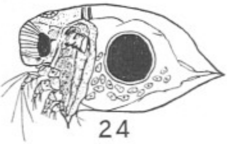
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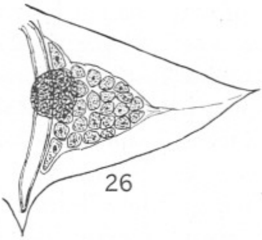
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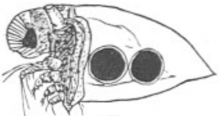
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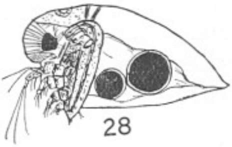
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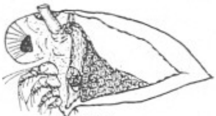
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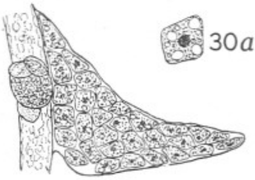
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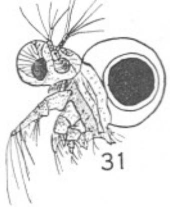
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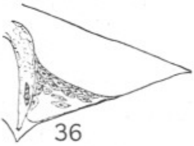
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FIG. 22.—Female *E. nordmanni* with two fully-developed winter-eggs of equal size in brood pouch. Nurse-cells entirely disappeared.

FIGS. 23 and 24.—Winter-eggs almost or completely developed, with thick shell. Shrunken remains of some nurse-cells in brood sacs.

FIG. 25.—Developing winter-egg within closely packed mass of nurse cells. Protective shell not yet begun to be formed.

FIG. 26.—Rather later stage than last—nurse-cells less numerous and less closely packed.

FIG. 27.—Two fully-formed winter-eggs escaping through ruptured wall of brood pouch into shell space.

FIG. 28.—Specimen containing two winter-eggs of unequal size.

FIG. 29.—Young winter-egg surrounded by other three cells of the tetrad. Brood pouch already filled with nurse-cells.

FIG. 30.—Detail of Figure 29 more highly magnified.

FIG. 30a.—One of glandular nurse-cells enlarged to show nucleus, fat globules and granules.

FIG. 31.—Specimen of *Podon ? polyphemoides* with winter-egg in shell cavity.

FIG. 32.—Growing winter-egg of *E. nordmanni* showing formation of envelope. (Brood sac and nurse-cells not indicated.)

FIG. 33.—Cast shell of Evadne containing a winter-egg.

FIG. 34.—Earliest stage in winter-egg formation observed. Ovary contains only a tetrad with third cell slightly enlarged but not noticeably different from others in texture.

FIG. 35.—Rather later stage than last. Third cell now definitely larger and filled with fat globules.

FIG. 36.—Stage between those shown in Figures 34 and 35. Brood pouch formed and partially filled with nurse-cells which are situated chiefly along its anterior wall.

FIG. 36a.—Shows detail of ovary shown in Figure 36. Third cell of tetrad filled with fat globules.

shows, during certain stages of brood sac formation, a condition similar to that described by Claus.

When the eggs first leave the ovary they lie at the posterior end of the shell cavity, just anterior to the caudal furca and closely surrounded by a fine membrane which forms the wall of the brood sac (Fig. 12). The eggs are thus pressed together and are not circular in outline as they become later. As the eggs develop, the wall of the brood pouch correspondingly expands and its cellular character becomes obvious. It is attached to the shell along its posterior border and becomes triangular in shape. The anterior wall appears thickened, and elongated spindle-shaped cells occupy the apex of the triangle (Figs. 5, 10, and 11). With further development of the embryos, the brood pouch lengthens until its attachment consists of a fine strand of tissue connecting its end with that of the shell (Fig. 6). When the brood sac contains only a small number of embryos its shape is not conspicuously altered, but when packed with many well-grown young its anterior side becomes rounded and it occupies a considerable portion of the shell space which is correspondingly altered in shape (Figs. 8 and 9).

As the development of the embryos nears completion the glandular cells of the brood sac wall are no longer visible (Fig. 7). When the young are fully formed and ready to be freed they are evidently capable of individual movement within the brood sac and the thin wall becomes ruptured, permitting their escape into the shell-space (Fig. 9).

From the torn appearance of the brood pouch after the embryos have passed out and from its very small size when the eggs first reach it, it appears to be used only once and renewed for the reception of each successive batch of eggs. Claus, quoting Lovén, mentions the immediate contraction of the walls of the brood pouch on the exit of the embryos, but that this does not occur invariably is evidenced by the torn remains of its walls visible in our preparations, and by the fact that a new batch of eggs may leave the ovary and be surrounded by a second tiny brood pouch while the embryos of the previous generation are still retained within theirs (Fig. 14).

That the complete freeing of the embryos takes place in two stages, as described by Lovén, is shown even from a study of fixed material. Following the first stage already described, the final freeing from the maternal shell space is brought about by ecdysis of the mother, when the embryos remain in the old shell, from which they can then make their escape.

Discarded shells containing one or more embryos have been observed as well as stages following the rupture of the brood pouch. One preparation, illustrated in Figure 13, shows a cast shell in which one embryo is retained together with what appear to be the cast cuticles of two other embryos, indicating that the young cast their skins at or about the beginning of their free existence. This is probably their first ecdysis, as the embryos are retained within the egg membrane during the greater part of their sojourn within the brood sac.

The number of embryos in a batch may vary considerably. That both ovaries shed their eggs simultaneously and that each of the large ovarian cells may, under favourable conditions, produce an embryo, is seen from the presence of as many as fifteen blastulæ and up to thirteen or fourteen advanced embryonic stages. (It is difficult to be sure of the exact number when so many embryos are packed together in the brood sac.) The usual number, however, is not nearly so large—generally six to eight or nine—while at times the majority of specimens carry only two to five embryos. An analysis of the samples taken at different periods shows this condition to be coincident with the several stages of the parthenogenetic phase. Ordinarily, during the period of more active metabolism, larger numbers of young are produced, while the depression mentioned as preceding the onset of the sexual phase is indicated by the presence of fewer embryos, as well as by the occurrence of males in the samples.

The number of embryos formed is, in the first place, dependent upon the number of ripe germ cells in the ovary, but it is apparent that it may be further regulated, especially towards the end of the agamic period, by some of these failing to develop. Although it has not been possible to demonstrate the fate of these cells, it is believed that they disintegrate before leaving the ovary, as batches of newly extruded eggs may consist of only two (Fig. 14).

The greatest number of embryos, i.e. twelve to fourteen, has been observed only in the large form of *E. nordmanni*, referred to as occurring occasionally among the ordinary population. As regards the others, carrying from two to nine or more young, there is no appreciable difference in body-size, although those containing large well-filled brood pouches have the shell distended into a more rounded contour instead of the typical triangular form of less heavily burdened specimens, thus making the body appear more bulky.

The progressive decline in activity during the parthenogenetic phase, here shown for *E. nordmanni*, as indicated by the decrease in the number of embryos produced, provides an explanation of the discrepancies between the accounts of various authors as to body shape and number of young borne by this species. In consequence, as noted above, it has been regarded as having a North Sea variety which produces seven or eight eggs and a Baltic variety with two to five. Also Claus, who examined Mediterranean specimens in September, gives the number of embryos as four to six. That he was dealing with material nearing the end of the parthenogenetic phase is evident, not only from the time of year when the specimens were taken, but also from his account of developing winter-eggs obtained at the same period.

The number of eggs in the first batch produced by a female while still in the maternal brood pouch apparently varies within only small limits. Claus gives the number as four to six. Kuttner figures an embryo bearing five blastulæ, and our material also gives examples varying from four to six eggs or blastulæ.

The presence of males was noted towards the end of the parthenogenetic period, but there are no special observations to record. They are readily distinguishable from the females by the absence of a brood pouch and by the rounded form of the paired testes which are easily discernible in stained preparations.

2. The Sexual Phase.

Claus' observations on the development of the winter-egg, which are incomplete due to lack of material, are here confirmed. There is no question as to the production of the gamic egg from one of a group of four ovarian cells as described by him, but our material includes quantities of females with such eggs in various stages of development, and a fuller account of the process is now possible.

The earliest stage seen shows the ovary to contain only four large cells arranged in a row, the third from the anterior end being already slightly broader than the others. No germarium is visible, the ovarian wall being closely apposed to the edges of the tetrad (Fig. 34). That this is an early stage in winter-egg production is indicated, as already stated, by the absence of the germarium, the size of the third cell and by the fact that the brood pouch contains only one embryo which appears to be a male as, although fully developed, it bears no eggs beneath the cuticle on its dorsal side.

There is at this stage no indication of the presence of the nurse-cells which later occupy the brood pouch prior to its reception of the growing winter-egg.

Claus noted the absence of any other cells in the ovary during the formation of the winter-egg and assumed therefrom that other oocytes formed at the same time as the one that gives rise to the tetrad must have passed out to become the glandular nurse-cells which nourish the growing egg in the brood sac. An examination of our material, however, shows the nurse-cells to have a different origin.

In the stage shown in Figure 34 the future winter-egg has the same granular appearance as the other three cells of the tetrad and is only distinguishable by its slightly larger size. There is no sign of the formation of the brood sac or of the presence of glandular cells. At a slightly later stage, that illustrated in Figures 36 and 36a, the winter-egg has assumed its characteristic appearance of being filled with globules of fat, and a brood pouch of moderate size has been formed. This contains a number of nurse-cells which partially fill it, and they, for the most part, are situated along its anterior border. That is to say that they arise in the same position as do the glandular cells present during the development of the parthenogenetic embryos. This would seem to indicate, in the absence of any other cells capable of nourishing the egg, that they are not derivatives of ovarian cells at all, but are actually the product of the wall of the brood pouch, arising, as in the former case, from an invagination of its anterior border. That they become markedly different from the cells which feed the parthenogenetic embryos in size, shape, number and contents will be seen by a comparison of Figures 5, 10 and 11 with Figures 25, 26, 29, and 30.

The slightly older stage shown in Figure 35 is drawn from a specimen in which the brood pouch is still only partially filled with nurse-cells; but when the stage represented in Figures 29 and 30 is reached and the egg, while retaining its original position, has increased in diameter to about the width of the intestine, the brood pouch has become packed with thirty to forty large glandular cells, polyhedral in shape through mutual pressure and having the appearance indicated in Figure 30a. A central nucleus is present, and a number of fat globules of various sizes are to be seen in the granular cytoplasm.

As the egg increases still more in diameter, a fine membraneous envelope appears, surrounding it closely on its dorsal side and drawn away from it ventrally, as shown in Figure 32, suggesting that it is the product of the ovarian wall. The three cells associated with the young winter-egg have now disappeared.

During the subsequent growth to its relatively enormous size the egg does not as a rule become far removed from the region of the ovary, but lies embedded, at the proximal end of the brood sac, in the mass of nurse-cells which now fill it. When, however, two eggs are developed simultaneously, one is placed more distally (Figs. 22, 27, and 28).

From the first appearance of fat globules in the egg, when it loses its ability to take up stains readily absorbed by the remainder of the body, and particularly the nurse-cells, it becomes difficult to distinguish, especially when it has come to be situated within the brood chamber. Due to this and the fact that the closely packed mass of nurse-cells may have the appearance of a large number of early embryos, it was not until a considerable quantity of material had been examined that the significance of these cells was appreciated and their presence in the brood pouch was found always to be coincident with the occurrence of a winter-egg in process of development.

As the winter-egg nears its limit of growth the nurse-cells decrease somewhat in size and number and become more sharply separated from one another (Fig. 26). The thick protective shell is then formed and when the development is completed a few shrunken remnants of the nurse-cells may still be present, as shown in Figure 23. When two eggs have been formed the brood sac is generally empty.

The fully-formed resting-egg breaks through the wall of the brood sac and lies in the maternal shell cavity. There is no production of an ephippium in Evadne, the winter-egg being simply left in the cast shell on the subsequent ecdysis of the mother. As cast shells containing winter-eggs have been taken in the plankton samples on several occasions (Fig. 33), it is possible that they do not immediately sink to the sea bottom as previously supposed and that, in the case of those formed in early summer, they may perhaps remain planktonic and develop comparatively rapidly without a marked resting period.

While the production of a single winter-egg is to be regarded as the normal condition, it is by no means rare to find two present—evidently one from each ovary—especially during the summer sexual period. When this occurs, the eggs may be sub-equal in size, both considerably smaller than the fully-grown single egg (Fig. 22), or they may be markedly different in size (Figs. 27 and 28).

A study of Geoffrey Smith's work (**73**) on the storage of glycogen and fat by Crustacea led to the making of preparations stained with neutral red and with osmic acid. As the material used was by no means ideal for the purpose, it was not expected to give particularly good results, but they were sufficiently convincing to be worthy of brief reference.

The osmic acid preparations showed the developing winter-egg to be more heavily loaded with fat than any other part ; also the nurse-cells and the gut took up the stain fairly strongly. Specimens carrying embryos showed a certain amount of fat to be present in these, but the neutral red preparations indicated that it is glycogen which is the predominating substance stored during the parthenogenetic phase. It is present at the bases of the limbs, in and about the intestine, and is particularly obvious in the ovaries (especially the germarium), and in the contents of the brood sac. Indeed, the neutral red served as a differential stain for the ovaries, showing up their contents as did none of the general stains previously used—such as borax carmine, alum cochineal, and methyl green.

Specimens in the sexual phase, treated with neutral red, showed glycogen to be present in the ovary during the tetrad formation, all four cells being deeply stained at first, but the young winter-egg ceases to take up the stain as soon as fat globules appear within it and thereafter remains unstainable. Some glycogen is present in the nurse-cells in addition to the fat, and also in the intestine.

These facts show that *E. nordmanni* behaves similarly to other Crustacea which have been investigated as regards alternating periods of fat and glycogen storage associated with the periods of sexual activity and of growth respectively.

The most interesting and striking feature of the analysis of the Northumberland material is the evidence of a definite double cycle in the annual history of marine Cladocera as shown for *E. nordmanni*. Except for Apstein, who touches briefly on the subject, no previous attempt has been made to work this out, to compare marine with freshwater forms in this respect or to correlate the phenomenon with environmental conditions.

General Conclusions.

The very considerable amount of work which has been done on the investigation of the life-cycle of Cladocera in relation to environmental conditions and to hereditary qualities, has been carried out almost entirely on freshwater forms. Observations on these under natural and experimental conditions have led to widely different theories as to the probable causes of the change from parthenogenetic to sexual activity.

Weismann was of the opinion that there is a definite inherent cycle which causes the production of a particular number of gamic generations —the number varying with the species—between every two gamic periods, regardless of external changes. On the other hand, the generally accepted idea has been that the life-cycle is intimately bound up with seasonal variations in the environment, and that the production of winter-eggs occurs at the onset of conditions unfavourable to continued activity of the organism, i.e. that in nature it precedes hot dry periods when small bodies of water are liable to become dried up, and cold spells when freezing may occur.

With regard to the effect on the organism of these conditions it is obvious that it is not the actual process of desiccation or freezing which brings about the development of the protected resting-egg, for to be of any value in preserving the species, its formation must be completed before the unfavourable conditions supervene, and the stimulus to sexual reproduction must be looked for in changes which take place some little time in advance.

If physical factors of the environment are regarded as being mainly responsible for changes in metabolic activity of the organism, it is necessary to consider what these are and to attempt to discover how they act. The more obvious changes are those of temperature and salinity*

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* A detailed discussion of the effects of normal variations in the percentage of dissolved oxygen and carbon dioxide and in the amounts of different chemical compounds present in the water is regarded as unnecessary. Such variations will not ordinarily be of sufficient magnitude to act as direct limiting factors of the activities of epiplanktonic animal forms of open waters, with which the present discussion is primarily concerned. A knowledge of these and of their indirect effect is assumed in the following consideration of changes in abundance of the phytoplankton in its relation to the nutrition of Cladocera.

and, having regard to climatic conditions in various parts of the world, it is evident that species living in different climatic zones may react differently if these factors exert a direct influence. That is to say that the gamic phase may be associated in some cases with an increase in the amount of the factor or factors concerned and in other cases with a decrease in the amounts of the same factors.

Due to the occurrence of large swarms of Cladocera which have been observed to congregate in restricted areas (even in large lakes) during the agamic period, two other factors have been regarded as of importance, namely the accumulation of excretory products and the possible scarcity of food, or changes in the constitution of available food material. The question of nutrition is of vital importance both as a direct factor and in its relation to physical changes, notably temperature, as stimuli influencing both the amount of food material obtainable and the organism's ability to use it.

Experimental work prosecuted with a view to determining the value of various physical and nutritional factors believed to be instrumental in bringing about the cessation of parthenogenesis, has resulted in many and conflicting conclusions. This experimental work has been summarised by Cutler (**14**) and more recently and completely by Schull (**63**), whose comprehensive and critical account makes it unnecessary to discuss it here.

As regards the theory of the inherent cycle in Cladocera, first formulated by Weismann and attributed to the effect of natural selection, there is again considerable difference of opinion resulting from more recent investigations. Papanicolau (on showing that early broods are strongly parthenogenetic in tendency, late broods gamic in tendency and intermediate broods easily influenced either way) assumed the existence of a graduated inherent cycle, but his results can also be interpreted in the light of changing environment, as shown by Agar (**1**) and others. Also Banta, having reared three hundred generations of Moina, found it no easier to induce the gamic phase then than in early generations.

Woltereck (**86**) takes the *via media*, being of the opinion that internal and external causes are equally contributory to the production of gamic forms. While retaining the idea of internal stimulus to periodicity and postulating the presence of " paralisators " and " activators " within the organism, acting in opposition to one another to produce alternating phases of its life-cycle, he permits these hypothetical substances to be set in operation by the action of physical factors of the environment.

That there is here an inherent cycle in the sense that periods of rapid somatic growth, of reproductive activity, and of comparative rest are characteristic of Cladocera as of living organisms generally, is obvious, but data relating to the behaviour of particular species in different types of natural habitat show plainly that nothing more need be claimed regarding the part played by heredity and natural selection. The work of Zschokke and of Ekman has demonstrated that a particular species of Cladocera may be dicyclic, polycyclic or even acyclic in varying freshwater conditions presented on the European plains, but is strongly and definitely monocyclic in high Alpine lakes and in lakes and ponds of the far North.

Beyond the fact that gamic reproduction must occur at some period (except possibly in " acyclic " forms), it is evident that the stimulus which induces the gamic phase must be sought in those environmental factors which necessarily limit or accelerate, directly or otherwise, the rate of metabolism of the organism at any given time. This would appear to be the idea behind von Scharfenberg's attempt to reconcile the two opposed views regarding the relative importance of internal and external factors, by assuming that the influence of food on the cycle is an inherited quality acquired through natural selection.

With regard to the conclusions drawn by various workers from the results of their experiments, one or two points appear to be worthy of further mention. Much has been made of the effect of the accumulation of excretory products, resulting from overcrowding, in inducing gamic reproduction (or at least depression), but it seems to the writer that this must be of far less consequence in nature than under experimental conditions. That it is probably a contributory cause of depression in small or in very stagnant bodies of fresh water at times of maximal population is not denied, but that such an accumulation can occur to any marked extent in large water masses, whether of fresh water or the sea, where there is considerable movement, at least near the surface, the writer is unable to appreciate. Also, in so far as carbon dioxide is to be regarded as an important excretory product in this respect, it might with equal probability be assumed to have the reverse effect in that it would tend to increase the supply of phytoplanktonic food-material.

Geoffrey Smith's experiments on the effect of temperature also call for remark in the light of our observations on Evadne. He states that a lowering of the temperature, which induces gamic reproduction, acts as a stimulus to the storage of fat in the tissues as opposed to glycogen. That decreased temperature need not be operative, or is not the only stimulus regulating fat storage, is shown by the incidence of the gamic phase in Evadne at two different seasons—one when the temperature is rising prior to its August maximum value and the other usually when this is well past. Similar conditions obtain in regard to salinity in the case of Evadne, the first gamic phase occurring about or before the period of the annual maximum, the second considerably later.

The fact that the question of food-supply has generally been considered of vital importance is brought out, as noted by Schull, by the event of more experimental attempts having been made to connect the life-cycle with nutrition than with any other external factor—temperature being a close second. As decreased temperature is generally regarded as acting either through its effect on the amount of food-material available or in reducing the rate of the organism's metabolic activity and consequently lessening the nutritive process, it may be assumed to be an important contributory factor in nature at those times at which low temperature and depression or the occurrence of the sexual phase supervene simultaneously. This does not however take into account those times when gamic individuals occur also during periods of comparatively high temperature.

It was evidently this difficulty which led Keilhack, arguing from observations in nature, to reject the idea of low nutrition as an important factor in the production of sexual forms. He remarks that *Polyphemus pediculus*, a dicyclic form, has a gamic phase in June " when food is abundant." His contention is supported by Strohl who states that a gamic phase in June could not be due to lack of nutrition. As to the abundance of food suitable to continued asexual activity of dicyclic Cladocera at these times, there must be considerable doubt and, from a study of recent work on the periodicity of freshwater Cladocera together with our records for Evadne, this contention must definitely be rejected.

From observations in the field, the general conclusion of Dr. Robert Gurney, with whom the writer has been in correspondence, is that shortage of food is the main direct limiting cause of the cessation of parthenogenetic development of freshwater Cladocera, as it appears to be in the case of marine species also. Leaving aside the special problems relating to food-supply in temporary ponds and the like, and in lakes situated at high altitudes and high latitudes where, compared with permanent water-masses of temperate regions, the periods suitable to food production are of relatively short duration, the periodicity of abundance and scarcity of food is closely parallel in both marine and freshwater habitats.

It will be sufficient here to draw attention to the similarity in number, times of appearance and relative productivity of the periods of maximal abundance of the phytoplankton of fresh and sea-water, without entering upon a detailed discussion as to the causes of the same, and to show the close relationship between these and the life-cycles of characteristic Cladoceran inhabitants. It has generally been supposed that marine Cladocera were monocyclic and that their activities, therefore, bore no relation in respect to periodicity, to limnetic forms. Also, as it is only comparatively recently that the dicyclic character of the latter has been correlated with changes in abundance of phytoplankton, no comparison has been drawn between fresh water and marine Cladocera in this respect until now.

Taking into consideration regions in which temperate climatic conditions obtain, a similar periodicity of phytoplanktonic activity is found to occur in freshwater lakes and in the sea. In the former the two periods of upheaval caused by temporary full circulation of the water in spring and autumn due to the development of a thermocline (and in certain cases to other causes as in Lough Derg) (**74**), give rise not only to the provision of nutritive substances required for the rapid multiplication of diatoms, green algæ, etc., but also bring increased supplies of food-material directly within the reach of detritus feeders among the animal plankton such as are many of the freshwater Cladocera. Thus, two periods of reproductivity of the zooplankton are possible. While this may be associated in some species with the one, in others with the second period of optimal nutritive conditions, certain forms such as Cladocera and Rotifers may take advantage of both periods (**11**) : here the agamic phases are coincident in time with both the aforesaid periods and thereafter the population suffers a reduction in numbers followed by the sexual phase.

In the sea, a similar series of events takes place, the spring and autumn maximal periods of parthenogenetic development of Cladocera being associated in time, at least in a general way, with the corresponding periods of diatom abundance, after which numbers decline and the gamic phase supervenes. This has been shown for *E. nordmanni* to be more strongly marked after the spring maximum than it is in autumn, thus indicating an association between Cladocera and phytoplankton in regard to relative quantity as well as to time. Another aspect of the effect of varying quantities of food on Cladocera, while not having a direct bearing on the present problem, is nevertheless interesting. Wolterek (**88**), in his recently published book, shows the possibility of inducing modifications in the form of *Daphnia cucullata* in response to abundance or scarcity of food.

That there is a definite relationship between times of food scarcity and corresponding periods of depression in the metabolic processes of plankton organisms generally is now evident. It has been shown by Dieffenbach and Sachse, as quoted by Carpenter ; is suggested by the findings of Gurney (**24**), Zschokke, and Ekman referred to above ; is indicated in the analysis of samples taken by Scourfield (**70** and **71**) and is of common occurrence among marine planktonic forms. In addition to being demonstrated in the case of Evadne, the Northumberland plankton samples show the presence of spring and autumn periods of reproductivity in the common acorn barnacle (not yet worked out in detail), as is the case in many holoplanktonic forms and littoral animals with pelagic larvæ, e.g. Mysis spp., *Crangon vulgaris* (**6**), *Sagitta elegans* (**47**).

The emphasis laid on the influence of the vernal and autumnal maxima of phytoplankton on the zooplankton generally and on limnetic and marine Cladocera in particular, is meant to detract in no way from the importance of the physical factors of the environment but is meant to draw a comparison between the similarity of the more important features regulating the cyclic activities of both marine and freshwater pelagic animals, and to draw attention to the effect of physical changes being generally indirect rather than direct in their influence. There is, of course, no question of the direct effect of decreased temperature, for example in lowering the rate of nutrition ; but so far as dicyclic Cladocera are concerned this is a secondary stimulus, brought to bear on the autumnal period of depression but not on the spring one.

As regards the results of experimental and other observations on the influence of increase or decrease in the intensity of physical and nutritional factors, it would appear that it is not necessarily or only the actual amount of any particular factor which affects the organism concerned, but rather " change as change." This is pointed out by Schull in reference to Whitney's work, and its importance in regard to the constitution of the available food-supply is shown by von Scharfenberg's experiments. That his conclusions are confirmed by the behaviour of plankton organisms in nature is indicated by the fact that while the spring increase of diatoms is followed by abundance of Peridiniæ in the summer, agamic reproduction in dicyclic Cladocera nevertheless comes to an end (or at least is greatly slowed down) and supervenes again at a rapid rate only when the diatom curve is once more on the up-grade in early autumn.

While the Northumbrian records of periodic abundance of Evadne show it to follow the trend of the general annual diatom curve, there is considerable variation in the times of maximal population from year to year, and it is not yet possible to show to what extent these variations are coincident with minor changes in the position of the cusps of the diatom curves in those years in which abnormal conditions have prevailed in the region under consideration.

SUMMARY.

PART I.

From an analysis of previous records of *E. nordmanni*, considered in conjunction with those furnished by the present investigation, the following points of interest emerge.

1. *E. nordmanni*, while being generally distributed in the North Sea and adjacent waters throughout the summer months, has been shown to breed freely in inshore waters in early summer and again in autumn when maximum numbers of individuals are obtained.

2. These two periods of maximal abundance are produced as the result

of successive parthenogenetic broods and alternate with periods of depression. This is indicated not only by the sexually-produced winter-egg, but also by a reduction in the number of embryos contained in the brood chamber and consequent change in body-shape. This serves to show that the supposedly distinct races, described as being characteristic of the North Sea and the Baltic, have no doubt been founded on material taken at different periods of the agamic phase.

3. The alternating periods of abundance and scarcity appear to be associated with transnatant movements of the population.

4. The earlier maximum is the more extensive one and the following period of scarcity of numbers in inshore waters is less marked and of shorter duration than that which follows the autumn maximum. Although the Northumberland records do not cover a sufficient number of months of any year to provide information as to the presence of *E. nordmanni* during the winter, it is evident from previous accounts that a certain proportion of the population is able to withstand both periods of depression and that these, together with new individuals produced from the resting-eggs and others entering the area from without, provide a stock from which the following early summer maximum is obtained.

5. The distribution of the species is affected by exceptional conditions wrought by changes in the current system of the area of distribution.

6. *E. nordmanni* is an inhabitant of both coastal and oceanic waters. It is present in great quantity on both sides of the North Atlantic, and it is suggested that its geographical distribution is intimately associated with the current system of that ocean. Its distribution beyond this region is merely indicated.

7. A comparison of the surface current systems of the southern North Sea, the Irish Sea, and the eastern English Channel is made in an attempt to explain the scarcity of Cladocera in these regions.

8. The material available for the study of the vertical distribution of Evadne is adequate to illustrate only diurnal conditions and shows the optimum light intensity to be very high for this form. There is no evidence that Evadne retires below the surface to any noticeable extent in rough weather.

PART II.

9. The account of the development of the parthenogenetic generations of *E. nordmanni* has reference to the formation of the oocytes; the development of the brood pouch and the production of the nutritive cells of its wall; the method of freeing of the embryos.

10. The presence of three generations of young within the mother and the fertility of the embryos are considered in relation to the rate of

increase of the population. The variation in number of embryos within the brood pouch is discussed in its association with the period of depression which is shown to precede sexual reproduction. The fact that the brood pouch may at times be empty is shown, and is correlated with the change from the agamic to the sexual mode of development.

11. A more detailed description of the formation and growth of the winter-egg than has been given heretofore is included, and has reference to the formation of a tetrad ; the disappearance of the germarium ; the production, derivation, constitution, and absorption of the nurse-cells and the freeing of the winter-egg. The significance of the production of two winter-eggs simultaneously is considered.

12. Evadne is shown to behave similarly to other Crustacea in the matter of fat- and glycogen-storage, being associated with alternating periods of active growth (parthenogenetic phase) and gamic reproduction.

13. The general conclusions arising out of the study of the life-cycle of Evadne which shows it to be definitely dicyclic, are concerned with the question of the relative value of internal and external factors as stimuli effecting the biannual series of changes which occur, and it is believed that food-supply is of primary importance and that other factors are of a secondary nature or are indirect in their influence.

14. A coincidence of the periods of maximal population of Cladocera with those of diatom abundance is shown to take place as regards both time of occurrence and relative productivity. A comparison is drawn between the behaviour, in relation to food-supply, of marine and limnetic species of Cladocera.

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Studies on the Monogenea of Plymouth. *Gastrocotyle trachuri* v. Ben. and Hesse, 1863.

By

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With 4 Figures in the Text.

In August, 1932, six specimens of this species were found on the gills of *Trachurus* [*Caranx*] *trachurus* taken at Plymouth. This is the first record of its occurrence in British waters.

The genus and species were first defined by van Beneden and Hesse (1864), their description being from young specimens, and incomplete in numerous details. No account of the internal organs is given, the genital opening is not described and the number of crotchets or hooks at the posterior end of the body is said to be four. This undoubtedly arises from the fact that their specimens were immature, being 1·5 mm. in length, whereas the specimens found at Plymouth are *circa* 4·7 mm.

Of subsequent authors Taschenberg (1879, a and b) refers to Gastrocotyle, but depends on van Beneden and Hesse's description and adds no new details. J. T. Cunningham (1887) refers to Gastrocotyle in a discussion on the systematic position of Stichocotyle, but again contributes no new details. Monticelli (1888) discusses its systematic position, depending on van Beneden and Hesse's description ; von Linstow (1889) mentions Gastrocotyle in his Compendium, but the first record of its occurrence after van Beneden and Hesse's discovery comes from Paroni and Perugia (1890, a) who found it on the gills of *Trachurus trachurus* at Genoa and later in the same year (1890, b) published a description of the species. This account is a big advance on that of van Beneden and Hesse, but is still incomplete. The reproductive organs are said to be similar to those of Microcotyle, but no description is given. Six crotchets are described at the posterior end of the body and the cotylophore bears 35 suckers. The measurements of their specimens are 3 mm. × 1 mm. Unfortunately the armature of the suckers is not figured. Braun (1893), Pratt (1900), Monticelli (1903), Nicoll (1915), and Brown (1929) all make references to the species, but no new data or records are added.

The specimens here described were found during an investigation at Plymouth on the trematodes of fishes. During this investigation it was repeatedly noticed that when copepods were present on the gills

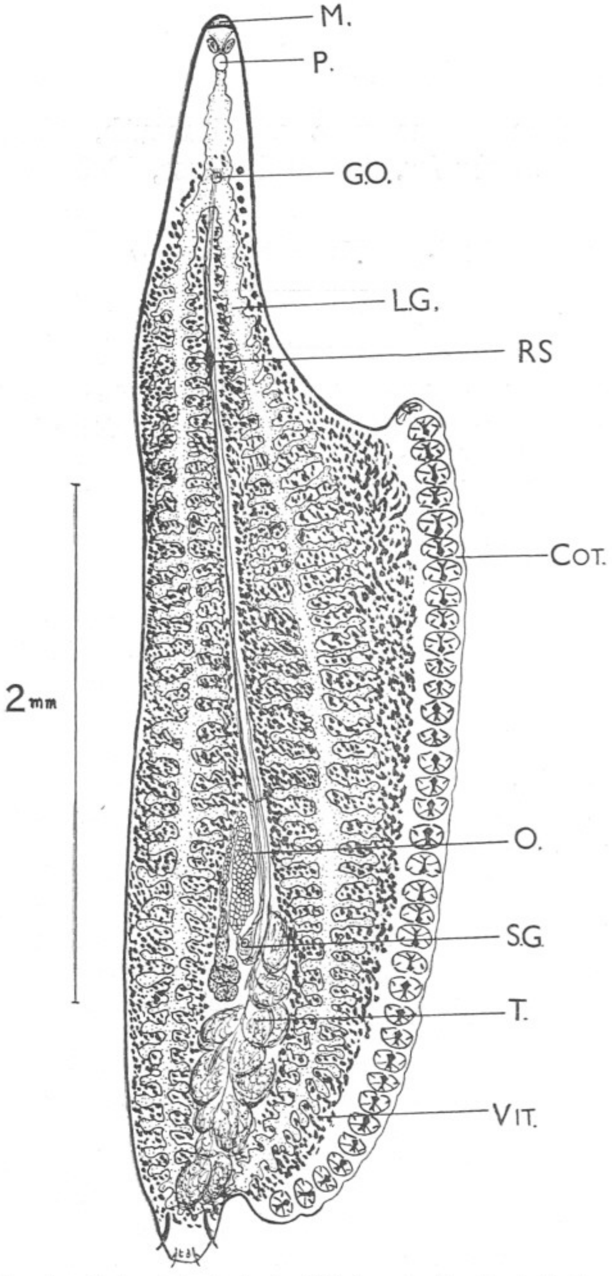

FIG. 1.—*Gastrocotyle trachuri*. Whole animal. Ventral view. COT.=cotylophore; G.O.=genital opening; L.G.=limb of gut; M.=mouth; O=ovary; P.=pharynx; R.S.=receptaculum seminis; S.G.=shell-gland; T.=testis; VIT.=vitellaria.

trematodes were seldom found and vice versa—a fact also noticed by W. H. Leigh-Sharpe (1933).

Gastrocotyle trachuri (Fig. 1) is an elongated worm 4·7 mm. long, narrow in its anterior third but considerably broader (1·2 mm.) in its posterior two-thirds along the left side of which is borne the cotylophore. The cotylophore bears one series of 32–40 suckers, each sucker measuring 0·08 mm. in diameter. Van Beneden and Hesse (1864) give the number of suckers as 31–38, and Paroni and Perugia (1890) as about 35. The armature of the suckers (Fig. 2, A) is very different from that described by van Beneden and Hesse. At the extreme posterior end of the body are 6 uncini, the lateral pair being large and stout and the two medial pairs small (Fig. 2, B).

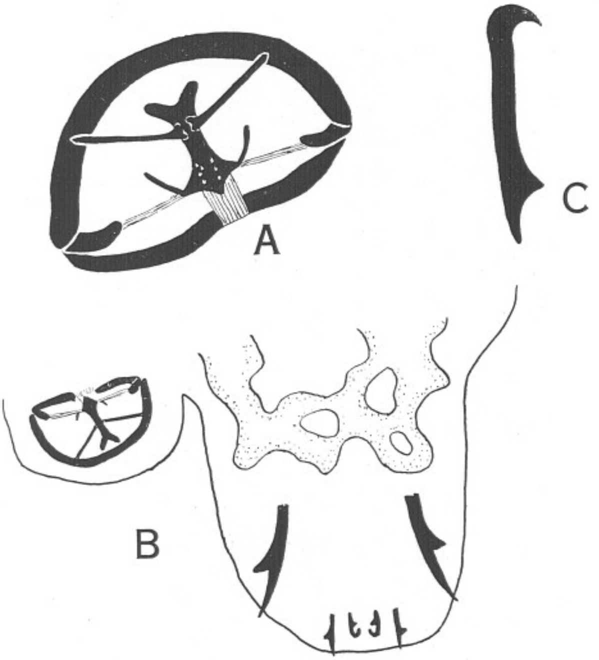

FIG. 2.—A. Armature of sucker; B. Posterior end of body; C. Crotchet from genital opening.

The Alimentary System. The mouth is terminal at the anterior end and leads into a buccal cavity in which are situated two lateral oval suckers measuring $23\mu \times 15\mu$. From the buccal cavity emerges the pharynx, measuring $46\mu \times 30\mu$, which leads into the œsophagus. The œsophagus is 0·2 mm. in length and has pouches in its walls but no actual diverticula. The gut extends down on either side of the body and has numerous diverticula and in the posterior end of the body the limbs of the gut anastomose (Figs. 1 and 2, B).

The Reproductive System (Fig. 3). The testes and ovary are situated in the posterior third of the body in the mid-line. The testes are situated more posteriorly and consist of closely apposed lobules. The vasa efferentia unite to form a fine vas deferens which passes in close apposition to the uterus up to the genital atrium into which it opens. The ovary is a ∩-shaped organ containing ripe ova in one extremity, from which emerges a short oviduct which leads into the shell-gland. From the shell-gland

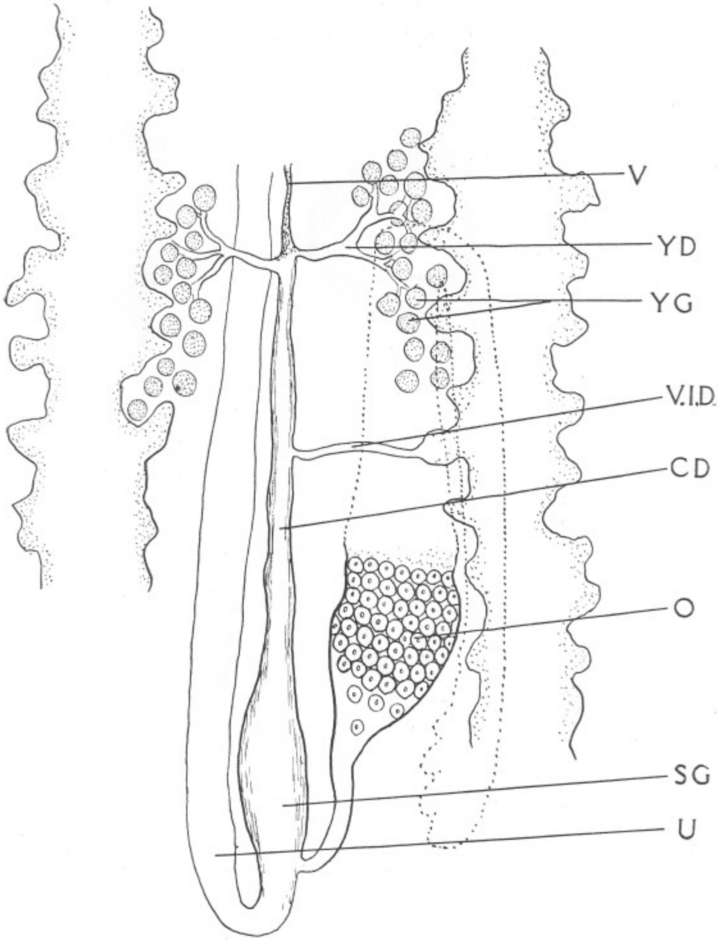

FIG. 3.—Shell-gland and associated structures. C.D.=connecting duct; O.=ovary (partially in outline); S.G.=shell-gland; U.=uterus; V.=vagina; V.I.D.=vitello-intestinal duct; Y.D.=yolk-duct; Y.G.=yolk-glands.

emerges the uterus which is a non-convoluted wide thin-walled tube leading up to the genital atrium into the base of which it opens (Fig. 4).

The genital atrium (Fig. 4) is a muscular sac 23μ in diameter, and at its apex is the genital opening which is situated in the mid-line ventrally, a short distance from the anterior end of the body. The opening is guarded by 12 crotchets arranged in a circle. Each crotchet (Fig. 2, C) has a bifurcate base and a hooked extremity, not a simple base and a flattened diamond-shaped extremity as described by Paroni and Perugia (1890, b).

The vagina opens in the mid-line on the dorsal surface a short distance behind the genital opening. It leads into a receptaculum seminis from which a duct emerges which proceeds downwards between the uterus and vas deferens and at the level of the upper border of the ovary receives the vitelline ducts on each side and then passes down into the shell-gland (Fig. 3), giving off the vitello-intestinal duct on the left.

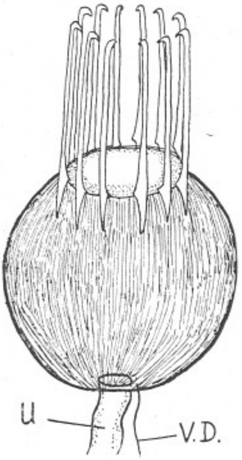

FIG. 4.—Genital atrium and opening. U.=uterus; V.D.=vas deferens.

The vitellaria are scattered diffuse lobules lying between the diverticula of the gut and a few lie anterior to the genital opening. None pass into the cotylophore.

The eggs are described by van Beneden and Hesse, and Paroni and Perugia as possessing two short filaments. No eggs were found in these specimens, so this fact cannot be confirmed.

I am indebted to my friend and former teacher, Mr. W. H. Leigh-Sharpe, for his help in finding these specimens.

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Rhopalura granosa sp. nov., an Orthonectid Parasite of a Lamellibranch *Heteranomia squamula* L., with a Note on its Swimming Behaviour.

By

D. Atkins, B.Sc.

With 4 Figures in the Text.

CONTENTS.

INTRODUCTION.

THE Orthonectida, a small group of rare parasites, have attracted considerable interest owing to their doubtful systematic position. In 1868 Keferstein (1868, pl. ii, fig. 8) figured, though he did not describe, a "problematic parasite"* from the digestive tube of *Leptoplana tremellaris*, but it was not until about 1877 that a serious investigation of these forms was undertaken by Giard (1877), who gave to the group the name of Orthonectida. Our knowledge of the organisation and life-history of these parasites, however, is in great part due to the admirable researches of Caullery and his collaborators. The Orthonectida are forms in which the sexual generation is formed asexually from germ cells produced in a parasitic plasmodium.

Some eight species of Rhopalura, and one of Stœcharthrum, are now known.

Rhopalura granosa sp. nov., parasitic in *Heteranomia squamula* L. (=*Anomia aculeata* Müller), in the Plymouth area, is the first Orthonectid

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* This species was named *Rhopalura* (*Intoshia*) *leptoplanæ* by Giard (1880, p. 236); it was rediscovered and described by Jourdain (1880)—under the name of *Prothelminthus hessi*—at Saint-Vaast-la-Hougue, and by Caullery and Mesnil (1901 c, pp. 399–400) in the bay of Saint-Martin, under the old fort of Saint-Germain-des-Vaux.

to be described from a Mollusc, members of the group being hitherto known from Annelids, Nemertines, a Planarian, and from an Ophiuroid, *Amphiura squamata*. The only previous record of an Orthonectid for the British Isles would seem to be that by McIntosh in 1873 (p. 129), when he described a curious parasite burrowing in the body wall of *Lineus gesserensis*. The specific name *granosa* has been given on account of the presence of characteristic refringent bodies in the male (see p. 237).

DESCRIPTION OF *RHOPALURA GRANOSA*.

In *R. granosa* the sexes are separate, and, as in other species of Rhopalura where the male is known, exhibit sexual dimorphism. Sexual dimorphism is so marked in the genus that Giard (1879, 1880) originally referred the two sexes in *R. ophiocomæ* to two genera, Rhopalura and Intoshia.

The Female.

The female (Fig. 1, A and B) is cylindrical, tapering anteriorly and posteriorly, and about 190 to 210μ long, and 60 to 75μ broad, not including the cilia. Individuals, however, vary somewhat in shape, doubtless partly owing to their considerable powers of contraction; a narrow elongated female, ca. 230μ long and 55μ broad, is shown in Fig. 1, B, but this is an extreme form, and rarely seen.

Fig. 1, A and B, of *R. granosa* recall Julin's figures of " femelle aplatie " and " femelle cylindrique " of *R. ophiocomæ* (Julin, 1882, pl. ii, figs. 2 and 1). The type of female shown in Fig. 1, A, is not flattened, however, for there is no appreciable difference observable in the width as it rotates in swimming; the rings are no less clearly marked than in the elongated form (Fig. 1, B). Both forms are found among those issuing naturally from their hosts. Caullery and Mesnil (1901 c, pp. 395–397) think that possibly the cylindrical females of *R. ophiocomæ* are a temporary state, leading to the flattened females: their specimens were apparently taken artificially from the host.

The body of the female *R. granosa*, which is entirely ciliated, shows eight rings, of which the first is the anterior, and the last the posterior terminal cone. The fourth and sixth rings seem to be formed of two rows of cells, while the second, third, fifth and seventh are formed of one row each. The anterior and posterior cones are formed of several rows. Between the rings there is a row of tiny cells, as in the male. The rings are superficial, involving the ectoderm only, the body not being segmented: they are more evident in some individuals than in others. When the animal is swimming forwards the cilia on the anterior cone are directed forwards, and those on the body posterior to it backwards (see Fig. 1, A). When the animal is swimming backwards, however, those on the second ring, as

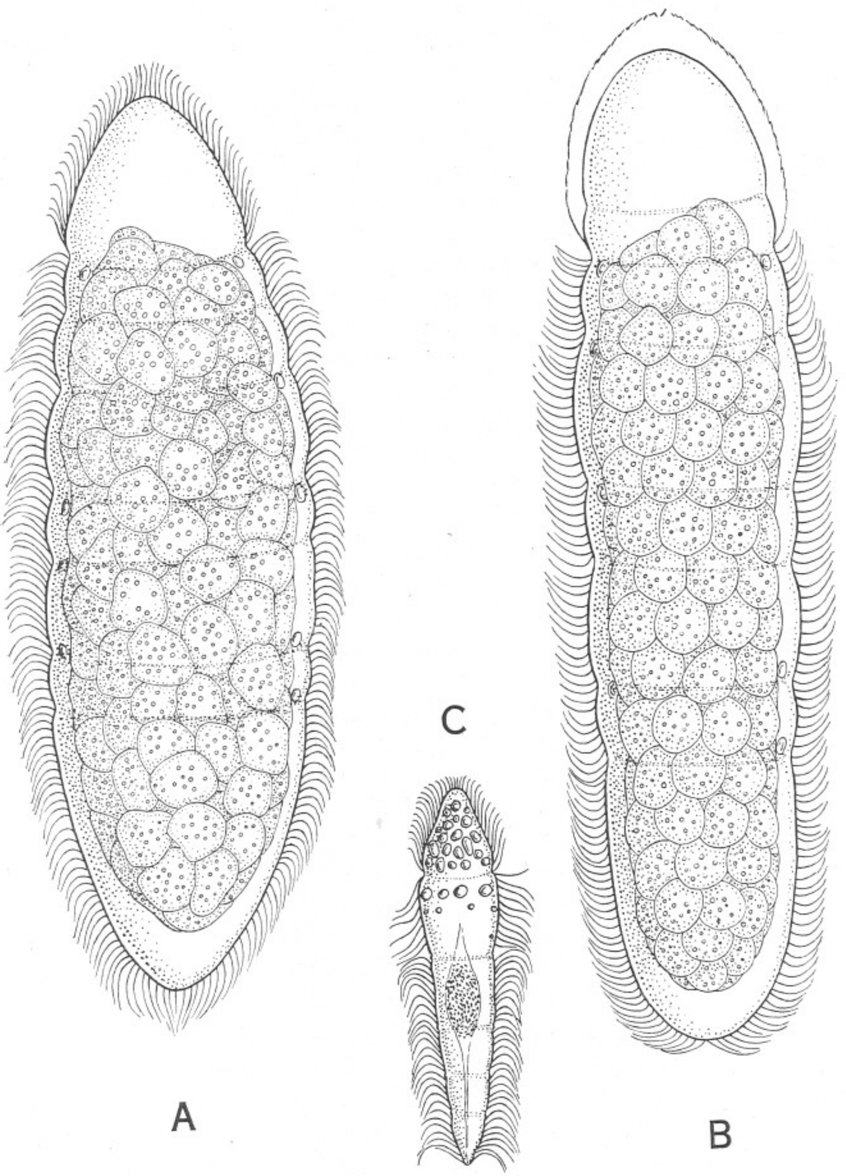

FIG. 1.—*Rhopalura granosa*. Sketches from life of individuals which had issued naturally from the host. The cilia are shown in profile only, although actually the animals are entirely ciliated: they are shown somewhat diagrammatically. × 573⅓.

A. Female. The cilia are shown as they appear during slow forward movement.

B. Rare, elongated form of the female. The cilia are shown as they appear during reversed swimming. In both forms the asymmetrical anterior extension of the mass of ova is due to the presence of the problematical organ, which is not shown in the figures.

C. Male.

well as those on the anterior cone, become motionless and are applied closely to the surface of the body, the tips being directed anteriorly (see Fig. 1, B, and also p. 247).

The ectoderm cells of the anterior and posterior extremities are deeper than those covering the rest of the body, the depth of the anterior cells being especially noticeable. The latter, in particular, contain a number of granules towards their outer ends, which become red if a trace of neutral red is added to the water. In sections of animals preserved in Bouin's fixative and stained with Heidenhain's iron hæmatoxylin and acid fuchsin the ectoderm cells appear much vacuolated, the vacuolation occurring sometimes at the inner ends, and sometimes at the outer ends of the cells. A problematical organ is present in the anterior cone; narrow prolongations from the organ appear to encircle the cone. It has been suggested by Metschnikoff (1881, p. 285) that this structure may be a remnant of an alimentary canal, and by Caullery and Lavallée (1908 b, p. 465) a nervous ring. A few, one to four, large vacuoles are generally observable in the cells of the anterior cone.

A small number of refringent bodies occur at irregular intervals, in a position between the rings of the body. These become orange with neutral red, and pale blue with methylene blue *intra vitam* staining.

The ova are numerous, very roughly about two hundred. They extend only slightly into the region of the anterior cone. They are about 14μ in diameter, with transparent cytoplasm containing a number of refringent granules, which become red with neutral red used *intra vitam*: it would appear to be these granules which in sections of material preserved in Bouin's fixative stain black with iron hæmatoxylin.

The embryos develop in the body of the parent: they are closely packed, and no movement of the ciliated larvæ is observable, such as occurs in *R. pelseneeri* (M. and C., 1905a, p. 429).

Embryos and ova have been observed, on several occasions, escaping from the parent in the region of the second and third rings. The fact that ova also have been seen to be expelled, points to the conclusion that these occurrences were not normal, but possibly due to unnatural conditions of observation; the position of emergence may, therefore, also be abnormal. A genital pore, such as described by Caullery and Mesnil (1901 c, p. 394) for *R. ophiocomæ*, could not be distinguished, at least in females sectioned while still within the host: no sections were made of those which had emerged.

The Male.

The male (Fig. 1, C) is cylindrical and slender, tapering anteriorly and posteriorly, the broadest region being the second ring. It is 87 to 95μ long and 20μ broad, not including the cilia. The body shows six superficial rings, of which the first is the anterior, and the last the posterior terminal cone. Between the rings is a row of tiny cells, the nuclei of which show clearly in sections. The anterior cone is formed of several rows of ectoderm cells, as is also the second ring.

A characteristic of the male is the presence of large irregular refringent bodies in the cells of the anterior cone, as well as in the first row of cells of the second ring. Occasionally smaller refringent bodies occur in other parts of the second ring. In *R. ophiocomæ*, the only other species in which the males are known to have these curious large refringent bodies in the cells, they are present in the second ring only (Giard, 1880, p. 229; Julin, 1882, p. 11). In sections of *R. granosa* preserved in Bouin's fixative these bodies frequently stain lightly with a dark periphery with iron hæmatoxylin and acid fuchsin, but others stain uniformly black. Caullery and Mesnil (1901 c, p. 393) found those of *R. ophiocomæ* disappeared in preparations treated with alcohol and xylol, a vacuole occupying their place. The fixative they used chiefly was a saturated solution of sublimate in sea-water, with the addition of 1% acetic acid.

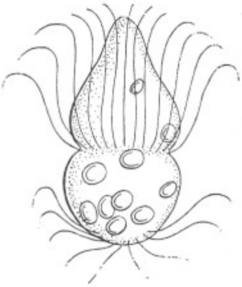

FIG. 2.—*Rhopalura granosa*. Ciliated larva, taken from the body of the parent. × 1470.

FIG. 3.—*Rhopalura granosa*. Fragment of a male producing plasmodium. × 70.

The male of *R. granosa* is entirely ciliated. The cilia on the anterior cone are rather shorter and denser than those on the rest of the body; they are directed forwards as in the female. Those on the second ring are much less closely set than those on the posterior rings, but appear to be as long. In *R. ophiocomæ*, the species which—of those so far described—seems most closely allied to *R. granosa*, the second ring is said to be unciliated, though Caullery and Mesnil (1901 c, p. 392 footnote) note that some isolated cells exceptionally bear long cilia. In sections the basal granules of the cilia stain very darkly and clearly with iron hæmatoxylin.

The "testis" is present about the middle of the body. The spermatozoa are flagellated.

The Larva.

The ciliated larva (Fig. 2) forced from the body of the female, by gentle pressure on the coverslip, is somewhat acorn-shaped,* being slightly constricted in the middle region, pointed anteriorly and broadly rounded posteriorly. (The pointed end is apparently anterior, as this is foremost when the larva swims.) It is about 19μ long. Ciliation is restricted to two bands of long cilia; one in the middle region about the slight constriction, and one posteriorly. Refringent bodies are present in both regions of the larva, but chiefly posteriorly. Cells could not be distinguished in the living state; larvæ were not sectioned.

The larva of *R. granosa* differs considerably in appearance from those so far described, namely, that of *R. ophiocomæ* (C. and L., 1905, p. 266; 1908 b, p. 432, and pl. xv, figs. 43, 44) and *R. pelseneeri* (M. and C., 1905 a, p. 429, and fig. 1), which appear to have no regular arrangement of the cilia, though Caullery and Lavallée (1908 b, p. 432), speaking of the very small size (12–15μ in diameter) and great transparency of the former larva, say: "La disposition des cils mêmes est à peu près impossible à fixer; ils paraissent longs et peu denses. Ils donnent à ces larves un mouvement rapide, souvent tourbillonnant."

Relationships.

Caullery and Mesnil (1901 c, p. 419) have distinguished three groups in the genus Rhopalura, characterised as follows:—

Cilia limited to narrow rings, *R. pterocirri* St. J. (I).

Cilia entirely (or nearly) covering the body.	Ova in compact mass. (II).	*R. ophiocomæ* Gd. *R. intoshi* Metchn.
	1 (or 2) linear row of ova. (III)	*R. leptoplanæ* Gd. *R. pelseneeri* C. and M. *R. linei* Gd. *R. metchnikovi* C. and M. *R. julini* C. and M.

R. granosa evidently belongs to the second group. It is intermediate in size in both sexes, between *R. intoshi* from *Lineus* (*Nemertes*) *lacteus* and *R. ophiocomæ* from *Amphiura squamata*. In the male it is clearly distinguishable from *R. intoshi* by the presence of large refringent bodies, and from *R. ophiocomæ* by having these bodies in the anterior cone, and the

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* Shaped like an acorn in its cup.

first row of cells of the second ring, while in *R. ophiocomæ* they are restricted to the second ring.

The female of *R. granosa* has not been observed to be without cilia on the second ring, as occurs in certain individuals of *R. ophiocomæ* (Giard, 1880, p. 232; Julin, 1882, p. 16; C. and M., 1901 c, p. 393): it has eight rings, while that of *R. intoshi* has nine (Metschnikoff, 1881, p. 284).

The larva differs from that of *R. ophiocomæ* both in the shape and the arrangement of the cilia: the larva of *R. intoshi* is unknown.

THE PLASMODIA AND THEIR DISTRIBUTION IN THE HOST.

In *Heteranomia squamula* the parasite is found replacing the gonad; it also occurs in the blood lacunæ and vessels in the mantle and the suspensory membranes of the gills, even extending into the dorsal ends of the gill filaments. In one host sectioned, numerous young plasmodia were present in the mantle margin in the posterior region. In heavy infections the parasitic plasmodia, containing the sexual forms of the Orthonectid, entirely replace the gonad of the host, rendering the determination of sex impossible. A fragment of a male containing plasmodium is shown in Fig. 3.

It would appear to be more usual for the males and females to occur in separate hosts, though it is by no means rare for them to be found together (see p. 244); when this occurs one sex generally predominates. Observations were mostly made on living Heteranomia, only two specimens being sectioned. One of the sectioned individuals was parasitised by plasmodia containing males only, many of them being nearly mature. It was well infected, plasmodia occurring in the mantle, visceral mass, suspensory membranes of the gills and dorsal ends of the gill filaments, but much of the gonad remained, sperm being recognisable among degenerating cells in some regions.

The second Heteranomia sectioned was very heavily infected, no gonad being recognisable. The great majority of the plasmodia in this host contained female Rhopalura, but in four separate regions of the visceral mass and mantle, males were present, many being nearly mature, and in at least two of these regions males and females occurred together in the same plasmodium (see Fig. 4). In one region (a), several branches or lobes of a plasmodium contained males, but in a very small portion only were the two sexes present together. In a second region (b), a small island of well-formed males, together with numerous germ cells and groups of germ cells, was present among females, and the males were not segregated in separate lobes of the plasmodium. In a third region (c), a few males were present in a small, almost empty plasmodial lobe, which was rather doubtfully traced into a female plasmodium. The fourth region (d), near the byssal muscle of the host, was by far the largest. This plasmodium appeared to contain males alone, though its considerable size made the tracing of its many branches difficult.

Where the males and females were present in the same plasmodium, the females yet appeared to contain unsegmented ova, so far as could be ascertained in the crowded condition of these. Caullery and Mesnil (1901 c, pp. 466–467) state that " dans des coupes d'une Amphiura, *qui renfermait des plasmodes des deux sexes* (of *R. ophiocomæ*), plusieurs femelles, à l'intérieur desquelles, au lieu d'ovules, on trouvait des corps plurinucléés ayant tout à fait l'aspect des embryons décrits ci-dessus, mais un peu moins avancés. Nous les interprétons comme tels. Il est parfaitement admissible que, lorsque les deux sexes de Rhopalura existent dans une même Ophiure, les femelles adultes puissent, avant d'arriver au dehors, être fécondées et renfermer des embryons."

It is impossible to be entirely certain that the presence of males and females in the same plasmodium is not due to the disappearance of host tissue dividing two originally separate plasmodia, but it seems not improbable that a plasmodium may produce males and females at different times, the two phases overlapping to some extent. When plasmodia are well established in the host, they ramify greatly, and it is practically impossible to determine their number and limits. The presence of plasmodia with males only in the less heavily infected host sectioned would seem to indicate that, if it should prove to be correct that the two sexes are produced by the same plasmodium at different times, the male phase precedes the female.

It may be noted that curious thread- or rod-like bodies, or regions, of darker staining protoplasm were present in some small portions of female producing plasmodia. Among masses of these occurred a few normal-looking groups of germ cells. The significance of these bodies is obscure ; they may be a normal occurrence, or possibly parasites.

Caullery and Mesnil (1901 c, p. 384 ; C. and L., 1912, p. 159) have described plasmodia which produce one sex only, such as are usually found in *R. ophiocomæ* from *Amphiura squamata*, as " unisexual," and those in which males and females develop side by side in the same plasmodium, as in *R. metchnikovi* from *Spio martinensis* (C. and M., 1901 c, pp. 384, 402), as " hermaphrodite." In *R. intoshi* from *Lineus* (*Nemertes*) *lacteus* an intermediate condition, between that of *R. ophiocomæ* and *R. metchnikovi*, seems to obtain, " male," " female," and " hermaphrodite " plasmodia frequently occurring in the same host (Metschnikoff, 1881, p. 284).

Most known diœcious species of Rhopalura apparently have " hermaphrodite " plasmodia (*R. leptoplanæ*, C. and M., 1901 c, p. 399, and *R. julini*, C. and M., 1901 c, p. 412, in addition to those already mentioned), *R. ophiocomæ* being the only one with generally " unisexual " plasmodia.

There appears, however, to be considerable variation in the condition of the plasmodia of this species in different localities. Giard (1880, p. 228) and Metschnikoff, 1881, p. 288) found that in *R. ophiocomæ* from *Amphiura squamata* from Wimereux, and from Naples and Spezzia respectively, a plasmodium produced Orthonectids of one sex only, males or females, though very occasionally the two sexes might be present in the same host. Julin (1882, p. 8), also working at Wimereux, says: "Je n'ai jamais rencontré dans le même hôte que l'une des deux formes, soit le mâle, soit la

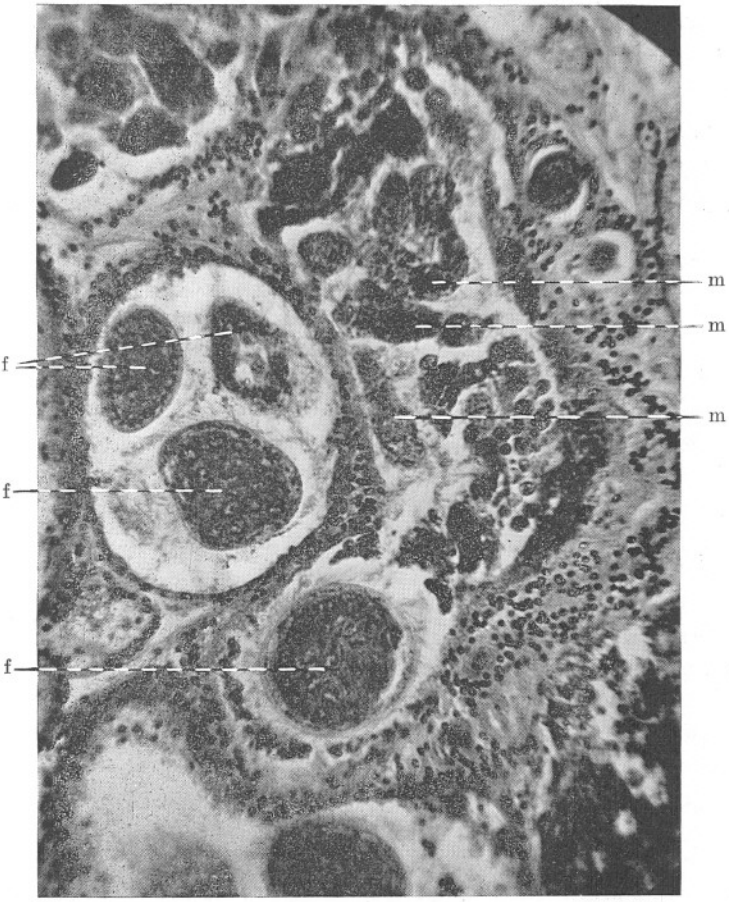

Photo. *D. P. Wilson.*

FIG. 4.—*Rhopalura granosa*. Section of part of a plasmodium containing both males and females. F., female (transverse section); m., male (longitudinal section). Bouin's fixative: Heidenhain's iron hæmatoxylin and acid fuchsin. × ca. 1012.

femelle, . . ." Caullery and Mesnil (1901 c, p. 392) found "Dans le cas de la *Rh. ophiocomæ*, chaque plasmode ne renferme que des individus d'un seul sexe, et souvent dans une même Ophiure, tous les plasmodes sont du même sexe," and in a foot-note add : "Dans l'anse Saint-Martin, un tiers environ des Ophiures parasitées renfermait uniquement des femelles, un tiers uniquement des mâles, un tiers à la fois des mâles et des femelles." On the other hand Koehler (1886, p. 609) working at Cette on the same species very frequently found males and females in the same Amphiura, the latter always being less numerous than the males. He rarely found one sex only ; in some fifty infected Ophiuroids only two contained males alone. He not only found males and females in the same host, but in the same plasmodium. Working in the same months of the year as Julin, he says (1886, p. 610) that the difference in their results can hardly be due to season, but that "Le genre de vie de ces remarquables parasites n'est donc pas le même à Cette qu'à Vimereux." In 1901 Caullery and Mesnil (p. 392) record that in an exceptional case they found adult males and females, together with developmental stages of both sexes, in the same plasmodium of *R. ophiocomæ*, thus confirming Koehler's observation of 1886.

In *R. ophiocomæ*, where the host is parasitised generally by Orthonectids of a single sex (with the exception of Amphiura at Cette), Caullery and Lavallée (1912, p. 163, foot-note) believe that the infection has mostly arisen from a single larva, and that the rare instances where males and females are present in the same host, have arisen from multiple infection by larvæ of different sexes. They think that one larva may possibly give rise to several amœboid germs, which spread the infection in the host (1912, p. 153).

When mature the males and females leave the host. Those from the gonad of Heteranomia would seem to pass out by way of the renal ducts, for in sections free forms have been recognised in them. The renal ducts opening into the exhalent chamber, the parasite will pass out safely in the exhalent current of the host. The way of escape of those parasites present in the blood-vessels and spaces has not been observed.

The males and females apparently meet outside the host and fertilisation is effected. The mode of fertilisation was not observed in *R. granosa*. It has, however, been studied in *R. ophiocomæ* by Caullery and Lavallée (1908 b, pp. 428–430). They found that on mixing mature males and females artificially taken from the host, "Au bout de 10 à 15 minutes, on observe *très fréquemment* que des mâles sont remorqués, aux flancs des femelles, dans la moitié postérieure de celles-ci, comme s'ils s'étaient accidentellement pris dans le revêtement ciliaire et n'avaient pu s'en dégager. Une femelle remorque parfois deux mâles ; nous en avons même observé, une fois, trois.

Ce phénomène, extrêmement commun dans les premiers temps du mélange, ne se retrouve plus ensuite. Nous avons pu nous convaincre que ces rencontres des mâles et des femelles étaient les circonstances mêmes de la fécondation. Et cependant, la façon dont nagent les deux catégories d'individus n'indique nullement qu'ils se recherchent. On voit les mâles passer très près des femelles sans a'y fixer. Il semble que ce soit purement le hasard qui produise les couples observés. Le contact des deux sexes n'est d'ailleurs jamais très long. Au bout de quelques minutes, les mâles se sont dégagés, les femelles sont de nouveau solitaires. Ce contact n'est jamais non plus intime. Le mâle paraît simplement retenu par sa ciliation à celle de la femelle.

. . . nous avons constaté, d'une façon indiscutable, que les spermatozoïdes sont émis, à ce moment, au dehors. . . .

Caullery et Mesnil (1901, p. 394, pl. x, fig. 2, og.) ont signalé, sur la surface de la femelle, un pore, appelé par eux *pore génital ;* . . . Nous avons lieu de croire que c'est par là que les spermatozoïdes pénètrent."

The embryos develop while in the body of the parent, being liberated as ciliated larvæ. To Caullery and his collaborators is due the discovery that in the Orthonectida the ciliated larvæ carry infection to fresh hosts ; Caullery and Lavallée (1910, 1912) have caused experimental infection of *Amphiura squamata* by *R. ophiocomæ*.

They (C. and L., 1912, p. 140) have discovered that in the life-history of the Orthonectida two generations alternate regularly :—

(1) a sexual generation, constituted in most species of males and females (some species, e.g. *R. pelseneeri*, are hermaphrodite) formed asexually from germ cells produced in the parasitic plasmodium.

(2) a generation produced from the fertilised ova of the preceding generation and carrying infection in the larval state to new hosts, where these larvæ are transformed into plasmodia, which give birth to the sexual generation.

It is puzzling to imagine how minute ciliated larvæ can effect safe settlement in a Lamellibranch. In the Anomiidæ the action of the lateral cilia on the gills is particularly furious, and the inhalent current rapid. One would not expect larvæ of not more than 19μ in length to be sufficiently strong swimmers to resist such a current, though it is possible that their cilia may interlock with those on the gills. If carried to the dorsal groove between the two demibranchs of each side they would in all probability eventually reach the mouth. It is possible, however, that after being thrown against the gills, they may be carried to the free edges of these, and then posteriorly in the rejection current, and dropped on the mantle margin in the posterior region. It may be noted that in one of the two Heteranomia sectioned, numerous young plasmodia were found in the mantle margin in this region, but the actual path of infection remains obscure.

If a number of Heteranomia from an infected batch be placed in a finger-bowl, numerous specimens of *R. granosa* may be obtained after a time. These will live quite happily in sea-water, whereas those obtained by opening the hosts, being not yet fully mature and ready for their free life, very quickly die. Even the cilia of immature forms frequently break down into droplets. It is remarkable that males, sufficiently mature for the sperm to be active, yet, when artificially liberated from the host die after a very few minutes in sea-water. In well-formed males obtained in this way sperm is frequently seen issuing from about the middle of the body (see also Julin, 1882, pp. 13–14), but this is almost certainly abnormal and not the true method of emission.

If a jet of air be passed through the bowl, the Heteranomia will live for weeks, and a supply of Rhopalura be available. A number of Heteranomia have been kept in this way for some fourteen weeks, though towards the end of that time specimens of Rhopalura were difficult to find, and females with segmented ova rare.

R. ophiocomæ issues from *Amphiura squamata* chiefly in the late afternoon; Caullery and Lavallée (1912, p. 143) suggest that the more or less fixed hour of emergence, providing for the simultaneous emission of the males and females, brings about the meeting of the sexes. No observations were made on the time of emergence of the Orthonectids from Heteranomia.

NUMBER AND DISTRIBUTION OF THE HOSTS INFECTED.

The infected Heteranomia, with one exception, have been obtained from masses of *Lepralia foliacea*. The Rhopalura was first found on November 25, 1932, infecting Heteranomia taken from a mass of Lepralia turned out of the Plymouth Aquarium, but which had most probably come from off Revelstoke Point or Stoke Point. Ten out of twenty-two (45·4%) of the Lamellibranchs were found to be infected. Of these seven were infected with plasmodia containing females, and three with plasmodia containing males. In an unnoted number of Heteranomia infected with female forms, males were also present. This high percentage of infection, which has so far not been reached in material examined direct from the grounds, may possibly have been artificially induced by favourable conditions in the tanks.

On February 2, 1933, 149 Heteranomia from fragments of Lepralia dredged from off Revelstoke Point were examined. Of these twenty-four (16·1%) were found to be infected; ten with males, ten with females (in one the plasmodia contained only immature forms, which from their size were probably female), and four with both males and females. When both sexes were present together the males were the more numerous, but as they are so much smaller than the females it does not necessarily follow that the plasmodia producing males occupied more space in the host than those producing females. The hosts varied from 3 to 10 mm. in diameter: that of 3 mm. was parasitised by male-bearing plasmodia.

The following animals, living either attached to, or sheltering in the crevices of the Lepralia obtained on February 2, were examined, but unsuccessfully, for the presence of Orthonectids: ten *Chlamys distorta*, ten *Ophiothrix fragilis*, five *Ophiocomina nigra*, and one *Antedon bifida*.

On February 6, 1933, 165 Heteranomia from fragments of Lepralia trawled from off Revelstoke and Stoke Points were examined. Of these only eleven (6·6%) were infected; four with males, five with females, and two with both males and females. In four the infection was slight. The hosts varied from about 6 to 12 mm. in diameter.

On February 13, 1933, all the Heteranomia of any size from three large pieces of Lepralia trawled from off Stoke Point were examined. Of the ninety obtained fourteen (15·5%) were infected; nine with males, two with females, and three with both males and females. Where the two sexes were present together the males were much more numerous than the females. The hosts varied from about 5 to 14 mm. in diameter.

The Heteranomia obtained on February 2, 6, and 13 were opened and carefully examined at a magnification of about 140, so that it is unlikely that even small numbers of well-developed sexual forms would have been overlooked, though tiny plasmodia most probably would have been.

Thirty-eight Heteranomia from twenty-four *Chlamys opercularis* from the "Corner" Ground off the Mewstone were examined on January 20, 1933: none were found to be infected.

An examination of seventy-three Heteranomia taken from the carapace of a single *Maia squinado* from the Mewstone Ground on March 20, 1933, showed only one to be infected, and that with plasmodia containing males alone.

It is possible that only those Heteranomia which occur in large communities, such as on masses of Lepralia, will be found to be generally infected. The branching colonies of the Polyzoan would also provide shelter from dispersing currents for the Orthonectids emerging from their hosts, thus facilitating the meeting of the males and females. Colonies of *Lepralia foliacea* were dredged and trawled chiefly off Revelstoke and Stoke Points at a depth of from 15 to 22 fathoms.

R. ophiocomæ, a species on which most work has been done, has been found to infect 2·5% to under 10% of *Amphiura squamata* (Giard, 1880, p. 227; Julin, 1882, p. 9; Caullery and Lavallée, 1908 b, p. 425), varying widely in different parts of the same locality (Caullery and Mesnil, 1901 c,

p. 391; Koehler, 1886, p. 609), and in different years (Metschnikoff, 1881, pp. 287, 288).

THE SWIMMING BEHAVIOUR OF *Rhopalura granosa*.

The Orthonectida were so named by Giard from their habit of swimming in a straight line. Giard states (1877, translated 1878, p. 182): "By the name of Orthonectida I have desired to recall their progression, which is so characteristic that it would of itself suffice for their recognition among the parasites with which they might be confounded."

In *R. granosa* this habit would seem to be very generally confined to animals travelling relatively slowly, as they frequently do on being artificially liberated from the host. It was apparently on individuals of *R. ophiocomæ* and *R. linei* obtained in this way that Giard made his observations. Observations on *R. granosa* have been made on individuals which had issued naturally from the hosts; mostly on females because of their larger size. The males swim more rapidly than the females, for although there is little difference in the length of the cilia in the two sexes, the males are less than half the size of the females.

The females, when normally active, continually take short flights upwards, often touching the bottom of the watch-glass or finger-bowl only to leave it almost immediately: the males less frequently touch the bottom. They turn in all directions, this apparently being due to bending of the body. It is only when their activity becomes much reduced that they travel largely in contact with the substratum, and then nearly always in a straight line. When swimming at speed these Orthonectids mostly, though not invariably, follow a gently spiral path. They may, on occasion, swim almost perpendicularly upwards, and on reaching the surface film (in a watch-glass of water) swim beneath it for a short distance, before diving downwards again. It is particularly when an animal is swimming perpendicularly upwards that it may be observed to follow a spiral path, for the anterior end of the animal is seen to describe tiny circles. *R. granosa* is symmetrical, with apparently no longitudinal differentiation of cilia, but any slight bending of the body out of a straight line—such as might well occur in an animal capable of muscular contraction—would, owing to the rotation of the animal on its own axis, result in a spiral path being followed.

The cilia on the body do not beat directly backwards, but obliquely, and the animal moves forwards, rotating on its own axis to the left. This is actual, and not apparent rotation due to the appearance of metachronal waves. During backwards swimming the animal rotates to the right.

Caullery and Mesnil (1901 c, p. 402) noted that the males of *R. metchnikovi* while in the plasmodia "montrent une assez grande mobilité; ils tournent sur leur grand axe à la façon d'une toupie." It is also of interest that they remark of the male, which is globular, measuring 40μ by 30μ, with the anterior extremity larger than the posterior, " En raison sans doute de sa forme globuleuse, il n'a pas le mouvement en ligne droite, si général dans le groupe et que nous avons constaté, en particulier, pour la femelle. Il est extrêmement mobile et il décrit des sortes de cercles ; il ressemble beaucoup à un Infusoire holotriche." It should be noted that Caullery and his collaborators—in common with previous investigators—in most of their work prior to that recorded in the 1912 paper, apparently used material obtained by opening the hosts.

As in other species of Rhopalura, there is in both sexes clear differentiation of the ciliation of the anterior cone from that of the rest of the body, in that when the animal is swimming forwards the cilia on the anterior cone appear to be directed forwards, while those on the rings posterior to it appear to be directed backwards (see Fig. 1, A). Over both regions, however, the effective beat is backwards, in spite of the difference in appearance. The appearance of the cilia on the anterior cone may be due to a restricted amplitude of beat ; when an animal is swimming slowly and the beat can be seen, they then certainly appear to beat through a small angle. That the effective beat is backwards over the anterior cone may be observed by the movement of particles caused by the action of these cilia in animals artificially liberated before maturity from their host, and in consequence have lost the rest of the cilia while in sea-water (see p. 244). It is of interest that the cilia on the anterior cone resist disintegration considerably longer than those on the rest of the body, and may frequently be seen intact and active, when the others have been shed. These cilia beating alone appear unable to move the animal. It is possible that they have a sensory function in addition to a locomotory one ; their differentiation from those on the rest of the body suggests this.

When the Orthonectids are swimming slowly forwards the appearance of the cilia is as shown in Fig. 1, A and C.

The cilia on the anterior cone, and in addition those on the second ring—though the latter during activity appear to be directed posteriorly with the cilia on the posterior rings—can be suddenly applied so closely to the surface that even at a magnification of 500 they appear as a thick, and but slightly striated cuticle (Fig. 1, B) ; during reversed swimming they were observed always to be motionless. In animals swimming forwards very slowly the cilia on the anterior cone have been observed, on occasions, to be motionless, but it is doubtful whether this occurs under normal conditions.

The cilia on the body posterior to the second ring rarely, if ever, become motionless, but the rate of beat may be much reduced temporarily so that the animal remains almost stationary. Females have been observed to remain for a time practically stationary, but with the body rotating.

This is apparently due to change of direction of beat of the cilia. They have also been seen to stand on end and rotate, being evidently attached posteriorly owing to some viscid property of the cilia in that region.

From observations it seems that the direction of beat of the cilia may be changed, for the Orthonectids are capable of swimming forwards and backwards, though the forward movement is the more usual. Frequently, however, females artificially liberated from their host may continue swimming backwards for the few minutes they live. McIntosh (1873, p. 129), one of the first observers of an Orthonectid, noticed the backward swimming of the parasite he found in *Lineus gesserensis*.

The change in direction of movement from forward to backward swimming is abrupt, the animal giving a sudden dart backwards as the cilia on the anterior cone and second ring are closed down ; during backward swimming these cilia have never been observed to beat, and would, therefore, seem to be incapable of reversing the direction of their beat.

In reversed swimming the cilia posterior to the second ring appear to be directed forwards (see Fig. 1, B)—that is in the opposite direction to that obtaining when the animals are swimming forward. Although it has been impossible to make observations on the movement of individual cilia, the change in direction of swimming would seem to be due to reversal of the effective beat of the cilia.

This power of sudden reversal of direction of movement is probably of value to the animal in rapid retreat from danger. On running into an obstacle, they have been observed frequently to swim in the reversed manner for a certain distance, then to turn round by muscular action, and continue the retreat in the same direction, but with the anterior end foremost. This reaction, however, does not invariably occur, for females at least appear to have a tendency to collect round debris, with the anterior end pushed against it, and the body cilia beating, though not at full speed. They frequently rub backwards and forwards against debris, at the same time contracting and expanding the body, and if the posterior extremity should come in contact, they have been observed to become caught—apparently by some viscid secretion or thread—and unable to free themselves, though the cilia, including those on the anterior cone, beat rapidly. The production of this viscid thread may perhaps be abnormal, due to the unnatural conditions of observation ; a female on one occasion was seen towing a male by such a thread, though at some considerable distance, and on other occasions females have been seen attached to each other posteriorly by a thread and tugging against each other, and so held stationary. It is just possible, however, that the viscid property of the cilia may play some part in the pairing of the males and females.

Males may frequently be observed continually reversing the direction of swimming, at very short intervals of time (a second or less). A characteristic movement of the male is that of sharply striking the water with the slender posterior region of the body: it is to this that the name Rhopalura refers (see Giard, 1880, p. 231).

I wish to thank the British Association for granting me the use of their table at Plymouth, and the Director and Council of the Marine Biological Association for facilities. For the microphotograph (Fig. 4) I am indebted to Mr. D. P. Wilson.

SUMMARY.

A new species of Orthonectid, *Rhopalura granosa* from *Heteranomia squamula* L., is described. The female is fusiform, and about 190 to 230μ long, and 55 to 75μ broad. The male is also fusiform, but less than half the size of the female, being only 87 to 95μ long and 20μ broad. *R. granosa* is distinguished from all other known species of Rhopalura by the presence in the male of large refringent bodies in the anterior cone, and in the first row of cells of the second ring. The male of *R. ophiocomæ* Giard, a species closely allied to *R. granosa*, has the refringent bodies in the cells of the second ring only.

The infected Heteranomia have been obtained from *Lepralia foliacea* trawled and dredged from off Revelstoke and Stoke Points. In Heteranomia examined direct from the grounds the infection in February, 1933, varied from about 6·6% to 16%, but in a number taken from Lepralia from the Plymouth Aquarium in November, 1932, the percentage of infection was as high as 45·4%.

The parasite is found replacing the gonad of the host; it also occurs in the blood lacunæ and vessels in the mantle, and in the suspensory membranes of the gills, even extending into the dorsal ends of the filaments. In heavy infections the Orthonectid may entirely replace the gonad of the host.

Male and female containing plasmodia usually occur in separate hosts, but it is not uncommon for the two sexes to be found together. From sections it would seem that males and females may on occasion be produced in the same plasmodium.

The swimming behaviour of *R. granosa* is described.

APPENDIX.

OTHER ORGANISMS OBSERVED IN *Heteranomia squamula.*

Few parasites and commensals, other than Rhopalura, were noticed in some four to five hundred Heteranomia examined. Those seen were :—

(1) Rounded masses, *ca.* 60 to 80μ in diameter, of tiny spores in the gonad of two individuals.

(2) A Coccidian in the kidney. The number of Heteranomia infected with this parasite was not noted.

(3) A Rhabdocœle from each of six individuals of the seventy-three taken from the carapace of a single Maia (see p. 245). This Rhabdocœle almost certainly was not *Graffilla gemellipara* Linton, which is common in the mantle cavity and in the gut of *Cardium edule* from the Yealm Estuary and Millbrook. Although the specimens were large they did not contain viviparous young as is characteristic of *G. gemellipara*, and were more opaque than that species: they were broadly rounded anteriorly and pointed posteriorly. In addition to these six specimens another two or three have been seen at different times.

(4) A few larval Trematodes were seen in two or three Heteranomia taken from the Maia mentioned previously.

(5) In a number of Heteranomia a ciliate, possibly a species of Boveria, was present on the mantle.

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On the Rate of Diatom Growth.

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With 3 Figures in the Text.

The series of events taking place in the sea which influence the growth of phytoplankton, and consequently the general fertility, has provided a fruitful study during recent years. Intensive surveys have been made since simple and sufficiently accurate methods of determining minute traces of phosphates and nitrates in sea-water became available. Over the greater part of the oceans the annual crop of phytoplankton seems to be limited by the quantity of these nutrient salts which arrive annually in the upper layers from below. This quantity depends upon vertical mixing, since nitrogen salts and phosphates are re-formed but slowly from dead organisms, which sink meanwhile to enrich the deep layers. Although this hypothesis gives a simple explanation why some areas are fertile, supporting a rich growth of phytoplankton and others not so much so, and the facts so far ascertained fit well with the explanation, recent investigations in the Southern Ocean (**1**, **2**) indicate that other causes limit the annual production there. The phosphates and nitrates are not fully utilised during the summer, whereas in equally high and higher latitudes in the North Atlantic they are, and, moreover, growth may be very rapid.

A wealth of observations has been collected in widely distant seas, and the questions, often rather nebulous, which have arisen from these require consideration in any attempt to envisage the skein of possible factors which regulate the growth of diatoms in various places.

Purely mechanical means by which phytoplankton organisms are transported vertically may play a leading rôle. Off the west coast of Norway (**3**a, **4**) it has been found that the spring outburst of diatom growth starts around the edges of the fiords and over the edge of the continental shelf, then extending across the 30 miles of sea between these foci; later it commences in the Atlantic water beyond. In the Gulf of Maine (**5**) the spring outburst starts close inshore and over the offshore banks. Between Russia and the Northern ice (**6**) growth starts first inshore and in the cold Arctic water which has originated from comparatively shallow areas, later in the tongues of warmer Atlantic water which penetrate eastward into the Arctic water. It has been suggested that water near the surface close inshore and over banks where there is upwelling is better seeded with diatoms and their spores, these having been kept better in suspension throughout the winter by turbulence than in the deep ocean. Another likely locus (**3**b) where the surface layers are well seeded at the beginning of sunny weather is close to ice, where the run off remains near the surface and may often contain diatoms which have been frozen in at the end of the previous summer.

Vertical transport in the turbulent water of the open ocean is of necessity greater in those regions where wave motion keeps the water so well mixed that the upper layers do not gain in temperature over the water below. The continuous drain on the phytoplankton population by being carried below the "compensation level," where there is sufficient light for photosynthesis to exceed respiration, is enhanced in such areas, where vertical mixing is not restrained during the summer months owing to density differences being set up (**3**). Further, the surface waters being kept cold, the rate of photosynthesis is kept low. This may to some extent influence the fertility over wide and turbulent expanses of the Southern Ocean, where owing to the great "fetch" of the waves their mixing effect may extend deeper than in the North Atlantic.

It has recently been found in the seas between Iceland and Greenland (**7**), in the Barents Sea (**8**), and in the English Channel (**9**) that ammonium salts occur at greater concentration in the upper layers than in the deeper water. Although the quantity is always very small, some material amount remains after all or practically all the nitrate has been used up by phytoplankton. Nitrate production, which presumably takes place only by bacterial action, has not yet been found to occur in the upper layers of ocean water, although it occurs readily enough in water in contact with bottom deposits. It is not clear how the plants get a sufficiency of nitrogen salts during the summer months, at least in such places as the upper layers of the English Channel, unless they utilise ammonium as it is being formed. In fact, the numerous and more accurate data now accumulated have added little to our knowledge of the processes involved in the nitrogen cycle in the seas.

Physical conditions may explain, either wholly or in part, a group of phenomena connected with the growth of diatoms in temperate and Northern seas. The date of the vernal outburst of growth in the English Channel and off the Isle of Man has been found to depend largely on the amount of sunshine in the early part of the year, yet in Loch Fyne it may occur a month earlier than in the near-by Loch Striven (**10**). Off the west coast of Norway, in materially higher latitude and colder water, it occurs earlier than in the English Channel. The date may depend upon the total amount of incident light, of which there are no observations yet available, or upon some other cause not yet recognised.

In general it appears that the growth of diatoms during the summer months in relatively shallow inshore waters is greater than in deeper waters out to sea. Although the amounts of nutrient salts at the beginning of the season may not be very different, in the shallower areas mixing due to tides and occasional strong winds keep the upper water layer better refreshed with these salts throughout the summer. In this connection Gran (**3**) has put forward the interesting theory that drainage from the land contains some growth-promoting factor, which would in part account for the great productivity of coastal waters, and perhaps for the inability of phytoplankton to consume all the available nutrient salts in the Southern Ocean which receives little land drainage compared with the Northern Atlantic. It had been found that the addition of a sterilised water extract of soil to a flask of sea-water containing ample phosphate and nitrate increased the growth of diatoms in it.

Mention should also be made of the successive outbursts of diatom growth in the sea, where one dominant species dies out to be replaced by another, and of how diatoms cultured in flasks tend after a time to die out, particularly if bacteria become numerous.

The experimental investigation of influences affecting the growth of diatoms *in vitro* cannot by itself solve the questions which arise from observations such as these. However, the effect of some chemical factors on the rate of growth lends itself to such investigation, and was undertaken in the hope that further knowledge of the physiology of diatoms may open up new lines of enquiry.

EXPERIMENTAL METHODS.

The diatom *Nitzschia closterium* was chosen as it grows well, is persistent, and was obtainable free from flagellates. On the other hand it is a neritic species typical only of inshore waters.

I am indebted to Dr. E. J. Allen for the parent culture, which had in its turn been subcultured over a number of years. Up to the present time a persistent culture of marine diatoms has never been obtained completely free from bacteria. In interpreting these experiments, the possibility has always to be borne in mind that differences in the rate of growth of the Nitzschia may have been caused by changes in the bacterial flora or their secretion into the water. It would seem, however, that the additions of the various substances to the sea-water act directly upon the diatoms, rather than indirectly through the bacteria, but this is, of necessity, a matter of opinion.

In order to follow the rate of growth, six flasks (A, Fig. 1) of equal volume, 293 c.c., were arranged in a carrier. Each was filled with the same culture and 20 c.c. withdrawn, leaving 273 c.c. of liquid and 20 c.c. of air. To one, acting as control, a trace of mercuric chloride or potassium cyanide had been added. The carrier was placed in a water bath kept at constant temperature, usually 16° C., and the whole continuously shaken to and fro by means of a motor. The shaking was sufficient to bring the gases in solution in the liquid into equilibrium with the 20 c.c. of air within a short time. The upper ends of the gauge tubes B were connected to a manometer and the pressure adjusted so that the height of liquid in the gauge tube of the control was at a convenient mark : then the heights in the other tubes were read, the motor being stopped meanwhile. The mark on the gauge tube of the control is so chosen that the 20 c.c. of air in the series of flasks is roughly at normal atmospheric pressure.

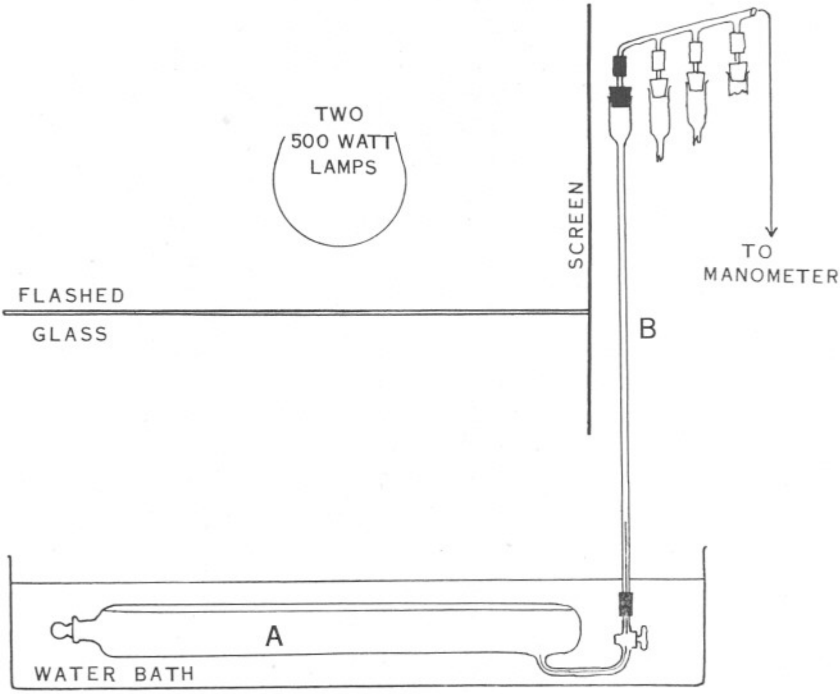

Fig. 1.

Illumination was obtained from two 500-watt gas-filled lamps with the light source 35 cm. above the tubes, and having a sheet of flashed glass immediately below the lamps. This provided more even illumination and reduced the heat radiated to the water bath. On the other hand it reduced the illumination some 50%. After a period of illumination the motor was again stopped, the manometer again adjusted so that the height of liquid in the control flask gauge was the same as before, thus obliterating the effect of any slight variation in temperature, and the heights in the other tubes read. The increases in height from the previous readings gave the increases in volume of the air above each flask, due to the oxygen given off by the diatoms. This distributes itself between the liquid and the air, increasing the volume of the latter.

The volume of oxygen produced per litre of liquid in each flask, subsequent to the first period of shaking, was calculated in the following manner.

If x c.c. of gas are evolved, mostly oxygen, it increases the volume of the 20 c.c. of air above the sea-water in the flask to $20+x$ c.c., the temperature being 16° C. and the pressure being taken as normal atmospheric pressure, the slight increase due to the rise of water in the gauge tube being neglected. Since the proportion of nitrogen in this air is slightly reduced by the oxygen given off, its partial pressure falls and a little nitrogen is given off from the sea-water. Let a c.c. be the nitrogen and $x-a$ c.c. be the oxygen evolved. The 273 c.c. of sea-water at 16° C. and normal atmospheric pressure in equilibrium with air contains 3·5 c.c. of nitrogen at 16° c. (Fox).

At the beginning the sea-water is in equilibrium with nitrogen at a partial pressure of approximately $\frac{16}{20}$ of 760 mm. Hg. After the evolution of x c.c. of gas it is in equilibrium with a mixture containing $16+a$ c.c. of nitrogen and $4+x-a$ c.c. oxygen, and the partial pressure of nitrogen becomes $\frac{16+a}{20+x}$ of 760 mm. Hg. Hence the volume of nitrogen remaining in the sea water is

$$3{\cdot}5\times\frac{(16+a)\ 20}{(20+x)\ 16}\ \text{c.c.}$$

and the loss is

$$3{\cdot}5-\frac{280+17{\cdot}5a}{80+4x}=a$$

From this the gas evolved contains roughly 14% of nitrogen and 86% of oxygen.

The 273 c.c. of sea-water at 16° C. contains when in equilibrium with air at normal pressure 1·74 c.c. of oxygen measured at 16° C. (Fox). After x c.c. of gas have been evolved it is in equilibrium with the $20+x$ c.c. of gas mixture containing $4+0{\cdot}86\ x$ c.c. oxygen. The dissolved oxygen then amounts to $1{\cdot}74\times\frac{5(4+0{\cdot}86x)}{20+x}$ c.c., being an increase of $\frac{5{\cdot}75x}{20+x}$ c.c.

Hence the total oxygen production approximates to $0{\cdot}86x+\frac{5{\cdot}75x}{20+x}$ c.c. measured at 16° C. per 273 c.c. of culture, or $\frac{78x+3x^2}{20+x}$ c.c. per litre measured at N.T.P.

If oxygen is being produced rapidly by the diatoms in the flasks there will be a certain lag in time before it attains equilibrium with the air with which the liquid is being shaken. In order to assess the error likely to arise from this cause the following experiment was carried out.

Two flasks were charged with sea-water approximately saturated with air at 16° C. and two flasks with sea-water which had been partially de-aerated. They were shaken in the water bath for 3 minutes before the first readings of the heights of liquid in the gauge tubes were read. Readings were taken at intervals. In this particular experiment the manometer was disconnected. In order to eliminate a slight change in temperature in the water bath, the readings of flask IV were subtracted from those in the other three flasks, this procedure being comparable with the use of a control flask and manometer in an ordinary experiment.

TABLE I.

Change in Volume of Air in Flasks Less Change in Flask No. IV.

	I.	II.	III.
After 10 min.	—0·451	—0·483	—0·021 c.c.
20 ,,	·506	·536	·023
30 ,,	·519	·542	·020
40 ,,	·520	·545	·020
50 ,,	·522	·546	·022
80 ,,	·520	·546	·020

The result indicates that equilibrium was quickly approached, and attained within the limit of experimental error in less than 30 minutes. In the above experiment gases were entering the water, while working with diatoms oxygen passes out of the water into the air above.

In many of the experiments qualitative differences in growth rate were observed on keeping the cultures in small flasks in a north window until a thick growth had developed. Visual inspection was sufficient to show any material differences, and this was in many instances confirmed by examination in a Dubosq colorimeter. In some cases counts were made by means of a hæmocytometer having a field of $\frac{1}{10}$ cubic millimeter. In order to obtain representative values it was necessary to count several hundred cells from each culture, or even several thousand when the difference was not very great although clearly seen on visual inspection. I am indebted to Mr. G. M. Spooner for mathematical analysis of several counts.

THE EFFECT OF DISSOLVED PHOSPHATE ON THE RATE OF CARBON FIXATION BY *Nitzschia closterium*.

Nitzschia was seeded into a flask of sea-water which had been passed through a Berkfeld filter and to which an excess of potassium nitrate had been added, equivalent to over 500 mg. of nitrate nitrogen per cubic metre. This was kept in a north window until vigorous growth had used up practically all the dissolved phosphate. Analysis was made difficult by the quantity of diatoms present, but there remained certainly less than 10 mg. P_2O_5 per cubic metre. This culture was then filled into two flasks. The third, fourth, and fifth flasks were filled with the same culture to which 10, 20, and 100 mg. P_2O_5 per cubic metre had been added respectively. The sixth flask, acting as a control, was filled with the same culture to which a little cyanide had been added. Exactly 20 c.c. was withdrawn from each. After standing overnight in the dark they were illuminated and shaken at 15° C., the first reading being taken 45 minutes later.

TABLE II.

EXCESS OF PHOTOSYNTHESIS OVER RESPIRATION.
c.c. oxygen produced by 1 litre during

	1 hr. 30 min.	2 hr. 25 min.	4 hr. 20 min.	6 hr. 20 min.
Without addition of phosphate . . .	0·12	0·24	0·49	0·67
Ditto . . .	0·15	0·26	0·53	0·75
With 10 mg. per m^3 P_2O_5 added . . .	0·19	0·32	0·66	0·96
20 mg.	0·24	0·41	0·76	1·24
100 mg.	0·25	0·43	0·85	1·26

These values indicate that the addition of phosphate caused an increased rate of photosynthesis as soon as illumination was commenced, having had all night in the dark in which to be absorbed by the diatoms.

With the aim of ascertaining the final increase in fixed carbon due to the addition of phosphate, two experiments were made. Nitzschia was grown in filtered sea-water enriched with nitrate until all, or practically all, the dissolved phosphate had been used up, as shown by analysis. The flasks were filled, the control poisoned with cyanide, 20 c.c. withdrawn from each, and they were brought to constant temperature in the water bath. After a short period of illumination to ascertain that the rate of growth in all was the same within the limits of experimental error, additions of potassium hydrogen phosphate were made to three of the tubes, an equal quantity of liquid being withdrawn. They were then subjected to alternating periods of light and darkness.

Figure 2 shows the rate of growth, that is the excess of photosynthesis over respiration, during illumination. The volumes of oxygen used up in the process of respiration during the periods of darkness do not enter into the values plotted.

It is seen that growth proceeds at a steady slow rate in the tubes having no added phosphate. The increase in rate due to the addition of 20 or 86 mg. P_2O_5 per cubic metre remains about the same for 10 hours or more, after which the effect of 86 mg. becomes markedly greater than the effect of 20 mg., although even after 20 to 25 hours only a small part of the 20 mg. has presumably been used up.

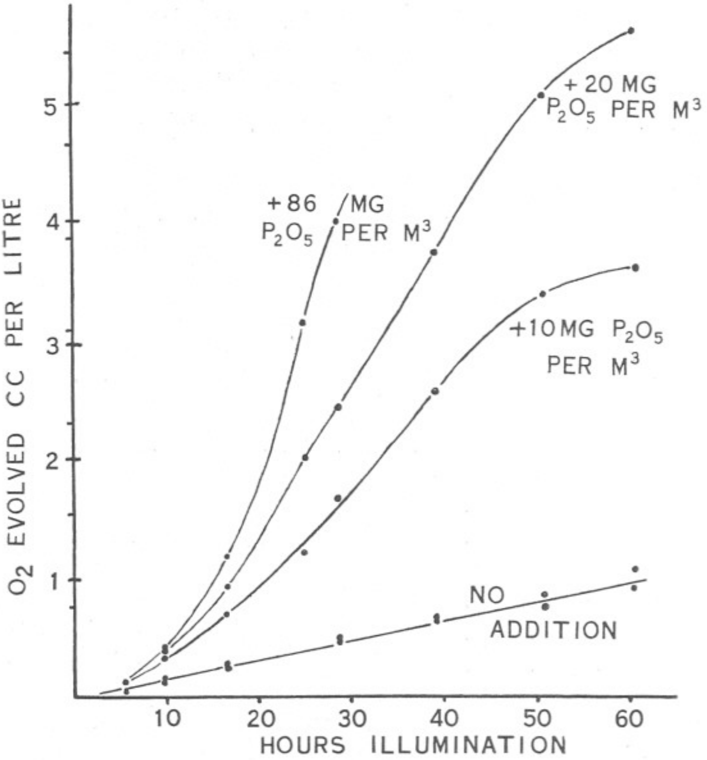

FIG. 2.

The last part of the curve, showing the growth where 10 mg. P_2O_5 per cubic metre had been added, runs parallel with the line or curve showing the growth of the diatoms without added phosphate. This indicates that the 10 mg. per cubic metre had all been utilised and that it gave rise to 2·6 c.c. per litre of oxygen more than in the tubes having no added phosphate. However, the respiration during the periods of darkness was greater in the flasks with added phosphate, the nett productions of oxygen being as follows :

TABLE III.

NETT OXYGEN PRODUCTION AT THE EXPIRATION OF 60 H. 45 M. LIGHT AND 69 H. 45 M. DARKNESS.

With no addition	$0{\cdot}40$	c.c. per litre.
Ditto	$0{\cdot}43_5$	,, ,,
With 10 mg. P_2O_5 per m.^{3} added	$2{\cdot}45$	,, ,,

This shows a nett increase of 2·0 c.c. per litre due to the addition of 10 mg. P_2O_5 per m^3.

In the next experiment filtered sea-water with excess of nitrate was seeded with Nitzschia and after some days in a north window filled into five of the flasks, one of which was poisoned with mercuric chloride and used as control. In order to deduce when practically all the phosphate was used up, and to see that all the flasks behaved alike, they were illuminated daily for about 12 hours for four days. The observed increases in volume were 0·445, 0·447, 0·435, 0·440 c.c. respectively, showing remarkably close agreement. To two flasks 10 mg. P_2O_5 per cubic metre was then added, and illumination continued daily for eight days, by which time the rate of growth was the same. The oxygen production, being the nett excess of assimilation over respiration during this eight-day period of alternating light and darkness, was as follows :

$$\text{Without added phosphate}\ \left.\begin{matrix}1{\cdot}80\\1{\cdot}50\end{matrix}\right\}\ \text{mean } 1{\cdot}6_5 \text{ c.c. per litre.}$$

$$\text{With 10 mg. } P_2O_5 \text{ per m.}^3\ \left.\begin{matrix}3{\cdot}9\\3{\cdot}9\end{matrix}\right\}\ \text{mean } 3{\cdot}9 \text{ c.c. per litre.}$$

The nett increase in oxygen, due to the addition of 10 mg. P_2O_5 per m.^{3}, is here $2{\cdot}2_5$ c.c. per litre, a value comparable with that of 2·0 c.c. found in the previous experiment.

A peculiar inference arises from these values. The addition of 10 mg. P_2O_5 per cubic metre gave rise to an observed increased growth equivalent to $2{\cdot}0$–$2{\cdot}2_5$ c.c. evolution of oxygen, or assimilation of the same quantity of carbon dioxide per litre, that is to say a fixation of 1·07 to 1·2 gm. of carbon per cubic metre. If the illumination had been continuous there is reason to suppose that this quantity would have been greater, the losses due to respiration during the periods of darkness being eliminated. The ratio of P_2O_5 added to carbon fixed is $\frac{1}{107}$ to $\frac{1}{120}$; even less if illumination were continuous. There are no analyses showing the ratio of P_2O_5 to carbon in the cells of *Nitzschia closterium*, but Raben's analyses of plankton consisting almost entirely of mixed diatoms gives a ratio of about $\frac{1}{15}$. The addition of phosphate brought about the fixation of seven times the amount of carbon that might have been expected.

THE EFFECT OF ADDED PHOSPHATE UPON THE RATE OF OXYGEN CONSUMPTION BY *Nitzschia closterium* IN DARKNESS.

Filtered sea-water, enriched with potassium nitrate, was seeded with *Nitzschia closterium* and kept in a north window until vigorous growth had developed. This was filled into the flasks, to three of which additions of phosphate were made. They were then covered with black cloth and shaken continuously at 16° C. in darkness. The results of this experiment are shown in Figure 3.

A second experiment was made in the same manner, but over a longer period of time. As in the previous experiment the oxygen consumption was roughly doubled where 200 mg. P_2O_5 per cubic metre had been added. The increase in rate of oxygen consumption tended to wane about 45 hours after its addition.

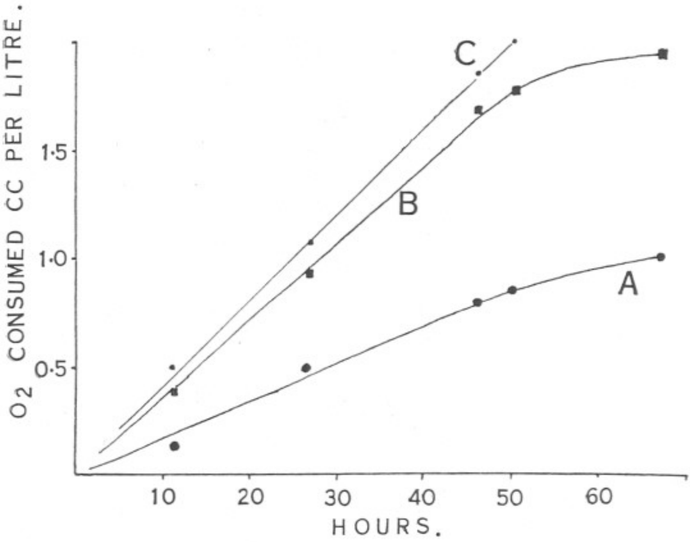

FIG. 3.—Oxygen consumption by Nitzschia in sea-water with excess nitrate in darkness. Curve A shows mean values for two flasks without addition of phosphate. Curve B shows mean values for two flasks with 200 mg. P_2O_5 per cubic metre added. Curve C shows values for flask with addition of 1000 mg. P_2O_5 per m.^{3}.

In another experiment the flasks were filled with a culture rich in nitrate which had used up practically all the available phosphate. They were exposed to alternating illumination and dim light, not complete darkness in this case. By taking the rate of photosynthesis as equal to the rate of oxygen produced under illumination plus the rate of consumption in dim light, as approximating darkness, the results may be epitomised as follows :

RATE OF PHOTOSYNTHESIS, C.C. O_2 PER LITRE PER HOUR, MEAN OF VALUES FROM TWO FLASKS IN EACH CASE.

	During first day	second day	third day of experiment.
Without addition . .	0·051	0·045	0·041
With 10 mg. P_2O_5 per m.^{3} .	0·081	0·089	0·087
Mean rate of oxygen consumption in dim light :			
Without addition . .	0·008	0·011	0·013
With 10 mg. P_2O_5 per m.^{3}.	0·017	0·022	0·022

From this it appears that the rates both of photosynthesis and of oxygen consumption in darkness are about doubled by providing phosphate even in such small quantity. It is improbable that the increases are wholly due to the increase in quantity of fixed carbon brought about during the periods of illumination, particularly as the first period only gave rise to a very small carbon dioxide assimilation.

Another experiment was made in the same way. Adding 10 mg. P_2O_5 per cubic metre about doubled the rate of oxygen consumption as in the previous experiment. Treating the values in the same way, and making the same assumptions, the rate of photosynthesis increased from nearly double to over treble during the third day. In the previous experiment it remained about double. More phosphate, 86 mg. per cubic metre, rather more than doubled the rate of oxygen consumption and this rate increased as a material quantity of new growth was formed.

Rate of Photosynthesis, c.c. oxygen per litre per hour.	During first day	second day	third day of experiment.
Without addition . .	0·026	·028	·028
With 10 mg. P_2O_5 per m.^{3} .	·048	·078	·10
20 ,, ,, ,, .	·050	·10	·15
86 ,, ,, ,, .	·056	·15	·29

In these experiments the rate of oxygen consumption in darkness is due to respiration by the diatoms and to bacterial and autolytic breakdown of dissolved organic matter. However there is no reason to suppose that the addition of these minute traces of phosphate affects the bacteria and oxidation of dissolved organic matter, and it seems safe to assume that the big differences found in the rate of oxygen consumption are due to the influence of phosphate upon the respiration of the diatoms.

It is considered that they had loaded up with fixed carbon in the form of storage products, which they could not convert into new growing tissue for lack of necessary phosphorus. As soon as this is provided the conversion takes place and in consequence the rate of respiration increases. The following experiments indicate that this conversion is accompanied by division of many of the cells, and the formation of new pigment, even if the diatoms are kept in the dark.

A culture of Nitzschia in filtered sea-water, heavily enriched with nitrate, was kept for several days in a window until growth had apparently ceased owing to lack of phosphate. This was divided between two flasks, to one of which phosphate was added to the extent of 100 mg. per cubic metre. Both were then kept in darkness for 48 hours. The addition of phosphate resulted in a 29% increase in the number of diatom cells, and the culture was browner in colour than the flask to which no addition had been made.

The experiment was repeated with a fresh culture. The addition of phosphate, after 48 hours in darkness, resulted in a 28% increase in the number of diatom cells. Equal quantities were filtered and the pigment washed out from the diatoms on filter papers by repeated passage of 80% acetone. Colorimeter readings of the two pigment extracts—yellow-green in colour—showed 45% more pigment in the culture to which phosphate had been added.

A consideration of Table II, p. 259, which is typical of several experiments where the culture stood some 18 hours in the dark with added phosphate before being illuminated, is suggestive. Hand in hand with the change of stored material into actively respiring protoplasm, the photosynthetic activity of the cells was increased. During the first hour and a half's illumination the effect of adding phosphate 18 hours previously is marked.

THE EFFECT OF NITRATE AND OF AMMONIUM UPON THE GROWTH OF *Nitzschia closterium.*

The results of two experiments with cultures of Nitzschia, in sea-water enriched with phosphate, are shown in Tables IV and V. It is seen that ammonium-nitrogen replaces nitrate-nitrogen in the case of this neritic diatom, and that its addition is equally effective in promoting growth.

TABLE IV.

OXYGEN IN C.C. PER LITRE PRODUCED DURING CONTINUOUS ILLUMINATION.

	After 18½ hr.	42½ hr.	90½ hr.	138½ hr.	Increase due to addition.
No addition	0·37	0·85	1·06	1·2	
With addition of 60 mg. per $m.^3$ of nitrate/N_2 .	0·52	1·7	2·4	2·5	1·3
60 mg. per $m.^3$ of ammonium N_2 ammonium .	0·51	1·8	2·7	3·1	1·9

TABLE V.

OXYGEN, C.C. PER LITRE, PRODUCED AFTER

	7 hr. illumination $24\frac{1}{2}$ hr. darkness 21 hr. illumination	54 hr. illumination $24\frac{1}{2}$ hr. darkness	93 hr. illumination $24\frac{1}{2}$ hr. darkness	Increase due to addition.
No addition	0·7	2·8	4·0	
60 mg. per cubic metre nitrate–N_2 added .	1·08	4·0	5·15	1·15
Ditto	1·16	4·2	5·45	1·45
60 mg. per cubic metre of ammonium N_2 added	1·08	4·0	5·23	1·23

The increase in oxygen production brought about by this addition of 60 mg. per cubic metre of nitrate-nitrogen in these two experiments was 1·3, 1·15, 1·45 c.c. per litre, the mean being equivalent to the fixation of 0·7 gm. carbon per cubic metre. The ratio of nitrogen added to carbon fixed is therefore $\frac{1}{12}$.

Analyses by Raben of plankton consisting mainly of mixed diatoms gave a ratio of nitrogen to carbon amounting to roughly $\frac{1}{5}$. As with phosphate, the addition of a small quantity of available nitrate gives rise to an unexpectedly large increase in the amount of carbon fixed.

During the vernal outburst of diatoms in the sea about two and a half times more nitrate-nitrogen than phosphate (as P_2O_5) is used up. Yet in these experiments the addition of roughly ten times more nitrate-nitrogen than phosphate is required to bring about the same increase in fixed carbon.

Under the conditions of these two experiments the addition of ammonium brought about a similar increase in growth to that brought about by the addition of nitrate.

THE EFFECT OF ARSENATE UPON THE GROWTH OF *Nitzschia closterium*.

The quantity of phosphate in sea-water as estimated by the Atkins-Denigès method includes any arsenate which may be present. After vigorous growth of phytoplankton in the summer, the phosphate content of the water, estimated by this method, may fall to less than 1 or 2 mg. P_2O_5 per cubic metre. Hence there is either practically no arsenic present as arsenate or the phytoplankton utilises it. With regard to the latter possibility, it is known that some plants can utilise arsenate partially in lieu of phosphate. In a single preliminary experiment, made in 1930 in daylight with rather crude apparatus, increased growth was observed due to the addition of sodium arsenate amounting to 20 mg. As_2O_5 per cubic metre. However, in six instances, when between 20 and 40 mg. As_2O_5 per cubic metre were added and the experiments carried out in the apparatus here described, the rate of photosynthesis was reduced.

EFFECT OF HYDROGEN ION CONCENTRATION.

An experiment was made with a vigorous dense growth of Nitzschia in filtered sea-water which had been enriched with phosphate and nitrate. The pH was reduced to varying degrees by blowing alveolar air through the culture. The oxygen production during illumination is shown in the following table.

TABLE VI.

Approximate pH measured colorimetrically. Initial.	Final.	c.c. oxygen produced per litre during 3 hr. 45 min. illumination.
8·4	8·45	0·48
8·1	8·1	0·50
7·9	7·9	0·57
7·45	7·4	0·55
less than 7·0		0·55

This experiment indicates that slight variations in pH in the tubes of culture are not likely to have invalidated any of the foregoing experiments.

THE EFFECT OF EXCESS BASE.

In many of the following experiments rich cultures were produced in small flasks where, from the nature of the experiment, the rate of growth may have been gradually slowed owing to excessive rise in pH. Since the addition of any base would hinder the rise in pH by increasing the buffering, it was desirable to find out if the addition of any substances used in the experiment had acted by altering the " excess base " in the sea-water and so affecting its buffering capacity. With this end in view an experiment was made in which a solution of sodium bicarbonate saturated with carbon dioxide was added to flasks of enriched sea-water inseminated with Nitzschia. This increased the excess base to ·0036, ·0046, and ·0086 Normal. No significant effect was noticeable upon the growth of Nitzschia.

THE EFFECT OF IRON.

Filtered open sea-water was enriched with phosphate and nitrate and inseminated with Nitzschia. Varying quantities of ferric ammonium citrate were added to flasks of this. After two days in a north window the effect of added iron was noticeable. On the ninth day the cells were counted by means of a Hæmocytometer with the following result :

Iron added. Mg Fe per c.m.	Number of cells per cubic mm.
none	5,340
8	7,070
80	9,540
1,600	13,870

It was realised from other experiments proceeding simultaneously with this one that the full effect of added iron was probably suppressed owing to lack of silicate. The cultures are thick and the diatoms require more than is initially present in the water (200–400 mg. SiO_2 per m.^{3}) and is being continually dissolved from the glass of the flasks.

A similar experiment was made in which the water was enriched with silicate as well as with phosphate and nitrate, and three series of flasks set up with additions of ferric ammonium citrate. After fifteen days in a window counts were made in one series with the following result :

Iron added. MgFe per c.m.	Number of cells per cubic mm.
none	7,370
1 mg.	16,360
3 mg.	16,540
5 mg.	28,000

From inspection as growth was proceeding in the three series of flasks it was clear that the rate of growth was about doubled in each case by the addition of 1 mg. Fe per cubic metre.

An experiment was made with a vigorous thick culture, in water enriched with phosphate nitrate and silicate, to see if the addition of iron caused division of the cells or formation of colouring matter when kept in the dark, but no evidence of this was found.

A number of experiments were made with the object of indicating in what form iron is available and effective. Iron ammonium citrate is slowly hydrolysed in sea-water, less rapidly if sodium citrate is also added, when it remains longer in solution as an " iron-citrate " complex. The addition of sodium citrate did not make a culture with iron ammonium citrate grow any faster, which indicates that the " iron citrate " complex itself is not available to the plants—a conclusion also arrived at by Hopkins (**13**). With regard to other iron compounds an experiment was made in which 800 mg. Fe per cubic metre was added in the form of ferric ammonium citrate (slowly hydrolysed), ferric alum, ferrous sulphate (both rapidly hydrolysed in sea-water) and dialysed iron, the colloidal hydroxide formed by hydrolysis. The citrate was most immediate in its action, but after twelve days in a window the iron alum and ferrous sulphate had brought about an increased growth similar to that due to the addition of citrate. Dialysed iron in this and other experiments was found to have no effect or only very little. Gran had found that hæmoglobin was without effect and the writer that hæmatin likewise did not promote growth. A small piece of steel was found to improve the growth in a culture, as it rusted. It would seem that these additions act through the iron-ions which they give off and which escape hydrolysis to the unavailable hydroxide.

The writer was unable to detect any ferric or ferrous ions in sea-water until it had been both made acid and subjected to vigorous oxidation, as by boiling with bromine water. It would seem that it mostly occurs as organic compounds (**14**) in solution and ferric hydroxide in suspension or colloidal solution (**4**), with only a small moiety in a form available to plants.

These experiments as a whole indicate that iron in an available form does not exist in sea-water in sufficient quantity for the most rapid growth of Nitzschia. There is sufficient, however, for a heavy final production. There is no evidence whether this is present *ab initio* or is formed from " unavailable iron " as the " available " is used up.

We have found that the addition of 1 mg. Fe per cubic metre in the form of citrate doubles the rate of growth of Nitzschia. Probably much of this addition exists in the form of iron-citrate complex and the hydroxide formed from it by hydrolysis, neither of which appear to be "available." It does not seem unreasonable to conclude from this that sea-water contains less than 1 mg. per cubic metre of iron in an available form. Analysis shows that the concentration of iron-ions is less than this amount. Hopkins considers that iron-ions are the only form in which iron is available, basing his conclusion on experiments with the freshwater alga Chlorella, which however requires much more iron for growth than do marine diatoms. He estimates that Chlorella requires some 82 mg. iron-ions per cubic metre in the culture solution to give satisfactory growth.

THE EFFECT OF ADDED SILICATE.

The filtered sea-water used in these experiments contained silicate in solution to the extent of 200–400 mg. SiO_2 per m.^{3}. A further supply of silicate arose from the glass vessels. Sea-water is known to dissolve silicate from glass, and after long use the flasks are seen to be corroded.

In a number of cases it was noticed that with a thick culture in glass flasks—2,000 to 5,000 cells per cubic mm.—increased growth was obtained if the water had been enriched with sodium silicate (2,000 mg. SiO_2 per cubic metre) in addition to phosphate and nitrate. The cells were rather larger and more regular in shape.

The solution of silicate from the glass was demonstrated in an experiment where sea-water inseminated with Nitzschia and enriched with phosphate and nitrate was kept in a north window in glass bowls. Two of the bowls were coated with paraffin wax inside while two were coated outside in order that the illumination in all four should be similar. During the first days there was no noticeable difference, but in seven days the growth had become significantly greater in the bowls which were waxed outside and where the water was free to dissolve silicate from the glass.

THE EFFECT OF A PREVIOUS GROWTH OF NITZSCHIA IN THE CULTURE MEDIUM.

A rich culture of Nitzschia was prepared in filtered sea-water enriched with phosphate and nitrate. This culture, several weeks old, was filtered through a membrane filter and the filtrate saturated with air. As control a sample of sea-water was filtered in the same way. Both were enriched with excess of phosphate and nitrate, then seeded with the same quantity of Nitzschia, and kept in a window. Growth was significantly greater in the water filtered from the previous growth of Nitzschia.

The experiment was repeated except that a Nitzschia culture was filtered as soon as a thick vigorous growth had taken place. The filtrate was low in dissolved silica, containing 210 mg. SiO_2 per cubic metre, while the control contained twice this amount. In this case rather more growth was obtained in the control than in the filtrate from the vigorous culture. However, when a trace of sodium silicate was added to both, bringing the SiO_2 content up to about 2,000 mg. per cubic metre in each case, significantly greater growth was obtained in the filtrate from the culture.

These experiments indicate that Nitzschia does not secrete substances into the surrounding water which are inimicable to the further growth of the same species, but rather that the cells secrete substances which accelerate growth.

THE EFFECT OF SOIL EXTRACT UPON GROWTH.

The influence of land drainage running into the sea upon the growth of diatoms has been noticed since many years. It used to be attributed to the supply of phosphates and nitrogen salts carried down from the soil, but the more recent analyses show that these often amount to little and that their effect would not extend far seaward. Gran suggests that land drainage acts largely by reason of the iron salts and colloidal iron which it brings into the sea, possibly also manganese. Atkins showed that it provides silicate, lack of which may hinder diatom growth, perhaps even preventing it in the open oceans of low latitude far from land, where diatoms give way to coccolithophores.

It has long been known that the growth of diatoms and other plants, moulds and other organisms in culture solution is accelerated by the addition of a little vegetable or soil extract (Miquel, Allen, Pasteur, Wildiers, Schreiber, Nielsen and Hartelius and others). It appears that some organic substance or group of substances, occurring rather widely in the breakdown products of living organisms, acts as a growth-promoting factor.

The foregoing experiments show that the silicate in solution in a soil extract may often increase growth, even in cultures in glass vessels from which silicate is continuously though slowly given off. They show that diatom growth will be accelerated if the addition of soil extract to sea-water increases the available iron. No experimental evidence has actually shown that it adds to the available iron, although this seems probable.

It is yet an open question what constituents of land drainage other than silicates, phosphates, nitrogen salts and perhaps iron influence diatom growth in the sea. The following experiments were made with the aim of throwing more light upon this.

Soil extract was prepared by boiling garden soil with water, filtering and bringing this filtrate to boiling point at intervals of two days or more to destroy bacteria.

Filtered sea-water, heavily enriched with phosphate and nitrate, about 1,000 mg. P_2O_5 and 3,000 mg. nitrate-nitrogen per cubic metre, was seeded with Nitzschia and 60 c.c. portions poured into five small flasks. Addition of soil extract was made to four of these. They were kept in a north window at room temperature for nine days, when the number of cells was great enough to make fairly accurate counting possible.

TABLE VII.

NUMBER OF CELLS PER CUBIC MILLIMETRE.

	After 9 days.	Increase due to addition
No. addition	860	
0·05 c.c. soil extract . .	1,030	170
0·10 c.c. ,, ,, . .	1,230	370
0·5 c.c. ,, ,, . .	1,380	520
2·0 c.c. ,, ,, . .	1,770	910

The increased growth was very apparent on inspection only, the colour of the culture being browner and the turbidity due to the tiny cells more marked. Later, as growth proceeds, the differences between the flasks became less noticeable—the cells tend to clump together and to adhere to the bottom and sides of the flasks, making accurate counting impossible.

Experiments were then made to investigate the effect of soil extract on the rate of growth and of respiration of an actively growing culture of Nitzschia in enriched sea-water. Table VIII shows the effect of 3 hours illumination, followed by 18 hours darkness, followed by 4 hours illumination and then 18½ hours darkness.

TABLE VIII.

OXYGEN PRODUCTION + OR UTILISATION − IN C.C. PER LITRE DURING PERIODS OF

	3 hr. illumination.	18 hr. darkness.	4 hr. illumination.	18½ hr. darkness.
No addition	+1·14	−0·48	+2·4	−0·68
No addition	+1·14	−0·48	+2·4	0·60
With 0·5 c.c. soil extract	+1·14	−0·53	+2·9	0·60
2·0 c.c. ,, ,,	+1·16	−0·65	+3·3	0·68
5·0 c.c. ,, ,,	+1·14	−0·75	+3·3	0·78

It is seen that soil extract did not affect the rate of photosynthesis during the first 3 hours illumination—it is not immediate in its effect. The respiration rate after this short period of illumination was however increased. The rate of photosynthesis was increased during the ensuing period of 4 hours illumination but the rate of respiration during the ensuing period of darkness was not materially affected.

The increase in respiration after the first short period of illumination is peculiar. The values are significant and regular. In order to see if it was due to the oxidation of the soil extract, the experiment shown in Table IX was made. Two flasks were charged with a rich growth of Nitzschia in enriched sea-water and two with filtered sea-water without diatoms. To one of each soil extract was added. After 48 hours shaking in darkness at 16° C. the lights were turned on to make sure that the soil extract was effective in promoting photosynthesis.

TABLE IX.

OXYGEN UTILISED −, IN C.C. PER LITRE

	After 24 hr. darkness.	After 48 hr. darkness.	Oxygen produced during subsequent period of 6 hr. illumination.
No addition	−1·25	−2·68	+2·2
With 5 c.c. soil extract	−1·31	−2·76	+3·3
Filtered sea-water only	−0·10	− ·17	
Ditto, with 5 c.c. soil extract	−0·15	− ·32	

Slow oxidation of dissolved organic matter in the filtered sea-water is demonstrated, greater where soil extract had been added. Taking this into account the values show that the addition of soil extract had no appreciable effect upon the rate of respiration, although the added soil extract was very effective in promoting photosynthesis during subsequent illumination.

The next step was to find whether addition of soil extract caused division of the cells or formation of colouring matter in darkness. Filtered sea-water was enriched with phosphate and nitrate, inseminated, and after a vigorous growth of Nitzschia had developed divided into two portions. To one 10% of filtered sea-water was added, to the other 10% of an extract of soil made with sea-water. They were then kept in the dark for 48 hours and the cells counted by means of a hæmocytometer. This experiment was repeated three times with the following results :

NUMBER OF CELLS PER CUBIC MM.

	With soil extract.	Without.	Increase.
Experiment I . .	1,540	1,320	16%
,, II . .	5,630	4,840	16
,, III . .	1,630	1,490	9

There was no noticeable increase in colouring matter due to the addition of soil extract.

A series of experiments indicated that soil extract did not act only through the silicate and iron which it contains. Filtered sea-water was enriched with phosphate, nitrate, silicate and iron (80 mg. Fe per cubic metre in the form of ferric ammonium citrate), and inseminated with Nitzschia. Growth was rapid and the final production great, yet the addition of soil extract caused a material increase in the rate of growth. There is reason to suppose that this increase was not due to the extra silicate and iron added in the soil extract, since there was already a large excess of silicate and a heavy enrichment with iron in the control.

That iron does not play the leading rôle is further suggested by the observation that an alkaline extract of soil is more effective than an acid one, both being neutralised previous to use.

There is indication that the growth-promoting factor is of organic nature, possibly a group of organic substances, often present in the breakdown products of animal or vegetable matter. Thus evaporation and ashing of soil extract destroys its growth-promoting properties. The addition of a very small quantity of yeast or Fucus or Nitzschia extract or of a very dilute solution of ovolecithin promoted growth in a culture rich in phosphate, nitrate, silicate and iron.

THE EFFECT OF ICE WATER.

A suggestion has been made by Barnes (**15**) that the production of diatoms may be influenced by trihydrone molecules in the water from recently melted ice or snow. He found that Spirogyra grew more rapidly in water which had been previously frozen than in water which had recently condensed from the gaseous state, and even than in water which had long been in the liquid state. In this preliminary communication details of the control of other factors, such as the supply of nutrient salts, are not given.

It is easy to experiment with Nitzschia in such a way that the only variables are the possibly different nature of the water molecules. Filtered sea-water was enriched with phosphate, nitrate, iron citrate, and sodium silicate and inseminated with the diatom. Fifty c.c. portions of this were filled into small flasks, to half of which were added 10 c.c. of recently distilled water and to the other half 10 c.c. of the same water which had been frozen and allowed to melt. The flasks were then kept in a north window at room temperature, which varied around 20° C. Between each pair of flasks the only difference was that recently distilled water had been added in the one case, and water from melted ice in the other.

The experiment was repeated several times and, except in the case of one pair of flasks, a greater growth could be distinguished after several days where ice water had been added. Counts were made of the number of diatoms in one pair of flasks after five days' growth with the following result :

With recently distilled water, 4,310 cells per cubic mm.

With recently distilled water previously frozen and melted, 5,430 cells per cubic mm.

In this experiment, with two pairs of flasks, the difference was very clearly distinguishable, equally so in each pair. In other experiments the difference was not always so marked although distinguishable.

The question was attacked in another manner. Filtered sea-water similarly enriched was filled into two flasks. One was partially frozen and allowed to attain room temperature. Then both flasks were inseminated with the same quantity of a thin Nitzschia culture and kept in a north window. In each of the experiments the growth was perceptibly greater in the water which had been partially frozen. It is possible that a minute trace of some constituent separated out from solution when the latter concentrated during the partial freezing, so these experiments do not form such good indication of the possible physiological action of trihydrone as the former series appear to do.

These experiments were all made at room temperature during the summer months under conditions of good illumination, the daylight lasting some 15 hours out of the 24.

A similar series of experiments was made in November, also at room temperature, the illumination being weaker and lasting only some 9 hours out of the 24. No difference was detected between the flasks with added ice water and the controls although good growth had taken place in a week.

I am indebted to Dr. E. J. Allen, F.R.S., and to my colleagues, particularly Dr. W. R. G. Atkins, F.R.S., Mr. F. S. Russell, and Mr. G. M. Spooner, for many suggestions and for the help which they have given me during the course of this research.

SUMMARY.

The neritic diatom *Nitzschia closterium* was grown at constant temperature under artificial illumination in filtered sea-water to which various additions had been made. The oxygen production or utilisation was measured by observing the change in volume of air with which the cultures were continuously shaken.

The addition of phosphate to a culture poor in this nutrient salt increased the rate of both photosynthesis and respiration.

If kept in darkness after the addition of phosphate, an increase in number of cells and of yellow-green pigments resulted.

The addition of 1 part P_2O_5 gave rise to an increased carbon fixation of 107 to 120 parts of carbon.

The addition of nitrate and ammonium increased the rate of photosynthesis.

The addition of 1 part nitrate-nitrogen gave rise to an increased carbon fixation of 12 parts of carbon.

The addition to sea-water, enriched with phosphate, nitrate, and silicate, of 1 mg. Fe per cubic metre in the form of citrate doubled the rate of growth.

The addition of silicate increased the production of Nitzschia in glass vessels from which the culture solution only slowly dissolves silica.

Experiments bearing on the effect of a previous growth of Nitzschia in the culture solution are described.

The addition of a sterilised extract of garden soil increased the rate of photosynthesis. It also caused multiplication of cells in the dark. Evidence is given suggesting that this may be due to the provision of silica and possibly iron in a form readily assimilated by diatoms, and also to a " growth-promoting factor."

Some evidence is given that the growth of Nitzschia proceeds faster,

under certain conditions, in water part of which had recently been in the form of ice.

The conclusions are tentative in that they are based on a limited number of observations of one species of diatom under a narrow range of experimental conditions; moreover, it is not improbable that this species may behave differently under different conditions, as of light, temperature, age and volume of culture. The aim of this preliminary investigation was to suggest new lines of enquiry and supplement current research concerning the productivity of the sea, rather than to study the effect under a wide range of conditions of any one factor upon this diatom.

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The Food Consumed by Shags and Cormorants around the Shores of Cornwall (England).

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With 2 Figures in the Text.

CONTENTS.

I. INTRODUCTION.

AT a meeting held in the County Hall at Truro, Cornwall, on 30th August, 1911 (**2**, *a*), the Cornwall Sea Fisheries Committee decided to offer a reward of one shilling for the head of every Shag and Cormorant killed within the limits of the sea fisheries district under the jurisdiction of the Committee, the reward to become payable on and after the first day of September—just two days later.

This action was taken as the result of many and bitter complaints having reached the Committee concerning the destruction of marketable fishes—especially young flatfishes—by these birds in Cornish waters. Within one month after the initiation of this scheme for reducing what was then believed to be a serious menace to Cornish inshore fisheries, 751 birds' heads were received. Although this heavy initial slaughter did not for long continue unabated, the Fishery Officer for the County, in his quarterly report submitted to the Committee at their meeting on 26th May, 1915 (**2**, *e*), stated that he had then paid for a total of 4,220 birds since the order was first issued in September, 1911. He also further stated in that report that " from information gathered along the coast it is the general opinion of the longshore fishermen that since the destruction of so many of these birds there is a marked improvement in the quantity of fish in our coves and estuaries."

In July, 1915 (**2**, *f*), owing to certain difficulties which had arisen in connection with the continuation of the scheme, the offer of rewards for the destruction of Shags and Cormorants was withdrawn.

The scheme was again brought into being in September, 1925 (**2**, *h*), and remained in operation until the end of 1929, when the payment of rewards was again discontinued (**2**, *j*). During this second period in which the reward was offered, 6,739 heads were received and paid for, making a total of 10,959 birds killed, payment for which had involved an outlay of approximately £550.

From time to time, while the scheme for the destruction of Shags and Cormorants was in operation, doubts were expressed in various quarters as to its efficacy, no appreciable beneficial effect having become evident in the fisheries. Apparently even the fishermen's previously avowed belief in its usefulness had also faded, for the Fishery Officer's report to the Committee, dated 12th December, 1929 (**2**, *j*), contains the following statement. "During my periodical visits throughout the County I have interviewed several fishermen as to the effect of the operation of the scheme on the fisheries. The consensus of opinion is that there is no positive evidence that the destruction of these birds has been sufficient to influence the fisheries to any appreciable extent."

This purely negative result of the Committee's action could be explained by the operation of either of two entirely different factors—(1) that although the birds are definitely harmful, their numbers had not been reduced sufficiently to have any appreciable effect upon the fish stocks; or (2) that the birds are not so harmful as the fishermen had stated and as the Committee had been led to believe. If the former explanation were the true one, the launching of a more intensive campaign against the offenders would probably have been the proper course to pursue; whereas if the latter hypothesis should be correct the destruction of the birds in the past had been entirely unnecessary and unjustifiable and ought in no circumstances to be continued.

In order to dissipate the fog of uncertainty in which the Committee had gradually become enveloped, Dr. E. J. Allen, Director of the Plymouth Laboratory, undertook to have the stomach contents of any birds sent to him examined and their food reported upon by members of his staff. Following upon this offer by Dr. Allen, 39 birds were received at the Laboratory during the autumn of 1929. They were examined by Mr. V. C. Wynne-Edwards, who submitted a report of his findings to the Committee at their meeting of 18th December, 1929. In this report Wynne-Edwards stated that "the Shags seem to be feeding almost entirely on inshore fishes and very seldom take any marketable species. Out of a total of 84 fishes which I have been able to name only 3 have been marketable and of these the one I have entered as 'Gadus sp.' was almost certainly a Poor-cod, and the 'Clupea sp.' was probably a Sprat. This leaves one small Dab on the black list."

Four of the Cormorants examined by Wynne-Edwards contained identifiable food in their stomachs but no food fishes were included. Too few birds had been examined, however, to justify his making any definite statement concerning them.

It was after consideration of this report that the Committee hurriedly issued a notice withdrawing their offer of rewards for the heads of Shags and Cormorants. At the same time, they agreed to contribute towards the cost of further investigations by the Marine Biological Association.

Shortly afterwards Mr. Wynne-Edwards left the country and the subsequent investigations have been carried out by the present writer.

The researches were continued until early in 1933, when it was considered that a sufficient number of both species had been obtained to justify definite conclusions being drawn from them concerning the normal food of these birds in this area. The total numbers of Shags and Cormorants examined in the years 1929–1933 inclusive are shown in Table I.

TABLE I.

NUMBERS OF SHAGS AND CORMORANTS EXAMINED IN EACH OF THE YEARS 1929–1933 INCLUSIVE.

	SHAGS.			CORMORANTS.		
	Stomach containing recognisable food.	Stomach empty.	Total number of birds examined.	Stomach containing recognisable food.	Stomach empty.	Total number of birds examined.
1929	23	11	34	4	1	5
1930	12	14	26	0	1	1
1931	35	8	43	1	0	1
1932	115	1	116	19	0	19
1933	3	0	3	3	0	3
Totals	188	34	222	27	2	29

II. METHODS EMPLOYED.

In 1929 birds shot from time to time in the neighbourhood of St. Austell and Mevagissey were sent to the Plymouth Laboratory for examination of their stomach contents. All the birds had been dead for some time, therefore, before their stomachs could be opened and their food recorded. Thirty-nine birds (34 Shags and 5 Cormorants) were dealt with in this way and one small Dab was the only food-fish found in them.

It was considered not unlikely that these results had been vitiated by the digestion which continues in the birds' stomachs for a considerable time after life is extinct. In order to eliminate this possible source of error arrangements were made in the summers of both 1930 and 1931 by which all birds were examined almost immediately after death. The results obtained after adopting this precaution were similar to those previously recorded. It can safely be concluded, therefore, that the 1929 results are perfectly reliable.

As most of the birds dealt with in the years 1929–31 had been shot during the summer months around rocky and exposed shores it was decided that, in order to make the investigation complete, birds shot during the winter months and in other localities ought also to be secured for examination. In the winter of 1931–32, therefore, an effort was made to obtain birds from sandy bays, harbours, and river estuaries, where flatfish are known to be numerous and where fishermen state that they frequently see Shags and Cormorants devouring large numbers of them.

By this means also it was hoped to receive a larger proportion of Cormorants than formerly when most of the birds shot were Shags. This was due to the fact that where shooting had been carried on Shags are plentiful and Cormorants relatively very scarce. The Shag is essentially marine, seldom venturing inland or even into the more or less enclosed waters of harbours and estuaries unless compelled to forsake its usual haunts by stormy weather. The Cormorant, on the other hand, normally frequents harbours, estuaries, and tidal rivers, and may even visit lakes and reservoirs far inland. Very occasionally it will venture out along the open coast but never goes far to sea.

In spite of these efforts, however, only four birds (two Shags and two Cormorants) were obtained from such localities during the winter of 1931–32, none of which contained any food-fishes.

As the following winter (1932–33) approached, a still more determined effort was made. In November, 1932, the reward offered for each bird shot in or near any harbour, sandy bay, or river estuary was increased from one shilling to two shillings and sixpence. The assistance of the Fishery Officer for Cornwall (Mr. W. H. Barron) was also enlisted. Mr. Barron was asked to select suitable men to shoot birds in specified localities around the coast and forward them to the Plymouth Laboratory. These measures were unexpectedly successful. Birds soon began to arrive in large numbers and in a very short time sufficient data had been collected to complete the investigation.

Throughout this work the numerical method of recording the stomach contents has been adopted, the number of recognisable organisms of a species or group being noted.* Many stomachs contained also a mass of highly comminuted and unrecognisable food fragments. No attempt was made to deal with this in any way. Identification of fishes from the otoliths† accumulated in the bottoms of the birds' stomachs were likewise not attempted as this was considered unnecessary in view of the numbers of food organisms directly and more accurately identifiable.

One point of considerable interest and of no little importance in the future conduct of the investigation came out clearly from the work done in the summer of 1930. Twenty-two Shags (12 adults and 10 young) were shot near Port Isaac on July 7th, all before 7 o'clock in the morning. Not one of these birds had a particle of food in its stomach; without doubt the birds had all been shot before feeding had begun. It was therefore decided that in future no shooting should take place very early in the morning. This precaution had the desired result, and very seldom afterwards were birds received whose stomachs did not contain recognisable food material.

III. FOOD OF SHAGS (*Phalacrocorax graculus graculus* (L.)).

In Table II are summarised the results of the examination of the 188 Shag stomachs which contained recognisable food. It will be seen that the food consisted almost entirely of fishes, with, in addition, a very small proportion of various crustaceans. Twenty-four kinds of fish have been recognised with sufficient accuracy to place them in their Genera, and in twenty cases the species also has been determinable. Ninety-six birds—or 51 per cent of those containing recognisable food—were found to have been feeding on Sand Eels (Ammodytes spp.), and 69 of them had *nothing but Sand Eels in their stomachs.* There can be no doubt that Sand Eels constitute the staple food of Shags in this area throughout the whole year. Wrasses, Gobies, Rocklings, Blennies, Dragonets, and other non-marketable species are also regularly eaten in smaller numbers.

In the winter months, however, Sprats and other Clupeoids also enter to some extent into the diet of Shags. In one stomach approximately 200 small Clupeoids up to about 2 inches in length (recorded as Clupeoid Britt) were found. Seven birds had devoured one or more Anchovies.

The Clupeoids are marketable species but, with the exception of the Anchovy which is not fished here, they are present in such large numbers that any depletion which Shags may be able to effect cannot possibly be

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* See also Appendix II, p. 291.

† Remarkably large numbers of otoliths (up to 73) frequently were found in the stomachs. Possibly they accumulate and are used for breaking up the food in somewhat the same way as fowls and pigeons use small pebbles.

TABLE II.

FOOD OF SHAGS (SUMMARY).

Total number of birds examined 222—of which 188 contained identifiable food organisms in their stomachs.

Name of food animal.*	Number of birds in which found.	Highest number found in one stomach.	Total number recognised in all the stomachs examined.
Sprat (*Clupea sprattus*)	**20**	**50**	**278**
Anchovy (*Engraulis encrasicholus*)	**7**	**15**	**24**
Britt (Small Clupea spp.)	**2**	**200** (estimated)	**350** (estimated)
Clupeoid (Herring, Sprat, etc.) Remains	**21**	—	—
Conger Eel (*Conger vulgaris*)	**2**	**1**	**2**
Bib (*Gadus minutus*)	**2**	**1**	**2**
Pollack (*Gadus pollachius*)	**2**	**2**	**3**
Ling (*Molva molva*)	**1**	**1**	**1**
Gadoid (Gadus spp.) Remains	**3**	—	—
Dab (*Pleuronectes limanda*)	**2**	**7**	**8**
Flatfish (Pleuronectid) Remains	**3**	—	—
Sea Stickle (*Spinachia vulgaris*)	2	1	2
Pipe Fish (*Syngnathus acus*)	1	1	1
Sand Eel (Ammodytes spp.)	96	30	440
Five-bearded Rockling (*Onos mustelus*)	1	1	1
Three-bearded Rockling (*Onos tricirratus*)	8	1	8
Blenny (Blennius spp.)	1	1	1
Blenny (*Chirolophis ascanii*)	3	1	3
Weever (*Trachinus vipera*)	1	1	1
Dragonet (Callionymus spp.)	19	5	36
Goby (*Gobius flavescens*)	1	1	1
Goby (*Gobius minutus*)	2	35	45
Goby (Gobius spp.)	3	1	3
Sea Scorpion (Cottus spp.)	2	2	3
Ballan Wrasse (*Labrus bergylta*)	12	5	17
Cuckoo Wrasse (*Labrus mixtus*)	3	4	7
Corkwing Wrasse (*Crenilabrus melops*)	3	5	11
Gold-sinny Wrasse (*Ctenolabrus rupestris*)	24	10	63
Wrasse (Labrid) Remains	5	—	—
Comber (*Serranus cabrilla*)	1	1	1
Unidentifiable Fish Remains	28	—	—
Prawns (Palæmonidæ)	9	5	16
Shrimps (Crangonidæ)	5	2	7
Miscellaneous Crustacea	3	—	—

* Marketable fishes in heavy type.

considered to constitute a menace to any commercial fishery for them which exists in this area.

Bib, Pollack, and Ling are other species, of more or less value commercially, which are occasionally eaten by Shags, but the numbers killed in this way are so small as to be quite negligible—more especially since these fishes, though marketable, are not very valuable.

Only 5 out of the 188 birds were found to have eaten flatfish. Two of those were shot in Mevagissey Bay, one on November 2nd, 1929, and the other on November 23rd, 1932. The former had eaten one small Dab and the latter had unidentifiable flatfish remains in its stomach. The three others, it is important to note, were all shot in river estuaries. Two of them were obtained from the Camel River in November, 1932, one of which contained the remains of a single flatfish (Flounder ?) and the other had in its stomach seven small flats—five of them obviously Dabs and the two others either Dabs or Plaice. The fifth bird, shot in the

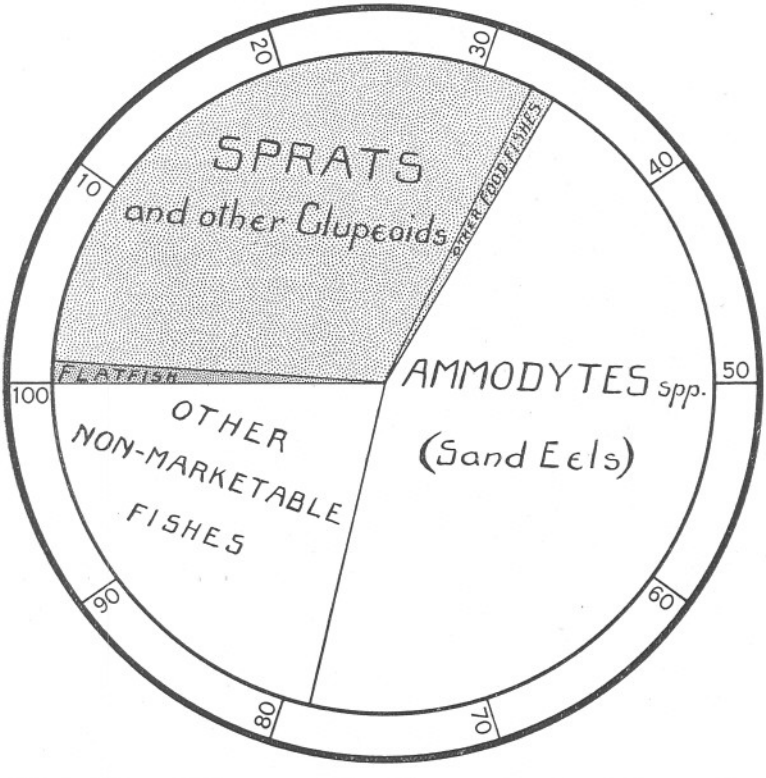

FIG. 1.—Diagrammatic representation of the percentage numerical composition of the food of Shags (Clupeoid Britt and Crustaceans omitted).

TABLE III.

Food of Cormorants.

Total number of birds examined 29—of which 27 contained recognisable food organisms in their stomachs.

Serial number of bird.	Date examined.	Locality where shot.	Herring (*Clupea harengus*).	Sprat (*Clupea sprattus*).	Freshwater Eel (*Anguilla vulgaris*).	Conger Eel (*Conger vulgaris*).	Grey Mullet (*Mugil chelo*).	Father Lasher (Cottus sp.).	Dragonet (Callionymus sp.).	Goby (Gobius spp.).	Flounder (*Pleuronectes flesus*).	Plaice (*Pleuronectes platessa*).	Dab (*Pleuronectes limanda*).	Flatfish remains.	Gurnard (Trigla sp.).	Pogge (*Agonus cataphractus*).	Ballan Wrasse (*Labrus bergylta*).	Corkwing Wrasse (*Crenilabrus melops*).	Gold-sinny Wrasse (*Ctenolabrus rupestris*).	Prawns (Palæmonidæ).	Shrimps (Crangonidæ).
	1929																				
1	July 15	Mevagissey			1				2												
6	,, 15	,,															1				
12	,, 26	,,															1				
19	September 20								1										1		
	1931																				
93	July 29	Newlyn															1				
	1932																				
113	February 4	River Erme (Estuary)																1	1		
114	,, 4	,, ,, ,,																		2	

115	October	18	Mouth of Yealm River	1																		
168	November	23	River Camel (Estuary)									8										1
172	,,	23	St. Austell Bay									1	1									
174	,,	23	,, ,,															3				
175	,,	23	,, ,,						5													+
192	,,	23	,, ,,		1						4	4									11	3
221	,,	24	River Camel (Estuary)								1	1										+
222	,,	24	,, ,, ,,									1										
224	,,	24	Mevagissey Bay				1															
227	,,	24	,, ,,							1				2		1					+	+
237	,,	26	River Lynher			1									1							
238	,,	26	,, ,,	4																		+
241	,,	29	River Tamar												3							31
242	December	5	River Tamar (Estuary)									1										
243	,,	5	,, ,, ,,											2			9					
244	,,	5	,, ,, ,,					1														
245	,,	5	,, ,, ,,											2								
	1933																					
248	January	12	River Lynher	4											+							+
249	,,	23	Sutton Harbour (Plymouth)										4									
251			River Lynher								26	1	6	1	7						+	4
Total number of birds in which present				3	1	2	1	1	1	3	3	7	3	4	4	1	1	4	1	2	4	9
Total number of fish recognisable in birds examined				9	1	2	1	1	5	4	31	17	11	7	12	1	9	6	1	2	15	44

+ signifies "present."

River Lynher on January 5th, 1933, had unidentifiable flatfish fragments in its stomach.

The accompanying diagram, Figure 1, shows the approximate percentage numerical composition of the total food eaten by the Shags examined—excluding Clupeoid Britt and a few Crustacea. A single glance at this diagram will immediately reveal how insignificant is the number of flatfish and other food-fishes which enter into the diet of Shags and how largely these birds depend upon Sand Eels and other non-marketable species for their sustenance. During periods of stormy weather, however, some of them are often compelled to forsake their normal feeding-grounds and driven to seek their prey in the more sheltered waters of harbours and river estuaries where they occasionally devour flatfish. But even in these circumstances they do not appear to do so if they can find other food. Eleven birds driven inland in this way have been shot and found to contain recognisable food, but only three of them had any trace of flatfish in their stomachs. The very last Shag examined was shot in the River Lynher at the same time and in the same place as a Cormorant. The two birds had obviously been feeding together, for both their stomachs contained many Gobies—the Shag 35 and the Cormorant 26 of them. But whereas the Shag's stomach contained only Gobies the Cormorant had eaten in addition no less than 15 small flatfish.*

IV. FOOD OF CORMORANTS (*Phalacrocorax carbo carbo* (L.)).

Twenty-nine Cormorants have been secured in the course of this investigation.† Twenty-seven of them contained recognisable food, the examination of which has yielded very definite and interesting results quite different from those obtained from the Shags. In Table III these results are shown in detail for each bird.

From this table it will be seen that 16 out of the 27 birds containing food material have been obtained from river estuaries as the result of the special efforts made to secure birds from such localities. Of these no less than 14 birds were found to have eaten one or more flatfish. It is clear, therefore, that flatfish form a large proportion of the food of Cormorants when they are feeding in the shallow waters of estuaries or harbours, which are their normal hunting-grounds. When foraging farther at sea, as they occasionally do, Cormorants devour the same kinds of fishes as Shags—with the exception of Sand Eels, which they appear seldom to capture; at any rate, not one of all the Cormorants examined had any trace of a Sand Eel in its stomach.

Figure 2 shows in graphic form the percentage numerical proportions

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* See Table III.

† See p. 280.

of marketable and non-marketable fishes eaten by all the Cormorants examined in the course of this investigation. Flatfish formed nearly 40 per cent of the total. Other marketable species, including Clupeoids, formed roughly 10 per cent of the fishes devoured by them. Thus *very nearly half of the fishes eaten by these birds were marketable species of greater or less value.*

V. Discussion of Results.

Because of their habit of frequenting harbours and river estuaries Cormorants are observed hunting their prey much more frequently than are Shags. There is therefore little doubt that the complaints which from time to time have been made by Cornish fishermen concerning the killing of marketable fishes, and flatfishes in particular, by Shags and Cormorants have been based almost entirely upon observations of the depredations of Cormorants alone. A grave and expensive mistake was made, therefore, in considering Shags

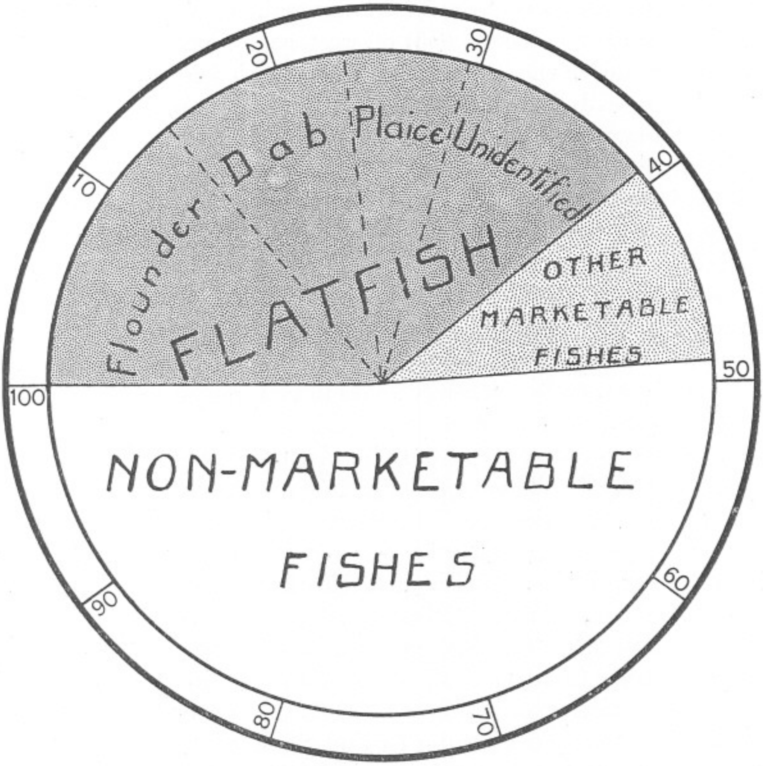

Fig. 2.—Diagrammatic representation of the percentage numerical composition of the food of Cormorants (Crustaceans omitted).

equally destructive. This error arose probably because Shags and Cormorants are very similar in appearance, and fishermen do not as a rule trouble to distinguish between them. It is just possible, however, that the published results of previous workers (applicable to other localities but not to this) had reached the fishermen or their Committee and helped to produce or confirm this erroneous belief. Witherby (**3**, p. 403), for example, states that the food of the Shag consists almost entirely of sea fish such as Plaice, Sillock, Wrasse, Eels (up to 2 ft. long), Herring, Garfish, Father-lasher, etc., and exceptionally also of crustacea and mollusca (Mytilus). Collinge (**1**, p. 220) examined the stomachs of 28 Shags,* 26 of which contained food material. He found that "excepting for a small percentage† (2·55) of crustacean remains and 1 per cent of algæ, the whole of the stomachs were filled with fish, cod, haddock, and whiting being easily identified." In a table (*op. cit.*, p. 221) showing the "monthly percentages of the principal food items of the adult Shag" the diet is recorded as varying between a maximum of 100 per cent food-fishes in November, December, and January and a minimum of 90·50 per cent in June, with an average of 96·45 per cent of food fishes over the whole year. These results are completely at variance with those obtained in the present investigation. The explanation of this disagreement may be that the staple food of Shags varies greatly in different localities, according to the different kinds of food organisms available. Haddocks, for example, are rarely found in this area, so they cannot form any part of the diet of sea-birds in Cornish waters.

With regard to the food of Cormorants, the statements of Witherby (*op. cit.*, p. 400) and Collinge (*op. cit.*, p. 218) and the results of this investigation are more in agreement. Witherby states that their diet consists almost entirely of fish, both fresh and salt water, including Trout, Eel, Pike, Flounder, Plaice, Sand-launce, 15-spined Stickleback, Haddock, young of Coal-fish, Mullet, and Conger (up to 2½ ft.), and that crustacea (including crabs and Pandalus) are occasionally taken. The absence of fresh-water fishes from the food of the birds examined in the course of the present investigation is due to the fact that no birds were obtained or sought from purely fresh-water feeding grounds.

As the result of the examination of 43 Cormorants with full stomachs, Collinge found that their largest food item consisted of food-fishes—95·80 per cent. Where identifiable they were found to be Cod, Haddock, and Whiting. Crustacean remains, believed by the author to be derived from the stomachs of the fishes eaten,‡ were found in 4 stomachs and represented 0·75 per cent of the total food. Miscellaneous unidentifiable matter

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* Presumably obtained from various parts of the country, although no details are given.

† See footnote, p. 292.

‡ Several of the stomachs examined by the present writer contained Shrimps, Prawns, etc., which could not possibly have been derived from the stomachs of fishes eaten.

amounting to 2·31 per cent, and 1·14 per cent of algæ were also found. Collinge therefore concludes that "if we regard a bird that feeds upon food-fishes as injurious, then there is nothing to be said in favour of the Cormorant." The evidence obtained in this area does not wholly support this downright condemnation of the birds. Around the shores of Cornwall Cormorants feed to no inconsiderable extent upon non-marketable species as well as food fishes.

Perhaps the most striking difference between the food of the Cormorants examined by Collinge and those at present under discussion is the very much greater range of fish species which had been eaten by the latter (*vide* Table III, p. 284).

As Cormorants are observed hunting their prey much more frequently than are Shags, a false impression of the magnitude of the Cormorant population—and therefore of the damage that they do*—is likely to be acquired. It is necessary to point out, therefore, that Cormorants are much less numerous than Shags in both Devon and Cornwall. My colleague, Mr. G. M. Spooner, M.A., an active member of the Devon Bird-watching and Preservation Society, informs me that in South Devon, between Plymouth and Start Point, a careful census has shown that Shags are roughly 10 times as numerous as Cormorants. Although no actual census of the Shag and Cormorant populations in Cornwall has been made, it seems probable that the proportion of Cormorants in that county is even smaller than in Devon. In the whole of Cornwall (excluding the Scilly Isles) there are probably not more than one thousand Cormorants as compared with from 10 to 15 thousand Shags.

VI. ACKNOWLEDGMENTS.

I have much pleasure in recording indebtedness to my colleagues, Messrs. E. Ford and G. M. Spooner, for coming to my aid on several occasions when pressure of work made it difficult for me to deal expeditiously with consignments of birds.

VII. SUMMARY.

1. 188 Shags and 27 Cormorants, which had been feeding around the shores of Cornwall and whose stomachs contained identifiable food organisms, have been examined.

2. The Shags were found to have been feeding principally upon Sand Eels (Ammodytes spp.), and other non-marketable fishes.

3. The proportion of flatfishes and other economic species which had been devoured by the Shags was negligible.

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* Still another factor operates to convey an exaggerated impression of their depredations among flatfish. Because of their shape, flats are difficult fishes to swallow. A bird's efforts to dispose of a large individual, therefore, often attracts the attention of onlookers, whereas ordinary round fishes are swallowed too quickly and easily to be seen and recognised except on very rare occasions.

4. During the winter months Clupeoids (Sprats, Anchovies, etc.) were included in their diet.

5. The Cormorants had been feeding largely upon flatfish and other estuarine food-fishes.

6. Cormorants, which are frequenters of more or less enclosed waters, are much less numerous than Shags in both Cornwall and Devon.

VIII. LITERATURE CITED.

1. Collinge, W. E. The Food of Some British Wild Birds, 2nd edition. York, 1924–27.

2. Cornwall Sea Fisheries Committee: Minutes of Meetings. (*a*) 30th August, 1911; (*b*) 29th November, 1911; (*c*) 29th May, 1912; (*d*) 27th August, 1913; (*e*) 26th May, 1915; (*f*) 24th November, 1915; (*g*) 30th May, 1923; (*h*) 23rd September, 1925; (*j*) 18th December, 1929.

3. Witherby, H. F. A Practical Handbook of British Birds, Vol. II. London, 1924.

IX. APPENDIX I.

As the food consumed by Shags and Cormorants in this area has been found to differ greatly in important respects, it will be useful here to tabulate the main features by which these birds are distinguished.

Cormorant.	Shag.
1. Body plumage bronze-brown and black (winter and summer).	Body plumage greenish black, the green gloss being less pronounced in winter than in summer but always present.
2. Sides of head and chin brownish white (colour produced by white feathers tipped with brown); in summer, pure white, the feathers having no brown edges.	Chin and round base of lower mandible only, may have varying amounts of white to brownish white; in summer, whole of chin and throat glossy green without any trace of white or brown.
3. In summer, large patch of white feathers at base of thigh.	Never has any white on thigh.
4. Has 14 tail feathers.*	Has 12 tail feathers.*
5. Overall length of adult bird usually between 33 and 38 inches.	Overall length of adult bird usually between 25 and 30 inches.
6. Weight of adult bird usually between $5\frac{1}{2}$ and $8\frac{1}{2}$ pounds.	Weight of adult bird usually between $3\frac{1}{2}$ and 5 pounds.
7. Frequents harbours, estuaries, and tidal rivers, or even inland lochs and reservoirs.	Entirely marine, frequenting open, exposed, and usually rocky sea-coasts. Occasionally is found feeding in sheltered waters when driven in from its usual haunts by stormy weather.

* These numbers are not absolutely constant.

In the field the Shag can be distinguished from the Cormorant by its noticeably smaller size, greenish black plumage, and smaller amount of white around the chin and neck. In breeding dress the Cormorant can readily be identified by the conspicuous patch of white feathers at the base of the thigh.

The immature birds are less easy to distinguish except by size. The breast and abdomen of the young Cormorant may, however, be dull white mottled with brown. The breast of the immature Shag is never white.

The Cormorant swims with its bill pointed upwards and when diving usually submerges its head and glides under water with scarcely a ripple. The Shag, on the other hand, often springs quite clear of the water in diving.*

X. APPENDIX II.

Collinge (*op. cit.*, p. 31) expresses the hope that in all future investigations into the food of wild birds the " volumetric or percentage by bulk " method of recording the stomach contents will be employed rather than any of the various modifications of the numerical system.† He urges the adoption of the former method because he is convinced of " its superiority and greater scientific accuracy over any other."

In the opinion of the present writer this conviction can be justified only when applied to the stomach contents of birds whose food consists of vegetable products either wholly or in part, and where the economic values of both plant and animal food materials have to be assessed and balanced against each other. According to Collinge (*op. cit.*, p. 27), however, " if we say that a bird's stomach contains sixty aphids and six bees the idea furnished is a ratio of 60 to 6, but if computed by the percentage of bulk the ratio would be more correctly stated by the figures 3 to 28 of the total food contents of the stomach," and this author believes the second expression to be much the more valuable for the purpose of assessing the usefulness or otherwise of the bird in question. In reaching this conclusion he has failed to take into consideration the fact that the sizes of organisms seldom or never bear any relation to their activities, whether beneficial or harmful, or to their marketable value, either actual or potential. In the present investigation, for example, one Cormorant was found to have eaten 15 small flatfishes between 5 and 10 cm. in length. The combined volume of all these fishes was less than that of a single fully grown adult. But they would have produced 15 adult marketable fishes had they been allowed to live. By destroying these young individuals, therefore, this particular bird had done quite as much *potential* harm to the fish stock as if it had eaten an equal number—*or over* 20 *times the volume*—of adults.

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* See also Witherby's " Handbook."

† See p. 280.

A further criticism levelled against the numerical method is that it cannot successfully be applied to finely comminuted animal or vegetable matter (**1**, p. 29). In my experience this applies also to the volumetric method, at any rate when dealing with fish-eating birds. Fragmentary food remains which are so far disintegrated as to make it impossible to ascertain from how many individuals they were derived are seldom or never in such a state that they can be accurately identified. To determine their volume, therefore, even when this may be possible with any degree of accuracy,* would add but little to the value of the record.

Again, a bird whose stomach contained, say, three tails of *Gobius flavescens* would, in the numerical computation, be recorded—and accurately so—as having eaten three of these fish. By volumetric computation, if the stomach contained any other food, the proportion of Goby would work out at considerably less than would have been produced by a single whole individual. If, however, no food were present, the percentage proportion by bulk would have to be recorded as 100 *per cent Goby* whether the stomach contained only one recognisable fragment or whether it was packed with a large number of the fish. A " volumetric " or " proportion by bulk " expression of the results in such instances can have no real meaning. Moreover, if such separate readings be taken into consideration when calculating the proportions of the total food eaten by all the birds examined they will produce, or tend to produce, totally false final values. If, on the other hand, in order to eliminate this grave source of error, all stomachs containing only one kind of food organism are disregarded, the final computations will be equally unreliable and misleading.

Ideally, of course, a combination of all possible methods of exact computation is desirable. In the present investigation this would have been quite impracticable. What was believed to be the most satisfactory of the various methods available was therefore chosen.

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* The accuracy obtainable is never such as to justify expressing the results correct to two places of decimals (see p. 288).

The Magnesium and other Inorganic Constituents of some Marine Invertebrates.

By

R. A. McCance and H. L. Shipp,
Biochemical Laboratory, King's College Hospital, London.

With 1 Figure in the Text.

The livers of some of the marine invertebrates are well known to contain unusually high concentrations of certain of the heavy metals, such as iron, which are normally found in smaller amounts throughout the animal kingdom. Other invertebrate animals contain relatively high concentrations of metals which are not usually found, or only in the merest traces, in the higher animals. The present paper describes what is believed to be a new observation not quite falling into either category.

In the course of some work on the organic and inorganic constituents of food the following marine invertebrates were subjected to analysis: Oysters (*Ostrea edulis*), Scallops (*Pecten maximus*), Winkles (*Littorina littorea*), Mussels (*Mytilus edulis*), and Whelks (*Buccinum undatum*). These were all analysed cooked, except the Mussels and Oysters, and nothing very striking was observed in their inorganic 'make up' except in the case of the Winkles and the Whelks. These animals were found to contain 414 and 160 mg. of magnesium respectively per 100 g. of wet cooked flesh. These figures are the mean of several analyses. In mammals, birds and fish the magnesium was found to lie between 10 and 35 mg. per 100 g. of live weight and to vary to some extent with the organ. Muscular tissue, for example, contained 22 to 35 mg. per 100 g. and mammalian kidney 16 mg. per 100 g., while eggs and fish roes (male and female) contained only 10 mg. per 100 g. The $\frac{\text{Na}}{\text{Mg}}$ ratios in fish and mammalian muscle lay between $\frac{3}{1}$ and $\frac{5{\cdot}5}{1}$.

The detection of these abnormal magnesium concentrations in the winkles and the whelks was considered of sufficient biological interest to warrant further investigation. With the assistance of the Director and Members of the Marine Biological Association's Laboratory at Plymouth, *Cardium edule, Pecten maximus*, and *Littorina littorea* were obtained in the raw state and the individual organs analysed. Water, sodium, potassium, calcium, magnesium and iron were determined. A complete survey of the methods used is in course of publication. (McCance & Shipp, 1933.) A brief note on the magnesium technique is, however, necessary. After incineration of the material and extraction with hydrochloric acid the solution was neutralised to phenol red, made just acid with acetic acid and the calcium removed as the oxalate. The magnesium was precipitated from the calcium free solution as magnesium ammonium phosphate, and the phosphate in the precipitate determined by Brigg's (1922) method.

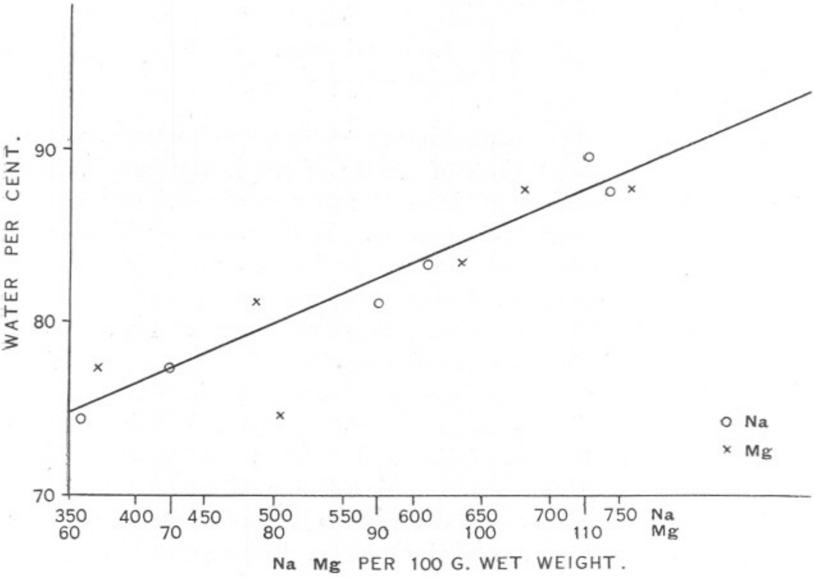

FIG. 1.—The relation between the water and the sodium-magnesium contents of the organs of *Pecten maximus*.

To ensure that the whole of the phosphate was present as the magnesium salt and not in combination with some quite unexpected metal, a large amount of the precipitate from the winkles was collected and weighed after ignition to the pyrophosphate. The weight of phosphate in the ignited salt corresponded with the theoretical amount required for magnesium pyrophosphate, and no metal other than magnesium was found when the precipitate was dissolved and subjected to qualitative analysis.

The results obtained may be found in Table I (p. 296).

The points to which we wish to draw attention are :—

(1) The very high concentration of magnesium in *Littorina littorea*. The $\frac{\text{Na}}{\text{Mg}}$ ratio in these animals is approximately $\frac{1}{1}$. The element appears to

be distributed throughout all the organs in amounts which would be fatal to higher animals. The physiological significance of this is at present quite obscure.

(2) The high but rather variable magnesium in the different organs of Cardium and Pecten. In Pecten $\frac{\text{Na}}{\text{Mg}}$ is roughly $\frac{6{\cdot}5}{1}$ and in Cardium $\frac{4{\cdot}3}{1}$. It will be observed that the magnesium, sodium and water tend to vary together. The relationship in Pecten is demonstrated by Figure 1.

(3) The low concentration of magnesium in mussels and oysters. The $\frac{\text{Na}}{\text{Mg}}$ ratios are about $\frac{14}{1}$.

(4) The potassium concentration in the various organs of these invertebrates runs parallel not with the water but with the dry matter. The potassium, as might have been expected, seems to form an integral part of the protoplasm and only small variations are compatible with life.

(5) The variations in iron from one animal to another and from one organ to another are striking and their importance unknown.

SUMMARY.

The sodium, potassium, calcium, magnesium and iron of a number of marine invertebrates have been determined and some of the findings are very briefly discussed.

The common winkle *Littorina littorea* contains 330–510 mg. of magnesium per 100 g. of live weight. All the organs appear to contain these high concentrations. Boiled specimens of whelks contained about 160 mg. of magnesium per 100 g.

We should like to thank the Director and Staff of the Laboratory of the Marine Biological Association for their assistance. R. A. McC. has held a part-time grant and H. L. S. a full time grant from the Medical Research Council during this work.

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McCance, R. A., and Shipp, H. L. 1933. Medical Research Council Special Report Series (in press).

TABLE I

Animal.	Organ.	Water %	Na.	K.	Ca.	Mg.	Fe.
			mg. per 100 g. of live wet weight.				
Mytilus edulis	Whole		290	315	90	23	5·8
Ostrea edulis	Whole		650	258	185	41	6·0
Littorina littorea	Foot	64·6	425	375	265	346	17·8
	Mantle	70·9	415	277	1266	334	18·7
	Gonad	65·2	342	390	168	460	26·8
	Stomach and Liver	67·7	438	473	550	507	33·6
Pecten maximus	Foot	83·6	612	250	42	97	2·8
	Mantle	87·9	742	148	52	104	0·9
	Muscle	77·4	424	387	26	63	1·8
	Gonad	81·1	566	283	38	78	5·8
	Gills	89·8	726	143	54	111	1·7
	Stomach	74·4	351	262	118	80	11·2
Cardium edule	Foot	77·4	510	305	41	93	15·5
	Mantle	84·5	610	180	180	117	17·5
	Muscle	73·5	482	300	70	84	3·9
	Gills	83·5	294	239	87	106	7·3
	Stomach, Liver, etc.	71·1	241	302	145	94	8·1

Abnormal Eyes in Wild *Gammarus zaddachi* Sexton.

By

R. Bassindale, M.Sc.

With 2 Figures in the Text.

During the course of a biological survey of the Tay Estuary collections of the species of Amphipoda found in the tidal zone were made from Bridge of Earn, near the limit of tidal waters in the River Earn, down to the confluence of the Rivers Earn and Tay, and thence to Tayport, near the sea. Between Newburgh and Bridge of Earn (from 23 to 32 miles from the sea) the only Amphipoda recorded were 198 specimens of Gammarus and one specimen of *Melita palmata* (Mont.). The water in this part of the Estuary, although tidal, is for the most part fresh, attaining at Newburgh at high tide an average salinity of only 3 or 4 gm. per 1000 gm.

Four collecting stations were investigated in the zone described and all the Gammarus were identified by Mrs. Sexton as *G. zaddachi* Sexton, a brackish-water species described by Mrs. Sexton herself (**1**). Of these 198 specimens, four were observed to have abnormal eyes. Although this condition has been previously described from a Laboratory strain of *G. chevreuxi* (**2**) this is the first occasion on which wild specimens have been recorded with similar abnormalities.

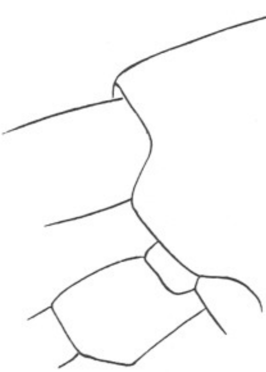

Fig. 1.

Fig. 2.

Of the four individuals, No. 1 was taken at the highest station at Bridge of Earn, and No. 2 was found at the second station some 3 miles lower down the Estuary. Nos. 3 and 4 both occurred at Newburgh, the lowest station at which *G. zaddachi* was found.

Specimen No. 1 is small, measuring about 5 mm. along the dorsal line. Both eyes are irregular, the left being rounded instead of reniform with the margin indented : the right eye is roughly triangular, very similar in shape to the one figured by Sexton (**2**) (Text-fig. 7, p. 356).

Specimen No. 2 is slightly larger (*ca* 7½ mm.) and is remarkable in having only one eye developed—on the right side—practically normal in size and shape. There is no trace of an eye on the left side (Fig. 1).

Specimen No. 3 is the largest (15 mm.) and has suffered damage after capture. The eyes, however, show distinct irregularities in size (the right being much smaller than the left), in shape and in the arrangement of the ommatidea.

Specimen No. 4 (6½ mm.). The head is much narrower in proportion to the body measurements than in the normal animal. The right eye is degenerate, closely resembling the albino mutation of *G. chevreuxi*, and consists of a few scattered colourless cones (Fig. 2). The left eye was evidently large and pigmented in life, but has suffered damage and the exact details cannot be determined.

SUMMARY.

Of 198 specimens of *Gammarus zaddachi* collected in the Estuaries of the Rivers Earn and Tay four individuals had abnormal eyes. This is the first record of abnormal eyes in wild specimens of a Gammarus species, although Laboratory strains of *G. chevreuxi* have developed them.

The investigation described in this paper was carried out as part of the programme of the Water Pollution Research Board of the Department of Scientific and Industrial Research, and is published by permission of the Department. My thanks are due to Dr. E. J. Allen and to Mrs. E. W. Sexton for their assistance in preparing the paper.

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2. Sexton, E. W. Degeneration and loss of the eye in the Amphipod *Gammarus chevreuxi* Sexton, Part I. Journ. Mar. Biol. Assoc., N.S., Vol. XVIII, No. 1, 1932, p. 355.

Notes on Some Copepoda from Plymouth.

By

Robert Gurney.

With 4 Figures in the Text.

Tisbe elongata A. Scott. Harpacticid inhabiting the Gill Chamber of the Lobster.

When examining the gills of a lobster for specimens of Nicothoe large numbers of copepods were found which, colourless and slender in form, had the sluggish and rather aimless movements which one would expect from a commensal removed from its natural habitat. It was somewhat of a surprise to find that they all belonged to a species already described —*Tisbe elongata* A. Scott. Scott obtained a few specimens from mud collected on mussel beds between Heysham and Morecambe. It appears, then, that we have here a species which is capable of free life, but its abundance, in all stages of growth, in the gill chamber of a lobster, proves that it is also to be considered a semi-parasite.

The occurrence is of some interest, as examples of parasitism are rare among Harpacticids. The closest parallel is the record of Kröyer of *Machairopus hippolytes* (Kröyer) in the gill chamber of *Spirontocaris grœnlandica* Fabr. Hansen* supposed that this occurrence was accidental; but it is probable that this is also a case of semi-parasitism.

Aurivillius has recorded the finding of *Tisbe furcata* in the Ascidian *Molgula ampulloides*, but this was no doubt simply accidental, as *T. furcata* is a ubiquitous littoral species. The only Harpacticid actually becoming a fixed and more or less degenerate parasite is also a member of the Tisbidæ—*Cholidya polypi* Farran parasitic on Octopus. Other more or less parasitic species are :—

Balænophilus unisetis Aurivillius, on Whales. *Sunaristes paguri* Hesse, in shells of Hermit Crabs. *Cancrincola jamaicensis* Wilson, on gills of the crab Cardisoma. *Cancrincola wilsoni* Pearse, on gills of the crab Sesarma. *Nitocrameira bdelluræ* Liddell, on gills of Limulus. *Nitocra divaricata* Chappuis, on gills of Potamobius. *Tisbe wilsoni* Seiwell, in the Ascidian Amaroucium.

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* 1923, *Ingolf Exped.*, iii, p. 74.

LARVAL STAGES OF *Misophria pallida* BOECK.

The systematic position of Misophria is still a matter of complete uncertainty, and it was to be expected that its nauplius, if it could be found, might throw light on the subject. At Plymouth *M. pallida* is extremely difficult to obtain, but can be found by diligent search of dredgings from the Sound. During two visits, however, none were to be found with eggs, and it was only on the third attempt, in July 1932, that egg-bearing females were taken and the eggs successfully hatched.

The female bears 2–4 large eggs, loosely attached to the genital somite, but not, apparently, enclosed in a definite egg-sac, and the eggs seem to be carried for a considerable time before hatching. Unfortunately the nauplius, after all, provides no definite evidence for the systematic position of the adult. It is without eye or mouth, the body filled with yellow yolk, and the appendages naturally without any masticatory processes (Fig. 1). The antennæ and mandibles are large, with 4-segmented exopods, and beneath the cuticle can be seen rudiments of legs 1 and 2. Within about a day it moults to the 1st copepodid stage which has the same habit as the adult of gliding movement on the bottom. The appendages, though not fully developed, are quite of the adult plan (Fig. 2).

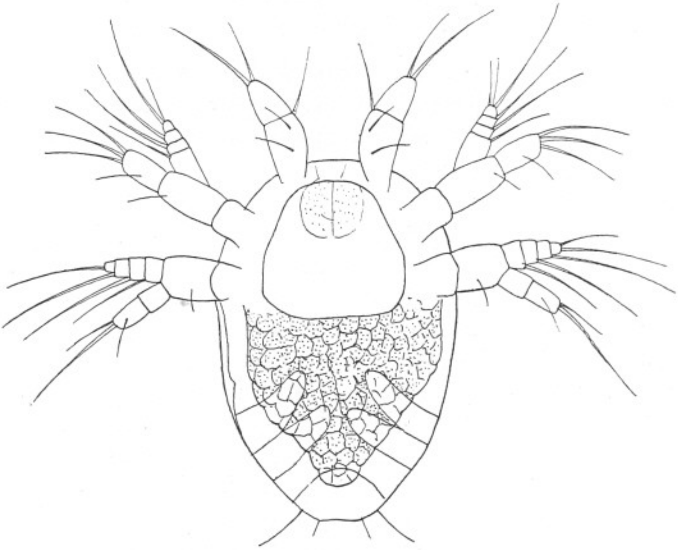

FIG. 1.—Nauplius of *Misophria pallida*.

What is of interest in this life-history is the almost complete cutting out of the nauplius stages. No Calanoid and no Harpacticid is known with a yolk-filled egg of this type and a non-feeding nauplius, a point which may be regarded as some evidence against relation to either of these groups. Among the Cyclopoida also nothing of the kind is known, except among the semi-parasites such as the Ascomyzontidæ, and there cannot be any question of any relation to them. The nauplius may be said to resemble much more closely the Cyclopoid type than that of the Calanoids, and to be quite unlike that of such Harpacticids as are known, and to

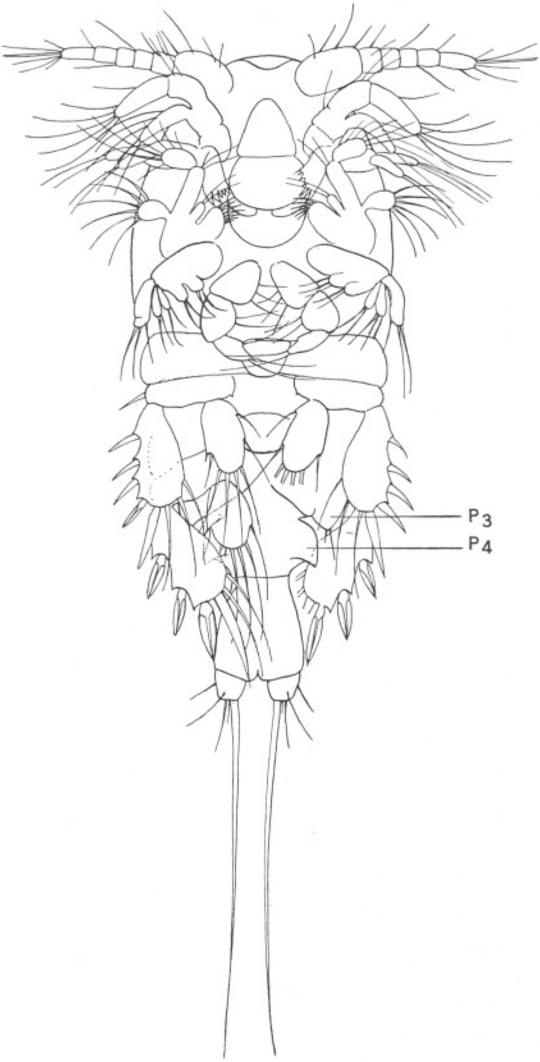

FIG. 2.—*Misophria pallida*, first Copepodid stage.

this very small extent relation to the Cyclopoida is suggested. The copepodid provides no useful evidence. The same plan in stage I is universal among Copepods, and the appendages already have the characters of the adult. If any conclusion can be drawn from the meagre facts, it seems to be that, in its larval history, as in its adult structure, Misophria holds an isolated place, which can best be expressed by regarding it as the type of a separate Order Misophrioida.

FIG. 3.—Nauplius of *Psamathe longicauda*.

THE NAUPLIUS OF *Psamathe longicauda* PHILIPPI.

Among a number of littoral Harpacticids handed over to me by Mr. John Colman were some nauplii of *Psamathe longicauda* which proved to have a structure of unusual interest (Fig. 3). This nauplius has already been described by Brian,* but without drawing special attention to the particular point of importance, which is the modification of the whole of the upper lip into a sucker. The upper lip is a hollowed circular disc the margins of which are strengthened by radial chitinous rods and fringed

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* *I copepodi Harpacticoidi del Golfo di Genova*, 1921, p. 25.

with very delicate hairs (Fig. 4). Anteriorly there is a gap in the disc which is closed by a pair of hairy pads. This sucking disc persists through the nauplius stages, but is lost at the moult to the copepodid, in which the upper lip is not modified. So far as I know a sucker of this kind is quite unknown in all other Harpacticids. In the closely allied *Aspidiscus littoralis* there is nothing of the kind, but in this case the margin of the dorsal shield has a delicate hyaline membrane which may serve to convert the whole body into a sort of sucker. On the other hand, suckers of strikingly similar form are found on the maxillæ of the Branchiura, which are not Copepods at all, on the anterior margin of the head in some Caligidæ, and in a number of parasitic forms at the apex of the mouth cone. In this last case, however, the sucking disc is largely, or wholly, the product of the modified lower lip, and the mandibles are enclosed in the mouth cone. The closest parallel to the disc of Psamathe seems to be found in Eunicicola. According to the figures given by Sars of *E. clausi* the disc is here, as in Psamathe, entirely formed by the upper lip, and the mandible, if it exists, is behind it. It is therefore simply an organ of adhesion and not, as in Lernæopods, for example, a sucking disc for feeding purposes.

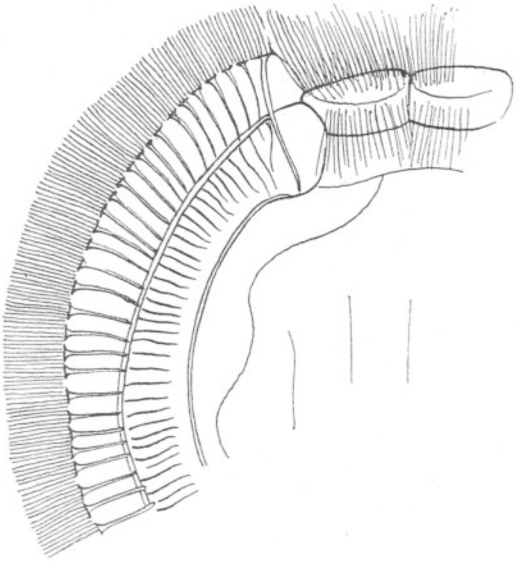

FIG. 4.—Structure of the Sucker of *Psamathe longicauda*.

THE NAUPLIUS OF NOTODELPHYS.

In his description of the nauplii of *Notodelphys agilis* and *Doropygus porcicauda** Mr. Peter Gray draws special attention to the absence of an

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* *Journ. Mar. Biol. Assoc.*, xviii, p. 519, 1933.

endopod from the mandible, which he claims to be otherwise unknown among nauplii. This is not altogether true, since an uniramous mandible is found in certain Branchiopod nauplii, but it is a remarkable feature in a Copepod. On the other hand Canu, in 1892,* gave excellent figures of the nauplii of *Notodelphys agilis* and of *Doropygus gibber*, and in both cases showed a small endopod on the mandible. I have myself seen the nauplius of *N. allmani*, and in this species (which is also figured by Canu) the endopod is quite distinct. A difference between the two species *D. porcicauda* and *D. gibber* in this respect is not impossible, but seems most unlikely, in view of the fact that an endopod is present in all the nauplii of Notodelphyids described by Canu—*Bonnierella longipes*, *Doroixys uncinata*, *Enterocola fulgens*, *Aplostoma brevicauda*, besides those mentioned above.

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* *Trav. Lab. Zool. Wimereux*, vi, 1892.

An Account of the Herring Investigations Conducted at Plymouth during the Years from 1924 to 1933.

By

E. Ford, A.R.C.Sc.,

Fisheries Naturalist at the Plymouth Laboratory.

With a Chart and 10 Figures in the Text.

CONTENTS.

INTRODUCTION.

THE Plymouth Laboratory is well situated for the study of the herring and its commercial fishery, and since the winter of 1924–25, advantage has been taken of the varied facilities for research thus afforded. From time to time reports have been published in the Journal of the Marine Biological Association as a series, entitled : " Herring Investigations at Plymouth " and these have dealt with many seemingly distinct subjects of study, including experiments with larvæ from laboratory-fertilised eggs ; studies of growth, migration and structure of young and old fish ; and accounts of the commercial operations during the winter drift-fishery at Plymouth. It has now been considered advisable to bring together the several results in one paper, in an endeavour to show their essential bearing upon the problems of the practical fishery.

The first part of the paper is a descriptive account of the actual winter fishery at Plymouth which is of sufficient commercial importance to warrant the collection of information on the essentially business matters of catching, landing and marketing. This fishery, however, no less than any other drift-net fishery, is perforce conducted under difficult conditions of uncertainty. Fishermen and merchants alike are only too well aware of the extent to which the yield is liable to fluctuate from day to day and from season to season, and their business operations are rendered even more difficult because they can neither foresee nor prepare for the circumstances, favourable or otherwise, which each new season holds in store. It will not be questioned, therefore, that if scientific enquiry can ultimately succeed in removing this uncertainty from the fishery, it will have accomplished an essentially practical service. But it may be stated with equal assurance that this practical end can only be attained through a very exhaustive study of the life-history, habits and migration of the

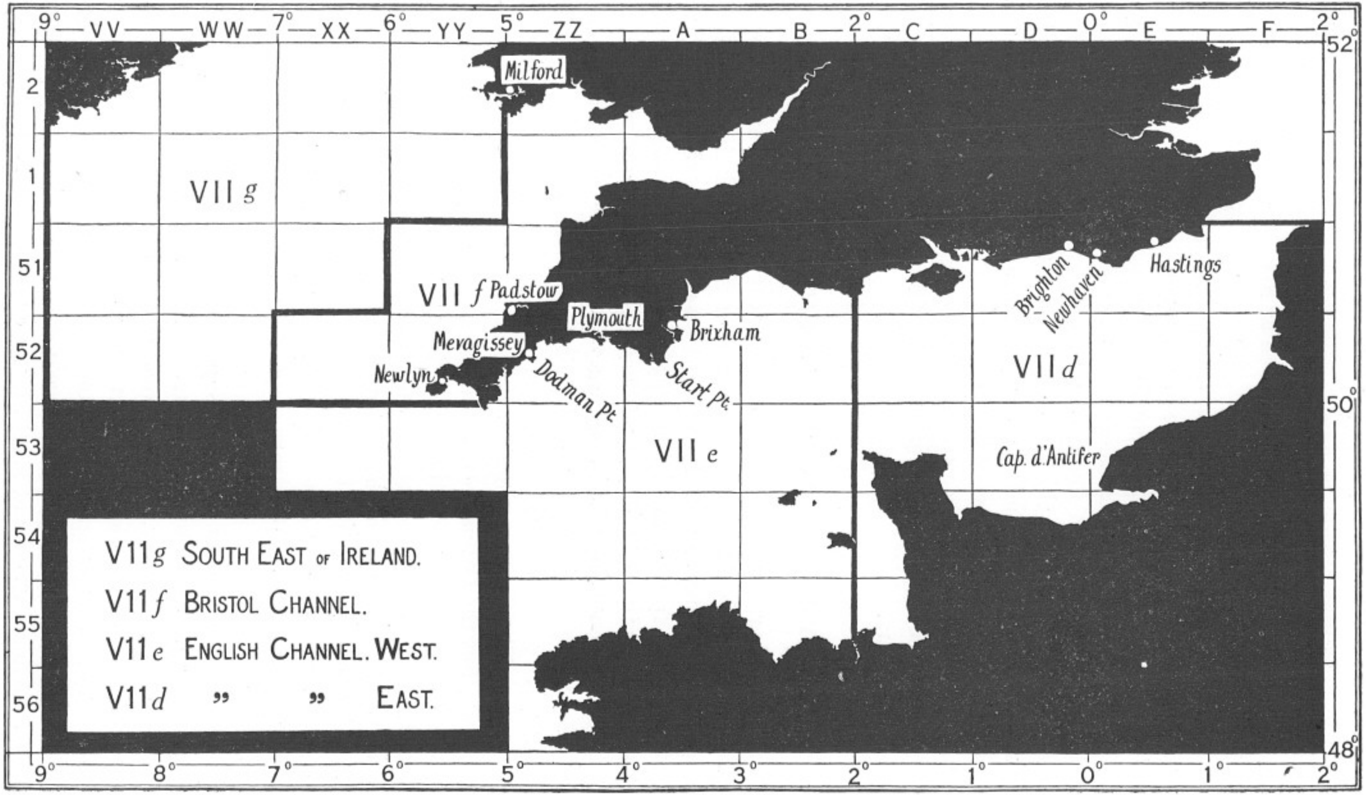

Chart showing Statistical Regions dealt with in this Paper.

herring itself. And in this study the task of the investigator is made hard because so much of the needed information has to be sought for in an indirect way. The development of this indirect technique involves a great deal of preliminary research which at first sight appears to have but little bearing upon the practical fishery, but it is none the less essential. In the pages which follow, much of the text is devoted to the nature and application of such basic investigation, and an endeavour has been made to show how the different lines of enquiry meet in the central study of the fluctuations of the fishery. With so many distinct topics to be considered, it has not been found easy to preserve full continuity from section to section, although this has been done as far as possible. For the same reason it has been found impossible to avoid technical treatment in some instances, so that the general reader may find certain sections less easy to read than others. The paper concludes with a consideration of the question of forecasting the yield of the fishery from information gathered in preceding years.

THE PLYMOUTH WINTER DRIFT-NET FISHERY.

From November until the end of January, Sutton Harbour at Plymouth functions as the base for a large number of drifters which fish the neighbouring inshore waters for herrings. The season opens with the arrival of motor drifters from Cornish ports, but as soon as daily results prove sufficiently attractive (usually at the beginning of December) steamers from Lowestoft and Yarmouth augment the fleet. At the height of the season there may be between two and three hundred drifters at work. Circumstances permitting, they fish each night and land their catches in the morning. The steamers work continuously throughout the seven days of the week, but the Cornishmen do not land on Sundays.

Sutton Harbour and the adjoining fishmarket are the property of the Sutton Harbour Improvement Company, whose officers control the movement of vessels to and from the fish quay and supervise market proceedings. Catches are sold by public auction on the evidence of small samples exposed on a tray in front of the auctioneer's rostrum. Fishermen bring their samples and queue up in front of the rostrum awaiting their turn for a sale.

The herrings are bought chiefly to supply a fresh-fish market either at home or abroad. Home buyers arrange to have their barrels and boxes stacked alongside the quay, so that purchases can be swung out of the ship in quarter-cran baskets and shot direct into the containers in which they are to be forwarded to their destination. The quantity taken out of the ship is checked basket by basket, and ice is strewn over the fish as packing proceeds. When packed and labelled, the consignment is conveyed by lorry to the railhead at one of the Plymouth stations. Herrings bought by the "Klondyke" trade for export to the Continent are not unloaded at the quayside but conveyed direct to the carrier-vessel by the drifters themselves.

QUANTITY AND VALUE OF FISH LANDED.

The quantity and value of the fish landed at Plymouth vary from season to season and from day to day. The extent of these variations is considered below.

Seasonal Variation.

The Ministry of Agriculture and Fisheries collects statistics of the landings at Plymouth, and Table I shows the weight, value and average price of herrings landed during the months of December and January in the course of the past quarter of a century :—

TABLE I.

Season (Dec.–Jan.)	Total Weight Landed. Cwt.	Total Value. £		Average Price per 1 Cwt. s.	d.
1906–07	32,913	8,040		4	11
1907–08	23,957	6,583		5	6
1908–09	4,257	2,521		11	10
1909–10	52,544	16,105		6	1
1910–11	37,741	17,048		9	0
1911–12	39,167	18,158		9	3
1912–13	8,171	3,594		8	10
1913–14	28,886	13,933		9	8
1914–15	7,585	6,021	War Period.	15	11
1915–16	11,582	13,062		22	7
1916–17	24,293	35,901		29	6
1917–18	38,108	88,453		46	5
1918–19	8,624	15,160		35	2
1919–20	29,425	40,045		27	3
1920–21	40,263	42,752		21	3
1921–22	16,922	14,792		17	6
1922–23	54,839	26,326		9	8
1923–24	98,684	65,290		13	3
1924–25	113,585	109,294		19	3
1925–26	105,643	89,334		16	11
1926–27	63,138	47,539		15	1
1927–28	122,419	65,451		10	8
1928–29	75,104	44,475		11	10
1929–30	86,955	63,569		14	7
1930–31	94,811	52,973		11	2
1931–32	45,865 + 40 by trawl	37,620*		16	5
1932–33	79,532 + 499 by trawl	41,025*		10	3

The figures show that the yield varies considerably from season to season. Even so, greater quantities have been landed since the war than before it, and the seasonal average price is still above that of 1913–14.

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* Value inclusive of trawled fish.

Daily Variation.

Information concerning daily variation in yield is obtainable from the daily returns of which the seasonal statistics given in Table I are the aggregate. It is found that there are many days in each season when the total weight of fish landed is comparatively small. For example, Table II is an analysis of daily statistics for the past five seasons :—

TABLE II.

		No. of days on which landings were of the following weights (cwt.)										
Season (Dec. Jan.)	Total No. of Days.	Less than 1000	1000 to 1999	2000 to 2999	3000 to 3999	4000 to 4999	5000 to 5999	6000 to 6999	7000 to 7999	8000 to 8999	10000 to 10999	13000 to 13999
1928–29	54	35	6	4	3	3	–	1	–	2	–	–
1929–30	54	30	15	3	–	–	2	–	1	1	1	1
1930–31	60	31	10	6	6	4	3	–	–	–	–	–
1931–32	60	44	11	2	1	2	–	–	–	–	–	–
1932–33	56	33	11	2	5	2	1	–	1	–	1	–

It is seen that on considerably more than half the total number of days when landings were made, the amount landed was less than 1,000 cwt. Indeed, further analysis of statistics shows that the daily weight was actually less than 500 cwt. on 26, 21, 22, 34 and 26 days respectively, during the five seasons. This being so, it is hardly surprising that the comparatively occasional large daily landings should tend to sell at glut prices. The figures for 1929–30 provide a good illustration. During December and January, a total of 86,955 cwt. was landed. Of this amount, 36,502 cwt. was landed in 48 daily lots of less than 3,000 cwt., and sold for £41,351. This represents an average price of 22s. 8d. per 1 cwt. for approximately 42 per cent of the season's total catch. The remaining 58 per cent., or 50,453 cwt., was landed in 6 lots only and realised £22,218, representing an average price of 8s. 10d. Of these 6 lots, 3 were on the consecutive days, December 17th, 18th and 19th, when a total of no less than 30,900 cwt. was landed and sold at an average price of 6s. 4d.

A second illustration is provided by the statistics for the period, December 10th to 16th, 1928 :—

Date. 1928. Dec.	Weight Landed. Cwt.	Total Value. £	Price per 1 Cwt. s.	d.
10	222	564	50	10
11	7	10	28	7
12	1,465	1,465	20	0
13	8,050	4,600	11	5
14	8,050	2,926	7	3
15	6,030	1,785	5	11
16	3,875	1,525	7	10

From these two illustrations it is clear that only limited significance can be attached to the seasonable average price per 1 cwt., obtained by dividing the total value for the season by the total weight sold. This average tends to mask the relation which exists between the weight of fish landed in any one day and the price which it commands.

The Intensity of Fishing.

One of the causes of fluctuation in yield is that the intensity of fishing varies. The number of fishing vessels which participate in the fishery is not constant from season to season, and conditions of weather often seriously curtail the activities of those which do come. These and other factors affecting the intensity of fishing will now be considered.

Changes in Fishing Power.

The composition of the fishing fleet in each season since 1918–19 is shown in Table III, the data being supplied by Mr. W. G. Nelder, Manager of the Sutton Harbour Improvement Company, Plymouth :—

TABLE III.

Season.	Number of East Country Steamers.	Number of West Country (Cornish) Motor Drifters.	Number of Local Motor Drifters.
1918–19	33	139	Average No. is 10, some years only 3.
1919–20	30	156	
1920–21	26	182	
1921–22	31	155	
1922–23	68	142	
1923–24	59	161	
1924–25	86	176	
1925–26	153	158	
1926–27	129	169	
1927–28	77	145	25
1928–29	81	170	12
1929–30	54	169	12
1930–31	75	177	14
1931–32	52	170	20
1932–33	85	161	12

Dealing first with the motor drifters (mostly Cornish vessels), it is seen that the number has been well maintained throughout all the post-war years. During the fifteen seasons from 1918–19 to 1932–33, they landed an aggregate weight of 400,355 cwt. of herring as compared with the corresponding aggregate of 635,226 cwt. landed by the steamers. Taking into account the number of motor drifters in comparison with that of the steamers, it is estimated that the steam fishery has been from four to five times as efficient as the motor fleet, so far as weight per fishing unit is concerned.

The number of steamers has not been so steady. The large number of arrivals in 1925–26 and 1926–27, for example, is in marked contrast with those of the seasons from 1929–30 to 1931–32. It is of interest to enquire into the reasons for this irregularity in the number of steamers which form so important a section of the fishing power. Data show that there is a rise in the number of steamers in the season which follows one of good fishing. Thus, fishing was good in 1924–25 when 86 steamers came, and in the following season 153 steamers made the trip. Similarly, the good fishing of 1929–30 was followed by the arrival of a larger number of steamers in 1930–31. But the reverse seems to hold good, the number of steamers becoming reduced in the season following poor fishing. In 1925–26 fishing was bad, so that fewer steamers came in 1926–27. It was again poor, and the number of steamers was still less in 1927–28.

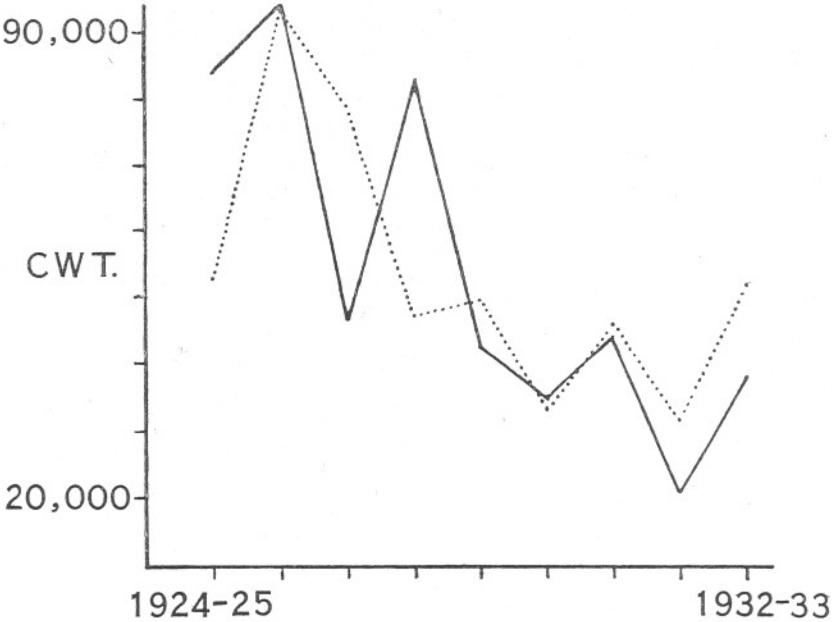

FIG. 1.—Total weight of herrings landed at Plymouth in each season from 1924–25 to 1932–33.

Continuous graph.....Actual weight landed.

Dotted graph........Hypothetical weight on basis of flat rate of 611 cwt. per steamer per season.

There are, of course, other influences which help to decide how many steamers will participate in the Plymouth fishery. The Plymouth season follows hard upon a strenuous and extended fishery in the North Sea, culminating in the great East Anglian season. Owners of steamers will know how they have fared thus far, and may or may not be prepared to carry an additional risk at Plymouth. In any event, they are unlikely to send the ships round before they receive some assurance by news from Plymouth that there is at least the chance of making a profitable voyage.

A matter of some practical importance is the extent to which the total weight of fish landed during a season is affected by changes in the number of visiting steamers. Out of the 1,035,581 cwt. of herrings landed during December and January from 1918–19 to 1932–33, the steamers obtained 635,226 cwt., or over 61 per cent. The latter amount represents the combined result of 1,039 separate steamer-visits, a single visit being the whole or some part of one season. Now if the aggregate weight of fish landed and the total number of steamer-visits had been equally distributed over the fifteen seasons, approximately 42,348 cwt. would have been landed each season as the result of 69 steamer-visits. One steamer-visit would thus have contributed about 611 cwt. to each season's catch. This "spread-over" average is admittedly only a rough estimate of a steamer's fishing efficiency, but it serves the purpose intended. In the following Table the theoretical weight as calculated on the basis of 611 cwt. per steamer-visit is shown in conjunction with the actual weight landed during the seasons from 1924–25 to 1932–33 :—

Season.	Number of Steamers.	Theoretical Weight Landed, on basis of 611 cwt. per Steamer. (Cwt.)	Actual Weight Landed. (Cwt.)	Discrepancy. Actual Weight is	
				More by :	Less by :
1924–25	86	52,546	83,647	31,101	
1925–26	153	93,483	94,248	765	
1926–27	129	78,819	45,932		32,887
1927–28	77	47,047	82,803	35,756	
1928–29	81	49,491	42,177		7,314
1929–30	54	32,994	34,264	1,270	
1930–31	75	45,825	44,071		1,754
1931–32	52	31,772	20,927		10,845
1932–33	85	51,935	47,793		4,142

It is evident from the above Table and the graph in Fig. I, that although the total weight landed yearly is dependent upon the number of steamers engaged, the fluctuation in yield from season to season, is not wholly due to this. In some years, particularly 1924–25 and 1927–28, fishing was much more productive than a flat rate of fishing would indicate, while in others, notably 1926–27 and 1931–32, much less fish was landed than would be expected.

Number of Landings.

It is common knowledge that the number of drifters which proceed to sea is different from day to day. Compulsory stoppages on account of inclement weather, and voluntary cessations from fishing over week-ends and holidays, result in an appreciable loss of fishing time. The motor fishery is the greater sufferer in these respects and anything from 15 to 30 days in December and January in each year pass without a single motor landing. The steam fishery is more fortunate, for the days are rare when at least one steamer does not land. The greater regularity with which the steamers are able to operate is exemplified by the following statistics for the period, December 23rd, 1931, to January 19th, 1932 :—

Date 1931–32.	Steamer Landings.	Motor Landings.	
Dec. 23	20	90	
24	20	–	
25	15	–	Christmas Day
26	26	–	Boxing Day
27	27	–	Sunday
28	28	10	
29	30	20	
30	35	50	
31	35	70	
Jan. 1	30	60	
2	30	12	
3	28	1	Sunday
4	31	–	
5	25	–	
6	25	–	
7	30	70	
8	31	95	
9	31	100	
10	3	–	Sunday
11	31	–	
12	28	80	
13	24	–	
14	28	70	
15	9	–	
16	31	90	
17	20	–	Sunday
18	31	4	
19	30	80	

The steadiness with which the steamers fish is a valuable asset to the fishery as a whole since it tends to secure that desirable evenness in daily supply of fish for the market. Withdraw the steamers from Plymouth and supplies would fluctuate very seriously from day to day, with the result that the market would cease to attract the important class of buyer who is mainly interested in large and regular supplies of fish. This in its turn might easily lead to the more frequent occurrence of a glutted market in which price falls to a very low level because of a weakening demand. If for no other reason than this steady fishing, the steamers are a highly important section of fishing power, and a permanent reduction in their numbers would be a disquieting factor.

SIZE OF CATCHES.

The amount of fish landed in any one season depends not only upon the amount of fishing power expended, but also upon the yield of the fishing. It is characteristic of the fishery that results are outstandingly good in some seasons and correspondingly bad in others ; that heavy catches are made on one day and light ones on another ; that on one and the same day, some boats land many fish, whereas others return to port empty.

Seasonal results.

The average weight per landing by steamers and motors in each of the seasons from 1924–25 to 1932–33 is shown in Table IV.

TABLE IV.

Season. (Dec. and Jan.).	Average Weight per Landing (Cwt.). Steamers.	Motors.
1924–25	40·0	20·5
1925–26	23·1	25·9
1926–27	16·6	15·9
1927–28	46·3	24·6
1928–29	27·5	23·5
1929–30	39·1	42·5
1930–31	32·7	23·3
1931–32	17·6	9·2
1932–33	34·2	20·2
	Average 30·8	Average 22·8

Looking down the results of the steam fishing it is seen that in the seasons 1924–25, 1927–28 and 1929–30, the average weight per landing was well above the mean value for the period, whereas in 1926–27 and 1931–32 it fell much below the mean. The same applies to motor landings with the single exception that the yield in 1924–25 was not outstanding. Full consideration of the probable reasons why fishing should have been very good in the three seasons mentioned, but bad in the other two, must be deferred until the biological investigations have been described. It may be said, however, that this is just what might be expected from a knowledge of the fishable stocks which frequented the grounds in those seasons.

The Drift-net as a Snare.

Variation in the size of catches arises in consequence of the nature of the fishing implement. Skippers, men of experience in the art of drifting, making full use of their knowledge and beliefs, may manœuvre their vessels to the berth they consider the best available at the moment for catching fish, but all their skill cannot ensure a good catch every time the nets are shot. This is because the instrument of capture, the drift-net, is a snare in which fish are caught only as they themselves enter it. Practical experience in drifting and a knowledge of local conditions are indispensable aids in deciding where it is best to set the snare, but the size of the catch depends upon the behaviour of the fish in the immediate neighbourhood of the set nets.

In an interesting paper, Graham (**22**) deals with the phenomenon of the "swim," which he defines thus: "Something happens limited in time, and space, the result of which is that herring are caught in the nets, in numbers from say five thousand to a quarter of a million per fleet of nets;

this phenomenon is called a 'swim' of herring." His provisional explanation of the swim is "that herring, in a normal state, can see the nets and avoid them, so that the sea may be full of herring, yet none caught. When, however, they are under the influence of crowd excitement (due to panic, sexual excitement or migratory impulse) herring are more or less unable to see the net, and are caught." Whether Graham's explanation holds good at Plymouth, it is impossible at present to say, but there is no doubt whatever about the fact that catches are very unequal among the vessels working in close proximity on the same night, or that catches are frequently heavier on some nights than on others.

The Effect of Gales.

A connection between stormy weather and herring catches has evidently been long recognised by Cornish fishers. Thus, Dunn (**3**) writes concerning herrings which annually visit Mevagissey Bay for spawning :—

> " One fact is certain, that they exist closely hidden near the shore ; and here they would live in undisturbed possession of their haunts but for the storms of winter, especially those blowing directly on the coast. When these happen the fish immediately leave their hidden recesses and move out into the open bay. It is only then our fishermen at Mevagissey are able to catch them ; hence our fishers are always waiting for a storm, their nets being moored with anchors at each end in the bay throughout the winter. If only an ordinary gale comes, the inside nets will get most of the fish caught ; after a violent storm the herrings will be caught in all the nets ; if there is only a strong breeze the fish will not move from their haunts. If a severe tempest is approaching the coast, the herrings by some intuitive knowledge will move out before it comes."

In an endeavour to test this belief, the strength of the wind as recorded by the Plymouth (Mount Batten) Station of the Royal Air Force and published in the Daily Weather Report of the Meteorological Office, London, has been studied in association with data on daily landings of herrings. The general procedure has been to note the wind at 1300 G.M.T., when boats are normally proceeding to sea, and at 1800 G.M.T., when the fleet is taking up position at sea on the fishing grounds. These records have then been entered in a table, opposite the catch made during the night and landed on the following morning. Working in this way through the data for the past few seasons, distinct correlation between wind and fishing results has been observed.

Reference has already been made to the fact that strong gales prevent the motor fleet from leaving harbour, but it has now to be noted that when the motors are able to resume fishing once more, catches for a few days are much above the average. Bearing in mind the suggestions made by Graham, it is as if a gale from a southerly quarter sets the fish on the move, so that many are caught. As a first example, the results for December, 1928, will be considered. There were two periods when the motor boats were prevented from fishing because of strong winds, viz. December 10th–11th, and December 22nd–26th. Table V gives data regarding the strength and direction of the wind,* and the fishing results for a few days before and after these enforced stoppages :—

TABLE V.

Wind Records and Fishing Results during December, 1928.

	Wind.				Fishing Results by Motor Boats.			
Day of Month.	1300 G.M.T.		1800 G.M.T.		Day of Month.	No. of Landings.	Average weight per Landing (cwt.).	
4	W	1	NW	1	5	60	17·5	Average weight prior to stoppage=17 cwt.
5	N	3	NNW	2	6	50	14	
6	SW	6	NW	3	7	30	6	
7	NW	3	ENE	2	8	30	19	
8	NNE	4	N	1	9	7	28	
9	–	0	SW	4	10	no fishing	–	
10	**S**	**7**	**SSE**	**6**	11		–	
11	E	2	SE	2	12	70	14·5	Average weight after stoppage =60 cwt.
12	NE	3	NE	3	13	70	59	
13	ENE	3	E	4	14	80	73	
14	SE	5	NE	4	15	30	96	
15	ENE	3	S	4	16	30	59	
18	ENE	3	SSW	4	19	40	19	Average weight prior to stoppage=19 cwt.
19	SW	3	W	3	20	30	17	
20	NNW	4	NNW	4	21	10	26	
21	–	0	E	2	22	4	15	
22	W	3	W	4	23	no fishing	–	
23	WNW	2	ESE	2	24		–	
24	**SW**	**6**	**SW**	**7**	25		–	
25	**SW**	**4**	**SW**	**6**	26		–	
26	W	4	NNW	4	27		–	
27	ESE	3	SE	4	28	10	52	Average weight after stoppage =54 cwt.
28	W	4	WSW	4	29	12	55	
29	W	5	WSW	6	30	14	43	
30	WNW	4	NNW	4	31	16	66	

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* For the convenience of readers, the following official description of the Beaufort Scale Numbers is given :—

Beaufort Scale No.	Statute Miles per hour.	Beaufort Scale No.	Statute Miles per hour.
0	Less than 1	7	32–38
1	1– 3	8	39–46
2	4– 7	9	47–54
3	8–12	10	55–63
4	13–18	11	64–75
5	19–24	12	Above 75
6	25–31		

It will be observed from Table V that the average weight per landing for the motor boats is very much greater on the days following a temporary stoppage of fishing than on those prior to the cessation. Moreover, during the stoppages themselves, the wind has blown for some time at strengths of Beaufort Scale Numbers 6 and 7 from a southerly quarter.

Similarly for the season 1929–30. During practically the whole of the first fortnight of December, 1929, the weather was wild and tempestuous, and only 3 landings were made in the 9 days from December 4th to December 12th, the market being blank for 7 days on end. On December 16th, however, 50 landings were made by motor boats with the remarkable average landing of 161 cwt. Next day there were 70 motor landings averaging 171 cwt. Thereafter, the weather remaining favourable, many motor boats were able to fish each night, but the average fell off each day, first to 83 cwt., then to 80 cwt., and was only 14 cwt. on December 20th, and 27 cwt. on December 21st. Only a few steamers had arrived at Plymouth in time for this heavy fishing, but those few obtained results similar to those of the motors. Thus, on December 16th, one steamer made a landing of 385 cwt.; on the 17th, 4 steamers averaged 350 cwt., per landing; on the 18th, 6 averaged 334 cwt., and on the 19th, a total of 17 averaged 288 cwt. But on December 20th, when 12 steamers landed, the average per landing fell to 50 cwt., and it stood at the still lower value of 24 cwt. on December 21st. During January, 1930, the steamers made extra heavy landings on the three days, January 12th, 13th and 14th, the averages being 70, 75 and 67 cwt. respectively. Winds from SSW and SW of Beaufort Scale Numbers 6 to 8 were blowing on January 9th and 10th, moderating on the 11th. Thus, with fishing resumed after the gale, catches were of a high order.

The season 1932–33 is of particular interest in this apparent connection between strength of wind and fishing yield. The following is an analysis of the season's catch :—

Period.	Number of Days.	Total Weight Landed. cwt.	Average Per Day. cwt.	Average per Landing. Steamer. cwt.	Average per Landing. Motor. cwt.
Dec. 1st to Dec. 6th	6	165	27	3	2
Dec. 7th to Dec. 11th	5	2,540	508	**45**	**23**
Dec. 12th to Dec. 18th	7	**36,525**	**5,246**	**67**	**32**
Dec. 19th to Dec. 26th	8	6,941	868	19	10
Dec. 27th to Jan. 3rd	8	6,760	845	21	10
Jan. 4th to Jan. 6th	3	**13,305**	**4,435**	**37**	**33**
Jan. 7th to Jan. 14th	8	11,750	1,469	22	14
Jan. 15th to Jan. 25th	11	1,546	141	14	11
Whole season	56	79,532	1,420	34·2	20·2

It is apparent from the above figures that daily results were very uneven. The two periods, December 12th to 18th and January 4th to 6th, were by far the most productive as regards total weight of fish landed.

Nearly one-half of the season's catch was landed in the seven days of the first of these periods, and another one-sixth in the three days of the second. The weight per landing for both steamers and motors was also very high. Although not so profitable in total yield, the period from December 7th to 11th was characterised by a heavy average weight per landing.

During the season, there were two periods of strong gales, the first in early December, and the second in the beginning of January.* From 1300 G.M.T. on December 6th until 0700 on December 12th the wind records taken three times daily at Mount Batten did not fall below Beaufort Scale 6 except on two occasions, and Beaufort Scale 8 was recorded throughout December 11th. The direction was mainly E.N.E. In consequence, there was no fishing by motor vessels from December 6th to December 11th except by a few larger ones on the night of December 10th. For the twelve landings made, the average was 23 cwt., which, as will be seen from the analysis given above, was fairly high. A number of steamers fished throughout the gale period, their results being good. With the gale moderating during December 12th, all vessels, both motor and steam, were able to fish that night, and on the following morning no less than 10,500 cwt. of fish were landed, representing an average steamer landing of 100 cwt. for 39 vessels, and an average motor landing of 66 cwt. for 90 vessels. Thereafter for 4 nights, a full fleet was able to work with very high yield. The second gale period extended from December 31st until January 4th, this time from the southward, with wind force from Beaufort Scale 6 to 8. There were no landings by motor drifters on January 1st, 2nd and 3rd, and although a good number of steamers continued to fish, the results were not unusually heavy. But with the return of fair weather, enabling full fishing by the motors, high average landings were realised, particularly by the motors. On January 4th, 20 motors made an average landing of 35 cwt. ; and on January 5th, 44 motors averaged 56 cwt. per landing, whereas not since December 19th had the average landing been higher than 25 cwt.

The two periods of greatest yield during the 1932–33 season, therefore, immediately followed occasions when the motor fleet had been weather-bound in harbour for some days on end. This experience, together with the other illustrations previously described, seems definitely to suggest that the herrings are in some way affected by the blowing of strong winds, so that fish are caught in great numbers in drift-nets which are set as soon as this becomes practical. There is little evidence as to what actually happens. Strong winds will, of course, increase the turbidity

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[*] Readers will be materially assisted by referring to Cooper's Fig. 1 on p. 56 of this Number. (Cooper, **1**.) It should be noted that Cooper adopts the "Mean Cube Beaufort Number" as an index of the capacity of the wind to cause mixing and turbulence in the sea.

of the water, and possibly this may result in the fish not being able to see the nets so readily. If the fish moved under these circumstances, they would thus be more likely to become enmeshed. Possibly, in addition to increasing the turbidity of the water, strong wind action may actually induce the fish to move, and so increase the chances of fish being gilled. Whatever the cause, the apparent relation between wind and density of landing is one of practical importance.

Inshore Fishing in Bigbury Bay.

On some days it is noted that the motor boats are making good landings, whereas the steamers are having a poor time. The following are a few examples from the returns of 1931–32 :—

	Steamers.		Motors.	
Date. (1931–32.)	No. of Landings.	Average Weight. (cwt.)	No. of Landings.	Average Weight. (cwt.)
Dec. 19	15	1·9	90	12
Jan. 20	30	1·4	120	35
Jan. 21	20	3·5	90	16
Jan. 27	18	3·5	90	12

This occurred when the herrings were located well inshore in Bigbury Bay. These grounds can be worked with safety by the smaller motor craft, but not by the steamers without risk of damage to both boat and gear.

Ray-netting and Trawling in Bigbury Bay.

Reference may here be made to complaints by drift-net fishermen of interference caused by other methods of fishing. It is alleged that a considerable amount of damage to drift-nets is sustained by fouling with the ropes and moorings of the large-meshed tangle nets set on the bottom in Bigbury Bay for catching rays and turbot. (*vide* Steven, **31**.) At the time of writing, negotiations are proceeding between the Sea Fisheries Committees of Devon and Cornwall, and it is hoped that a satisfactory solution of the difficulty will eventually be reached.

There is also some feeling among local drifting interests that motor trawlers fishing for spawning herrings in Bigbury Bay are doing harm to the stocks. No sound case for this objection can be made out, however, and the Devon Sea Fisheries Committee have decided to take no action.

CONCLUSION.

The yield of the Plymouth winter drift-net herring fishery is subject to daily and seasonal fluctuation. Among the contributory causes of these fluctuations are (1) variation in the number and character of the boats engaged in the fishery, and (2) variations in the intensity with which the boats are able to fish. These causes, however, do not fully account for the observed fluctuations in yield, since the results of fishing, good or bad, ultimately depend upon the number and behaviour of the fish on the grounds. It follows, therefore, that it is impossible to give a complete explanation of past fluctuations in yield, or to predict what seems likely to happen in the future, until adequate knowledge of the fish stocks has been acquired.

STUDIES OF THE FISHES LANDED.

It is convenient to commence this section with a brief summary of the more general facts concerning the herrings caught at Plymouth. Catches include fishes of three classes in varying proportions: (1) "full" fish, in which the roes and milts are sufficiently developed so as to fill or almost fill the body-cavity, (2) spawners, or "maizey" fish, in which the reproductive glands are fully mature and actually in the running condition, (3) spent fish, which for the most part have quite recently spawned. Examination of the stomachs of the fishes shows that there is no feeding. These facts prove that the fishery depends upon a concentration of fish intent on spawning. The fish have not come to feed.

But while the fish agree in the purpose for which they have come, they differ in practically all other respects. In length, individuals vary from 21 cm. to 31 cm. (8 in. to 12 in.) although a sample taken at any time during the season will probably include 50 per cent or more individuals between the lengths of 25 cm. and 28 cm. With regard to weight, Orton (**28**) has shown that for 1075 individuals the total range of variation is from 72 grm. to 218 grm. ($2\frac{1}{2}$–$7\frac{1}{2}$ oz.). Age is also variable. Fishes are mostly in the 3rd to the 7th or 8th winter of life, but an occasional individual in its 2nd winter may occur, and those in their 9th, or even older, are not uncommon. In structure and body proportions, individuals differ in such features as the size of the eye, the depth of the body, and the number of bony rays in the fins. They also differ in their number of vertebræ, and it has been shown (Orton, **28** and Ford, **8**) that, exclusive of the terminal portion of the backbone known as the urostyle, the number varies from 53 to 58. Another internal difference is in the number of pyloric cæca (Ford, **6**).

The interpretation of these differences forms an essential part of the study of the fluctuations of the commercial fishery, and in the pages which follow, an account is given of the conclusions reached.

SPAWNING AND SPAWNING-TIME.

Direct evidence that spawning takes place in the Plymouth district is provided by records of naturally-deposited herring spawn taken by

Laboratory research vessels, although such records are surprisingly few. Only once in the past ten years has spawn been taken, when on March 3rd, 1930, eggs were brought to the surface in the trawl of s.s. *Salpa*, working on the Mewstone Grounds. Nevertheless, there are many other observations to show that spawning is intensive locally. It is of interest first to note that Matthias Dunn, the gifted fisherman-naturalist of Mevagissey in Cornwall, has given a description (Dunn, **4**) of what he believed was the actual spawning of herrings in Bigbury Bay. He says : " As to the actual spawning of Herrings, we have many times seen this going on on cold nights in December and January, in Bigbury Bay, in from fifteen to twenty fathoms of water. At such times male and female Herrings will congregate together in multitudes, and form themselves into vast columns —possibly slightly pyramidal in form—reaching from the surface to near the bottom, when they will commence a violent perpendicular action. Sometimes the top will be more than one hundred yards in diameter, and, when the column is in full swing, the mass often appears like a boiling cauldron. The uninitiated could not surmise the cause of such a perpetual din and clatter from this up-and-down motion as may be heard near by. This goes on without any horizontal movement being visible. Nor will any ordinary noise disturb them, so intent are they on their work ; and the relative position of the fish and the fishing-boats near them will often remain the same for an hour or more together. This action, no doubt, presses out the milt and roe from the male and the female, which is evidently dropped in the sea ; and the congress of life happens as the ova is sinking to the lower depths, for the spermatozoa floats—or is only of the specific gravity of the water—while the eggs are heavier, and instantly sink. Often the net will come in contact with these columns of spawning fish near their base, some fifty feet under water, and there Herrings will enter the net as thick as at the surface. When such masses are spawning, the whole sea in the neighbourhood will have a milky whiteness, caused by the surplus milt of the male." Whether or not Dunn was right in believing that he had witnessed herrings in the act of spawning, it is impossible to say, but when this talented and experienced observer describes so remarkable a phenomenon, for which no equally satisfactory alternative explanation can be advanced, it is difficult to say that he is wrong.

The presence of large quantities of maizey (spawning) fish in both drift-nets and the trawl, and the numbers of newly-hatched larval herrings which are taken in tow-nets used by the research vessels, bear out the limited direct evidence of spawning grounds inshore at points along the neighbouring coast from off Gribbon Head in Cornwall to the eastward at least as far as Exmouth in Devon. Bigbury Bay has long been regarded as one of the principal areas, no doubt because it is here that spawning shoals are most usually located, but considerable spawning must take place in other parts. Dunn (**3** and **4**) refers to spawning in Mevagissey Bay, while Wallace (**36**) records a catch of no less than 4210 recently-hatched larvæ in one ½-hour haul of the young-fish-trawl by s.s. *Salpa*, working Rame Head, bearing E. 12 miles, on February 5th, 1923—a record which strongly suggests the presence of a spawning ground near at hand. Early larvæ have also been taken in quantity at points off the Devon coast. Herrings running with spawn have been taken in Plymouth Sound and the estuaries of the Lynher and Tamar, while every year in late December and January, small drifters working out of their home ports of Exmouth, Sidmouth, Beer, etc., and fishing just off the shore in the waters of the Great West Bay, secure catches consisting almost entirely of running fish. These and other records support the belief that spawning takes place over a wider area than is commonly supposed.

It is important to fix the time at which spawning occurs. Running fish have been taken as early as September 30th (Plymouth Sound, 1925 and 1926), and as late as May 14th (trawled by s.s. *Salpa*, 1930), representing an extreme range of 7½ months. Moreover, in any one season, spawners and spents may occur in the catches at any time, making it a matter of some difficulty to decide when spawning is most general over the grounds. Observations conducted during the season 1924–25 (Ford, **9**, p. 284) indicated that spawners were chiefly in evidence in the catches of late December and the whole of January. The results of later work confirm this, but also show that considerable numbers of spawning fish are in the neighbourhood in February and March, after the drifting season has come to an end, and that these can be, and are, caught in the trawl. There is reason to believe, too, that the amount of spawning which takes place in October and November is considerably less than that in subsequent months. Although no explanation can at present be offered, it may be stated that during the past three seasons (1930–31 onwards), " maizey " fish are almost entirely absent from drift-net landings, even during the months of December and January when they would be expected. Good catches of spawning fish, however, were later secured in the trawl.

It is clear, therefore, that from October onwards, a concentration of herrings, bent on spawning, occurs off the Plymouth coasts. Many of the shoals must arrive some considerable time before the individual fishes are ready to spawn, for the catches in the earlier part of the season consist almost exclusively of " full " but not ripe herrings. Probably these shoals remain in the vicinity until spawning has been accomplished, but it is not unlikely that they are later joined by shoals which are ready to spawn almost as soon as they arrive on the grounds. In any case, it is only possible to explain the " mixed " character of landings by assuming that spawning takes place shoal by shoal throughout the season, with the result that on the same day, one boat will land " full " fish and another "spents," while one and the same catch will include fulls, spawners and spents.

VARIATION IN WEIGHT.

In 1914–15, a comprehensive biometric investigation of a total of 1075 herrings was carried out at the Plymouth Laboratory (*vide* Orton, **28**), which included the determination of the weight of each fish to the nearest gram. The weight was that of the ungutted fish, and the individual variation thus depended not only on the size of the fish, but also on its sexual condition. Variation due to unequal weights of stomach and gut-contents may be ignored since the winter fish at Plymouth hardly ever contain food. Fraser (**16**, p. 251) worked out a formula linking weight with length, on the basis of the data given in Orton's Table III. He found that for the total of 550 records,

$$W = 0{\cdot}00000337 \times L^{3{\cdot}149}$$

$$\text{Where } W = \text{Weight in grammes.}$$

$$L = \text{Length in millimetres.}$$

Fraser's formula does not take into account the individual differences in sexual condition which occur among a season's catches, but may be taken to apply to "full" fishes. From an analysis of the data given in Orton's Table IV, where the weights refer particularly to spawning fish (maturity stage VI) and spents (maturity stages VII and II), it appears as if spawning females are slightly heavier than spawning males of a similar length, while, as expected, the spents of both sexes are not so heavy as the fulls. But as the standards of sexual maturity are not sufficiently precise, no useful purpose is served in making more detailed comparisons.

THE AGE OF FISHES LANDED.

During each of the eight seasons from 1924–25 to 1931–32, estimates of the age of the herrings landed were made from their scales. Two or three scales from each fish, separately picked from the anterior region of the body near the tip of the pectoral fin, were cleaned between finger and thumb in water and mounted on a numbered glass slide, using a mixture of egg-albumin and glycerine as the adhesive. In reading a scale, the number of "summer zones" and the number of "winter rings" were both recorded (see Ford, **7**, p. 243), the clear winter-edge being counted as a completed ring. Records of age were then grouped into year-classes according to the calendar year in which the first summer zone was formed on the scale. For example, fishes caught during the season of 1924–25 which showed five summer zones and four winter rings within the winter edge, were recorded as "5 zoned 5 ringed" and assigned to the 1920 year-class. Normally, fishes older than " 6-zones 6-rings " were recorded as " old " fish without any attempt to fix the age with precision.

In actual practice it was found that catches taken during the two most important months of December and January of any one season agreed sufficiently closely to warrant the calculation of a seasonal average age-composition, giving in the form of percentages the relative numbers of fishes of different ages likely to be taken in a catch at any time during that season. In the following Table VI the average percentages, according to age, are given for the eight seasons :—

TABLE VI.

Season.	Percentage Numbers of Fish at the following Age.				
(Dec.–Jan.)	3	4	5	6	Older than 6
1924–25	7·0	12·3	56·0	15·3	9·4
1925–26	5·3	15·2	14·1	47·5	17·9
1926–27	4·7	27·9	22·9	10·7	33·7
1927–28	18·6	20·4	30·9	12·0	17·1
1928–29	3·3	30·8	19·5	26·6	19·3
1929–30	1·9	18·1	35·9	15·4	28·8
1930–31	4·4	10·2	23·8	33·2	28·3
1931–32	3·4	12·6	15·0	21·3	47·7
Means	6·1	18·4	27·3	22·7	25·3 (Total=99·8%)

It is evident from the figures that the composition by age varies considerably from one season to the next. An important feature of this age-variation, however, is more clearly seen when the age data are rearranged according to the year-classes which they represent. This has been done in Table VII :—

TABLE VII.

Age of Year-class (Zones and Rings).	Percentage Numbers contributed by each of eleven Year-classes during months of December and January.											
	1919	1920	1921	1922	1923	1924	1925	1926	1927	1928	1929	Means
3	–	–	–	7·0	5·3	4·7	18·6	3·3	1·9	4·4	3·4	6·1
4	–	–	12·3	15·2	27·9	20·4	30·8	18·1	10·2	12·6	–	18·4
5	–	56·0	14·1	22·9	31·9	19·5	35·9	23·8	15·0	–	–	27·3
6	15·3	47·5	10·7	12·0	26·6	15·4	33·2	21·3	–	–	–	22·7

Looking down the columns of Table VII it is seen that year-classes agree almost without exception in the order of the rise and fall of the percentage from the third to the sixth year. The percentage is comparatively low in the third year, rises to a maximum in the fifth, and commences to fall in the sixth. There is but one departure from this, in that year-class 1924 gave a greater percentage in its fourth year than in its fifth.

This agreement among year-classes was noted in an earlier report (Ford, **11**, p. 14) when only the results for the four seasons 1924–25 to 1927–28 were available for study. That it should hold good over the longer period of eight seasons suggests that we have to deal with something more than a fortuitous coincidence of figures, the observed agreement strongly indicating that younger year-classes replace older ones in a regular manner as the seasons go by. In considering this process of replacement, however, it is important to remember that the data relate to *commercial catches* as distinct from the *fish-stocks* from which the catches were drawn. It is true that the characters of a catch bear real relationship to the characters of the stock fished, but the former are also dependent upon the size of mesh in the nets used. Since no important alteration from season to season in the size of mesh is known to occur, the selective action of fishing may be ignored, provided that the distinction between *catch* and *stock* is recognised. The results summarised in Tables VI and VII thus show the process of replacement of older year-classes by younger, *in the fishery*. Each year-class in turn enters the fishery in its third year, reaches its maximum proportion in the catches during its fifth year, and begins to fall out in its sixth.

Further reference to Table VII shows that there is little uniformity in the contributions made by successive year-classes at the same age. Those of 1920, 1923 and 1925 gave comparatively large percentages throughout the third to the sixth years of life, whereas those of 1921, 1927 and 1928 gave correspondingly poor ones. This outstanding importance of certain year-classes and the comparative absence of others are highly significant matters which will be dealt with more fully at a later stage (p. 370). It will suffice at present to point out that in their fifth and most important year, fishes of year-classes 1920, 1923 and 1925 formed 56·0%, 31·9% and 35·9% respectively, of the season's catch. Not only this, for each in its turn remained a most important element of the catches for two or even three seasons in succession.

Before leaving this study of age-composition, attention must be drawn to the fact that all the above considerations have had to do with percentage-composition of catches and not with absolute numbers. The data tell us how many out of every hundred fish caught are of a certain age or belong to a given year-class, but they give no idea as to the absolute numbers of such fishes landed. This fact will also be recalled later.

LENGTH IN RELATION TO AGE.

It has already been stated that the length of the herrings at Plymouth varies between the limits of about 21 cm. to 31 cm. Since length increases with age, one might have expected that fishes of the same age-group would be of approximately the same length, but it is actually found that there is a wide variation in the length of fishes of the same age-group. The result is that it is quite impossible to obtain anything approaching a reliable estimate of the length of a fish merely by noting its age, or vice-versa. For example, a 3-zoned 3-ringed fish may be any length from 21 cm. to

29 cm., while an individual measuring 25 cm. in length might prove to be any age from 3 years upwards. The following Table VIII summarises results obtained during the four seasons from 1924–25 to 1927–28, and will serve to show the range and extent of the length-variation according to age :—

TABLE VIII.

Age-group.	Season.	Year-class.	No. of fishes in each of 11 length groups (cm.).											Total No.	Average length. (cm).
			21	22	23	24	25	26	27	28	29	30	31		
3-zoned 3-ringed	1924–25	1922	–	3	19	39	68	36	15	3	1	–	–	184	25·5
	1925–26	1923	2	10	9	32	44	13	3	–	–	–	–	113	24·9
	1926–27	1924	–	–	4	11	33	27	12	–	–	–	–	87	25·9
	1927–28	1925	4	18	57	71	34	4	1	1	–	–	–	190	24·2
4-zoned 4-ringed	1924–25	1921	–	–	6	13	34	67	72	53	10	2	–	257	27·0
	1925–26	1922	–	4	11	33	59	94	87	22	–	–	–	310	26·4
	1926–27	1923	–	2	13	59	88	46	19	14	2	–	–	243	25·7
	1927–28	1924	–	2	26	49	66	32	9	3	1	1	–	189	25·3
5-zoned 5-ringed	1924–25	1920	–	–	–	11	96	304	481	251	33	4	1	1181	27·4
	1925–26	1921	–	–	–	10	35	58	79	37	12	2	–	233	27·1
	1926–27	1922	–	–	3	21	54	65	48	25	2	–	–	218	26·5
	1927–28	1923	–	–	2	25	120	105	44	5	–	–	–	301	26·1
6-zoned 6-ringed	1924–25	1919	–	–	1	2	12	59	140	65	26	–	–	305	27·6
	1925–26	1920	–	–	–	6	37	106	250	304	97	6	–	806	27·9
	1926–27	1921	–	–	–	4	10	21	34	18	9	2	–	98	27·4
	1927–28	1922	–	–	–	7	27	31	31	8	5	–	–	109	26·7

That fishes of the same age-group may differ in length to the degree indicated in Table VIII is a matter which requires further consideration. A certain amount of this difference in length may be due to the fact that fishes of the same *age-group* are not necessarily all of the same absolute *age*. And this is because the method of estimating age from the number of rings and zones on the fish's scale is not able to distinguish between fishes born at different times during the same spawning season. With an extended spawning season like that at Plymouth, fishes of the same year-class may thus differ in absolute age by as much as five to six months.

Length, however, is not solely a function of age, although it is known that a herring adds something to its length during every year of its life. There is little reason for believing that two fishes, born on the same day, will reach exactly the same length after a given interval of time.

The interpretation of observed differences in length therefore necessitates enquiries in a number of different directions, the more important of which will now be dealt with.

Length (l_1) at formation of First Winter Ring.

It is characteristic of the Plymouth fish that the length l_1 at which the first winter ring is formed on the scale varies within wide limits. (Ford, **9**, p. 294.) Thus, for a total of 1122 fishes of year-class 1920 examined in the winter of 1924–25, l_1 varied from 6·5 cm. to 18·5 cm. Similarly, a total of 244 fishes of year-class 1921, also examined in the winter of 1924–25, varied from 8·5 cm. to 17·5 cm. In both instances, the individual values were widely dispersed over the total range of variation, so that the averages were subject to a large probable error.

Length (l_2) at formation of Second Winter Ring.

The length l_2 is also very variable. Thus, for the 244 fishes of year-class 1921 in which l_1 varied from 8·5 cm. to 17·5 cm., the value of l_2 varied from 16·5 cm. to 25·5 cm., and the average l_2 was also subject to a large probable error.

Correlation between the Values of l_1 and l_2.

In an individual fish, the difference between l_1 and l_2 is the total amount added to the length during the year which intervenes between the formation of the first and second winter rings on the scale. But, as has already been shown, the absolute age of the fish at the time when this increment was added cannot be stated with complete precision. Hence, a comparison between the observed values l_1 and l_2 for a number of fishes is in reality a comparison of the growth of fishes which probably differ in absolute age. Error from this source can be reduced to the minimum by first subdividing the fishes into groups according to the value of l_1 and then noting the value of l_2 for each of the groups. For the 4-zoned 4-ringed fishes of year-class 1921 referred to above, the following are the results :—

Values of l_1	9·5	10·5	11·5	12·5	13·5	14·5	15·5	16·5
Average Values of l_2 .	17·93	18·87	19·58	20·15	20·82	21·22	22·29	22·69
$(l_2 - l_1) = t_2$	8·43	8·37	8·08	7·65	7·32	6·72	6·79	6·19

It is seen that the size of the growth increment (t_2) depends upon the length l_1, so that the larger the value of l_1, the smaller the increment. Statistical treatment of the data shows that the correlation between l_1 and the increment t_2 is significant. Hence it is possible to determine a regression equation of the form $l_2 = ml_1 + c$ which will give values of l_2 closely approximating to the observed data. Similar regression equations may be determined linking l_3 with l_2, l_4 with l_3 . . . etc. (Ford, **7**, p. 249.)

"Compensatory Growth."

This correlation between the length of a herring at the formation of a given winter-ring and the increment of length which will be added before the next ring is laid down, has been noted by other workers. For example, Watkin (**37**) writes : "It is a feature of the growth of the herring that each succeeding year's growth is less than that of the preceding year. . . . It also seems to be a general feature that the herring should approach a certain length at the completion of each of the various years' growth. If for some cause or other the fish was unable to complete this amount of growth in a particular year then it will in some measure make up the deficiency the following year, so that what may be called the phenomenon of *compensatory growth* is characteristic of the herring."

More recently, however, Hodgson (**26**) has studied the matter in an interesting way, to arrive at the conclusion that this so-called "compensatory growth" is simply explained as the natural result of comparing the growth of fishes which are at different ages. For convenience, his Fig. 30 is here reproduced as Fig. 2 below. He draws a curve AB, which he terms "the curve of ability to grow," passing through a value 8·5 cm. on the axis XY. This curve intersects the ordinate OP at point G.

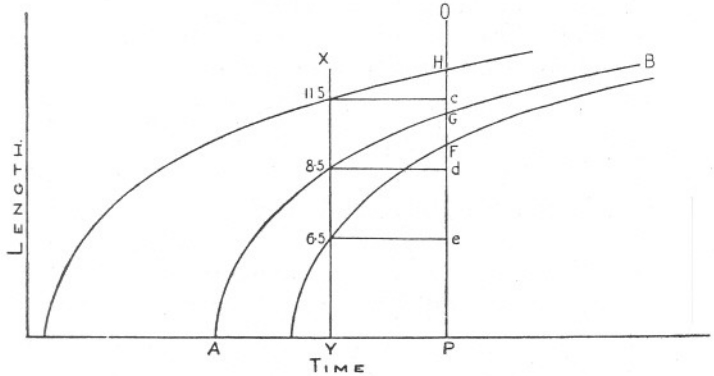

FIG. 2.—Reproduction of Fig. 30 in Hodgson (**26**). For explanation see present Text, above.

The growth made in the interval of time YP is thus given by the length Gd on the ordinate OP. Hodgson now moves curve AB to the left, keeping point A on the time-axis, until the curve cuts the XY axis at a value of 11·5 cm. instead of 8·5 cm. Under these circumstances, the growth made in the time-interval YP is given by the length Hc on the ordinate OP instead of Gd. Alternatively, the curve AB is moved to the right, still keeping point A on the time-axis, until it cuts XY at 6·5 cm. In this case the growth in the time-interval YP is given by Fe on the ordinate OP. With these things done, it is seen that Fe>Gd>Hc. That is to say, the growth made during the time YP is dependent upon the value on the XY axis through which the curve passes, the largest growth being given by the smallest value, 6·5 cm., and the smallest growth by the largest value, 11·5 cm. The sole explanation of this is that the curve AB has been started at a different point in time on the time-axis. There is no question of a difference in growth-rate, or any kind of compensatory growth, for the form of the curve has been unchanged.

The first point to be raised in connection with Hodgson's study is his "curve of ability to grow." The growth of the herring from year to year is not continuous and uniform. Seasons of growth alternate with seasons of no growth. The measurements of scales provide information as to the amounts added from year to year, but they tell us nothing concerning the time and rate at which individual increments are laid down. These facts are, of course, well known to Hodgson, and it may be assumed that he intends his curve merely as a geometric curve to show how the length increases from year to year, rather than as a growth-curve in the stricter sense.

A second point is that Hodgson gives no indication of the particular "form" of his curve AB. Admittedly, this does not affect the validity of the fact that $FE > GD > HC$, but it is important to note that the *amount* by which $FE > GD > HC$ is dependent upon the "form" of the curve as well as upon its position with relation to the time-axis.

Consider the regression equations which show the relation between l_1 and l_2, l_2 and l_3, l_3 and l_4 . . . . l_n and l_{n+1}. They are all of the general form : $Y = MX + C$

where X=Length of a herring at formation of n^{th} winter ring.
Y= ,, ,, ,, ,, $n+1^{\text{th}}$,, ,,
M=A constant of positive value less than 1.
C=A constant of positive value greater than 1.

Treating the equation $Y = MX + C$ purely as a mathematical expression, let us now apply it continuously so that having determined the value of Y for an initial value of X, we use this as a new value of X for a further calculation of Y, and so on, indefinitely. These are the results :—

Number of times the equation is operated.	Values of X.	Values of Y. ($Y = MX + C$).
1	$X_1 = 0$	$Y_1 = C$
2	$X_2 = C$	$Y_2 = C(1 + M)$
3	$X_3 = C(1 + M)$	$Y_3 = C(1 + M + M^2)$
4	$X_4 = C(1 + M + M^2)$	$Y_4 = C(1 + M + M^2 + M^3)$
5	$X_5 = C(1 + M + M^2 + M^3)$	$Y_5 = C(1 + M + M^2 + M^3 + M^4)$
....	....	....
n	$X_n = C(1 + M + M^2 + M^3 + \,..\, M^{n-2})$	$Y_n = C(1 + M + M^2 + M^3 + M^4 + \,..\, M^{n-1})$

Thus at the nth operation of the equation,

$$Y_n = C(1 + M + M^2 + M^3 + M^4 \ldots M^{n-1})$$
$$= \frac{C(1 - M^n)}{1 - M}$$

In Fig. 3 the successive values Y_1, Y_2, Y_3 . . . Y_6 when the initial value X_1 is 0, are shown graphically, with a smooth curve passing through them.

It is seen that at the first operation of the equation, as represented by one unit along the time-base, the value of Y is C. After the second operation, Y has increased by an additional amount MC, which is less than C

because M is less than unity. The third operation adds a further amount M^2C, which is again a proportionate part of the previous increase. After the sixth operation, the total increments which have been added are C, MC, M^2C, M^3C, M^4C and M^5C, each of these being equal to M times the previous increment. Clearly, therefore, the continuous operation of the equation is bringing the value of Y nearer and nearer to a limiting value by permitting an increase in Y which is always M times the previous increase. It is simple to ascertain what the limiting value actually is, by observing that $Y_n = \frac{C(1-M^n)}{1-M}$. As n is increased, M^n decreases, so that ultimately M_n becomes zero, and hence the limiting value $Y_x = \frac{C}{1-M}$.

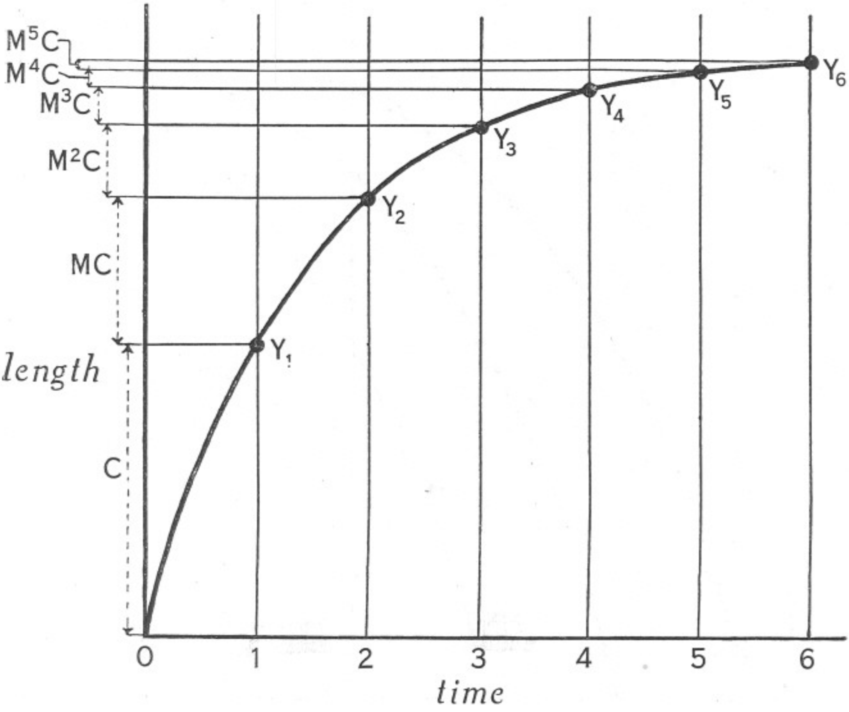

FIG. 3.—For explanation, see Text, p. 330.

In Fig. 4, on p. 332, the curve given in Fig. 3 has been re-drawn in triplicate from three points along the time-base. It is seen that on the ordinate at time 5, $BA > CB > DC$. This is clearly a repetition of Hodgson's result and, like his, is entirely due to the fact that the three curves occupy different positions in relation to the time-axis. But in Fig. 4, the actual "form" of the curve is known, whereas in Hodgson's figure it is not.

Attention is now directed to Fig. 5, which resembles Hodgson's figure in that three curves commence from different points along a time-base and intersect the ordinates XY and OP. Here again, Fe>Gd>Hc, but for a different reason. Whereas in Hodgson's figure and also in Fig. 4, a single curve is drawn in three alternative positions, in Fig. 5 *the three curves are all different*. Curve 1 is that resulting from the continuous operation of the equation $Y = \cdot 5X + 15$; curve 2, from the equation $Y = \cdot 6X + 12$; and curve 3 from the equation $Y = \cdot 7X + 9$. All three curves are gradually approaching the limiting value of $\frac{C}{1 - M}$, which in each case is 30. In consequence of the order in which the curves are placed with regard to time, they can be extended indefinitely to the right without ever meeting. Wherever the ordinate OP is erected, Fe will always be greater than Gd, and Gd greater than Hc. But the *amount* by which these increments will differ will depend not only upon the length of time the curves have been extended from their commencement, but also upon their "forms."

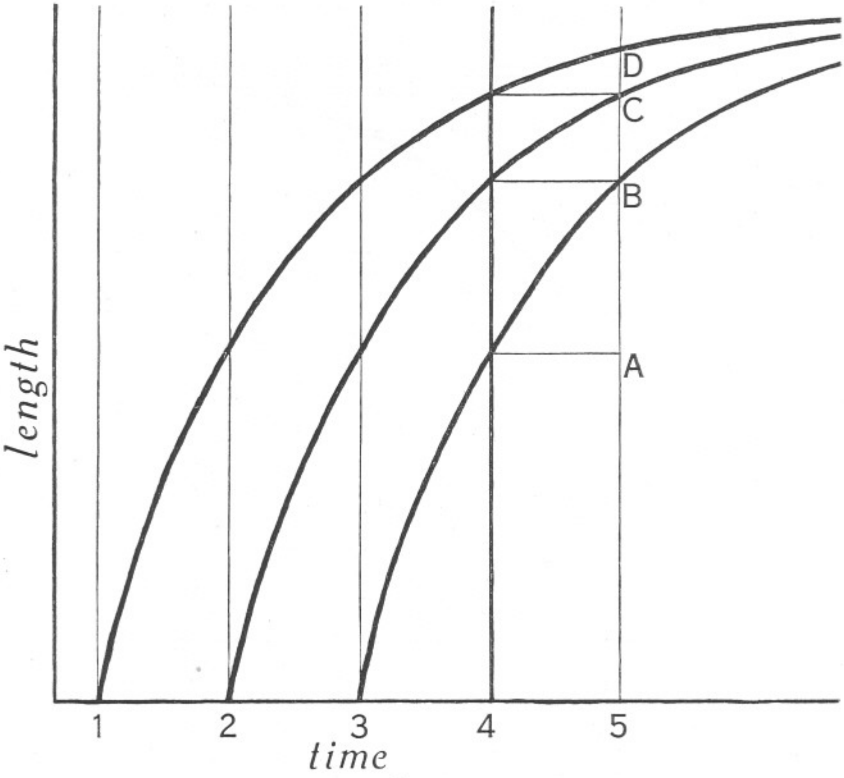

FIG. 4.

These theoretical considerations show that Hodgson's explanation of "compensatory growth" in the herring is subject to reservation. He says: "If we call the curve AB, the curve of ability to grow, we see that with increase of age there is less ability to increase length and consequently the larger and older fish of any given growth period will grow less than the smaller and younger fish." But it is necessary to add that the "curve of ability to grow" may itself be subject to variation from fish to fish, with important consequences.

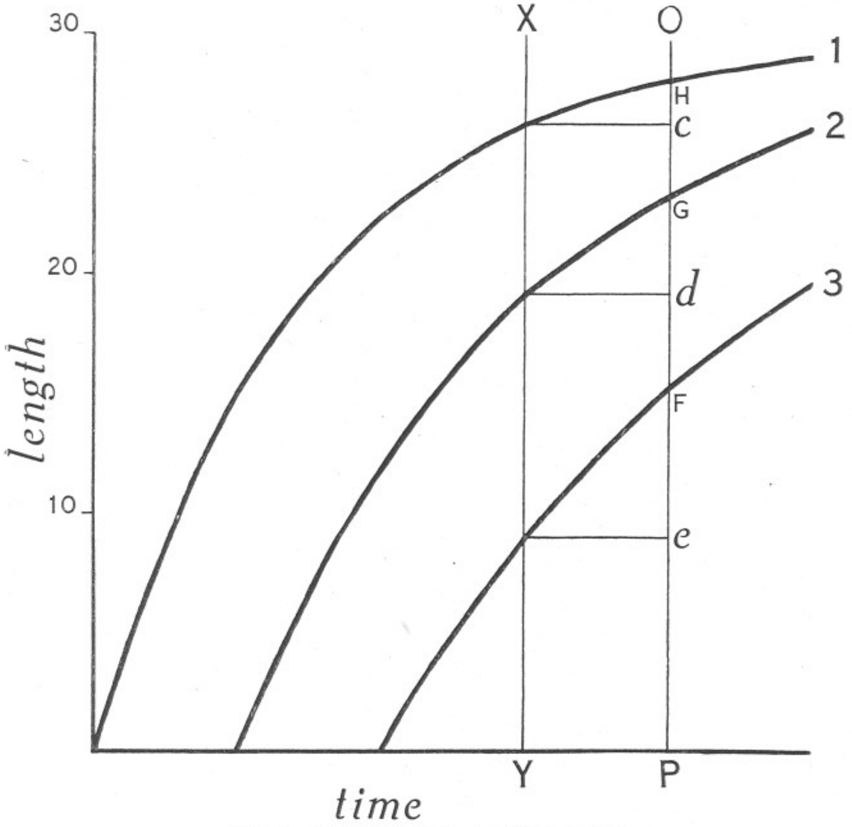

FIG. 5.—For explanation, see Text, p. 332.

GROWTH IN LENGTH IN DIFFERENT GEOGRAPHICAL AREAS.

In earlier papers an endeavour was made to show that regression equations can be used as a technique for the comparison of growth in length in different geographical areas. The method has since been developed with rather instructive results. In illustration, data given by Gilson (**21**, p. 50, in Table XIII) regarding the mean lengths from l_1 to l_9 for spent herrings taken from the region Griz-Nez to Ostende will now be used. Take the equation $Y = \cdot56X + 11\cdot5$ and substitute Gilson's l_1 of 9·96 cm. for X. The value of Y (representing l_2) is given by $\cdot56\ (9\cdot96) + 11\cdot5 = 17\cdot08$ cm. as against the observed value of 17·19 cm. Next, using the value 17·08 as a new value of X, a new value of Y (this time representing l_3) is given by $\cdot56\ (17\cdot08) + 11\cdot5 = 21\cdot06$ cm., as compared with the actual l_3 of 21·05 cm. Similarly, the substitution of 21·06 for X will provide a value of Y which represents l_4. Working in this way, a complete alternative set of calculated values for $l_2, l_3 \ldots l_9$ can be obtained and compared with Gilson's data :—

	l_1	l_2	l_3	l_4	l_5	l_6	l_7	l_8	l_9
Gilson's means	9·96	17·19	21·05	23·14	24·29	25·20	25·58	26·00	26·50
By equation	9·96	17·08	21·06	23·29	24·54	25·24	25·64	25·86	25·98

It is seen that with the exception of the period from l_8 to l_9 the equation has given values which closely approximate to the observed data. That is to say the herrings represented by Gilson's data had, on average, added to their length yearly in a regular manner, whereby the increment of length added in each succeeding year was approximately ·56 times the increment added in the previous year.

The single equation $Y = \cdot56X + 11\cdot5$ is thus all that is necessary for determining how the Belgian fish add to their length from year to year. It is especially convenient as a means for comparing the Belgian results with those from other places where the average l_1 may be higher or lower than 9·96 cm. For instance, Gilson gives Hodgson's data for herrings of the southern North Sea ($l_1 = 8$ cm.), and also those of le Gall's *Type côtier* ($l_1 = 11\cdot88$ cm.) and *Type atlantique* ($l_1 = 12\cdot49$ cm.) from the English Channel. By determining the values of Y when X is 8, 11·88 and 12·49 respectively, using the Belgian equation, and comparing them with Hodgson's and le Gall's l_2 values, any difference in growth is at once revealed. In the following table Hodgson's and le Gall's data are fully compared with those given by continuous operation of the Belgian equation :—

Southern North Sea.		Type Côtier.		Type Atlantique.	
(Hodgson.)	Equation.	(le Gall.)	Equation.	(le Gall.)	Equation.
$l_1 = 8$	8·0	$l_1 = 11\cdot88$	11·88	$l_1 = 12\cdot49$	12·49
$l_2 = 16$	16·0	$l_2 = 18\cdot46$	18·15	$l_2 = 19\cdot19$	18·49
$l_3 = 20–21$	20·45	$l_3 = 21\cdot72$	21·66	$l_3 = 22\cdot46$	21·85
$l_4 = 23$	22·95	$l_4 = 23\cdot30$	23·62	$l_4 = 24\cdot25$	23·74
		$l_5 = 24\cdot50$	24·72	$l_5 = 25\cdot40$	24·79
		$l_6 = 25\cdot54$	25·34	$l_6 = 26\cdot17$	25·38
		$l_7 = 26\cdot40$	25·69	$l_7 = 26\cdot94$	25·72

It is seen that Hodgson's data as a whole and le Gall's data for the *Type côtier* as far as l_6 are well fitted by the Belgian equation. The only important difference between the fishes in the three cases is in the value of l_1. On the other hand, the rate of increase in length of le Gall's *Type atlantique* is distinctly faster than that given by the Belgian equation.

Good material for a second illustration is provided by a sample of Icelandic herrings of the year-class 1906, taken 3 km. N. of Siglunaes on July 25th, 1908. Data are given by Hjort (**23**, p. 119, Collection 16). The mean values of l_1 to l_{12} as recorded by Hjort, and the corresponding values calculated from the continuous operation of the equation $Y = \cdot742X + 9\cdot57$ are given below :—

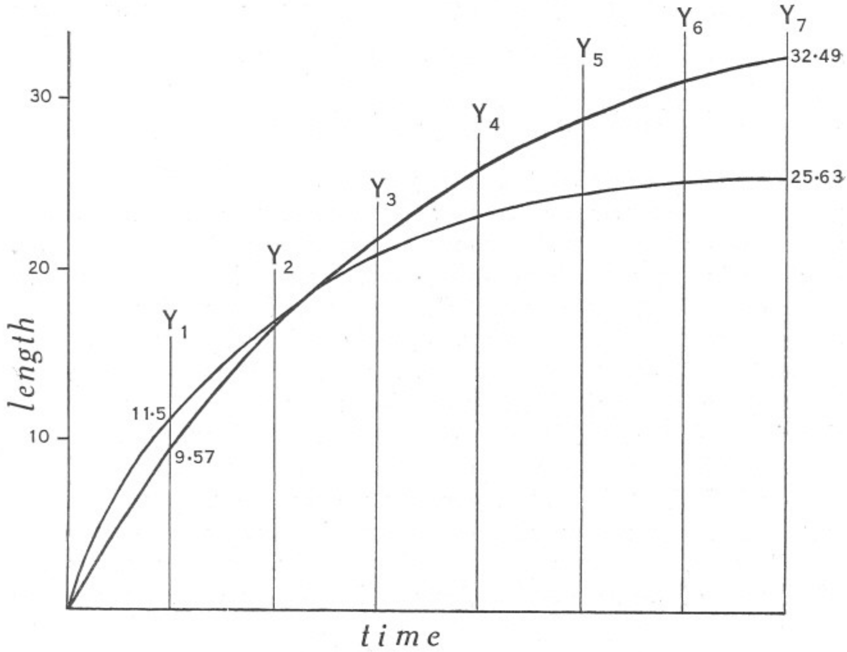

FIG. 6.—Comparison of growth in southern North Sea with that in Iceland.

	l_1	l_2	l_3	l_4	l_5	l_6	l_7	l_8	l_9	l_{10}	l_{11}	l_{12}
Hjort	8·7	15·7	21·4	26·0	29·0	30·8	32·2	33·2	34·2	35·0	35·8	36·3
Equation	8·7	16·0	21·5	25·5	28·6	30·8	32·4	33·6	34·5	35·2	35·7	36·1

Here again a single equation has yielded a close approximation to observed data. But this equation is not the same as the one which satisfied Gilson's, Hodgson's and le Gall's data. The difference between them may be demonstrated by continuously operating both from a commencing value X=O. In effect this is equivalent to starting two curves from the same point in time, as in Fig. 6. The degree to which the curves diverge is a measure of the difference in the rate which at length is added. The results are as follows :—

Equation.	Y_0	Y_1	Y_2	Y_3	Y_4	Y_5	Y_6	Y_7
$Y = {\cdot}742X + 9{\cdot}57$	0	9·57	16·67	21·94	25·85	28·75	30·90	32·49
$Y = {\cdot}56X + 11{\cdot}50$	0	11·50	16·94	20·98	23·25	24·52	25·23	25·63

The Icelandic growth is clearly of a totally different order from that of the southern North Sea and English Channel, both in the successive yearly increments and the limiting value towards which the total length tends to approach each year. The Icelandic limit $\frac{C}{1-M}$ is $\frac{9{\cdot}57}{1-{\cdot}742} = 37{\cdot}1$ cm., whereas the southern North Sea limit is $\frac{11{\cdot}5}{1-{\cdot}56} = 26{\cdot}1$ cm.

The above examples indicate (1) that in many cases the successive yearly increments which a herring adds to its length decrease in magnitude in something very nearly approaching geometric progression, and (2) that there are real differences in growth between herrings of different geographical areas. The first of these points is hardly what might be expected at first sight. And yet, when it is seen how closely the Icelandic data are matched by the equation values over a period of twelve years, it is impossible to ignore the observation. The result would seem to suggest that the Icelandic fish had succeeded in growing, as it were, "according to plan," whereby each succeeding year an increment of length is to be added which shall always be about ·742 times the increment added the year before. Returning to the original data and noting the actual annual increments, it is possible to determine how much they deviate from those which would have been added if growth had been strictly according to "plan" :—

Actual Increments.	Increments given by Growth-Equation.	Difference.
$t_2 = l_2 - l_1 = 7{\cdot}0$ cm.	7·3 cm.	·3 cm.
$t_3 = l_3 - l_2 = 5{\cdot}7$	5·5	·2
$t_4 = l_4 - l_3 = 4{\cdot}6$	4·0	·6
$t_5 = l_5 - l_4 = 3{\cdot}0$	3·1	·1
$t_6 = l_6 - l_5 = 1{\cdot}8$	2·2	·4
$t_7 = l_7 - l_6 = 1{\cdot}4$	1·6	·2
$t_8 = l_8 - l_7 = 1{\cdot}0$	1·2	·2
$t_9 = l_9 - l_8 = 1{\cdot}0$	·9	·1
$t_{10} = l_{10} - l_9 = {\cdot}8$	·7	·1
$t_{11} = l_{11} - l_{10} = {\cdot}8$	·5	·3
$t_{12} = l_{12} - l_{11} = {\cdot}5$	·4	·1

The difference, sometimes positive and sometimes negative, is not very large when expressed in absolute lengths as above, and therefore gives the impression that growth follows the geometric law with consistent regularity, leaving but little evidence of any variation resulting from annual differences in conditions for growth. Some light is thrown on this matter, however, if the proportion between a given increment and the preceding one is compared with the theoretically fixed value of ·742 :—

$$\text{Ratio}: \frac{t_{n+1}}{t_n}$$

$$\begin{aligned}
\frac{t_3}{t_2} &= \frac{5{\cdot}7}{7{\cdot}0} = {\cdot}81\\
\frac{t_4}{t_3} &= \frac{4{\cdot}6}{5{\cdot}7} = {\cdot}81\\
\frac{t_5}{t_4} &= \frac{3{\cdot}0}{4{\cdot}6} = {\cdot}65\\
\frac{t_6}{t_5} &= \frac{1{\cdot}8}{3{\cdot}0} = {\cdot}60\\
\frac{t_7}{t_6} &= \frac{1{\cdot}4}{1{\cdot}8} = {\cdot}78\\
\frac{t_8}{t_7} &= \frac{1{\cdot}0}{1{\cdot}4} = {\cdot}71\\
\frac{t_9}{t_8} &= \frac{1{\cdot}0}{1{\cdot}0} = 1{\cdot}00\\
\frac{t_{10}}{t_9} &= \frac{{\cdot}8}{1{\cdot}0} = {\cdot}80\\
\frac{t_{11}}{t_{10}} &= \frac{{\cdot}8}{{\cdot}8} = 1{\cdot}00\\
\frac{t_{12}}{t_{11}} &= \frac{{\cdot}5}{{\cdot}8} = {\cdot}625
\end{aligned}$$

The values of the ratio $\left(\frac{t_{n+1}}{t_n}\right)$ vary between the limits of ·6 and 1·0, thus causing the length l_n to be sometimes greater and sometimes less than the value which would be attained if the ratio had remained steady at ·742. These annual fluctuations in growth rate are not very large when expressed in absolute units in length, particularly in the later years of life. Nevertheless, they must be regarded as real differences due to annual changes in conditions for growth. The geometric law making the best fit to the observed results may be regarded as the smoothing out of real fluctuations which are likely to recur year after year. Viewed in this light there should be no occasion for surprise, either that it should be possible to formulate a law fitting growth with the passage of time, or that individual increments of growth should differ from those indicated by that law. If there is anything unexpected in the matter it is that the law arrived at should be of the particular nature indicated above, although even here it is not necessary to insist that herring-growth is strictly of the geometric type whereby annual increments become less and less in constant ratio. Very possibly the total length does not truly approach an asymptotic limit, although its value at each year for many years in succession may for all practical purposes be sufficiently closely portrayed by a mathematical law which *does* demand an asymptotic limit.

Practical Application of Technique.

Using this technique on data given by Hjort (**23**), comparisons of growth have been made between samples of herrings obtained from various places in the North Sea. The results are shown in Table IX, the appropriate equation, its period of operation and the limiting value set by it, being given in each instance :—

TABLE IX

Locality.	Reference to Sample (Hjort, **23**).	Period of operation of equation.	Equation.	Limiting value. (cm.)
Lowestoft	Collection 25, pp. 147 and 149			
	Year-class 1904	l_1 to l_5	$Y = \cdot 6X + 11 \cdot 0$	27·5
	Year-class 1902	l_1 to l_7	$Y = \cdot 635X + 10 \cdot 0$	27·4
Grimsby	Collection 26, p. 155			
	Year-class 1904	l_1 to l_5	$Y = \cdot 62X + 10 \cdot 5$	27·6
Faroes	Collection 21, p. 136			
	Year-class 1904	l_1 to l_4	$Y = \cdot 6X + 12 \cdot 6$	31·5
Shetlands	Collection 24, pp. 141–144			
	Year-class 1904	l_1 to l_5	$Y = \cdot 6X + 12 \cdot 6$	31·5
	Year-class 1903	l_1 to l_6	$Y = \cdot 6X + 12 \cdot 6$	31·5
	Year-class 1900	l_1 to l_8	$Y = \cdot 6X + 12 \cdot 6$	31·5
	Year-class 1902	l_1 to l_7	$Y = \cdot 62X + 11 \cdot 8$	33·1
Iceland	Collection 15, p. 111			
	Year-class 1895	l_1 to l_{13}	$Y = \cdot 74X + 9 \cdot 5$	36·5
	Collection 16, p. 119			
	Year-class 1896	l_1 to l_{12}	$Y = \cdot 742X + 9 \cdot 57$	37·1
Iceland	Collection 17, pp. 123 and 125			
	Year-class 1901	l_1 to l_8	$Y = \cdot 74X + 9 \cdot 8$	37·7
	Year-class 1897	l_1 to l_{12}	$Y = \cdot 74X + 9 \cdot 4$	36·2

It is seen that the limiting value rises from about 27·5 cm. off Lowestoft to 37–38 cm. in Iceland. In the equations there is a marked change in the value of M and a less pronounced change in C. This alteration in limiting value and form of equation from southward to northward brings to mind the fact that the number of vertebræ shows a similar tendency. (*Vide* Schnakenbeck **29** and **30**.)

One important matter not taken into account in the results of Table IX is the possibility that individual samples are " mixtures " which ought not to be treated as homogeneous for the study of growth in length. It is emphasized, therefore, that these results are in no sense to be regarded as a critical analysis of the growth in the different regions dealt with. They are merely intended to show the kind of regional differences in growth which are revealed by using growth equations. The samples considered are a selection from Hjort's invaluable data which lend themselves fairly easily to treatment.

" Mixed " Growth.

Many of Hjort's samples cannot be fitted with a single equation in the manner illustrated in previous pages. Nevertheless it is found that two equations instead of one will satisfy the data. Hjort's Collection 27, Year-class 1900, caught off North Shields (Hjort, **23**, p. 159), may be used as an initial illustration :—

l_1	l_2	l_3	l_4	l_5	l_6	l_7	l_8	l_9
9·0	16·1	20·0	22·3	23·6	24·6	25·3	26·0	26·6

t_2	t_3	t_4	t_5	t_6	t_7	t_8	t_9
7·1	3·9	2·3	1·3	1·0	0·7	0·7	0·6

$\frac{t_2}{t_1}$	$\frac{t_3}{t_2}$	$\frac{t_4}{t_3}$	$\frac{t_5}{t_4}$	$\frac{t_6}{t_5}$	$\frac{t_7}{t_6}$	$\frac{t_8}{t_7}$	$\frac{t_9}{t_8}$
·56	·55	·59	·565	·77	·70	1·0	·86

Looking at the values of the ratio $\frac{t_{n+1}}{t_n}$, it is seen that up to l_5 it varies only between ·55 and ·59, but that there is then a marked rise to ·77. Not at any subsequent time does the ratio fall to the level at which it remained during the earlier years. Using the equation $Y={\cdot}57X+10{\cdot}9$ from a commencing value of $X=9{\cdot}0$ we get

l_1	l_2	l_3	l_4	l_5
9·0	16·0	20·0	22·3	23·6

These values are almost identical with the observed values, and represent growth which is steadily falling off towards an asymptotic limit of $\frac{10{\cdot}9}{{\cdot}43}=25{\cdot}3$ cm. It is obvious, however, that a change occurs at l_5. Let us therefore try a second equation, $Y={\cdot}75X+6{\cdot}95$, commencing with $X=23{\cdot}6$:—

l_5	l_6	l_7	l_8	l_9
23·6	24·6	25·4	26·0	26·5

These results are a close approximation to the observed values, and represent growth which is steadily falling off towards a limiting value of $\frac{6{\cdot}95}{{\cdot}25}=27{\cdot}8$ cm., as compared with the limit of 25·3 cm. towards which the curve of growth up to l_5 was approaching.

The Norwegian samples provide numerous cases of growth which cannot be fitted by a single growth equation. Hjort's data concerning fishes of year-class 1904 make an instructive study in this connection. In the following table his data of Collection 5 from Leinæs Hammerö (p. 52) and of Collection 9 from 60° 30′ N. 3° 30′ E. (p. 71) are compared. In the case of the increments t_1, t_2, etc., the year when the increase was made is shown :—

						1905.	1906.	1907.	1908.
	l_1	l_2	l_3	l_4	l_5	t_2	t_3	t_4	t_5
Collection 5	7·0	11·9	15·4	19·3	22·7	5·0	3·4	3·9	3·4
Collection 9	8·4	15·9	21·9	25·3	27·6	7·5	6·0	3·5	2·2

Consider the two equations beneath in connection with the growth from l_1 to l_3:—

$$(1)\quad Y = \cdot 695X + 7\cdot 1 \qquad \text{and } (2)\quad Y = \cdot 80X + 9\cdot 18$$

$$\text{The limiting value for (1) is given by } \frac{7\cdot 1}{\cdot 305} = 23\cdot 3 \text{ cm.}$$

$$\text{The limiting value for (2) is given by } \frac{9\cdot 18}{\cdot 20} = 45\cdot 9 \text{ cm.}$$

Applying equation (1) for a commencing value of 7·0 cm. and equation (2) for a commencing value of 8·4 cm. we get

	l_1	l_2	l_3
Equation (1)	7·0	11·96	15·41
Equation (2)	8·4	15·90	21·90

Comparing these results with Hjort's data it is seen that equation (1) reproduces the values for Collection 5 and equation (2) those for Collection 9. Thus the growth of the fishes of Collection 5 during the years 1905 and 1906 was quite different from the growth of the fishes of Collection 9 during the same two years.

Next, consider two further equations in connection with the growth from l_3 to l_5:— $(3)\quad Y = \cdot 87X + 5\cdot 9$ and $(4)\quad Y = \cdot 615X + 11\cdot 9$

The limiting values are :—

$$\text{for (3)} \ldots\ldots \frac{5\cdot 9}{\cdot 13} = 45\cdot 4 \text{ cm.}$$

$$\text{for (4)} \ldots\ldots \frac{11\cdot 9}{\cdot 385} = 30\cdot 9 \text{ cm.}$$

Applying equation (3) for a commencing value of 15·41, and equation (4) for a commencing value of 21·90, the following values are obtained :—

	l_3	l_4	l_5
Equation (3)	15·41	19·3	22·7
Equation (4)	21·90	25·37	27·5

That is to say the growth of the fishes of Collection 5 from l_3 to l_5 is reproduced by equation (3), and that of the fishes of Collection 7 by equation (4). Hence in 1907 and 1908, as well as in 1905 and 1906, the growth was different for the two collections.

Summarising, it is now seen that Collection 5 shows a growth from l_1 to l_3 towards a limit of about 23 cm., followed by a growth from l_3 to l_5 towards the much higher limit of about 45 cm. The change in growth rate results in the increment t_4 added during 1907 being greater than t_3 laid down in 1906. In contrast, Collection 9 shows a growth from l_1 to l_3 towards a high limit of approximately 46 cm., followed by a growth from l_3 to l_5 towards a much lower limit of about 32 cm. The change in growth rate at l_3, however, is not so self-evident as in Collection 5 (where the dominance of t_4 over t_3 is visible) and only becomes apparent when growth is analysed.

How are these results to be interpreted? A reasonable answer to this question is twofold in nature :—

(*a*) That the fishes of Collection 5 were under quite different conditions for growth during 1905 and 1906 from those under which the fishes of Collection 9 were growing during the same period. Similarly during 1907 and 1908.

(*b*) That the fishes of the same Collection, whether 5 or 9, were not under the same conditions for growth during 1905 and 1906 as they were during 1907 and 1908.

Growth in Length as Evidence of Migration.

If the conclusions (*a*) and (*b*) just given are substantially correct, it seems to follow that the growth characters revealed by the study of scale-measurements can be used as clues to herring migrations. This point has been strongly advocated by Lea (**27**). The Norwegian investigator contends that the history of growth of the different year-classes occurring in a catch may exhibit certain extremely characteristic and striking peculiarities which, precisely because they deviate from the normal, may very easily be observed and recognised. He has no hesitation, therefore, in asserting that Norwegian herrings occurred in the spawning condition off the Faeroes in 1910, intermixed with non-Norwegian (Faeroese) herrings, and also suggests that spring-spawning herrings taken off the Shetlands in March-April, 1923, were also Norwegian fish, especially of the year-class 1918. He also shows how the fish caught in the Skagerak by Swedish and Norwegian vessels fishing independently agreed in growth characters not only with one another but with those from shoals met with at the west coast of Norway a little south of Cape Stadt. All belonged to shoals or groups of immature Norwegian herring. Thus Lea arrives at the conclusion that ". . . it is possible to identify or recognise Norwegian herring even if they occur in localities where one would not have expected them." The investigations of Storrow (**32**) also, in distinguishing between growth in "narrow seas" and that under "oceanic" conditions, follow very similar lines as regards their underlying principle. All that is claimed for the method of calculating growth equations in this type of investigation is that it provides a convenient and practical technique of growth-analysis which will readily reveal the characteristics of growth in different places, and facilitate the carrying out of growth-comparisons. While Lea and Storrow would be directly influenced in their judgment by the absolute size of the increments added to its length by a fish during a period of time, the investigator using the equations would review the same basic facts, but in terms of the growth-equations reproducing the increments, rather than of the increments themselves. As with any other method which seeks to trace the migrations of herrings by indirect means, however, one needs to consider when the technique can be legitimately applied and how the results of its use must be interpreted.

The Plymouth Shoals.

In this discussion on growth in length we have been drawn away from the situation at Plymouth. Growth studies of the herrings visiting Plymouth waters have shown that the shoals are " mixed " in a complex manner as regards growth in length. It is impossible to give a single equation which, by continuous operation, will give successive values l_2, l_3, etc., that may be considered as a " type " of growth representative of the Plymouth fish. There is no such " type." On the other hand, it has previously been suggested (Ford, **9**, p. 299) that if the spawning shoals visiting Plymouth are assumed to have come partly from the more enclosed waters of the English Channel and partly from the more open waters at the Atlantic end of the Channel (conditions for growth in these two areas being different), the complex growth-data can be interpreted in terms of migratory changes.

It has already been demonstrated (p. 334) that at the extreme eastern end of the Channel and the Southern Bight, growth is not greatly different from that reproduced by the equation $Y = \cdot56X + 11\cdot5$. It has also been shown (Ford, **12**) that fishes caught off the Sussex coast, as well as those which Hodgson terms his " Channel type," differ from the above only in the length l_1, growth being otherwise of a similar order. Coming westward to Portland and Plymouth, le Gall (**18**, p. 47) gives data concerning samples taken from catches off Brixham in Portland Bay, and in the bay of Plymouth :—

	l_1	l_2	l_3	l_4	l_5	l_6	l_7
Brixham . .	12·20	18·30	21·00				
Plymouth . .	11·88	18·46	21·72	23·30	24·50	25·54	26·40

The Brixham sample is satisfactorily fitted by the equation $Y = \cdot56X + 11\cdot5$ and the Plymouth data, which Gilson refers to as le Gall's " type côtier," have already been shown (p. 334) to be in accordance with this same equation. That is to say, samples at Brixham and Plymouth, examined by le Gall, have been found which show growth of the same character as that of fishes from the Southern Bight and eastern English Channel. But le Gall in the same paper also gives data from the coast of Brittany :—

	l_1	l_2	l_3	l_4	l_5	l_6
Audierne	10·98	17·40	21·20	22·98	24·40	25·17
Penmarc'h	11·50	17·50	20·30	22·00		
Le Croisic	12·17	18·60	22·00	23·70	25·00	25·50

Of these it can be said that the samples from Audierne and le Croisic are reasonably well fitted by the equation used above, and even those from

Penmarc'h are not greatly different. From the Southern Bight to Brittany, therefore, herrings have been taken which have all grown according to one and the same growth curve, although differing in the length l_1.

But while this is true, it must be observed that not all the herrings in the Plymouth area have growth-characters which are fitted by the equation $Y=\cdot56X+11\cdot5$. Thus, it was shown above on p. 334 that herrings caught in the Bay of Plymouth by le Gall and called by him the "type atlantique" do not conform to the equation. Nor will all the data collected at the Plymouth laboratory be thus satisfied. On the contrary, it becomes necessary to utilise fresh equations which give a higher limiting value than that imposed by the equation $Y=\cdot56X+11\cdot5$. In this connection, it is of interest to refer to data brought together by Watkin (**48**) and referring to herrings taken in south-western waters. In his Table XX, on p. 87, Watkin records the average size at the formation of each winter ring for (*a*) drift herrings caught mainly in statistical region VIIg off the south-west coasts of Great Britain, (*b*) trawled herrings of the "Smalls," and (*c*) drift herrings taken at Plymouth and examined by Ford (**9**, p. 295) :—

	l_1	l_2	l_3	l_4	l_5	l_6	l_7	l_8	l_9
(*a*)	12·6	20·2	24·0	26·2	27·4	28·2	28·8	29·5	29·9
(*b*)	15·9	23·6	25·4	27·2	28·0	28·7	29·6	29·8	30·0
(*c*)	13·88	21·03	24·64	27·02					

Considering (*a*) above, it has been found that the lengths l_1 to l_5 are in accord with the results of the repeated operation of equation $Y=\cdot53X+13\cdot5$, and the lengths l_5 to l_9 to a second equation $Y=\cdot85X+4\cdot87$. That is to say, the drift fish in region VIIg grow from l_1 to l_5 towards an asymptotic limit of $\frac{13\cdot5}{1-\cdot53}=28\cdot7$ cm., and from l_5 to l_9 towards a higher asymptotic limit of $\frac{4\cdot87}{1-\cdot85}=32\cdot5$ cm. The observed values of l_5 to l_9 and the values calculated from the two equations are given together below, and it will be seen that they are in close agreement :—

	l_1	l_2	l_3	l_4	l_5	l_6	ll_7	l_8	l_9
Observed . .	12·6	20·2	24·0	26·2	27·4	28·2	28·8	29·5	29·9
Equation . .	12·6	20·18	24·20	26·32	27·45	28·20	28·84	29·39	29·86

Turning next to the fish from the "Smalls," (*b*) above, it is found that except for the one period l_1 to l_2, the growth corresponds with that of the drift fish from VIIg, in that from l_2 to l_5 the equation $Y=\cdot53X+13\cdot5$ applies, and from l_5 to l_9, the equation $Y=\cdot85X+4\cdot87$:—

	l_1	l_2	l_3	l_4	l_5	l_6	l_7	l_8	l_9
Observed . .	15·9	23·6	25·4	27·2	28·0	28·7	29·6	29·8	30·0
Equation . .	19·06	23·6	26·0	27·28	27·96	28·64	29·22	29·71	30·12

The "Smalls" fish thus differ from the drift fish from VIIg in that they are on an average larger at l_1 and grow to a greater size at l_2; subsequently, however, their growth is of a similar order.

The Plymouth data, (*c*) above, like those of the drift fish from VIIg are satisfied by the equation $Y = \cdot 53X + 13\cdot 5$ from l_1 to l_3:—

	l_1	l_2	l_3	l_4
Observed . . .	13·88	21·03	24·6	27·02
Equation . . .	13·88	20·86	24·56	26·52

All the foregoing observations have a bearing upon the composition of the herring shoals which come to Plymouth in the winter and spring for spawning. Some of the fish are indistinguishable in growth from fishes taken in the Atlantic fisheries; others resemble fishes taken in the eastern part of the English Channel, while others, again, show a "mixed" growth in the sense that they resemble Atlantic fish at some part of their growth, and the more easterly fish at another. A reasonable interpretation of these variations in growth character is that the Plymouth spawning grounds are visited by shoals coming both from the westward and the eastward. Those fishes coming from the westward will have fed and grown under Atlantic conditions during the summer preceding spawning, and will have grown more than those of a corresponding size and age which have remained within the more enclosed waters of the Channel. Furthermore, it is necessary to believe that fishes which come from the east or west to spawn do not necessarily return always to the same feeding grounds from which they come. In other words, the study of the growth in length from year to year is an indirect means of determining the nature and extent of the migrations between the Plymouth spawning area and the feeding grounds of the Channel and Atlantic. Concerning these migrations, Matthias Dunn (**4**) has written:—

> "On our coast (Devon and Cornwall), after spawning, Herrings generally take off into deep water, and seldom remain in one locality unless food is plentiful; and, as the summer advances, they generally find themselves far out in the deep waters of the Channel or in the Atlantic. When the autumn arrives . . . they gather themselves in large schools and move landwards to the necessary weedy coral or stony bed wherein to deposit their eggs. . . . One of the largest migrations ever noted on our southern coasts was in the autumn of 1892. Late in October our fishing boats fell in with quantities of Herrings some fifteen miles south of the Eddystone, while fishing for mackerel there, and, although only mackerel nets were at first used, so plentiful were they, that it was nothing uncommon for boats nightly to catch ten thousand herrings in them. Nothing seemed to disturb them, and, although apparently wandering at leisure, eventually it was found that they gradually but

surely kept up a northerly course, and early in December finally reached their spawning grounds on the Devon coast—to the east of Plymouth. . . . This is a sample of how Herrings generally migrate around the coasts; and, probably, the events connected with the migrations of the Herrings in the North Channel (i.e. off north coast of Cornwall) in their various stages, move much on the same lines. For some years past these northern fish have been in greater numbers than the southern schools, and in their spawning migration seem to strike the land somewhere to the north and east of Port Isaac. When their intuitions tell them that the range of ground for spawning purposes is unfit or insufficient for their wants in that immediate neighbourhood, they gradually drop down the coasts, leaving ample numbers to cover grounds near Padstow, Newquay, St. Ives, and Mounts Bay. Moreover, I think there can be no doubt that sometimes they have been in such numbers as to necessitate their moving further along the coast into the English Channel, and to have joined their friends near Plymouth in Bigbury Bay. For many years, off and on, when pilchards are migrating late in November, quantities of herrings will sometimes pass with them; and at other times Herrings will migrate along distinct from the pilchards. We have many times traced these fish from the Lizard to beyond Plymouth."

This scheme of migration, visualised by Dunn, appears to express, as clearly as possible, the general conception arrived at by the comparison of growth-rates among the fishes concerned, and there seems no necessity to suggest any radical alteration in the events described. The only addition considered necessary is that shoals do not always return to the grounds from which they came, with the result that "mixed" growth is a characteristic of the fishes over the whole area of distribution covered by the migratory cycles.

Genotypes in the Herring.

In foregoing pages, differences in rate of growth in length from one geographical region to another were discussed. Throughout the discussion, however, it was assumed that a "herring" was a "herring," the distinction between *phenotype* and *genotype* being ignored. The degree to which the observed variation in growth in length among the Plymouth fishes is genotypic as opposed to phenotypic, that is to say, the degree to which it is due to qualities inherited from the ancestors of the fish as opposed to qualities due directly to the conditions under which the fish has grown up, is a question for future investigation, but much work has already been done in an endeavour to recognise genotypes at Plymouth by analysing counts of the number of vertebræ. Many samples, taken at random from commercial catches, have been examined, and appreciable differences in number of vertebræ have been found, but the difficulties in interpreting the differences have been great. The facts as they appear to the writer will now be presented.

Variation in the Number of Vertebræ from Sample to Sample.

Adopting some arbitrary standard of counting, including or excluding the urostyle according to choice, the "number of vertebræ" for each fish in a sample may be determined, and a frequency table prepared which summarises the individual counts. In its simplest form this table will show the number of individuals having (x), (x+1), (x+2) . . . etc. vertebræ respectively, but it is a simple mathematical operation to reduce the original numbers to a percentage basis, as if the sample really consisted of exactly 100 fishes. The percentage-frequencies may also be presented graphically, plotting the values of (x), (x+1), (x+2) . . . etc., as abscissæ and the corresponding percentages as ordinates. Alternatively, recognised statistical methods may be followed for the calculation of the "arithmetic mean number of vertebræ" for a sample, together with the "standard deviation" and "standard error."

Whichever way one elects to summarise sample-data, whether as a table of frequencies, a graph of percentage-frequencies, or an arithmetic mean, one is free to make direct comparison between sample and sample and thus to establish the extent of agreement or disagreement. The circumstances governing a particular investigation will, of course, decide which form of summary is the most convenient to adopt for the purpose of comparison. Sample A may be found to differ from sample B by an amount *a*, but the *significance* of the difference *a* cannot be accurately assessed without much detailed information concerning the samples themselves.

The samples to be discussed were taken from the regions shown in the chart on p. 307. Details of these samples are to be found in Ford (**8**), and also in Table XIX at the end of this paper in p. 383, and we shall first consider the total range of variation in number of vertebræ for all the samples examined, irrespective of locality and time of capture, or the length, age and sexual condition of the fishes taken. The individual number of vertebræ varies from 53* to 58* and the arithmetic mean from 55·48* to 55·99*. Fishes with 55 or 56 vertebræ together account for 78 per cent or more of every sample, while those with 57 vertebræ only rarely exceed 20 per cent. Fishes with 54 vertebræ hardly ever number more than 2 or 3 per 100, while those with 53 or 58 are very uncommon indeed.

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* These numbers do not include the urostyle. Throughout this paper, unless otherwise stated, the number of vertebræ, whether individual or as an average, is always exclusive of the urostyle.

Expressing the percentage frequency of each sample in the form of a graph, it is found that the shape of the graph varies between the extremes shown at the top and bottom of Fig. 7, with intermediates such as those indicated in the figure. The change in shape of the graph is clearly due to the fact that the percentage of fishes with 55 vertebræ which is so dominant in sample A becomes progressively reduced (see also Fig. 8),

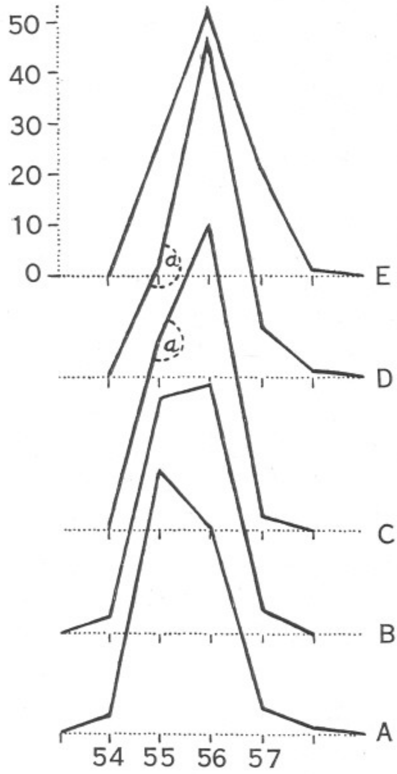

FIG. 7.—Five percentage frequency graphs of the number of vertebræ, representative of the range of variation in form.

A... Sample from statist. region VIIg. July, 1926.
B... ,, ,, Mounts Bay. March, 1926.
C... ,, ,, Brighton. December, 1926.
D... ,, ,, Plymouth. February, 1925.
E... ,, ,, statist. region VIIg. June, 1926.

In graph C, the angle *a* is less than 180°.
In graph D, the angle *a* is more than 180°.

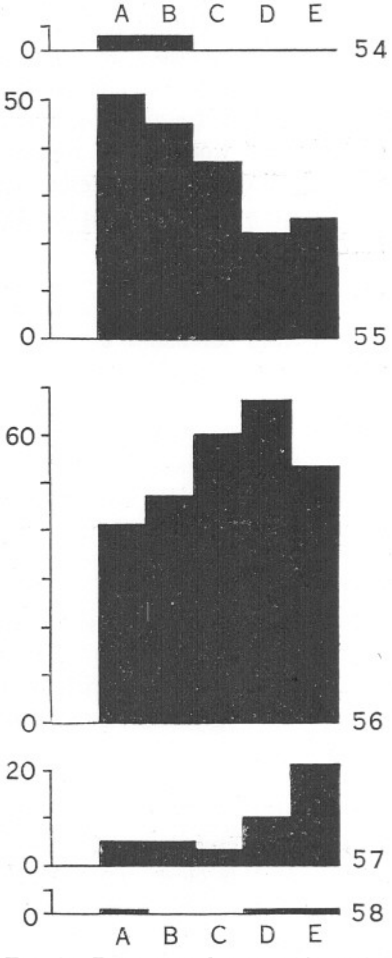

FIG. 8.—Percentage frequency in vertebral number for samples A to E. (See also Fig. 7.)

while the percentage of fishes with 56 vertebræ is increased. The percentage with 57 vertebræ increases from sample A to sample E.

Schnakenbeck (**29** and **30**) has strongly advocated the extensive use of percentage-frequency graphs of the kind shown in Fig. 7, and it is not denied that a pictorial representation of percentages will conveniently and plainly convey to the mind the composition of a sample with regard to the number of vertebræ. But when graphs of the "single-peaked" type, such as C and D in Fig. 7, are superimposed one above the other, an artificial "sameness" in appearance is apt to be created which may mask considerable differences in vertebral composition. For detailed comparison of frequency-graphs, therefore, some description criterion of "shape" would seem to be desirable. This is particularly needed when dealing with the present samples, the majority of which give the single-peaked type of graph. The following arbitrary* standards have been adopted :—

Class 1.

Percentage of fishes with 55 vertebræ is greater than that of fishes with 56 vertebræ. The frequency graph is illustrated by A in Fig. 7.

Class 2.

Percentage of fishes with 56 vertebræ is greater than that of fishes with 55 vertebræ, but the difference does not exceed 10%. The frequency graph is of the "truncated" type illustrated by B in Fig. 7.

Class 3.

Percentage of fishes with 56 vertebræ exceeds that for fishes with 55 vertebræ by more than 10 %, although it is less than twice the percentage for 55 vertebræ. Fishes with 57 vertebræ account for not more than 13%. Graph C in Fig. 7 belongs to this class.

Class 4.

Percentage of fishes with 56 vertebræ is at least twice that for 55 vertebræ. Percentage with 57 vertebræ is not more than 13%. In graphs of this class, represented by D in Fig. 7, the angle a is greater than 180°, whereas in graphs of class 3, angle a is less than 180°.

Class 5.

Percentage of fishes with 57 vertebræ is at least 14%, while the percentages for vertebræ 55 and 56 may agree with those of class 3 or 4. The frequency graph is typified by E in Fig. 7.

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* It should be understood that the classification is quite arbitrary and artificial, and is used merely as a convenient standard for the purpose in hand.

The total of 103 samples examined may thus be split up according to the above five classes :—

Class 1	1
Class 2	7
Class 3	30
Class 4	53
Class 5	12

It is seen that the bulk of the samples falls into classes 3 and 4, indicating that fishes with 56 vertebræ are usually in decided predominance. But this segregation of samples according to vertebral distribution proves to be a segregation according to the geographical regions in which the samples were taken. This is shown in Table X :—

TABLE X

Region.		Number of Samples according to Vertebræ-Class.					Totals.
		1	2	3	4	5	
VIIe.	(Sussex coast)	–	–	8	–	1	9
VIIe.	(Brixham and Exmouth)	–	–	5	3	–	8
VIIe.	(Plymouth area)	–	2	10	37	1	50
VIIe.	(Mevagissey)	–	–	–	2	–	2
VIIe.	(Mounts Bay)	–	1	–	2	–	3
VIIg.	(Between English and Irish coasts southward of 52°N.)	1	3	1	4	10	19
VIIf.	(Port Isaac Bay)	–	1	6	5	–	12
	Totals	1	7	30	53	12	103

It will be observed from Table X that the samples from region VIIg and VIIe (Sussex coast) are different both from one another and from those of other areas. Of the 19 samples from VIIg no less than 10 are of class 5, as against only 2 of this class in the 84 samples taken elsewhere. Furthermore, only 1 of the VIIg samples is of class 3, whereas in VIIe (Sussex coast) 8 out of the total of 9 are of this class. In other words, samples from the Atlantic end of the English Channel (region VIIg) are characterised by a higher number of vertebræ than samples from the eastern end of the Channel (region VIIe, Sussex coast).

The majority of the Plymouth samples fall into class 4 which is intermediate in character between classes 5 and 3. But, geographically, Plymouth occupies an intermediate position between VIIg and VIIe (Sussex coast). Similarly, the Brixham and Exmouth samples are intermediate between those from Plymouth and Sussex, and so, also, are the geographical positions.

This tendency for the number of vertebræ to rise from east to west in the English Channel has been shown in an earlier paper (Ford, **8**) by using the arithmetic means for the samples, instead of the percentage-frequencies.

Although in region VIIg samples of class 5 are so much in evidence, it is in this same region that samples of classes 1 and 2 are the most common. Hence, in one and the same region, there is wide variation in the number of vertebræ. Although somewhat less pronounced, the range in vertebral variation in the other regions is also considerable. While, therefore, there is a tendency for the number of vertebræ to rise from east to west in the English Channel, there is wide variation between samples taken in close proximity to one another.

The Conception of " Races " of Herrings.

Having noted the extent of the differences in number of vertebræ between samples, it is helpful to enquire how such sample differences might conceivably be brought about. It is generally believed that the number of vertebræ, once fixed in the early life of an individual, remains unaltered, so that the difference in vertebral number between *samples* of fish must be due to the manner in which fish group themselves during the successive phases of their life-history. The *shoal*, as usually conceived, is a naturally formed group of herrings composed of individuals which differ in age but do not vary greatly in length or swimming capacity. But for how long a given shoal retains its distinctive identity without becoming merged into a greater entity or split up into groups, it is difficult to say. Nor is it easy to determine at what rate the composition of a shoal is changed as the result of the replacement of older members by recruits. Yet such changes might conceivably result in marked changes in vertebral distribution. Consider a spawning shoal arriving at a spawning place. It will show a certain vertebral distribution, and, presumably, will have all its members in approximately the same state of sexual maturity. If that shoal spawned by itself, we should have a parental spawning population of given vertebral distribution giving rise to a new generation. More probably, however, the spawning stock will consist of more than one shoal. Nevertheless, the vertebral distribution of the total spawning population might still remain fixed at a certain value provided that each and every shoal showed the same vertebral distribution. If such were the case, it is logical to think that the shoals which leave after spawning would also be alike in vertebral distribution, even if the retiring shoals were quite different as regards their individual members from those which came to spawn. The conceivable contrast is that of a complex spawning population made up of a number of shoals which differ in vertebral distribution, and of retiring shoals for which the vertebral distribution is different from that of the ones which contributed to the spawning population.

On a feeding ground, as opposed to a spawning ground, the only character in common which it is necessary to attach to individual shoals is that all have come to feed. It is of little moment that they may differ in vertebral distribution. But later on, when the call of spawning occasions the concentration of fish prior to a movement inshore to the spawning place, the facts are otherwise. If smaller shoals join forces to form greater ones there arises the possibility of the coming together of " groups " of herrings which have hitherto been distinct in their number of vertebræ, unless there be some inherent character in the fishes which impels them to make a deliberate choice of their associates for spawning. In this event, the period when shoals concentrate for the spawning migration could be regarded as a " sorting-out " time when genotypes come apart.

This brings us face to face with all the problems associated with the hypothesis of " races " in the herring. In his important theses, Schnakenbeck (**29** and **30**) considers the division of the herring species into a number of races which are to be regarded as morphologically and physiologically distinct entities. He suggests that each race is characterised by its number of vertebræ, which can be expressed in the form of a distinctive frequency graph. Members of a race spawn at a given time of year in given places, the continuity of the race from generation to generation being preserved by the strict inheritance of the number of vertebræ and by the fact that no two races spawn on the same ground at the same time.

If the basic premises for this conception of herring races were proven facts, it would be permissible to treat all samples of catches as race-samples, of which some might be homogeneous in race but others mixtures of races. Differences between samples would thus be manifestations of differences in racial composition. Indeed, this has been done already by Schnakenbeck himself who has postulated two distinct races within the geographical area covered by the Plymouth data. He includes all the herrings of the English Channel in one race, " The Channel Sea Herring," but refers those of the Smalls to a second race, designated " The Smalls Herring." Reserving judgment as to the validity of the premises on which Schnakenbeck has established these races, it is instructive to treat the Plymouth samples as if they were race-samples.

The " Channel Sea Herring " and the " Smalls Herring."

From Schnakenbeck's Fig. 33 (**30**, p. 516), which is here reproduced as Fig. 9 on p. 352, the form of the frequency graph typifying the number of vertebræ for the two races may be seen. It must be noted, however, that Schnakenbeck's count of the vertebræ is always one vertebra greater than the Plymouth count, since he includes the urostyle. Series A to the left of the figure represents the " Smalls " race, and series B on the right, the

"Channel" race. Reference to Schnakenbeck's legend to his Fig. 33 shows that the samples of Series A are actually the class 5 samples from region VIIg already referred to above, while it is evident from the figure itself (reproduced here as Fig. 9) that the Series B are class 3 samples from region VIId and e. The vertebral frequencies which Schnakenbeck uses as types of the races is given in p. 550 of his paper (**30**) :—

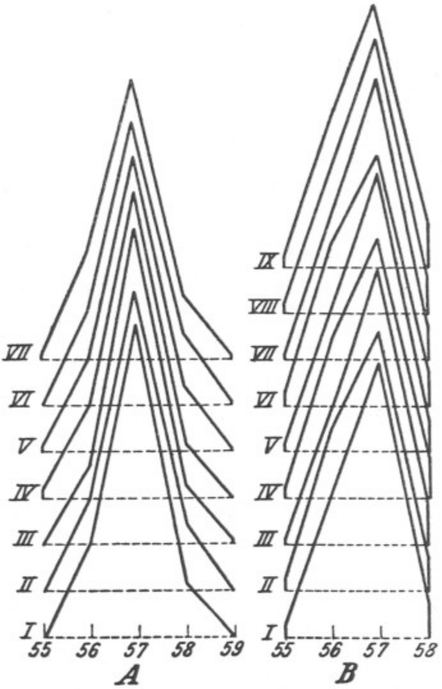

Fig. 9.—Reproduction of Fig. 33 from Schnakenbeck (**30**).
Series A.....Samples from "Smalls," region VIIg.
Series B.....Samples from Eastern English Channel.

		Number of Vertebræ.				
	Schnakenbeck's count	55	56	57	58	59
	Ford's count	54	55	56	57	58
"Smalls" race		–	20	64	14	1
"Channel" race		3	31	59	7	–

Here again it is seen that the vertebral frequency is of class 5 for the "Smalls" race and class 3 for the "Channel." The difference between these two frequencies and their graphic representation is so pronounced that no one will question their separation, even if doubts are retained as to their racial significance.

But since samples of classes 5 and 3 occur in other regions, it would seem necessary to stipulate that fishes of the " Smalls " race (or some other race having a similar vertebral frequency) may occur at Plymouth and even to the eastward of Plymouth as far as off the Sussex coast, and also that fishes of the " Channel " race (or another race having a similar vertebral frequency) are to be found off Exmouth and Plymouth and in the western regions VIIf and g. The inevitable conclusion from this is either that there is an extensive overlap in the range of distribution for the two races named, or that races other than the " Smalls " and the " Channel " are represented in the samples. The same difficulty arises if we accept the findings of le Gall (**17**), who some years ago distinguished between " Hareng type Atlantique, variété côtière " inhabiting the Channel proper, and " Hareng type Atlantique, variété du large " which were confined to deeper water and included the fish trawled at the Smalls and elsewhere in region VIIg.

But all the samples taken within the area of investigation are not of classes 5 and 3 alone. There are the samples of classes 1, 2 and 4 to be considered, and each region presents difficulties on this account. In regions VIIf and g, in Mount's Bay and at Plymouth, samples of classes 1 and 2 occur for which the vertebral frequency graph is quite unlike that of either class 5 or class 3. Schnakenbeck has remarked on this (**30**, p. 516) and definitely excluded them from his two main races. Perhaps the greatest difficulty arises, however, when we come to consider the samples of class 4, for which the vertebral frequency graph is of a form intermediate between those of classes 5 and 3. How are they to be interpreted ? This question is of especial import in the Plymouth area where 37 out of the total of 50 samples belong to this class. Why in this area where the shoals are unquestionably assembled for spawning should there be such a dominance of samples which differ in vertebral distribution from the type-distributions characterising the " Channel " race and the " Smalls " race ? If, as Schnakenbeck suggests (**30**, p. 518), the great majority of the Plymouth herrings in the winter months belong to the same race (i.e. the " Channel " race) as the herrings of the eastern Channel one would have expected close agreement in number of vertebræ between the majority of the Plymouth samples and those from off the Sussex coast. Instead, it is found that the Sussex samples are almost entirely of class 3, those of class 4 being absent, whereas at Plymouth class 4 samples outnumber those of class 3 by nearly 4 to 1. It will be necessary in a moment to note the degree to which the " number of vertebræ " for a sample of class 4 differs from that of a sample of class 3, but even if the difference were but slight, the fact remains that there *is* a difference, and that the Plymouth samples as a rule contain fewer fishes with 55 vertebræ and more than 56 than is shown by the Sussex samples. If, then, the " Channel " race actually exists, which are the purer samples of the race, those from Plymouth or those from Sussex? Furthermore, how does the difference between samples of class 3 and class 4 arise?

As a step in the study of these questions let us determine the extent of the difference between the vertebral distribution shown by the Plymouth samples and those from Sussex, restricting attention to those of classes 3 and 4. In the following Table XI samples are tabulated according to the percentage of fishes with 55 and 56 vertebræ respectively, in the form of a correlation table. The data relating to Sussex samples of class 3 are shown in the bolder clarendon type, those relating to Plymouth samples of class 3 are in italics, while the plain numbers refer to Plymouth samples of class 4 :—

TABLE XI

NUMBER OF SAMPLES ACCORDING TO PERCENTAGES OF FISHES WITH 55 AND 56 VERTEBRÆ.

Percentage of fishes with 55 vert.	Percentage of fishes with 56 vertebræ.																				Totals.		
	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71			
20																				1	–	–	1
21																			2		–	–	2
22																1			1		–	–	2
23													1								–	–	1
24													1		2	1					–	–	4
25									1	1	1	1				1					–	–	5
26										1			1	2				1			–	–	5
27										3			2		1	1					–	–	7
28												1		1							–	–	2
29							1		2		1										–	–	4
30											1		1								–	–	2
31									**1**	*1* **1**		1									**2**	*1*	1
32						**1**		*1*			1										**1**	*1*	2
33									*1*												–	*1*	–
34				*1*					*1*												–	*2*	–
35	*1*	*1*		**1**				*1*													**1**	*3*	–
36																					–	–	–
37		**1**	**1**			**1**			**1**												**4**	–	–
38																					–	–	–
39					*1*																–	*1*	–
40																					–	–	–
41																					–	–	–
42		*1*																			–	*1*	–
Totals	–	**1**	**1**	**1**	–	**2**	–	–	**2**	**1**	–	–	–	–	–	–	–	–	–	–	**8**		
	1	*2*	–	*1*	*1*	–	–	*2*	*2*	*1*	–	–	–	–	–	–	–	–	–	–		*10*	
	–	–	–	–	–	–	1	–	3	5	4	3	6	3	3	4	–	1	3	1			37

Sussex samples of class 3 are shown thus : **1**
Plymouth ,, class 3 ,, ,, ,, *1*
Plymouth ,, class 4 ,, ,, ,, 1

It is seen from Table XI above that there is very little overlap between the Sussex samples of class 3 and the Plymouth samples of class 4. Whereas the former show from 31–37% of fishes with 55 vertebræ and from 53–61% of those with 56 vertebræ, the latter show from 20–32% with 55 vertebræ and from 58–71% with 56 vertebræ. On the other hand, the class 3 samples from the Sussex coast agree very well with the class 3 samples from Plymouth.

There appear three possible explanations of this definite difference between the Plymouth and the Sussex samples :—

1. The Sussex samples are "pure" samples of the Channel race, whereas the Plymouth samples are mixtures of Channel and some other race.
2. The Plymouth samples are "pure" samples of the Channel race, whereas the Sussex samples are mixtures of races.
3. Both the Sussex and the Plymouth samples are mixtures of races.

There is evidence from other sources that, at the eastern end of the English Channel and entrance to the North Sea, samples of herrings vary considerably in vertebral character. Thus, le Gall (**19**, p. 254), dealing with the French fisheries, has had to divide his area into three regions, in each of which the herrings differ in number of vertebræ. In the region southward of the Somme, from that river to Cap Antifer, the herrings are assigned to "Groupe II," for which the number of vertebræ as determined by samples during the past few years is as follows :—

	Percentage number of Vertebræ.					
le Gall's count . .	54	55	56	57	58	59
Ford's count . .	53	54	55	56	57	58
1928	—	0·9	29·3	59·1	10·1	0·4
1929	0·2	1·2	30·7	57·7	9·9	0·2
1930	—	0·6	30·8	61·8	6·8	—

Fishes of this "Groupe" are regarded as of a distinct "Channel" race, and it is seen that they conform very closely with Schnakenbeck's figures. It is also worth noting that the number of vertebræ on average tends to be on the low side as compared with the Plymouth samples of class 4. Thus, the percentage of fishes with 56 vertebræ does not amount to 62%, while the percentage with 55 vertebræ is not less than 29% (cf. Table X on p. 349).

Le Gall's second region is to the northward of the Somme between Cap Griz-Nez and the Somme, and the herrings are here referred to "Groupe I" : —

	Percentage number of Vertebræ.					
le Gall's count .	54	55	56	57	58	59
Ford's count . .	53	54	55	56	57	58
1928	1·2	3·4	44·4	45·8	5·2	—
1929	—	2·5	35·3	55·3	6·7	—
1930	0·2	1·8	35·0	56·4	6·3	0·2

There is in this group more variation. It is seen that by comparison with the classification used in this paper, the 1928 analysis is of our class 2, while those of 1929 and 1930 are of our class 3. Le Gall regards these as varying admixtures of two races, namely, his " Channel " type and " The Southern North Sea " type, the latter being mainly confined to the Southern North Sea, and characterised by an average number of vertebræ lower than that of the Channel type. His " Southern North Sea " type would show a frequency graph of the " truncated " type somewhat similar to those given by our classes 1 and 2.

Le Gall's third group is the " Groupe Dyck-Sandettié," coming from the region Dyck–Sandettié–Ruytingen, and captured mainly in the trawl :—

	Percentage number of Vertebræ.						
le Gall's count	54	55	56	57	58	59	
Ford's count	53	54	55	56	57	58	
1928	0·8	2·5	35·3	55·3	6·7	0·2	
1929	0·3	4·5	43·7	47·3	3·8	0·1	(also 0·3 less than 53 vert.)
1930*			39·0*	52·7*	6·5		

Here again, le Gall is led to regard these samples as mixtures of the two races named above, for it is impossible to assign them to either one or the other.

Le Gall has thus been able to interpret his results only by extending the range of the " Channel " race into the North Sea and introducing North Sea fish into the Channel. Tesch (**35**), in his investigations of young herrings in the southern sea entrances of Holland, and of adult herrings from the southern North Sea and the eastern part of the English Channel, also finds it necessary to assume considerable overlap in range between races of the North Sea and those of the Channel, even going so far as to suggest " kinship " between the young fish from the Ooster-Schelde and the Plymouth fishes.

Gilson (**21**), too, investigating the Belgian fishery for " spent " herrings between Ostende and Cap Gris-Nez, obtained counts of vertebræ which cannot be reconciled with a single race.

Leaving the eastern end of the Channel to return to the Plymouth samples, it cannot be said that the samples show any greater tendency to conform to type than those in the localities just dealt with. Some of the Plymouth samples could be referred to the " Channel " race, but there remain others which could not, either because the number of vertebræ is too low (class 2 samples) or because it is too high (samples of class 5 and a proportion of those of class 4). If races exist, then the Plymouth samples provide evidence of race mixture.

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* There is an obvious error in the setting up of this table in the original, but the figures given appear to be the correct interpretation.

Summarising the conclusions reached in this section, it appears that :—

1. Not all the samples from VIIg conform with the " Smalls " race.
2. Not all the samples from the Plymouth district conform to the " Channel " race.
3. Not all the samples at the eastern end of the Channel conform to the " Channel " race.
4. The number of vertebræ tends to be higher in samples from the Atlantic end of the Channel than in those from the eastern end, although there is an appreciable range of variation in the sample-averages in each region investigated.

Samples from Plymouth and District.

Seeing that the Plymouth district is an important spawning ground, it is just here that one would most expect to obtain pure race samples. Furthermore, since spawning fishes may occur at Plymouth from the end of September until late in the spring, there would seem to be reasonable time for more than one race to spawn without overlap. But as the Plymouth samples were not specifically collected as part of a " race " enquiry, it is, perhaps, hardly surprising that they do not prove very satisfactory for this latter purpose. The majority of them are heterogeneous in the sense that they are composed of fishes which vary in the condition of the gonads, and none of them are sufficiently large to warrant the breaking-up into components.

There is some evidence, however, for believing that in the year 1925, fishes with a comparatively low number of vertebræ spawned within Plymouth Sound from the end of September until the beginning of November. On the nights of September 30th, October 8th, and November 1st, stop-nets set in the Sound beneath the Laboratory took catches which included a number of spawning fish, and on October 25th a drift-net catch in Cawsand Bay also included spawners. Further evidence of this local spawning was afforded by the capture of " spent " fish in the Tamar estuary on November 20th. The low number of vertebræ characterising these samples is exemplified by the following results :—

Date.	Locality.	Percentage number of Fishes with number of Vertebræ as follows :				
(1925).		54	55	56	57	58
October 25th	Cawsand Bay . .	3	42	53	3	–
November 1st	Below Laboratory . .	1	45	50	5	–
November 20th	Tamar Estuary . .	–	39	56	4	–

In the following year, 1926, a sample from the Sound below the Laboratory on October 21st, and samples from Cawsand Bay on October 18th and 25th included a few spawners, although not so many as in the previous year. Of these three, the Cawsand Bay sample of October 18th showed a low number of vertebræ, but the remaining two did not :—

Date. (1926).	Locality.	Percentage number of Fishes with number of Vertebræ as follows : 53	54	55	56	57	58
October 18th	Cawsand Bay . .	–	–	46	47	7	–
October 21st	Below Laboratory .	–	–	28	63	8	1
October 25th	Cawsand Bay . .	1	3	23	64	10	–

Samples taken on the open drifting grounds outside Plymouth Sound during October and November in 1925 and 1926, were composed entirely of "full" fishes at maturity-stages IV and V. Only one of these samples, namely that taken in East Bay on November 18th, 1925, showed a vertebral distribution comparable with the low values given by the samples from the Sound and Cawsand Bay. The remainder included a higher proportion of fishes with 56 vertebræ :—

Date.	Locality.	Percentage number of Fishes with number of Vertebræ as follows : 53	54	55	56	57	58
November 4th, 1925	Whitsand Bay . . .	–	1	24	67	8	1
November 18th, 1925	East Bay	–	2	35	59	5	–
November 3rd, 1926	Off Looe	–	–	28	65	7	–
November 4th, 1926	Off Rame Head . .	–	–	27	64	9	–
November 15th, 1926	Rame–Eddystone .	–	2	27	61	10	–
November 23rd, 1926	Rame–Eddystone .	1	1	29	62	7	–

Putting these facts together, there may be some justification for suspecting that in October and November, fishes which are low in number of vertebræ spawn in the neighbourhood of the Sound. But, outside the Sound on the usual drifting grounds, shoals are present which are not yet ready to spawn and which have a higher number of vertebræ. The difference in vertebral character between these two kinds is shown graphically in Fig. 10, the "flat-topped" graphs applying to the early spawners.

In contrast with this, it has been found almost impossible to make a similar separation of samples taken during December, January and February, when the main fishery is in progress. Considerable spawning occurs all the time, but vertebral distribution appears to vary without relation to the stage of maturity. In Table XII, data are given for ten samples, selected because they each consist for the most part of fishes in the spawning condition, i.e. at maturity-stage VI :—

TABLE XII

Sample.	Percentage number of Fishes with number of Vertebræ as follows : 54	55	56	57	58	Arithmetic Mean No. of Vertebræ.
1	2	34	55	8	1	55·72
2	1	32	62	4	–	55·70
3	2	31	61	5	1	55·72
4	–	30	62	8	–	55·77
5	1	29	60	10	–	55·80
6	2	27	61	10	–	55·79
7	–	27	64	9	–	55·83
8	2	24	64	10	–	55·82
9	–	23	63	14	–	55·91
10	1	20	71	8	–	55·86

Comparison between samples shows :—

1. The percentage of fishes with 55 vertebræ varies between 34% and 20%
2. ,, ,, ,, ,, 56 ,, ,, ,, 55% ,, 71%
3. ,, ,, ,, ,, 57 ,, ,, ,, 4% ,, 14%
4. The arithmetic mean no. of vertebræ varies from 55·70 and 55·91.

The differences between the samples is thus quite considerable, and yet all of them consisted mainly of spawning fishes. That is to say, it is hardly permissible to regard the samples as representative of one and the same race, unless the differences in vertebral composition are overlooked. Nor as an alternative, is it any easier to accept the vertebral differences as evidence of the presence of, say, two races, for this would mean that two races must be spawning together on the same grounds at the same time.

Vertebral Variation among Spawning Fishes.

In an endeavour to obtain fuller knowledge concerning the variation in the number of vertebræ among fishes spawning together, two larger samples of actually spawning fish were analysed during January, 1931. To obtain the first of these samples, the writer proceeded to Sidmouth in Devon, where the chances of obtaining spawners in the requisite quantity appeared to be most favourable. On January 6th, a drift-net catch of several thousands was landed, and as soon as possible after landing, a start was made in the process of going through the catch, fish by fish, gently squeezing the abdomen to determine whether or not ripe eggs could be expressed. All the fishes which had thus been proved to be females fully ripe for spawning were retained, and a total of 355 individuals

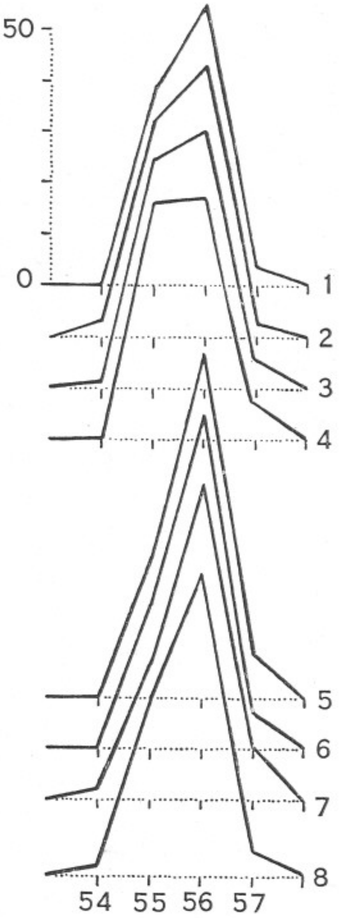

FIG. 10.

Percentage frequency graphs of number of vertebræ.

1. R. Tamar, November, 1925.
2. Cawsand Bay. October, 1925.
3. Sound. November, 1925.
4. Cawsand Bay. October, 1926.
5. Whitsand Bay. November, 1925.
6. Off Looe. November, 1925.
7. Rame–Eddystone. November, 1925.
8. Bigbury Bay. November, 1925.

was collected before the catch must needs be packed for transport. It may be explained that the restriction of the sample to females only was largely a matter of convenience. It is well known that at maturation the eggs become translucent and the ovaries lose their firmness—eggs escape easily from the body in response to slight pressure, giving a sure indication of ripeness. In the case of the males, there is not that certainty in distinguishing ripe from unripe—or so it appears to the writer.

The sample having been forwarded to Plymouth, the length of each fish was determined, the age was read from the scales, and the number of vertebræ in the cleaned skeleton was counted. In reading the age from the scales, some disappointment was felt when it was found that by no means every fish could be referred with certainty to a definite year-group. Since it was undesirable to reject any part of the sample on this account, additional age-classes had to be created so that every fish would be included in the final summary of age.

The sample as a whole and in its age-components gave the following results :—

TABLE XIII

	Number of Fishes in each of the following Vertebræ-Classes :							
Age-Group.	54	55	56	57	58	Abnormal Skeletons.	?	Total Counts.
?	–	–	1	–	–	–	–	1
2	–	1	2	1	–	–	–	4
3	–	32	51	2	–	4	1	85
3 or 4	–	14	35	3	–	–	–	52
4	1	24	36	9	–	2	1	70
4 or 5	–	6	10	4	–	1		20
5	–	11	31	8	1	4	–	51
5 or 6	–	4	11	2	–	–	–	17
6	1	9	16	3	–	–	–	29
6 or 7	–	1	4	–	–	–	–	5
Older than 6	–	5	1	1	–	1	–	7
Total Sample	2	107	198	33	1	12	2	341

Although the numbers of fishes in the separate age-groups are not as large as could be wished, the following calculations of arithmetic means and errors serve their purpose in demonstrating that the vertebral distribution is subject to appreciable variation :—

Age Groups.	Total Number of Fishes.	Arithmetic Mean Number of Vertebræ.	Standard Error of Mean.
Whole sample	341	55·777	·067
Younger fishes (Age-groups 2, 3, 3 or 4)	141	55·709	·046
Older fishes (Age-groups 4 or 5, and all older groups)	129	55·860	·060
3	85	55·647	·057
5	51	55·980	·095
5 and 6	80	55·900	·078

Whether or not these differences in average number of vertebræ may be considered significant is shown by the results of tests of independence given in Table XIV :—

TABLE XIV

Age Groups compared. I	with II	Arithmetic Means. M_2	M_1	Difference. (M_2-M_1)	Standard Error of Difference.	Ratio : Difference / Standard Error.
5	3	55·980	55·647	0·33	0·11	ca. 3
5 and 6	3	55·900	55·647	0·25	0·096	> 2
whole sample	3	55·777	55·647	0·13	0·067	ca. 2
5	whole sample	55·980	55·777	0·20	0·10	ca. 2
Older fishes	Younger fishes	55·860	55·709	0·15	0·075	ca. 2

From these results one is at least justified in hesitating to regard the total samples as " homogeneous " in vertebral distribution. The fishes of age-group 3 appear not to agree with those of age-group 5, or with those of groups 5 and 6 taken together, and younger fishes do not agree with older ones. Recalling that every fish in this Sidmouth sample was a fully-mature female, ready to spawn if not actually doing so, it is difficult to escape the conclusion that the spawning population sampled was a mixed assembly of fishes which differed in vertebral distribution from age-group to age-group.

The second sample came from a total of about one thousand herrings caught by s.s. *Salpa,* using the otter trawl in Bigbury Bay on January 14th, 1931. With the assistance of four colleagues at the Plymouth Laboratory, a total of 623 fishes from this catch were subjected to an analysis of length, sexual condition, age and number of vertebræ. In all, 439 individuals were ripe (Stage VI), while the remaining 184 included " full " fishes at stage V, and " spents " at stage VII.

It was found that the male fish were generally shorter in length than the females :—

Sex.	Stage of Maturity.	Length Classes (cm.) 21	22	23	24	25	26	27	28	29	30	Mean Length Male.	Female.
♂	VI	–	–	2	3	13	74	103	64	17	2	27·45	
♀	VI	–	–	–	1	2	29	66	47	13	3		27·79
♂	V	–	–	–	1	5	28	33	17	7	1	27·42	
♀	V	–	–	–	–	2	15	24	15	5	1		27·65
♂	VII	1	–	–	1	1	–	3	1	–	–	26·07	
♀	VII	–	–	–	–	2	4	4	5	6	2		28·15

Finding that the difference in length between male and female persisted even when age was also taken into account, it was decided to treat the sexes separately in the investigation of their number of vertebræ, as in Table XV :—

TABLE XV

	No. of Fishes in following Vertebræ Classes.					Arithmetic Mean No. of Vertebræ.	Total No. of Fishes.
	54	55	56	57	58		
A. Whole Sample							
Males only	3	121	226	27	–	55·735	377
Females only	–	76	143	26	1	55·805	246
Both sexes	3	197	369	53	1	55·762	623
B. Fishes at Stage VI							
Males only	2	97	159	20	–	55·709	278
Females only	–	50	94	17	–	55·795	161
Both sexes	2	147	253	37	–	55·740	439
C. Fishes NOT at Stage VI							
Males only	1	24	67	7	–	55·808	99
Females only	–	26	49	9	1	55·823	85
Both sexes	1	50	116	16	1	55·815	184

It is clear from Table XV that the females were not only of a greater average length, but had a higher average number of vertebræ. The male fish at maturity stage VI gave interesting results. Of the total of 278, no less than 142 were old fishes exceeding the age of 6 zones, 6 rings, and having the following number of vertebræ :—

No. of Vertebræ	54	55	56	57	58
No. of Fishes	1	56	77	8	–

Arithmetic Mean No. of vertebræ = 55·648
Standard Error of Mean = 0·050

The male and female fish at maturity stage VI thus gave the following averages :—

	Arithmetic mean No. of vertebræ.
"Old" Males	55·648
Other Males	55·772
Females	55·795
All	55·740

Statistical test shows that the difference of 0·147 vert. between the mean for the old males and that for the females can hardly be attributed to chance. This being so, not much significance can be attached to the actual value of the arithmetic mean number of vertebræ for all the fishes of stage VI taken together. Thus, as was the case with the Sidmouth sample, there is reason to doubt whether the spawning population sampled was really homogeneous in vertebral character.

It cannot be claimed that the results given by these two samples definitely prove that spawning populations may be mixed in vertebral character, but they certainly demonstrate that just as much care is needed when comparing samples which are homogenous in sexual condition as is demanded when samples are not homogeneous in that respect. It is seen that the arithmetic mean number of vertebræ for the total Sidmouth sample of spawners is almost the same as that for the spawners among the Plymouth sample. The samples were taken within a few miles of each other and at practically the same date. Everything thus appears to favour the view that fishes belonged to a single stock. But the analysis of the samples has shown that it is doubtful whether, under the circumstances, the means for the samples as a whole can be legitimately compared at all.

Herrings of the " O " Group.

The number of vertebræ of the offspring from a spawning stock is a matter of importance. Many counts of vertebræ in samples of late post-larval and metamorphosing herrings have been made at Plymouth, and large differences have been observed. Two facts have been recorded (Ford, **14**, p. 748) concerning the number of vertebræ in samples taken from neighbouring estuaries during 1927 and 1928 from April until June :—

1. The number of vertebræ tended to be higher in later months.
2. Within the same day's sampling, the number of vertebræ changed with the length of the fishes.

The extent of the difference which may be shown between samples taken at different times is exemplified by the data for samples taken on May 26th, 1927, and April 5th, 1928 :—

	Body-length* Distribution.			Vertebral Distribution.			
	30 mm.	35 mm.	54	55	56	57	58
April 5th, 1928	50	49	2	41	46	10	–
May 26th, 1927	51	50	–	3	58	38	2

The very high number of fishes with 57 vertebræ in the sample of May 26th may occasion some surprise, as this does not usually much exceed 10% in samples of adults at Plymouth. The correspondingly low number with 55 vert. is also unusual. The data given, however, have been confirmed by the counting of a second sample. Perhaps a more typical case is provided by a comparison between the above sample of April 5th, 1928, and one taken on May 18th of the same year, and even here the difference is self-evident :—

	Body-length Distribution.			Vertebral Distribution.			
	30 mm.	35 mm.	54	55	56	57	58
April 5th, 1928	50	49	2	41	46	10	–
May 18th, 1928	55	50	–	14	70	11	–

The second feature, that of difference in vertebral distribution within one and the same sample, is exemplified by samples taken on May 27th

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* The " body-length " is equivalent to the total length less the caudal fin. Defects in the caudal fin of many specimens necessitated the use of this alternative method of expressing length (*vide* Ford, **10**, p. 307).

and June 25th, 1928 (Ford, **14**, p. 749). In the May sample, fishes less than 35 mm. in body-length had a higher average number of vertebræ than those exceeding 35 mm., while in the June sample, fishes from 50 to 55 mm. had a higher average than those from 60 to 65 mm.

The Sample and the Race.

The various forms of investigation described above agree in showing that in an attempt to use the " number of vertebræ " given by random samples as a clue to the racial composition of the populations sampled, there is the persistent difficulty of apparent race-mixture. This leads us to enquire into the validity of the basic proposition that the number of vertebræ as given by a sample can be accepted as an estimate of a race character. For convenience in writing, we will refer to the sample estimate as the " sample-number " and to the race character as the " race-number."

Having determined a large number of sample-numbers, an investigator may decide to place some of them in a group apart from the rest *because they agree.* He may make a special note of the absolute value of the number of vertebræ which is characteristic of the members of the group he has created and decide to establish this as a " type " to which future samples of the same vertebral composition may be referred. But this " type " is nothing more than a quite arbitrary standard, and the " constancy " with which the members of the group conform to type is solely the result of the deliberate exclusion of samples which differ from standard. The mere sorting-out of sample-numbers into types according to a criterion of vertebral distribution of itself proves nothing beyond the fact that a certain number of the samples are alike in their number of vertebræ, but differ from others in this respect. It is simply and solely a technique for the assessment of the amount of variation in vertebral distribution.

Alternatively, the investigator may first segregate his samples according to some character *other than the number of vertebræ*, only to find that in one of the resulting groups all the samples also agree in vertebral distribution. In this instance the agreement between the " sample-numbers " is not merely the result of a deliberate choice of sample according to an arbitrary standard of vertebral distribution, but a sequel to a selection of samples according to some other criterion. It shows, moreover, that there is a correlation between the character used for the sorting of the samples and the number of vertebræ.

The fundamental difference between the above two alternatives is self-evident, but it needs to be remembered in the present discussion of " sample-numbers " and " race-numbers." Were it proven that the principle of "race-numbers" is valid, the first alternative would be a legitimate method for conducting racial analyses, but unless and until that principle is established, the results of such analyses remain entirely speculative. By the adoption of the second of these alternatives and paying due regard to the sexual condition of the fishes in the samples he utilises, Schnakenbeck has accumulated a wealth of valuable information which he offers as substantial evidence for the "race-number." Certainly, he has shown that sexual condition and "sample-number" are interdependent, but it is a matter of opinion as to whether or not he has proved either that the number of vertebræ is strictly inherited, or that spawning populations are homogeneous in vertebral composition—and these two premises are the fundamental elements of the theory of unalterable "race-numbers."

Without more knowledge than is at present available concerning the inheritance of the number of vertebræ, there must remain some uncertainty as to the real significance of observed difference between "sample-numbers." There is at least the possibility that some part of this difference is phenotypic—a possibility which may increase the difficulty of using "sample-numbers" as "race-numbers" in seeking to establish genotypes. This explains the present writer's hesitation in accepting the system of herring races postulated by Schnakenbeck, or, at the present time, to proceed further with a racial analysis of the Plymouth samples than has been indicated in the foregoing pages. It may well be that Schnakenbeck has in broad outline already mapped out the different races as they actually exist, and that his technique is basically sound, but he has given no proof.

Until this proof is forthcoming, it is held that "sample-numbers" should be treated merely as characters of the temporary populations from which the samples are drawn and not as "race-numbers." They can be used in conjunction with data on age and growth as clues to the movements of the shoals which result in the formation of those temporary populations, and persistent work of this kind ought ultimately to reveal the different entities represented in the populations. The Scottish investigations on the autumn-spawning and spring-spawning herrings in Scottish waters provide an excellent example of the application of this method.

Concerning the Plymouth spawning population, there remains no doubt that it is very complex. Whatever character is considered, it is found that the Plymouth fishes have something in common with those taken in regions to the eastward and westward. Just as some of the Plymouth fishes are indistinguishable in growth from those caught at the eastern end of the Channel, while others resemble those taken in the Atlantic fisheries, so also there is a relation between the "sample-number" of vertebræ in the three districts. On the whole, also, growth in length in western regions tends towards a higher limiting value than that in eastern regions; similarly, the number of vertebræ tends to rise from east to west. Many of the Plymouth herrings exhibit "mixed" growth, suggesting that in the seasons between successive spawnings they have visited different feeding grounds; so, too, the number of vertebræ varies from sample to sample, as if to confirm the belief that the Plymouth spawning population is drawn from a number of different sources. The explanation which seems best to fit these results is that the shoals which arrive in succession to spawn off Plymouth come both from the deeper parts of the English Channel proper and from the more open waters at the Atlantic entrance. After spawning, they return to off-shore waters, although not necessarily to the same grounds from which they came. Accepting the view that the Plymouth spawners spend the whole of their lives within a fairly definable and comparatively limited geographical area, and that the number of spawning places is also limited, it might be permitted to speak somewhat loosely of a "south-western" herring which differed, say, from a Norwegian herring. Nevertheless, there will be marked individual variation among "south-western" fishes in both growth and number of vertebræ, since the size of annual increments of growth depends upon the feeding grounds visited when fishes are a given age and size, while the number of vertebræ, although in a measure dependent upon the parental number, may yet be affected by the environmental conditions under which fishes are born and develop.

The Rearing of Young Herrings.

Great advance in our knowledge of genotypes in herrings might be expected if it were possible to rear herrings of known parentage under controlled conditions. In practice it is a comparatively simple process to express eggs from a ripe female and to fertilise them with the milt from a ripe male. The eggs thus "set" will develop quite normally in sea-water and give a plentiful yield of active and apparently strong larvæ. No special care is needed to secure this result other than that usually taken in the experimental rearing of marine animals. Whenever opportunity has permitted at Plymouth, eggs have been fertilised and incubated until larvæ have appeared. Eggs have been incubated in plunger-jars; in running water and still; in the light and in the dark; in water of different temperature and salinity. Unfortunately, however, no larvæ have ever been reared much beyond the stage at which the yolk-sac is absorbed, and it has become increasingly evident that the problem of rearing cannot be treated as an incidental to other enquiries if success is to be achieved. It must be undertaken as a major research. As an aid in this it was thought that Plymouth could assist by acting as a distribution centre for fertilised eggs and supply workers in laboratories elsewhere, where facilities for rearing are available.* Thanks to the co-operation of Mr. Storrow at Cullercoats; Professor Orton of Liverpool University, and Mr. Smith of Port Erin; Mr. Elmhirst of Millport; and Mr. Weller of the Municipal Aquarium at Brighton, trial consignments were sent to the above places and reports made on subsequent incubation. Ripe eggs were expressed from females into glass jars (breffits) partly filled with water, the jars being moved about meanwhile so as to distribute the eggs as evenly as possible in a single layer over the inside of the jar. The eggs were then fertilised by pouring into each jar a small quantity of a suspension of sperm in sea-water. After fertilisation had been effected, the water was changed. Two breffits containing eggs and securely capped with glass covers and muslin, were packed in a hamper and despatched by rail to each of the four Laboratories mentioned. The hampers for Brighton, Cullercoats and Millport left by passenger train, and that for Port Erin went first to Liverpool by rail and was then transferred to the steamer for Douglas in the Isle of Man. Upon arrival at their destination, the eggs were housed according to the facilities available. Excellent hatchings were reported.

The Number of Myomeres in Larval Herrings.

Being unable to rear larval herrings of known parentage until the number of vertebræ could be counted, an attempt was made to determine how the number of myomeres varied, but with equally disappointing results. It is well known that an error of one or two in the counting of myomeres is unlikely to lead to a mistaken identification of a herring as distinct from a sprat or a pilchard. But no such latitude in precision of count is permissible when studying myomeral variation within a herring brood—the counts must be reliable statistics—and in practice there was no assurance on this important point. It is thought, however, that with opportunity for closer investigation, interesting results might be forthcoming.

Incubation of Herring Eggs in Waters of different Salinities.

Despite the failures referred to above, it has been shown (Ford, **13**) that fertile eggs of the same parentage can be made to yield larvæ which differ in specific gravity as the result of incubation in waters of different

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* There is, of course, nothing very new in this. As early as 1879, Dunn (**4**) forwarded some thirty or forty thousand eggs to the Brighton Aquarium in connection with a proposal to "enrich Australian waters with the English Herring," and he states that whereas full ninety days was required for the journey with the transported eggs still unhatched, it was found possible to "repress life" for only forty days. In later years, ova fertilised at Plymouth were the material for trial transportation to New Zealand, and were successfully taken as far as Cape Town.

salinities. This opens up the question as to what anatomical variation, if any, might be expected to reveal itself in the fishes at a later stage of life, in consequence of this difference in environment during embryonic development. At present, nothing further can be added to the original report.

The Metamorphosis of the Herring.

Leaving the larva and turning to the stage in the life of a herring when it becomes transformed into a silvery and scaled adolescent, there is considerable variation to be explained. The marked changes in form during metamorphosis can be regarded as the consequences of differential growth in length (Ford, **14**) and it is suggested that any circumstances which will affect the relative proportions of the different parts of the larval body, or which will influence the rate at which these different parts grow, must induce a difference in the form of the adolescent. It has been shown that at Plymouth the length at which metamorphosis occurs is by no means constant, and that early larvæ at an arbitrary stage of metamorphosis are larger and have a lower number of vertebræ than those at the same stage of transition in later months. To what extent these changes are genotypic or phenotypic remains to be determined.

The Adult Fish.

After the adolescent, there is the adult fish. Whether it has grown much or little ; whether it has matured early or late ; whether it agrees with or differs from a second fish in its number of vertebræ : there remains the ever-present difficulty regarding the interpretation of differences between individual herrings.

Technique.

It remains to speak of the technique by which the investigator seeks to recognise genotypes in the herring. Stated simply ; he has to devise means for distinguishing between fishes which differ in factorial constitution. The manner in which he essays to solve the problem is immaterial, provided that his method is reliable. The " number of vertebræ " is a character much used in this connection, but it appears that there is still much to learn about this character. In a communication to the *Journal du Conseil,** now in the press, the present writer has discussed the "number of vertebræ " as the sum of a series of bony elements which differ one from the other. Two individuals may have the same total number of vertebræ, but yet be different in the structure of the vertebral column. Reference must also be made to an important paper by Wollaston (**39**), recently published, in which the statistical treatment of sample data on the number of vertebræ is most critically examined.

* *Journal du Conseil*, Vol. VIII, No. 2, 1933.

FORECASTING THE YIELD OF THE FISHERY.

It would be of practical advantage to the fishing industry if, at some time in advance of the opening of a new season's fishing, fishing prospects could be announced with regard to the following :—

(*a*) The date when profitable fishing might be expected to begin.
(*b*) The expected quality of the catches.
(*c*) The estimated yield of the fishery.

If events during the fishing season were repeated year after year with unbroken regularity, knowledge during any one season would be quite sufficient to indicate what would happen in the next. We know, however, that no such uniformity actually occurs. Even so, if it could be shown that the variation from season to season followed some rule, it might yet be possible to discover that rule from the study of past data, and hence to predict what is likely to occur in the future.

Is there any " law and order " governing the whole or some part of the fluctuations in fishing yield which can be discovered from the study of past data on the Plymouth fishery ? Is there any certainty that future events will continue to follow the same course ? Until positive answers can be given to these questions, any forecasting is pure speculation, and therefore without scientific value.

It can be regarded as certain that fishing results are dependent upon the weather, but in the present state of meteorological science, we cannot hope to receive much advance information regarding weather conditions during a forthcoming season. Hence, every form of fishery forecast which can be issued at the present time must of necessity include an important reservation dealing with the weather. Nevertheless, the official weather forecasts which are broadcast daily are themselves in the nature of fishery predictions. Thus, a gale warning is not solely an indication that an interruption of fishing is imminent, but also a portent of heavy catches when fishing is resumed after the enforced suspension. Alternatively, the prediction of a spell of calm weather may be interpreted as an indication of lighter catches. It is certain that a detailed study of the relation between weather and fishing yield will form an important part of future work on fishery prediction.

But however favourable the weather may be for fishing, the size and number of catches made are dependent upon the fish stocks. There is reasonable assurance that some fish, at any rate, will be found on the grounds as early as October, and that not until at least the end of January will it be possible to say that none can be caught in drift-nets. Moreover, during the intervening four months the condition of the fish will vary from individuals with half-filled roes and milts to fish which have spawned. But beyond these two general statements, it is almost impossible to be sure of anything except that the quantity and quality of fish caught varies from season to season, day to day, and from boat to boat, in a bewildering fashion.

It is believed that the fish come in successive shoals, partly from the English Channel proper and partly from the neighbouring Atlantic waters. After spawning, the fish will return once more to the deep. Year after year this inshore migration for spawning, and the return journey to the offshore feeding grounds, is repeated. An observer at Plymouth, therefore, by studying samples of fish taken during the winter fishery, can obtain a working idea of the changes which occur from one season to the next. He sees how the stock alters in character by the gradual replacement of older fish by younger ; how that fishes born in a given year outnumber those born in other years ; and he learns to distinguish between fishes which have come from different feeding grounds. From these detailed studies, conducted over a number of years, he finds that he can formulate an empirical cycle of events which will, to a useful degree, account for the observed changes in the fishable stock. Let us examine some of the results obtained in this way.

On p. 325 data were given on the age of fishes caught during the seasons 1924–25 to 1931–32, and it was there shown (1) that fishes born in certain years were much more important to the fishery than those born in others ; and (2) that fishes of any given year-class are of the greatest importance to the fishery in their fifth winter of life. Now these are observations which, strictly speaking, refer only to the period in which they were noted. That is to say, there is no certain proof that they will apply at some future date. On the other hand, there is no real necessity to assume that they will not. Accordingly, there can be no objection to the experiment of attempting to forecast the age-composition of catches during a future season on the basis of past observations. In the year 1929, an experiment of this kind was made, utilising data taken during the four seasons 1924–25 to 1927–28. (*vide* Ford, **11**, p. 14.) It was predicted that the rich year-class 1923 would begin to decline in 1928–29 and that in its stead the very successful 1925 year-class would predominate in the catches of 1929–30. Furthermore, dates were given when year-classes 1922 to 1925 would cease to be important elements in the catches, and the opinion was expressed that by 1932–33 practically the whole of the stock represented in the catches of 1927–28 would be replaced by new stock. Concerning these experimental predictions it is now possible to say from actual experience that they were substantially correct. Since this first attempt it has been the custom at the end of each season to form an opinion as to the probable age-composition of the catches in the following year, and it may be said that there has been no fundamental discrepancy between forecast and fact.

It may not appear of great practical utility to be able successfully to forecast the age-composition of catches, nor is there any value in so doing, if the work is to stop at this point. But if it is remembered that as a fish gets older it increases in size, then it will be realised that a forecast of age-composition is also a forecast of "quality" of catch. For example, if catches during an impending season are expected to include a high proportion of old fish it means that big fish will outnumber small. Conversely, the prediction of a high percentage of young fish in future catches is only another way of saying that the average size of the fish will be small. But at Plymouth this is merely a generalised truth, for it is at present very difficult, if not impossible, to convert predictions of age-composition into precise predictions of size-quality, because fishes of the same age-group vary considerably in size. Of course, a high average age usually means a high average size, but an individual length is no criterion of age any more than an individual age is a criterion of length (cf. p. 326). Size will depend upon the feeding grounds which the fish have frequented in past years, so that the average size of the fishes taken during any season at Plymouth will depend upon the regions from which the shoals have come. And in the present state of knowledge there is little justification for assuming that each year sees an unaltered proportion of migrants from the Channel proper and from the Atlantic regions. If in some years there is a greater proportion of migrants from the Atlantic feeding grounds the average size for any given year-class is likely to be larger than in the years when the Channel migrants are in greater evidence. The winter of 1932–33 provides a case in point. From the observations made during the preceding season it was anticipated that the catches of 1932–33 would include a high proportion of old fishes, since there had been no important replenishment of stock by younger year-classes in recent years. At the same time it was felt that unless the brood of the winter of 1929–30 had proved very successful in its survival the outlook for the fisheries of the immediate future was very disquieting. Now if these anticipations were to become realised facts the catches of 1932–33 should have shown an appreciable percentage of fishes of the larger sizes, as well as a fair quota of small individuals—the former being the old fishes remaining from previous stock and the latter the new arrivals of the young 1929–30 brood. Fishes of medium size, representing fishes from 4 to 6 years of age, should be few in comparison. These results were actually obtained during the fishery, but in a manner which was not, and could not have been foretold. Old fishes certainly predominated in the catches of 1932–33, so much so that samples taken from catches in several instances consisted of from 50% to 80% of individuals over the age of 6 years, whereas the average percentage for fishes over 6 years during the previous eight seasons was only 25%. With so large a percentage of old fish it was quite according to expectation that the average size of the fishes in the catches should also be large, but it came as a surprise to see *how* large they really were. Individuals of 28 cm. to 30 cm. in length outnumbered others, while those from 25 cm. to 27 cm. were less in evidence than in perhaps any year since 1924–25. The explanation which most satisfactorily accounts for this fact is that shoals coming from the Atlantic regions were more numerous than in recent years.

Young fishes of the 1929–30 season made their appearance in a very marked manner during the months of September, October and November, 1932. During that period catches were landed at Plymouth and at a number of places off Cornwall which included anything from 30% to 60% of the 3-year-old fishes of this year-class. The frequency and the characters of these fishes were altogether unusual, at least in the Plymouth area. They were of large average size in comparison with fishes of the same age usually caught at Plymouth, being about 25 cm. long on average. But more noticeable still, they had a much higher average number of vertebræ than is usual in the district. Fishes having 57 vertebræ actually outnumbered those with 55 vertebræ, and the average number of vertebræ exceeded 56·0 in four out of the five samples taken from Plymouth landings. Such high vertebræ averages are not ordinarily obtained in Plymouth waters and can only be matched by averages in the Atlantic region VIIg. (*vide* p. 349). Samples from Mevagissey and Port Isaac, taken during the same period, showed very similar characters, and it seems most natural to conclude that these and the Plymouth fish were of like origin.

From these observations it would appear that the fishable stock on the Plymouth grounds during the 1932–33 season had come more from westerly sources than had been the case for a number of years. But this change was not predictable because there was no available evidence upon which to judge. Hence, although a knowledge of the age-composition of catches in previous years proved sufficient to prepare a forecast of the age-composition in 1932–33 there was no means of expressing more than a generalised opinion on the probable size-quality of the catches. In other words, the prediction of a high percentage of old fish implied that the average size would tend to be high, but it was impossible to state that the fishes would be mostly 28 cm. to 30 cm. in length, because it could not be foreseen that the shoals would be predominately westerly in character.

For the same reason there is at present a limitation to the accuracy with which forecasts of the *quantity* of fish can be given. As will be indicated below, extremely useful general indications as to the quantity of fish to be expected can be extracted from analyses of past records, but these are all dependent upon the underlying assumption of unaltered conditions between present and future. Four times out of five, or perhaps nine times out of ten, that assumption may be sufficiently near to the truth, but at the fifth or the tenth time it may fail. For example, a marked alteration in the migration of herrings such as is thought to have occurred during 1932–33 might well upset any prediction of quantity which did not take into account the possible effects of the migratory change. As to the causes which might induce these migratory changes, it has been suggested that the cyclic activity of Atlantic waters is one of the most important. Thus Storrow (**34**, p. 20) says : " In the study of fluctuations of the herring fishery we are confronted with the problem of associating changes in fisheries with changes in waters, and these with changes in other phenomena such as the association of pressure distribution and winds." French investigators (*vide* le Gall, **20**) have gone so far as to associate the fluctuation of the herring fisheries in the English Channel with rhythmic movement of Atlantic water over the Continental plateau, and to predict the success or failure of the fishery in consequence of this rhythm. Many will think, however, that our knowledge of the factors which govern the movements of herring shoals has not yet reached that stage when it can be used in the practical forecasting of fishing yield. But the fact remains that such knowledge will have to be sought after, despite the complexity of the problems awaiting solution.

But even if the significance of these unknown factors governing the movement of shoals is admitted, there is much to be learned from past results of actual fishing. In Table IV, on p. 315, the average weight per landing by steamers at Plymouth during each of the seasons 1924–25 to 1931–32 was given. Using these figures as the best available estimate of density of catch, and placing them alongside the corresponding age-composition of the catch, we have the following material for study :—

	Season.							
	1924–25	1925–26	1926–27	1927–28	1928–29	1929–30	1930–31	1931–32
Average weight per steamer-landing (cwt.)	**40·0**	23·1	16·6	**46·3**	27·5	**39·1**	32·7	17·6
Age composition of catches expressed as percentage-numbers of fishes of following year-classes :—								
1919	15·3							
1920	**56·0**	**47·5**						
1921	12·3	14·1	10·7					
1922	7·0	15·2	22·9	12·0				
1923		**5·3**	**27·9**	**30·9**	**26·6**			
1924			4·7	20·4	19·5	15·4		
1925				**18·6**	**30·8**	**35·9**	**33·2**	
1926					3·3	18·1	23·8	21·3
1927						1·9	10·2	15·0
1928							4·4	12·6
1929								3·4

It will be seen from the above table that there is a relationship between the density of steamer-landing and the percentage-number of fishes in the three year-classes 1920, 1923 and 1925. The steamer-landing was heaviest in the three seasons 1924–25, 1927–28 and 1929-30, and in these same seasons the most important part of the catch consisted of fishes of 1920, 1923 and 1925 year-classes, respectively, when those fishes were at the age of 5 years. In 1926–27 and 1931–32, the steamer-landing was very low, and it was in just those seasons that fishes of the above-mentioned year-classes were comparatively weakly represented. Thus, in 1926–27, the year-class 1920 had reached the age of 7, so that the time had passed when it might be expected to make a heavy contribution to catches. Moreover, the 1923 year-class was only aged 4, and therefore not yet yielding its full quota, while year-class 1925 was not due to appear in the catches until the following year. In 1931–32, all three classes had passed their zenith—it is probable that those of 1920 and 1923 were little more than nominally represented in the catches, if at all, while that of 1925 had reached its maximum two seasons previously. The data further show that the fishery from 1924-25 onwards has depended far more upon year-classes 1920, 1923 and 1925 than upon any others.

Putting these observations together, there seems good reason for thinking that the yield of the Plymouth fishery (as represented by the average weight per steamer-landing) fluctuates in accordance with the strength of a limited number of highly-successful year-broods, occurring only at intervals. The yield will reach a maximum when one of these rich broods is in its fifth winter. It follows from this that the moment an observer can learn of the arrival of a new and successful brood, he is in the position to forecast when fishing is likely to benefit from that event. Thus, when in the season 1927–28 the present writer (Ford, **11**, p. 16) noted that the percentage of 3-zoned 3-ringed fishes of the year-class 1925 was unusually high, he could have gone on to predict that the fishery in 1929–30 would be good. And the prediction would have been realised, although made two years in advance.

The converse case must also be noted, for if during successive seasons no evidence is forthcoming that an important new brood is about to take the place of those passing out of the fishery, then it must be concluded that the fishery will suffer in consequence. In this connection it is of interest to consider the progress of the Plymouth fishery during the past four seasons (1929–30 to 1932–33). In 1929–30, when fishes of the rich year-class 1925 at the age of 5 years made up 35·9% of the catch, the average steamer-landing was 39·1 cwt. During the following season of 1930–31, fishes of the same year-class, now 6 years old, were again dominant, but the average weight per steamer-landing fell to 32·7 cwt. In 1931–32 the steamer yield was lower than it had been since 1926–27, while the catches consisted of no less than 47·7% of fishes older than 6 years. These results plainly show that fishes of year-classes 1926, 1927, 1928 and 1929 were not present on the Plymouth grounds in anything approaching the density with which those of year-class 1925 had been. There are two ways of explaining these results. Either the broods of the winters 1925–26 to 1928–29 were poor in survival-rate as compared with that of 1924–25, or the four former broods did not visit Plymouth to the same extent as did the latter brood, but went elsewhere to spawn. Of the two explanations, the first appears the more likely since there is independent evidence that the dominance of the year-classes 1920, 1923 and 1925 was widespread (*vide* Storrow, **33** and **34**).

The position at the end of the 1931–32 season at Plymouth, therefore, appeared anything but favourable for the fishery of 1932–33. What remained of the previously fished stock was old, while there was little to be expected from the oncoming younger broods. The only possible prediction which could be made was that the fish of the 1932–33 seasons would consist of a greater proportion than ever of old fish, and that the average yield would be low. As has already been shown, the proportion of old fish did prove to be exceptionally high, but it has to be noted that the average weight per steamer-landing was considerably heavier than might have been expected. Yet it must be said that this discrepancy between forecast and fact was more apparent than real because, unfortunately, the average of 34·2 cwt. per steamer-landing does not convey a fair estimate of the season's fishing. On p. 318 it was shown that fishing was only really productive during two periods, the first from December 7th to December 18th, and the second from January 4th to 6th. Admittedly, during the 12 days of the first period and the 3 days of the second, the steamer-landings were very good, averaging 53 cwt. per landing (and this good result has been shown to have been dependent upon good fishing weather), but there were 36 other days during the season when the steamers were far less successful, and for which the average is only 20 cwt. as compared with the 9-year seasonal average of 30·8 cwt. The results of the motor fishery tell a similar story, for whereas there were 12 days on which the average weight per landing was equal to or greater than the seasonal average of 20·2 cwt., there were 27 days when the daily average was much below this figure. For the 12 days the average weight per landing was 36·5 cwt., but for the 27 days it was only 11·6 cwt., and there were an additional 17 days when no landings at all were made. Thus, when some two-thirds of a working season gives decidedly poor results, too much significance ought not to be attached to a seasonal average like the weight per steamer-landing which, in effect, spreads the heavy landing of a few days over a long period of poor yields. The result, as in the present instance, is apt to be misleading.

From these observations it may be concluded that although the average weight per steamer-landing fluctuates from season to season in accordance with the changing age-character of the fishable stock, its limitation as a precise estimate of fishing yield creates some difficulty in forecasting future results. It will therefore be necessary for prediction purposes to find some better criterion of the density of fishing.

Now it is a self-evident fact that forecasts of quality and quantity which are determined in the manner just described are concerned only with the expected remains of previously-fished stock. They have nothing to do with that entirely fresh stock which enters the fishery for the first time in any one year. At Plymouth there is at present no means of anticipating the strength of the 3-year-old stock in an impending season, but this is of little practical consequence because the proportion of 3-year-old fishes in the catches is relatively unimportant. Elsewhere, however, where the catches always include a high proportion of 3-year-old stock (off the Sussex coast, for example), it would be necessary to discover some means of determining the relative richness of an oncoming year-class before it had reached its third year as well as to obtain an indication of the expected yield from previously-fished year-classes.

There remains to be considered the question of the time at which fishing in any season may be expected to begin. This matter of early and late seasons was given some attention in an earlier paper (Ford, **11**) when it was suggested that the temperature of the sea may provide a clue. It was found that at temperatures above 13°C. fishing tended to be poor, but that it improved as the temperature fell towards 11°C. and became good as soon as the temperature was less than 11°C. The "normal" date at which 11°C. is reached is about December 19th. An individual season would thus be early or late in starting according as the temperature of 11°C. is attained before or after the "normal" date. It has not been possible to examine this question in further detail, but it is worth noting that on December 6th, 1932, the temperature over the Bigbury Bay area of the fishing grounds was round about 11°C. and on the next day, December 7th, the steamers made the first big landing of the season. This suggests that the matter may be worthy of more critical and detailed investigation.

Having reviewed the present possibilities and limitations connected with the general question of predicting catches, it is convenient to consider available data in somewhat greater detail. The average age-composition of catches during the eight seasons from 1924–25 to 1931–32 was given in Table VI on p. 325, and at the foot of that table the following means for the 8-year period were stated :—

Percentage Numbers of Fish at following Age :

3	4	5	6	Older than 6
6·1	18·4	27·3	22·7	25·3

The figures are seen to increase from the 3rd to the 5th year, but to begin to decline in the 6th. Assuming that the decline is continuous from the 6th year onwards at a fixed rate of about 54% annually, the percentages at ages 7, 8 and onwards may be estimated as follows, making the total percentage of fishes older than 6 amount to 25·4 instead of 25·3 :—

Percentage Numbers of Fish at following Age :				
7	8	9	10	11
12·3	6·6	3·9	1·9	1·0

The above may be regarded as representing the "normal" life of a year-class *in the fishery*, and suggests that this life commences with a minor contribution at the age of 3 years, growing to a maximum at 5 years, and dwindling to a merely nominal representation from the age of 8 years onwards.

This hypothetical "life-table" is not only useful in giving an estimate of the length of time and the extent to which the fishery may be expected to profit or suffer by the presence of a "normal" year-class, but also in showing the manner in which oncoming year-classes must increase their quotas in order to make good the losses sustained by the passing out of the older classes. It is seen that of the nine year-classes which contribute to the catch of any one season, only those at the ages of 3 and 4 will increase their contributions during the next season, whereas the seven classes at the ages of 5 to 11 will contribute less than hitherto. Hence, if in actual experience a numerically weak year-class enters the fishery, its weakness will be almost immediately reflected in the density of the catch, while the effect upon the catch of two weak year-classes in succession will be very apparent. Conversely, the arrival of a rich year-class will lead to an early rise in the catch.

TABLE XVI.

Season.	Percentage by Weight contributed by Year-classes at the following Age :					
Dec.–Jan.	3	4	5	6	Older than 6	
1924–25 .	5·6	11·7	55·8	15·7	11·3	
1925–26 .	3·9	13·4	13·4	49·1	20·2	
1926–27 .	4·2	24·2	21·8	11·3	38·5	
1927–28 . .	14·9	18·6	32·0	12·9	21·6	
1928–29 . .	2·6	27·6	19·4	27·7	22·7	
1929–30 . .	1·5	16·0	34·7	15·9	31·8	
1930–31 . .	3·5	9·4	22·8	33·3	31·0	
1931–32 . .	2·8	10·6	13·8	21·7	51·1	
Average . .	4·9	16·4	26·7	23·4	28·5	Total=99·9%

When one comes to consider the density of actual catches in relation to their composition by age, there is the difficulty that the catches are expressed in terms of either volume (crans) or weight (cwt.), whereas the age composition is given in numbers. Since no actual data are available as to the weight of fishes at different ages (and such would be difficult to obtain in practice), the alternative has been adopted of obtaining a working idea of the age-composition of catches, *by weight*, by assuming that weight is proportional to the cube of the length and then calculating the weight of fishes at different ages from the corresponding lengths. Table XVI, on page 377, is thus an expression by weight of the numerical age-composition given in Table VI, on p. 325.

Dividing up the average weight per steamer-landing according to the above percentages, season by season, we obtain the following :—

TABLE XVII.

Season.	Average weight per steamer-landing. (cwt.)	Weight of Fish at following Age (cwt.). 3	4	5	6	Older than 6
1924–25	40·0	2·2	4·7	22·3	6·3	4·5
1925–26	23·1	0·9	3·1	3·1	11·3	4·7
1926–27	16·6	0·7	4·0	3·6	1·9	6·4
1927–28	46·3	6·9	8·6	14·8	6·0	10·0
1928–29	27·5	0·7	7·6	5·3	7·6	6·2
1929–30	39·1	0·6	6·3	13·6	6·2	12·4
1930–31	32·7	1·1	3·1	7·5	10·9	10·1
1931–32	17·6	0·5	1·9	2·4	3·8	9·0
Average	30·4	1·7	4·9	9·1	6·75	7·9
%	99·9	5·6	16·1	30·0	22·2	26·0

With the seasonal catch thus split up into age-components, it becomes possible to estimate how much the fishery depended upon the three year-classes 1920, 1923 and 1925 :—

TABLE XVIII.

Season.	Average weight per steamer-landing. (cwt.)	Weight of Fish of following Year-classes. 1920	1923	1925	Total.	Percentage.
1924–25	40·0	22·3	–	–	22·3	56
1925–26	23·1	11·3	0·9	–	12·2	53
1926–27	16·6	3·5*	4·0	–	7·5	45
1927–28	46·3	3·0*	14·8	6·9	24·7	53
1928–29	27·5	1·0*	7·6	7·6	16·2	59
1929–30	39·1	·5*	6·7*	13·6	20·8	53
1930–31	32·7	·3*	4·0*	10·9	16·2	50
1931–32	17·6	·2*	2·0*	4·9*	7·1	40

It is thus estimated that in each season from 1924–25 to 1931–32, the year-classes 1920, 1923 and 1925 accounted for approximately one-half of the catch. A measure of the superior yield of these three classes is provided by comparing their quotas at the age of 5 and 6 when they were

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* These values are estimates on the assumption that rate of decrease each year after the 6th is about 54% annually.

making their fullest contribution to the fishery, with the corresponding quotas of other year-classes :—

	Year-classes.						
	1920.	1923.	1925.	1921	1922.	1924.	1926.
Weight contributed to steamer-landing during 5th and 6th years	33·6	22·4	24·5	5·0	7·6	11·5	11·3

It is seen that the quotas contributed by the year-classes 1920, 1923 and 1925 were individually much in excess of those given by the classes 1921, 1922, 1924 and 1926. The largest quota, that of 1920, was over six times as great as the smallest, viz. that of 1921, while the quotas of 1923 and 1925 were each from four to five times the heavier.

With this measure of the inequality of the contributions to the catch made by successive year-classes, and the knowledge of the extent to which the density of the catch is dependent upon the contributions made by a limited number of year-classes, the chances of being able to predict the trend of future fishing would seem to be favourable, provided that it is possible to learn in advance which year-classes are the ones of promise. Looking over the results of the past eight seasons, one must conclude that a good year-class hardly makes itself evident in catches before it is in its fourth year, although the impending importance of year-class 1925 became evident when that class was at the age of 3. Nevertheless, this is one year's prior notice of an important influence upon the size of the catch. Earlier indication, however, may be forthcoming by the examination of catches taken during the months from September to November, when it is usual for local boats to land catches of younger fish. Certainly in the late autumn of 1932, fishes of year-class 1930 were particularly in evidence, and it is upon this class that one expects the fishery of the near future to depend in no small measure. Admittedly, they were not generally strong in the commercial catches of December, 1932 and January, 1933, although occasional catches were landed which included a good percentage of small fish, but if the year-class is to be as important as the October samples suggested, then the catches in 1933–34 should show an appreciable percentage of 4-year-old fish, while in 1934–35, this year-class, now in its fifth winter, should be a dominant element in the catches. Accordingly, the yield of the fishery should show a new and satisfactory maximum in 1934–35, subject, of course, to the reservations discussed above.

From these observations at Plymouth it has been concluded that the continuous study of the changes in the character and density of commercial landings provides clues to the size and quality of future landings, despite the fact that the results of a season's fishing so obviously depend to an appreciable degree on circumstances which cannot as yet be foreseen. The limitations of the average weight per steamer-landing as an estimate of the density of the fishable stock are large, but they do not mask the fact that fishing-yield fluctuates in accordance with the varying richness of successive year-broods. In practice it is possible to obtain advance information of the relative richness of broods and hence of the relative success of future fisheries. But there still remain possible influences which may militate against a forecast of yield based entirely on this evidence, chief among these being the factors which govern the migrations of herrings. These call for investigation.

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TABLE XIX.

Statistical Region	Fishing Ground.	Method of Fishing.	Port of Landing.	Date of Sample.	Percentage No. of fishes in 6 Vertebræ Classes.						Total No. of Fishes in sample (n).	Arith. Mean No. of Vertebræ (m).	Standard Deviation σ	Standard Error of m $\frac{\sigma}{\sqrt{n}}$
					53	54	55	56	57	58				
VIIg	" Smalls "	Trawl	Milford	Aug. 19th, 1925	1	–	25	55	19	–	100	55·91	0·73	0·073
		,,	Haven	Sept. 1st, 1925	–	–	20	68	12	–	95	55·92	0·56	0·056
		,,	,,	Sept. 14th, 1925	–	–	17	69	13	1	144	55·97	0·58	0·048
		,,	,,	Sept. 30th, 1925	–	1	20	64	14	1	95	55·94	0·65	0·066
		,,	,,	Oct. 19th, 1925	–	–	21	62	16	1	140	55·97	0·63	0·054
		,,	,,	July 28th, 1926	–	1	43	46	10	–	90	55·64	0·68	0·076
		,,	,,	Aug. 10th, 1926	–	2	34	52	11	–	96	55·73	0·69	0·070
		,,	,,	Aug. 18th, 1926	–	3	42	43	12	–	86	55·63	0·73	0·078
		,,	,,	Aug. 24th, 1926	–	–	31	50	18	1	98	55·90	0·72	0·073
		,,	,,	Sept. 2nd, 1926	–	–	26	55	20	–	97	55·94	0·67	0·068
		,,	Plymouth	Sept. 7th, 1926	–	–	20	65	15	–	112	55·955	0·59	0·056
		,,	Milford	Sept. 28th, 1926	–	2	26	60	12	–	85	55·81	0·85	0·072
		,,	Haven	Nov. 15th, 1926	–	1	23	61	14	1	134	55·91	0·65	0·056
VIIg	Between English	Drift	Newlyn	April 24th, 1926	–	1	20	60	17	2	96	55·99	0·70	0·072
	and Irish Coasts	Nets	Milford	April 26th, 1926	–	2	40	49	9	–	157	55·65	0·67	0·053
	southwards of	,,	Haven	June 16th, 1926	–	–	23	62	14	1	126	55·93	0·63	0·057
	latitude 52° N.	,,	,,	June 23rd, 1926	–	–	25	53	21	1	95	55·98	0·71	0·073
		,,	Newlyn	June 23rd, 1926	–	2	29	61	8	–	131	55·74	0·62	0·053
		,,	Milford Haven	July 13th, 1926	–	3	51	41	5	1	155	55·48	0·67	0·053
VIIf	Port Isaac Bay and	Drift	Padstow	Nov. 5th, 1925	–	2	20	66	12	–	119	55·88	0·61	0·056
(ZZ 51)	Vicinity	Nets	,,	Nov. 11th, 1925	–	1	29	65	5	–	118	55·75	0·56	0·051
		,,	,,	Nov. 17th, 1925	–	1	30	58	12	–	118	55·805	0·64	0·059
		,,	,,	Nov. 25th, 1925	–	–	31	63	6	–	118	55·75	0·56	0·051
		,,	,,	Dec. 11th, 1925	–	2	26	61	11	–	115	55·82	0·64	0·060
		,,	,,	Nov. 10th, 1926	–	1	32	60	7	–	111	55·75	0·60	0·057
		,,	,,	Nov. 16th, 1926	–	1	33	60	6	–	112	55·715	0·59	0·056
		,,	,,	Nov. 24th, 1926	–	3	38	50	9	–	116	55·66	0·68	0·064
		,,	,,	Nov. 29th, 1926	–	1	30	66	4	–	108	55·72	0·54	0·052
		,,	,,	Dec. 7th, 1926	–	–	33	58	9	–	106	55·76	0·61	0·059
		,,	,,	Dec. 20th, 1926	–	–	35	53	11	1	116	55·78	0·67	0·062
		,,	,,	Dec. 28th, 1926	–	2	43	44	11	–	110	55·645	0·70	0·067
VIIe	Mounts Bay	Trawl	Plymouth	Mar. 9th, 1926	–	3	45	47	5	–	113	55·55	0·64	0·060
(YY 52 & 53)		,,	,,	Mar. 17th, 1926	–	1	27	63	8	1	117	55·80	0·62	0·057
		,,	,,	Mar. 22nd, 1926	–	1	29	64	7	–	132	55·76	0·57	0·051
VIIe (ZZ 52)	Mevagissey Bay, 6 miles E.S.E. of	Set- Nets	Mevagissey	Oct. 26th, 1925	–	3	31	62	4	1	135	55·69	0·62	0·052
	Mevagissey	Drift	,,	Jan. 8th, 1926	–	–	23	68	9	–	95	55·85	0·55	0·056
VIIe	Area covered by	Set-	Plymouth	Nov. 20th, 1924	–	1	27	67	5	–	115	55·77	0·55	0·051
(ZZ 52	local fishery at	Nets·	,,	Dec. 3rd, 1924	–	1	31	63	6	–	99	55·75	0·56	0·056
A 52)	Plymouth	Seine	,,	Dec. 9th, 1924	–	2	24	66	8	–	97	55·80	0·60	0·061
		Drift	,,	Dec. 16th, 1924	–	–	26	65	9	–	100	55·83	0·57	0·057
		Nets	,,	Jan. 5th, 1925	–	–	26	64	10	–	98	55·85	0·58	0·059
		,,	,,	Jan. 8th, 1925	–	2	27	61	10	–	100	55·79	0·64	0·064
		,,	,,	Jan. 13th, 1925	–	–	29	60	10	1	98	55·84	0·64	0·064
		,,	,,	Jan. 20th, 1925	–	–	23	63	14	–	99	55·91	0·61	0·061
		,,	,,	Jan. 27th, 1925	–	–	27	64	9	–	97	55·825	0·57	0·059
		,,	,,	Feb. 2nd, 1925	–	1	32	62	4	–	95	55·695	0·58	0·058
		,,	,,	Feb. 9th, 1925	–	–	25	63	12	–	99	55·87	0·60	0·060
		,,	,,	Feb. 18th, 1925	–	–	22	67	10	1	99	55·90	0·60	0·060
		,,	,,	Feb. 20th, 1925	–	–	34	60	6	–	97	55·72	0·57	0·058
		,,	,,	Mar. 2nd, 1925	–	2	25	67	6	–	97	55·77	0·59	0·060
		,,	,,	Oct. 25th, 1925	–	3	42	53	3	–	118	55·57	0·61	0·056
		,,	,,	Nov. 1st, 1925	–	1	45	50	5	–	107	55·58	0·60	0·058
		,,	,,	Nov. 4th, 1925	–	1	24	67	8	1	120	55·83	0·61	0·056
		,,	,,	Nov. 18th, 1925	–	2	35	59	5	–	107	55·66	0·59	0·057
		,,	,,	Nov. 20th, 1925	–	–	39	56	4	–	117	55·65	0·56	0·052
		,,	,,	Dec. 1st, 1925	–	2	25	60	13	1	117	55·86	0·65	0·060
		,,	,,	Dec. 6th, 1925	–	1	26	65	8	–	119	55·81	0·59	0·054
		,,	,,	Dec. 15th, 1925	–	1	30	64	5	–	115	55·74	0·56	0·052
		,,	,,	Dec. 21st, 1925	–	1	25	62	12	–	114	55·86	0·62	0·058
		,,	,,	Dec. 23rd, 1925	–	2	21	70	7	–	118	55·84	0·60	0·055
		,,	,,	Jan. 1st, 1926	–	–	32	59	8	–	118	55·76	0·59	0·055
		,,	,,	Jan. 6th, 1926	–	1	27	66	7	–	113	55·79	0·57	0·054
		,,	,,	Jan. 10th, 1926	–	1	29	60	10	–	118	55·80	0·62	0·057
		,,	,,	Jan. 14th, 1926	–	–	30	62	8	–	119	55·77	0·57	0·052
		,,	,,	Jan. 18th, 1926	–	1	27	61	11	–	114	55·825	0·63	0·059

TABLE XIX—*continued.*

Statistical Region.	Fishing Ground.	Method of Fishing	Port of Landing.	Date of Sample.	Percentage No. of fishes in 6 Vertebræ Classes.						Total No. of Fishes in sample (n).	Arith. Mean No. of Vertebræ (m).	Standard Deviation σ	Standard Error of m $\frac{\sigma}{\sqrt{n}}$
					53	54	55	56	57	58				
VIIe (ZZ 52 A 52)	Area covered by local fishery at Plymouth	Set-	Plymouth	Jan. 25th, 1926	–	2	22	70	6	1	116	55·83	0·59	0·055
		Nets	,,	Jan. 28th, 1926	–	2	24	64	10	–	115	55·82	0·61	0·057
		Seine	,,	Feb. 2nd, 1926	–	–	24	66	9	1	110	55·87	0·59	0·056
		Drift	,,	Feb. 4th, 1926	–	1	20	71	8	–	115	55·86	0·54	0·051
		Nets	,,	Feb. 10th, 1926	–	–	20	70	10	–	117	55·91	0·54	0·050
		,,	,,	June 8th, 1926	–	3	29	58	10	–	92	55·74	0·68	0·071
		,,	,,	Oct. 18th, 1926	–	–	46	47	7	–	109	55·615	0·62	0·061
		,,	,,	Oct. 21st, 1926	–	–	28	63	8	1	113	55·81	0·61	0·057
		,,	,,	Oct. 25th, 1926	1	3	23	64	10	–	110	55·79	0·69	0·066
		,,	,,	Nov. 3rd, 1926	–	–	28	65	7	–	118	55·79	0·55	0·051
		,,	,,	Nov. 4th, 1926	–	–	27	64	9	–	112	55·82	0·58	0·054
		,,	,,	Nov. 15th, 1926	–	2	27	61	10	–	105	55·80	0·62	0·060
		,,	,,	Nov. 23rd, 1926	1	1	29	62	7	–	106	55·73	0·68	0·067
		,,	,,	Nov. 30th, 1926	–	–	33	60	7	–	118	55·74	0·58	0·053
		,,	,,	Dec. 6th, 1926	–	2	25	61	12	–	114	55·84	0·64	0·060
		,,	,,	Dec. 20th, 1926	–	–	26	61	12	1	107	55·88	0·64	0·062
		,,	,,	Dec. 20th, 1926	–	2	31	61	5	1	119	55·72	0·62	0·057
		,,	,,	Dec. 30th, 1926	–	3	35	52	10	–	119	55·70	0·69	0·063
		,	,,	Dec. 30th, 1926	–	–	26	69	5	–	100	55·79	0·52	0·052
		,,	,,	Jan. 4th, 1927	–	2	34	55	8	1	112	55·72	0·67	0·063
		,,	,,	Jan. 19th, 1927	–	3	35	53	9	–	117	55·67	0·68	0·062
VIIe (A 52)	River Dart Great West Bay	Seine	Brixham	Dec. 10th, 1925	–	1	33	55	11	–	97	55·76	0·66	0·068
		Set-	,,	Nov. 10th, 1925	–	1	22	67	9	–	76	55·84	0·59	0·068
		Nets	,,	Nov. 26th, 1925	–	2	32	56	10	–	116	55·72	0·67	0·062
		and	,,	Dec. 16th, 1925	–	1	30	63	5	–	92	55·73	0·58	0·060
		Drift	,,	Jan. 4th, 1926	–	–	38	50	12	–	64	55·75	0·66	0·083
		,,	,,	Oct. 27th, 1926	–	2	26	66	6	–	107	55·76	0·58	0·056
		,,	,,	Nov. 23rd, 1926	–	–	34	61	5	–	116	55·71	0·56	0·052
		,,	,,	Dec. 14th, 1926	–	2	37	56	5	–	119	55·65	0·61	0·055
VIId (D 51 E 51)	Off Sussex Coast	Set-	Plymouth	Dec. 9th, 1924	–	2	27	55	16	–	98	55·86	0·70	0·071
		Nets or	Brighton	Oct. 19th, 1925	–	1	37	54	8	–	124	55·69	0·63	0·056
		Drift	,,	Nov. 10th, 1925	–	2	31	60	7	–	97	55·72	0·65	0·066
		,,	,,	Dec. 1st, 1925	1	3	37	53	5	1	118	55·62	0·72	0·066
		,,	,,	Nov. 1st, 1926	–	3	35	55	7	–	119	55·66	0·64	0·059
		,,	,,	Nov. 5th, 1926	–	1	31	61	7	–	97	55·74	0·60	0·061
		,,	,,	Dec. 2nd, 1926	–	–	37	60	3	–	97	55·66	0·54	0·054
		,,	Hastings	Dec. 10th, 1926	–	2	32	57	10	–	115	55·74	0·65	0·061
		,,	Brighton	June 29th, 1927	–	3	37	57	3	–	99	55·60	0·56	0·056

Observations on the Reactions of Marine Plankton to Light.

By

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With 22 Figures in the Text.

CONTENTS.

FOREWORD.

That light is among the more influential elements in the environment of the smaller marine organisms is widely recognised. While laboratory investigation has revealed its kinetic action in specific ways, its capacity for stimulating behaviour responses, and its orientating action on directed movement, the observations of field-workers are providing a growing body of evidence that light does indeed act as an important factor in the bionomics of species in the wild.

The effect of changes in illumination on vertical distribution is an obvious case in point. Now, this line of investigation, as is characteristic of such marine ecological studies, deals essentially with the movement of populations, or groups. The sort of conclusion to be derived from the results is that changes in the distribution of a population correlate significantly with changes in illumination. In practice, it is usually possible to go beyond generalisations of this kind, but doing this involves assumptions concerning the behaviour of individuals composing the group. Indeed, the closer the correlation, the more necessary it becomes to think in terms of the behaviour of individuals. This is a general necessity in the study of populations which form quite unorganised groups, since the behaviour of the whole is merely a reflection of the units composing it.

Hence appears a demand for knowledge of the behaviour of individual plankton animals. Since, however, insurmountable difficulties exist in the direct observation of these animals in their natural habitats, there is little possibility of obtaining the required information other than by investigation in the laboratory. To offset the advantages of controlled experiment, laboratory conditions, always more or less restricted and unnatural, are particularly so in the case in point, and more than usual care has to be exercised in ascribing significance to results obtained under them.

Still, granted that the behaviour of a population is to be rendered intelligible by knowledge of what the individuals composing it are doing, and granted that the behaviour of individuals in the laboratory bears at least some kind of ascertainable relation to that of animals in the wild, it is concluded that data derived from the laboratory is not altogether without ecological value.

Turning now to what can be observed with regard to plankton animals confined in glass containers, one has to admit that the behaviour is, for the most part, featureless. There is little amongst the varied contrasts and changes to which the animals may be subject that can modify, or give added direction and coherence to their activity. Consequently, particular significance must be attached to any factor of the environment which exerts consistent marked effects. It so happens that light proves to be just such a factor. Sudden changes in light intensity may produce shock reactions as readily as mechanical contact, while the clustering on the lighted side of glass containers is familiar to all who have had anything to do with plankton. Since, in the laboratory, the behaviour is perhaps more subject to conditions of illumination than to those of any other single factor, there is a maximum scope for experiment if behaviour in relation to light is chosen for study. This consideration is entirely independent of what has been said above with respect to the evident importance of light in nature. There is thus a twofold incentive for the study of behaviour in relation to light in marine organisms.

DIRECTION AND INTENSITY AS FACTORS IN RESPONSE TO LIGHT.

One of the most readily noticed characteristics of collections of small marine animals is the formation of groups heading towards (or away from) the light. In any glass container a concentration of animals will be found on that side which faces a window, or artificial light-source, as the case may be. This applies to a great range of forms from various phyla. At the same time a greater or lesser concentration, of the same or different species, may occur on the opposite side of the container, in the part furthest from the source. The former group consists of individuals which move more or less directly up to the bright region where they collect and which at this stage may be simply called "positive," the latter of individuals which keep away from the source and may be called "negative." This grouping in relation to simply-defined conditions of illumination provides a suitable starting-point for more detailed study of the influence of light on the behaviour of the animals concerned.

Observers of this photopositive and photonegative behaviour are generally soon led to enquire how far the animals are influenced by the directional properties of the light, and how far by successive changes of intensity experienced during the course of their movement. This opens up one side of an intricate problem which has assumed several shapes at one time or another, namely—to state it briefly, if crudely—the question of the relative importance of *direction* as opposed to *change of intensity*. It appears to be an appropriate enquiry in the present case, in view of the evident effects of diurnal changes in intensity on the distribution of the wild populations of various plankton organisms. Let us see, then, in what precise ways the problem is applicable to these animals in confined spaces. For simplicity we will restrict considerations to photo-positive behaviour, but they apply equally, *mutatis mutandis*, to photo-negative.

A. *As concerns the group.* The collection formed on the lighted side of the vessel may have formed because (*a*) it is nearest the light-source, or (*b*) it is in the brightest part of the vessel. It usually happens that movement towards the source is accompanied by increase in intensity, but conditions can be devised in which the two factors are dissociated. In the one case the group should form along the line of incidence of the light, in the other, in a region of maximum illumination irrespective of direction of incidence. Experiments bearing on this point are described below.

B. *As concerns the individual.* In so far as the group is homogeneous (and in this case it is so to be regarded), a complete interpretation of its behaviour will be given from the study of a typical individual composing it.

The varieties of individual behaviour that lead directly to the formation of groups in regions of some definite illumination are as follows.

(I) Activity may vary with light intensity, and so the animals may tend to concentrate in that intensity in which the movement is slowest. This is a purely *photokinetic* effect. Its success in bringing about formation of groups is not great unless very marked differences in activity are produced. Thus (for a negative case) *Gonionemus murbachi* collects in the shaded part of a tank, partly because of decrease in activity. (YERKES, 1903 ; MURBACH, 1909.)

(II) The direction of movement may still be random, with the exception that reversal reactions are given to abrupt changes of intensity. Thus it is well known that *Euglena viridis* collects in (not too strongly) lighted regions owing to avoiding reactions when entering a shadow (see JENNINGS, 1906). Similar behaviour is claimed for *Bacterium photometricum* and various Protista, and probably occurs more than is suspected among Metazoa such as Isopods.* For the appearance of this kind of group it is necessary that there should be an abrupt change from light to shade in the field of illumination.

(III) The animal may exhibit, to a greater or lesser degree, some form of *phototaxis*. That is to say, the light influences the *direction of movement*. So long as it is reactive, the animal, as it moves, is constantly making some sort of adjustment in relation to the light, so that the course it follows bears some definable relation to the conditions of illumination. Various forms of phototaxis have been distinguished. They have been classified by KUHN (1919) and reviewed by FRAENKEL (1931). In light of these publications, and of other contributions to the literature of subject, the varieties of phototactic behaviour that we must be prepared to find may be conveniently grouped as follows :—

(a) *The animal is capable of at least fairly accurate orientation, in a strict sense, in the direction of incidence of the light.* It is not necessary that the animal should be in some way capable of directly appreciating the direction of the light, as, for example, by adjusting the position of a certain transparent tissue to the direction of the light passing through it. Nor is it necessary that the light should directly alter the tonus of the muscles, thus forcing the organs into certain positions, so that the animal is as passive an agent as is a dead body in the way it acts in respect to gravity. It is, indeed, sufficient that the animal can somehow appreciate differences in intensity on the two sides of the body. By nervous response it tends to adjust its course so that bilateral photoreceptors receive equal illumination. One of the first detailed quantitative investigations on

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* Shock reactions on passage from shadow to light are recorded by Müller (1925) for negative Oniscus.

phototaxis, namely that of PATTEN (1914) on blowfly larvæ, demonstrates this method of orientation. The more clear-cut cases of *tropotaxis* are included in this category. They appear to be widespread, occurring in various kinds of animals. One might expect that animals with eyes sufficiently developed to discriminate some sort of visual field will be able to orientate more efficiently, displaying less searching movement, than, for example, a blowfly larva, which has no eyes, or a Calanoid Copepod, which has a single median eye.

(b) *Orientation may be very inaccurate, and so the path followed irregular, but the animal still be capable of distinguishing differences in intensity on the two sides of the body.* The irregularity may be the result either of intermittent sensitivity, or due to the fact that the animal can only appreciate large differences in intensity.

(c) *The animal moves in a course directed in the path of the light, not in the above manner, but through response to changes in intensity as its photic-sensory area moves into the shadow of the body.* This type of movement was originally ascribed by JENNINGS to Protista, such as *Euglena viridis*. Though BANCROFT (1913) brings forward good evidence that Jennings' explanation is inadequate for that organism, a genuine case appears to be provided by tadpoles of the Ascidian Amaroucium studied by MAST (1921). In this case the response is not to differences between right and left sides, but to changes in illumination of the photic-sensory area as a whole.

(d) As in (c), the animal is only sensitive to changes in intensity on its sensitive surface as a whole. While it is incapable of any exact orientation, yet, because of the shading effect of the body, the mean direction of its course tends to be in the direction of the light-rays, rather than to the area of maximum illumination (if the latter is dissociated from the former).

(e) As in (d), *but the light receptors are such, or the behaviour so adapted, that the intensity changes appreciated by the animal approximate to those that " exist in the physical surroundings." A positive animal will therefore collect in the brightest region, and not at the point nearest the light-source, if these two are dissociated.* Though this behaviour undoubtedly takes place with respect to the chemical sense, viz. typical examples of " chemophobotaxis " (e.g. cheese-mite, HENSCHEL, 1929), it is very doubtful whether it is likely ever to occur with respect to light. At one time more than one investigator, using a graded filter, has claimed that certain Crustacea collect in the brightest area and not in the path of incidence of the light, but the experimental conditions seem in no case to exclude other explanations (see p. 424).

These five types may be grouped together in various ways to suit taste or convenience. Thus (a) and (b) are logically grouped apart from (c), (d), and (e), since in the former differences in illumination on the two sides of the body are detected, in the latter only differences in total illumination from moment to moment. This seems to be the most rational line of distinction between *topotaxis* and *phobotaxis*, though presumably Kuhn's classification would group (c) with (a) and (b) as contrasted with the two others. However, the point is of no consequence for our present purpose, though it serves to illustrate the chimæroid form of biological definitions, according as the emphasis falls on the logical or empirical implications. Or again, in (a) and (c) orientation is in a fairly accurately directed course along the path of incidence of the light ; in (b) and (d) the course is irregular about an axis coinciding approximately with the direction of incidence ; in (e) there is no connection between direction of movement and direction of light. A grouping of this sort is more appropriate when the cause of aggregations of the animals is the main point at issue.

During examination of the light responses of various plankton animals, an attempt has been made to relate the observed behaviour, by the aid of the above categories, to that of animals that have received more thorough attention, while at the same time to note how far the categories meet the requirements of the species investigated here. It has been considered useful to do this before attempting detailed analysis of the behaviour of any particular species.

Two terms are freely employed in this paper : " phototaxis," meaning that the direction of movement is in some way or another affected by light ; and " (photo)topotaxis," a special type of phototaxis in which the direction of movement is controlled by the direction of the light rays. The term " phototropism," formerly used, is avoided, as this has been restricted to the orientation of sessile animals.

METHODS AND MATERIAL.

In the usual circumstances, such as in the straightforward case of a light-source on a dark background, the light intensity increases in the direction of the source. The two factors are not separated. It is not difficult, however, to devise conditions in which one factor is eliminated, or set against the other. In the case of a parallel beam of light, if loss due to absorption be disregarded, the approach to the source is accompanied by no change of intensity ; in a convergent beam, the light intensity *diminishes* towards the source ; in a gradient of light given by a filter increase of intensity* can be opposed to direction ; the light source can be made to diminish as the animal moves towards it ; both direction and change of total intensity can be eliminated by opposed parallel beams ; while direction is eliminated but change of intensity maintained if a convergent is opposed to an exactly similar divergent beam. If persistently

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* It should be made clear that the conception of light intensity at a given place means the *sum total illumination falling from all directions*. The expression is so employed all along. It is referred to as " total intensity " when added emphasis is required.

photosensitive organisms, exhibiting some definite movement in relation to light, are subjected to such varied conditions, an analysis can be made of the light response in question. The external conditions essential for the response will be shown ; in particular, it will be possible to estimate the relative importance of direction and change of intensity. Such, in its essence, is the method underlying the experiments of which account is given below.

The various light conditions that were reproduced may be summarised as follows.

(1) *Parallel beam.* This was procured by means of a wide convergent lens of 20 cm. focal length. Placed against a square glass dish of water, at a distance of 42 cm. from an electric bulb, this lens produced a beam which slightly converged from the parallel. The convergence may be regarded as adequate to counteract any loss of intensity due to absorption. The essential details are reproduced in Fig. 1.

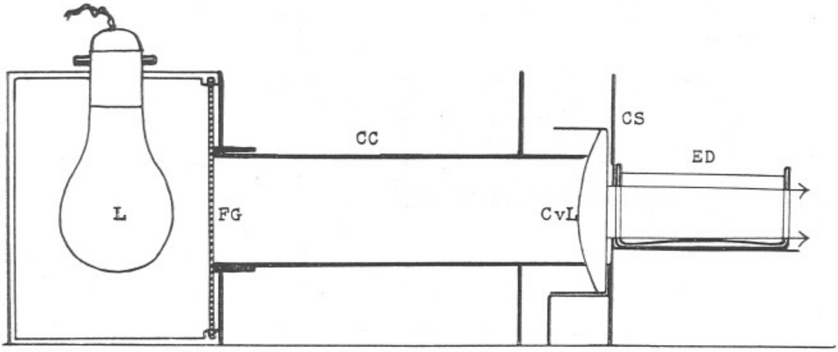

FIG. 1.—Apparatus for procuring parallel beam.

L, daylight bulb, 100 watt. FG, frosted glass screen. CC, cardboard cylinder. CvL, convergent lens. CS, cardboard screen. ED, experimental dish.

It was not found necessary to use a filter for infra-red rays, as over reasonably short periods there was no appreciable change of temperature, and no significant difference was observed in the behaviour of the animals even over long periods. The lens itself must have absorbed a large proportion of these rays. However, if lights were to be kept on for long periods, a battery-jar of water was placed between the light and the lens. The jars shown in Fig. 3 are for this purpose.

On occasions the screen of frosted glass placed close to the lamp was omitted from the apparatus.

(2) *Convergent beam.* Apart from preliminary experiments in which a cylindrical jar of water was used, a convergent beam was procured by substituting, in the above apparatus, a convergent lens of much greater refracting power (see Fig. 2a and b, and p. 400).

(3) *Convergent opposed by divergent beam.* The convergent beam was produced with the same lens as in (2), and passed through a dish 7 cm.

wide. A divergent beam was obtained from a second light-source on the opposite side of the dish, the correct amount of divergence being secured by means of cardboard screens suitably placed. The intensity of the second light was reduced by a sheet of ground glass (Fig. 3). An adjustable resistance was fitted to the lead of the first light-source, so that the intensities of the beams could, if required, be equalised. A grease-spot on a piece of white paper provided an adequate indicator for the latter purpose.

(4) *Light gradient.* Methods involving the use of a triangular glass dish filled with an absorbing liquid, or some kind of screen of graded absorbing capacity, have in the past been employed by investigators desirous of obtaining an intensity gradient antagonistic to the direction from which the light is coming. The apparatus employed in the experiments here described consisted of a triangular dish filled with an appropriate solution (Figs. 11, 12, and 13) placed horizontally between the light-source and a long glass dish containing the animals. The latter dish stood on a dark board marked in squares. A screen was fitted around the filter in such a way that no direct light reached the experimental dish from the light-source other than that which passed through it. Suitable precautions were taken to minimise light reflected from the sides of the dish. The triangular dish was filled with either ammonia copper sulphate solution or diluted Indian ink. The one gave a clear passage to the light, of which all that came through except at the extreme bright end was deep blue; the other caused differential scattering of the components of the radiation, so that the light that came through became increasingly red towards the dark end, until only the red outline of the filament showed. The concentration of the solution was so adjusted that an obvious gradient was shown on a plain white surface. In the case of the copper solution, the

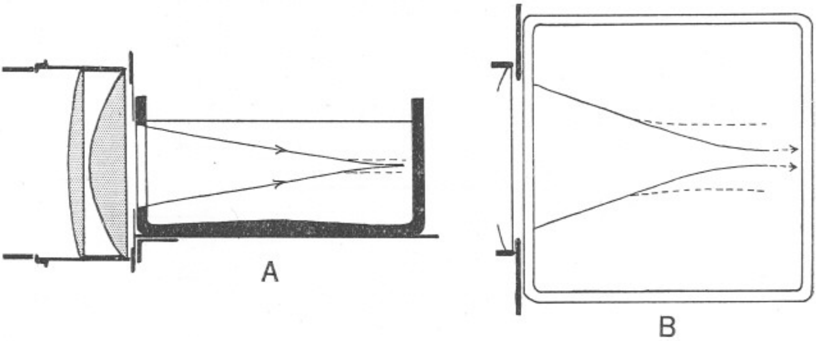

FIG. 2.—Apparatus for procuring convergent beam.
(*a*) side view of lens and dish.
(*b*) convergent beam from above.

actual concentration was measured. Methylene blue solution was also tried.

Various other lighting conditions were also set up at one time or another, some of which are referred to in this paper. For instance, two parallel beams, procured by a duplication of the apparatus in (1), have been opposed to one another, and the intensity of one, or both, varied by means of an adjustable resistance. Again, two such parallel beams have been placed at right angles to one another. Certain such modifications of the above four main varieties of apparatus employed are mentioned during the course of description of the experiments.

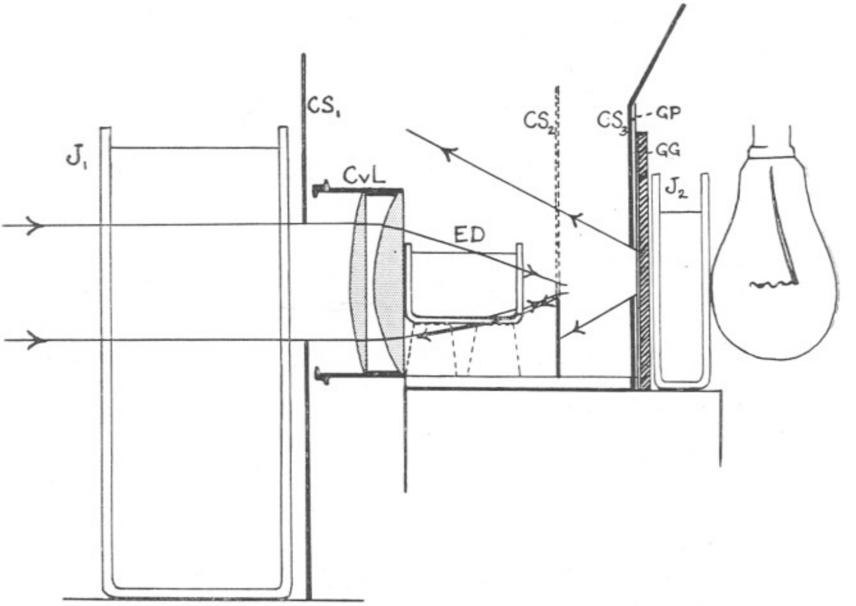

FIG. 3.—Apparatus in which a convergent is opposed by a divergent beam. J, jars of water. CS, cardboard screens. CvL, convergent lens. ED, experimental dish. GP, sheet of grease-proof paper. GG, sheet of ground glass.

Notes on apparatus. The sources of light consisted of 100 Watt daylight electric bulbs, either Osram or Mazda, gas-filled.

Glass dishes. Rectangular, moulded, dishes of $15\frac{1}{2} \times 15\frac{1}{2} \times 7$ cm. were most frequently in use. Selection was made of those in which the glass of the sides was most regular. The dish shown in Fig. 11, etc., was $47 \times 12 \times 7$. Use was also made of a special cemented dish, $11 \times 6 \times 15\frac{1}{2}$, in which the glass was perfectly free from blemishes.

Water. The water in the dishes was always pure " outside " sea-water, which had reached room temperature.

Scattered light. The experiments were carried out in darkened rooms in which extraneous sources of light were negligible, if not entirely absent. The sources of light in the experimental apparatus were always adequately screened. But more difficult to deal with is the light which diffuses from the beams themselves or which is reflected from the sides and corners of the dishes. Precautions to eliminate the effects of such light were taken where necessary, and as far as the experiments go, the results are not complicated by such effects. Perhaps, however, one exception to the latter statement is in respect to the light-gradient dish, where light reflected from the back side many to a certain extent assist scattered light in producing a deviation from the path of the direct light (see p. 414).

Preliminary experiments, and such in which apparatus 3 was concerned, were conducted during the spring of 1931 in a cellar. Here the temperature fluctuated little and remained conveniently cool. The room could be darkened completely. In the second part of 1932 the greater part of the work was conducted in another room which provided better facilities. It was darkened for the purpose. The temperature here varied from 22·5° C. in August to 14° C. in October, but was not subject to large diurnal changes.

The plankton animals investigated were taken from groups of healthy survivors in fresh tow-nettings from the English Channel off Plymouth Sound. They were transferred to dishes of clean sea-water and left for a time to become habituated to the new conditions. As a rule it was then merely a matter of selecting those specimens which were showing persistent aggregation towards, or away from, the lighted side of the dish, or showing any kind of response to light. Their behaviour in one or more of the experimental situations was then recorded, but only *in so far as the particular response remained.* Specimens which lost activity or became erratic in their behaviour were discarded. Since it was the primary aim to investigate the responses themselves, and not the extent to which any given animal would exhibit them, it was beside the point to consider how the experimental conditions compared with those in nature, or how fluctuations in light intensity or temperature might affect the appearance of a certain response. It was sufficient that the animal continued to show it.

All along care was taken to observe that the animals were consistently exhibiting the response under investigation. In general this presented no difficulty. One of the most likely changes that would have upset results would have been sudden changes from positive to negative behaviour, such as is readily induced in some species, e.g. *Temora longicornis.* But such behaviour was very infrequent, and quite obvious when it did occur. It may be noted that the light intensities in the dishes were always low, as compared with daylight, and well below the limit that might have induced species living in the upper levels of the water to revert from positive to negative. Again, there may be temporary or intermittent loss of sensitivity to light, so that movement becomes more or less random. But this did not occur under experimental conditions if it was not also observed in ordinary illumination.

The animals were handled as carefully as possible with a fairly wide-mouthed pipette, and the water in the dish to which they were introduced disturbed as little as possible during the procedure. They could be attracted to any required position in the dish with the help of a subsidiary light; so that, once they were in the experimental dish, no further handling as a rule was necessary.

When not crowded, most of the plankton which survive under these conditions generally remained healthy for two or three days, if not more. For the most part, however, those investigated had been captured the previous day.

The names of the species investigated are in all cases those adopted in the Plymouth Marine Fauna, Second Edition (1931).

In identification of specimens I am indebted to Dr. M. V. Lebour and Mr. D. P. Wilson for the help, on various occasions, of their special knowledge. It also gives me pleasure to record my obligations to Dr. E. J. Allen, Dr. W. R. G. Atkins, and Mr. F. S. Russell for helpful criticisms and suggestions.

BEHAVIOUR OF PHOTOPOSITIVE SPECIMENS.

I. In Divergent and Parallel Light.

In proceeding with the account of certain laboratory observations to be described, it is proposed to start with a survey of the various species of plankton animals which have been noticed during the course of the work to give positive movements to light. It was soon clear that animals forming positive groups are very largely, if not always, forms which exhibit some definite *phototactic* movement. At any rate, among the variety of forms studied, no cases were encountered in which grouping was effected by methods I and II (see p. 388). All light response with which we are here concerned falls under the broad category of phototaxis.

In the ensuing account of the characteristic behaviour of different species, it is implied that the direction of the light is horizontal.

Centropages typicus, a medium-sized species of Copepod, is often persistently attracted to the light. It shows two main types of movement: (*a*) regular steady swimming, keeping a straight course in the direction of the light; (*b*) rapid darts, which may be carried over a considerable distance, and in which the course is more or less zigzag. The straight, steady movement is typically interrupted by short pauses, which correspond to the sinking phase of the up-and-down movement observed when the light-source is from above. When orientated horizontally, the animal may have either dorsal or ventral surface uppermost. Indeed the latter position seems to be more frequent than the former. The habit of swimming indiscriminately front or back-side uppermost appears to be quite general among Copepods.

The two above-mentioned types of movement, rapid and slow steady, are to be seen in other species of Copepoda. *Temora longicornis* progresses either rapidly in a zigzag course, as though hurling itself to the light, as well as by slow, steady movement interrupted by pauses. *Paracalanus parvus* swims a straight steady course, with fewer checks than is usual in Centropages, or else, particularly in a beam of light, may move in quick jerks. *Calanus finmarchicus*, again, moves either slowly and steadily in a straight line for the source of light, or rapidly, by jerks, in a rather zigzag course.

Another Copepod, the abundant *Acartia clausi*, behaves in quite a distinctive manner. Its movement to the light, usually rapid, is accomplished by a series of jerks (between which there may be, if movement is slow, a considerable pause), the path followed being somewhat zigzag. The noteworthy feature is that no constant orientation of the body is maintained during this lightward movement. The animal perhaps most frequently assumes a more or less vertical position, the head uppermost, and the dorsal surface facing the light-source ; but during the course of movement no one position is kept for any length of time. The animal may come to face in almost any oblique direction : upwards, sideways, diagonally, or even downward. There is therefore no question here of the course of movement being dependent on the direction in which the body is orientated. And further, when the animal remains still there is no orientation ; it is only after movement has begun that a lightward direction can be detected.

Corycaeus anglicus, a small species with excessive development of the eye lenses, is spasmodically attracted to light. It moves with fair speed, somewhat jerkily but without pauses, characteristically keeping a straight course. This movement is more vigorous than the slow steady straight movement observed in other Calanoids, but in either case there is constant orientation of the body in the direction of the light rays.

Occasional positive specimens of *Anomalocera patersoni* have been observed. In this species locomotion is strikingly different from that in other Copepods investigated, being stronger and more deliberate—a difference that is no doubt associated with predatory habits.

Euterpina acutifrons, a Harpacticoid Copepod abundant in fine townettings from the Sound, moves by a rapid succession of short jerks. Though sometimes they keep in a straight path, their course is often erratic, deviating from one side to the other. However, on account of their activity, and because it has been possible to observe numbers at a time, they have given satisfactory results in certain experiments described later.

Males of the parasitic *Caligus rapax* are, as a rule, photopositive. When swimming with dorsal or ventral side uppermost they move in a straight line towards the source, the body orientated in the direction of the rays.

If, however, as often happens when the light is horizontal, they turn and swim on their side, the direction of movement is *at an angle* to the path of the light, the dorsal side facing the source. At intervals the animal turns over, " tacking " in the opposite direction. As a result, the course followed is zigzag and leads the animals towards the light-source (Fig. 5). In a parallel beam the angle is approximately 45°, the turns being thus made through a right-angle. This instance is evidently to be classed among those light reactions to which the term *menotaxis* has been applied. It is the only example that has come under notice.

The nauplii of *Balanus balanoides* progress with the jerky motion characteristic of Crustacean nauplii. The lightwards path is more or less straight, but if a specimen is watched closely a good deal of deviation from side to side may be seen. On account of the persistency of the photopositive movement, these animals provide favourable material for laboratory experiments. The same persistent photopositive tendency was found in the newly hatched nauplii of the freshwater *Cheirocephalus diaphanus*. A specimen of an unidentified Cirripede metanauplius moved towards a light-source in a straight path.

Among the immature stages of Decapod Crustacea, the planktonic forms seem as a rule to be strongly reactive to light. Mention may first be made of the larvæ (first and second stages) of *Galathea squamifera* and *dispersa*. These were found to move straight to the light with their *posterior end foremost*. In the best performers the body is held accurately orientated, the path taken direct, and the movement continuous. Either ventral or dorsal side may be uppermost.

As in the case of other species capable of accurate orientation, the paths may often undulate considerably—even in a specimen which has only just previously moved in a straight path.

The first larvæ of Upogebia sp. (probably *stellata*) also orientate and move backwards, and are also capable of swimming in a straight path up a beam, but were found to be more erratic than Galathea. This curious habit of swimming backwards was pointed out by LYON (1906), who found that Palæmonetes larvæ move to light in this way.

The first Zoeas of *Carcinus maenas* have been found to be strongly photopositive, moving up a beam in a steady, and remarkably straight, course. They orientate in a normal manner, anterior end facing the light and dorsal surface uppermost. The elongate 1st Zoeas of Porcellana sp. (probably *platycheles*) also react persistently, moving straight forward towards a light-source or up a parallel beam. Owing to their long anterior spine it is easy to observe the exact direction of orientation in these larvæ, and it seems typical for them continuously to sway from side to side as they travel along. But this swaying is through a small angle only, and the mean direction of movement is in a straight line to the light source.

Specimens were sometimes seen to move backwards, but in this were not in the least handicapped in maintaining a direct path. The abdomen was moved rapidly, and the body swayed from side to side a great deal, but the speed was much the same as in direct forward movement. One specimen, perhaps with a limb hampered in some way, rolled over continuously to the left, and thus progressed in a spiral. And yet it kept a straight course up the beam.

Various other Zoea larvæ of crabs have shown photopositive behaviour, several moving in a straight line towards the source. Some of these swim backwards, the long posterior spine pointing ahead.

In addition, a specimen of a *Pandalus montagui* larva, which, though not altogether healthy, deserves mention as it remained persistently positive when tested in a parallel beam, went straight to the source with very little tendency to deviate, although—and this is the point emphasised —orientating at various oblique angles.

The larvæ of the herring (*Clupea harengus*), during the first fortnight of life, show marked tendency to cluster on the lighted side of their tank. Their responsiveness to light appears to be strongest when their activity is greatest. In lowest intensities, not only is there a falling off in activity, but, curiously, a reversal to negative phototaxis. Examination of the movement of individuals in relation to a single light-source, or in a parallel beam, was handicapped by the fact that the intensity was clearly too low. Though all active specimens before long moved up toward the light-source, they did not steer a straight course towards it and deviated considerably from side to side. After having been kept in the dark for three days their progress up a beam was more definite, but still there was a good deal of random movement.

The young larvæ of a species of goby (Gobiidæ) showed more definite phototactic movement. When active, specimens frequently swam towards the light up a parallel beam, moving in a characteristic way. They progressed by a series of jerks, the direction of each jerk (corresponding to one flick of the tail ?) being different from the one before, alternating to right and left so that the path was decidedly zigzag. The mean direction of the path was, however, straight and coincided with the direction of the incident light (Fig. 8).

Small Polychæt larvæ provide further examples of forms which can be strongly photopositive. They move continuously and directly towards the source, the course taken varying from a straight line to one which undulates regularly. An undulating course is characteristic of a species of Polydora, in which the body is constantly swayed from side to side, so that the head is all the time moving to and fro through a wide arc. A similar type of movement is seen in small free-swimming Turbellarians, single specimens of which have from time to time been under observation, In these the path followed deviates irregularly, but an average direction in the axis of the light is maintained. The anterior end of the body is constantly swayed from side to side, suggesting trial and error behaviour. Strong photopositive movement has also been observed in an Autolytid bud carrying eggs, and a Polychæt metatrochophore. In the latter specimen the anterior end moved through a very wide spiral. An unusual example is provided by the Disomid, *Poecilochaetus serpens*, a young specimen of which was found to be decidedly positive to light and to exhibit quite a unique type of topotaxis. It proved capable of moving straight up a parallel beam, although swimming so vigorously that its movement can only be described by saying the worm threw itself into convulsions.

It was placed by pipette at the far end of the beam. At first it lay extended on the bottom ; then rhythmic body movements began, which gradually increased in intensity until the worm was, so to speak, coiling on itself. Rising in the water, it swam straight up the beam, coiling vigorously. This procedure was repeated five times with an exactly similar result. Thus, in this example, the path of the animal is direct, whereas no part of the body is orientated to the light. The means whereby the direction of the path is maintained is quite obscure.

For completeness it may be added that further instances of observed photopositive movement are provided by Oithona sp. (Copepoda), *Sagitta elegans*, Mollusca larvæ, and Annelid trochophores. By this time sufficient has been said to show that indisputable phototactic behaviour can be evoked in a wide selection of smaller planktonic animals. This fact remains whatever the extent and significance of such behaviour under natural conditions.

The majority of the above species have been tested in a parallel beam of light (apparatus as in Fig. 1), and in no case was any difference in behaviour observed from that in ordinary divergent light. Since it has been found convenient to use a parallel beam in examination of methods of movement, the data from such tests have been freely included in the above account. Positive movement in a parallel beam has previously been found by ROSE (1925) for Balanus nauplii, etc., and by FRIEDRICH (1931) for *Calanus helgolandicus* and *Corycaeus anglicus*.

In reviewing the above account, attention may be drawn to the variety there is to be found in the movements of different positive phototactic forms. Some, such as most Copepods when moving slowly, and Decapod larvæ, are constantly orientated towards the source ; others are not orientated to the source although the path followed may be quite straight (*Acartia clausi*, *Poecilochaetus serpens*). Some keep the body rigid (Crustacea), others sway the anterior end from side to side (Turbellaria) ; some move jerkily (Euterpina, various nauplii), others smoothly and continuously (Decapod larvæ, Polychæt larvæ). The course followed may be straight (Decapod larvæ, some Polychæt larvæ), zigzag (some Copepods, Sagitta, Gobiid larva), undulating (Polydora sp.), or spiral (Trochophore) ;

varying regularly (Polychæt larvæ) or irregularly (Euterpina). Several Crustacea swim with either ventral or dorsal side uppermost. It is further to be noted that movement may be to the side (Acartia), or backward (prawn larvæ, Zoeas), or obliquely (specimen of Pandalus larva), and yet a straight course be maintained.

II. In Convergent Light.

It has been noted above that photopositive plankton animals will readily move up a parallel beam of light, although in doing so they are not continually passing into light of increasing intensity. Throughout they are subjected to constant illumination. One may next enquire what happens when the beam of light is made to converge, so that movement towards the source necessitates passing from higher to lower light intensities. Accordingly examination was made of the animals' behaviour in a convergent beam.

In the apparatus employed (Fig. 2) a convergent beam passing through a rectangular opening of 8·8 cm.×4·5 cm., shrank from 7·8×4·2 (dimensions on entering the water in dish) to 1·2×0·8 cm. in a distance of 10 cm. When allowance is made for loss of light due to scattering, etc., the increase in intensity over this region was calculated as approximately 25 times.

The results obtained for various species tested are given below. In all cases care was taken that the specimens chosen were reacting positively to ordinary light.

Centropages typicus. On several occasions positive specimens were placed in a convergent beam, always with the same result. Provided they did not stay motionless, they moved up the beam towards the source, and showed no tendency to stay in the brightest region. In short, they reacted just in the same way as to divergent or parallel light, thus showing the importance of the direction of incidence as against change of intensity. Notes on the behaviour of 24 adult specimens are shown in Table I. Moreover, their average courses followed the paths of the light-rays; that is to say, starting in the brightest region the paths taken spread out in a fan coinciding with the direction of the converging light. In nearly all cases the animal kept at the edge of the beam, either at the side, or above, or on top. When left undisturbed, the animals congregated against the area of entry of the light (PQ, Fig. 4), where again they exhibited a tendency to collect at the edges. Movement was either very slow, steady, and straight; or more rapid, steady, continuous; or in rapid jerks.

Specimens placed carefully by pipette in one of the far corners of the dish (19-viii-32) behaved as expected if supposed to follow the course of the light-rays or the maximum diffuse light. The tracks of nine individuals are shown in Fig. 7.

TABLE I.

Centropages typicus.

Notes on movement up a *convergent beam* of 24 adult specimens (including 10 ♂♂ and 14 ♀♀).

The apparatus is that described on p. 391. (For the first 12 specimens the opaque glass filter was present, for the rest it was absent ; but this does not affect results.) Specimens were placed singly by pipette in the narrowest part of the beam. Unless stated to the contrary, all were photopositive, moving up to the light source. The point at which movement started is recorded : l.p.—on leaving pipette, e.b.—on entering beam, t.b.—on touching bottom.

Specimen.	Started to move.	Movement.	Position of path.
(with opaque glass filter)			
1.		slow, with some hesitation	side edge of beam.
2.	t.b.	continuous slow steady	lower edge, in centre.
3.	l.p.	paused, then continuous slow steady	side edge.
4.	l.p.	,, ,, ,, ,,	side edge.
5.	l.p.	swooping movement, then slow	inside beam.
6.	l.p.	slow steady	side edge.
7.	l.p.	slow steady	centre, top edge.
8.	l.p.	slow steady	centre, top edge.
9.	l.p.	slow steady	centre, top edge.
10.	l.p.	slow steady	centre, lower edge.
11.	l.p.	slow steady	centre, top edge
12.	t.b.	movement at first irregular started on bottom, swam up and across beam, then hesitated ; then swam slowly and steadily to light	side edge.
(without opaque glass filter)			
13.	l.p.	rapid, then slow	centre, top edge.
14.	l.p.	slow steady	centre, top edge.
15.	t.b.	slow steady	lower edge.
16.	l.p.	swoop, then slow steady	side edge.
17.	l.p.	2 or 3 rapid darts, then zigzag, then slow up side edge, gradually carried away from beam ; checked, recovered, swam along edge of beam to source	
18.	l.p. swerved at start	slow steady	top edge.
19.	l.p.	slow steady	top edge.
20.	l.p.	slow steady	top edge.
21.	l.p.	(paused, fell through beam, only giving very slight jerks on coming in contact with the beam. Fell to bottom, from which it moved a little later)	
22.	e.b.	(started positive on side of beam, but tended to move in a circle, and was carried into darker part of dish)	
23.	l.p.	rapid	centre, top edge.
24.	l.p.	slow steady	centre, top edge.

When the convergent beam was reflected back on itself by a mirror, so that the directive quality of the light must have been counteracted to a large extent, it was found that the Centropages still swam towards the main source. Evidently the intensity of the direct beam exceeded that of the reflected light enough for the excess to be detectable by the animals. This affords an example of an effect which was observed on several occasions—when light is coming from various directions, the animal moves in the direction from which the light is relatively strongest.

Acartia clausi. In this species again no difference of behaviour was detected in divergent and convergent light. In the latter case animals moved towards the light as readily as in the former. Specimens were tested on several occasions, embracing both adults and immature, winter broods, spring broods, and late summer broods. Both slow and rapid movement were observed, as well as the characteristic lack of orientation. When collected at the light-source they showed a marked tendency to select the outer edges of the beam (as in the case of Balanus larvæ, Fig. 9).

Temora longicornis. Positive specimens of this species, again, were found to move up a convergent beam. Several tested (15-vii-32) moved for the most part with rapidity in a zigzag course (though slow, steady movement was also observed); and showed decided tendency to keep to the outer part of the beam, both during movement and when left to congregate.

On another occasion (21-v-31) several specimens had been tested alternately in convergent and divergent light of equal intensities in the apparatus figured on page 393. Each specimen was kept on the move for some while by the switching over from one light to the other. On the whole the animals moved distinctly faster up the divergent than up the convergent beam, as indicated below.

	DIVERGENT.	CONVERGENT.
Specimen 1.	Rapid, rather zigzag.	Slow steady.
,, 2.	Rapid.	Partly slow, partly rapid.
,, 3.	Very rapid.	Rapid.
,, 4.	Rapid, with slight exception.	Slow, interspersed with rapid.
,, 5.	Rapid and slow.	Relatively slower.
,, 6.	Rapid.	Slow, except at end of path.
,, 7.	Partly rapid, partly slow.	Less rapid, more slow.

It is not known, however, if any significance is to be attached to this difference. Movement up the convergent beam was, as usual, in the direction of the light-rays, i.e. the paths radiated outwards from the narrow end of the beam.

Euterpina acutifrons. Specimens which moved in a direct line for the light likewise moved directly up a convergent beam. The immature and nauplii also moved up the beam as readily as to an ordinary source.

Calanus finmarchicus. Positive specimens were found to swim to the

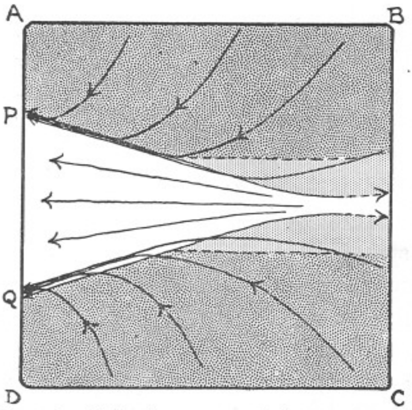

FIG. 4.—Paths in convergent beam—mean direction of those animals which move in the direction of the rays.

ABCD, square dish. PQ, entrance of convergent beam.

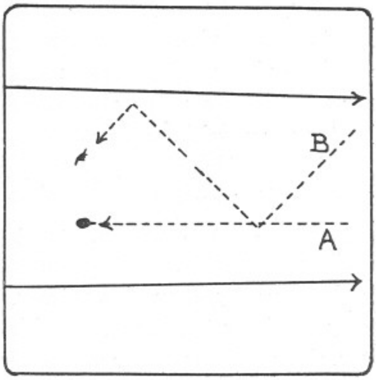

FIG. 5.—*Caligus rapax* ♂—paths in lateral parallel beam.

A, dorsal or central surface uppermost.
B, one of the sides uppermost.

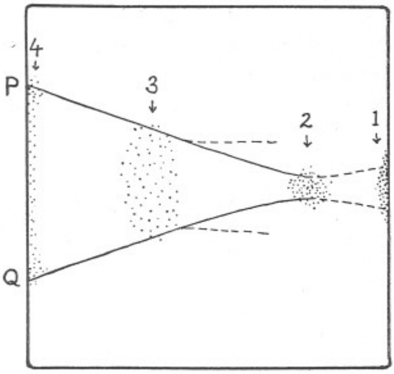

FIG. 6.—*Balanus balanoides* day-old nauplii —four successive positions (1 to 4) in movement up a convergent beam. PQ, entrance of beam.

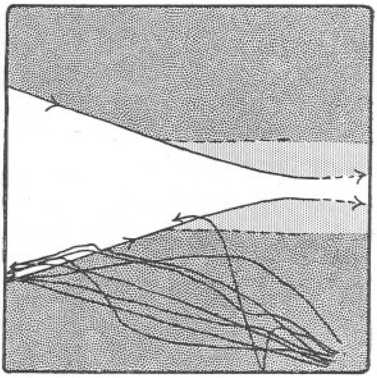

FIG. 7.—*Centropages typicus*—paths of 8 specimens in diffuse light coming from convergent beam.

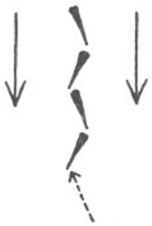

FIG. 8.—Path of Gobiid larva, showing successive positions of the body.

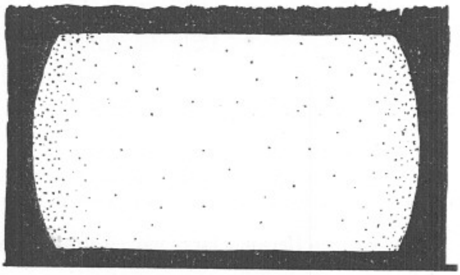

FIG. 9.—*Balanus balanoides* day-old nauplii—congregation at entrance of convergent beam.

light by steady continuous motion, following the direction of the rays. The tracks in the beam approached the ideal shown in Fig. 4. It may be added that positive specimens have also been found to continue lightward movement when the source was steadily dimmed during the time they were travelling towards it.

Balanus balanoides nauplii. A group of day-old larvæ, strongly positive, gave very clear results in a convergent beam (27-vii-32). They moved up the beam towards the light, the group spreading out in the beam, but not passing outside it. (The region outside the beam could be explored by the light reflected from a mirror.) Four successive positions of the main body are shown in Fig. 6. Within 2½ minutes from the switching on of the light they had moved from position (I) and congregated against the glass at the entrance of the beam. When collected in this way they tended to accumulate at the edges of the lighted area (Fig. 9), an effect which has been observed in various other species. When the beam is reflected back by a mirror, the larvæ still move towards the direct source, though considerably more slowly and in a more irregular course.

Zoea larvæ. Zoea larvæ that have been tested in a convergent beam have been found to move as straight and quickly towards the light as to an ordinary source. As in other forms, they follow the direction of the rays. Their paths conform closely with the idealised paths shown in Fig. 4.

Other positive animals which definitely swam towards the source in a convergent beam, thus behaving in a manner comparable with the species described above, include the following :—

CRUSTACEA	*Corycaeus anglicus*
	Paracalanus parvus
	Oithona sp.
	Caligus rapax ♂
	Nauplius of *Cheirocephalus diaphanus* (freshwater)
	Podon intermedius
CHÆTOGNATHA	Sagitta sp.
ANNELIDA	small Spionid larvae
	Polychæt metatrochophore
	,, trochosphere
PLATYHELMIA	small Turbellarian

To these may be added the following :—

An elongate Copepod nauplius, whose forward movement was regularly interspersed with pauses, remained positive in a convergent beam, the pauses being distinctly longer and more frequent.

An unidentified Decapod larva moved straight backwards up the beam in the same way as it moved to other light sources.

Very small cercaria larvæ from *Littorina littorea** were found to collect gradually towards

* I have to thank Miss M. Rothschild for these specimens.

the light. When a convergent beam was thrown through the beaker containing them, the larvæ gradually collected as before. For considerable periods the larvæ were seen to hang motionless in the water, but every now and then a sudden dart for a short distance was made in the direction from which the light was coming.

Among the various animals tested all gave comparable results, namely positive specimens move up a convergent beam as to any other source of light. There was not a single exception found. This uniform result is all the more striking, as a variety of types were investigated, representing several phyla, and exhibiting a variety of modes of progress (see p. 399).

There were no discrepancies from the general rule that, in so far as the animal normally moves straight in the direction of the light, so, in the convergent beam, its possible paths follow the fan-shaped arrangement of the conventionalised light-rays (as shown in Fig. 4). There was also shown a decided tendency to keep to the outer side of the beam rather than in the centre, and for collections to concentrate most on the outer edges of the beam at its point of entry ; probably to be explained on the grounds that the light was somewhat more concentrated at the edge of the beam.

The results, therefore, emphasise the primary importance of directional properties of the light in photopositive movement of the type considered. Not only is the increase of intensity which usually happens to be associated with the approach to a light-source unessential, but an appreciable *decrease* (such as produced by a convergent beam) does not affect the result.

III. In Convergent opposed by Divergent Light.

With a parallel beam of light, change of intensity in the physical environment is eliminated while direction is maintained. Direction, too, may be eliminated by opposing two beams of exactly equal strength. If it is required to preserve the change of intensity, it is only necessary that one of the beams should be convergent and the other divergent. Thus a convergent beam exactly opposed by a divergent of corresponding intensity gives a condition in which intensity change is preserved but direction, in one plane, eliminated.

As figured on p. 393 (Fig. 3), a convergent beam, produced as before, was passed through a dish 7 cm. across, and a direct light-source was opposed to it, screened with opaque glass and cardboard slits in such a way that a divergent beam was produced coinciding in position with the convergent. An adjustable resistance (a pair of triangular copper plates which could be moved up and down in a battery-jar of water) was connected with the second light, so that the intensity of the divergent beam could be adjusted to that of the other. A grease-spot, made by a small drop of medicinal paraffin on white paper, provided an effective indicator.

The animals investigated were placed in the glass dish and their positive behaviour checked by switching on one or other of the lights. Throughout the course of the experiment it was possible to check the persistence of this behaviour in the same way. It has to be acknowledged that the double-sourced beam was of twice the intensity of one light alone, but the behaviour with which we are here concerned was clearly not influenced on this account. Doubling the intensity of a single light-source was found, on occasions when tested, in no way to desensitise or otherwise to alter the general phototropic movement of the animal.

Acartia clausi. Tested on several occasions, this strongly photo-positive species was found to lose orientation altogether in the double-sourced beam. The movement of individuals appeared to be quite random, the jerks being made in any direction. When several were left in the beam, they distributed themselves at random through it.

Euterpina acutifrons is also quite disorientated. Specimens were observed to move to and fro in various directions as well as round in circles. As soon, however, as one light was dimmed (an opaque glass filter being interposed), a drifting away from the dimmed source was at once apparent, divergent and convergent source being treated alike.

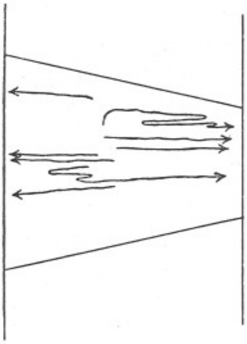

FIG. 10.—*Corycaeus anglicus* ♀—paths in convergent opposed by divergent beam.

Contrasting strongly with the above two species, *Corycaeus anglicus* keeps strictly orientated to one or other of the two light-sources. Positive (or, for that matter, negative) specimens move to and fro in the beam, always in the axis of the light. Fig. 10 is typical of results obtained. This shows the paths taken by a ♀ which was placed by pipette 8 times in the centre of the beam. It travelled straight towards one or other of the lights, and on occasions when it changed direction a complete turn through 180° was made. As far as tests with this species went, no preference for one or other of the lights was noticeable.

Centropages typicus, again, retains orientation along the path of the light rays, moving without preference to either source. The characteristic behaviour of actively positive specimens is movement from one side to the other along the length of the beam with longer or shorter intervals spent at either source. As a typical illustration may be cited the behaviour of an active ♀ (20-1-31) on being placed in the centre of the beam 35 times in succession.

	No. of trials	to convergent source.	to divergent source.
(1) Both lights on . . .	8	4	4
(2) Divergent only . . .	8	0	8
(3) Convergent only . . .	8	8	0
(4) Both lights on . . .	11	8	3

On arriving at the side of the dish it either remained for some time at the light or else soon turned and swam to the opposite source.

Precisely the same sort of behaviour was found with specimens placed in opposed parallel beams—they oriented to one source or the other. With a parallel beam reflected on itself, either the direct source or the reflection can act as a source of attraction.

Temora longicornis, as Centropages, orientates its course in a very noticeable manner to one or other of the sources. Individuals were observed to move to and fro in the beam from one source to the other.

A particularly clear-cut instance is that of a specimen which, after being placed in the beam and left undisturbed, swam alternately from one end of the beam to the other. Watched for 2 or 3 minutes, it was seen to move to one source, swim against the glass for a little, then turn and swim straight to the opposite source. During this whole period it made no fewer than 18 journeys, 9 times to each source. Then, for a period of half a minute, the single lights were tried in turn, and the positive behaviour of the animal verified. After this, both lights were again switched on together, and for another two minutes the to-and-fro course was continued. Again, in the same way, 18 journeys were made.

Zoea larvæ of an unidentified species were tested on one occasion. A number of specimens were watched, and the characteristic behaviour found to be as follows. To either divergent or convergent source alone they move fairly straight and quickly ; when both lights are on they are to a large extent disoriented : they move in various directions, but apparently oftener up and down the beam than across. Thus, because their movements are not altogether random, but more frequently towards one or other of the sources, they are intermediate between Centropages and Acartia.

Some of the smaller planktonic forms appeared, like Acartia, to be disoriented in the double-sourced beam. Among these are : Balanus nauplii, *Paracalanus parvus*, and Oithona sp. It may be added that *Podon intermedius* and larvæ of Polydora sp. lost orientation in a double-sourced parallel beam, moving in circles.

No other species were investigated, and no further examples can be given of behaviour like that shown by Corycæus, Centropages, and Temora. It is probable, however, that prawn larvæ of various kinds would be found to act in the same way. A specimen of the larva of

Pandalus montagui was found to steer straight to one or other end of a double-sourced parallel beam.

There was no tendency found, among species investigated, to collect in the brighter part of the beam (divergent source), but it cannot be claimed that the experiments were sufficient to exclude absolutely the possibility of this occurring. At any rate, it is certain that this does not happen in the case of *Acartia clausi,* specimens of which species distribute themselves at random through the beam. With Acartia, then, we have definite evidence from this source that photopositive movement depends on the directional properties of the light, and not on the change of intensity encountered in passage through the beam. Again, with species which maintained orientation and moved to one source or the other, on no occasion was there any indication of preference for either one of the lights.

These experiments go far enough to bring out two points. In the first place, there is the fact that, in a double-sourced beam, two quite distinct types of behaviour occur. Some species, on the one hand, lose orientation and move about in any direction ; some, on the other hand, still orientate to either source. It may be supposed that this difference between these two groups of species results from differences in the light receptors. If the latter structure is affected by the light from all directions more or less equally, then light from two opposed directions may be expected to upset orientation. If, however, the receptor is affected, say, from one direction only, so that when facing that quarter it is screened from the light behind, then orientation to each source in turn is possible. It can be understood that, among various forms of lower animals, some might be affected by light coming from almost any direction, while others might show decided differential selection, being, for example, more receptive to light coming from in front than from the sides, and from the sides more than from behind. Among the former might be included the more transparent and the smaller forms with a single median eye ; among the latter, forms with larger paired eyes with a definitely restricted field of view, forms with a single median eye whose field is reduced by the opacity of the body, or owing to the presence of pigment, forms with well-developed lenses which concentrate light from one direction at the expense of others, or with any other characteristic which may induce inequality in the optical field. This supposition receives support from results given by the species which have been investigated. Those that are disoriented include (i) small transparent forms with a single median eye, such as Balanus nauplii, Euterpina, and *Paracalanus parvus*, and (ii) the larger, but transparent, *Acartia clausi*, which, as noted above, does not maintain orientation in any fixed direction when on the move, and so would come under the influence of both lights equally. Those that still orientate themselves are species which happen both normally to move straight in the axis of the beam, following the path of the rays, their body orientated towards the light-source, and, at the same time, to give reason to suppose that their eye is wholly or partly screened from the light falling posteriorly. *Temora longicornis*, though rather small, is pigmented; Centropages is by no means transparent and of considerable size; while Corycæus possesses a pair of prominent lenses which concentrate the light from one direction at a time.

The second point to be brought out is that those species which move to and fro to one or other of the sources are evidently still sensitive to the *direction* of the light. They will continue, moreover, swimming up a convergent beam even though there is divergent light from the opposite direction.

IV. In a Light Gradient crossing the Path of the Light.

By means of the apparatus described above (p. 392) it is possible to produce a gradation of intensity from one end to the other of an elongated glass dish or glass tube, in such a way that the brightest end is furthest from the light-source, and the passage in the direction of the light involves passing into decreasing intensity. Two phases can be observed in the behaviour of the animals studied: (i) the direction of their path across the dish, (ii) the area in which they congregate when left undisturbed for an adequate period.

(i) When an animal is introduced somewhere along the length of the side away from the light-source, it first crosses the dish, until in contact with the glass of the side facing the source. The course followed may be compared with the known direction of the light and any possible effect of intensity difference noted.

(ii) Assuming that it remains active after coming in contact with the side of the glass facing the light-source, the animal will continuously swim against the glass in the effort of continuing lightward movement. In the ordinary way, that is, if there is no light filter, the result of its movements will be to bring it gradually to the region immediately opposite the light-source, where random variations in direction will be made equally to the right or the left. The animal will, in effect, work its way along the edge of the glass by degrees, until in the region nearest the light-source. A group of animals left to themselves will gradually collect and concentrate in this region. Now, in the ordinary way, the animal is all the time moving into increasing light intensity; whereas when a graded filter is used, the intensity *decreases* as the region opposite the source is approached. Where, it may be asked, will the animals collect in the latter case? If the region of highest intensity is chosen, they will collect at the end of the dish *furthest* from the source ; if influenced by the direction of the lig alone, they will collect *opposite* the source.

Centropages typicus. The first trials were made with comparativel highly diluted Indian ink in the filter. The apparatus is shown in Fig. 11 Individual animals were placed by pipette in the region of the dish

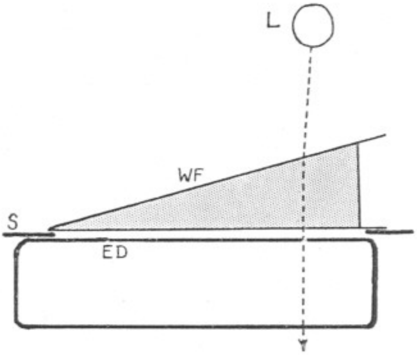

FIG. 11.—Light gradient apparatus.
L, daylight bulb, 100 watt. WF, filter.
S, screen. ED, experimental dish.

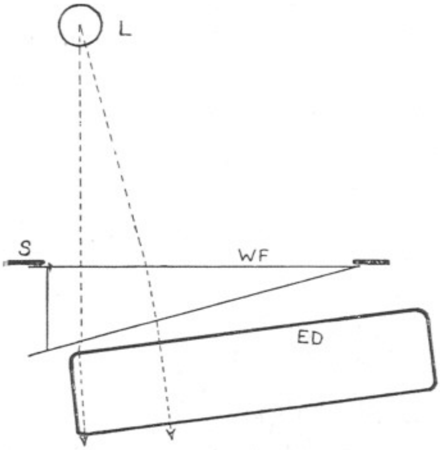

FIG. 12.—Light gradient apparatus. Lettering as in Fig. 11.

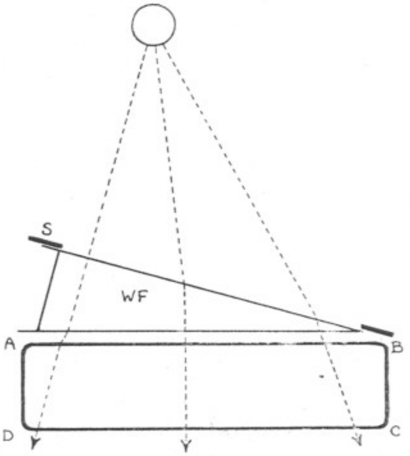

FIG. 13.—Light gradient apparatus. Lettering as in Fig. 11. Corners of experimental dish marked ABCD.

furthest from the source and their subsequent movement noted. The paths of the 25 specimens tested are shown in Figs. 14A and B. It will be seen that the paths coincide closely with the direction of the light-rays. No marked deviation towards the brighter region (i.e. in the direction of Z) can be detected. Furthermore, the animals did not take long to work up the dish to the region opposite the light, where they then collected. This behaviour—moving in path of the light-rays and collecting at the point nearest the source—is what is to be expected of animals whose photopositive movement is regulated by the direction of the light rather than by change of intensity.

When, however, the strength of the Indian ink solution was increased, so that a more pronounced gradient was procured, and very little light penetrated direct into the darker end, the paths of specimens tested (this time liberated in middle region of the dish) showed a noticeable deviation to the left, that is, towards the brighter part of the gradient.

This deviation was then demonstrated more accurately. The same solution of ink was used, and the apparatus arranged as in Fig. 13. Twenty-five specimens were released immediately opposite the point of direct incidence of the light. Note was taken of the point at which they arrived at the opposite side.

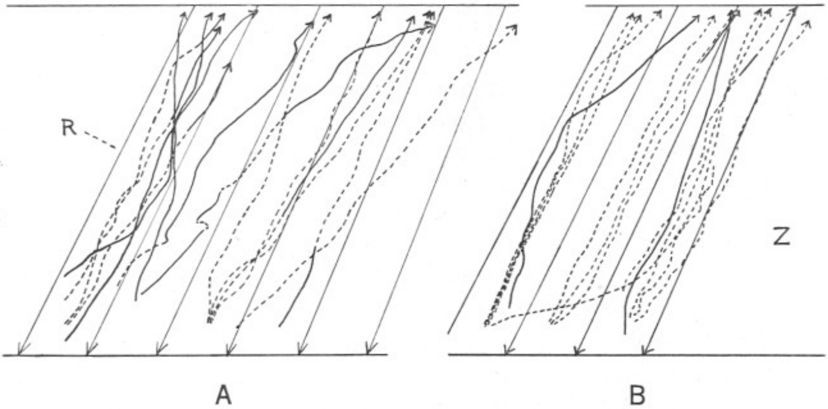

FIG. 14, A and B. *Centropages typicus*—paths in light gradient.
R, arrows indicating direction of the light.
Z, direction of brighter end of gradient.

The distance of the direct path was 11 cm. A dark board underneath the dish was marked in 2-cm. squares, the scale being expressed in cm., 0 to 46. In this case the point opposite the source, where the light fell at right angles to the dish, was at 25. The points of arrival were grouped in 2 cm. lengths.

It became clear that the animals deviate slightly towards the brighter end of the dish (i.e. in this case to the right), as the results given in Table II show. There was, in fact, an average deviation of 1·2 cm. to the right over the direct course of 11 cm. The next day the experiment was repeated, the same batch of animals being used, with similar results, shown in the same table. No record of the actual tracks was kept, but it was most noticeable that such deviation as was apparent occurred mainly in the last

4 or 5 cm. of the path. An estimated mean path is shown in Fig. 16. That a deviation should be found is not surprising; the cause of it is discussed below. In the majority of animals the movement was slow, and at the same time jerky.

TABLE II.

PATHS OF *Centropages typicus* ACROSS LIGHT GRADIENT.

Point of arrival along AB	Animals released at **25**. 20–22	22–24	**24–26**	26–28	28–30	Average deviation.
Number of specimens						
12–x–32	0	3	7	12	3	1·2 to Right (25 to 26·2)
13–x–32	0	1	**10**	11	3	1·3 to Right (25 to 26·3)

NOTE.—In each series the same animal may have been used on more than one occasion. Very few gave no results, i.e. remain inactive.

When some Centropages were left in the dish, they did not concentrate exactly opposite the light-source (at **25**), but kept distinctly to the right. This behaviour was also shown, and more obviously, by a number of Acartia in the dish at the same time.

It is not difficult to account for the occurrence of this deviation from the path of the direct light; for it is clear that, if body-orientation in some way depends on a balance of the light falling on the two sides of the animal's body, excess of diffuse light on one side will cause a deviation of orientation in that direction. In the darker part of the dish the amount of diffuse light coming from the brighter end must have a strength of an order comparable with that of the direct light, and so introduce an appreciable lateral component into the light effective in regulating the animal's course. The excess of diffuse light on one side will also influence the position round which the animals tend to congregate—for at the point nearest the source random movement will now tend towards the brighter side rather than the other. This question is fully treated later, after some experiments with Euterpina have been described.

Euterpina acutifrons. In a preliminary test, with the filter arranged as in Fig. 11, and containing methylene blue solution, it was noted that immature animals moved obliquely across the dish more or less in the direction of the rays and steadily accumulated at the dimmer end of the dish round a point almost opposite the light source. As in Centropages, the brighter end was ignored.

With diluted Indian ink in the filter, it was observed that now, on the whole, the paths of adults and immatures, moving across the dish at the brighter end, noticeably deviated to the left. Then, when left to congregate, the animals were found concentrated in an area opposite the light-source—or somewhere to the left of it.

When the filter, filled with half-strength ammonia copper sulphate solution, was arranged as in Fig. 18 (except that the dish was placed parallel with the lighted side of the filter, so that the point nearest the source was at the extreme left end), adults, immatures, and nauplii aggregated quite rapidly to the left side of the dish opposite the source of light. The paths of individuals, judging from the way a group expanded from the point at which introduced, on the average appeared to approximate well with the path of the light rays. The behaviour was no different when a length of opaque glass was stood between the filter and the dish. The animals even continued to congregate at the left-hand end (1 to 18) when the opaque glass was stood obliquely, as shown in Fig. 17, in a way which greatly accentuated the gradient. Further, when the apparatus was arranged as in Fig. 13, the animals congregated in the neighbourhood of 25 ; and again when it was arranged as in Fig. 12, they collected about 18, that is, once more approximately opposite the light-source. With

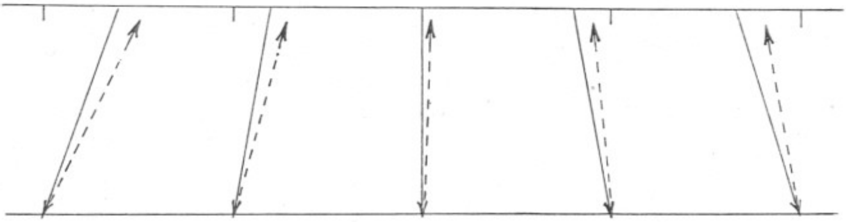

FIG. 15.—Balanus nauplii—paths in light gradient. Continuous line, path of direct light ; broken line, path of larvæ.

FIG. 16.
Centropages typicus mean direction of path across light gradient.

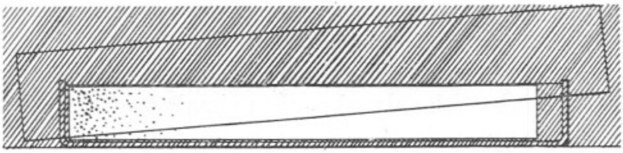

FIG. 17.—*Euterpina acutifrons* in light gradient (see text).

this filter, therefore, there was shown no marked deviation from the path of the direct light; though it should be added that the average paths of individuals placed in the dark end (at 5) or opposite the light (2) seemed consistently to show a slight trend to the right of the order of 1 cm.

By contrast, a very noticeable deviation towards the brighter end was found when Indian ink was placed in the filter. Six different mixtures of increasing concentration were tried in turn. No. 1 mixture was just strong enough to give a perceptible gradient; while no. 6 so dense that the filament of the electric bulb was only just visible in the darkness of the left-hand end of the dish, and it was only the right-hand third of the dish that received any appreciable illumination. No. 2 was twice the concentration of 1, 3 twice that of 2, while 4 and 5 were intermediate between 3 and 6. In each case a group of Euterpina were given adequate time to form a cluster opposite the light, and the position of the midpoint of the cluster was recorded. In each case, also, active specimens were introduced opposite the light-source and the trend of their movement observed. The results, which are graphically shown in Fig. 18, A to F, are as follows:—

Solution.	Midpoint of photopositive cluster.	Deviation to right.
1	27	2
2	28	3
3	30	5
4	31	6
5	37	12
6	39	14

The figures also show the trend of the paths of specimens traversing the dish. In all cases, when starting from 25, they veer towards the point at which the group is formed. The mean path is at right angles to the length of the dish only when the animals are liberated opposite the centre of the group.

The point clearly brought out is that, as the thickness of the filter increases, so the direction of the animals' movement deviates increasingly from the path of the direct light, until a stage is reached at which the animals are, so to speak, driven far into the brighter end of the dish.

It should be pointed out that there is no question of the animals becoming negative to light in the lower intensities. Some tests were made with the same animals used in this experiment and it was found that the animals remained sensitive to light of very low intensity, reacting positively all the time. Moreover, any possibility of the animals having become negative or desensitised during the experiment is entirely annulled from the fact that the animals continued to cluster on the side of the vessel facing the source. Negative animals would have grouped on the opposite side, while desensitised animals would not have formed clusters at all.

It is noteworthy that even in the condition shown in Fig. 18F, the brighter (right-hand) corner is avoided by the animals. The group does not extend into it. By this fact we are assured that the animals are still not grouping in the region of highest light-intensity as such, any more than in other cases.

In respect to the light conditions to which the animals in the dish were subject, it is important to emphasise that the ink suspension in the filter has a considerable scattering effect on the light, thus increasing the amount of diffuse light at the expense of the direct. One would therefore expect the paths of the animals to show more deviation with Indian ink in the filter, than with a clear solution such as ammonia copper sulphate. The deviation would necessarily become greater as the thickness of the solution increases. A further point is that the filtered light becomes

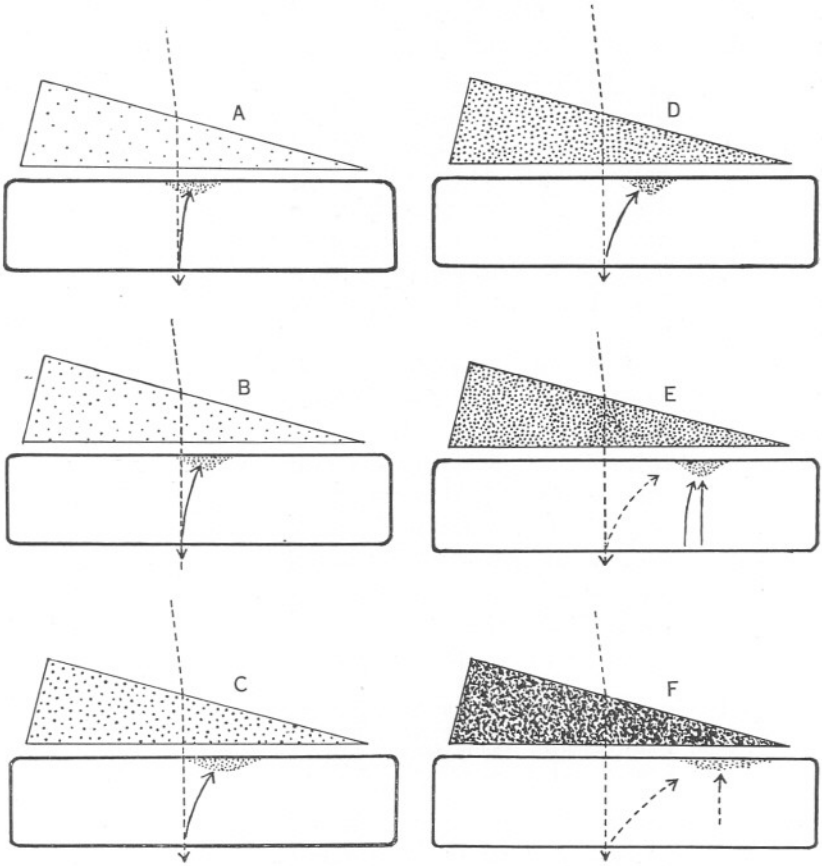

FIG. 18, A to F. *Euterpina acutifrons*—mean paths and groupings in light gradient with increasing concentration of filter.

increasingly redder the more it is absorbed: it gets more and more reddish from the brighter end of the gradient to the dark. Since the Euterpina are presumably less sensitive to this than other parts of the spectrum (some experimental evidence on this was obtained), the gradient will, if anything, be accentuated from their point of view. And such accentuation would tend to increase the deviation of their paths.

After the above considerations it is sufficiently clear that the cause of the deviation is the excess of diffuse light coming from the right-hand side of the dish. In Fig. 18F, it is particularly obvious that an animal, moving in a path in which illumination on its two sides is balanced, if starting in the middle, will move diagonally across the dish towards the region where the group actually formed. There is no question here of the significance of the diffuse light coming from the brighter end of the dish. The other conditions in the Figs. 18E, to 18A, differ from this case only in degree. By gradual stages the importance of the diffuse light diminishes, and we see the accompanying decrease in the deviation of the animals' paths and centre of grouping.

These results are treated in some detail as they provide an explanation of the discrepancies in the work of some previous investigators who have used graded filters (see p. 424).

Balanus (?) *balanoides* nauplii. Some observations were made on batches of the latest nauplius stage of Balanus, and the results fit in well with those described above. The filter contained a fairly concentrated solution of ammonia copper sulphate, and the dish was placed as in Fig. 13. The procedure in this case was to place pipette-fulls of larvæ at various points along the side of the dish furthest from the light-source, and to note the mean point of arrival on the opposite side.

In crossing the dish the group continuously spread fanwise. The animals reached the opposite side (AB) over a stretch of a few cm. But they were most numerous about a half-way point, which could be readily determined to the nearest ½-cm. This point is given in the table below. It represents the average of three trials.

The results are shown in Fig. 15 and in Table III. It is to be noted that the path is all the time deviated to the right-hand side of the course of the direct light-rays. The right-hand side is the side towards the brighter end of the gradient. The amount of deviation tends to increase towards the brighter end. When left undisturbed the larvæ were found to congregate in the middle part of AB, the centre of the group being slightly to the right of the point nearest the source of light (25). With Balanus nauplii, then, a constant deviation is found, which is no doubt to be ascribed to the same cause as noted above, i.e. scattered light from the bright end of the gradient.

TABLE III.

SHOWING DIRECTION OF MOVEMENT OF BALANUS NAUPLII ACROSS LIGHT GRADIENT.

Point along CD.	Deviation of path from perpendicular (cm.).	Deviation of direc light from perpendicular (cm.).
5	5½ to R.	4 to R.
15	3 ,,	2 ,,
25	½ ,,	0 ,,
35	1 to L.	2 to L.
45	2 ,,	*3½ ,,

Caligus rapax ♂. An actively photopositive specimen gave particularly clear results in the light gradient (apparatus as in Fig. 13 with ammonia copper sulphate solution in the filter). Crossing the dish rapidly, orientated dorso-ventrally, it moved in a straight course which corresponds well with the direction of the light. It then worked its way along the edge of the glass in a comparatively short time and stopped in the region nearest the light-source. For some time afterwards it remained in the latter region. Its behaviour was in exact accord with the expected behaviour of an animal moving in the direction of the light irrespective of the change of intensity, and thus resembled that of the two species already considered.

When the animal swam on its side, the same menotactic behaviour was observed as noted above (p. 397).

Larvæ of the herring (*Clupea harengus*). Considerable difficulty was encountered in obtaining clear results from these larvæ, owing in the first place to their tendency to lose activity and ability to orientate well in low intensities of light. But a further complication appeared in the first trials. Active specimens taken from a positive group and placed in the region of C (Fig. 13) first moved, as expected, across the dish approximately in the direction of the light-rays, and then proceeded to work their way along BA towards the centre of the dish. But instead of remaining in the centre they continued to work their way to A. Before long, all active specimens had collected in the dark end of the dish, the majority clustered around D. The procedure was repeated several times, all precautions being taken to eliminate any source of light that might attract positive specimens to corner D. But the results were consistent. Soon the explanation became apparent —most of the larvæ in the darker part of the dish had become *negative* to light. (That herring larvæ become negative to light of very low intensity was found on other occasions also.) So the only chance of making a successful test with this species was to obtain specimens that had become more adapted to light of low intensity. These were found among larvæ a few days older that were still fit and active. Though it was impossible to reduce the characteristic element of randomness in their movement (see p. 398), the results obtained with them were satisfactory. They moved across the dish roughly in the direction of the light and grouped along AB on either side of the centre line. The group was widely spread, but not enough to give reason for doubt that the bright end as well as the dark end were being avoided. It was quite clear that, in so far as they exhibited phototactic movement, they followed the direction of the light and did not select the region of highest intensity. Their behaviour therefore is essentially similar to that of other phototactic plankton animals treated here.

Observations on behaviour in the light gradient of several other species,

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* Repeated with extra precautions to eliminate scattered light from the sides of the apparatus. The result was the same.

to be mentioned below, were obtained. In all cases the same characteristics were to be seen, namely, movement across the dish in a course approximating to that of the light rays and grouping at the region nearest the light-source. Deviations of the kind described for Centropages and Euterpina were noticed as often as they could have been expected to show.

Acartia clausi grouped somewhat to the right of the path of the direct light (apparatus as in Figs. 12 and 13 and dilute Indian ink in filter). *Corycaeus anglicus* swam in a characteristic straight course, but there was considerable variation in the direction of the course taken in different trials. Individual paths of *Paracalanus parvus* also showed variation in direction. This species, at the same time as Acartia, showed tendency to group to the side of the path of direct light (Indian ink in filter). A small Turbellarian moved across the dish in a direct, slightly undulating, path, and gradually worked its way to the region opposite the light-source; as did also a Polychæt metatrochophore (apparatus as in Fig. 13; ammonia copper sulphate in filter). Other forms include: *Temora longicornis*, Balanus larvæ, Zoea larvæ, Copepod nauplii, an Autolytid bud with eggs, and some Mollusc larvæ.

Thus, again, all photopositive animals tested showed the same general behaviour.

BEHAVIOUR OF PHOTONEGATIVE SPECIMENS.

The influence of the direction of the light is particularly well shown by photonegative animals. As ROSE (1925) has noticed at Roscoff, negative specimens in jars of plankton are far less plentiful than positive. And especially is this the case in the low light intensities of the laboratory. The following species are included among the animals that have been studied: *Centropages typicus*, *Calanus finmarchicus*, *Temora longicornis*, and Balanus nauplii, as well as the small bottom-living Harpacticoid, *Nitocra typica*.

In divergent light, it is characteristic that negative specimens of the animals considered in this paper move away from the source, the mean direction of the course taken being along the path of the light rays. If a beam is passed through the water, animals collected at the light source swim down the beam to the opposite side of the dish, and do not immediately pass to the darker regions. This may be illustrated by the paths taken by negative *Temora longicornis*, swimming slowly and steadily, orientated away from the source (Fig. 19).

In a parallel beam (apparatus as in Fig. 1), Temora showed similar behaviour, travelling down the beam away from the source. The specimens tested were moving somewhat irregularly, and the course taken was consequently rather twisty, but the mean direction was straight in line with the path of the light. Not until after reaching the wall of the dish opposite the source did random movements take them into the darker parts of the dish to the sides of the beam. An excellent example of the same behaviour was provided by some negative *Calanus finmarchicus*, which, tested individually, swam straight down the beam with steady uniform motion.

The small Harpacticoid, *Nitocra typica*, a strongly negative species, taken from a bowl in which Amphipods were being reared, also swam down the beam, quite rapidly. The body sways continually, so that the anterior end is always moving from side to side through a wide angle. They first accumulate at the side opposite the source, and then gradually, through the random component of their movement, work their way to the edges of the beam and into the darker parts of the dish.

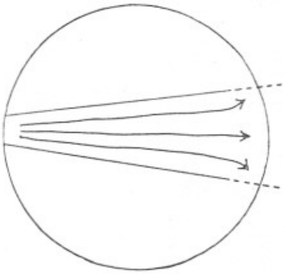

FIG. 19.—*Temora longicornis* —direction of movement of negative specimens in beam passing through circular dish.

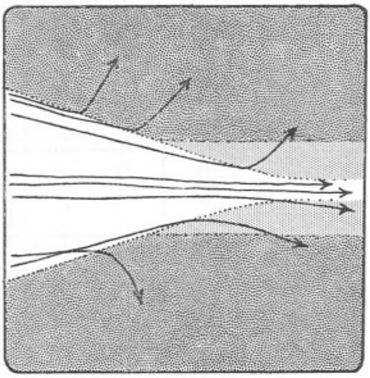

FIG. 20.—*Nitocra typica*—paths in convergent beam.

More instructive still is the behaviour in a convergent beam. *Nitocra typica* may be considered first, as numbers were examined at a time. The mean direction of the paths followed is represented schematically in Fig. 20. It will be seen that, so long as the animals remain in the beam, the course followed inclines towards the centre of the dish, while as soon as random movement happens to take the animal clear of the beam, the course bends abruptly to one side. This is just what is to be expected if the direction of the light-rays is followed, and is, indeed, exactly the type of figure that is obtained from photopositive specimens (Fig. 4), only the movement is then towards, instead of away from, the source.

Temora longicornis gave precisely similar results, the individual paths approximating closely to the ideal. They swim in the direction of the rays, and either enter the narrowest part of the beam, or if they approach the edge before this, turn and swim away to the side of the dish. So too with *Centropages typicus*. Again, *Calanus finmarchicus* swim down the beam in the same way, and show no hesitation on entering the brightest region. Several were observed moving steadily, in a perfectly straight course, following the path of the rays.

Comparable results have been found by KALMUS (1931) to be given by the negative larvæ of *Sabellaria spinulosa*. The latter move down a convergent beam away from the source and concentrate towards the brightest region.

Behaviour in the light gradient (arranged as in Fig. 13) was studied in the case of *Nitocra typica*. Specimens placed anywhere along the edge of the dish facing the light (Fig. 21, AB) move across to the opposite side, their course on the average approximating to the direction of the light-rays. (It cannot be said whether deviations such as have been found for some positive forms occur.) Then they gradually congregate towards the right or the left-hand corner, according to which side of the middle line (where the light passes directly across the dish) they may happen to be. There is no congregation in corner A, although the intensity here is scarcely greater than at D, and very much less than at C: the importance of the direction of the light is once more apparent.

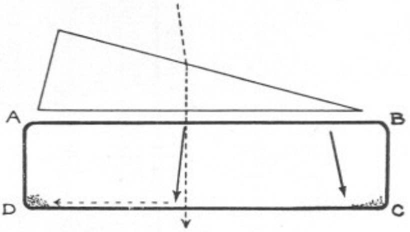

FIG. 21.—*Nitocra typica*—mean paths and groupings in light gradient. Corners of dish marked ABCD.

Thus, in all cases studied, the course of negative movement is found to be the exact opposite of that of positive. It would appear that the same orientating mechanisms are involved in both. And just as positive specimens will move into lower intensities as they approach the source, so too negative specimens will move into higher intensities in travelling away from it. The importance of the direction of the light is shown by the fact that negative animals do not take the most direct route to the darker parts of the dish.

SUMMARY OF PREVIOUS WORK.

I. PHOTOTAXIS.

In the foregoing section examples are given of phototactic behaviour observed in marine plankton animals. Examination of the literature reveals a considerable number of scattered records of such behaviour. The better attested of these may now be summarised.

COPEPODA. That many Copepods show positive or negative movement to light has long been known (LOEB, 1893; FRANZ, 1911; ESTERLEY, 1919; ROSE, 1925). No attention had, however, been paid to the paths followed by individuals until FRIEDRICH (1931) described observations on the behaviour of *Calanus helgolandicus* and *Corycaeus anglicus* in parallel beams of light.

CIRRIPEDIA. The phototaxis of the nauplii of Balanus species has for some time been a favourite subject of investigation (GROOM and LOEB, 1890; MOORE, 1909; EWALD, 1912; ROSE, 1913, 1925). But even with these animals the small size has prevented exact study of the " mechanism " of the behaviour.

MALACOSTRACA. The larvæ of *Palæmonetes vulgaris* have been found to move straight to the light source (G. M. WHITE, 1924); so too the strongly reactive Zoeas of *Maia squinado* (Rose, 1925) and the larvæ of *Pinnotheres maculatus* (WELSH, 1932).

PROTOCHORDATA. The tadpole larvæ of Amaroucium species move directly, in a close spiral, towards a source of light (MAST, 1921), the orientation apparently being effected by regular shock-reactions in the way Jennings had supposed for Euglena, and not by topotaxis in the true sense. Amphioxus is described by G. H. PARKER (1906) as being negatively phototropic.

PISCES. FRANZ (1910) found that phototactic behaviour is shown to a greater or lesser extent by various fish larvæ, particularly in small vessels, *Cyclopterus lumpus* and *Trachinus vipera* being among the most reactive. There are other records of certain fish larvæ collecting towards a source of light, or the reverse; but little, if anything, appears to have been done by way of analysing this movement.

MOLLUSCA. The larvæ of the squid, *Loligo pealii*, move straight towards a light-source (G. M. WHITE, 1924).

ANNELIDA, etc. Phototaxis has been recorded in Polygordius larvæ (LOEB, 1893), and Spionid larvæ (ROSE, 1925). *Tomopteris helgolandica* are predominately negative (ROSE, 1925). The negatively phototactic larvæ of *Sabellaria spinulosa* have been studied in some detail by KALMUS (1931).

PLATYHELMINTHES. Cercaria floridensis moves in the direction of the light (MILLER and McCOY, 1929).

CŒLENTERATA. YERKES (1903) mentions that the Medusa, *Gonionema murbachii*, when moving upwards in the water, was subject to the directive action of the light. MURBACH (1909), however, criticises this statement, and is of the opinion that the animal never reacts to the direction of the light, but only to changes in intensity.

There are various other instances in which mention is made of positive or negative reaction without further particulars on the relation of the course of movement to the light conditions : e.g. negative ♀♀ of *Labidocera æstiva* (G. H. PARKER, 1901) ; positive Cyprid larvæ of Balanus (VISSHER and LUCE, 1928) ; Sagitta species (ESTERLEY, 1919).

It may be noted that in several cases the phototactic behaviour has been used as a basis for the elucidation of more special problems involved in light response. Thus LOEB and NORTHROP (1917) used Balanus larvæ for testing the validity of the Bunsen-Roscoe law of resultants in reactions to two sources of light; WHITE (1924) observed the distribution of *Palæmonetes vulgaris* and *Loligo pealii* in crossing beams of different monochromatic lights ; VISSCHER and LUCE (1928), in an admirable piece of work, examined the relative stimulating effects of different wave-lengths by a somewhat similar method in the Cyprid larvæ of Balanus ; while WELSH (1932) has measured the effect of temperature and different light-intensities on the rate of swimming in Pinnotheres larvæ. Further, a good deal has been done on the external agencies effective in reversing the " sign," or direction, of taxis (particularly LOEB, 1893 ; ROSE, 1925).

These references should serve to add further evidence to the widespread prevalence, among the smaller free-swimming marine organisms, of phototactic movement ; or, at any rate, of the capacity for such behaviour. One important reservation appears necessary, namely, that this generalisation should, at the present state of knowledge, be restricted to bi-laterally symmetrical animals. It is quite doubtful how far radially-symmetrical animals, such as Medusæ, are influenced by the direction of the light. No experiments on Medusæ are here recorded, partly because they do not survive well, but chiefly because they are not disposed to phototaxis in the manner of other plankton. This, in itself, may be of some significance. Apart from earlier observations on *Gonionemus murbachii*, there is no help to be obtained from past literature.

With regard to the occurrence of more unusual methods of orientation during phototaxis, two examples among Arthropods may be recalled. In the fiddler-crab, *Uca pugnax*, strong positive movement towards a light-source is shown. The animal, however, is all the time orientated sideways (HOLMES, 1908). A case somewhat comparable with *Acartia clausi* is provided by the freshwater larva of the fly *Corethra plumicornis*, which under certain conditions moves in the direction of the incident light, locomotion being accomplished by a succession of jerks in a direction oblique to the axis of the body at the phase of rest. Movement to light occurs because the jerks are predominately to the most illuminated side, and thus are, on the whole, successively to right and left. Thus only accidentally does the animal come to orientate its body exactly in the direction of the light, which, nevertheless, is the average direction of its path.

II. Analysis of Phototaxis.

Very little experimental work has hitherto been published which may help to elucidate the exact nature of the light responses of the animals with which we are concerned. The publications to which reference has been made in the previous section contain only two in which analysis of the phototactic movement has been carried to any length. One of these (KALMUS, 1931) requires further mention, as the experimental methods are of the same kind as those adopted in the work described here. The negative movement of the larvæ of *Sabellaria spinulosa* was investigated. The behaviour of the larvæ was observed in a convergent beam, between two sources of light, and in a light gradient produced by a wedge-shaped filter. The results are in complete agreement with those obtained here with negative forms (p. 418); and they are such as to satisfy the investigator that the movement is definitely a *topo*taxis, and not some kind of *phobo*taxis.

Reference should also be made to a contribution by M. GOLDSMITH (1921), who observed the behaviour of some typical marine plankton animals under the conditions of a light gradient. From the results of this and certain other experiments, she concludes that the reaction to light of these animals is essentially a matter of random movements which bring the animals into a brighter region, and not of orientation to the direction of the light-rays. This is directly contradictory to the results and conclusions stated here, and so requires careful examination. There are good reasons for believing the interpretation to be fallacious, but these are best stated after something has been said of the former work which has involved the use of graded filters.

ON THE USE OF GRADED FILTERS.

Following Strasburger's classical experiments on the swarm-spores of Algæ (STRASBURGER, 1878; and see ROSE, 1929, p. 15), several workers attempted to apply his method on other photoreactive organisms. The main object was to obtain a gradient of intensity in a contrary direction to the incident light, and to discover whether the animals still moved in the path of incidence, or whether they moved up the gradient towards an optimum intensity. At that time "phototaxis" and "photopathy" were the terms used to describe these alternative forms of behaviour, though the latter expression was susceptible of more definitions than one, and very loosely employed. The term "phototaxis" is now used in a wider sense to include all kinds of movement in relation to light, and the sense in which the term was contrasted with "photopathy" is that conveyed in the expression "photo*topo*taxis."

It seems generally recognised that the results obtained by use of this method have not attained the desired objective. In certain cases, notably among Protista and Crustacea, the organisms appeared to be responsive to the light gradient irrespective of the direction of the rays, and so to exhibit "photopathy." But these cases are each open to suspicion, and indeed have been subjected to criticism both at the time by workers in the same field and by later investigators, such as ROSE (1929). It seems that not only are we without sufficient evidence that "photopathic" behaviour does in fact occur, but, if it does, it may be often open to question whether the light gradient in use could adequately show it. The essential difficulty is that the animals concerned may always be capable of moving in the direction of incidence, and experimental conditions have to be very carefully devised to ensure that, while a sufficiently steep gradient is obtained, apparent "photopathic" effects are not produced as a result of behaviour that is essentially topotactic. This consideration applies especially to a case, dealt with below, in which marine plankton animals are concerned.

At the same time it is not to be implied that experiments with graded filters can give no kind of positive result. The results, for instance, have distinct value if definite topotactic behaviour is still shown; for if the animals still orientate accurately in the direction of the rays, and if they congregate away from the brightest end, as close as they can get to the light-source—just as would happen if no gradient existed—then information is provided on two points: (i) on the independence of topotactic response of gradual changes of intensity in the surroundings, and (ii) on the dominance of topotactic behaviour over any phobotactic behaviour that the animal may be capable of showing. The observations described above (pp. 400–418) should be viewed from this aspect.

It has been seen how various planktonic animals behave in a horizontal light gradient, produced by an Indian ink or ammonia copper sulphate filter, and how the behaviour can be explained completely on the supposition that the animals move in the direction of incidence of the light (and see further the discussion on p. 426 *et seq.*). It was found that an apparent irregularity was clearly to be explained as the effects of light scattered and reflected from the brighter end of the gradient. With Indian ink in the filter the latter effects increased as the mixture was made more concentrated, until, under the conditions represented in Fig. 18C, the animals grouped close to the brighter end of the gradient. The disturbing effect of scattered light was also sometimes observed, though to a less extent, with the copper solution in the filter.

These results render intelligible M. GOLDSMITH'S observations (1921). She gives a brief report on the use of a gradient-apparatus, consisting of a dish painted over with black varnish and covered with a piece of smoked glass of graded opacity. No light could enter the dish except through the cover, which thus acted as a graded filter. The dish was placed near an electric light shining obliquely down on it, with the darkest end of the cover nearest the light. Thus the end of the dish nearest the light was situated at the darkest end of the gradient. Goldsmith's results may be quoted in full :—

" Les Convoluta, les Mysis, les zoé de Maia se groupaient en très grande majorité (il faut noter que l'éclairement était assez faible) dans la partie la plus transparente du vase, qui est en même temps la plus éloignée de la source. Pour les Copépodes planktoniques, il en est de même à la lumière solaire ; à la lumière électrique, la région optima se trouve à mi-chemin entre les deux extrémités du vase."

Considering that the smoked glass must have scattered the light very considerably, the result is quite in harmony with the present observations, and accordingly is not in any way inconsistent with the idea that the animals' response could have been purely topotactic. For one would have expected at any rate the zoeas and Copepods to follow in the mean direction of the light-rays, and the fact that they are brought into the brighter half of the vessel is almost certainly due to the effects of scattered light. The above results are thus essentially comparable with those obtained by DAVENPORT and CANNON (1897) with Daphnia, and E. TOWLE (1900) with Cypridopsis. (Both of these investigators deal with light shining on the filter obliquely from above, and in both cases the animals clearly move in the direction of incidence of the light.)

M. Goldsmith, however, felt justified in the conclusion that the reactions to light of the animals she observed do *not* consist in orientation to the direction of the light-rays depending on a symmetrical influence of the light, but in various random movements which bring them into the brightest region. This verdict is remarkable considering that the animals included such strikingly phototactic forms as Balanus nauplii, *Centropages hamatus*, *Acartia clausi*, Zoeas of *Maia squinado*, etc. Actually it is based on two main pieces of evidence : one has already been adequately dealt with by ROSE, who has carried the experiment in question a stage further, and simply demonstrated that the results are otherwise explicable (1929, pp. 152–153) ; the other piece of evidence is from the behaviour in the light gradient, and this, in view of the above considerations, is seen to be invalid.

With respect to other work involving the use of graded filters, especially that on freshwater Crustacea, it seems likely that if the results were considered in the light of the criticism applied above, some of the apparent inconsistency would be removed. It may be legitimately doubted whether any of the so-called photopathic effects (YERKES, 1899; DITLEVSEN, 1907) are anything but the result of topotactic movement. Still it may be significant that YERKES found a complete contrast in the behaviour of *Cyclops parvus* (" phototactic ") and *Simocephalus vetulus* (" photopathic ") under the same conditions.

INTERPRETATION OF THE RESULTS.

It is now necessary to consider what the observations described in this paper, together with previous work along similar lines, may have succeeded in demonstrating. Our procedure, it may be recalled, has been to observe behaviour under different conditions of illumination designed so that the intensity gradient and the direction of incidence bore different relations to one another. In other words, the data include (*a*) conditions of illumination described as a character of the physical environment, and (*b*) the behaviour of the animals *in relation to* (*a*). It is necessary to be clear on this point when, later, consideration is given to the sensory responses of the animals in question; for the light conditions as " appreciated " by the animal may differ considerably from those thus described, owing to the specialisation of the light-receptors.

Where the Groups Form.

The results on pp. 400–418 show that in no case did positive animals group in the brightest region when this was away from the point nearest the light-source. In a convergent beam, groups always settled at the entrance of the beam, and not in the narrowest, brightest, part. Though fewer species have been tested in the light-gradient, the results obtained were quite consistent (p. 418). The group collected away from the brighter end somewhere in the region opposite the light-source, or, more strictly, in the region of the " axial line " at which the direct light from the source passes across the dish at right angles. This " axial line " in the dish can be found in a simple way by interposing a screen with a narrow slit. It is of significance in that it represents the line along which the direct light is equally balanced on both sides (at least as detectable by a sufficiently small photoreceptive mechanism).

It is to be noted, however, that the groups do not usually form exactly round this point, but at a greater or lesser distance towards the brighter end of the dish. It has been seen how this effect is undoubtedly due to scattered light, of which considerably more will come from the brighter end than the darker, depending on the nature and concentration of the solution in the filter. This scattered light will result in shifting the *effective* " axial line " a little way towards the brighter end.

One may speak of an " effective axial line," defined practically in some such way as follows. Supposing suitable methods of measurement were devised, small arrows could be placed in various parts of the dish indicating the direction in which the light falling on the two sides of the arrow is equal in amount. If one imagines that these arrows are liberally distributed and placed in horizontal rows, it is easy to see that in each row, somewhere near the region of the point close to the light-source, one arrow will point at right angles to the long axis of the dish. A line joining such arrows is what is understood by the expression " effective axial line " (see Fig. 22). It may be straight, or somewhat curved, but in any case it will be nearly, if not quite, at right-angles across the dish, a little to the side of the simple straight axial line of the direct light.

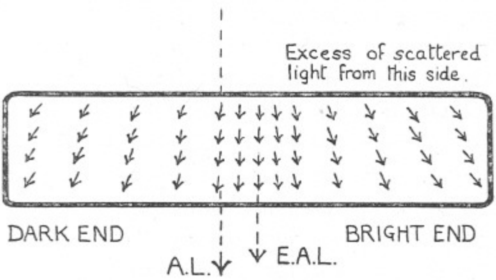

FIG. 22.—Light conditions in light gradient apparatus. At each point the direction of the light is the resultant of two components : (i) direct light from source, (ii) excess scattered light from bright end.

A.L., axial line. E.A.L., effective axial line.

We are now in a position to define more precisely the position at which the group forms. If the effects of scattered light were quite negligible, one would expect it to form about the direct axial line ; since, however, they are not, the group instead forms about the " effective axial line." This appears to express adequately the observed behaviour of those animals tested in the conditions of the light gradient.

To state the evidence provided by these results more generally : *positive groups of the plankton organisms investigated primarily collect around a point in the mean line of incidence of the light.* The point in the line will of course be that beyond which the confines of the vessel prevents the animals from passing. *It is immaterial whether this happens to be the brightest region of the dish accessible, or not.* The amount of scattering of the group on either side of the point will vary with the degree of diffuseness of the light. Negative forms show just the expected reverse behaviour.

BEHAVIOUR OF INDIVIDUALS.

How the groups come to collect in the above way is explained by examination of the behaviour of the individuals composing them. When the movement of individuals is considered, two points emerge clearly enough.

First, the various animals tested were able to maintain their normal movement in the direction of incidence of the light, whatever the changes of total intensity encountered during their passage. As they moved up a convergent beam, and as they moved towards the axial line in the gradient dish, the intensity was diminishing. The removal of the intensity factor did not noticeably affect their capacity for movement in the direction of the light-rays. Secondly, if the animals have opportunity of " selecting " one of two paths, namely either one of increasing intensity or one in the path of incidence of the light, they will chose the latter.

An animal following the path of incidence will, on the average, maintain an equal balance of the light falling on the two sides of the body, or, strictly speaking, of its photoreceptive surfaces. It is this orientation, exact or approximate, of their path that brings these animals into illuminated regions. They first cross the dish in the path of the rays, and then work their way along the side towards the " effective axial line." The latter phase is naturally the slowest, as the animals are continually moving against the glass, and it is only the excess of random movements in one direction that enables them to progress. At the " effective axial line " random movement in either direction is equally probable ; hence the animals accumulate here. It can now be fully appreciated why the groups form in the positions in which they have been found.

NATURE OF THE PHOTOTACTIC MOVEMENT.

Looking further into the observations on the behaviour of individuals, we may enquire how far the characteristic behaviour of species observed fits into any of the five categories distinguished above (pp. 388–9). This is a matter of more than academic interest, in that if an animal can be assigned definitely to one of these categories, various predictions as to its behaviour become possible. There will, for instance, be an opportunity for speculating what it does in the sea.

In this procedure we are faced with the question, hitherto evaded, as to how the light conditions are to be viewed from the aspect of the animal. So far we have considered the light conditions as a character of the physical environment, for as such they can be measured and described in a straightforward manner. They can be mapped out in a framework representing dimensions of space and time, total intensity indicated by contours and mean direction by a series of arrows. But the simplicity of this scheme is, after all, only because it is, operationally considered, an idealised construction. The specified light conditions of a point within this optical field mean nothing if it is not that they are to be detected by an object placed at that point. And the optical field, described as above, actually represents the conditions of illumination detectable by a hypothetical photometer that is sensitive to light from all directions equally, and is ideally small.

If we regard light-sensitive animals in their capacity of photoreceptive mechanisms, we can discover how they tend to differ from the above-mentioned hypothetical photometer. And we find that the chief difference is that they may by no means be sensitive to light from all directions equally. With motile, bilaterally symmetrical animals, it is generally the case that photoreceptor organs are concentrated at the anterior end and may be largely, if not altogether, shaded from the light falling on the posterior surfaces. Of course the degree to which this happens varies among different forms, but the general tendency is beyond dispute. With such specialised distribution of light-sensitivity over its surface, a photoreceptive mechanism loses its ability to record the changes of light intensity that occur in its surroundings, unless provision is made to allow for its direction of orientation. For now it will record different intensities at the same position according to the direction in which it is facing—as, to take an extreme example, a camera placed at a given point in the beam of a motor head-lamp. We can therefore see, in the first place, how a change of intensity recorded by the animal will be a combination of the change in the physical field and that due to change in orientation of the body in relation to the main source; and, in the second place, how the resultant direction of the light may also vary—according to the dominance in stimulating power of light falling along the axis of body-orientation over that falling laterally.

All this is to show how the light conditions capable of stimulating an animal as it passes through an optical field may by no means coincide with those reproducible by an ideally small photometer, that is, with the light conditions of the environment stated in physical terms. The animal is here regarded purely in its capacity of an automatic light recorder. It should not, however, be overlooked that further " complications " may be expected from such phenomena as threshold stimulation and state of adaption of the sense-organs; while, on the other hand, even if the light conditions appreciated may not coincide well with those of the physical surroundings, the behaviour of the animal may be so adapted that its movements will nevertheless be such as to compensate for the difference.

Applying these considerations to the special problem of phototaxis, it becomes apparent that the behaviour observed in the convergent beam and in the light gradient (i.e. direction of light chosen against intensity gradient) is not a conclusive proof of topotaxis (III*a* and *b*, p. 388). It is conceivable that an animal could follow such a path merely by reacting to changes in intensity affecting its sensitive area as a whole owing to small deviations in the direction of orientation of its body, or of its sensitive anterior end. It might all the time be avoiding movement into a position which, to it, involves decrease of illumination. Such behaviour would be classed under (*c*), and justifiably termed *phobotaxis*, although the resulting path the animal follows may be well directed towards the source.

To distinguish this behaviour from true topotaxis is not simple, for in many respects the net result will be identical. But certain distinctions are bound to follow. First may be mentioned a characteristic that provides a useful laboratory expedient for distinguishing between the two types. Unilateral blinding results in circus movements in the first case, not in the second. On these grounds HERTER (1926) has good evidence that *Nereis diversicolor* is enabled through its hind ocelli to move topotactically, but if these are put out of action and the front ocelli left intact, the worm still orientates, though less accurately, by this phobotactic method. In the second place, orientation is evidently more difficult in phobotaxis, and considerable deviations from the mean path are to be expected. Also where movement is not in a spiral path, it is difficult to see how this method of orientation could work at all without considerable side to side movement of the head. It is evidently to be ruled out of the question if the animal orientates accurately towards the source of light and proceeds to move straight towards it without any side movements, as may be observed in the case of most Copepods and various larvæ of Decapods. A further consideration is applicable to an animal which can maintain a fairly well directed path phobotactically ; for it follows that the light intensity it appreciates varies greatly with the position of the body. If it should happen to move into an intensity that is too strong, it has only to turn its body slightly to the side to reduce the appreciated intensity considerably. It could therefore achieve the same result by merely turning the body as by moving further away from the source. Clearly, then, an animal of this kind would encounter difficulties in keeping within an optimum zone of intensity. Thus, paradoxically, an animal sufficiently sensitive to changes in intensity to maintain a path directed towards a source, would not easily arrive at a region where the intensity is " optimum."

Returning now to the interpretation of the observed behaviour, we may recall that all cases dealt with are to be classed as *taxis* (III, p. 388). We may further state that no behaviour remotely suggesting (*e*) or (*d*), (p. 389) was noticed ; and since all the species moved to, or from, the light in a more or less well-directed path, (*b*), too, is of no account. The latter condition is indeed sometimes approached by animals which normally move in a straight course, but which, for some reason or other, are not reacting well.

We are therefore left with alternatives (*a*) and (*c*). Something has already been said of the distinctions between these two modes of behaviour. It may be repeated that any animal maintaining accurate orientation and moving in a straight line in the direction of incidence, with no sideways or "searching" movements, cannot possibly be classed under (*c*). True topotaxis is, therefore, exhibited by :—

various Copepods : *Centropages typicus*
Temora longicornis
Paracalanus parvus
Corycaeus anglicus
Caligus rapax ♂
Decapod larvæ : Galathea spp.
Upogebia sp.
Pandalus montagui
Zoea larvæ of Porcellana sp. and other crabs
Cirripede metanauplius
At least some Polychæt larvæ.

These animals are presumably capable of appreciating differences between light falling on the right and left sides, and of adjusting their position so that the intensity is equally balanced. It is of interest to note that whereas the Decapod larvæ possess paired compound eyes of some size, Calanoid Copepods have but a small single median eye. Yet for slow movement the latter are capable of orientating with considerable accuracy. *Corycaeus anglicus* has large paired lenses focussing on small paired eyes, and it is evident that the light falling straight from the direction in which the animal happens to be facing will be far more effective than that falling laterally or from behind. That this is actually the case is indicated by certain features of the animal's behaviour.

The species in the above list, as well as others, which, as emerges later, should be classed with them, may be expected to exhibit characteristics which appear to be generally typical of topotactic behaviour: for instance (i) ready reversal from positive to negative, and *vice versa*, under the influence of appropriate stimulation, such as temperature change, chemical change, mechanical shock, increase of light-intensity, etc.; (ii) movement in a diagonal line between two light sources, or movement in the resultant line when the light is falling from various directions or greatly scattered. Such behaviour has actually been tested and observed in several of the above species. *Corycaeus anglicus* is less inclined than others to keep to a diagonal between two sources, owing without doubt to the fact that its lenses are so constructed as to concentrate light from one direction.

It may also be noted that when the light is broken up and made to fall from various directions, the paths are more varied, and the groups formed more scattered, but the average direction of movement approximates to the direction from which the greatest amount of light is coming and on either side of which the total amount of light is fairly equalised.

Two other cases of topotaxis stand quite on their own. First, the strongly positive *Acartia clausi* is, as we have seen, capable of moving in a reasonably straight path in the direction of a light-source, without keeping its body orientated in any fixed direction. Movement is in " jerks," and successive " jerks " are not necessarily in the same direction, so that the course is somewhat zigzag (see p. 396). During movement the body may be orientated in almost any direction, though positions in which the anterior end is above the lower are most frequent. The appearance is as though the animal were being forcibly pulled to the light in whatever direction it attempted to move. The fact that *Acartia* moves likewise in the path of incidence of the light in a convergent beam and across a light-gradient proves that the animal is not reacting to changes in intensity—i.e. its phototaxis is not type (*c*) ; for its transparent body and constant body-orientation ensure that it is affected by light from all directions fairly equally. The movement is thus a variety of true topotaxis, but how exactly this is brought about presents a problem that cannot be answered by the usual interpretations of this category of behaviour. Secondly, *Poecilochaetus serpens*, writhing vigorously, so that no part of its body has any constant relation to any other part, is able to move straight up a beam of light (p. 399). Again we are presented with the phenomenon of orientation of the path in absence of orientation of the body.

It appears, then, a distinction should be drawn between cases of true topotaxis in which orientation of the path is the result of orientation of the body, and those in which it is not. That cases of the latter type should occur at all is of some interest, and the fact by no means simplifies the theory of phototaxis. Perhaps it occurs more frequently than may be suspected. It has been noted (p. 398) how a Pandalus larva moved straight up a beam although orientating at various oblique angles.

The foregoing paragraphs deal with clear examples of true topotaxis (Type *a*), which stand out because of the accuracy with which orientation can be effected. Since a number of such examples occur, one may confidently expect to find along with them many others in which orientation is not so efficient, though effected in essentially the same way. The animals, though exhibiting true topotaxis, will not keep such a straight course. There can be little doubt that the bulk, if not all, of the other species referred to fall into this class. For instance :—

Copepoda : all species in more rapid movement
Euterpina acutifrons
Nitocra typica
Cirripedia : Balanus nauplii
some Polychæt larvæ
Decapod larvæ.

Thus the whole range of species investigated is practically covered ; and the evidence is strong that true topotaxis (*a*) is the primary type of response of these animals to light.

But whatever closer study on the distinction between (*a*) and (*c*) may show, it is for most purposes sufficient that the animals examined fall into one or other of these categories. For it means that all have one important characteristic in common. That is, that the response to light is such that movement is always in the direction of the rays. The influence of the direction of incidence is such that the changes of light intensity encountered during progress are of no significance with respect to direction of movement. That this statement should not be misunderstood, it is perhaps necessary to point out that it is by no means implied that changes of intensity have no influence at all. Such would be contrary to fact. Reactions, for instance, may occur to sudden changes, such as when an animal enters a beam or a shadow ; movement may be activated or inhibited by variation in light intensity, or the direction of phototaxis reversed. And since in nature the animals are subject to sudden shadowing, to fairly rapid changes at dawn and dusk, and to increase in light-intensity as they move upwards in the direction of incidence, such behaviour is undoubtedly of importance. The point, however, with which we are here concerned is that changes in intensity in the environment are of no significance for the maintenance of the sort of phototactic movement that a wide range of plankton animals show. The path of the animal is orientated in the direction from which the light is coming, or, if the light is scattered and falling from various directions, to the resultant of the total incident light. And whether the actual mechanism of this movement is that of class (*a*) or class (*c*), the general course of movement is the same.

These conclusions are based primarily on the observations here described, but they also receive some support from those that are to be found in the literature. It may be pointed out that, in general, observers of the behaviour of plankton animals have been struck by the apparent topotactic nature of characteristic light responses. In particular, reference should be made to M. ROSE (1925, 1929), who has paid as much attention to this subject as anyone. One gathers from his publications that he regards the directional properties of the light as of primary significance. The experimental evidence here provided justifies this opinion.

RELATION TO THE PROBLEM OF VERTICAL MIGRATION.

It is not unreasonable to assume that the animals exhibit the same *kind* of response in the sea as in the laboratory, though the *extent*, or the *intensity*, or the *persistence* may differ in the two cases. If this is so, then movement in the direction of the incident light, whether positive or negative, should at least figure prominently among the light responses of the animals in nature.

Accurate field-work, in which a valuable lead has been given by F. S. Russell, is showing that movements of the plankton are related to changes in the light conditions more readily than to any other environmental factor. Some species, indeed, tend to " follow " an optimum intensity. In so far as this is the case, we can now point to topotactic behaviour as one important means whereby such an " optimum " is reached. Positive topotaxis is of itself sufficient to bring animals from low intensities up towards their " optimum," and may alone be adequate to keep persistently positive forms such as *Acartia clausi* high in the water. When the light-intensity increases beyond the " optimum," one must suppose, in so far as light conditions regulate behaviour, either that the animals become negatively topotactic (Loeb's original theory), or that movement is inhibited and the animals sink back into their " optimum " zone (as first put forward by EWALD, 1912). Be that as it may, the prevalence of the kind of orientated movement to which prominence has here been given, could account in a large measure for the correlations that are found between vertical distribution and light-intensity.

SUMMARY.

1. The most noticeable response of marine plankton to light, under laboratory conditions, is the formation of groups on the lighted (or opposite) side of the vessel containing them.

2. Specimens from such groups were tested under different conditions of illumination, and in all cases they moved in the *direction* of the light quite irrespective of accompanying changes of *intensity* in the surroundings.

3. Groups form around the line of direction of the light, or the resultant direction when the light is scattered or falling from more directions than

one, this being the direct result of individuals moving along the mean path of incidence of the light.

4. The behaviour of individuals was examined more closely to distinguish between the two possible ways in which the directed movement could have been brought about, viz. (i) reactions to bilateral inequalities of illumination (here called " true topotaxis "), and (ii) reactions to changes in total illumination of light-receptors (a type of " phobotaxis "). For a number of species it was clearly a case of " true topotaxis," and very probably for at least the majority of the rest.

5. In two very different cases, namely, *Acartia clausi* and *Poecilochaetus serpens,* there was no orientation of the body, but nevertheless efficient orientation of the path of movement. It is believed that this is the first occasion on which such behaviour has been described.

6. The observations described point to the fact that movement in the direction of incidence of the light, however this may be affected, is general among a wide range of the smaller, free-living, bilaterally symmetrical, marine animals, and would tend to dominate other possible response to light. This behaviour on the part of individuals provides a substantial basis for attempted explanations of the correlations, that have been demonstrated by ecological workers, between the vertical distribution of populations and light-intensity.

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Abstracts of Memoirs

RECORDING WORK DONE AT THE PLYMOUTH LABORATORY

The Loxosomatidæ of the Plymouth Area, including *L. obesum* sp.nov.

By D. Atkins.

Quart. Journ. Micr. Sci., Vol. LXXV, 1932, *pp.* 321–391.

FOUR known species of Loxosoma, *L. phascolosomatum* Vogt, *L. crassicauda* Salensky. *L. singulare* Keferstein, and *L. claviforme* Hincks, and a new species *L. obesum* found in the Plymouth region, are described.

In *L. crassicauda*, which lives in the tanks in the Laboratory, males only were found during the year they were kept under observation.

L. claviforme is considered a valid species.

A small group of Loxosoma, found on *Aphrodite aculeata*, were intermediate in form between *L. singulare* and *L. claviforme*, and peculiar in retaining a number of their buds. The sex of such buds in several instances differed from that of the parent.

L. obesum sp.nov., found on the dorsal surface of *Aphrodite aculeata*, may reach a length of 2·4 mm., and averages rather more than 1·0 mm. in length. The lophophore is small, and bears almost invariably eight tentacles. Longitudinal muscles only are present in the stalk, which ends in a small disc of attachment. A foot-gland is present in the bud, and is frequently preserved as a vestige in the adult. The buds are near the lophophore, and may be as many as six on each side. The larva resembles that of *L. singulare*.

Two main forms are distinguishable, differing in shape of the calyx and development of the stomach.

The ovary may contain six well-developed ova on each side, and the vestibule twenty-six embryos.

Females, with one exception, greatly exceeded males in number, and it is probable that the male becomes sexually mature at a smaller size than does the female.

D. A.

The Ciliary Feeding Mechanism of the Entoproct Polyzoa, and a comparison with that of the Ectoproct Polyzoa.

By D. Atkins.

Quart. Journ. Micr. Sci., Vol. LXXV, 1932, *pp.* 393–423.

An account is given of the ciliary feeding mechanism of the Entoproct Polyzoa, and of the structure of the lophophore and tentacles. The long lateral cilia cause a current of water to pass inwards between the tentacles, and throw particles on to the short frontal cilia of the inner surface, which carry them to the vestibular groove leading to the mouth.

The behaviour of the lateral cilia of the tentacles of *L. crassicauda* is described, and it is suggested that they are under the nervous control of the animal.

A résumé of Borg's work on the ciliary feeding mechanism of the Ectoprocta is given, a note on *Flustrella hispida* being added. It is pointed out that the method of feeding in this group differs widely from that of the Entoprocta.

D. A.

The Nematode Genus *Ascarophis* van Beneden.

By H. A. Baylis.

Ann. & Mag. Nat. Hist. (10), *XI*, *pp.* 111–117.

Two female specimens obtained from the stomach of a gurnard (*Trigla lineata*) at Plymouth are referred to the very imperfectly-known species *Ascarophis morrhuæ* van Beneden, 1871, which had been recorded previously from the cod, haddock, halibut, and father lasher. The literature dealing with this species and with *Ascarophis helix* Cobb, 1928, is reviewed. In the light of the present material the description of the female is amplified (the male being unknown), the doubtful systematic position of the genus is discussed, and an emended generic diagnosis is given.

H. A. B.

The Osmotic Relations between White and Yolk in the Hen's Egg.

By J. B. Bateman.

Journ. Exp. Biol., 9, 1932.

Vapour-pressure determinations on white and yolk of the hen's egg, (*a*) by direct comparison, (*b*) by reference to an intermediate salt solution, and (*c*) by dialysis against known salt solutions, have confirmed the existence of a real osmotic difference between these two substances. These experiments show A. V. Hill's vapour pressure thermopiles to be reliable when used with viscous protein solutions such as egg yolk, and that a recent criticism is unfounded.

The vapour pressure changes which occur on mixing white and yolk indicate a removal of osmotically active substances; they disagree, therefore, with Straub's freezing-point determinations (1930). Dilution of white and yolk with water and with various salt solutions is studied from this point of view and also in connection with the problem of bound water. It is concluded that the amount of bound water in both white and yolk is small, and this is confirmed by the effect of solid sodium chloride on the vapour pressure of white and yolk. Other substances (urea, sodium lactate) produce abnormal effects resembling their effects on blood. Glucose behaves normally.

The result of mixing white and yolk, mentioned above, is discussed in relation to the osmotic changes occurring in the fertilised and unfertilised egg.

J. B. B.

The Heat Production and Economy of Maintained Contractions in Crustacean Muscle.

By D. W. Bronk.

Journ. Cell. & Comp. Physiol., II, pp. 285–294, 1932.

The heat production of crustacean muscle has been measured during the course of a short tension by means of a single thermocouple thrust into the adductor muscle of the claw of Maia. It has been found that there is a marked increase in the economy of maintaining tension, as represented by the ratio of tension developed to heat produced, as a result of previous activity of the muscle. This striking increase in economy is shown to be due to a very marked slowing of the muscle as a result of previous contractions. The slowing is very much greater in this type of muscle than in vertebrate striated muscle. It is pointed out that this would make it possible for the animal economically to maintain powerful contractions for considerable periods of time in spite of the fact that the motor nerve fatigues rapidly, as has previously been shown to be the case by A. V. Hill.

D. W. B.

The Effect of Veratrine on the Electrical Response of Crab's Nerve.

By S. L. Cowan.

Jour. Physiol., 77, 27*P.*

After soaking for half an hour in aerated sea water (pH 8) containing 1 in 10 millions to 1 in 100 millions of veratrine, a nerve from a walking leg of Maia gave a much increased initial action current, as measured with a galvanometer of 3·8 sec. period.

For autumn crabs the optimum concentration of veratrine was 1 in 25 millions to 1 in 50 millions; the initial response was about 200 times that of untreated nerve and the area of the deflection × time curve was increased more than a hundredfold. The "retention of action current" lasted for nearly half an hour.

Asphyxiation, previous to stimulation in oxygen, did not affect the response. (Compare Fromherz, H., and Hill, A. V. *J. Physiol.*, 77, 25 P.)

S. L. C.

Note on the Occurrence of *Graffilla gemmelipara* Linton (Turbellaria) at Plymouth.

By W. Harold Leigh-Sharpe.

Parasitology, Vol. XXV, No. 1, 1933.

On 28.viii.1932 seven specimens of *Graffilla gemmelipara* Linton 1910 were found by Miriam Rothschild on the body inside the mantle cavity of a specimen of *Cardium edule* from Millbrook, Plymouth.

Though only taken previously in America and on a different host, *Modiolus plicatulus*, Linton's excellent figure leaves no doubt that these specimens belong to the same species.

The mother, a perfect oval, is uniformly ciliated, colourless and transparent, with a pair of typical Turbellarian bean-shaped eyes, and contains within her body eight bubble-like, transparent, spherical cysts. Each of these contains a pair of ciliated young, complete with eyes like their mother; and the young of each pair are arranged head to tail and slowly revolve within the cyst. W. H. L.-S.

A Second List of Parasitic Copepoda of Plymouth with a Description of Three New Species.

By W. Harold Leigh-Sharpe.

Parasitology, Vol. XXV, No. 1, *pp.* 113–118, 1933.

The following constitutes a supplement to my previous list (Leigh-Sharpe, 1926), and consists of a few records previously omitted, and also an account of some Copepoda taken by me during a visit to the Laboratory of the Marine Biological Association, Plymouth, Aug.–Sept. 1932, with notes on these and previously recorded species. Three new species are described: *Lernæocera phycidis*, *Clavella deliciosa* and *C. typica*, and an account of normal and abnormal specimens of *Lernæocera lusci*. Notes are given on the eggs and nauplii of the Dichelesthiidæ. W. H. L.-S.

On the Mitraria Larva of *Owenia fusiformis* Delle Chiaje.

By Douglas P. Wilson.

Phil. Trans. Roy. Soc. B., Vol. 221, 1932, *pp.* 231–334.

THIS is a detailed histological study of the development from the early trochosphere to the young worm a few days after metamorphosis. The larva is of a most unusual type, in which the normal mode of Polychæte development is masked by an exaggeration of some larval structures associated with a peculiar disposition of certain parts of the developing worm trunk. The prototroch beginning as a simple ring becomes folded into a sinuous tract simulating the ciliated band of an Echinoderm larva. The blastocœl is spacious. Long provisional bristles probably protect the larva during its month of pelagic life. The worm trunk develops in such a way that the anterior segments are turned inside out and are folded back to envelop the posterior segments. The head is widely separated from the trunk, but is connected with it by the circumœsophageal nerve commissures and by a pair of retractor muscles, as well as by the larval tissues of the blastocœl wall. The development culminates in a metamorphosis of cataclysmic violence and rapidity in which during the course of a few seconds the trunk is straightened out while the head is drawn down on to its anterior end and there subsequently fuses with it. The provisional bristles are thrown off and lost, but the softer larval tissues—the prototroch and other structures—break down in rapid histolysis and are swallowed by the newly-formed worm during the first few minutes of benthonic life. Laboratory experiments indicate that in the sea it is usual for this metamorphosis to take place only when the fully developed larva comes into contact with a suitable sandy bottom, and that it is delayed for a time if the larva has not reached the sea-bed or if the bottom conditions are unsatisfactory. Such a power of suspending metamorphosis must greatly add to a larva's chance of ultimately reaching the right kind of bottom for adult life. D. P. W.

The Autonomic Nervous System of Selachians.

By J. Z. Young.

Quart. Jour. Micr. Sci., Vol. 75, *p.* 571.

An analysis of the visceral motor nerves of Selachians was made, with a view to comparison with the arrangement in mammals. Very little evidence was found of the existence of functionally antagonistic sympathetic and parasympathetic systems, and it is suggested that these systems in Tetrapods represent specialisations within a single segmental set of visceral motor fibres, running primarily through the dorsal roots, but coming to pass through the ventral roots in those segments in which the roots join.

In the trunk region of Selachians the rami communicantes contain only pre-ganglionic fibres, i.e. there are no grey rami, and in accordance with this it was found that the melanophores of the skin are not innervated.

The structure of the autonomic neurons is described in detail. In the case of the post-ganglionic cells which innervate the suprarenal bodies the processes can sometimes be followed all the way from nerve cell to nerve ending so that the hypothesis of Elliott, that the chromophil cells themselves represent post-ganglionics, is disproved. J. Z. Y.

Comparative Studies on the Physiology of the Iris. I. Selachians. II. Uranoscopus and Lophius.

By J. Z. Young.

Proc. Roy. Soc. London, Ser. B, Vol. 112, *p.* 228, 1933.

It was found that the sphincter muscle of the iris of Selachians is not under nervous control but contracts in direct response to illumination. The dilatator muscle, on the other hand, receives motor fibres from the oculomotor nerve. The action of various drugs on these muscles was then tested and it was found that whereas adrenaline, acetyl choline, pilocarpine and eserine all caused contraction of the dilatator muscle, none of these substances caused any contraction of the sphincter. This is held to be evidence that these drugs act at the mioneural junction and not on the muscle fibres themselves.

Both of the muscles of the iris of Uranoscopus and Lophius are under nervous control and a study of the effects of drugs in these forms gave results in agreement with the above hypothesis. J. Z. Y.

Nervous Degeneration and Regeneration in Cephalopods.

By E. Sereni and J. Z. Young.

Pubbl. Staz. Zool. Napoli., Vol. 12, *p.* 173, 1932.

A study was made of the effects of sectioning the mantle connective or stellar nerves in various Cephalopods. The process of degeneration and regeneration of the nerves is described in detail and an analysis made of functional components of the nerves in question. After section of the mantle connective degeneration proceeds as far as the stellate ganglion but not into the stellar nerves, and this fact demonstrates that there is no continuity between the axons of the connective and the neurons of the stellate ganglion. In agreement with this the actual terminations of the fibres in the stellate ganglion (" boutons terminaux ") were recognised, this being the first time that such structures have been described in invertebrates. J. Z. Y.

Notices of Books.

Origin and Environment of Source Sediments of Petroleum. By Parker D. Trask, assisted by Harold E. Hammar and C. C. Wu. Gulf Publishing Co., Houston, Texas, 323 pp., 1932.

THIS book contains much interesting matter, not to be found elsewhere, based upon the examination of sediments from about 1600 localities from all parts of the world.

The organic content of a marine deposit depends upon the supply of organic matter in the overlying water, due allowance being made for the effects of transportation and decomposition. The importance of the upwelling of deep water rich in phosphates, nitrates and other nutrient salts has been made evident, so that bottom deposits in such regions rich in plankton are themselves rich, save where steepness of slope may hinder deposition ; basins on the other hand are richer in organic matter.

The organic content of recent marine sediments ranges between 0·3 per cent in deep ocean oozes and 7 per cent in deposits of the Channel Islands region of California. Pelagic sediments contain very little organic matter.

In the surface layers nitrogenous components form 40 per cent of the organic matter and lignin-humus complexes comprise 30 per cent. Oils and fats comprise less than 0·3 per cent. Changes take place in the organic matter before the deposits have become consolidated, so that much of the matter deposited disappears. It is considered that petroleum arises owing to the conditions to which the organic matter is subjected after consolidation.

About 130 recent and 30 past sediments were distilled in iron retorts, the results being remarkably alike. The oil production varies directly with the organic content. In recent marine sediments the maximum yield is 3 gallons per ton and in past deposits 6 gallons. In rich sediments, both past and recent, 25 per cent of the organic matter is converted into oil, but less than 5 per cent in poor deposits. Oil is formed in the retorts between about 260 and 525° C., its specific gravity lying between 0·88 and 0·98. Water and gas, mainly methane and hydrogen, are also produced.

In this work researches in marine biology find a direct application and the results obtained by the authors are of interest to a field far wider than that of petroleum technology.

W. R. G. A.

The Marine Shells of Port Alfred, S. Africa. By Lt.-Col. W. H. Turton, D.S.O. Oxford University Press, London: Humphrey Milford, 331 pp., 1932, Pl. I–LXX, 18s. net.

This is an account of shells collected for many years at Port Alfred. It is valuable because they all came from this one very rich locality, and among them are some hundreds of new species which are figured in photographic plates at the end of the volume. It is the result of an enormous amount of work, but is purely conchological. Apparently no effort whatever was made to discover the form of the animal, natural habitat or general biology, and most of the shells were collected when dead, the numerous minute forms having been obtained by sifting sand.

The wonderful variety of these small shells makes us wish for some good notes on their living inhabitants. Some of the minute new species are almost certainly larval forms, for instance *Trophon ornatus* is much more like a larval Philbertia than a Trophon, having almost the exact sculpture and shape of some of the British species; *Triphora retusa* may easily be still a veliger, and many others of these we should like to see alive before admitting them as new species. M. V. L.

British Museum (Natural History). Instructions for Collectors. No. 12—Worms. 22 pp., 1932, 6d.

This is a new edition of a familiar handbook on the collection and preservation of worms, the latter term being used in its widest sense. It has been thoroughly revised, and is a most attractively produced as well as useful publication. Brief non-technical descriptions of each of the main worm groups, illustrated by nineteen clear and well-chosen illustrations, should help the non-specialist collector in classifying his specimens before looking up the appropriate methods of preservation. The methods given are simple and good, but exception must be taken to the statement that Arrow-worms fixed in Bouin for histological study should be stored in formalin (page 12). It should also have been clearly stated that when Bouin's fluid is used it must be washed out with strong alcohol and not with water, as readers unfamiliar with the fixative will probably assume. The handbook ends with a useful descriptive list of fixatives and instructions as to labelling and packing. D. P. W.

Marine Biological Association of the United Kingdom.

Report of the Council for 1932.

The Council and Officers.

Four meetings of the Council have been held in London during the year, at which the average attendance was sixteen. The meetings were held as usual in the rooms of the Royal Society at Burlington House, and the thanks of the Association are due to the Royal Society for the accommodation provided. A Committee of the Council, consisting of six members, including the Chairman, Professor E. W. MacBride, F.R.S., visited and inspected the Plymouth Laboratory.

The Plymouth Laboratory.

The good state of repair of the Laboratory buildings and fittings has been maintained ; the woodwork of the north building and north side of main building, and the interior of the tankroom have been repainted throughout. Much interior painting of the north building has been carried out by direct labour. The approach from the main gate to the entrance of the building has been levelled and paved with tarred stone.

The motor pump, which was installed in place of the old gas engine, has worked satisfactorily and the circulation of water and air throughout the tanks has proved sufficient.

Extension of Laboratory Buildings.

The new series of laboratories forming an extension of the north building, which have been built through the generosity of the Rockefeller Foundation, who made a grant of £4,642 for the purpose, were completed and taken into use at the beginning of the summer. The new block contains two large laboratories, one for physiology and one for biochemistry, a special room for photographic work and experiments on the effects of light on the reactions of marine animals, and five smaller laboratories for general purposes. It constitutes a most valuable addition of working space, for which the Association is deeply indebted to the Rockefeller Trustees.

The Ship and Motor-Boat.

The steam drifter *Salpa* has been steadily at work during the year, with the exception of the customary and necessary periods in harbour for refit and overhaul. Both hull and engines are in very good order.

The motor-boat *Gammarus* has been in regular use throughout the year and is maintained in sound condition.

The Staff.

The Council desire to congratulate Dr. C. M. Yonge on his appointment to the newly-constituted chair of Zoology in the University of Bristol. Dr. Yonge has done most useful work at Plymouth for a number of years and he will be greatly missed at the Laboratory.

Mr. J. E. Smith's term as Student-Probationer was completed in September and he has since taken up an appointment in the Zoological Department of the University of Manchester.

Mr. O. I. Green of Oxford has been appointed Student-Probationer to succeed Mr. J. E. Smith.

Occupation of Tables.

The following investigators have occupied tables at the Plymouth Laboratory during the year :

Miss D. Atkins, London (Pinnotheres and Lamellibranch gills).
Dr. J. R. Baker, Oxford (Pharmacology of sperms).
R. Bassindale, Middlesbrough (Identification of Tees Estuary Invertebrates).
J. B. Bateman, Cambridge (Osmotic regulation in shore crabs).
Dr. H. A. Baylis, London (Parasitic worms from fishes).
Miss E. D. Beavis, Darley Dale (Marine Algæ).
Mrs. M. P. Beresina, Leningrad (Heat production in crustacean nerves).
Dr. N. J. Berrill, Montreal (Ascidian embryology).
Miss A. M. Bidder, Cambridge (Digestive system of Loligo. Vital staining of Cephalopod larvæ).
Miss M. V. Bishop, London (Development of Buccinum).
R. Boto, Lisbon (Chemical Constituents of Sea-water).
Prof. D. W. Bronk, Philadelphia (Fatigue of muscles of Maia through stimulation).
H. A. Cole, Bangor (Morphology of fishes).
S. L. Cowan, London (Chemical exchanges in crustacean nerve).
Dr. C. Crossland, Ghardaqa Marine Laboratory, Red Sea, Egypt (General Zoology).
D. D. Dasen, Liverpool and Madras (Fish eggs and larvæ).
J. H. Day, Liverpool and S. Africa (Plankton. Growth of Crabs and Sacculina).
W. J. R. Deeks, London (General Zoology).
Dr. G. P. Eggleton, Edinburgh } (Phosphate in crab nerve. Car-
Dr. P. Eggleton, Edinburgh } nosine in invertebrate muscle).
T. P. Feng, London (Heat production in crustacean nerves).
Dr. M. Florkin, Liége (Hæmerythrin in Phascolosoma).
Miss E. Georgeson, Leeds (Ascidians).

F. M. Ghazzawi, Liverpool (Histology of intestines of Mullet).
A. Graham, Sheffield (Patella).
J. Gray, Cambridge (Movements of fishes).
O. I. Green, Oxford (Food of fishes. Natural history of *Lepidorhombus whiff*).
Dr. R. Gurney, Oxford (Copepod nauplii).
J. E. Harris, Cambridge (Cinematography of fish movements and eggs of marine animals).
J. C. Hayes, Manchester (Young marketable marine fishes).
H. Henson, Leeds (Development of Haliclystus).
Prof. A. V. Hill, London (Chemical exchange in crustacean nerve. Heat production in crustacean nerve).
Mrs. Greta Hörstadius, Stockholm (Proteolytic enzymes of Aplysia and Helix).
Dr. Sven Hörstadius, Stockholm, Ray Lankester Investigator (Heredity in sea-urchins. Development of Luidia. Phagocytosis in Gastropods).
A. F. W. Hughes, Cambridge (Injection of fishes).
Dr. Walther Huth, Berlin (Ophryotrocha).
Miss P. M. Jenkin, Cambridge, Ray Lankester Investigator (Correlation of photosynthesis of diatom cultures in the sea with photoelectric measurements of light penetration).
E. I. Jones, London (Fish Trematodes).
Dr. T. Kamada, Tokyo (Pedal waves of Gastropoda).
J. A. Kitching, London (Wembury Bay Fauna. Contractile vacuoles of Protozoa).
Mrs. M. K. Krainska, Warsaw (Behaviour of yolk in crab's egg).
W. H. Leigh-Sharpe, London (Parasitic Copepods).
A. G. Lowndes, Marlborough (Movement of sperm in Ostracods).
G. I. Mann, Plymouth (General Zoology).
B. J. Marples, Manchester (Anatomy of the vascular system in Elasmobranchs).
G. A. Millikan, Cambridge (Maia blood).
C. C. A. Monro, London (Polychæte worms).
C. F. A. Pantin, Cambridge (Osmotic control in Amphipods).
L. E. R. Picken, Cambridge (Osmotic regulation in Sipunculids).
Dr. H. H. Poole, Dublin (Measurement of submarine illumination).
P. Powers, Pennsylvania (Parasitic Protozoa in Echinus).
Miss N. Reed, London (Sporozoan parasites in Annelids).
A. D. Ritchie, Manchester (Pecten and Oyster muscle).
Miss M. L. Rothschild, London (Parasitic Trematodes).
J. P. Scott, Oxford and Wyoming (Cleavage of Echinus).
Miss F. E. Smith, Plymouth (Nemertines).
F. G. W. Smith, London (Development of Patella).
S. Smith, Cambridge (Nitrogen excretion of *Carcinus mænas*).
Dr. E. A. Spaul, London (Relation of the thyroid and pituitary body in fishes).
Miss F. A. Stanbury, Plymouth (Diatom cultures).
Miss E. M. Stephenson, Birmingham (Colour change in Crustacea).
Dr. S. Takatsuki, Tokyo (Physiology of the oyster).
Miss M. J. Thomas, London (Feeding mechanisms).
R. C. Vernon, Plymouth (General Zoology).
Prof. J. Paul Visscher, Cleveland, Ohio (Distribution and periodicity of Cirripedia).
G. P. Wells, London (Action of salts on invertebrate muscle).
Mrs. D. P. Wilson, Plymouth (Marine Algæ).

Dr. Sven Hörstadius of Stockholm was appointed Ray Lankester Investigator, and with his wife, Mrs. Greta Hörstadius, worked at the Laboratory for five months during the summer. Subsequently Miss P. M. Jenkin of Cambridge was appointed to the same investigatorship and commenced work in October.

A meeting of the Society for Experimental Biology was held at the Laboratory in July and was well attended.

The usual Easter Vacation Course in Marine Zoology was conducted by Mr. D. P. Wilson and Mr. G. A. Steven, and was attended by forty-one students from Oxford, Cambridge, London, Edinburgh, Liverpool, Manchester, Birmingham and Exeter.

A Course in Marine Biology was also held during the Summer Vacation, conducted by Prof. J. H. Orton, of Liverpool University, and was attended by fifteen students from Cambridge, London, Liverpool, Exeter, and Portsmouth.

During the Easter Vacation, Mr. J. M. Branfoot brought five students from Oundle School, one from Clifton College, and one from Winchester College; Mr. M. W. Barr, three from Harrow; Dr. E. W. Shann, eight from Rugby, two from Stowe School, and one from Wellington College; Mr. H. P. Ramage, three from Gresham School; Mr. C. T. Prime, two from Whitgift School; Mr. I. Hamilton, one from Dauntsey School; and Mr. H. C. Wilson, three from Monkton Combe. Mr. A. S. Gillespie and Mr. A. S. Turner, from Rydal Mount School, Colwyn Bay, also came as visitors.

At Whitsuntide Mr. E. I. Jones of the Chelsea Polytechnic conducted a class of nine students.

The Scientific Work of the Plymouth Laboratory Staff.

As in last year's report the descriptions of the different investigations have been arranged so as to indicate their bearing on the general plan of work that is being undertaken by the staff. The investigations on the physical and chemical characters of the environment are first described, then those on the vegetable and animal plankton, which form the basis of the food supply of the sea. Researches on the ecology, physiology, and genetics of the invertebrates of the sea-floor which feed on the plankton and on each other are then described. These invertebrate animals constitute the food of the bottom-living fishes and lead naturally to an account of studies on the fishes themselves and the commercial fisheries.

Physics and Chemistry of the Environment.

Dr. Atkins and Dr. H. H. Poole have continued their work on the measurement of submarine illumination and an arrangement has been devised whereby the colour filters can be changed at various depths, so that alterations in intensity can be determined more nearly simultaneously for various colours. This method avoids errors introduced by a possible drift of the ship between the depth-series carried out with one colour filter after another. The photo-electric cells used in these investigations have now been standardised in terms of "mean noon sunlight," as defined by the Seventh International Congress of Photography, so that photo-electric measurements made at various places may be truly comparable. A laboratory study was also carried out upon the behaviour of the new type of photo cell described by Lange. This is used without a high-tension battery and is highly sensitive, but the current is not linearly proportional to the illumination over an extended range and there is a considerable temperature coefficient. Bearing such limitations in mind a cell of this type was mounted in a handy form of submarine photometer which was carried about under water by Mr. J. A. Kitching and Mr. Gilson while using the diving helmet in their survey of a submarine gully near Wembury. The photometers were calibrated against a vacuum photo-electric cell and precautions were taken to minimise the temperature effect.

Dr. Atkins has also shown that diphenylbenzidine is a serviceable reagent for estimating nitrate in sea-water. The reagent is readily prepared, the colour intense and stable to light. Since iodate reacts in a quantitatively similar manner it must be removed, if present.

Attention has also been given to the determination of the copper-content of sea-water on account of the recognition of the importance of this element in plant growth, in the utilisation of iron in the animal organism and as the stimulus, according to Prytherch, for the attachment of oyster larvæ. By means of electro-deposition and colorimetric estimation with sodium diethyl-dithiocarbamate sea-water was found to contain 10 mg. of copper per cubic metre. A more rapid method whereby the copper salt of the reagent is extracted with an organic solvent has also been used and a river water at low tide was found to contain 36 mg. as against 16 mg. per cubic metre at high tide.

The hydrographic records between Plymouth and Ushant, commenced in 1921, have been continued. These are published yearly in the *Rapport Atlantique* of the International Council for the Exploration of the Sea. They are also worked up by Mr. H. W. Harvey in conjunction with the surface data, collected for the Ministry and for this Association by cross-Channel steamers. Charts of the salinity distribution at the mouth of the Channel are drawn for each month. Reports on the major changes which have taken place are published in the Journal of the Association at intervals.

Much of Dr. L. H. N. Cooper's time has been spent in working up the mass of data on the minor constituents of sea-water obtained during 1931. Calculations of the phytoplankton crop in the Channel, based on seasonal changes in phosphate, nitrate, oxygen, and carbon dioxide and agreeing closely with one another, show that each square kilometre produces about 1,400 metric tons wet weight. The crop calculated from silicate data is less than one-tenth of this. Since silicate is seldom found completely exhausted and diatoms predominate in the phytoplankton, it is concluded that silicate takes part in the life-cycle several times in the course of the season. This is supported by the rapid re-solution of silicate after the spring outburst to give a summer maximum about July or August. The detailed results of this work are being published in the Journal of the Association. Work has been continued on certain of the nutrient salts. The summer maximum for silicate was again observed in 1932.

Plankton.

Mr. Harvey has continued an investigation concerning the influence of various factors upon the rate of assimilation and respiration by the diatom *Nitzschia closterium*. It was found that the addition of phosphate to a culture which had used up all or nearly all the available phosphorus, caused, in the dark, an increased rate of respiration and a division of cells.

In the light the addition of 10 mg. per cubic metre P_2O_5 brought about an increased fixation of some 115 mg. of carbon. The addition of either nitrate or ammonium to a culture which had used nearly all the available nitrogen caused a similar increase in the rate of growth in the light, the addition of 1 mg. of nitrogen bringing about an increased fixation of some 12 mg. of carbon. It was found that the addition of 1 mg. of iron per cubic metre, in the form of citrate, roughly doubled the rate of growth, and some evidence was obtained that iron is only available in ionic form, of which sea-water probably contains considerably less than one part in a thousand million. The addition of a sterilised extract of soil to a culture, enriched with nutrient salts, iron and silica, caused a material increase in rate of growth. If kept in the dark the addition caused a multiplication of the diatom cells. The presence of a "growth-promoting factor" in extract of soil, yeast, seaweed, and the diatom itself seems probable.

To a Nitzschia culture additions were made of recently distilled water and of an equal quantity of the same water which had been frozen and allowed to melt and attain room temperature. An increased growth was observed where the added water had previously been frozen. An increased growth was also observed where the culture fluid was partly frozen and then allowed to attain room temperature before inoculation with the diatoms. Further experiments on the apparent physiological action of trihydrone are being made.

Mr. F. S. Russell has made progress with his research on the biology of the plankton animal Sagitta. It has been possible to show that a number of broods are produced during the year the adults of which appear to grow to different sizes, those maturing in April and May being the largest. There are two species of Sagitta commonly occurring at Plymouth, *S. elegans* and *S. setosa ;* in their annual life-cycles the two species differ slightly. Both cease breeding for a period in the winter, but *S. setosa* continues to breed later than does *S. elegans*, an adult brood of the former appearing in October while the last brood of the latter to mature in the year appears in September. *S. setosa* would seem therefore to have one more brood than *S. elegans* during the twelve months. Both species show variation in the size to which adults of the different broods grow, but the range of this variation is greater in *S. elegans* than in *S. setosa.* These results have been published in the Journal, Vol. XVIII, No. 1. An examination of the Sagitta population over a number of years has shown that there has been a gradual change over from a population in 1930 in which *S. elegans* predominated to that of 1932 in which *S. setosa* predominates. An attempt has been made to find the actual relative abundance of the Sagitta throughout the year ; results based on oblique hauls with the 2-metre stramin ring-trawl appear to show a considerable dying down of the Sagitta stock during the winter months. Collections made with a stramin net fished very close to the bottom, however, show no such diminution and seem to suggest that the apparent diminution in the oblique catches may be due to the descent of the Sagitta to the deeper water-layers.

By piecing together the results of the above research and further results obtained from collections made in 1926 to study the vertical distribution, it has been possible to produce a preliminary picture showing the whole cycle of events in a Sagitta population throughout a year. Of especial interest in this is the rise of Sagitta into the upper highly illuminated layers in July, August, and September. This is a phenomenon that Mr. Russell has already shown for other plankton animals, notably the copepod *Calanus finmarchicus.* In its vertical distributions *S. setosa* always appears to live slightly higher in the water than does *S. elegans.* An account of the results of the above work is now in the press.

As an outcome of the researches on the pelagic young of teleostean fishes a record has been made of the occurrence of the fixed Chalimus stages of the Caligid parasitic copepods. It appears that two fishes, *Gadus merlangus* (whiting) and *Ammodytes lanceolatus* (sand-eel), are especially liable to parasitisation during their pelagic existence.

The weekly observations on the seasonal abundance of young fishes

larvæ have been confirmed, and a considerable quantity of material of all stages has been fixed and preserved. This material is at present being sectioned with a view to a detailed histological study, particularly of the curious metamorphosis.

Mr. Wilson has completed and published in the Journal an account of the development of *Nereis pelagica* based on a rearing made in 1927. He has also again reared *Notomastus latericeus* from the egg to an early bottom stage, confirming previous observations and making a few additions. A paper on the development of this species has been prepared for the Journal.

The work on the Mitraria larva having directed attention to the desirability of acquiring some knowledge of the development of Maldanids, a family whose embryology is as yet unknown, a special effort has been made with this end in view. A good patch of the worm *Caesicirrus neglectus* was, during the spring, located at Salcombe and has been visited at regular intervals ever since. Unfortunately these particular worms have not yet spawned, but it is hoped to obtain fertilisations as soon as they are ripe.

Invertebrates of the Sea Floor (*Ecology, Physiology, Genetics*).

The ecological survey of the Eddystone shell gravel which Mr. J. E. Smith commenced in January, 1931, was concluded in February of this year. The investigation included a study of the relations of the animals living in the gravel to their environment, and a discussion of the origin and nature of the gravel bottom in the immediate vicinity of the Eddystone reef. It is of interest that the shell constituent of the gravels consists only of the shells and tests of animals which normally live on the ground—evidence that the "shell gravel community" of animals is of a permanent and limited nature. A paper describing the survey and containing a discussion of the results has been published in the Journal of the Association.

During the summer months Mr. Smith has confined his attention to the collection of material for embryological work on Nemertines. Larvæ of *Cephalothrix rufifrons* (Johnstone) have been reared successfully to an advanced stage, and the early stages of segmentation have been studied both from living and preserved material. It is hoped ultimately to prepare for publication an account of the "direct" method of development of this Palæonemertine.

In July Mr. F. S. Russell paid a visit to Portsmouth to make a biological survey of H.M.S. *Champion* at the instigation of the Corrosion Committee of the Iron and Steel Institute. This was a preliminary examination to study the possible effects of the growth of marine organisms on corrosion of metal.

Dr. C. M. Yonge has made considerable progress with his investigations into the nature and permeability of crustacean chitin. A first paper on this subject on "The Chitin Lining the Foregut of Decapod Crustacea and the Function of the Tegumental Glands" was recently published in the Proceedings of the Royal Society. The integument was shown to consist of two distinct regions, a thin superficial cuticle and a much thicker, lamellated chitin. The former, as indicated in the Report for

1931, is formed by the tegumental glands which are everywhere abundant under all chitinous areas in the body of Crustacea (and also many other Arthropods), while the latter is secreted by the chitinogenous epithelium. The function of these glands has hitherto been a matter of speculation. The cuticle differs in chemical and physical properties from the chitin. Its true nature is still uncertain, but it is certainly *not* chitin. Experiments on the permeability of chitin are still proceeding (though approaching completion), and when they are published will establish definitely that the cuticle is of fundamental importance in controlling the permeability of the uncalcified chitin in the Crustacea and possibly in many other, or indeed all, Arthropoda.

In addition to the main objects of this research several interesting facts have been discovered. In the lobster, onwhich the great part of the work has been done, the formation of new chitin has been found to be preceded by the dissolution of the undermost layers of the old chitin. This is brought about by the agency of cells which migrate into it from the tissues and which apparently secrete a chitinase. It has also been possible to establish the true nature of the membranes which surround the eggs of Decapod Crustacea after they are attached to the pleopods of the female, and also the method of attachment, on both of which subjects there has, in the past, been much uncertainty. As the eggs pass down the oviduct they are covered with a thin layer of chitin and after extrusion they are wrapped round and secured to the pleopods by thin sheets of " cuticular " material secreted by the tegumental glands which are especially abundant in these appendages. The material used in the formation of nests by various Amphipoda and the cement secreted by the Cirripedia both appear to be of the same nature as the cuticle in the Decapoda. It is hoped to produce a paper shortly on the membranes and attachment of the eggs in the Decapods and, in the course of time, to follow up the preliminary investigations on the Amphipoda and Cirripedia.

Further progress has been made with the preparation and publication of work done during the Great Barrier Reef Expedition, and two papers, " The Relationship between Respiration in Corals and the Production of Oxygen by their Zooxanthellæ " (in collaboration with Mrs. Yonge and Dr. A. G. Nicholls) and " Notes on Feeding and Digestion on Pterocera and Vermetus with a Discussion on the Occurrence of the Crystalline Style in the Gastropoda," have been published in the Scientific Reports of the Expedition (British Museum Nat. Hist.). Short papers dealing with work done or observations made during the expedition have also been published in the Journal of the Malacological Society of London and in Natural History. A short account of the Crystalline Style in the Mollusca has been published in Science Progress. Some observations on planulation and early development in *Balanophyllia regia*, our only Eupsammiid coral, have been published in the Journal of the Association. Certain observations have also been made by Dr. Yonge on the iso-electric point of the mucus in ciliary feeders and the relation of the viscosity of the mucus to the hydrogen-ion concentration in various regions of the gut. This work will be incorporated in a forthcoming paper dealing with various aspects of digestion in ciliary feeders which differ from many other animals in that they feed *continuously*, which involves important correlations in the digestive processes.

The Mendelian work on *Gammarus* has been carried on by Mrs. Sexton with the assistance of Miss A. R. Clark, particular attention being directed during the past year to the question of the origin of recessive characters, especially as to how far they are present in the wild. A considerable amount of data has been collected which it is hoped will soon be ready for publication.

The paper, in collaboration with Mr. G. M. Spooner, referred to in last year's Report, dealing with the different stocks where variations in eye-pigmentation have occurred, has been published in the Journal, and has aroused considerable interest amongst those who are studying similar problems. In another paper Mrs. Sexton has given an account of a long series of degenerative changes grading from the perfect eye to the entire absence of one or both eyes. It is noteworthy that all these changes, which occurred in the same stock, took place within the short period of eight years.

Fish and Fisheries.

Mr. E. Ford followed the progress of the drift-net fishery for herrings during the winter of 1931–32. The commercial results were disappointing, the total quantity of fish landed and the total value both being the lowest since the season of 1921–22. The average weight of fish per landing was also low, comparing very unfavourably with the average of the past ten years, particularly in the case of the West-country motor-drifters. These results were not unexpected in view of the fact that there appears to have been a limited replenishment of the fish stocks by incoming recruits during recent years, so that the fishery has latterly been dependent upon a stock that is getting older and numerically weaker. The excellent fishery of 1929–30 was due in large measure to the presence of a high proportion of herrings of the successful year-class 1925, then in its fifth winter. The fisheries of 1930–31 and 1931–32 had also to rely for the most part on what still remained of this same year-class, since younger fishes of the broods of the years 1926, 1927, 1928, and 1929 were not entering the shoals to any noteworthy degree. Naturally, therefore, there was a marked fall in the average weight of fish per landing. The extent of this fall and the corresponding changes in the age composition of the catches are shown by the following figures :—

SEASON	AVERAGE WEIGHT PER LANDING		AGE COMPOSITION OF CATCHES		
(Dec.–Jan.)	Steamer (cwt.)	Motor (cwt.)	3, 4 and 5 years °/₀	6 years °/₀	Older than 6 years °/₀
1929–30	39·1	42·5	55·9	15·4	28·8
1930–31	32·7	23·3	38·4	33·2	28·3
1931–32	17·6	9·2	31·0	21·3	47·7

In face of these results, the outlook for the immediate future of the fishery would appear to be serious, unless and until there are signs of an early renewal of the stocks by a big influx of young fish.

Fortunately, there are indications that the brood born during the winter of 1929–30 is about to enter the fishable stocks in good numbers, although final confirmation of the richness of the brood will not be forthcoming until the season of 1932–33 has opened. The examination of samples from an unusual run of herrings inshore during September and October of 1932 showed an exceptionally high proportion of the brood in question—a circumstance which is the basis of the hopes expressed above. Should the 1929–30 brood prove a rich one, the turn of the tide in the fisherman's favour may be expected next season, if not in this coming one.

In January last, Mr. Ford tried the experiment of forwarding developing herring eggs to the Laboratories at Cullercoats and Port Erin (Isle of Man) and to the Brighton Municipal Aquarium, in order that trials might be made to hatch out and rear the larvæ under the normal local conditions. The eggs were forwarded attached to the inside of glass jars (breffits) in which they had been fertilised, the travelling containers being ordinary hampers. They arrived safely at their destination and good hatching results were reported in each instance, although it was found impossible to rear the larvæ. The experiment was quite satisfactory in demonstrating that fertilised eggs can be sent considerable distances by the ordinary methods of transport, whereby the facilities afforded by other laboratories for rearing researches become available.

In addition to this new work, Mr. Ford has been preparing a comprehensive account of the different branches of herring research which have been conducted and reported on in this Journal in a series of separate papers entitled "Herring Investigations at Plymouth." This account which is nearing completion will serve the double purpose of co-ordinating the separate studies made, and of indicating the lines along which further investigation is needed.

An increase in the opportunity for members of the staff of the Laboratory to take part in the public work of the administration of the fisheries of

Devon and Cornwall has been afforded by the appointment of Mr. Ford as a member of the Devon Sea Fisheries Committee, and of the invitation of the Cornwall Committee for him to attend their meetings.

Mr. G. A. Steven has continued his researches on the rays and skates of the western area of the English Channel, and a report embodying many of the results so far obtained was published in the Association's Journal in May of this year. It has often been observed, and became evident again in these researches, that female fish considerably outnumber the males in ray landings. An effort has been made to ascertain whether or not this preponderance of females in the catches is due to excess of females in the ray population in the sea or to differential capture of the two sexes. Data have been collected which show that, in these waters at any rate, the young of the commonest species (*R. clavata*) are born with the sexes approximately equally represented. As growth proceeds and maturity is reached the sexes segregate to a greater or less extent, and the females, when in a gravid or "spawning" condition, form more compact shoals than do the males and therefore tend to be captured in greater numbers. What is true of *R. clavata* probably holds good also for all the other ray species. This fact has a direct practical bearing upon the commercial fishery for these species, which are now of considerable and steadily growing importance as national food fishes. For the maintenance of any animal stock the female is, from the numerical point of view, the more important sex. In the Raiidæ, therefore, the greatest drain of the fishery upon the fish population is falling upon its most vulnerable part. A report of this work has been prepared for publication in the Journal of the Association. During the year, as weather and tidal conditions permitted, determined efforts have been made to obtain ray eggs in a locality which is believed to be a "spawning" ground. In spite of every endeavour, no eggs have been found although large numbers of empty cases and not a few full ones are thrown up on adjacent shores during heavy autumn and winter storms. The liberation of marked rays, with a view to following their migrations and determining their growth-rate, has been continued and very satisfactory returns of recaptured specimens are being obtained. Most of the fish which have so far been marked have been in an immature condition and the recaptures have shown that they migrate but little, at any rate, until maturity is reached. Numerous fish have been recaptured in the exact place of liberation after periods of freedom varying from a few days up to a year or more. Growth is slow, apparently averaging about 4 cm. in width across the disc in one year in half-grown individuals (20 to 30 cm. disc width) of *Raia clavata*. Most of this growth takes place during the summer and autumn months. Many more data are required, however, on these points and are steadily being accumulated.

In order to disentangle the movements of immature and sexually mature fish, the state of maturity of all males which have been marked—as indicated by the size and condition of the claspers—has been recorded. But as there is no external evidence of the state of maturity in the female fish, this could not be done with them. Investigation has now revealed that certain changes in the size and condition of the cloaca and uterus, which take place at sexual maturity and which can be ascertained by digital examination of the live fish, form a ready means of separating mature from immature female individuals. This method will be applied in future marking experiments and should greatly add to the extent and value of the data acquired.

In continuation of his investigations on the food of Shags and Cormorants Mr. Steven endeavoured to obtain birds from certain harbours and sandy bays and estuaries around the Devon and Cornwall coasts. It is in such situations that fishermen claim most frequently to see these birds devouring flatfish, particularly during the winter season when they are driven in from their usual feeding-grounds by stress of weather. It has been found very difficult to obtain the birds from such places, but 2 Shags and 2 Cormorants were shot and secured in the sandy estuary of the river Erme on 2nd February, 1932. Although shot *inside* the estuary where young flatfish are numerous, these birds had obviously been feeding around the rocky shores *outside*, for the contents of each of the four stomachs was made up of rock-dwelling species. No evidence has yet been obtained, therefore, in support of the fishermen's claim that these birds make serious inroads on the flatfish population around these shores.

The preservation of fishing-nets has continued to receive attention from Dr. Atkins and a short report was made to the Advisory Committee on Vegetable Fibres concerning sisal, hemp, and Phormium fibre for trawl twines. Nets treated with copper resinate, dissolved in gasworks benzene or in solvent naphtha, have retained their colour and original strength intact for a year under the usual test conditions, under which the preservative comes off the surface at least, in the case of other reagents, unless bound with tar. The resinate costs one shilling per pound and gives a greenish coloured net, quite clean to handle and not greasy. A net treated by Dr. Olie's method and re-treated every four months has now remained in good condition for six years, the breaking strength of the twine averaging 16 lbs. as against 18 lbs. when new.

River Tees Survey.

Field work connected with the Biological and Chemical Survey of the River Tees Estuary was continued until the early summer of 1932. Methods of reducing the toxicity of cyanide-containing effluents were investigated and a large-scale experiment was successfully carried out with the help of Messrs. Dorman Long Ltd. at their Acklam works. Some 5000 gallons per hour were rendered innocuous by the addition of lime and spent pickle liquor, a local by-product containing ferrous iron. Unfortunately, considerations of expense did not allow the whole of the cyanide containing effluent discharged into the estuary to be treated during the period of the smolt run, and the projected investigation of the effect upon the mortality of smolt during their migration of rendering the cyanide innocuous had to be abandoned. The rest of the year has been devoted to finishing various parts of the experimental work and to writing a report of the survey. The investigation has been carried out at Middlesbrough under the direction of Dr. B. A. Southgate, with Mr. R. Bassindale as biological assistant, and Mr. H. W. Harvey has visited Middlesbrough from time to time and keeps in contact with the various investigations and with the administration by means of such visits and by correspondence.

The Library.

The thanks of the Association are again due to numerous Foreign Government Departments, and to Universities and other Institutions at home and abroad for copies of books and current numbers of periodicals presented to the Library, or received in exchange for the Journal. Thanks are also due to those authors who have sent reprints of their papers, which are much appreciated.

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Finance.

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Vice-Presidents, Officers and Council.

The following is the list of gentlemen proposed by the Council for election for the year 1933–34:—

President.

The Lord Moyne, P.C., D.S.O.

Vice-Presidents.

The Duke of Bedford, K.G.
The Earl of Stradbroke, K.C.M.G., C.B., C.V.O.
The Earl of Iveagh, C.B., C.M.G.
Viscount Astor.
Lord St. Levan, C.B., C.V.O.
The Right Hon. Sir Austen Chamberlain, K.G., M.P.
Lord Noel-Buxton.
Major The Right Hon. Walter E. Elliot, M.C., M.P.
Sir W. B. Hardy, F.R.S.
George Evans, Esq.
Sir Nicholas Waterhouse, K.B.E.
G. A. Boulenger, Esq., F.R.S.
J. O. Borley, Esq., O.B.E.

COUNCIL.

Elected Members.

Prof. Joseph Barcroft, F.R.S.
Prof. H. Graham Cannon, SC.D.
R. A. Fisher, Esq., SC.D., F.R.S.
Prof. H. Munro Fox.
Prof. F. E. Fritsch, F.R.S.
Michael Graham, Esq.
Robert Gurney, Esq., D.SC.
Prof. C. R. Harington, F.R.S.
S. Kemp, Esq., SC.D., F.R.S.
J. R. Norman, Esq.
C. F. A. Pantin, Esq.
E. S. Russell, Esq., D.SC.
Prof. G. I. Taylor, F.R.S.
J. Z. Young, Esq.

Chairman of Council.

Prof. E. W. MacBride, D.SC., F.R.S.

Hon. Treasurer.

Nigel O. Walker, Esq., 38, Regent Street, Cambridge.

Secretary.

E. J. Allen, Esq., D.SC., LL.D., F.R.S., The Laboratory, Citadel Hill, Plymouth.

The following Governors are also members of the Council :—

G. P. Bidder, Esq., sc.d.

E. T. Browne, Esq.

George Evans, Esq.

The Lord Moyne, p.c., d.s.o.

H. G. Maurice, Esq., c.b. (Ministry of Agriculture and Fisheries).

Robert Corrie Evans, Esq. (Prime Warden of the Fishmongers' Company).

Nigel O. Walker, Esq. (Fishmongers' Company).

Guy Wood, Esq., m.b., m.r.c.p. (Fishmongers' Company).

(Oxford University).

J. Gray, Esq., m.c., sc.d., f.r.s. (Cambridge University).

Sir P. Chalmers Mitchell, Kt., c.b.e., d.sc., f.r.s. (British Association).

Prof. E. W. MacBride, d.sc., f.r.s. (Zoological Society).

Sir Sidney Harmer, k.b.e., f.r.s. (Royal Society).

THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM

INCOME AND EXPENDITURE ACCOUNT YEAR ENDED 31st MARCH, 1933.

	£ s. d.	£ s. d.
To Salaries, including Institutions Contribution to Superannuation		6,696 11 7
,, Laboratory Wages, including National Insurance and Institutions Contribution to Superannuation		2,100 5 9
,, Depreciation of Library		493 12 1
,, Scientific Publications, *Less* Sales		631 2 11
,, Upkeep of Laboratories and Tank Rooms:		
Buildings and Machinery	308 15 8	
Electricity, Gas, Coal, Oil and Water	402 12 5	
Chemicals and Apparatus	342 15 5	
Rates, Taxes and Insurance	105 1 6	
Travelling	65 16 1	
Stationery, Postage, Telephone, Carriage and Sundries	327 11 3	
Specimens	180 10 0	
		1,733 2 4
,, Maintenance and Hire of Boats:		
Wages, including Diet Allowance, National Insurance and Casual Labour	1,568 4 6	
Coal, Water, Oil, Petrol, etc.	217 3 9	
Maintenance and Repairs, with Nets, Gear and Apparatus	439 10 7	
Purchase of Material for Nets for Sale, excluding Labour	119 19 8	
Boat Hire and Collecting Expenses	18 17 0	
Insurance	300 13 0	
		2,664 8 6
,, Transfer to Depreciation Reserve Account		263 3 9
,, Balance, being Surplus for the Year		195 4 3
		£14,777 11 2

	£ s. d.	£ s. d.
By Grants:		
Ministry of Agriculture and Fisheries, Grant from Development Fund	11,258 6 10	
Fishmongers' Company	600 0 0	
British Association	50 0 0	
Royal Society	50 0 0	
Physiological Association (2 years)	60 0 0	
		12,018 6 10
,, Subscriptions		237 0 11
,, Donations		8 16 0
,, Sales:		
Specimens	1,173 16 5	
Fish (*less* expenses)	65 14 6	
Nets, Gear and Hydrographical Apparatus	253 9 1	
		1,493 0 0
,, Table Rent		454 3 9
,, Tank Room Receipts		497 17 6
,, Interest on Investments and Bank Deposits		40 19 1
,, Sale of Dr. M. V. Lebour's Book	4 15 10	
,, Sale of "Marine Fauna of Plymouth"	12 4 0	
		16 19 10
,, Refund of Income Tax		10 7 3
		£14,777 11 2

BALANCE SHEET 31st MARCH, 1933.

		£ s. d.	£ s. d.
Sundry Creditors:			
On Open Account		145 1 3	
Wages accrued		53 1 3	
			198 2 6
Building Fund:			
As at 31st March, 1932		285 8 7	
Add: Rockefeller Foundation Grant		1,849 17 8	
do. for Apparatus		141 8 7	
Sundry Donations		2 0 1	
		2,278 14 11	
Less: Expenditure:			
Library and Laboratory	287 8 8		
Rockefeller Laboratories	1,849 17 8		
Rockefeller Apparatus	141 8 7		
		2,278 14 11	– – –
Reserve for Depreciation of Boats and Machinery:			
As at 31st March, 1932		500 0 0	
Add: Transfer from Income and Expenditure Account		263 3 9	
			763 3 9
Bank Overdraft:			
Coutts & Co. (Secured by Deposit of Investments)			173 2 7
Surplus:			
As at 31st March, 1932		5,625 1 9	
Add: Composition Fees		31 10 0	
Surplus for the year as per Income and Expenditure Account		195 4 3	
			5,851 16 0
			£6,986 4 10

	£ s. d.	£ s. d.
Boats and Equipment, as per Valuation as estimated by the Director at 31st March, 1931:		
S.S. *Salpa*	2,000 0 0	
Motor-boat	150 0 0	
Nets, Gear and General Equipment	27 0 0	
		2,177 0 0
Laboratory Apparatus, Engines and Pumps:		
As per Valuation as estimated by the Director at 31st March, 1931, plus additions at cost		
As at 31st March, 1932	540 12 8	
Additions during the year	39 10 2	
		580 2 10
Library:		
As per Valuation as estimated by the Director at 31st March, 1931, plus additions at cost less Depreciation		
As at March, 1932	1,985 11 5	
Additions during the year	590 1 10	
	2,575 13 3	
Less: Depreciation	493 12 1	
		2,082 1 2
Stock of Specimens, Chemicals and Journals as estimated by the Director		350 0 0
Sundry Debtors		133 8 1
Prepayments		98 7 6
General Fund Investments, at Market Value as at 31st March, 1931:		
£410 14s. 8d. New Zealand 4% 1943/63	344 15 0	
£352 2s. 3d. Local Loans 3%	232 7 10	
(Market Value at Date—£734 18s. 6d.)		
		577 2 10
Depreciation Fund Investments at Cost		
£590 6s. 0d. Local Loans 3%	506 10 9	
£263 1[illegible] s. 1d. Conversion Loan 3%	256 13 0	
(Market Value at Date—£783 0s. 2d.)		
		763 3 9
Composition Fee Fund Investments at Cost:		
£18 8s. 6d. Local Loans 3%	15 15 0	
£32 9s. 6d. Conversion Loan 3%	31 10 0	
(Market Value at Date—£48 6s. 11d.)		
		47 5 0
Cash at Bank and in Hand:		
Lloyds Bank Limited	161 10 3	
Cash in Hand	16 3 5	
		177 13 8
		£6,986 4 10

To the Members of the Marine Biological Association of the United Kingdom:

We report that we have examined the above Balance Sheet with the books of the Association and have obtained all the information and explanations we have required. Capital expenditure on erection of Buildings on Land held on lease from the War Department is excluded. Subject to this remark we are of opinion that the Balance Sheet is properly drawn up so as to exhibit a true and correct view of the state of the Association's affairs, according to the best of our information and the explanations given to us and as shown by the books of the Association.

34 and 35 Bedford Street,
Plymouth. 8th April, 1933.

(Signed) R. A. Fisher } *Members of*
Guy Wood } *Council.*

(Signed) Price, Waterhouse & Co.

List of Annual Subscriptions

Paid during the Year, 1st April, 1932, to 31st March, 1933.

	£	*s.*	*d.*
Dr. W. M. Aders, O.B.E.	1	1	0
E. J. Allen, Esq., D.SC., F.R.S.	1	1	0
G. L. Alward, Esq. (the late)	1	1	0
Dr. Ikusaku Amemiya (1932 and 1933)	2	2	0
Aquario Vasco da Gama (1933 and 1934)	2	2	0
J. W. Arbuthnot, Esq.	1	1	0
Prof. J. H. Ashworth, D.SC., F.R.S.	1	1	0
Miss D. Atkins	1	1	0
Prof. J. Barcroft, F.R.S. (1931 and 1932)	2	2	0
W. H. Barrett, Esq.	1	1	0
Dr. J. B. Bateman (1933 and 1934)	2	2	0
G. R. de Beer, Esq.	1	1	0
J. Bělehrádek, Esq., M.D.	1	1	0
Mrs. M. G. Bidder (the late)	1	1	0
Birkbeck College (1932 and 1933)	2	2	0
W. Birtwistle, Esq.	1	1	0
Dr. H. Blaschko (1933 and 1934)	2	2	0
H. H. Bloomer, Esq.	1	1	0
H. Moss Blundell, Esq.	1	1	0
Mrs. H. Moss Blundell	1	1	0
Captain R. J. B. Bolitho	1	1	0
Dr. J. Borowik	1	1	0
L. A. Borradaile, Esq., SC.D.	1	1	0
C. L. Boulenger, Esq. (1932 and 1933)	2	2	0
E. G. Boulenger, Esq. (1930–1932)	3	3	0
Prof. G. C. Bourne, D.SC., F.R.S. (the late), (1932 and 1933)	2	2	0
Col. Sir Henry Bowles, Bart.	1	1	0
A. Bowman, Esq., D.SC.	1	1	0
Prof. A. E. Boycott, F.R.S.	1	1	0
Sir J. Rose Bradford, Bart., K.C.M.G., M.D., D.SC., F.R.S.	1	1	0
Brighton Public Library	1	1	0
R. Brown, Esq.	1	1	0
Miss E. M. Brown	1	1	0
R. H. Burne, Esq., F.R.S.	1	1	0
Carried forward	46	4	0

	£	s.	d.
Brought forward	46	4	0
M. Burton, Esq.	1	1	0
R. R. Butler, Esq.	1	1	0
L. W. Byrne, Esq.	1	1	0
Prof. H. Graham Cannon, SC.D.	1	1	0
J. N. Carruthers, Esq.	1	1	0
Dr. G. S. Carter (1930–1932)	3	3	0
Paymaster-Capt. R. Charles, R.N. (retd.)	1	1	0
Dr. J. Clark	1	1	0
Coastguard and Fisheries Service, Alexandria	1	1	0
Prof. F. J. Cole, D.SC., F.R.S.	1	1	0
J. S. Colman, Esq.	1	1	0
L. R. Crawshay, Esq.	1	1	0
Miss D. R. Crofts, D.SC. (1932 and 1933)	2	2	0
Norman Cuthbertson, Esq. (1932 and 1933)	2	2	0
Sir H. H. Dale, C.B.E., M.D., F.R.S. (1931 and 1932)	2	2	0
F. M. Davis, Esq.	1	1	0
Director of Agriculture and Fisheries, Travancore	1	1	0
F. A. Dixey, Esq., F.R.S.	1	1	0
C. C. Dobell, Esq., F.R.S.	1	1	0
Prof. J. C. Drummond (1931 and 1932)	2	2	0
Prof. L. Eastham	1	1	0
P. Eggleton, Esq., D.SC.	1	1	0
Major the Rt. Hon. W. E. Elliot, M.C., M.P.	1	1	0
C. E. D. Enoch, Esq. (1932 and 1933)	2	2	0
George Evans, Esq.	1	1	0
Prof. C. Lovatt Evans, F.R.S.	1	1	0
G. P. Farran, Esq.	1	1	0
Dr. Hussein Faouzi (1930–1932)	3	3	0
Fisheries Survey Committee, Capetown	1	1	0
E. Ford, Esq.	1	1	0
Dr. G. Herbert Fowler	1	1	0
Dr. E. L. Fox	1	1	0
Prof. H. Munro Fox	1	1	0
Miss E. A. Fraser, D.SC.	1	1	0
Prof. F. E. Fritsch, F.R.S.	1	1	0
Prof. J. Stanley Gardiner, F.R.S.	1	1	0
John S. Gayner, Esq. (1931 and 1932)	2	2	0
Ghardaqa Marine Laboratory	1	1	0
R. D'O. Good, Esq.	1	1	0
Carried forward	97	13	0

	£	s.	d.
Brought forward	97	13	0
Prof. E. S. Goodrich, D.SC., F.R.S.	1	1	0
Alastair Graham, Esq.	1	1	0
David H. Graham, Esq.		14	11
Michael Graham, Esq.	1	1	0
Ronald Grant, Esq.	1	1	0
Dr. A. M. H. Gray	1	1	0
Dr. H. P. Hacker	1	1	0
Wilfred Hall, Esq.	1	1	0
Ian I. Hamilton, Esq.	1	1	0
Prof. A. C. Hardy	1	1	0
Prof. C. R. Harington, F.R.S.	1	1	0
J. E. Harris, Esq.	1	1	0
T. J. Hart, Esq. (1933 and 1934)	2	2	0
H. W. Harvey, Esq.	1	1	0
Prof. L. A. Harvey	1	1	0
G. T. D. Henderson, Esq.	1	1	0
C. C. Hentschel, Esq.	1	1	0
Prof. S. J. Hickson, D.SC., F.R.S.	1	1	0
Prof. A. V. Hill, F.R.S.	1	1	0
Prof. J. P. Hill, F.R.S. (1931 and 1932)	2	2	0
W. T. Hillier, Esq., M.R.C.S.	1	1	0
Prof. K. Hirasaka	1	1	0
Dr. E. G. Holmes	1	1	0
C. E. P. Hopkins, Esq.	1	1	0
N. H. Howes, Esq.	1	1	0
P. Hoyte, Esq. (1931 and 1932)	2	2	0
Hull University College	1	1	0
O. D. Hunt, Esq.	1	1	0
Prof. J. S. Huxley	1	1	0
J. J. Judge, Esq.	1	1	0
Stanley Kemp, Esq., SC.D., F.R.S.	1	1	0
Mrs. A. Redman King	1	1	0
P. Kirtisinghe, Esq.	1	1	0
J. A. Kitching, Esq.	1	1	0
Dr. E. M. Kreps (1932 and 1933)	2	2	0
Dr. G. Lapage	1	1	0
Prof. R. D. Laurie (1931 and 1932)	2	2	0
A. G. Lowndes, Esq.	1	1	0
C. E. Lucas, Esq.	1	1	0
Carried forward	143	10	11

	£	s.	d.
Brought forward	143	10	11
Adrian Lumley, Esq.	1	1	0
Prof. E. W. MacBride, D.SC., F.R.S.	1	1	0
Prof. D. L. Mackinnon, D.SC.	1	1	0
G. I. Mann, Esq.	1	1	0
B. J. Marples, Esq.	1	1	0
D. J. Matthews, Esq.	1	1	0
Capt. W. N. McClean	1	1	0
Milford Haven Trawler Owners & Fish Salesmen's Association, Ltd.	1	1	0
W. S. Millard, Esq.	1	1	0
Sir P. Chalmers Mitchell, Kt., C.B.E., D.SC., F.R.S.	1	1	0
F. W. Moorhouse, Esq.	1	1	0
C. C. Morley, Esq.	1	1	0
Dr. J. Mukerji	1	1	0
National Institute of Turkish Fisheries (balance)		1	0
National Museum of Wales, Cardiff	1	1	0
Miss G. L. Naylor	1	1	0
Dr. A. G. Nicholls	1	1	0
J. A. Nicholson, Esq.	1	1	0
J. R. Norman, Esq.	1	1	0
Office Scientifique et Technique des Pêches Maritimes	1	1	0
Charles Oldham, Esq.	1	1	0
Prof. Yô Okada (1933 and 1934)	2	2	0
G. W. Olive, Esq.	1	1	0
R. Palmer, Esq.	1	1	0
The Hon. John H. Parker	1	1	0
C. W. Parsons, Esq.	1	1	0
Messrs. Pawlyn Bros.	1	1	0
T. A. Pawlyn, Esq.	1	1	0
Messrs. Peacock & Buchan Ltd.	1	1	0
Pease Laboratories Incorporated	1	1	0
F. T. K. Pentelow, Esq.	1	1	0
Prof. E. Percival	1	1	0
Plymouth Corporation (Museum Committee)	1	1	0
Plymouth Educational Authority	1	1	0
Plymouth Public Library	1	1	0
Plymouth Proprietary Library	1	1	0
Port of Plymouth Incorporated Chamber of Commerce	1	1	0
Portsmouth Municipal College	1	1	0
Carried forward	183	9	11

	£	*s.*	*d.*
Brought forward	183	9	11
W. Proctor, Esq.	1	1	0
W. P. Pycraft, Esq. (1930–1932)	3	3	0
Dr. A. Ramalho (1933 and 1934)	2	2	0
George Rayner, Esq.	1	1	0
H. C. Regnart, Esq.	1	1	0
D. M. Reid, Esq.	1	1	0
E. A. Robins, Esq.	1	1	0
E. S. Russell, Esq., D.SC.	1	1	0
F. S. Russell, Esq., D.S.C., D.F.C.	1	1	0
Capt. the Hon. Lionel St. Aubyn, M.V.O.	1	1	0
The Rt. Hon. Lord St. Levan, C.B., C.V.O.	1	1	0
J. T. Saunders, Esq.	1	1	0
R. E. Savage, Esq.	1	1	0
Dr. F. F. Schacht	1	1	0
Edgar Schuster, Esq., D.SC.	1	1	0
W. L. Sclater, Esq.	1	1	0
B. Sen, Esq.	1	1	0
Lt.-Col. R. B. Seymour Sewell, C.I.E., I.M.S. (1932 and 1933)	2	2	0
Miss Lilian Sheldon	1	1	0
Prof. W. Rae Sherriffs, D.SC.	1	1	0
N. Smedley, Esq.	1	1	0
J. E. Smith, Esq.	1	1	0
States Committee for Fisheries, Guernsey	1	1	0
A. C. Stephen, Esq.	1	1	0
Mrs. N. S. Steven	1	1	0
E. J. Stream, Esq.	1	1	0
Eric J. Tabor, Esq.	1	1	0
Harold E. Tabor, Esq.	1	1	0
J. M. Tabor, Esq.	1	1	0
Prof. W. M. Tattersall, D.SC.	1	1	0
Prof. G. I. Taylor, F.R.S.	1	1	0
Sir Charles Howell Thomas, K.C.B., C.M.G.	1	1	0
Harold Thompson, Esq., D.SC.	1	1	0
Sir Herbert F. Thompson, Bart.	1	1	0
Torquay Natural History Society	1	1	0
Philip Ullyott, Esq.	1	1	0
A. Walton, Esq.	1	1	0
Sir Nicholas E. Waterhouse, K.B.E.	1	1	0
Prof. D. M. S. Watson, F.R.S.	1	1	0
Carried forward	228	12	11

	£	s.	d.
Brought forward	228	12	11
Mrs. F. J. Weldon	1	1	0
Dr. K. B. Williamson	1	1	0
D. P. Wilson, Esq.	1	1	0
R. S. Wimpenny, Esq.	1	1	0
Ronald Winckworth, Esq., F.R.G.S.	1	1	0
V. C. Wynne Edwards, Esq.	1	1	0
Prof. C. M. Yonge, D.SC.	1	1	0
John Z. Young, Esq.	1	1	0
Total	£237	0	11

List of Donations to the General Fund

For the Year, 1st April, 1932, to 31st March, 1933.

	£	s.	d.
Dr. S. Hatta	1	10	0
News Chronicle	5	5	0
Mrs. C. H. Roberts	2	1	0
Total	£8	16	0

List of Donations towards the Building Extension Fund

Paid during the Year 1st April, 1932, to 31st March, 1933.

	£	s.	d.
Trustees of Rockefeller Foundation	1,991	6	3
Sundry Donation	2	0	1
Total	£1,993	6	4

List of Composition Fees

Paid during the Year, 1st April, 1932, to 31st March, 1933.

	£	s.	d.
Prof. Dr. H. Boschma	15	15	0
Miss M. L. Rothschild	15	15	0
Total	£31	10	0

Marine Biological Association of the United Kingdom.

LIST
OF
Governors, Founders, and Members.

AUGUST, 1933.

* Member of Council. † Vice-President. ‡ President.

Ann. signifies that the Member is liable to an Annual Subscription of One Guinea.

C. signifies that he has paid a Composition Fee of Fifteen Guineas in lieu of Annual Subscription.

I.—Governors.

The British Association for the Advancement of Science, *Burlington House, W.* 1	£1,090
The University of Oxford	£920
The University of Cambridge	£1,182 10*s.*
The Worshipful Company of Clothworkers, 41 *Mincing Lane, E.C.* 3	£625
The Worshipful Company of Fishmongers, *London Bridge, E.C.* 4	£22,755
The Zoological Society of London, *Regent's Park, N.W.* 8	£505
The Royal Society, *Burlington House, Piccadilly, W.* 1	£1,065
Bayly, Robert (the late)	£600
Bayly, John (the late)	£600
Thomasson, J. P. (the late)	£970
*G. P. Bidder, Esq., Sc.D., *Cavendish Corner, Cambridge*	£3,508
*E. T. Browne, Esq., B.A., *Anglefield, Berkhamsted*	£2,045
‡*The Lord Moyne, P.C., D.S.O., 10 *Grosvenor Place, London, S.W.* 1	£1,000

II.—Founders.

1884	The Corporation of the City of London	£210
1884	The Worshipful Company of Mercers, *Mercers' Hall, Cheapside, E.C.* 2	£341 5*s.*
1884	The Worshipful Company of Goldsmiths, *Goldsmiths' Hall, E.C.*	£100
1884	The Royal Microscopical Society, *B.M.A. House, Tavistock Square, W.C.* 1	£152 10*s.*
1884	Bulteel, Thos. (the late)	£100
1884	Burdett-Coutts, W. L. A. Bartlett (the late)	£100
1884	Crisp, Sir Frank, Bart. (the late)	£100
1884	Daubeny, Captain Giles A. (the late)	£100
1884	Eddy, J. Ray (the late)	£100
1884	Gassiott, John P. (the late)	£100
1884	Lankester, Sir E. Ray, K.C.B., F.R.S. (the late)	£101
1884	The Rt. Hon. Lord Masham (the late)	£100
1884	Moseley, Prof. H. N., F.R.S. (the late)	£100
1884	The Rt. Hon. Lord Avebury, F.R.S. (the late)	£100
1884	Poulton, Prof. Edward B., M.A., F.R.S., *Wykeham House, Oxford*	£110
1884	Romanes, G. J., LL.D., F.R.S. (the late)	£100
1884	Worthington, James (the late)	£100
1885	Derby, the late Earl of	£100
1887	Weldon, Prof. W. F. R., F.R.S. (the late)	£100
1888	Bury, Henry, M.A., *The Gate House,* 17 *Alumdale Road, Bournemouth West*	£100
1888	The Worshipful Company of Drapers, *Drapers' Hall, E.C.* 2	£315
1889	The Worshipful Company of Grocers, *Poultry, E.C.* 2	£120
1889	Thompson, Sir Henry, Bart. (the late)	£110
1889	Revelstoke, The late Lord	£100
1890	Riches, T. H., B.A., *Kitwells, Shenley, Herts.*	£430
1892	Browne, Mrs. E. T., *Anglefield, Berkhamsted, Herts*	£100
*1902	Gurney, Robert, D.Sc., *Bayworth Corner, Boars Hill, Oxford*	£109 1*s.*
1904	Shaw, J., K.C., *Adderbury House, Banbury, Oxfordshire*	£113
1909	Harding, Colonel W. (the late)	£115 15*s.*
1910	Murray, Sir John, K.C.B., F.R.S. (the late)	£100
1912	Swithinbank, H., F.R.S.E., F.R.G.S. (the late)	£100
1913	Shearer, Dr. Cresswell, F.R.S., *Anatomy School, Cambridge*	£100
1913	Heron-Allen, E., F.R.S., F.L.S., F.R.M.S., F.G.S., *Large Acres, Selsey Bill, Sussex*	£125 15*s.*
†*1918	Evans, George, 1 *Wood St., London, E.C.* 2	£103
1920	McClean, Capt. W. N., 1 *Onslow Gardens, S.W.* 7	£100
1920	Buckland of Bwlch, The Right Hon. Lord (the late)	£105
1920	Llewellyn, Sir D. R., *The Court, St. Fagan's, Glamorgan*	£105
1921	Harmer, F. W. (the late)	£100

1898 Worth, R. H., 42 *George Street, Plymouth* .... £120 15*s.*
1924 The MacFisheries, Ltd., 125 *Lower Thames Street, E.C.* 3......... £100
1924 Murray, Lady £100
1925 The Institution of Civil Engineers, *Great George Street, Westminster, S.W.* 1 .... £100
1927 Bidder, Miss Anna, *Cavendish Corner, Cambridge* £105
†1899 Iveagh, The Rt. Hon. the Earl of, 11 *St. James's Square, S.W.* 1 £145 15*s.*

III.—Members.

1900 Aders, Dr. W. M., O.B.E. .... £5 and Ann.
1928 Aikawa, Hiroaki, *Imperial Fisheries Experimental Station, Fugakawa, Tokyo, Japan* .... Ann.
*1895 Allen, E. J., D.Sc., LL.D., F.R.S., *The Laboratory, Citadel Hill, Plymouth* .... £25 10*s.* and Ann.
1925 Amemiya, Dr. Ikusaku, *University of Tokyo* (*Agriculture and Fisheries Department*), *Tokyo, Japan* .... Ann.
1927 Amirthalingam, C., Ph.D., *Indian Museum, Calcutta, India* £1 1*s.* and Ann.
1932 Aquario Vasco da Gama (Director, Dr. A. Ramalho), *Dafundo, Lisbon, Portugal*.. Ann.
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*1928 Barcroft, Prof. J., F.R.S., *Glenveagh, Grange Road, Cambridge* £2 and Ann.
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1930 Barrett, W. H., *Brickfields, Harrow, Middlesex* .... Ann.
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1929 Bayliss, L. E., Ph.D., *The Laboratory, Citadel Hill, Plymouth* £13 3s. and *C.*
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1928 Beer, G. R. de, 6 *High Street, New Headington, Oxford* .... Ann.
1926 Bělehrádek, J., M.D., *Docent of General Biology, Masaryk University (Medical Faculty), Brno, Czechoslovakia*.................. Ann.
1925 Berrill, N. J., D.Sc., *McGill University, Montreal, Canada* ...... Ann.
1903 Bidder, Colonel H. F., *Ravensbury Manor, Mitcham, Surrey*...... Ann.
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1931 Birtwistle, W., o/c. *Fisheries Department, P.O. Box* 744, *Singapore* .... Ann.
1930 Blaschko, Dr. H., *Kaiser Wilhelm Institut, Heidelberg, Germany* Ann.
1910 Bloomer, H. H., "*Longdown,*" *Sunnydale Road, Swanage, Dorset* .... Ann.
1921 Blundell, H. S. Moss, *Ministry of Agriculture and Fisheries,* 43 *Parliament Street, London, S.W.* 1 .... Ann.
1922 Blundell, Mrs. H. Moss, *Callipers Hall, Chipperfield, King's Langley, Herts*.......... Ann.
1930 Bogorov, Dr. B. G., *State Oceanographical Institute, Herzen str.* 6, *Moscow, U.S.S.R.* .... Ann.
1932 Bolitho, Capt. R. J. B., *Ponsandane, Penzance* .... Ann.
†1910 Borley, J. O., O.B.E., M.A., 5 *Queen Anne's Chambers, Dean Farrar Street, S.W.* 1.......... £1 1*s.* and Ann.
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1923 Boulenger, E. G., *Zoological Society, Regent's Park, London, N.W.* 8.......... Ann.
1898 Bowles, Col. Sir Henry, Bart., *Forty Hall, Enfield, Middlesex* £8 4*s.* 8d. and Ann.
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1902 Brighton Public Library (Henry D. Roberts, Chief Librarian)... Ann.
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1931 Cattell, Dr. McKeen, *Cornell University Medical College,* 477 *First Avenue, New York City, U.S.A.* .... *C.*
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1924 Clark, R. S., D.Sc., *Marine Laboratory, Wood Street, Torry, Aberdeen* ....£2 2s. and Ann.
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1886 Coates and Co., *Southside Street, Plymouth*.............. £5 5*s.* and *C.*
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1933 Cole, H. A., *Fisheries Experiment Station, Castle Bank, Conway* Ann.
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1930	Cuthbertson, N., 3 *Blenheim Road, Plymouth*	Ann.

1922	Dale, Sir Henry H., C.B.E., M.D., F.R.S., *National Institute for Medical Research, Hampstead, London, N.W.* 3	Ann.
1919	Damant, Captain G. C. C., R.N., C.B.E., *Thursford, Cambridge Road, East Cowes, Isle of Wight*	£6 1s. and *C.*
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1931	Dawes, B., D.Sc., *Dept. of Zoology, King's College, Strand, London, W.C.* 2	Ann.
1915	Dick, G. W., J.P., c/o P.O. Box 28, *The Point, Durban, Natal, South Africa*	*C.*
1915	Director of Agriculture and Fisheries, *Travancore, Quilon, S. India*	Ann.
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1910	Duncan, F. Martin, 19 *Staverton Road, Brondesbury Park, London, N.W.* 2	Ann.

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1927	Eggleton, P., D.Sc., 36 *Gillespie Crescent, Edinburgh*	£1 and Ann.
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1929 Faouzi, Dr. Hussein, *Fisheries Research Laboratory, Kayed Bay, Alexandria, Egypt* .... Ann.
1933 Fellowes, Miss R., *The Cloisters, Windsor Castle, Berks.* ...... Ann.
*1928 Fisher, Prof. R. A., Sc.D., F.R.S., *Galton Laboratory, University College, London* .... Ann.
1929 Fisheries Survey Committee, *Capetown, S. Africa* .... Ann.
1929 Foot, Dr. Ernest, 50 *Norman Avenue, Stoke, Plymouth, Devon*... Ann.
1928 Ford, E., *The Laboratory, Citadel Hill, Plymouth, Devon* £2 2*s.* and Ann.
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1920 Fox, Dr. E. L., 9 *Osborne Place, Plymouth*.......................... Ann.
*1912 Fox, Prof. H. M., *Zoological Department, The University, Edgbaston, Birmingham* .... £1 1*s.* and Ann.
1924 Fraser, Miss E. A., D.Sc., *Dept. of Zoology, University College, Gower Street, W.C.* 1 .... £3 3*s.* and Ann.
*1930 Fritsch, Prof. F. E., F.R.S., *Botanical Laboratory, East London College, London, E.C.* 1 .... Ann.
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1932 Ghardaqa Marine Laboratory of the Egyptian University, *Ghardaqa, Egypt* .... Ann.
1925 Gibbons, S. G., *Elora, Milltimber, Aberdeen* .... Ann.
*1910 Goodrich, Prof. E. S., D.Sc., F.R.S., 6 *Park Town, Oxford* £12 and Ann.
1926 Graham, A. P., "*Inglenook*," 43 *Oakfield Road, Newport, Mon.* 10*s.* and Ann.
1931 Graham, Alastair, *Zoology Dept., Birkbeck College, London, E.C.* 4 Ann.
1933 Graham, David H., 718 *King St., Otago, New Zealand* .... Ann.
*1931 Graham, Michael, *Fisheries Laboratory, Lowestoft, Suffolk* ...... Ann.
1930 Grant, R., 19 *South Hill Rd., Hemel Hempsted, Herts* .... Ann.
1930 Gray, Dr. A. M. H., 69 *Harley St., London, W.* 1 .... Ann.
*1912 Gray, J., M.C., Sc.D., F.R.S., *King's College, Cambridge* £15 5*s.* and Ann.
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*1929 Harington, Prof. C. R., F.R.S., *Greenfield, Bexmoor, Herts* ...... Ann.
*1885 Harmer, Sir Sidney F., K.B.E., D.Sc., F.R.S., *The Old Manor House, Melbourn, near Royston, Herts* .... £39 11*s.* and *C.*
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1924 Harvey, H. W., *The Laboratory, Citadel Hill, Plymouth* £5 5*s.* and Ann.
1933 Harvey, Prof. L. A., *Dept. of Zoology, University College of S.W., Exeter* .... Ann
1931 Henderson, G. T. D., D.Sc., *Dept. of Oceanography, University College, Hull* .... Ann.
1925 Hentschel, C. C., 10 *Newcastle House, Northumberland St., London, W.* 1 .... £1 1*s.* and Ann.
1926 Hickling, C. F., *Fisheries Laboratory, Lowestoft, Suffolk* £4 4*s.* and Ann.
1884 Hickson, Prof. Sydney J., M.A., D.Sc., F.R.S., 26 *Barton Road, Cambridge* .... Ann.
1926 Hill, Prof. A. V., F.R.S., *Physiological Laboratory, University College, Gower Street, London, W.C.* 1 .... £5 and Ann.
1919 Hillier, W. T., M.R.C.S., 23 *Francis Road, Edgbaston, Birmingham* .... £1 1*s.* and Ann.
1921 Hindle, Prof. E., Sc.D., 32 *Belsize Av., Hampstead, London, N.W.* 3 .... £1 1*s.* and *C.*
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1932 Hopkins, C. E. P., 41 *Gladstone Place, Aberdeen* .... Ann.
1933 Horne, F. R., *Seale-Hayne Agricultural College, Newton Abbot, Devon* .... Ann.

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1918 Hoyte, P., "*Nutley,*" *Elburton Cross, S.O., Devon*.................. Ann.
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1897 Lanchester, W. F., B.A.. *C.*
1928 Lapage, Dr. G., *School of Agriculture, Cambridge* .... Ann.
1928 Laurie, Prof. R. D., M.A., *Department of Zoology, University College of S. Wales, Aberystwyth* .... Ann.
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1931 Lucas, C. E., *Dept. of Oceanography, University College, Hull*... Ann.
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*1910 MacBride, Prof. E. W., M.A., D.Sc., F.R.S., *Imperial College of Science, South Kensington, S.W.* 7 ....£5 and Ann.
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1885 Marr, Prof. J. E., M.A., F.R.S., *St. John's College, Cambridge*...... *C.*
1933 Marsden, Sir John D., Bart., J.P., *The British Trawlers' Federation Ltd., Grimsby* .... Ann.
1910 Matthews, D. J., *Hydrographic Department, Admiralty, London, S.W.* 1 .... Ann.
*1912 Maurice, H. G., C.B., *Ministry of Agriculture and Fisheries,* 43 *Parliament Street, S.W.* 1 .... £1 1*s.* and Ann.
1910 McClean, Capt. W. N., 1 *Onslow Gardens, S.W.* 7........ Ann.
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1931 Menon, A. P. .... Ann.
1923 Milford Haven Trawler Owners' Association, Ltd. .... Ann.
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1930 Moorhouse, F. W., *The University, Brisbane, Queensland*........ Ann.
1915 Morley, C. C., *Trelawne, Duloe, R.S.O., Cornwall*........ Ann.
1931 Mount Desert Island Biological Laboratory, *Salisbury Cove, Maine, U.S.A.* .... Ann.
1929 Mukerjii, Dr. J., *Zoological Laboratory, University College of Science,* 35 *Ballygunge Circular Road, Calcutta* .... Ann.
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1884 Napier, Mrs., *Upton House, Sandwich, Kent* .... £20 and *C.*
1930 National Institute of Turkish Fisheries, Balta Liman, Rumeli Hissan, Istanbul, *Turkey* .... Ann.
1924 National Museum of Wales, *Cardiff*........ Ann.
1928 Naylor, Miss G. L., 261 *Trinity Road, London, S.W.* 8........ Ann.
1928 Neill, R. G., 434 *Liverpool Road, Birkdale, Southport*........ Ann.
1921 Newth, H. G., *The University, Edgbaston, Birmingham* .... Ann.
1930 Nicholls, A. G., Ph.D., *Marine Station, Keppel Pier, Millport, Buteshire* .... £1 1*s.* and Ann.
1931 Nicholson, J. A., 1 *Engadine Villas, Saltash, Cornwall*........ Ann.
1929 Nicol, Miss E. A. T., Ph.D., *Dept. of Zoology, The University, West Mains Road, Edinburgh* .... £3 3*s.* and *C.*
*1928 Norman, J. R., *Natural History Museum, Cromwell Road, S.W.* 7 Ann.

1931 Office Scientifique & Technique des Pêches Maritimes, *Laboratoire de Lorient, Port de Lorient-Keroman, France*........ Ann.

1933 Okada, Prof. Yaichiro, *Zoological Institute, Normal College, Koishikawa, Tokyo, Japan* .... Ann.
1911 Oldham, Chas., *The Bollin, Berkhamsted, Herts*............ £5 and Ann.
1930 Olive, G. W., *Dauntsey's School, West Lavington, near Devizes, Wilts*.. Ann.
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1928 Otter, G. W., *Selehurst, Horsham, Sussex*... .... £5 and *C*.

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1924 Pantin, W. A., *Dept. of History, Oriel College, Oxford*......... £10 10*s*.
1927 Parker, The Hon. John H., *Saltram, Plympton, Devon* .... Ann.
1928 Parsons, C. W., *Zoology Department, The University, Glasgow* £1 1*s*. and Ann.
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1925 Pawlyn, T. A., *Mevagissey, Cornwall*..................... £1 1*s*. and Ann.
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1931 Pease Laboratories Inc., 39–41 *West 38th Street, New York City* Ann.
1925 Pentelow, F. T. K., *Ministry of Agriculture & Fisheries*, 43 *Parliament Street, London, S.W.* 1.................. 10*s*. 6*d*. and Ann.
1929 Percival, Prof. E., *Canterbury College, Christchurch, New Zealand* Ann.
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1924 Plender, Sir William, Bart., G.B.E., 51 *Kensington Court, W.* 8 £10 10*s*.
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1928 Proctor, W., *Bar Harbor, Maine, U.S.A*.............................. Ann.

1932 Quick, Dr. H. E., M.B., B.S., B.Sc., F.R.C.S., 130 *Eaton Crescent, Swansea* .... Ann.

1932 Ramalho, Dr. A., *Aquario Vasco da Gama, Dàfundo, Lisbon, Portugal* .... Ann.

1928 Ray, H. N., *Zoological Department*, 35 *Ballygunge Circular Road, Calcutta, India* ....£1 1s. and Ann.
1933 Rayner, G. W., c/o "Discovery" Committee, 52 *Queen Anne's Chambers, Dean Farrar Street, London, S.W.* 1 .... Ann.
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1922 Robson, G. C., *British Museum* (*Natural History*), *S. Kensington, S.W.* 7 .... Ann.
1932 Rothschild, Miss M. L., 4 *Palace Green, London, W.* 8 .... *C*.
1931 Rothschild, Victor, 4 *Palace Green, London, W.* 8 .... Ann.
1928 Roughley, T. C., *Technological Museum, Sydney, N.S.W*.......... Ann.
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1930 Storrow, B., *Dove Marine Laboratory, Cullercoats.*

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