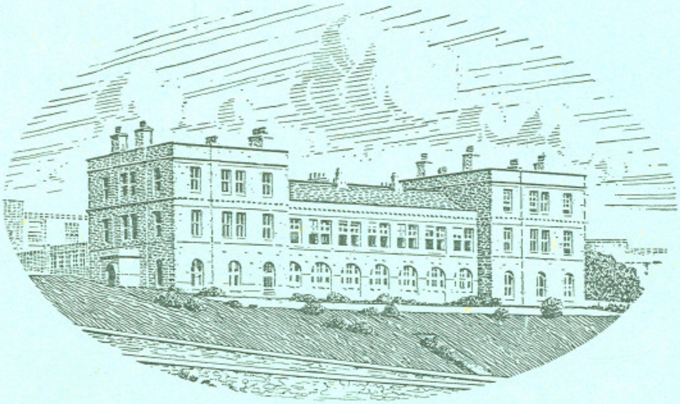
JOURNAL OF THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM



THE PLYMOUTH LABORATORY

VOLUME XXVIII, No. 1

(issued June 1949)

CAMBRIDGE
AT THE UNIVERSITY PRESS
1949

Price Thirty Shillings net

MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM

PATRON

HIS MAJESTY THE KING

OFFICERS AND COUNCIL

President

Prof. J. Gray, C.B.E., M.C., Sc.D., LL.D., F.R.S.

Vice-Presidents

The Earl of Iveagh, C.B., C.M.G.
Viscount Astor
Sir Nicholas E. Waterhouse, K.B.E.
Sir Sidney F. Harmer, K.B.E., Sc.D., F.R.S.
Col. Sir Edward T. Peel, K.B.E., D.S.O., M.C.
The Right Hon. Tom Williams, M.P.
G. P. Bidder, Sc.D.
W. T. Calman, C.B., D.Sc., F.R.S.
Vice-Admiral Sir John A. Edgell, K.B.E., C.B., F.R.S.
Prof. A. V. Hill, C.H., O.B.E., Sc.D., F.R.S.
H. G. Maurice, C.B.
E. S. Russell, O.B.E., D.Sc.
Sir Edward J. Salisbury, Kt., C.B.E., D.Sc., Sec.R.S.
Admiral Sir Aubrey C. H. Smith, K.B.E., C.B., M.V.O.

COUNCIL

Elected Members

Anna M. Bidder, Ph.D.
Prof. J. Rogers Brambell, D.Sc., F.R.S.
J. N. Carruthers, D.Sc.
G. E. R. Deacon, D.Sc., F.R.S.
H. Cary Gilson
Prof. J. E. Harris, Ph.D.
C. F. Hickling, Sc.D.
Edward Hindle, Sc.D., F.R.S.
O. D. Hunt
N. A. Mackintosh, D.Sc.
Morley H. Neale
Prof. Lily Newton, Ph.D.
J. E. Smith, Ph.D.
R. S. Wimpenny
Prof. J. Z. Young, F.R.S.

Governors

G. P. Bidder, Sc.D.
P. D. H. Dunn, C.M.G., O.B.E. (Ministry of Agriculture and Fisheries)
The Worshipful Company of Fishmongers:
  The Prime Warden
  Major E. G. Christie-Miller
  Alfred R. Wagg
Prof. A. C. Hardy, D.Sc., F.R.S. (Oxford University)
C. F. A. Pantin, Sc.D., F.R.S. (Cambridge University)
Prof. H. Gordon Jackson, D.Sc. (British Association)
H. G. Maurice, C.B. (Zoological Society)
Prof. A. V. Hill, C.H., O.B.E., Sc.D., F.R.S. (Royal Society)

Hon. Treasurer: Major E. G. Christie-Miller, 38 Hyde Park Street, London, W.2

Secretary: F. S. Russell, D.S.C., D.F.C., F.R.S.

SCIENTIFIC STAFF

Director: F. S. Russell, D.S.C., D.F.C., B.A., F.R.S.

Head of Department of General Physiology:
W. R. G. Atkins, O.B.E., Sc.D., F.R.I.C., F.Inst.P., F.R.S.

H. W. Harvey, Sc.D., M.A., F.R.S. (*Hydrologist*)
G. A. Steven, B.Sc., F.R.S.E. (*Zoologist*)
D. P. Wilson, D.Sc., F.R.P.S. (*Zoologist*)
L. H. N. Cooper, D.Sc., F.R.I.C. (*Chemist*)
G. M. Spooner, M.B.E., M.A. (*Zoologist*)
Mary W. Parke, B.Sc., Ph.D. (*Botanist*)
D. K. Hill, M.A. (*Physiologist*)
P. G. Corbin, B.A. (*Zoologist*)
H. G. Vevers, M.B.E., M.A., F.Z.S. (*Bursar and Zoologist*)
N. A. Holme, B.A. (*Zoologist*)

FURTHER OBSERVATIONS ON FISH GROWTH IN A FERTILIZED SEA LOCH (LOCH CRAIGLIN)

By F. Gross, D.Sc.
Department of Zoology, University of Edinburgh

(Plate I and Text-fig. 1)

In a previous paper (Gross, 1947) an account was given of studies on fish growth in Loch Craiglin under conditions of fertilizer application in 1942/43. From 1944 onwards Drs Marshall and Orr continued to apply fertilizers of different kinds and in varying quantities, and investigated the subsequent growth of phytoplankton (Marshall & Orr, 1948). The sampling of the bottom fauna and of the fish population was much reduced owing to our preoccupation with an experiment carried out in the open Kyle Scotnish (Gross, Raymont, Nutman & Gauld, 1946). However, analysis of the data obtained has established a few interesting points, briefly described here.

GROWTH OF FLOUNDERS FROM 1944 TO 1947

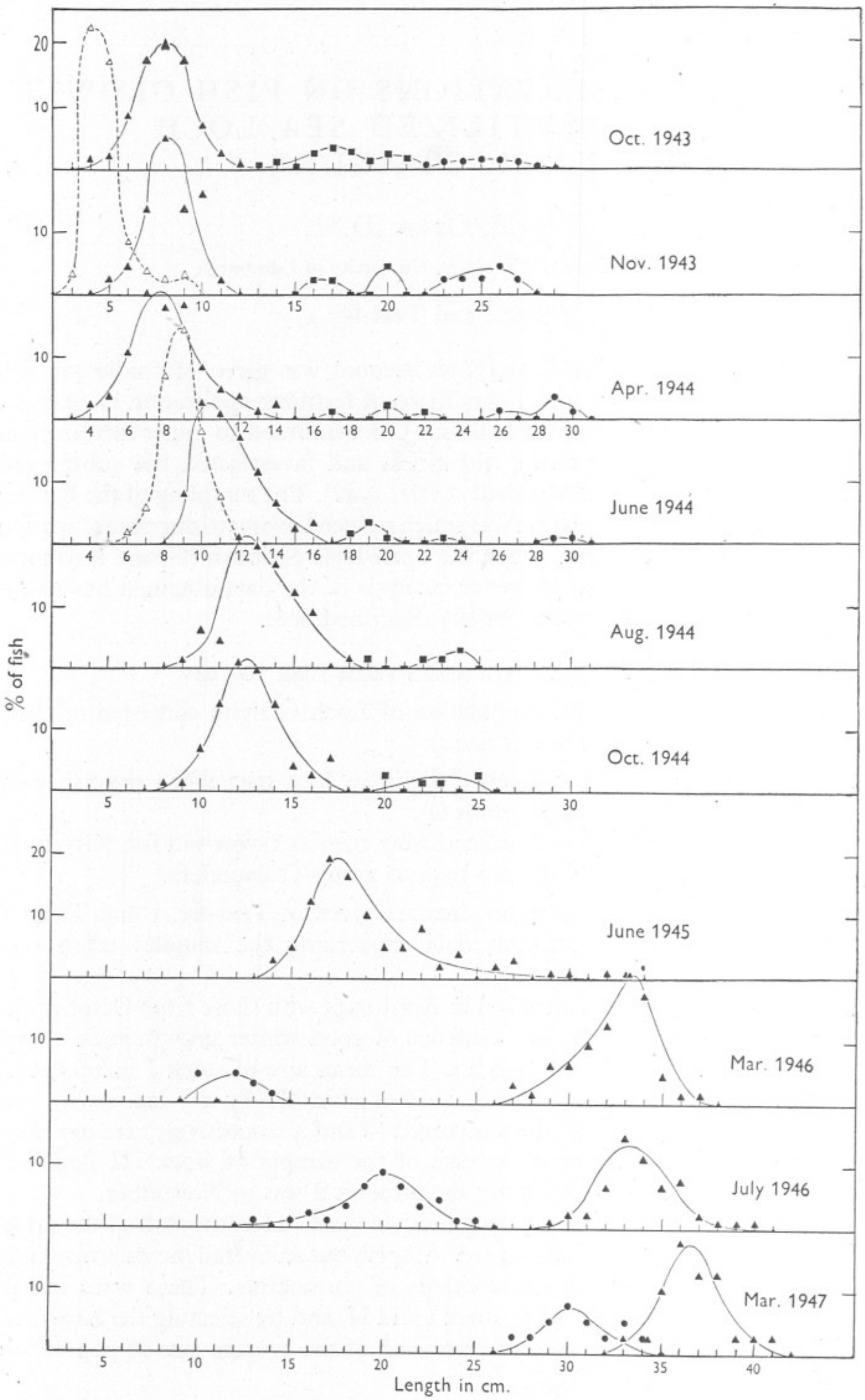
At the end of 1943 the fish population of Loch Craiglin consisted of three stocks of flounders (*Pleuronectes flesus*):

Stock I, transferred to Loch Craiglin in July 1942 when the fish were a few months old (age-group O).
Stock II, transferred in April and May 1943 as 1-year-old fish (Group I).
Stock III, transferred in July 1943 as group-O flounders.

Their size distibutions and mean sizes are given in Text-fig. 1 and Table I, which also contain the relevant data concerning the samples taken subsequently.

Comparison of the fish obtained in April 1944 with those from October and November 1943 gives no clear evidence of good winter growth such as was observed during the winter 1942/43. The mean size of stock I increased by 3·3 cm. (13%), and 65 g. (35%), that of stock II by 1·5 cm. (9%), and 19.5 g. (28%), but the numbers involved (6 and 4 respectively) are too small to be of significance. The mean size of the sample of stock III flounders (75 specimens) was almost exactly the same as it was in November.

There is an indication of winter growth of stock III in the shift of the upper limit of range of size to 13 and 14 cm. in April, but an overall increase may have been counteracted by the depredations of cormorants. These were mainly responsible for the reduction of stock I and II, and by selecting the larger fish of stock III may have caused a depression of the average size of population.



Text-fig. 1. The growth of flounders in Loch Craiglin (*full lines*) and in the estuary of the River Add (*broken lines* and *open triangles*). *Black triangles* refer to stock III, *squares* to stock II, *circles* to stock I in 1943/4 and to the native stock in 1946/7.

TABLE I. MEAN SIZE AND CONDITION FACTOR OF FLOUNDERS FROM LOCH CRAIGLIN

	Stock III					Stock II					Stock I				
Date of capture	No.	Age group	Length (cm.)	Weight (g.)	*K*	No.	Age group	Length (cm.)	Weight (g.)	*K*	No.	Age group	Length (cm.)	Weight (g.)	*K*
1943:															
Oct.	215	O	7·9	6·8	1·38	45	I	17·5	66·0	1·23	20	I	25·0	197·3	1·26
Nov./Dec.	34	O	8·2	7·3	1·33	4	I	18·2	68·7	1·14	6	I	25·4	184·5	1·13
1944:															
Apr.	75	I	8·2	7·5	1·36	4	II	19·7	88·2	1·15	6	II	28·8	259·0	1·08
June	114	I	11·6	16·9	1·08	8	II	19·3	72·5	1·01	2	II	29·2	268·5	1·08
Aug.	61	I	13·0	23·0	1·05	4	II	22·5	114·2	1·00					
Oct.	65	I	12·7	23·6	1·15	6	II	22·4	122·7	1·16					
1945:															
June	98	II	19·2	93·3	1·31										
						'Native stock'									
1946:															
Mar.	54	II	32·3	408·6	1·21	9	O	11·8	20·0	1·22					
July	52	III	34·0	463·0	1·18	37	I	20·0	96·1	1·20					
1947:															
Mar./Apr.	26	III/IV	36·8	580·0	1·16	13	I/II	30·6	353·0	1·23					

The symmetry of the curve relating to the size distribution of the 114 stock III flounders caught in June is even more distorted by the reduction in numbers of the size classes 11–16 cm. than the corresponding curve for the recaptures in April. In contrast to this, the sample of 52 flounders of the same age, caught during the same month in the estuary of the River Add, shows a very symmetrical size distribution around the mean of 8·8 cm., 7·8 g. Therefore the median (12·5 cm.) might be a more accurate estimate of the growth attained by stock III.

Even so, the size of stock III flounders was much smaller than that of stock I at the same age in June 1943 (18·2 cm., 76 g.). The reduction of growth rate was almost certainly due to the deterioration of hydrographic conditions caused by prolonged closure of the dam. The position was aggravated by the distribution on 1 August 1944 of ten times the usual quantity of fertilizers (1344 lb. sodium nitrate and 448 lb. superphosphate), most of which was taken up by, and converted into, sea weed and *Zostera*. The lack of circulation, the consequent drastic reduction in oxygen content and the development of high concentrations of H_2S in the deep water and of very high pH values near the surface, recorded by Marshall & Orr (1948), caused conditions unfavourable for the growth of fish. This continued to be very poor throughout 1944. The growth increment of stock III from June to August was negligible, while from August to October 1944 growth seems to have ceased altogether. The mean value for length was, in fact, a little less in October than in August (Text-fig. 1 and Table I).

Stock I and II specimens became very scarce in 1944. From the few fish (Stock II) obtained it would appear that no growth had taken place from April to June, a slight increase from June to August, and again practically no growth from August to October. The growth increment for the whole year, October 1943 to October 1944, amounted to 4·8 cm., 17 g., in stock III, and to 4·2 cm., 54 g., in stock II, and was thus of the same order as that recorded for flounders in natural waters.

During the following autumn and winter (1944/45) the sluice gate of the dam was opened to allow interchange of the water with the main loch outside. This led to an improvement in hydrographic conditions and to a striking improvement in fish growth.

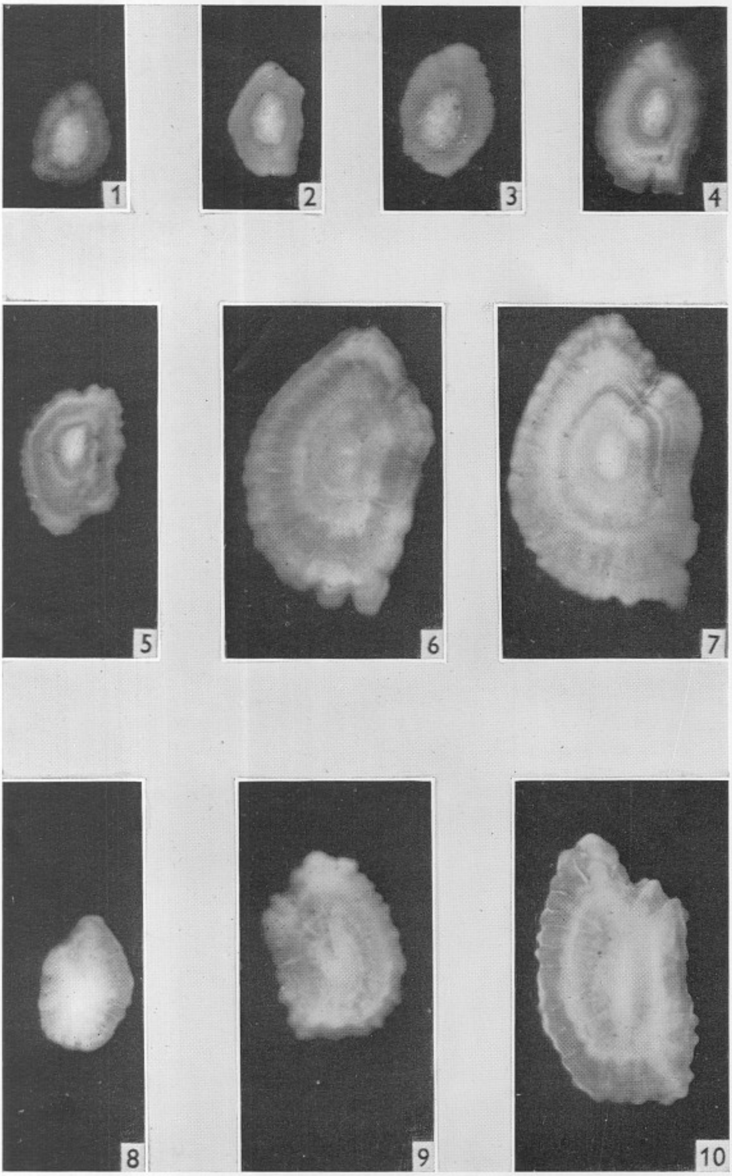
In June 1945 a sample of 99 flounders was obtained (Fig. 1, Table I). Examination of their otoliths, all of which were removed after the fish had been measured and weighed, showed that with the possible exception of one fish (27·4 cm.) all belonged to stock III. Their distribution curve is very asymmetrical. Comparison with the previous curves shows that the growth increment of stock III was greater during the period October 1944 to June 1945 than during the whole of 1944.

The next sample (63 flounders) was caught in March 1946. Of these 54 were 3-year-old stock III specimens. The mode of their size distribution was 33 cm., i.e. 16 cm. greater than in June 1945, a marked improvement over the normal annual growth increment of 4–7 cm. in unfertilized waters. Their growth slowed down again after March 1946. By July of that year they had added very little to their size, and by March/April 1947, at an age of 4 years, their modal class reached 36 cm.

The sample of March 1946 contained 9 group-O flounders of a mean size of 11·8 cm., 20 g. They were obviously 'native' fish which most likely had developed from eggs spawned in Loch Craiglin in 1945. Another sample of 37 of the same native stock, caught the following July, had a mean size of 20·0 cm., 96 g.; and 13 specimens, netted in March/April 1947, had attained an average of 30·6 cm., 353 g., a remarkable growth for 2-year-old flounders.

GROWTH OF OTOLITHS

Examination of the otoliths showed that both the poor growth of the flounders in 1944 and the excellent growth in 1945/46 was clearly recorded by the width of the otolith rings. In 1944, stock III specimens laid on narrow bands similar to fish caught in areas outside Loch Sween (Pl. I, figs. 1–4; see also Gross, 1947), while the bands formed in 1945 were broad and strongly plicated (Pl. I, figs. 6, 7). The extremely wide range of size of stock III flounders caught in June 1945 is illustrated by figs. 5 and 6 (Pl. I) which show otoliths of a small (14·5 cm., 43 g.) and a very large specimen (33·0 cm., 408 g.), both belonging to group II. The very rapid growth of the 'native' flounders in 1946 and 1947, illustrated by three otoliths (Pl. I, figs. 8–10), represents a marked contrast to that of stock III in 1944 (Pl. I, figs. 1–4).



Otoliths of flounders from Loch Craiglin. Magnification of all figures × 5·5.

Fig. 1. Group O; caught on 16. x. 43; size 10·1 cm., 11 g.
Fig. 2. Group I; caught on 10. iv. 44; size 10·8 cm., 14 g.
Fig. 3. Group I; caught on 8. iv. 44; size 13·5 cm., 28 g.
Fig. 4. Group I; caught on 11. x. 44; size 17·1 cm., 59 g.
Fig. 5. Group II; caught on 5. vi. 45; size 14·5 cm., 43 g.
Fig. 6. Group II; caught on 4. vi. 45; size 33·0 cm., 408 g.
Fig. 7. Group II; caught on 15. iii. 46; size 32·2 cm., 354 g.
Fig. 8. Group O; caught on 20. iii. 46; size 12·9 cm., 27 g.
Fig. 9. Group I; caught on 8. vii. 46; size 23·4 cm., 145 g.
Fig. 10. Group I; caught on 28. iii. 47; size 32·9 cm., 457 g.

CONDITION FACTOR

Comparison of the relation between length and weight of the flounders, expressed by the condition factor (Table I, *K*; see also Gross, 1947) reflects the unfavourable conditions for fish growth in 1944, especially during the summer. Condition factors were as low as 1·05 and 1·08 in June and August, rising to 1·15 in October. The condition factor of stocks I and II was very low throughout 1944. In 1945 rapid growth was accompanied by a high condition factor (1·31 in June 1945). It dropped to 1·21 in March 1946, to 1·18 in July 1946, and to 1·16 in March/April 1947. This last, relatively low value may have been correlated with the circumstance that the fish were ripe and may have begun spawning before they were caught. The native stock possessed a fairly high condition factor (1·2–1·23) in all three samples caught.

SEXUAL MATURITY OF THE FLOUNDERS

Of the 52 3-year-old stock III flounders obtained in March 1946 all but 3 females were fully mature: all males and some females were 'running ripe', and while the rest possessed fully developed ovaries the eggs did not run out freely when the animals were stripped. The 4-year-old stock III flounders caught in March/April 1947 (11 females and 15 males) were all mature, 3 of the females spent. Of the 13 'native' fish, just 2 years old, 12 were males, and 11 of these were fully mature, 1 immature, and 1 was an immature female. Thus the onset of maturity occurred in males at the age of 2 years, in females at the age of 3.

DISCUSSION

The observations recorded above represent a postscript to those described and discussed in a previous paper (Gross, 1947) which must be taken into consideration in assessing the growth rate of flounders in manured water as compared with that in natural conditions. The new data are instructive from the point of view of judging the effects of different factors on the growth of flounders. It has been recorded (Marshall, 1947) that a very heavy growth of phytoplankton took place in Loch Craiglin in the spring of 1944, but this did not lead to an improvement in fish growth. The distribution of ten times the usual quantity of fertilizers in August 1944 brought about a disproportionately small increase of phytoplankton crop and marked the beginning of a period of complete cessation of fish growth. There is every reason to believe that fish growth did not slow down and finally stop owing to shortage of food, but because of extremely bad hydrographic conditions consequent upon the prolonged closure of the dam. The growth increment of stock III flounders for the year October 1943 to October 1944 amounted to merely 4·8 cm., 16·8 g., which is approximately the annual growth increment of flounders in natural waters.

In 1945, after several months of interchange of water through the open sluice, the chemical and physical conditions in the loch improved, and during the period October 1944 to March 1946 the flounders increased by 19·6 cm. (155%) in length and by 385 g. (1660%) in weight, a very marked improvement on any records of marine fish growth in natural waters. Fertilizers were applied only on four occasions during that year, all during the period February-April 1945, 23 lb. N and 3·4 lb. P being added each time. During 1946, fertilizers were applied on two occasions only (superphosphate along with ammonium chloride on one occasion and urea on the other); these had little effect on phytoplankton density (Marshall & Orr, 1948). During the same year the growth of stock III flounders slowed down considerably. The growth increment from March 1946 to March 1947 amounted to only 4·5 cm., 171 g. On the other hand, the 'native' stock increased during the same period by 18·8 cm., 333 g., to 30·6 cm., 353 g., at an age of 2 years. They were thus about 5 cm. longer, and 150 g. heavier than stock I flounders at the same age. The slower growth of stock III specimens during 1946 may have been due to their sexual maturation and subsequent spawning, and perhaps also to the predominance of *Hydrobia*, not taken readily by flounders, and the relative scarcity of *Cardium* and chironomid larvae, favoured by these fish, and especially perhaps by larger specimens.

The new data, in conjunction with the results obtained in 1942/43, lead to the conclusion that distribution of fertilizers can bring about a very great increase in the growth rate of flounders, provided the hydrographic conditions are favourable. Though the last application of fertilizers was made in January 1946, the fertility level represented by the growth of fish remained high throughout 1946 and 1947, and, though declining, will probably remain above the pre-fertilization level for some years owing to the regeneration of nutrients locked up in great accumulations of organic material, remains of previous fertilizations.

There seem to be very few records concerning the relation of size, age and sexual development of fish. If maturity is correlated with a certain age and not with size, fish which grow more rapidly under conditions of fertilization would reach a considerable size, well above the minimum limit for marketing, before spawning. The maintenance of fish stocks, on the other hand, depends to a great extent on the size of the breeding stock, i.e. on the number of fish which have spawned before they were caught.

From the few published data it would appear that flounders, like plaice, normally mature at the age of 4–5 years, and that males reach maturity a year earlier than females. Kändler (1932) found that, in 1931, flounders of the Oder Bank reached maturity one year earlier than in 1925, the majority of females at the end of the fourth year, some males already at the end of the third year. He correlates the acceleration of maturity with an increase in growth rate from 1925 to 1931, due to thinning out of stock. In the Danzig area and in the central parts of the Baltic the flounders reached maturity at a higher age, males at 5, females at 6, and the size of the various groups was markedly smaller (Kändler, 1932). Molander (1932) investigated the flounder stocks off the Swedish coast in 1930/31 and found no spawning females of lesser size than 22 cm. and younger than group IV. Males were ripe at a length of 18–22 cm. and belonged to group III. In previous years spawning males, 13–15 cm. long, were also recorded. These presumably were also group-III flounders which had grown more slowly than those caught in 1930/31.

The fish obtained in Loch Craiglin also provide some useful evidence concerning the relationship between size, age and maturity. In March 1946 the great majority of 3-year-olds, both males and females, were fully ripe, and in March 1947 2-year-old males were ready for spawning. Only one 2-year-old female was obtained which was immature. Thus the males, at any rate, under conditions of fertilization and greater abundance of food, have matured at an age of 2 years. The data suggest, therefore, that sexual development in flounders goes with size rather than with age.

SUMMARY

Flounders grew much more slowly in 1944 than during the previous 2 years. From October 1943 to October 1944 their mean size increased from 7·9 cm., 6·8 g., to 12·7 cm., 23·6 g., an increment which was if anything smaller than under normal conditions. The reason for the reduction in growth rate is attributed to the increasingly unfavourable hydrographic conditions resulting from the prolonged closure of the dam, in particular to the high H_2S concentration, the high pH and the low oxygen concentration of the water.

In the autumn of 1944 the sluice gate of the dam was opened for several months. In 1945/46 the growth of stock III flounders was very rapid. They reached a mean size of 32·3 cm., 409 g., in March 1946 and 36·8 cm., 580 g., in March/April 1947. Native flounders reached a mean size of 30·6 cm., 353 g., in 2 years.

The poor growth in 1944 was reflected in narrow bands laid on by the otoliths and in low condition factors (1·05–1·15), the subsequent great improvement in growth rate was correlated with broad rings and high condition factors (1·31–1·16 in stock III, 1·2–1·23 in the native stock).

In March 1946 most females and all males were ripe at an age of 3 years. In March/April 1947 10 males were fully ripe at 2 years of age. These observations, in conjuction with those recorded by Kändler (1932), suggest that sexual maturity is correlated with size and not with age.

REFERENCES

GROSS, F., 1947. An experiment in marine fish cultivation: V. Fish growth in a fertilized sea-loch (Loch Craiglin). *Proc. Roy. Soc. Edin.*, B, Vol. LXIII, pp. 56–95.

GROSS, F., RAYMONT, J. E. G., NUTMAN, S. R. & GAULD, D. T., 1946. Application of fertilizers to an open sea loch. *Nature*, Vol. 158, p. 187.

KÄNDLER, R., 1932. Veränderungen im Flundernbestand der Ostsee durch die Fischerei. *Cons. Perm. Int., Rapp. et Proc.-Verb.*, Vol. LXXVIII (III), pp. 1–45.

MARSHALL, S. M., 1947. An experiment in marine fish cultivation: III. The plankton of a fertilized loch. *Proc. Roy. Soc. Edin.*, B, Vol. LXIII, pp. 21–33.

MARHSALL, S. M. & ORR, A. P., 1948. Further experiments on the fertilization of a sea loch (Loch Craiglin). The effect of different fertilizers on the phytoplankton. *Journ. Mar. Biol. Assoc.*, Vol. XXVII, pp. 360–79.

MOLANDER, A. R., 1932. Der Flunderbestand in der südlichen Ostsee und der Einfluss, den die Fischerei auf ihn ausübt. *Cons. Perm. Int., Rapp. et Proc.-Verb.*, Vol. LXXVIII (V), pp. 1–15.

FURTHER OBSERVATIONS ON CHANGES IN THE BOTTOM FAUNA OF A FERTILIZED SEA LOCH

By J. E. G. Raymont
University College, Southampton

(Text-fig. 1)

Introduction

An account has already been given (Orr, 1947; Marshall, 1947; Marshall & Orr, 1948; Gross, 1947; Raymont, 1947) of the changes resulting from the application of fertilizers to a small sea loch (Loch Craiglin) during 1942 and 1943. Remarkable increases in plankton production were observed, and these were followed by a considerable increase in the bottom fauna, the most obvious rise occurring during the second summer of fertilization. All the more important species of the bottom fauna exhibited increases and an average density of some 16,000 animals/m.^{2} was reached during August 1943, as compared with less than 5000 in the previous summer. The population declined with the approach of winter, but the average winter population for 1943–44 of a little over 7000 animals/m.^{2} showed an increase of 300 % over the 1942 corresponding winter population (Raymont, 1947).

The last regular samplings were made in February 1944, but a further series was taken in May. Thereafter, as heavy applications of fertilizers had been made throughout the summer of 1944 and again during the early spring of 1945 (Marshall & Orr, 1948), the series of grab samples was repeated every summer and continued until September 1947 in order to investigate the long-term effects of accumulated fertilizers on the bottom population.

Methods

The samples were taken at the same stations in the loch as in 1942 and 1943, except that Station VI was abandoned at the beginning of 1944. The bottom fauna there was very similar both in species and density to that at St. VII. A few samples were taken at a new station (St. VIII) sited fairly close to the north-west shore near the edge of the sparsely populated zone (see Raymont, 1947), as it was considered that the changes in that part of the loch had not been closely followed in the early work.

The samples were taken with the modified Petersen grab removing $\frac{1}{16}$th m.^{2} of the bottom, the material was washed through a 1 mm. sieve, and all the animals were preserved and counted later.[1] The results are therefore strictly comparable with those obtained in 1942 and 1943.

---

[1] I wish to thank the Department of Scientific and Industrial Research for a grant in respect of an assistant for 1946–47.

CHANGES IN THE BOTTOM POPULATION

The density of the bottom fauna in May 1944, as revealed by the grab samples, showed an unexpected drop as compared with the previous winter value. Some increase with spring reproduction might have been expected by May, but on the contrary, Sts. III–V and VII all showed declines, the population at St. IV being almost halved (Table I). By August, chironomid larvae and *Hydrobia ulvae* did show some increase at Sts. II and III, but the density of individual species and the total population at these stations was far below the 1943 summer level: at St. II the total population was only one-fourth, at St. III only one-half of that of the previous year. Even more striking were

TABLE I. THE BOTTOM FAUNA OF FIVE STATIONS, EXPRESSED IN NUMBERS OF ANIMALS/M.^{2}, SHOWING CHANGES FROM SUMMER 1943 TO SUMMER 1947

	Aug. 1943	Feb. 1944	May 1944	Aug. 1944	Sept. 1945	Sept. 1947
			Station II			
Chironomids	8,128	—	360	1,520	496	—
Hydrobia	5,888	1,360	1,520	2,096	2,528	7,632
Cardium	592	—	—	—	64	—
Crustacea	32	—	—	—	80	—
Other organisms	160	—	—	—	—	—
Totals	14,800	1,360	1,880	3,616	3,168	7,632
			Station III			
Chironomids	11,584	—	944	7,024	9,152	40
Hydrobia	3,904	5,664	800	3,744	9,936	5,320
Cardium	6,528	—	—	272	2,224	—
Crustacea	128	—	—	32	1,152	—
Other organisms	160	—	—	288	—	—
Totals	22,304	5,664	1,744	11,360	22,464	5,360
			Station IV			
Chironomids	7,568	10,816	6,896	3,504	23,568	1,496
Hydrobia	2,304	1,984	1,384	1,648	14,704	8,848
Cardium	8,624	16	8	—	2,000	48
Crustacea	1,776	1,264	16	16	2,000	216
Other organisms	736	6,992	2,856	112	80	64
Totals	21,008	21,072	11,160	5,280	42,352	10,672
			Station V			
Chironomids	11,952	2,256	4,544	560	12,176	2,488
Hydrobia	7,280	6,016	3,032	2,944	31,280	8,704
Cardium	2,704	—	8	144	3,296	—
Crustacea	48	80	—	48	272	8
Other organisms	80	592	400	—	48	—
Totals	22,064	8,944	7,984	3,696	47,072	11,200
			Station VII			
Chironomids	15,216	4,176	4,216	768	14,544	2,280
Hydrobia	4,656	4,560	4,288	1,168	20,608	27,048
Cardium	3,680	—	128	16	3,536	48
Crustacea	—	—	16	32	464	96
Other organisms	608	1,008	448	—	592	192
Totals	24,160	9,744	9,096	1,984	39,744	29,664

the changes in the region of the usually rich stations (Sts. IV, V and VII). The sharp decline continued there from May to August, when only 2000–5000 animals/m.^{2} were present along this normally rich zone. This density may be compared with 21,000–28,000 in the same region in the previous August.

The average population of Loch Craiglin, calculated from the populations at Sts. I–V (i.e. assuming as before that each station represents one-fifth of the population of the loch), showed a decline from 16,000/m.^{2} in August 1943 to under 5000 in 1944 (Table 2). The decrease affected almost every species of the bottom fauna, and in particular the normal summer spatfall of *Cardium*, and the rise in *Idothea* and *Gammarus* practically failed to occur.

Considerable deoxygenation occurred during 1944. Therefore from September the dam separating Loch Craiglin from Loch Sween was left fully open for several months so that a fairly complete exchange of sea water could take place. Early in 1945, when healthy conditions had been fully re-established, the dam was closed and several fertilizations were made which were followed by good phytoplankton increases (Marshall & Orr, 1948).

TABLE II. THE AVERAGE BOTTOM POPULATION OF LOCH CRAIGLIN FROM 1942 TO 1947, EXPRESSED IN NUMBER OF ANIMALS/M.^{2}; CALCULATED FROM GRAB SAMPLES TAKEN AT STS. I–V.

	Sept. 1942	Aug. 1943	May 1944	Aug. 1944	Sept. 1945	Sept. 1947
Chironomids	3,302	7,850	2,549	2,522	9,078	806
Hydrobia	920	3,875	1,347	2,086	11,693	6,578
Cardium	62	3,690	3	83	1,517	10
Crustacea	97	397	3	19	701	45
Other organisms	385	227	651	80	25	14
Totals	4,766	16,039	4,554	4,790	23,014	7,451

A full series of grab samples in September 1945 revealed a general and great rise in population density. The average calculated from the densities of Sts. I–V reached 23,000 animals/m.^{2} which is nearly 50 % higher than even the peak population obtained in the summer of 1943. Further, all the more important species of the bottom fauna (chironomid larvae, *Hydrobia*, *Cardium*) responded, the average density of *Hydrobia* being three times the population two years before (Table II). Along the whole rich east shore there was an average population of well over 40,000 animals/m.^{2} (Table I, Sts. IV, V and VII): this was nearly double the population of 1943 and represented the highest density recorded up to that time in Loch Craiglin.

There is fairly strong evidence that the high productivity was maintained throughout 1946. In September of that year a further series of grabs was taken, but unfortunately a number were lost during transport to the laboratory. Reliable counts can be given only for Sts. I, V, VII and VIII (Table III). At Sts. V and VII the total population of chironomid larvae, *Hydrobia* and *Cardium* (the number of other organisms was probably very small), was 29,000 and 52,000 respectively. St. V had thus declined from the 1945 peak value, but St. VII had increased again and the population was the highest ever recorded at any time. While it is impossible to calculate from these few samples an average population for Loch Craiglin for the summer of 1946, it seems fairly safe to assume that the general population did not decline very obviously during that year.

Table III shows that for the first time since 1942, St. I had a significant population composed almost entirely of *Hydrobia*. Also at Sts. V, VII and VIII, more than 90 % of the bottom fauna (at St. VIII practically 100 %) was made up of *Hydrobia*. Already in 1945 it was clear that *Hydrobia* had increased far more relatively than either chironomid larvae or *Cardium*, but the rise in *Hydrobia* in 1946 was far more striking.

A final series of grabs was taken in the following summer. The population at St. V was only 11,000 as compared with 29,000/m.^{2} in 1946. At St. VII there was a similar drop from 52,000 to 30,000/m.^{2} Comparable figures are not available for the other stations owing to the loss of samples in 1946, but we may compare the populations at these stations with the 1945 values. Thus St. III dropped from 22,000 to only 5000, and at St. IV there was a similar decline to approximately one-quarter of the 1945 population—from 42,000 to 11,000/m.^{2} (Table I).

TABLE III. THE BOTTOM FAUNA OF FOUR STATIONS IN SEPTEMBER 1946, EXPRESSED IN NUMBERS OF ANIMALS/M.^{2}

	St. I	St. V	St. VII	St. VIII
Chironomids	16	2,128	1,040	32
Hydrobia	448	27,264	50,592	20,288
Cardium	—	32	96	—
Other organisms	?	?	?	?
Totals	464	29,424	51,728	20,320

Station II was, however, exceptional, showing a rise in population from 3000 in 1945 to over 7000/m.^{2} in 1947 (Table I). At St. I also the population rose to some 2400 animals in 1947, all consisting of *Hydrobia*. The actual density is somewhat doubtful, as the two samples taken at St. I differed considerably when counted. Probably one grab struck the side of the deep pit round St. I and gave the higher count. Nevertheless, what is significant, is the fact that the recolonization of the azoic zone round St. I which was foreshadowed in 1946 continued throughout 1947.

Excepting Sts. I and II, there was a very sharp decline in 1947 from the peak 1945 levels and the average population for Loch Craiglin, calculated from the densities at Sts. I–V, decreased to about one-third of the 1945 density—from 23,000 to 7500/m.^{2} (Table II).

So far only the changes in numbers of the bottom fauna have been given. It is clear, however, that from the point of view of fish food it is the *weight* of the organic matter in the bottom fauna (i.e. excluding the shells and other indigestible matter) rather than numbers which is really significant.

The dry organic weights of the bottom fauna (i.e. dry weight less shell) have therefore been calculated approximately for the years 1944 to 1947. The method used previously (Raymont, 1947) has again been employed so that the data for earlier years are comparable. The average dry weight of all the commoner members of the bottom fauna was determined and the average numbers of bottom fauna given in Table II have been converted into dry weights. The results are shown in Table IV.

In the summer of 1942 the average dry weight of bottom fauna in Loch Craiglin was only 3 g./m.^{2} The weight fell to a minimum of 1 g./m.^{2} during the following winter, but rose rapidly during the summer reaching over 9 g./m.^{2} in August 1943 when a high density of some 16,000 animals/m.^{2} was present. This higher weight was maintained during autumn, but by February 1944 the average weight was reduced to 5 g./m.^{2} By May 1944 the dry weight had fallen further to below 3 g./m.^{2}, and in August there was only a very slight recovery to 3·5 g./m.^{2}

TABLE IV. THE AVERAGE DRY WEIGHT, IN G./M.^{2}, OF THE BOTTOM FAUNA OF LOCH CRAIGLIN (CALCULATED FROM THE NUMBERS OF ORGANISMS AT STS. I–V, WEIGHT OF SHELLS OF MOLLUSCA EXCLUDED).

	Feb. 1944	May 1944	Aug. 1944	Sept. 1945	Sept. 1947
Chironomids	1·3	1·3	1·3	4·5	0·4
Hydrobia	3·1	1·4	2·2	12·1	6·8
Cardium	—	—	0·1	2·2	0·1
Crustacea	0·3	—	—	0·8	—
Other organisms	0·2	0·1	—	—	0·2
Totals	4·9	2·8	3·6	19·6	7·5

The change in dry weight between 1944 and 1945 is striking: by September 1945 the average dry weight of the bottom fauna was between 19 and 20 g./m.^{2} Of the few counts made in 1946 the large numbers of *Hydrobia* recorded would suggest that a considerable weight of bottom fauna was present at that time. By September 1947, however, the dry weight had fallen markedly to an average of 7·5 g./m.^{2}

DISCUSSION

It is clear from Tables I and II that, with the exception of the deoxygenated pit round St. I, there was a very marked and general rise in the density of bottom fauna over the whole of Loch Craiglin from the summer of 1942 to summer 1943, but that every station experienced an equally obvious drop in population in the following summer (August 1944).

It might be claimed that, since the 1942 and 1944 summer populations are approximately equal and that fertilization was practised over all three years, the very high population of 1943 was not due mainly to a general increase in the amount of food, consequent upon fertilization, but was merely due to annual variations caused by other factors. This is unlikely in view of the fact that *all* the important bottom fauna species in Loch Craiglin showed marked increases in 1943. Nevertheless, it is true that the sharp decline in 1944 occurred in spite of a peak production of phytoplankton in the early months of that year, and despite the fact that the loch was still very rich in nitrates and phosphates which would indicate a very high *potential* productivity. But it must be admitted that however high the potential productivity of a body of water may be, factors other than the amount of food available may limit the actual production. It is possible, therefore, that the drop in bottom fauna density in the spring and summer of 1944 was due to some deleterious factor operating then but not during previous years, and that in the absence of this factor the population in 1944 would have been as high (or even higher) as in the previous year. That some depressing factor was acting seemed likely also from the observations by Gross (1949) that the growth of flounders in Loch Craiglin during the spring and summer of 1944 fell off very considerably.

From the autumn of 1943 the deoxygenation of the deep pit around St. I became progressively more marked, and throughout the spring and summer of 1944, there was a considerable production of hydrogen sulphide. It is believed that these unhealthy conditions spread out from this area during 1944, and, in contrast to previous years, affected a large proportion of the loch. This deoxygenation was caused mainly by the decay of exceptionally heavy growths of *Zostera* and sea weeds. These rich growths resulted from excessively heavy fertilizations in 1944, one summer fertilization, for example, consisting of ten times the normal quantity of fertilizers applied (Marshall & Orr, 1948).

The widespread deoxygenation even so was probably confined mainly to the mud surface. Although, therefore, a large part of the bottom fauna died, some animals living normally well above the bottom survived. This may account for the fact that *Hydrobia* showed a smaller drop in population from 1943 to 1944 than any other species (cf. Fig. 1), for *Hydrobia* typically lives on the weed in Loch Craiglin. On the other hand, chironomid larvae which are known to be able to withstand very low oxygen concentrations were very greatly reduced in number, but these were living in the mud surface.

If deoxygenation really did limit the production in 1944, the re-establishment of 'healthy' conditions should have led to an increased productivity. It is very significant therefore that following a full exchange of sea water later in 1944 between Loch Craiglin and Loch Sween, fertilization in the next spring produced very marked plankton increases, and further that the bottom fauna density rose very rapidly and generally over the loch to values higher than any previously recorded. Along the eastern side of Loch Craiglin the average population reached more than 40,000 animals/m.^{2} The average population in September 1945 was five times the average density in 1942 and 1944, and nearly 50 % higher than that of 1943. The great increase in 1945 may be attributed to a general raising of the level of productivity by fertilization and this rise in productivity is reflected also in the excellent growth of flatfish (Gross, 1949) over the same period.

Although these flatfish continued to feed heavily upon the bottom fauna, and despite the fact that only a very little fertilizer was applied to the loch during 1946, there is some evidence for the view that the bottom fauna productivity was maintained at a fairly high level over the summer of 1946.

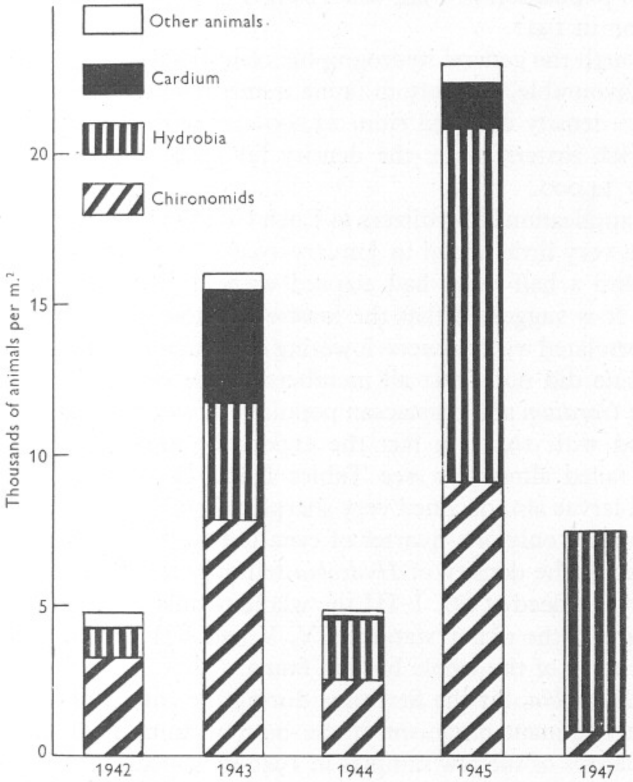


Fig. 1. Variation in the average density and composition of the bottom fauna in Loch Craiglin for the summers 1942–47, calculated from the populations at Sts. I–V. (Samples from all stations were not available for 1946.)

Thus, of the few records available, St. V showed a decline but St. VII an equally marked increase. The population at St. VII (52,000/m.^{2}) was indeed the highest recorded during the course of the investigation.

The fact that St. I also showed a population of some 400–500 *Hydrobia*/m.^{2} in the summer of 1946 is strong evidence for the view that the good hydrographic conditions established in 1945 continued throughout the following year. No animals of any kind were recorded around St. I from the summer of 1942 to 1945 owing to the deoxygenation of that region, but in 1946 *Hydrobia* was able to maintain itself.

By 1947, the population at St. I, still consisting entirely of *Hydrobia*, had increased five times. Thus we may conclude that good oxygenation and other favourable hydrographic factors, apart from dissolved nutrients, existed throughout 1947 also. In support of this conclusion, none of the samples taken in Loch Craiglin in 1947 smelled strongly of H_2S. Further, St. II, which bordered the previously deoxygenated zone and showed a very marked reduction in population in 1944 when oxygen was low, actually showed a rise in population in 1947.

Yet, although the general hydrographic conditions in 1947 would appear to have been favourable, the bottom fauna numbers in general fell very sharply. The average density dropped from 23,000/m.^{2} in 1945 to 7500 in 1947, and along the rich eastern shore the density fell from about 40,000/m.^{2} to approximately 14,000.

The last application of fertilizers to Loch Craiglin was made in spring 1945, except for a very little added in January 1946. Thus by the summer of 1947 some two and a half years had elapsed without any significant addition of fertilizers. It is suggested that the lowered bottom fauna density in 1947 is therefore correlated with a general lowering in the amount of nutrients available.

The decline did not affect all members of the bottom fauna to the same extent. The *Cardium* and crustacean populations were extremely small in 1947 as compared with 1945; in fact the expected summer spatfall of *Cardium* apparently failed altogether (see Tables I and II). The average density of chironomid larvae also declined very sharply: from 9000 to only 800/m.^{2}, this population being only one-quarter of even the 1942 summer population. On the other hand, the density of *Hydrobia* fell only to about a half of the 1945 peak density. Indeed at Sts. I–III the whole population in 1947 was virtually *Hydrobia* and at the richer stations (IV, V and VII) this species comprised from 75 to 90 % of the whole bottom fauna.

In 1945 *Hydrobia*, for the first time during the course of the investigation, became the dominant organism of the bottom fauna in Loch Craiglin (see Fig. 1). Analysis of the few samples in 1946 indicated that its dominance was increasing, and this apparently continued throughout 1947. It is believed that the rise in *Hydrobia* originally was due to its ability to avoid the low O_2 tensions near the bottom. But probably from 1946 to 1947, when with somewhat lowered productivity a stronger competition existed between the species of the bottom fauna for the food available, the large population of *Hydrobia* progressively crushed out its competitors.

There is also the differential grazing effect of the bottom fauna by the flounders. In Loch Craiglin chironomid larvae and *Cardium* were always favourite foods, but *Hydrobia* was not taken so readily. The very great reduction in chironomids in 1947 was probably due to intensive grazing outstripping production. *Cardium*, as well as being eaten, was also killed off to a considerable extent in Loch Craiglin by winter frosts (cf. Raymont, 1947).

Thus by September 1947 the density of *Hydrobia* was eight times that of chironomid larvae, and the total density of all other animals was quite insignificant.

Although fertilization of Loch Craiglin began in 1942, peak values of the bottom fauna were achieved only in 1945. Perhaps similar high values would have been reached in 1944 had healthy conditions existed then. But it would seem that when fertilizers continue to be added, at least 2–3 years are necessary to achieve anything approaching maximum productivity from the bottom fauna. Similar conclusions have been drawn from other fertilization experiments in an open sea loch (Raymont, 1948). Whether higher densities would have been obtained had fertilization continued it is impossible to tell. We can say that after more than two years' lack of fertilization there would appear to be a real falling off in bottom productivity. But even then, a fairly high productivity, certainly greater than pre-fertilization values, is still maintained. Table II shows that the average bottom density in 1947 was 7500/m.^{2} as compared with less than 5000/m.^{2} in 1942 when some beneficial effect of fertilization had probably already been experienced.

Even clearer, however, is the increase in bottom fauna productivity from 1942 to 1947 if the dry weights are considered. The rise in numbers from 1942 to 1943 was paralleled by a trebling of the average weight of bottom fauna. The decline during the following winter was due mainly to the reduction of chironomid larvae and young *Cardium*. *Hydrobia* was much less affected, probably because it was not eaten very much.

The expected rise in dry weight in the summer of 1944 did not occur; the increase from May to August was only 0·5 g. and the weight of the bottom fauna was then almost identical with that in 1942.

The rise in the summer of 1945 is therefore all the more striking, and the average dry weight of nearly 20 g./m.^{2} recorded in September compares very favourably with the weights of bottom fauna given by Zenkewitch, Brotzky & Idelson (1928) and Petersen (1918) for the rich White Sea and Limfjord regions. Their figures of 20–100 g. and 50 g./m.^{2} represent total *wet* weights, and a reasonable estimation of the dry weights is about 10 % or less, giving thus 2–10 g. and 5 g. respectively. It is true that Zenkewitch *et al.* found some areas with 20–30 g. (dry weight). Loch Craiglin would appear to be almost as rich as this.

By 1945 the weight of bottom fauna in Loch Craiglin indicated that it had become an exceedingly rich feeding ground. The weight was just over double what it was in the summer of 1943, and more than six times the 1942 value (Table IV). On the other hand, the average number of bottom animals in 1945 (23,000/m.^{2}) is only some 45 % greater than that of 1943 (16,000/m.^{2}). The difference lies in the fact that *Hydrobia*, which has a higher dry organic weight than either chironomid or very young *Cardium*, made a much greater contribution to the bottom fauna in 1945. Of the total average weight of 19·6 g./m.^{2}, *Hydrobia* contributed no less than 12 g., chironomid larvae 4·5 g. and *Cardium* only 2·2 g. The weight of *Cardium* seems especially small, but it must be remembered that in Loch Craiglin the vast proportion of *Cardium* were less than 5 mm. long. Thus, in 1945, of an average population of 1520 *Cardium*/m.^{2}, some 1260 were less than 5 mm. and only 45 were over 10 mm. in length. The average dry weight of *flesh* in cockles of less than 5 mm. length is very small—approximately only 0·2 mg. per individual.

It has been suggested that by 1947 there was a real and significant fall in productivity in Loch Craiglin. The dry weight in 1947 was somewhat below the 1943 summer value (9 g.), but the difference was not great. On the other hand, the number of organisms in 1947 was less than half the 1943 density. Once again the apparent discrepancy is explained by the fact that *Hydrobia* contributed to a very much greater extent in 1947: 6·8 g./m.^{2} out of the total 7·5 g. is made up by this one species.

The importance of dry-weight determinations is thus clear in these bottom fauna investigations. Although numbers and weight were declining in 1947, by September, some two and a half years after the last significant quantity of fertilizers had been applied, Loch Craiglin was still more than twice as rich in weight of bottom fauna as it was in 1942.

From the summer of 1942 onwards the weight of bottom fauna in Loch Craiglin was made up almost entirely of chironomid larvae, *Hydrobia*, crustacea and *Cardium*. Had a considerable proportion of the cockles been of large size, they would not have been available to relatively small-mouthed fishes such as flounders. Even the very rich feeding grounds investigated by Zenkewitch *et al.* may be only *apparently* rich, since it is uncertain how much of the bottom fauna was edible and available (cf. also Ford, 1925). In Loch Craiglin, however, the vast majority of *Cardium* were very young individuals in any year, and the other common organisms were all readily available. Therefore the weights of bottom fauna given can be regarded truly as the quantities of food available to the feeding fishes.

SUMMARY

An account is given of the further changes in the bottom fauna of a fertilized sea loch (Loch Craiglin) from 1944 to 1947, and the results are compared with those obtained from 1942 to 1944.

The bottom fauna density fell markedly during 1944, despite the addition of very large quantities of fertilizers. Unfavourable hydrographic conditions, especially low oxygen tensions, are considered to be responsible for the decrease.

Densities higher than ever obtained before in Loch Craiglin were found in the summer of 1945 (average of 23,000 animals/m.^{2}), when favourable hydrographic conditions once more existed.

The little evidence available suggests that the high productivity was maintained during 1946, although only a very little fertilizer was added during that year.

By 1947 the average density of bottom fauna had fallen to only 7500 animals/m.^{2} and it is suggested that this drop was correlated with less nutrients being available, since no fertilizers were added after January 1946.

Hydrobia ulvae became progressively more important from 1944 onwards, and was the dominant member of the bottom fauna from 1945. Reasons are advanced for the progressive rise in numbers of this species.

The average dry weight of flesh of the bottom fauna rose from 3 g./m.^{2} in 1942 to 9 g./m.^{2} in the summer of 1943. It fell to 3·5 g. in 1944, rose to 19·5 g. in 1945 but declined again to 7·5 g. in the summer of 1947.

The results suggest that with constant application of fertilizers at least two to three years are necessary to achieve maximum production from the bottom fauna. Further, even after two and a half years had elapsed since regular fertilization was practised, the bottom fauna production was still more than twice as great as under 'natural' conditions.

REFERENCES

FORD, E., 1925. On the growth of some lamellibranchs in relation to the food-supply of fishes. *Journ. Mar. Biol. Assoc.*, Vol. XIII, pp. 531–59.

GROSS, F., 1947. An experiment in marine fish cultivation: V. Fish growth in a fertilized sea-loch (Loch Craiglin). *Proc. Roy. Soc. Edin.*, B, Vol. LXIII, pp. 56–95.

—— 1949. Further observations on fish growth in a fertilized sea loch (Loch Craiglin). *Journ. Mar. Biol. Assoc.*, Vol. XXVIII, pp. 1–8.

MARSHALL, S. M., 1947. An experiment in marine fish cultivation: III. The plankton of a fertilized loch. *Proc. Roy. Soc. Edin.*, B, Vol. LXIII, pp. 21–33.

MARSHALL, S. M. & ORR, A. P., 1948. Further experiments on the fertilization of a sea loch (Loch Craiglin). The effect of different plant nutrients on the phytoplankton. *Journ. Mar. Biol. Assoc.*, Vol. XXVII, pp. 360–79.

ORR, A. P., 1947. An experiment in marine fish cultivation: II. Some physical and chemical conditions in a fertilized sea-loch (Loch Craiglin, Argyll). *Proc. Roy. Soc. Edin.*, B, Vol. LXIII, pp. 3–20.

PETERSEN, C. G. J., 1918. The sea bottom and its production of fish food. *Rept. Dan. Biol. Stat.*, Vol. 25, pp. 1–62.

RAYMONT, J. E. G., 1947. An experiment in marine fish cultivation: IV. The bottom fauna and the food of flat-fishes in a fertilized sea-loch (Loch Craiglin). *Proc. Roy. Soc. Edin.*, B, Vol. LXIII, pp. 34–55.

—— 1948. A fish-farming experiment in Scottish sea lochs. *Journ. Mar. Res.* Vol. VI, pp. 219–227.

ZENKEWITCH, L., BROTZKY, V. & IDELSON, M., 1928. Materials for the study of the productivity of the sea-bottom in the White, Barents and Kara Seas. *Journ. Cons. Int. Explor. Mer.*, Vol. 3, pp. 371–79.

NOTES ON THE GENERAL BIOLOGY OF *TUBULARIA LARYNX* ELLIS & SOLANDER

By K. A. Pyefinch and F. S. Downing

Anti-Fouling Section, British Iron & Steel Research Association.
From the Marine Station, Millport

(Text-figs. 1–6)

CONTENTS

INTRODUCTION

Though *Tubularia* has been extensively used as material for experimental studies of regeneration (Barth, 1940), and though detailed accounts are available of the cleavage of the ovum and of the early stages of development of the actinula larva (Allman, 1871; Ciamician, 1879; Conn, 1882; Brauer, 1891; Lowe, 1926), little attention has been given to the general biology of this gymnoblast, though Allman (1871), Ciamician (1879) and Salensky (1911) have given some details of post-liberation changes in the actinula and Klugh (1929) has briefly described certain factors which affect the vitality of the fully developed colony. Studies of the settlement of marine organisms on toxic surfaces have shown that *Tubularia* is one of the organisms most resistant to such poisons as copper (Barnes, 1948), and this fact has led to investigations of various aspects of the general biology of this genus. The preliminary results of these investigations are presented in this paper.

The material upon which this study has been based can most satisfactorily be included in the species *Tubularia larynx* Ellis & Solander, though the colonies which settle and develop upon suitable exposed surfaces at Millport differ in certain respects from the characters of this species as listed by Allman (1872). He gives the average height of a colony of this species as 1½–2 in. and states that the stems bear 'more or less distinctly marked annulations at intervals'. Colonies of this species at Millport generally exceed 3 in. and may reach 4 in. in height, and annulations are very difficult to detect on the stems; they are rarely clearly visible on the stems of a living colony, but a few shallow annulations can be seen on the bare stems after the polyps have been shed and the colony has died down to the condition in which it lives through the winter. It is felt, however, that differences of this character do not warrant the formation of a separate species for this material, though it is perhaps important that their existence should be mentioned. One further difference may be added. Mr J. Corlett (personal communication) has recently found, in the course of studies on the settlement of marine organisms in the Mersey, that there *T. larynx* does not flourish unless the water temperature exceeds 60° F. As at Millport this temperature is attained, under favourable conditions, only for a few days in the year, the temperature requirements of *T. larynx* at Millport appear to differ from those elsewhere, since there is no doubt that this species is able to settle in abundance and grow rapidly when the water temperature is well below 60° F.

Elmhirst (1923) states that the breeding period of *T. larynx* at Millport extends from May to September; our observations, made in greater detail over the past 5 years, are in general agreement with this estimate. Settlement is rarely at all heavy, however, until late in July. This period of heavy settlement continues through August and September and may extend into the first weeks of October. Some settlement may occur until the end of December.

During August and September, any suitable surface soon acquires a number of young colonies which grow rapidly. All the experimental material used in the present survey was taken from surfaces immersed from rafts moored close inshore. Sometimes colonies were removed from their substratum and brought into the laboratory for experiment. At other times, when it seemed essential to disturb the material as little as possible, colonies were used which had grown from settlements on ground-glass microscope slides immersed in the sea.

The use of settlement surfaces immersed from a raft is in some ways advantageous, in others the reverse. It is possible, using this method, to provide a surface, uncolonized by other organisms, for the attachment of the settling larva. Thus it is possible to obtain large numbers of settled individuals but, because of the conditions of immersion of these surfaces hung from a raft, the environment is not wholly normal. Continuous immersion is assured, but the immersed specimens remain at a constant depth below the surface of the water and consequently may be exposed to high light intensities for longer periods than are individuals growing normally just below low-water mark on a fixed object.

Liberation of the Actinula Larva

As Lowe (1926) has shown, the developing actinula is orientated with its aboral pole pointing towards the opening of the gonophore and its oral pole, sheathed in the aboral tentacles, pointing inwards. Allman (1872, p. 407) has stated that in *T. larynx* the oral tentacles are not formed until after liberation, but it is clear from our material and from *T. larynx* from Plymouth that this statement is erroneous. The aboral pole thus emerges first as the actinula is expelled and the tips of the aboral tentacles last; as each aboral tentacle is freed, it stands out from the body of the larva, so that the newly liberated actinula has a number of aboral tentacles radiating stiffly outwards (Fig. 1A). Allman (1872) for *T. indivisa* L. and Ciamician (1879) for *T. mesembryanthemum* Allman, state that in these species the oral pole of the larva emerges first.

The factors affecting the liberation of the actinula larva are still largely unknown, but two possibilities have been investigated in the course of this work. Early laboratory experiments suggested that change in light intensity stimulated the liberation of actinulae, since the rate of liberation was increased immediately after transfer from light to darkness or from darkness to light. Later work, however, has not wholly substantiated this result, the average rate of liberation (i.e. the number of larvae liberated per hour) is greater in darkness than in light, but a change of light intensity does not invariably increase the rate of liberation of actinulae. This point requires fuller investigation under carefully controlled conditions.

The other factor investigated which affects the rate of liberation of actinulae was variation in current speed. The range of current speed that could be used was limited, and was generally low in comparison with that to which colonies are exposed during the ebb tide at Millport, but the results obtained strongly suggest that larval liberation is markedly reduced in quite moderate currents. At a water speed of 1 cm./sec. the rate of liberation was greater than that which occurred in still water, but if the speed of the current was increased to 3 cm./sec. liberation of actinulae practically stopped. These preliminary results suggest that liberation may only take place in the sea over slack-water periods. This point is of some importance in the distribution of larval settlement round a mature colony and will be discussed more fully later (p. 35).

Large numbers of actinula larvae can readily be obtained for experimental purposes by suspending mature colonies, polyps downwards, in fresh sea water. If the sea water is frequently renewed, liberation of actinulae will continue for several days. Thus, a group of colonies containing approximately 150 polyp heads liberated about 1000 larvae over a period of 6 days in the laboratory, an average of about seven larvae per polyp. This is almost certainly an underestimate, as it is reasonable to assume that some larvae had been shed before the colonies were collected and that the full development of others was doubtless affected by the artificial conditions of the laboratory. Further, this estimate assumes that all the polyps in the colony liberated actinulae during the period of observation; as will be shown later, this is not likely to be true, so that it can be safely assumed that one polyp produces many more than seven larvae.

The Actinula Larva

Morphological changes before settlement

Immediately after liberation from the gonophore, the actinula larva of *T. larynx* consists of an ovoid body with the mouth, surrounded by four or five short oral tentacles, at one pole, and some distance below it a number of long aboral tentacles which radiate stiffly outwards (Fig. 1A). The tips of these tentacles are swollen and within the superficial tissues of these swellings are large numbers of nematocysts. The number of these aboral tentacles varies. In a series of some 200 actinulae, the number of aboral tentacles varied from six to thirteen, most (32 %) had ten aboral tentacles and over 75 % had nine, ten or eleven aboral tentacles.

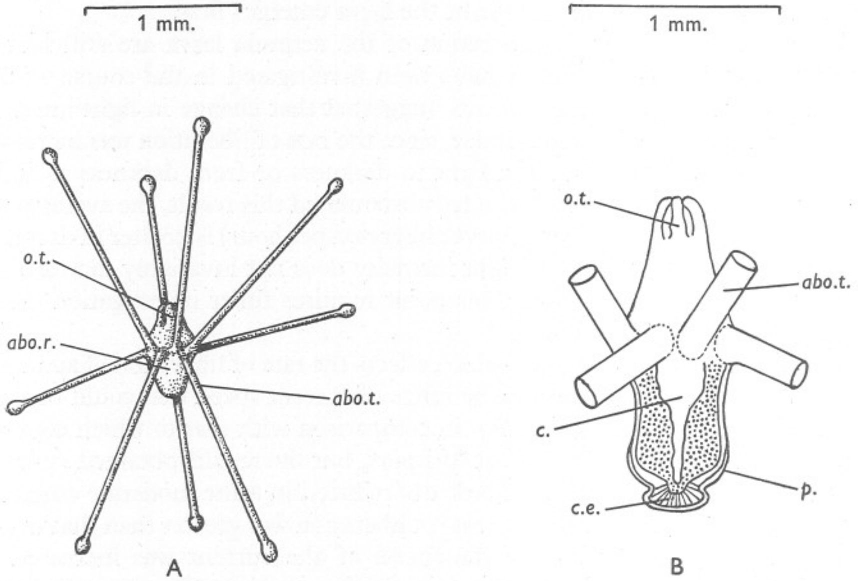


Fig. 1. A, actinula larva of *Tubularia larynx*, immediately after liberation. B, semi-diagrammatic sketch of the body of the actinula larva of *T. larynx*, shortly before settlement. The aboral region is shown in optical section. *abo.r.*, aboral region; *abo.t.*, aboral tentacle; *c.*, coelenteron; *c.e.*, columnar ectoderm; *p.*, perisarc; *o.t.*, oral tentacle.

Shortly after liberation, that part of the body below the aboral tentacular ring (the aboral region) begins to elongate. Immediately after liberation this aboral region measures 0·3 mm. in length and is 0·32 mm. in diameter at its widest part. When settlement occurs, this part of the larval body has increased in length to 0·43 mm. and its diameter has decreased slightly, now being 0·28 mm.; it is thus distinctly cylindrical in form (Fig. 1B).

The surface of the aboral pole of the actinula can be seen to be covered by a thin membrane immediately after liberation. By the time this region of the body has elongated, this membrane, which is the first appearance of the perisarc, can readily be distinguished (Fig. 1B). Some of the properties of this sheath were investigated using larvae which had settled on the substratum, since the sheath is then attached and can be manipulated more easily. If such larvae are placed in 10% NaOH, rapid and extensive maceration of the tissues takes place and the body of the larva can be drawn out of the sheath, leaving the latter as a short cylinder, closed at one end, attached to the substratum. The sheaths may then be washed several times and can be stored either in tap water or in 4% sea-water formalin.

When treated with Mallory's triple stain, the sheath stains a deep blue; it dissolves slowly in cold concentrated HCl; it is not wholly soluble in 50% NaOH at 60° C., and it gives a faint positive reaction to the chitosan test (the difficulty in obtaining a more satisfactory result to this test lies in the manipulation of the material). These properties are such as strongly to suggest that this sheath is chitinous in nature. One further point of interest emerges from these experiments; when treated with warm, concentrated alkali, the sheaths do not dissolve (though they become appreciably more delicate), but they always become detached from the substratum, suggesting that they are attached by a substance soluble in concentrated alkali. It is, therefore, possible that attachment is secured by means of an extra-chitinous cement similar to that found in arthropods. Mr B. W. Sparrow (personal communication) has demonstrated the existence of dihydroxyphenols in the attachment cement of *T. larynx*, an observation which strongly supports this possibility. There are indications (see also p. 29) that the cement used for the attachment of a number of marine animals belonging to different phyla may consist of a mucoprotein, and that this mass of cement hardens in a manner similar to that described for the arthropod cuticle by Pryor (1940). Ciamician (1879) suggested that the chitinous perisarc itself served to attach the actinula larva of *T. mesembryanthemum* to the substratum, but this seems unlikely to be true for the recently settled actinula of *T. larynx*.

General biology of the larva

After liberation, the actinula larvae sink slowly through the water. Measurements indicate that they sink at a rate of about 1 mm./sec., so that, although they may be carried in a slight current a little distance from the parent colony, it is probable that many will come into contact with a substratum not far from their point of liberation.

The aboral tentacles of the unattached actinula are held alternately pointing away from the substratum and towards it (Fig. 1A) and the larva can move slowly on the tips of the latter set of tentacles. Progress in this way is slow, but appears faster in light (of the order of 0·3 cm./hr.) than in darkness (roughly 0·1 cm./hr.). Critical experiments have not yet been made, but an examination of the results of these preliminary experiments suggests that the larvae are photokinetic rather than phototactic.

During this period of free movement over the substratum the orientation of the larva is mainly that which is eventually assumed, namely with the aboral pole towards the substratum. This point was specially examined as other accounts of the orientation of actinula larvae (e.g. Allman, 1872, for *T. indivisa*) suggest that the oral pole is directed towards the substratum and that a reversal of this orientation takes place just before settlement.

Temporary attachment to the substratum can take place by means of the tips of the aboral tentacles, but it would seem that these tentacles do not become attached immediately the larva comes into contact with a substratum. An actinula larva, placed in a dish of sea water and allowed to sink to the bottom, can at first be moved by the slightest current, but if larvae are left in contact with the substratum for a period of 2 hr., and are then subjected to a current which is very gradually increased in speed, they can withstand much faster currents. Most of the larvae became dislodged when the current speed was increased to 1–2 cm./sec., but some could withstand currents up to 8 cm./sec. before being dislodged. These results were obtained using smooth glass surfaces; under natural conditions, where the substratum may be more suitable for attachment and where the rate of increase of current speed is probably less, it may be that much stronger currents can be withstood without the larva becoming dislodged. It was frequently noted that when a larva became dislodged in a weak current it did not move far, but became attached again within a short distance (e.g. 3 cm.) of its original point of attachment. Much stronger currents were then needed finally to dislodge such larvae.

In the laboratory a considerable time interval may elapse before an appreciable proportion of actinulae become attached permanently to the substratum. Table I gives typical examples of the progress of attachment.

TABLE I. SETTLEMENT OF ACTINULAE OF *TUBULARIA LARYNX*

First-crop larvae		Second-crop larvae	
Estimated time after liberation (hr.)	Percentage attached	Estimated time after liberation (hr.)	Percentage attached
14	5	6	44
18	12	11	84
22	39	16	96
28	71	25	100
37	96		
46	100		

To obtain actinula larvae for these experiments, mature colonies of *T. larynx* were collected during the morning and inverted in fresh sea water for approximately 6 hr. The actinulae shed during this period were then collected and form the 'first-crop larvae' of Table I. The sea water bathing the colonies was then changed and the colonies were allowed to stand overnight. Actinulae were again collected the next morning and form the 'second-crop larvae'. There is clearly a very considerable difference in the rate at which these two batches of larvae become attached; this point is discussed more fully in the next section. It is evident, however, that the period for which the larvae are unattached may be greater than that recorded by Ciamician (1879) for the actinulae of *T. mesembryanthemum* (4–6 hr.). It will be noted that all the larvae eventually succeeded in becoming attached. Such results were typical of these larvae; under normal environmental conditions the proportion which settled successfully was rarely less than 90%. Other factors affecting settlement are discussed in the next section.

SETTLEMENT

It is not possible to give an account of the actual process of settlement, since this stage in the life history is apparently accomplished without the appearance of any marked structural changes or the initiation of any characteristic reactions. Sometimes the aboral tentacles lose their rigidity at about the time that settlement occurs; but this does not always seem to be so, and it is possible that this change is due to the artificiality of laboratory conditions. Larvae have frequently been watched carefully over the whole period between liberation and settlement, and it has not been possible to observe any marked or invariable change in structure or habit which would indicate that a larva was about to settle.

The effect of a number of factors on settlement has been investigated. The results obtained are briefly summarized below.

(i) *Hypotonic Sea Water*. Actinula larvae of *T. larynx* are not capable of withstanding hypotonic conditions for prolonged periods but, although degenerative changes were evident in the mixtures containing smaller proportions of sea water, there was also a tendency for settlement to be accelerated in such solutions (Table II).

TABLE II. SETTLEMENT IN FULL AND DILUTED SEA WATER

Estimated time after liberation (hr.)	Percentage attached		
	Sea water	70% sea water	60% sea water
7	0	24	20
9	3	42	20
20	7	43	36

(ii) *Copper and Mercury*. Grave & Nicoll (1939) have recorded that copper stimulated the attachment of ascidian larvae, and Prytherch (1934) considered that increased amounts of copper present at low water caused the settlement of the larvae of *Ostrea virginica* in Milford Harbour, though his conclusions have been severely criticized by Korringa (1940). A number of rough experiments on the effect of the addition of small amounts of copper and of mercury to sea water on the attachment of actinula larvae were carried out and the results suggest (Table III) that both of these poisons stimulate attachment to some extent.

TABLE III. EFFECT OF COPPER AND MERCURY ON SETTLEMENT

(1) Copper

Estimated time after liberation (hr.)	Percentage attached				
	Sea water	0·05 mg./l. Cu	0·075 mg./l. Cu	0·1 mg./l. Cu	0·25 mg./l. Cu
6	0	0	3	14	?81
9	3	0	6	16	80
19	7	0	39	46	100
28	24	35	50	60	100

(2) Mercury

Estimated time after liberation (hr.)	Percentage attached				
	Sea water	0·01 mg./l. Hg	0·05 mg./l. Hg	0·1 mg./l. Hg	0·25 mg./l. Hg
10	0	36	40	82	100
27	80	53	66	90	100

The range of copper and of mercury concentrations used in these experiments includes concentrations that are toxic. The median lethal concentration of copper (for an exposure period comparable with the total length of the experiment recorded in Table III) is approximately 0·09 mg.Cu/l., whereas the corresponding figure for mercury is 0·03 mg.Hg/l. Attachment is, therefore, stimulated at concentrations below the median lethal concentration for both poisons and, though the larvae in the highest concentrations were dead at the end of the experiment, attachment had taken place before death occurred.

(iii) *Benzoquinone and Ascorbic Acid.* If small amounts of these compounds are added to sea water in which actinula larvae have been placed, there is, up to concentrations which are toxic, a stimulatory effect on attachment. Table IV shows the results of one experiment using benzoquinone.

TABLE IV. EFFECT OF BENZOQUINONE ON SETTLEMENT

Estimated time after liberation (hr.)	Percentage attached				
	Sea water	0·01 mg./l. BQ	0·1 mg./l. BQ	1·0 mg./l. BQ	10·0 mg./l. BQ
15	23	36	37	0	0
27	40	74	91	0	0

At concentrations higher than 0·1 mg. benzoquinone/l. this compound killed the larvae very shortly after immersion in the solution.

Comparable results were obtained using ascorbic acid.

A brief explanation should perhaps be given of the reasons why the effect of these two rather unusual reagents was tested. Observations by one of us (K. A. P.), referred to in Harris (1946), suggest that the cement which is used to attach a number of sedentary marine animals (barnacles, mussels) to the substratum is formed from a mucoprotein basis, which is 'tanned' by the action of a quinone, in a manner similar to that described by Pryor (1940) for the cuticle of insects. It seemed possible that the cement which attaches the stolonial perisarc of *Tubularia* to the substratum was of a similar nature and the effect of these compounds was therefore investigated to test this possibility. Benzoquinone was used to provide a quinone already present in solution (in the insect cuticle the quinone is formed by oxidation from the corresponding dihydroxyphenol) and so possibly to 'tan' the mucoprotein rapidly and so prevent attachment because the mucoprotein cement had not spread sufficiently. The effect of ascorbic acid was investigated because this compound has been found (Evans & Raper, 1937) to be capable of reducing dopa quinone to dopa in the tyrosinase—tyrosine reaction (which in some respects parallels the reactions which occur as a mucoprotein becomes 'tanned'). The effect of the addition of ascorbic acid might, therefore, be to prevent 'tanning' of the mucoprotein of the cement by the prevention of oxidation of the dihydroxyphenol to the corresponding quinone. Apart from the stimulatory effects noted in Table IV, no particular effect on attachment was produced by either of these reagents.

(iv) *The presence of bacterial slime.* All the experiments on the rate of settlement of the actinula larva so far described were carried out in clean glass vessels. Such a substratum is probably highly abnormal, and an attempt was made to produce a substratum which was slightly more normal by carrying out settlement experiments in glass dishes in which sea water had been allowed to stand for a week. When this was poured away, a thin slime film, probably bacterial in origin, was present over the bottom and sides of the dish. Settlement was appreciably heavier on this surface than on a clean glass surface 24 hr. after the addition of freshly liberated actinula larvae.

The general impression gained from this series of experiments is that a variety of conditions can stimulate attachment. In fact, the reaction of an actinula larva to a disadvantageous environment seems to be that it becomes permanently attached. The reason for this may well be in the sequence of changes that takes place between liberation and settlement. The ectoderm at the tip of the aboral pole of the actinula larva is deeply columnar and its cells are packed with dark granules. The general appearance of this tissue, which is clearly discernible before the larva is liberated (Lowe, 1926), suggests that it is secretory in function. It would seem likely that this region of the ectoderm secretes the attachment cement, and it begins to do so when the aboral pole of the larval body comes into contact with the substratum. Normally this cannot happen until this region of the body has elongated, since the stiff aboral tentacles hold it away from the substratum. If, however, the aboral tentacles were to lose their rigidity for any reason, this 'fixation area' would prematurely be brought into contact with the substratum. As one of the first effects of a disadvantageous environment is to cause the aboral tentacles to lose their rigidity, it seems plausible to suggest that this is the reason why such a diverse series of conditions produce a similar effect.

The suggestion advanced in the preceding paragraph involves the assumption that the secretion of cement is possible whenever the aboral pole of the larva comes into contact with the substratum. Direct experimental proof that this assumption is correct is not yet available, but a number of observations, both under laboratory and under field conditions, suggest that this is so. Under laboratory conditions the high percentage settlement almost invariably obtained suggests that attachment is a passive process in the sense that it occurs as soon as the requisite part of the body comes into contact with a substratum, and, under field conditions, the wide range of substrata upon which settlement can occur also supports this suggestion. Settlement will not only take place readily on smooth surfaces such as glass or bakelite, and not only on rather rougher and more irregular surfaces such as ground glass or the compartments and opercula of barnacles, but also on substrata which are unstable and upon which practically no other sedentary animal seems able to settle. For example, the surface of certain types of resin-containing compositions soon becomes coated with a thick layer of jelly-like slime, which is probably bacterial in origin and which forms a most unstable substratum; actinula larvae settle in numbers on such slimes, though the young colonies are lost as soon as the slime layer peels away from the paint surface beneath. Again, anti-fouling compositions containing cuprous oxide which have a leaching rate which lies between 10 and 20 mg. copper/m.^{2}/day, acquire a felt-like algal settlement (formed, at least in part, by *Ectocarpus*) which soon completely covers the paint surface: *Tubularia larynx* is one of the few organisms which can settle and grow on this type of surface.

Algal growth of other kinds, such as *Enteromorpha* or the more normal tufted growth form of *Ectocarpus*, generally prevents settlement, but this effect is only evident if the algae exceed a certain length. In the course of exposures made to study the settlement and growth of *Tubularia larynx*, which are described more fully in the next section, it was found that settlement of the actinulae occurred readily in the presence of these algae if the latter did not exceed 2 mm. in length. This suggests that sporelings of greater length, provided their settlement was sufficiently dense, were perhaps capable of preventing contact between the actinula and the substratum. Occasionally actinula larvae succeed in settling *on* the filaments of well-grown *Ectocarpus*, and settlement will occur readily on the fronds of *Laminaria*, observations which suggest there is little inimical in an algal surface *per se*.

POST-SETTLEMENT CHANGES

Growth and maturity

The changes which take place in the actinula larva immediately after settlement are shown in Fig. 2. Fig. 2A shows a young form very shortly after settlement has taken place; Fig. 2B the same individual just over 7 hr. later, and Fig. 2C its appearance after a lapse of a further 12 hr. These figures emphasize the extremely rapid elongation which occurs immediately after settlement; over a period of some 19 hr. the overall length increased from 0·98 to 1·65 mm. The cell layers of the body wall become much thinner during this process and it would, therefore, seem that this elongation is due rather to the redistribution of tissue already formed than to the production of new tissue.

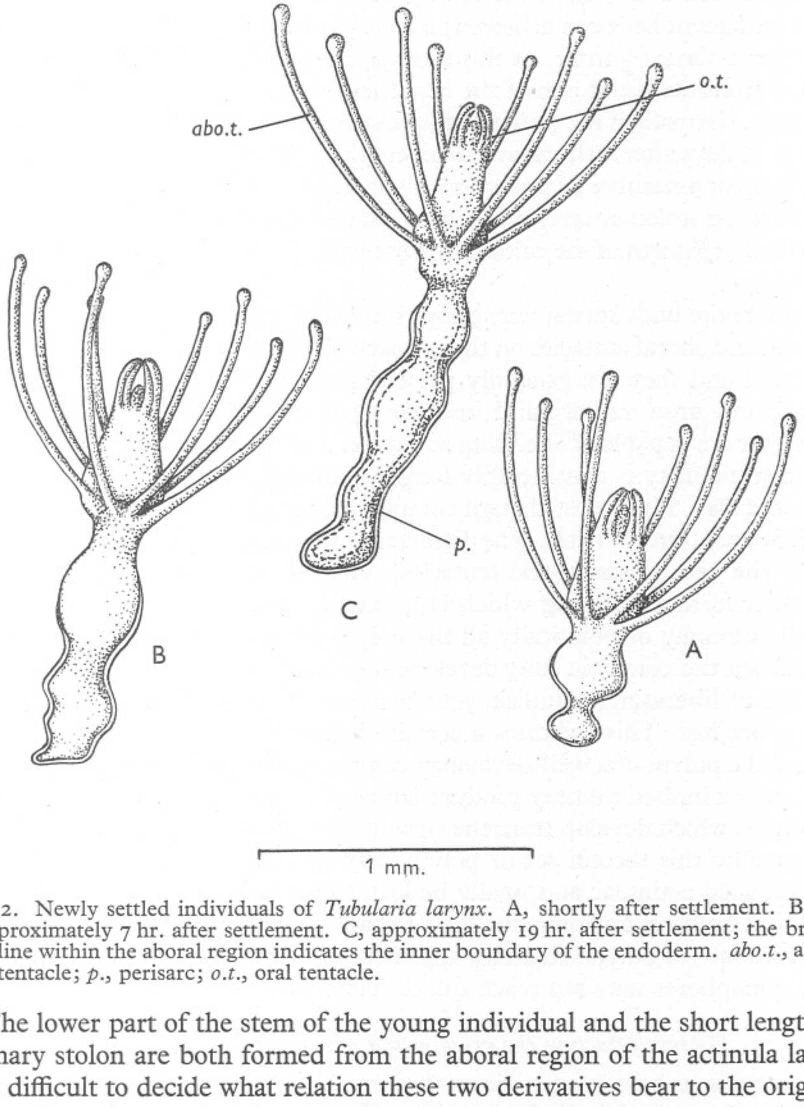


Fig. 2. Newly settled individuals of *Tubularia larynx*. A, shortly after settlement. B, approximately 7 hr. after settlement. C, approximately 19 hr. after settlement; the broken line within the aboral region indicates the inner boundary of the endoderm. *abo.t.*, aboral tentacle; *p.*, perisarc; *o.t.*, oral tentacle.

The lower part of the stem of the young individual and the short length of primary stolon are both formed from the aboral region of the actinula larva. It is difficult to decide what relation these two derivatives bear to the original point of attachment, but it seems plausible to suggest that elongation on one side of this point leads to the production of stolon, whereas elongation on the other side leads to the production of stem. For the latter, it must be presumed that elongation is initially not equal at all points, since the stem bends sharply away from the substratum. The aboral tentacles, it will be noted, are now all directed away from the substratum, but their tips are still swollen at this stage; they lose this characteristic later.

Following this stage of elongation there is one in which growth of the stolon predominates. This part of the colony may measure 0·3 mm. in length shortly after settlement has been achieved; 2 days later its length is 0·8 mm., and after a further 2 days 1·3 mm. At this stage a second polyp often appears, usually arising from the tip of one of the branches of the stolon and growing rapidly upwards. Growth of the stolon continues to predominate for some time longer, so that 11 days after settlement a total length of stolon of 7 mm. may be present (made up of a number of branches) associated with about eight polyps. Once a branching stolonial system has been established in this way, it is probable that further growth of the colony chiefly results in the production of stems and polyps.

Gonophore buds appear very early. For example, buds were visible between the oral and aboral tentacles on the primary polyp by the time the second polyp appeared and they are generally present some 7 days after settlement. The gonophores grow rapidly and just over 3 weeks (24 days) after settlement a number are capable of shedding actinulae. This estimate of the period taken to reach maturity is considerably longer than that found by Orton (1929) at Cawsand Bay, Plymouth, though comparable with the estimate he gave in an earlier paper (Orton, 1914). The diameter of the polyps is then 2 mm. measured across the base of the aboral tentacles. Growth of the polyps continues for a further fortnight during which large numbers of actinulae are shed, after which autotomy of practically all the polyps occurs. It is of interest to note that, when the colony is fully developed, only a proportion of the polyps are capable of liberating actinulae, yet when autotomy occurs, practically all the polyps are lost. This indicates a certain degree of differentiation of function among the polyps of a well-developed colony, in that while all can presumably feed, only a limited number produce larvae. The polyps lost are later replaced by others, which develop from the tips of the stems of the established colony. Presumably this second set of polyps may themselves grow, develop gonophores, shed actinulae and finally be lost, but it has not yet been possible to carry out field observations for long enough to prove this point. Successive 'generations' of polyps certainly appear under laboratory conditions, though their gonophores may not reach full development.

Factors affecting the growth and development of the colony

Observations have been made on the general biology of colonies of *Tubularia larynx* by exposing standard microscope slides (3 × 1 in.), with one face slightly roughened (using 80-mesh carborundum powder), on painted steel plates adapted to act as carriers for these slides. Each side of each plate can accommodate 27 slides, arranged in three rows, 9 slides to a row. These steel carriers can readily be bolted to the standard frames used for the exposure of painted steel plates; extensions to the frames allow carriers to be immersed at a number of depths. Exposures of this kind were made in 1946 and 1947, four carriers being used on each occasion; they were immersed at depths of 27, 45, 64 and 84 in. (approximately 0·7, 1·1, 1·6 and 2·1 m.) below the water surface. One slide was withdrawn from each row of each face of each carrier at approximately weekly intervals (the period between withdrawals was varied slightly according to the amount of change that was taking place at the time) and replaced by a clean slide. These slides which were withdrawn at intervals over the whole period of the experiment are termed the basic series in the description below. The slides which replaced them were themselves later withdrawn, some at approximately weekly and some at approximately 3-weekly intervals—these slides formed the weekly and the 3-weekly series mentioned later. After withdrawal, each slide was examined in detail and its various settlements and their characteristics recorded.

The slide series were immersed on 31 July both in 1946 and 1947. In 1947 immersion was continued until 10 October, but in 1946 the exposure period only lasted until 19 September.

Fig. 3 gives the general results of growth-rate measurements in 1946 and 1947. It was clearly impossible to attempt to measure growth by measurements of individual colonies, as only a few colonies could be dealt with in this way at the expense of a great amount of labour. As a rough estimate, therefore, the volume of *Tubularia* on each slide was determined. Using this method the growth on a number of slides could be rapidly estimated; the disadvantage was that reliable measurements were not possible until some time after settlement, as volumes less than 0·2 ml. could not be measured with sufficient accuracy. The results shown in Fig. 3 indicate that the initial growth rates were substantially the same in both years.

When, however, the numbers of new settlements per slide on the basic series of slides are compared for the 2 years (Fig. 4), considerable differences are evident. In 1946 the numbers of new settlements recorded showed a sharp increase between 4 and 5 weeks after the experiment began, whereas in 1947 the increase was much smaller, though it occurred at approximately the same time after immersion. Evidence will be presented later which suggests that the number of new settlements depends upon the state of maturity of the polyps in the immediate vicinity, i.e. those on the same slide or on its neighbours. The results obtained in 1946, therefore, indicate that considerable numbers of actinulae were released at almost the same time; but those obtained in 1947 may mean either that the numbers were much smaller (owing to poor development of the polyps) or simply that the actinulae were not able to settle.

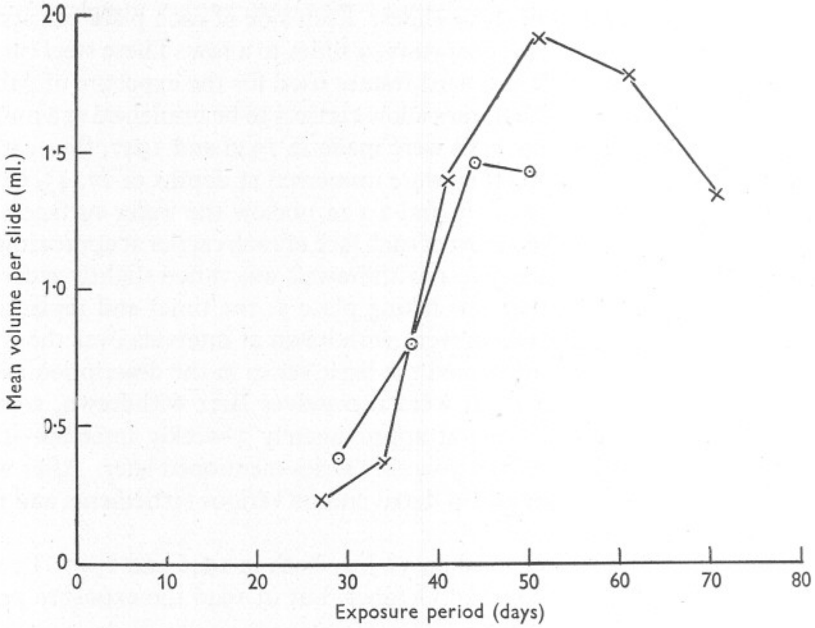


Fig. 3. Growth rates of *Tubularia larynx* in 1946 and 1947 (as indicated by increase of volume of the colonies) on the basic series of slides. —⊙—, 1946; —×—, 1947.

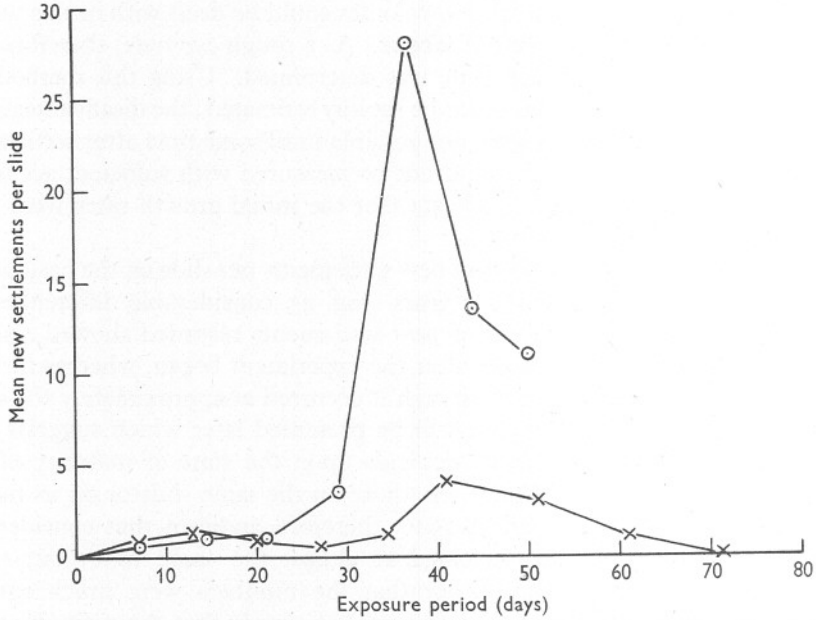


Fig. 4. New settlements of *Tubularia larynx* in 1946 and 1947, on the basic series of slides. —⊙—, 1946; —×—, 1947.

Other evidence suggests that the second explanation is probably correct. The first 5 weeks of the exposure period in 1947 were characterized by an unusually high proportion of sunny, calm days and the light intensity down to the depth covered by these slide exposures was probably greater than that for the corresponding period in 1946. This difference in environmental conditions would favour the growth of algae and, as is shown in Table V, their settlement was certainly heavier at all depths, and growth, at least of *Ectocarpus*, greater at all depths in 1947 than in 1946.

TABLE V. SETTLEMENT AND GROWTH OF ALGAE AT VARIOUS DEPTHS, AUGUST 1946 AND AUGUST 1947

Depth below sea level		*Enteromorpha* sp.		*Ectocarpus* sp.	
In.	M.	1946	1947	1946	1947
27	0·7	V. Fr. (4·8)	V. Fr. (2·5)	V. Fr. (6·6)	V. Fr. (7·6)
45	1·1	Occ. (s)	Fr. (s)	Occ. (s)	Fr. (5·6)
64	1·6	Rare (s)	Fr. (s)	Rare (s)	Fr. (3·8)
84	2·1	V. Ra. (s)	Fr. (s)	V. Ra. (s)	Rare (1·0)

V. Fr., Very Frequent; Fr., Frequent; Occ., Occasional; V. Ra., Very Rare.
The figures in parentheses are the mean lengths (in mm.) of the algal filaments. (s) indicates present only as sporelings.

These results refer to the basic series of slides; the 3-weekly and the weekly series, since their exposure periods are shorter and their chances of extensive algal colonization therefore less, should, if this suggestion is correct, indicate numbers of settlements which are more comparable for the 2 years. The results shown in Fig. 5 are in agreement with this suggestion. As might be expected, the difference between the 3-weekly series of 1946 and that of 1947 is greater than that between the weekly series; the numbers of new settlements on the latter are, within the limits of accuracy of an experiment of this sort, closely similar in 1946 and 1947.

Counts of the number of new settlements on slides exposed at various depths in 1946 showed that settlement did not take place predominantly at any of the depths investigated, but measurements of the mean volume of colony per slide at different depths suggested that the colonies attained a greater size when growing at depths greater than 4 ft. (1·2 m.) than they did when growing nearer the surface.

The presence of a mature colony contributes substantially to the amount of settlement which takes place in its immediate vicinity. When the experiments described earlier in this section were started, surfaces only a few feet away from the slide carriers bore large numbers of mature colonies of *Tubularia larynx*, yet settlement on the slides did not become heavy until some weeks later. This result might have been due to one of two causes; either the surfaces were, for some reason, not suitable for settlement immediately after immersion, or heavy settlement must be dependent upon the close proximity of mature colonies.

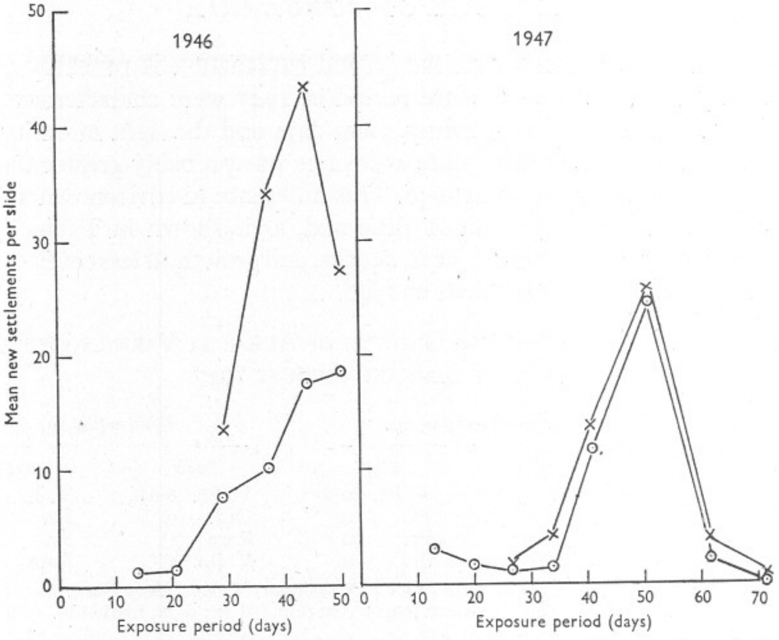


Fig. 5. New settlements of *Tubularia larynx* in 1946 and 1947, on the weekly and 3-weekly series of slides. —⊙—, weekly series; —×—, 3-weekly series.

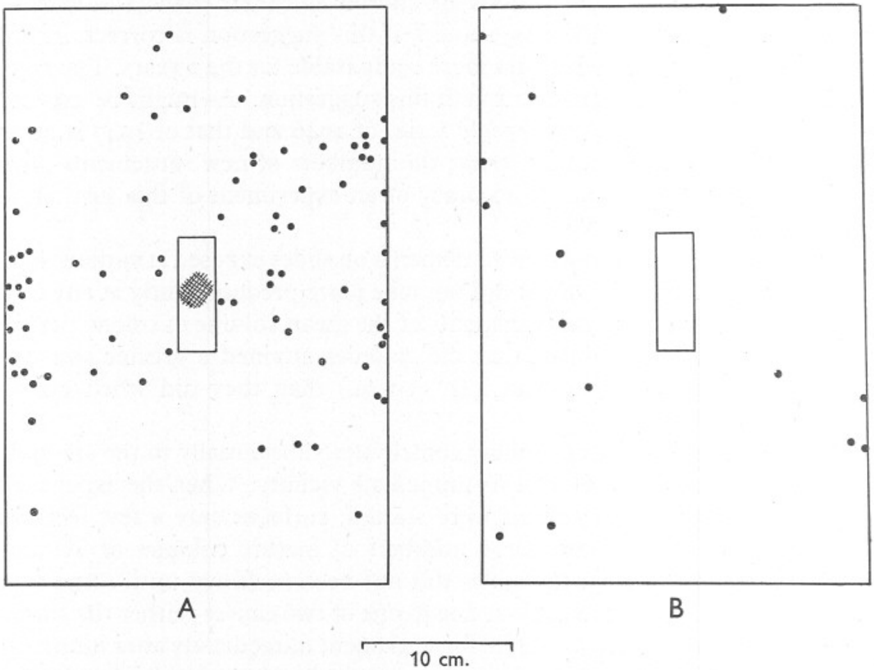


Fig. 6. New settlements of *Tubularia larynx* on (A) a wooden panel with a glass microscope slide fixed centrally bearing a colony of *T. larynx* and on (B) the same with the microscope slide clean. The position of each new settlement is indicated by a black circle.

Moore (1939) has described the lag in colonization of a newly prepared artificial surface, and it seemed conceivable that newly immersed glass slides might show a comparable lag. That this was not the factor which delayed settlement of the actinulae of *T. larynx* was clearly shown by an experiment in which freshly prepared slides were immersed beside slides which had been in the sea for some weeks, but which had their gross fouling removed. Settlement and growth on the two series was found to be closely similar.

This result suggests that the second possibility is the more likely and this is supported by the following experiment. A glass slide, bearing a mature colony of *T. larynx*, was set in the middle of a wooden panel, 10 × 15 in., and immersed from a raft which itself bore practically no *Tubularia*; a control exposure consisting of an uncolonized slide set in the middle of a similar panel was immersed close beside it at the same time. The amount of settlement on the two surfaces after a period of 11 days' immersion is shown in Fig. 6, and clearly indicates the heavier settlement which occurs in the vicinity of a mature colony.

BIOTIC ENVIRONMENT

Once settlement has been achieved and growth begun other organisms soon begin to be associated with, or to prey upon, the colony of *Tubularia larynx*. Under the conditions in which most of the colonies were studied in this investigation, where the colony of *T. larynx* was the largest colonizing form, the bases of the colonies soon began to accumulate the muddy tubes of *Jassa* sp., and also frequently bore clusters of small mussels (*Mytilus edulis* L.) which are usually settling in some abundance at the time that settlement of *Tubularia larynx* is becoming intense. The stems of the colonies quickly became colonized by Suctorians, chiefly *Ephelota* sp. and *Acineta* sp. The settlement of these Protozoa appeared to be successive in 1946, as *Ephelota* sp. predominated until early September, whereas *Acineta* sp. was more common later in the season. Diatoms, especially *Licmophora* spp. and *Striatella* sp., were also conspicuous on the stems of well-grown colonies, especially towards the end of September or early in October; the colonies of *Tubularia larynx* were then sometimes dark brown in colour due to the dense covering of these diatoms.

All these forms are merely associated with the colonies of *T. larynx*, and do not appear to have any predatory or parasitic relationships with the hydroid. Others, however, are predators or parasites.

The pycnogonid, *Phoxichilidium tubulariae* Lebour, is commonly to be found among colonies of *Tubularia larynx*, a habitat similar to that recorded by Lebour (1945) for *Phoxichilidium tubulariae* at Plymouth. The larvae of this pycnogonid occur within the gastral cavity of *Tubularia larynx* and, though a few larvae can usually be detected in this situation late in September, they seem only to be really abundant if well-developed colonies of *Tubularia* are present in some abundance at this time. Normally *T. larynx* is beginning to die down at the end of September, but if, as in 1945, it is flourishing early in October, practically every colony has several polyps which contain the larvae of *Phoxichilidium tubulariae*. Development of the latter must be rapid, as on one occasion colonies of *Tubularia larynx*, collected from a surface that had been immersed for only 24 days, contained advanced larvae of *Phoxichilidium tubulariae*. As some part of this immersion period must have been occupied by settlement and initial growth of the *Tubularia* colony, it is reasonable to suppose that the larvae of *Phoxichilidium* must have developed to this stage in less than 20 days. Lebour (1945) states that these larvae do not appear to harm the polyp in which they occur. We have found that such a polyp is usually abnormally distended, but that it seems otherwise normal. Because colonies of *Tubularia larynx* are so resistant to copper, experiments have been carried out in which this hydroid was immersed in copper solutions of different concentrations; on some occasions colonies with polyps containing the larvae of *Phoxichilidium tubulariae* were used for these experiments, but the sensitivity of infected colonies to this poison did not differ appreciably from that of colonies in which the polyps were uninfected.

The Holotricha, *Choenia* sp. and *Loxophyllum* sp., are also commonly found on colonies of *Tubularia larynx*. *Choenia* sp. is the more abundant: it feeds on newly settled forms, and is to be found in large numbers on mature polyps shortly before these are lost and also on and in moribund stems.

Numbers of nudibranch molluscs, particularly *Cratena aurantia* (Alder & Hancock) and *Dendronotus frondosus* (Ascanius), occur about the time that settlement and growth of *Tubularia larynx* reaches its maximum. Both feed on the polyps; the numbers of *Cratena aurantia* which occur suggest that this species may play a significant part in the reduction in the numbers of polyps which takes place at the end of the season. It would seem unlikely, however, that *C. aurantia* is the primary cause of this reduction.

Discussion

General observations in the field, as well as the results of experimental work, indicate that settlement of actinula larvae is heaviest in the immediate vicinity of a mature colony, which suggests that settlement occurs shortly after liberation. Laboratory observations, on the other hand, indicate that a period of the order of 24 hr. must elapse before an appreciable proportion of the larvae become attached. This discrepancy may occur because of the unnatural conditions under which laboratory observations must be carried out, but as observations suggest that in a healthy actinula larva elongation of the aboral pole of the larva must occur before the attaching surface can come into contact with the substratum, it would be expected that an interval should elapse between liberation and attachment in the sea. In fact, it is conceivable that under field conditions the interval might be slightly longer, since the water temperature is lower in the sea than in the laboratory. It is not known how the larva remains in contact with the substratum during this interval, but experiments carried out in the course of this investigation suggest that it is capable of remaining attached, even to a smooth, clean glass surface, in moderate water currents. In a more natural environment, attachment is likely to be more secure.

The actual means whereby this initial attachment is effected are not yet certainly known. It is possible that the tips of the aboral tentacles adhere to the substratum by means of an adhesive secretion (Orton (1929) speaks of the actinula larva of *Tubularia larynx* as 'highly adhesive'), but the experimental results do not agree well with such a hypothesis. For, if an adhesive secretion is produced, it is perhaps possible that the amount of this secretion might be increased under the stronger stimulus of faster water-flow, but it is more difficult to see why a decrease in the current, followed by a more sudden increase, should almost always cause the larvae to be dislodged. Another possibility is that attachment may be effected by means of nematocysts. The swollen tips of the aboral tentacles contain large numbers of nematocysts which, to judge by the extreme ease with which this part of these tentacles becomes attached to a needle, may be very sensitive to mechanical stimuli. Ewer (1947) has recently shown that the tentacles of the buds of *Hydra vulgaris attenuata* become attached temporarily to the substratum by means of atrichous isorhizas which lie in the nematocyst batteries in the tentacles; it would seem possible that at least some of the nematocysts in the tips of the aboral tentacles of the actinula larva have a similar function.

The results of the experiments on the effect of different current speeds on the rate of liberation of actinulae (though these experiments can only be regarded as preliminary in nature) are of interest, in that they suggest that larval liberation takes place only at periods of the tide when the larvae are least likely to be swept away in rapid tidal currents. They are in agreement with observations made on plankton hauls taken in the vicinity of mature *Tubularia* colonies. Tow-nettings have regularly been taken, during the ebb tide, from a point only a few yards from a raft bearing hundreds of mature colonies of *T. larynx*, but only individual larvae have been found when the haul was examined. Even if a plankton net is placed close against the side of a plate bearing large numbers of mature colonies, the result is much the same. This suggests that the number of larvae present in the water when the tide is running strongly is very small but, whilst this supports laboratory observations on the effect of current speed on the liberation of actinulae, these field results must be cautiously interpreted since many larvae may be caught up in the meshes of the net.

If further work substantiates the preliminary results of the effect of different current speeds on the rate of liberation of larvae, the question is then raised of the nature of the stimuli which initiate and stop liberation. Liberation of actinulae can be almost completely inhibited (in still water) by the addition of small amounts (0·5 %) of NaCl, KCl and $CaCl_2$; the effect of potassium in this respect can partly be antagonized by the simultaneous addition of $MgCl_2$. These results, which are closely parallel to the effects of these metallic ions on the contraction of smooth muscle, suggest that the immediate cause of liberation is contraction of the muscular elements of the gonophore, but do not indicate the nature of the stimulus responsible for initiation of the contraction. Further work is needed on this point.

A number of the observations made in the course of this work suggest that the colony of *T. larynx* should be regarded as a unit to a degree greater than that which is sometimes accorded to a hydroid colony. Some degree of functional differentiation among the individual polyps (in that only a small proportion bear mature reproductive organs) and the possibility that the life period of a single polyp is shorter than that of the colony both suggest that the unit is the colony rather than the polyp, and that the activities and development of the latter depend upon the general state of the former. When the colonies die down at the end of September or at the beginning of October, it is not easy to discover any external cause of this change. No rapid changes are taking place in water temperature and, though the depredations of *Cratena aurantia* (A. & H.) and other nudibranchs cause the loss of some polyps, such effects are commonly no greater then than they have been for some time earlier. Further, the fact that, at the time when the main mass of *Tubularia* colonies which have provided the bulk of the season's growth are dying down, a small number of new settlements are growing makes it unlikely that any external factor is the cause of the general decline. Hammett (1946) concludes that endogenous factors play an important part in the general economy of *Obelia* colonies towards the end of their period of abundance, and it is difficult to resist the conclusion that such factors also play an important part in causing the degeneration of colonies of *Tubularia larynx* at the end of the summer.

Settlement and growth of *T. larynx* at Millport normally reach their maximum during August and September, but the general seasonal sequence is not always regular. In 1945 heavy settlement began early rather than late in July, but at the beginning of August all the colonies became moribund, and autotomy of the polyps occurred. Regeneration did not take place until the middle of September and then the main mass of the *Tubularia* settlement persisted until towards the end of October. There were some signs that a similar phenomenon was about to take place early in August 1947, but the process of decline was arrested at an earlier stage and the period of vigorous growth and development was not substantially interrupted. The causes of such variations in the normal seasonal sequence are unknown, since no disadvantageous environmental factor, either edaphic or biotic, could be detected over the period when the interruption occurred. The observation that vigorous growth can persist through October, if the normal seasonal sequence has been interrupted by a period when the colonies are dormant does, however, offer some support for the suggestion that endogenous factors play a part in the autumnal decline of this hydroid.

We are indebted to the Marine Corrosion Sub-Committee of the British Iron and Steel Research Association for permission to publish this work, which was carried out in the course of an investigation of the general biology of fouling organisms. One of us (F. S. D.) was assisted by an expenses' grant from the Research Association, for which grateful acknowledgement is made. We should especially like to record our acknowledgement of the interest shown by Prof. J. E. Harris, Chairman of the Sub-Committee, and by the late Mr R. Elmhirst, Director of the Marine Station, Millport, in the progress of this work. We should also acknowledge the help of the Director of the Plymouth Marine Laboratory in providing a sample of *Tubularia larynx* for comparison with our own material.

SUMMARY

A description is given of a number of observations and experiments on the larvae and colonies of *Tubularia*. The experimental material could best be referred to the species *T. larynx* Ellis & Solander. Its characters are not wholly consistent with the diagnosis of this species, but the differences which exist are not great enough to warrant the erection of a new species.

Liberation of the actinulae takes place more freely in darkness than in light, and there is evidence which suggests that it only occurs in still water or in weak currents.

Immediately after liberation the body of the actinula is spherical and it rests on the tips of those aboral tentacles which point away from the mouth. Growth of the aboral region takes place and permanent attachment is possible when this region is long enough to come into contact with the substratum. This elongation takes place over a period of 24–48 hr. under laboratory conditions.

Temporary attachment can take place by means of the tips of the aboral tentacles; it seems likely that this is accomplished by the eversion of nematocysts.

A thin sheath of perisarc is present over the aboral region of the actinula when it is liberated. The perisarc is chitinous in nature, and permanent attachment is secured by means of an extra-chitinous cement, probably secreted by the glandular ectoderm of the aboral pole.

Exposure of the actinula larva to hypotonic sea water, low concentrations of copper and mercury and some organic compounds stimulates permanent attachment. These abnormal environmental conditions cause a decrease in the rigidity of the aboral tentacles; this allows the aboral pole of the larva to come into contact with the substratum prematurely.

Growth is rapid once permanent attachment has taken place. An extensive stolonial system is first established, followed by the production of a number

of stems and polyps. Gonophore buds appear on the primary polyp 2 days after settlement and some polyps can liberate actinulae 24 days after settlement. Most of the actinulae produced by a colony settle, if suitable substrata are available, in its immediate vicinity.

Only some of the polyps in any one colony liberate actinulae. Liberation continues for some days and is followed by autotomy of all the polyps in the colony. These are later replaced.

The biotic environment of the grown colony is briefly described.

REFERENCES

ALLMAN, G. J., 1871–72. *A Monograph of the Gymnoblastic or Tubularian Hydroids.* Parts I and II. London.

BARNES, H., 1948. Studies on anti-fouling compositions. IV. The relationship between leaching rate, copper loss and anti-fouling performance under raft and service conditions. *J. Iron and Steel Inst.*, 1948, pp. 175–85.

BARTH, L. G., 1940. The process of regeneration in hydroids. *Biol. Rev.*, Vol. XV, pp. 405–20.

BRAUER, A., 1891. Über die Entstehung des Geschlechtsapparates und die Entwicklung von *Tubularia mesembryanthemum. Zeitschr. f. Wiss. Zool.*, Bd. LII, pp. 551–79.

CIAMICIAN, J., 1879. Ueber den feineren Bau und die Entwicklung von *Tubularia mesembryanthemum* Allman. *Zeitschr. f. Wiss. Zool.*, Bd. XXXII, pp. 323–47.

CONN, H. W., 1882. Development of *Tubularia cristata. Zool. Anz.*, Bd. V, pp. 483–84.

ELMHIRST, R., 1923. Notes on the breeding and growth of marine animals in the Clyde sea area. *Ann. Rep. Scot. Mar. Biol. Assoc.*, 1922, p. 20.

EVANS, W. C. & RAPER, H. S., 1937. The accumulation of 1-3:4-dihydroxyphenylalanine in the tyrosinase-tyrosine reaction. *Biochem. Journ.*, Vol. XXXI, pp. 2162–70.

EWER, R. F., 1947. On the functions and mode of action of the nematocysts of *Hydra. Proc. Zool. Soc. Lond.*, Vol. CXVII, pp. 365–76.

GRAVE, C. & NICOLL, P. A., 1939. Studies of larval life and metamorphosis in *Ascidia nigra* and species of *Polyandrocarpa. Pap. Tortugas Lab. Wash.*, Vol. XXXII, pp. 1–46.

HAMMETT, F. S., 1946. Correlations between hydranth components of *Obelia* colony populations. *Growth*, Vol. X, pp. 89–172.

HARRIS, J. E., 1946. Report on anti-fouling research, 1942–44. *J. Iron and Steel Inst.*, 1946, II, pp. 297P–333P.

KLUGH, A. B., 1929. The effect of the ultra-violet component of sunlight on certain marine organisms. *Canad. J. Res.*, Vol. I, pp. 100–09.

KORRINGA, P., 1940. Experiments and observations on swarming, pelagic life and setting in the European flat oyster, *Ostrea edulis* L. *Arch. Néer. Zool.*, Vol. V, pp. 1–249.

LEBOUR, M. V., 1945. Notes on the Pycnogonida of Plymouth. *Journ. Mar. Biol. Assoc.*, Vol. XXVI, pp. 139–65.

LOWE, E., 1926. The embryology of *Tubularia larynx* (Allm.). *Quart. Journ. Micr. Sci.*, Vol. LXX, pp. 599–627.

MOORE, H. B., 1939. The colonization of a new rocky shore at Plymouth. *J. Anim. Ecol.*, Vol. VIII, pp. 29–38.

ORTON, J. H., 1914. Preliminary account of a contribution to an evaluation of the sea. *Journ. Mar. Biol. Assoc.*, Vol. X, pp. 312–26.

—— 1929. Experiments in the sea on the growth-inhibitive and preservative value of poisonous paints and other substances. With some chemical analyses by the Government Chemist. *Journ. Mar. Biol. Assoc.*, Vol. XVI, pp. 373–452.

PRYOR, M. G. M., 1940. On the hardening of the cuticle of insects. *Proc. Roy. Soc. London*, B, Vol. CXXVIII, pp. 393–407.

PRYTHERCH, H. F., 1934. The role of copper in the setting, metamorphosis and distribution of the American oyster, *Ostrea virginica*. *Ecol. Monogr.*, Vol. IV, pp. 49–107.

SALENSKY, W., 1911. Solmundella und Actinula. *Mém. Acad. Sci. St.-Pétersb.*, Ser. 8, Vol. XXX, pp. 1–70.

ON THE BIOLOGY OF THE SMALL COPEPODS IN LOCH STRIVEN

By S. M. Marshall, D.Sc.

From the Marine Station, Millport

(Text-figs. 1–32)

CONTENTS

INTRODUCTION

The importance of copepods in the economy of the sea is generally recognized, but our knowledge of their seasonal variations in breeding and growth is as yet very incomplete. The object of the present investigation is to study throughout a year the variations in the small copepods of Loch Striven in the Clyde sea area. Fortunately, the tow-nettings which had already been studied for *Calanus finmarchicus* (Marshall, Nicholls & Orr, 1934) were available and offered an opportunity of comparing the seasonal changes in the small copepods with those in *Calanus* and in the phytoplankton. The hauls were therefore re-examined and the small copepods picked out and separated into their developmental stages.

Details of the method of taking the hauls are given in the paper mentioned above. It is sufficient to say here that on each occasion five vertical hauls were taken with a modified Standard International Net of fine silk (200 meshes to the inch), and that from 27 March to 21 August inclusive one of the five was taken in two parts, the first from the bottom (60–70 m.) to 10 m., and the second from 10 m. to the surface. The five hauls were examined by eye, and if the four undivided hauls appeared to be similar they were mixed together; if one appeared decidedly different from the rest, it was kept separate and either not counted, or its figures not included in the final estimate. The divided haul was of course always counted separately.

Figures and tables giving data for temperature and numbers of phytoplankton organisms on the dates when the hauls were taken are given in the paper cited above.

Methods of preservation, sampling and measurement were the same as described by Nicholls (1933) and Marshall (1933). In all but the first five stations where, for *Oithona*, only one-fifth of the catch was counted, the procedure was as follows. One-tenth of the catch was examined, and all stages of all copepods picked out. If the total number of any stage reached 100 in this tenth, it was not separated from the remaining nine-tenths of the catch. Subsequent tenths of the catch were examined and the other stages of the copepods picked out until a hundred of each stage had been separated from a known fraction of the catch or until the whole catch had been examined.

On a few occasions when the nauplii of a species were very numerous they were counted in one-twentieth of the catch. Winsor & Walford (1936) have shown that counting individuals beyond the number of 100 adds very little to the accuracy of the estimate of the population.

It frequently happened that the numbers in the divided haul were lower than those of the undivided haul average, and I am much indebted to Dr H. Barnes for studying the statistics of these variations in number. The results of his examination are not yet complete. However, it may be tentatively stated that there is considerable evidence that a proportion of the catch is lost in the divided hauls; this loss affects the numbers below 10 m. only. The loss was not constant throughout the season, but on occasion it was of the order of 50 % of the total catch below 10 m.

The figures for the vertical distribution determination have necessarily to be obtained from the counts of these divided hauls, and the actual proportions above and below the 10 m. level may therefore be subject to a variable error; qualitatively the seasonal changes are accurately represented.

When, according to the counts of *Calanus* already made by Dr A. G. Nicholls (1933), the divided and undivided hauls did not differ much, only the former was counted. This was so on ten dates between 27 March and 21 August; on twelve the undivided were also sampled and counted. In plotting the total numbers and percentage distribution of the stages (Figs. 1–14) throughout the season the estimates from the undivided hauls were used when available; those from the divided haul only are marked with an asterisk.

THE SPECIES AND THEIR REPRODUCTION

Nine species occurred in Loch Striven, six of them in abundance. *Pseudocalanus* and *Microcalanus* occurred throughout the year. Following With (1915) *Pseudocalanus minutus* (Krøyer) is taken to include *P. elongatus*, and *Microcalanus pygmaeus* G. O. Sars to include *M. pusillus* G. O. Sars.

Paracalanus parvus (Claus) occurred also, but, apart from nauplii of which a few were probably always present, not in numbers until July. Two species of *Centropages* occur. *C. hamatus* (Lilljeborg) was the common species; *C. typicus* Krøyer appears occasionally in the Clyde sea area, but it was not observed in the Loch Striven catches. *Temora longicornis* (Müller) and *Acartia clausi* Giesbrecht were the common representatives of their genera. *A. discaudata* (Giesbrecht) has been observed in the Clyde sea area, but not in Loch Striven.

Oithona similis Claus was the most abundant copepod and occurred the whole year round. This species is the one named by Sars (1918, p. 207) *O. similis* (emended from his description of it as *O. helgolandica* Claus (*ibid.*, p. 8)). There are slight discrepancies in the literature about the armature of the exopods of the swimming feet by which the species are distinguished, so the Loch Striven form was examined.

The exopods are three-segmented, and one of the distinguishing characters is the number of external spines and internal setae on the terminal segments of these exopods. In the key given by Wilson (1932, p. 311) the number of external spines on the terminal segments of the first four swimming feet in the female *O. similis* is said to be 2, 1, 1, 1, but in his description of *O. similis* on p. 314 it is given as 2, 1, 1, 0. Rosendorn (1927), in her study of the genus from the material of the *Valdivia* expedition, agrees with Wilson's key. Sars, in his description (1918, p. 8), mentions a spine on the terminal exopod segment of the fourth foot but does not show one in his figure (Pl. III, p. 4). In the Loch Striven specimens the number of external spines on the terminal exopod segments of the first three swimming feet is 2, 1, 1, and on the fourth there is, not a spine, but a fine seta which often lies close to the apical spine and is difficult to see.

Rosendorn gives the number of internal setae on this same terminal exopod segment as 5, 5, 5, 5, for the first four swimming feet, but Sars, in the figure already mentioned, shows only four on the first swimming foot and this agrees with the Loch Striven specimens.

Oithonina nana (Giesbrecht) also occurred; it was most common in February and March, decreased in April and almost disappeared during the summer. Its numbers began to rise again slightly in September and October. In the end of March and in April, when one haul was divided at 10 m., it was almost invariably found in the bottom part of the haul and might there be almost as numerous as *Oithona similis*, which at that time was concentrated in the top 10 m. The nauplii were not distinguished and the numbers of these given for *O. similis* probably include a small number of *Oithonina* nauplii, but even in February and March they were not numerous enough to affect the general result.

The nauplii of *Calanus*, *Pseudocalanus*, *Paracalanus* and *Microcalanus* are difficult to distinguish except by size. When only *Pseudocalanus* and *Micro-*

calanus were present their nauplii could be distinguished fairly easily, but when *Paracalanus* was present also it was much more difficult, and the numbers of nauplii are certainly less accurate than those for copepodites.

The five copepodite stages and the adults (male and female) were all separated, but the six nauplius stages of each species were lumped together. Copepods pass through the nauplius stages so quickly that since visits were made only once a week the proportions of the nauplius stages present could give no information about the development of broods.

The paper by Oberg (1906) was found very useful for identifying the nauplii and that by Kraefft (1910) for distinguishing the sexes of the copepodite stages.

Pseudocalanus minutus (Krøyer)

(Table III and Figs. 1 and 2)

The female does not normally develop a fifth leg, so the sexes can be distinguished easily in copepodite Stages IV and V. Occasional female specimens are found, both adult and Stages IV and V, which have a small fifth leg, but in such females the legs do not resemble those of the males, being smaller. Such specimens have already been described by With (1915). In the Loch Striven samples less than 1 % showed this abnormality (4 Stage IV, 13 Stage V, and 4 adult females).

The percentage distribution of the various stages is shown in Fig. 1 and the variation in total numbers in Fig. 2. It was not found possible to count the eggs in those species of copepod which do not carry an egg-sac, and, for the sake of uniformity, eggs are not shown in Fig. 1. As can be seen in Fig. 2, nauplii usually outnumbered eggs considerably, which is to be expected from the greater length of time (judging from *Calanus*) spent in the nauplius stages. During a good part of June and July, however, eggs were slightly more numerous than nauplii.

In the Fig. 1 type of diagram a developing brood is clearly indicated when the peaks for successive stages move to the right from bottom to top. The peaks for several developmental stages may occur on the same date, since the maximum abundance of any one stage is naturally often missed, but when all the peaks, or a majority of them, occur on the same date it indicates merely a sudden drop in the proportion of nauplii which is usually the most abundant stage.

In most Figures the times when diatoms were rich (arbitrarily fixed as over 100 cells/ml.) are marked along the foot of the diagrams by thick black lines.

When observations began in the middle of January, 50 % of the stock of *Pseudocalanus* consisted of Stage V copepodites, and almost all the rest was made up of eggs, nauplii and adults (Table III, Figs. 1, 2). During the next 4 weeks the Stage V moulted into adults, the females then spawned, and on

20 February over 80 % of the stock was present as eggs and nauplii (Fig. 1). These eggs and nauplii began to develop and the early copepodite stages became more numerous during February and March. From Fig. 1 it looks as if the earlier nauplii of this brood did not complete their development, whereas the later nauplii did (Stage III appeared in numbers first on 27 February, Stage IV not till 4 April), becoming Stage V and adult about the beginning of April. It may be noted that the spring diatom increase began on 13 March

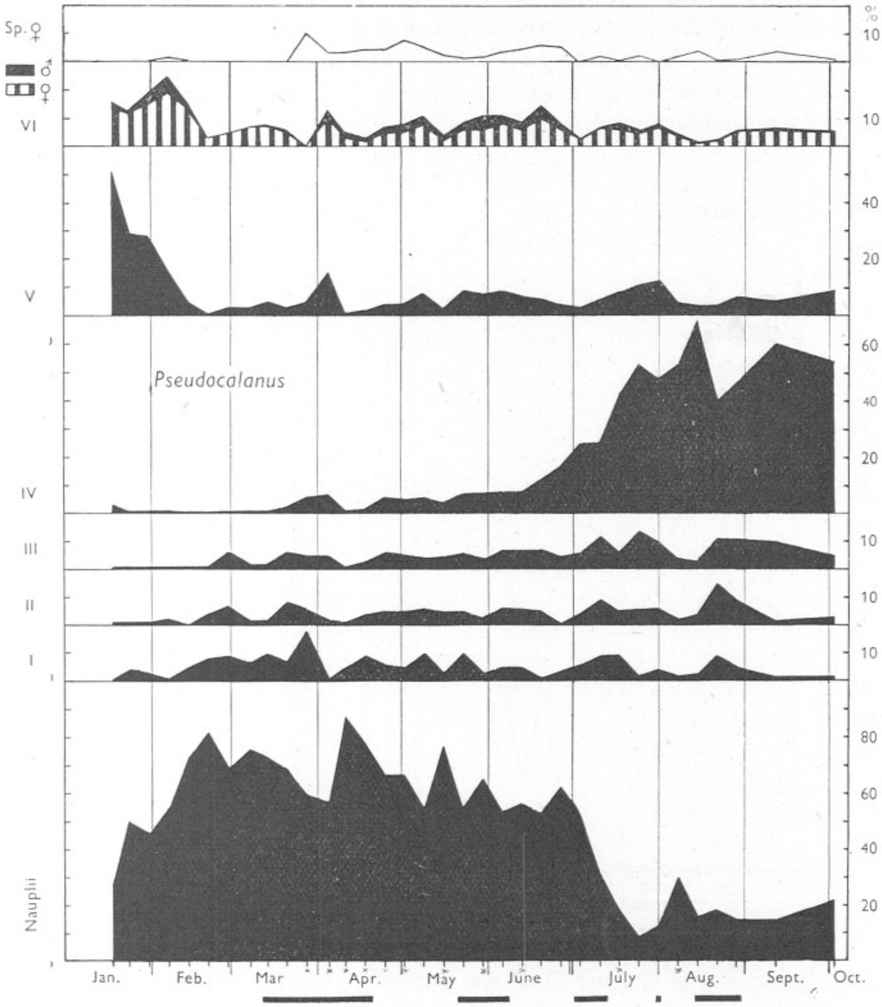


Fig. 1. *Pseudocalanus minutus*. Diagram showing the percentage of the developmental stages during the year. The percentage of adult females with spermatophores (*Sp.* ♀) is shown at the top. An asterisk indicates that counts were from a divided haul only (see p. 46). Periods of main diatom outbursts are marked by thick lines at the bottom of the Figure.

and would supply food for the later-produced nauplii and copepodites but not for the earlier. The actual numbers of the whole of this first brood were small, only a few hundred, and therefore it does not show on Fig. 2.

The adults of the beginning of April gave rise to another increase of nauplii in the middle of the month, whose development can be traced in the succeeding weeks. After this the percentage of nauplii remains high though variable, there are no distinct series of peaks on the curves for copepodite stages and breeding probably goes on continuously until July, when it falls off markedly.

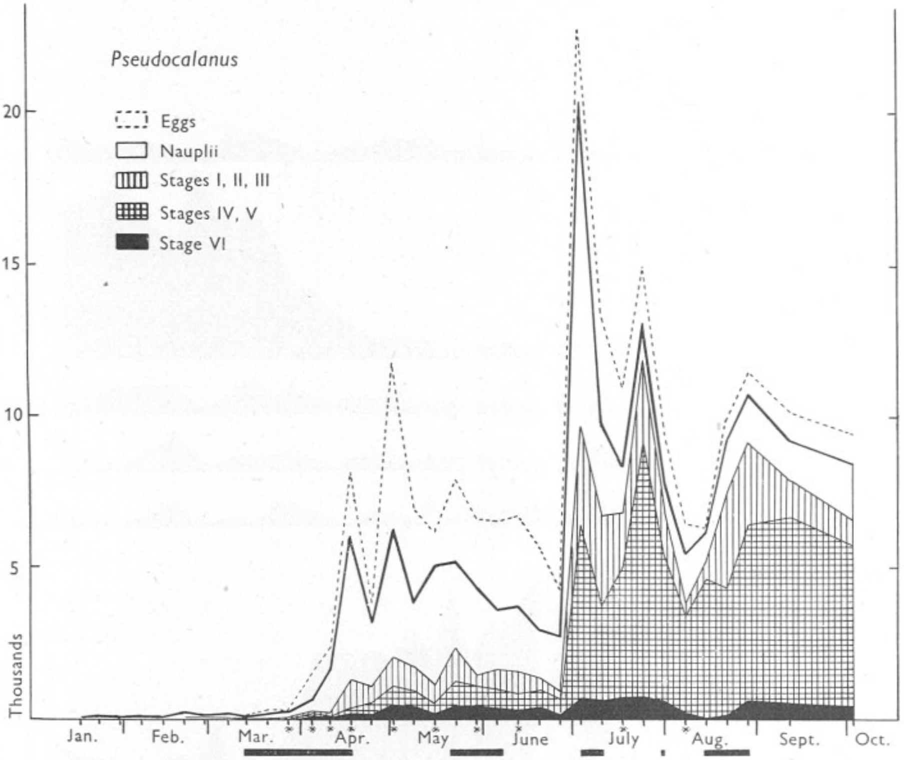


Fig. 2. *Pseudocalanus minutus*. Total number per haul throughout the year.

At the beginning of August there was a small but well-defined rise in the percentage of nauplii, followed a fortnight later by a rise in the percentage of early copepodites. This autumnal brood, however, does not get beyond Stage IV. Even from the beginning of July there was a very marked fall in the proportion of nauplii, and at the same time the number of Stage IV copepodites began to increase and continued to do so throughout the month and till the middle of August. From then till observations stopped at the beginning of October the proportion of Stage IV remained consistently high, usually between 40 and 60 % of the total catch. It is obvious that the majority of these copepodites were not completing their development but were accumulating to form the autumn stock. In *Calanus* (Nicholls, 1933; Marshall *et al.*, 1934) the stock in autumn consisted almost entirely of Stage V, and later observations are required to find out when *Pseudocalanus* moults into Stage V and adult. As shown in Fig. 1 the change to Stage V had been completed by mid-January, and a certain proportion had even become adult by then.

The increase in total numbers (Fig. 2) is very marked with the arrival of the second brood in the middle of April, and there is another great increase to the maximum for the year at the beginning of July. The number of copepodites on 3 July does in fact seem greater than can be accounted for by the comparatively small number of nauplii in the two previous weeks, considering the natural mortality which must be taking place all the time. It is possibly an instance of the uneven distribution of plankton which must always be taken into account in this type of work. There is another increase in total numbers in the second half of August following the increase in nauplii then. It consisted mainly of copepodites, Stages I, II and III being abundant as well as IV.

The relation of the first brood to the spring diatom increase has already been pointed out. The April increase in copepod numbers came just at the end of this spring maximum, which, although it was much poorer than usual, continued for over a month. The second great increase in copepod numbers was accompanied by a shorter diatom maximum composed, like the spring one, of *Skeletonema costatum*. During the period when *Pseudocalanus* numbers were at their maximum there were several outbursts of diatom growth, although the predominant species were then *Chaetoceros* spp. and *Leptocylindrus* sp. On the other hand, a marked diatom maximum from 22 May to 5 June (again mainly *Skeletonema*) was not followed, as one might have expected, by an increase in copepods.

Pseudocalanus shows several interesting points both of resemblance to and of difference from *Calanus* in its breeding cycle. Both had a first brood, very small in numbers, beginning to develop in March about the time of the spring diatom increase. The next brood appeared earlier in *Pseudocalanus* than in *Calanus*, and whereas that of *Calanus* did not develop, that of *Pseudocalanus* did. It is possible that the diatoms, abundant in the first half of April only, may have accounted for this.

Calanus had much more distinct breeding periods than *Pseudocalanus*; between its successive broods egg production died away almost completely, whereas in *Pseudocalanus* the proportion of eggs and nauplii remained comparatively high till July and breeding and development were probably continuous. In *Pseudocalanus* the building up of a winter stock began in July, and it consisted in October of Stage IV; in *Calanus* the building up did not begin till mid-August and it passed the winter as Stage V.

In the Loch Striven hauls a number of *Pseudocalanus* eggs were found free, but the majority were in egg-sacs, most often attached to the genital segment of the female. In the North Sea and English Channel, *Pseudocalanus* does not normally carry an egg-sac,* although two or three eggs are sometimes found attached to the genital segment. Fish (1936*b*) also states that in the Gulf of Maine the female is found only occasionally carrying two or three eggs. Sars (1903, Pl. X) figures the female *P. elongatus* with an egg-sac containing about seven or eight eggs and says in the text: 'Ovisac present of irregular rounded form but easily detached and containing a very limited number of ova.' In his figure of *P. gracilis* (Supplement, Pl. I), which, according to With (1915), is the same as *P. minutus*, the egg-sac is shown with twenty or more eggs. This variation in number is, however, within the range found in Loch Striven specimens. Females there were sometimes found with only two or three eggs attached, but it was assumed that these were in the act of laying, or had lost the main portion of the sac and they were counted as 'free' eggs.

Fish (1936*b*) says that to account for the large numbers of free eggs in the plankton each female must lay several hundred eggs. Since this seems, on the Loch Striven figures, too large a number for a single laying, each female may spawn several times, as has been suggested for *Calanus* (Marshall *et al.*, 1934).

The eggs in each egg-sac were counted throughout the year in order to estimate the average number laid by one female at a time and the seasonal variation. The average number varied considerably (Fig. 3), rising gradually from 9·5 on 13 February, to a maximum of 38·4 on 17 April. After this there was a gradual fall, interrupted by several very small increases, to a minimum of 8·0 on 11 September. The highest numbers occurred during the spring diatom increase and for a week or two afterwards; the slight interruptions of the downward curve are probably not significant, although they occur on, or just after, the dates of the secondary diatom maxima. It is not surprising that a well-fed copepod should produce more eggs than a starved one, but the variation seems to be dependent rather on the size of the female *Pseudocalanus*. The correlation between size of females (Fig. 16) and number of eggs is highly significant (0·98; 30 pairs of observations).

The free eggs were also counted and, assuming that the average number per egg-sac on each date holds for them also, it is possible to calculate the percentage of egg-bearing females present in any catch. This is a number, however, which shows violent fluctuations from week to week, and the variations do not seem to be related to any ascertainable factor. The maximum was 81 % on 12 June, a date on which the number of eggs, although high, was not at its maximum.

The number of females carrying spermatophores was also counted in a sample from each catch (that used for measurement) and is shown at the top of Fig. 1. The percentage was, with one exception, surprisingly low during the production of the first and second broods but was higher from April to June.

---

* Private communications from Mr R. S. Wimpenny, Lowestoft, and Mr P. S. B. Digby, Plymouth.

It was above 10 % only once, just before the appearance of the first brood females.

Males are usually much fewer than females in the catches, but this is probably because of their shorter life rather than because of any real discrepancy in actual numbers produced. When the proportions of the sexes are examined in copepodite Stages IV and V it is found that of the total number averaged over the year the percentage varies little from 50 % of each (Table I, p. 57). In the early part of the year, however (January to March), the proportion of males in Stage V is only 35 %, although slightly over 50 % in Stage IV. In several other species also males were scarcer during the early part of the year.

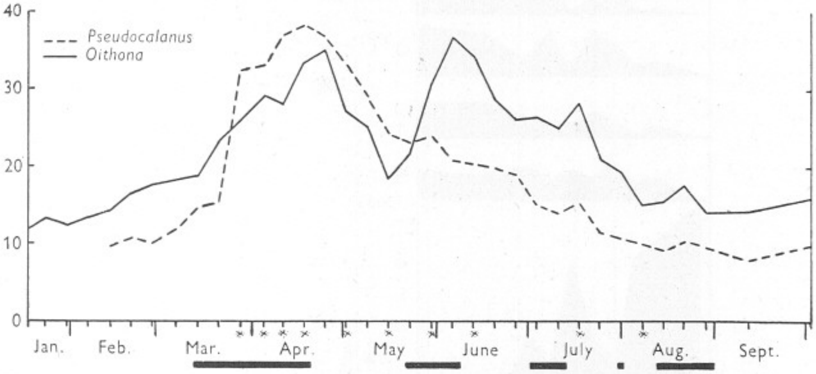


Fig. 3. Average number of eggs per female in *Pseudocalanus* and *Oithona*.

Paracalanus parvus (Claus)

(Table IV and Fig. 4)

Nauplii occurred throughout the year, but until July in small numbers only. Some of them were probably included among the *Microcalanus* nauplii, but they were separated from July onwards, and from the figures at that time it may be said that the percentage wrongly included is less than 10 and probably less than 5. Only an occasional copepodite stage was seen before the middle of July, but from then till 2 October, when observations stopped, they increased steadily (Fig. 4). The maximum total number (more than half nauplii) came on 31 August, but copepodites were at their maximum on 2 October. However, the decreasing proportion of nauplii and the fact that the majority were Stage V and IV indicates that reproduction was over for the season and that, like *Calanus* and *Pseudocalanus*, *Paracalanus* passes the winter in a late copepodite stage. No distinct broods can be made out and breeding was probably continuous during the period of observation.

The percentage of males was low, only 13·5 %. *Paracalanus* females, like those of *Pseudocalanus*, sometimes show abnormalities of the fifth leg. Several specimens were seen in which it was four-segmented and not two-segmented as normally.

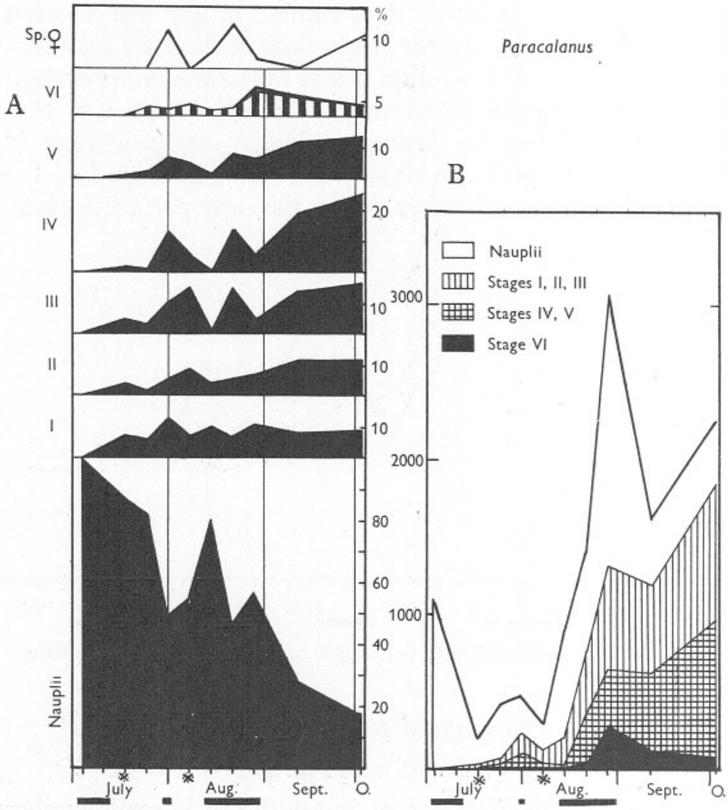


Fig. 4. *Paracalanus parvus*. A. Diagram showing the percentage of the developmental stages from July to October. The percentage of adult females with spermatophores is shown at the top. B. Total number per haul from July to October.

Microcalanus pygmaeus G. O. Sars

(Table V and Figs. 5 and 6)

This species differs from *Pseudocalanus* and *Paracalanus* and resembles *Calanus* in that it has well-marked breeding periods between which the proportion of nauplii and young stages falls to a low figure (Figs. 5, 6). It differs from all the other copepods studied in having its first breeding period well before the date of the spring diatom increase. When observations began (17 January) nauplii formed nearly 70 % of the catch, and the remaining 30 % was fairly evenly divided among all the copepodite stages. These nauplii, and the later nauplii found in February, grew up to adults during February and

March, and the second brood, beginning with a great increase in nauplii, came at the beginning of the spring diatom increase in March-April, and reached the adult stage in the beginning of May. Nauplii formed between 80 and 90 % of the catch during most of June; as in *Calanus* there seems to be a gap of several weeks between the time the adults appear and the time of maximum egg production as indicated by the number of nauplii; the eggs of this species were not counted. Diatoms were abundant at the end of May and again at the beginning of July, and it seemed to be mainly the later-produced of the June nauplii that grew up to form the third brood. The production of a brood in January, however, indicates that *Microcalanus* is less dependent on phytoplankton than the other species.

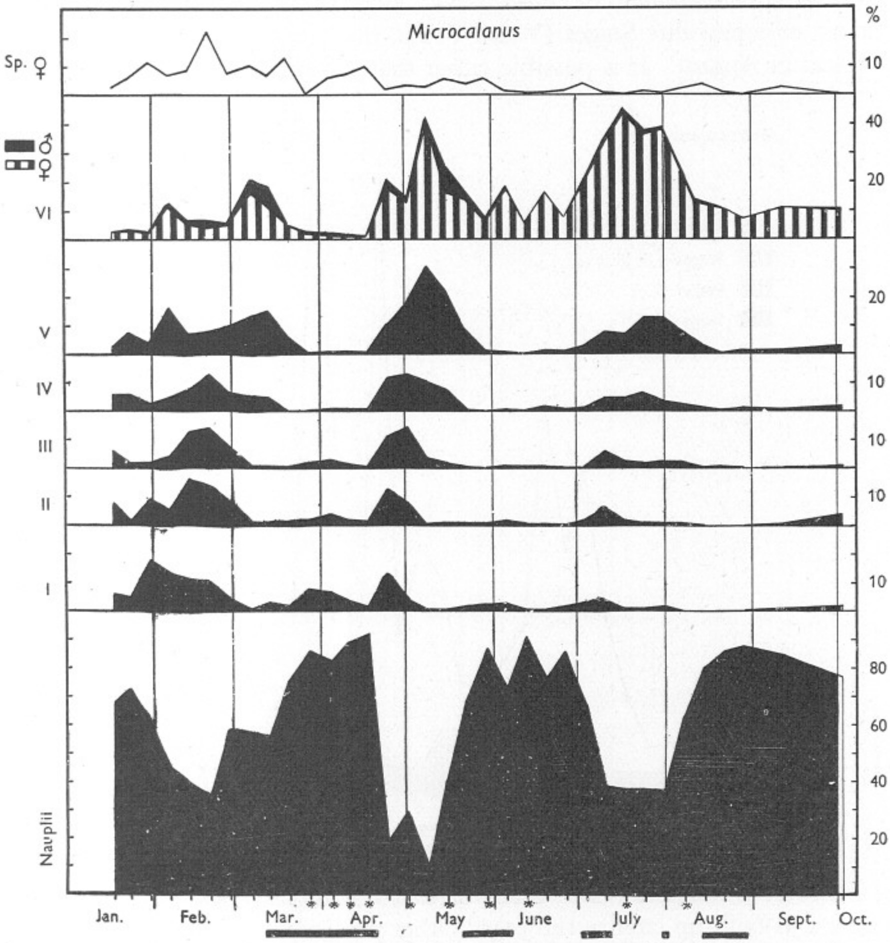


Fig. 5. *Microcalanus pygmaeus*. Diagram showing the percentage of the developmental stages during the year. The percentage of adult females with spermatophores is shown at the top.

The July peak of adults was followed in the last half of August by another steep rise in nauplii, which, although the actual numbers were much lower than in summer, made up as large a proportion of the catch. When observations stopped in October nauplii were still the most abundant stage (77 %), with adult females next. This is a very different state of affairs from that found in *Calanus*, *Pseudocalanus* or *Paracalanus*, where the winter stock consisted mainly of copepodite Stages IV and V, and that stock was already built up by the end of August. It is possible either that *Microcalanus* went on breeding at intervals throughout the winter, or that a winter stock of late copepodite stages was built up later in the year. Other possibilities are that *Microcalanus* passed the winter mainly in the nauplius or in the adult female stage. Observations during the winter are needed to decide which of these is correct.

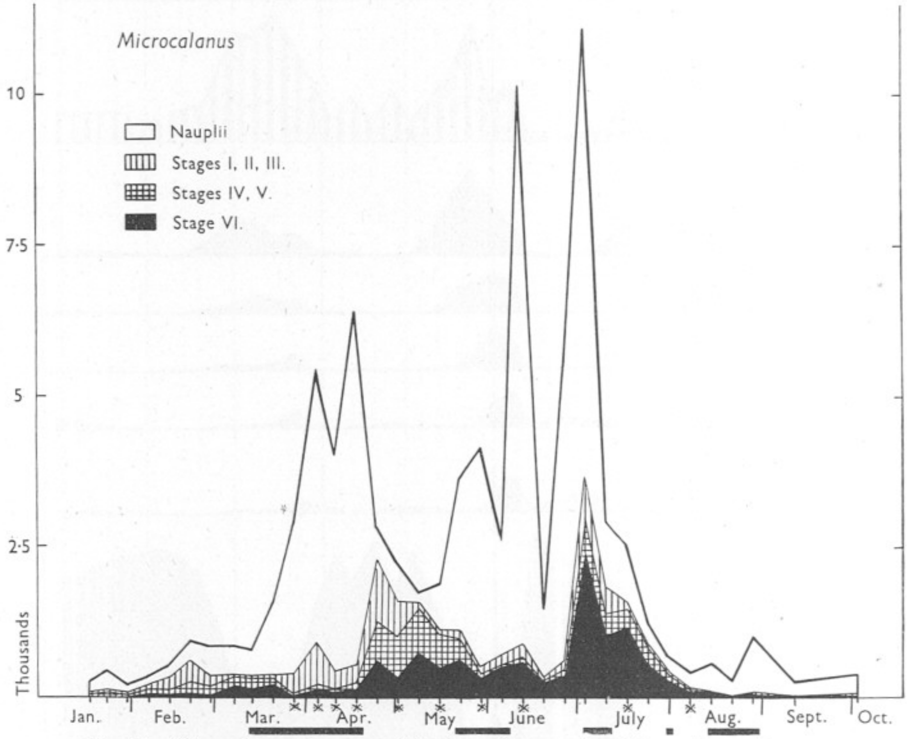


Fig. 6. *Microcalanus pygmaeus*. Total number per haul throughout the year.

On account of the very early first brood the total numbers of *Microcalanus* rose before any of the other copepods except *Oithona* became abundant. Already in February and the beginning of March the total number was nearly a thousand per haul compared with the two or three hundred *Pseudocalanus* present at that time. There were two maxima during the year, one in April, and one June to July, both consisting mainly of nauplii, but the second also the maximum for copepodites and adults. The second and larger maximum was interrupted by a sharp fall in nauplius numbers on 19 and 26 June.

The relative proportions of the different stages showed some peculiarities. There was evidently a high mortality among nauplii, which is only to be expected and is shown in most copepods. From May onwards, however, the normal proportions of the copepodite stages were reversed, and the adult females and also Stage V were in general more numerous than the younger stages. Perhaps this indicates a longer life for females and Stage V than in the early part of the year, and gives some slight support to the suggestion that adult females may survive the winter. Adult males were always scarcer than females (although equally numerous in Stages IV and V) and became much more so after May. From January to May the percentage of males among the adults was about 23, from June to September it dropped to about 4 (Table I).

The proportion of females carrying spermatophores was highest in the early part of the year, but bore no apparent relation to broods (Fig. 5).

TABLE I. PERCENTAGE OF MALES PRESENT

Species	Stage IV Jan.–Oct.	V Jan.–Oct.	VI Jan.–Mar.	VI Jan.–Oct.	Otten (1913)
Calanus	—	—	17·8	34·3	—
Pseudocalanus	47·7	50·2	11·1	23·1	18·3
*Paracalanus**	45·0	40·3	—	13·5	16·4
Microcalanus	49·2	52·8	29·4	11·2	—
Centropages	—	56·1	—	63·8	20·7
Temora	49·9	55·7	—	57·8	20·7
Acartia	46·5	45·7	7·7	48·3	5·3†
Oithona	—	—	2·1	12·8	4·6

* In Loch Striven, from July to October only.
† *Acartia bifilosa*.

Centropages hamatus (Lilljeborg) and *Temora longicornis* (Müller)

(Tables VI and VII, Figs. 7–10)

Breeding is so similar in these two species that they may be taken together. From January until the middle of March the stock, apart from an occasional early copepodite, was represented entirely by nauplii. These were few in number, rising from 10 or 20 in January to 100 or 200 in March. In March copepodites appeared in numbers for the first time, a little earlier in *Temora* than in *Centropages*, and in the following weeks this first brood grew to maturity to reach the adult stage in April. It may be noted that the spring diatom increase began on 13 March and lasted till the middle of April. In the middle and second half of April, nauplii again predominated, and a second brood grew up during late April and May (*Temora*) or May (*Centropages*), reaching the adult stage about 10 and 22 May respectively. At this time diatoms were not abundant. Another great increase of nauplii in both species causing the maximum numbers of the year for *Centropages* (1900 per haul) coincided with the next diatom increase, but apparently no brood developed from these nauplii. A marked increase in the proportion of adults in *Centropages* and of adults and copepodites in *Temora* on 19 June (Figs. 7, 9), seen in *Acartia* and *Oithona* also, was caused by a sudden drop in the number of nauplii, since the actual numbers of the older stages remained constant or even fell. The fourth brood, marked only in *Centropages*, developed from nauplii produced at the end of June, and during July and August breeding in both species seemed to be continuous. In *Centropages* the last distinct brood reached maturity at the end of August, and when observations stopped in October three-quarters of

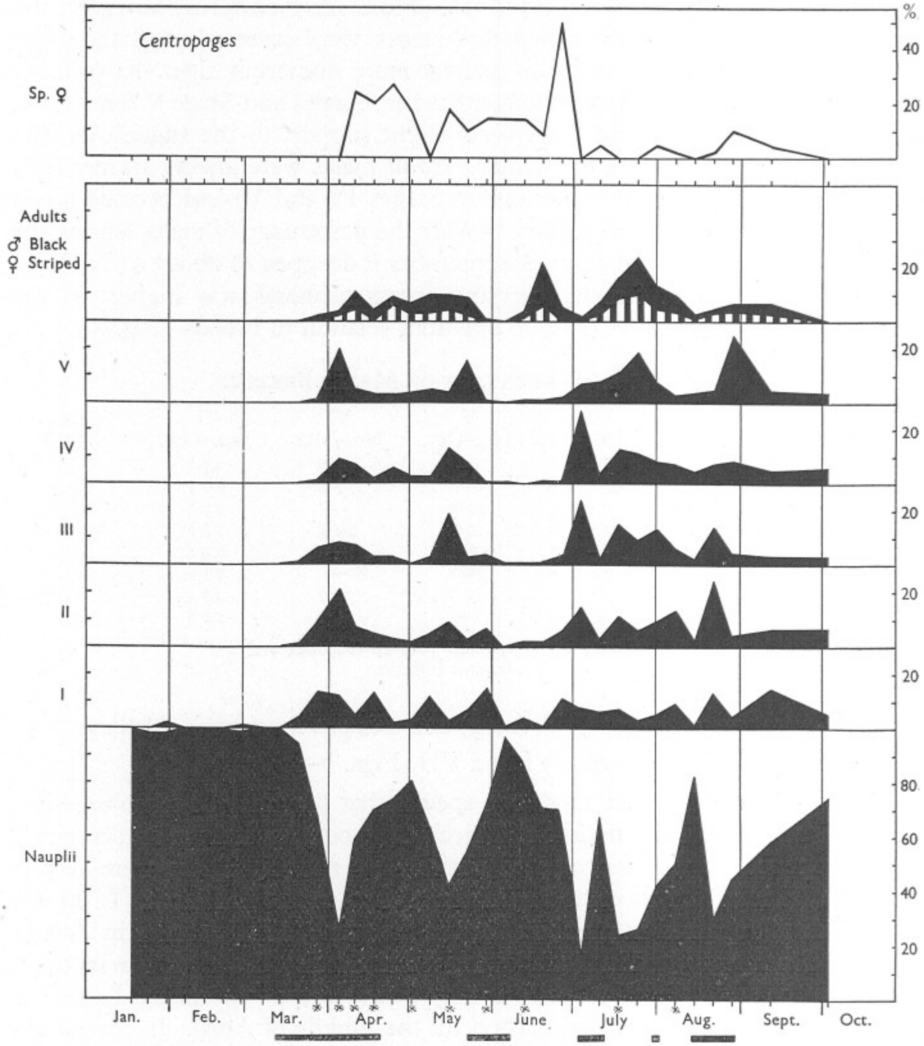


Fig. 7. *Centropages hamatus*. Diagram showing the percentage of developmental stages during the year. The percentage of adult females with spermatophores is shown at the top.

the catch was nauplii and the remaining quarter was fairly evenly divided among Stages I–V. In *Temora* there was no distinct August brood, but in October the distribution was much the same as in *Centropages*, nearly 70 % of the stock being nauplii. This is a very different distribution from that found at the end of the winter, and it is possible that breeding can go on later in the year. Otten (1913), however, mentions that in his catches (in Kiel Bay) there were at the end of September and in November large numbers of *Centropages* nauplii with no corresponding copepodites. The nauplius seems an unlikely stage in which to pass the winter (cf., however, *Microcalanus*), and it is possible that adults survived in small numbers, living so near the bottom that the vertical tow-net did not catch them, and producing a small number of eggs and nauplii throughout the winter. Another possibility is that some sort of resting egg is produced which can survive for long periods (see Fish & Johnson, 1937, p. 307).

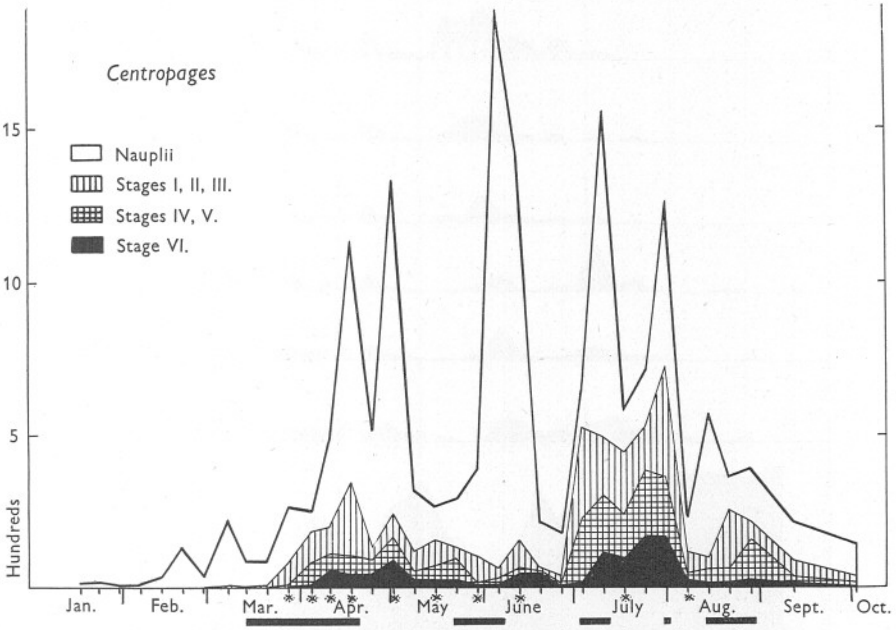


Fig. 8. *Centropages hamatus*. Total number per haul throughout the year.

Otten (1913) mentions *Temora* as carrying an egg-sac with four to eight eggs and says the sac breaks up readily. No sign of a sac was ever seen on the female *Temora* in Loch Striven.

Nauplii were responsible for most of the peaks in numbers during the summer (Figs. 8, 10), since they often formed over 70 % of the catch of *Centropages* and even more in *Temora*. In both species there were maxima of copepodites and adults in April at the time of the first brood and in July with the third or fourth. In *Centropages* the numbers in July were the higher (700 copepodites and adults per haul on 31 July) and in *Temora* the April to May numbers (500 per haul on 1 May).

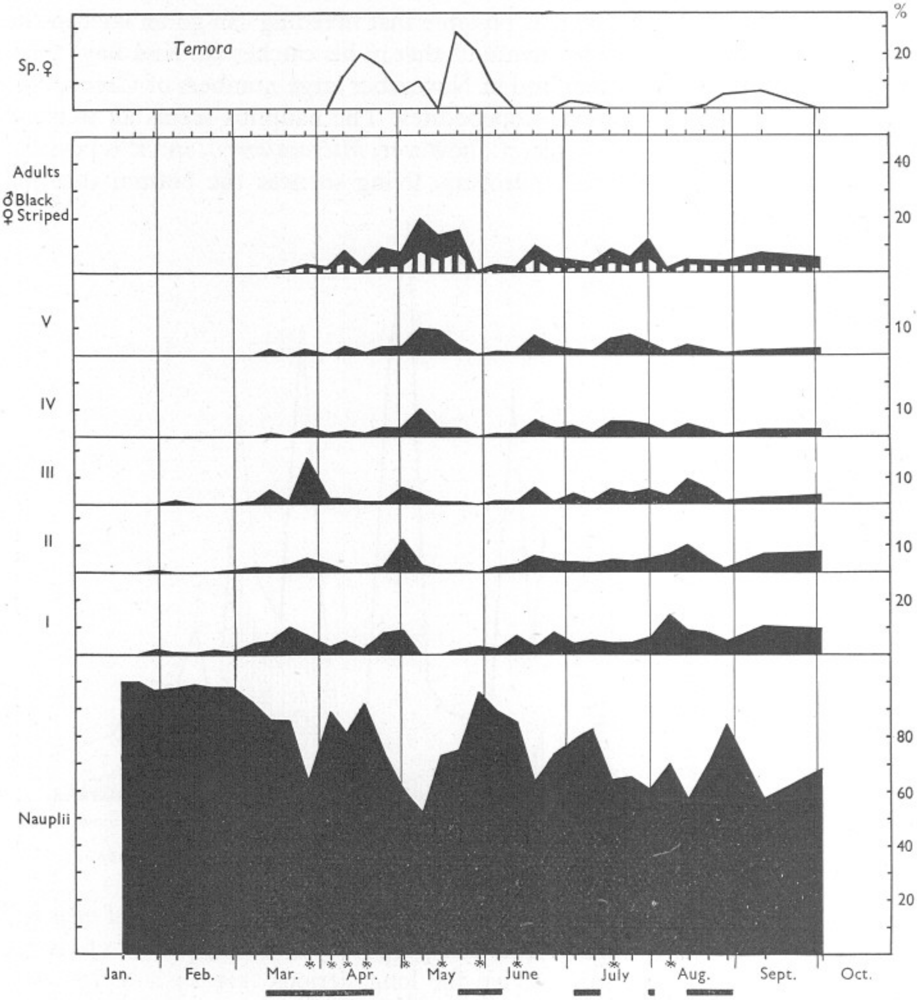


Fig. 9. *Temora longicornis*. Diagram showing the percentage of development stages during the year. The percentage of adult females with spermatophores is shown at the top.

Centropages and *Temora* differ from the other species of copepod examined in that males are more abundant than females throughout the year (Table I, p. 57). This was true also in the Nordåsvatn Fjord near Bergen (Wiborg, 1944). Even in Stage V there was a slight tendency for males to be more numerous. Taking the average over the year males formed 64 % of the *Centropages* adults and 58 % of the *Temora* adults. In Stage V they formed 56 % in both species. In spite of this the number of females carrying spermatophores, although higher than in *Pseudocalanus* and *Microcalanus*, was lower than in *Acartia*, where the sexes were about equal, or in *Oithona* where males formed only 13 %. The number of spermatophore-bearing females is shown at the top of Figs. 7 and 9, and it is on the whole highest on the appearance of the first brood and varies irregularly throughout the summer. The peak in *Centropages* on 26 June means little, for only two females were caught, one with a spermatophore.

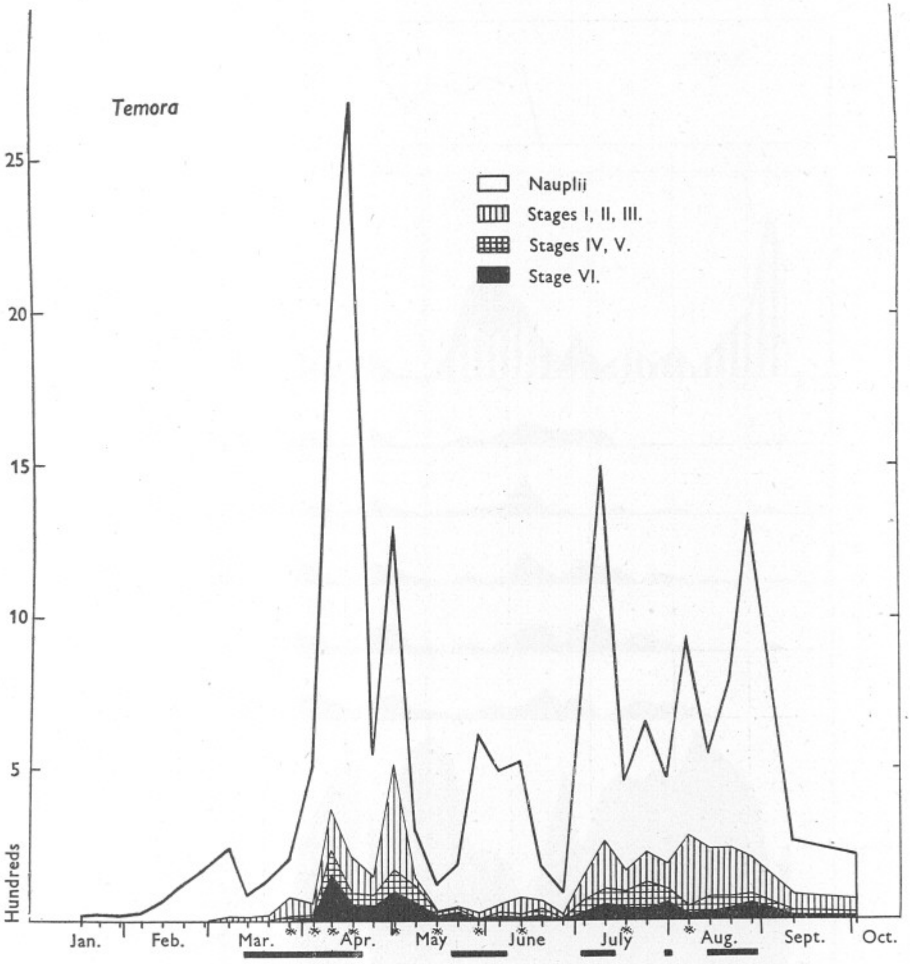


Fig. 10. *Temora longicornis*. Total number per haul throughout the year.

Acartia clausi Giesbrecht

(Table VIII, Figs. 11 and 12)

The stock of *Acartia* in January, unlike the other species examined, consisted almost entirely of adult females and nauplii. In February and March nauplii predominated, and in the latter half of March (along with the spring diatoms) the first brood grew up. The period of reproduction was rather spread out, or else there were two broods in close succession, of which the second

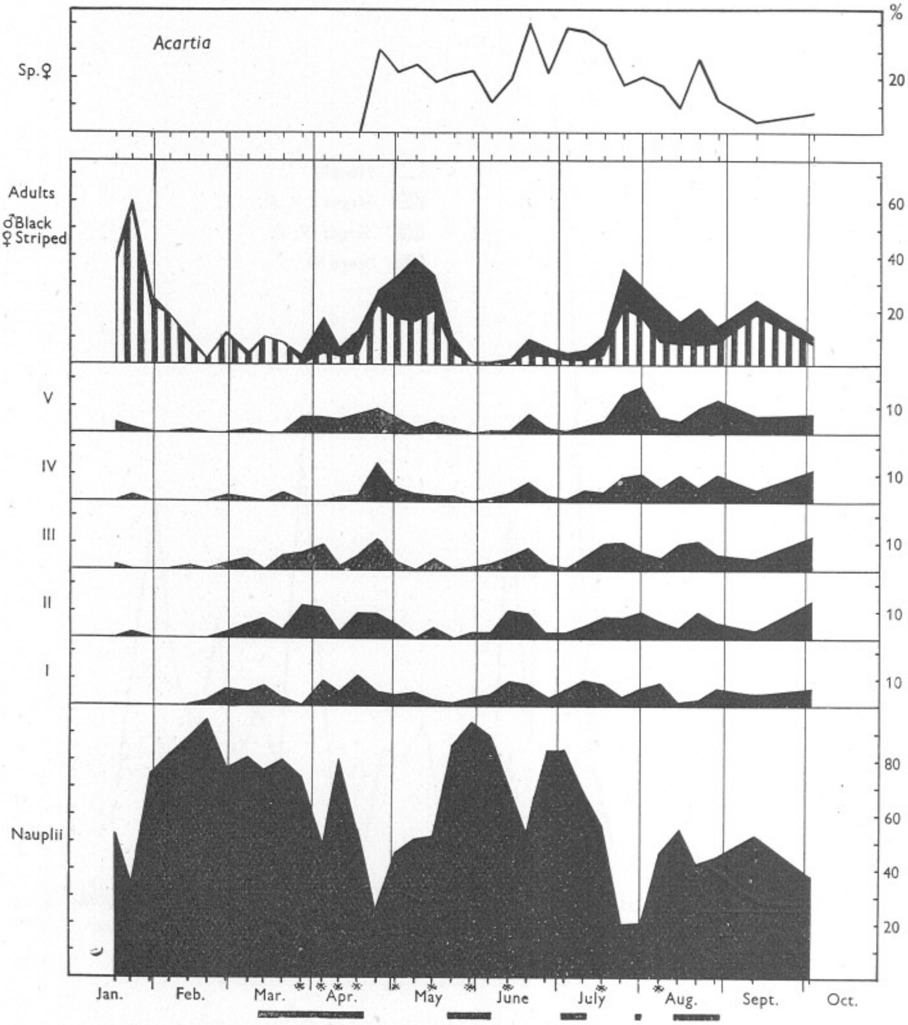


Fig. 11. *Acartia clausi*. Diagram showing the percentage of developmental stages during the year. The percentage of adult females with spermatophores is shown at the top.

came to maturity at the beginning of May. The numbers at this time were, however, very small and hardly show in Fig. 12.

Another peak in nauplius production came with the diatom increase at the end of May, and this brood began to grow up during June. It is difficult to follow it to maturity, however, because of the sudden change (already mentioned) on 19 June in the proportions of nauplii and late copepodites.

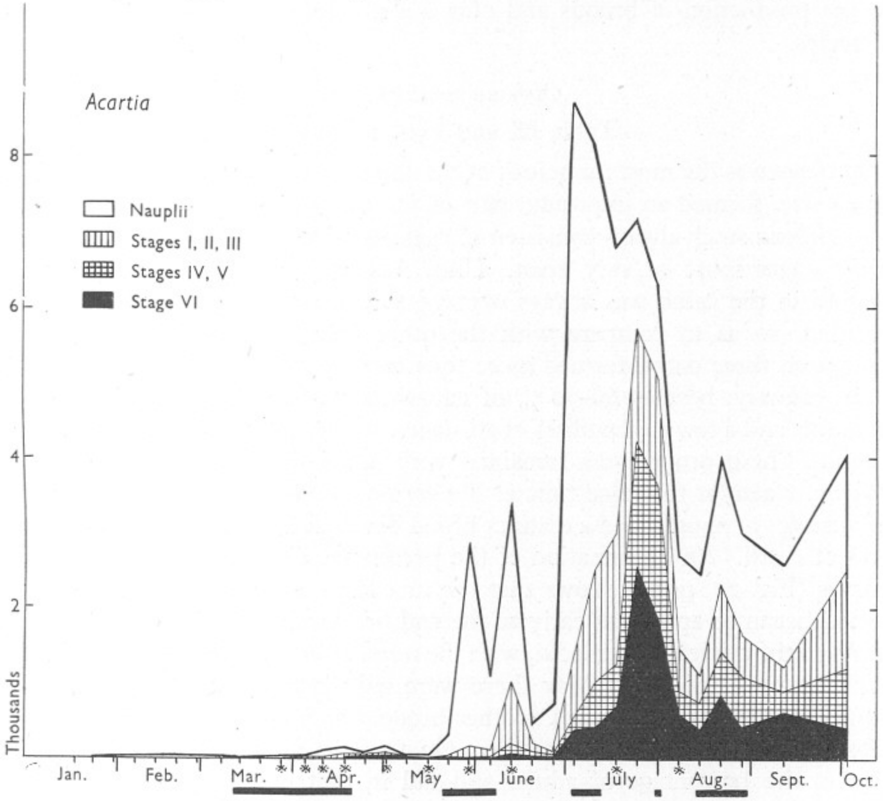


Fig. 12. *Acartia clausi*. Total number per haul throughout the year.

The peak in nauplius production at the beginning of July coincided with a diatom increase, and a brood, the third or fourth, developed during the month and reached the adult stage at the end of July and beginning of August. After this, breeding seemed to be continuous and the number of copepodites and adults remained high. When observations stopped in October there were less than 40 % of nauplii and the other 60 % was fairly evenly distributed among the different copepodite stages, so that in *Acartia*, too, it is possible that breeding may go on well into the winter.

The maximum number for the year occurred in July, as nauplii at the beginning of the month and as copepodites and adults (5000 per haul) at the end.

Taken over the year the sexes were almost equal in number in all stages where they are distinguishable (Table I, p. 57). Although among adults females predominated up to April and after August, during the summer months males often outnumbered females. There were no females carrying spermatophores in January and February, but from the end of April the number was high, especially during June and July, but it seemed to have no relation to the production of broods and only a slight relation to the predominance of males.

Oithona similis Claus

(Table IX and Figs. 13 and 14)

Oithona was the most numerous of the small copepods, and so, in spite of its small size, formed an important part of the plankton. A large proportion of the *Oithona* stock always consisted of eggs and nauplii; the mortality in these early stages must be very great. Until August the percentage of eggs and nauplii in the catch was always over 75 and often over 90. When eggs are omitted (so as to compare with the other copepods studied) the nauplii, except on three dates, formed more than half the catch.

In January, besides 60–70 % of nauplii the stock contained nearly 20 % of adults and a few copepodites of all stages, so that breeding may already have begun. These proportions remained very much the same until the end of March, when (at the same time as the spring diatoms) there was a rise in the percentage of nauplii and a distinct brood developed, reaching maturity at the end of April. An examination of the percentage size-frequency distribution curves (Fig. 29, p. 81) shows that the first large adult females of the spring brood began to appear as early as the end of March. From then till the end of April the curves are bimodal, with the number at the larger mode increasing until on 24 April and 1 May there were only large females present. These adults immediately produced another brood which grew up during May, but after this breeding was continuous. On 19 June there was the same abrupt rise in the percentage of adults and fall in that of nauplii as occurred in *Temora*, *Centropages* and *Acartia*. From July onwards the proportion of nauplii was lower than during the earlier part of the year. When observations stopped, adults and copepodites formed 60 % of the stock, and breeding may have continued throughout the winter.

Although *Oithona* was numerous throughout the year the numbers rose sharply only at the beginning of July, and the total stock (excluding eggs) on 3 July was 18,000 per haul. Numbers fell again to the beginning of August and then rose to the maximum for the year on 21 and 28 August when there were about 30,000 copepodites and nauplii, with 13,000 and 6000 eggs in successive weeks.

Males were always much scarcer than females, the discrepancy being most marked in early spring (Table I, p. 57). In January and March the males numbered only 2 % of the adults, for the whole year 13 %. The number of females with spermatophores was about 10 % or less until April, but after this, with the higher proportion of males, it remained consistently high. The figure probably means little, however, for among the females carrying egg-sacs some had spermatophores and some had not (see p. 69).

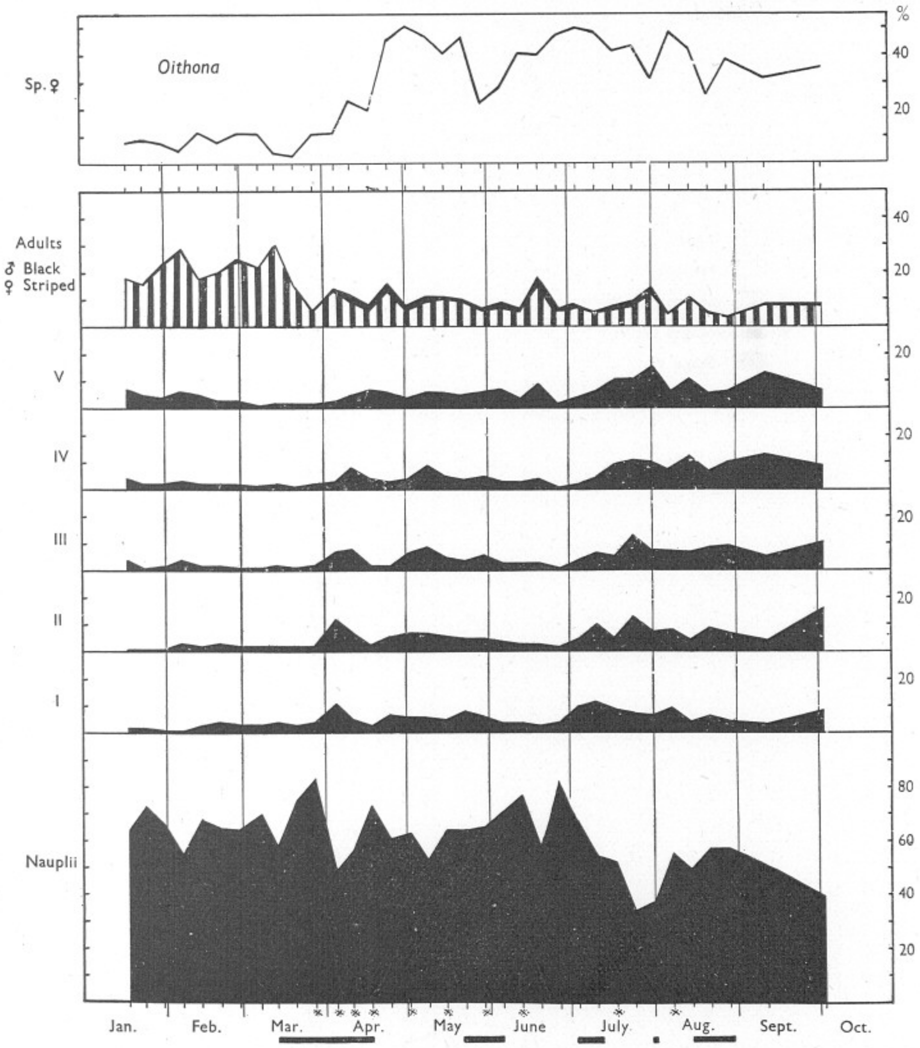


Fig. 13. *Oithona similis*. Diagram showing the percentage of developmental stages during the year. The percentage of adult females with spermatophores is shown at the top.

The eggs are carried by the female in a pair of egg-sacs attached to the genital segment, so it is possible to count the number of eggs per sac and per

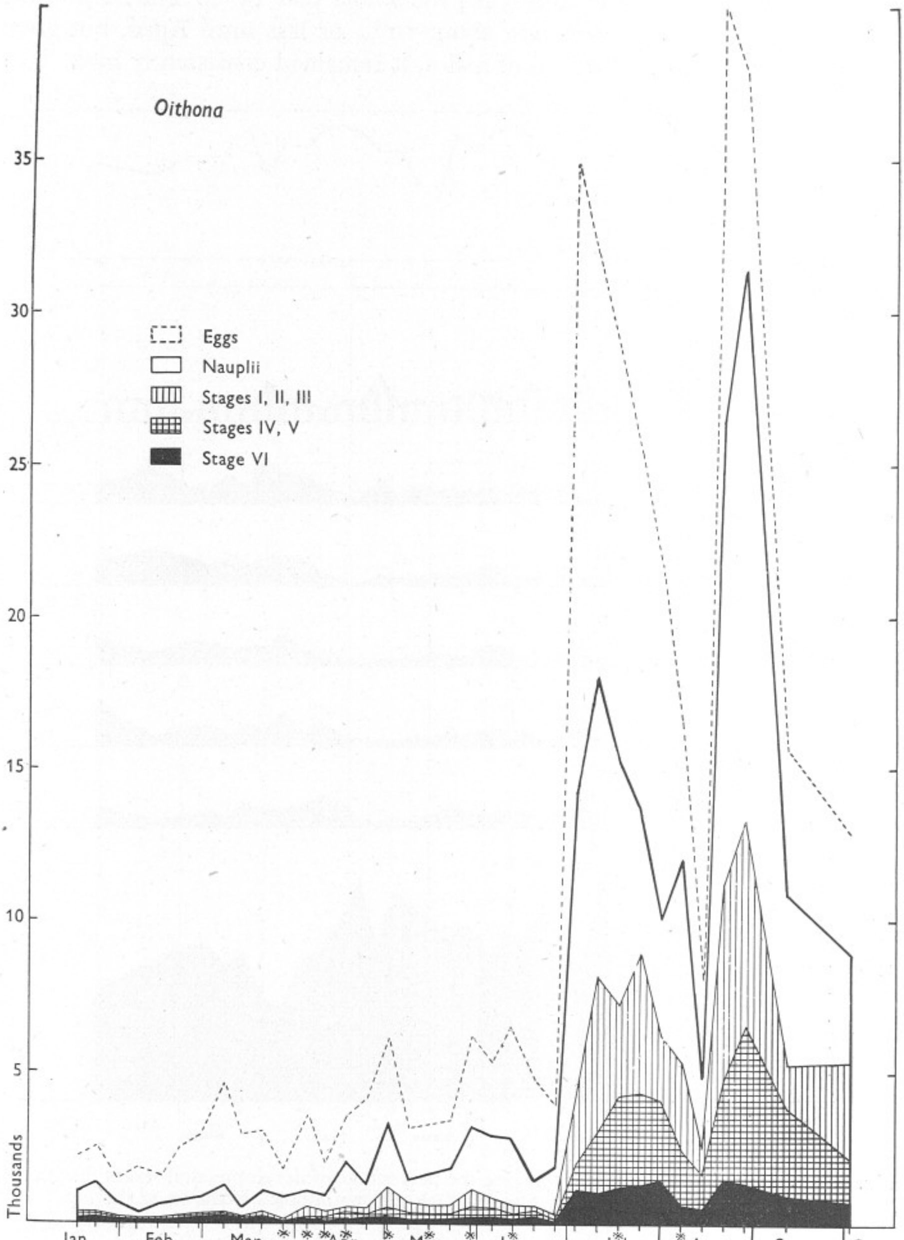


Fig. 14. *Oithona similis*. Total number per haul throughout the year.

female, and the latter is shown in Fig. 3 (p. 53). As in *Pseudocalanus* the number increased gradually to a maximum at the end of April, at the end of the spring diatom increase, when females were about their maximum size. There was then a rapid decrease in number until the middle of May, but from then till 5 June, unlike *Pseudocalanus*, there was a sharp rise to a second maximum. Thereafter numbers decreased gradually till the autumn, although there were two slight checks on the curve on the same dates as those found in *Pseudocalanus*.

The paired sacs did not always contain the same number of eggs, although they were usually nearly the same. The number per egg-sac varied from four to thirty-four, and almost the whole range might be covered in one catch. Over 100 egg-sacs were usually counted.

The curves indicate that the relation between number of eggs and size of female is less close than in *Pseudocalanus*, although the correlation coefficient is still highly significant (0·75, 35 pairs of observations). An examination of Figs. 3 and 28 shows that whereas egg numbers rose to a well-marked peak on 5 June the size of females showed only a slight rise at that time. Diatoms were abundant while the egg numbers were rising, and were scarce after 5 June, so that it is probable that the food supply has an effect on egg production. Diatoms were abundant also on the dates in July and August when the downward trend of egg number is checked, but the differences in egg number are not significant. Otten (1913) counted the number of eggs per sac and found that this varied throughout the year, being, like the nauplii, highest in April and October and lowest in August.

In considering the reproduction of the copepods as a whole, we can see that there are two types of breeding. In one the broods are distinctly separated by periods when eggs and nauplii are scarce. To this type belong *Calanus* and *Microcalanus*. In all the other copepods examined the broods were less distinctly separated and in the second half of the year were indistinguishable. In the second type there seems to be a shorter time between the appearance of adult females and the production of eggs and nauplii. In *Calanus* (Fish, 1936*a*; Marshall *et al.*, 1934) the maturing of the eggs is supposed to take about 3–4 weeks, and the same seems to be true of *Microcalanus*. In the other copepods a peak in nauplius numbers followed more closely (in two or three weeks) upon the appearance of adults, and two broods might appear in quick succession. In the late summer when breeding was continuous, no gap could be distinguished (see, however, Fish, 1936*b*, on *Pseudocalanus*).

In *Calanus* the time occupied in development from egg to adult was estimated, partly from the data from the Loch Striven hauls and partly from laboratory experiments, at about a month. There are no laboratory data for the small copepods, and since visits to the loch were made only weekly, estimates must be uncertain, but the time seems to be little shorter than in

Calanas. In most species the time from a peak in nauplius production to a peak of adults is 3–4 weeks. The great differences between spring and summer mentioned by Fish (1936*c*) do not occur here.

In all species the spring diatom increase seems to have had an important effect on reproduction. Although *Microcalanus* and possibly *Oithona* were breeding before it, yet during or at the end of the diatom-rich period (which in 1933 was long-drawn out—13 March to 17 April), every species showed an increase, in most of nauplii, and in all a successive development of early and late copepodites and adults. The date varied from one species to another between the middle of March and the middle of April. In *Pseudocalanus* and *Acartia* the actual numbers of the first brood were very small; in *Microcalanus*, *Centropages* and *Temora* they were considerable, especially when compared with the numbers occurring later in the year. In all species nauplii form a large proportion of almost every catch, and the greatest mortality must take place at this early stage. Fish (1936 *a*, *b*) suggests that another dangerous period in the life of a copepod is during the maturing of the eggs, and that in *Calanus* the mortality is actually greatest at that stage, and is important also in *Pseudocalanus*.

The maximum number of all species of copepod except *Temora*, and sometimes *Calanus* (Nicholls, 1933), came during the summer, in July or August, but the date varied from species to species. This was true for the maximum numbers both of nauplii, and of copepodites and adults, which in *Microcalanus* and *Oithona* occurred on the same date. Besides this summer maximum there was usually a secondary maximum earlier in the year, in April or May, but this was smaller and more variable. In *Acartia* and *Oithona* it was small, in *Temora* it was more important than the summer maximum.

The proportion of the sexes varied among the different species, and it varies also from place to place. Otten (1913) gives figures for seven copepods (Table I, p. 57), mostly the same species as those in Loch Striven, but in his samples males were much scarcer. In both places, however, *Oithona* had the smallest, and *Centropages* and *Temora* the highest, proportion.

In Loch Striven (Table I) the percentage of males in *Calanus*, *Pseudocalanus*, *Acartia* and *Oithona* was lowest from January to March. In *Calanus* and *Pseudocalanus* it was highest from April to June, but in *Acartia* and *Oithona* the proportion did not vary much from April onwards. *Centropages* and *Temora* were too scarce before April for the number of males to be reliable, and after April the proportion remained fairly constant. In *Microcalanus*, on the other hand, their percentage was highest in April and was very low after June.

If, as seems most probable, these very varying proportions indicate the length of life of the adult, then in some species the female is the longer lived, in others the male. The length of life also varies at different times of the year, and this we already know to be true of some of the earlier stages such as Stages IV and V of the autumn stock of *Calanus*, *Pseudocalanus* and *Paracalanus*.

In *Calanus* (Marshall *et al.*, 1934) the percentage of adult females carrying spermatophores was highest before the production of each brood of eggs, and it was observed that the spermatophore was usually lost before the eggs were ripe for spawning. No such relation was made out in the small copepods. In one species (*Oithona similis*) the spermatophore was often retained even after the eggs had been spawned, and this may be so in other species also. It is curious, too, that the very varying proportion of males seems to have little influence on the number of females carrying spermatophores.

VERTICAL DISTRIBUTION

From 27 March to 21 August one of the five hauls was taken in two parts, from the bottom (60–70 m.) to 10 m., and from 10 m. to the surface. It must, however, be remembered (see p. 46) that there may have been a considerable and variable loss from the bottom haul which means that the proportion of copepods below 10 m. may be greater than appears from the figures. It is felt that despite this disadvantage the results obtained are substantially true.

In Fig. 15 is shown for all stages of each species the percentage above and below 10 m. No allowance has been made for the much greater depth of water sampled below 10 m. It is felt that the copepods are very unlikely to be evenly distributed throughout the column, and there are in fact indications that they may have been confined to the top 20 or 30 m. A series of samples taken at 10 m. intervals from top to bottom would give a truer picture of their distribution.

It will be seen that from the end of March till the middle of June the great majority of all stages of all species except *Microcalanus* was above 10 m. There was then a rapid descent, and in July most stages of all species were wholly or largely below 10 m. In August there was a gradual rise again in most species, more marked in the younger stages, but when observations stopped on 21 August the distribution had not yet returned to the state shown at the end of March.

Although this gives a general picture of the copepod distribution, there was considerable variation in detail between the different species and the different stages of the same species. *Microcalanus* was unlike any of the others, since during almost the whole year all stages remained consistently below 10 m. On 22 and 29 May the proportion of Stages II and III above 10 m. increased, but the numbers then present were too small to be significant, and on the last two dates in August Stages I and II were absent altogether. The rise of the nauplii in August, however, was based on considerable numbers and seems to be real. On the first two dates, 27 March and 4 April, a considerable proportion of all stages except males and nauplii was found above 10 m., and this may mean that there is a period during the winter when *Microcalanus*, like the other copepods, lives mostly near the surface. Further observations are needed to

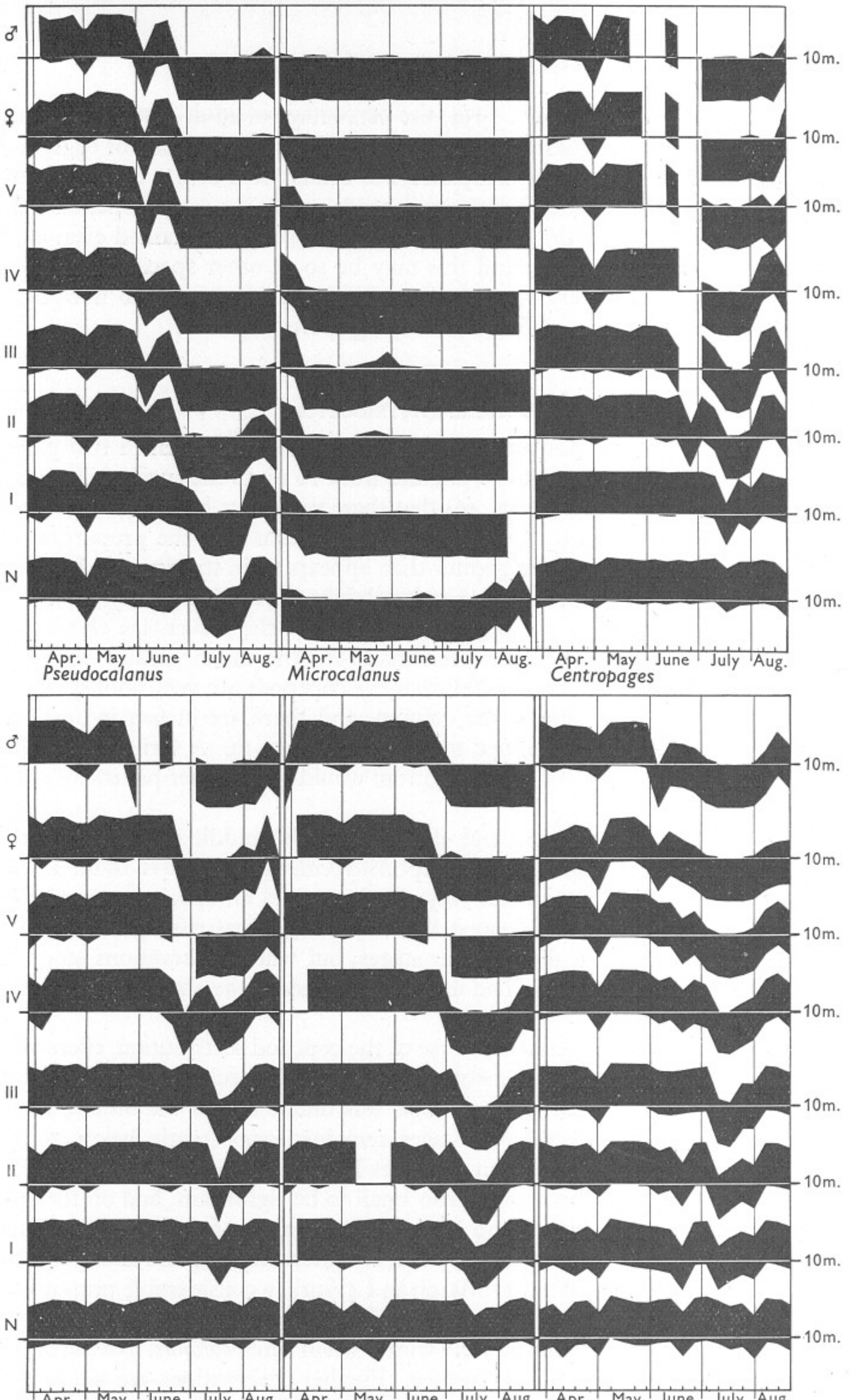


Fig. 15. Diagram showing the percentage of copepods above and below 10 m. from 27 March to 21 August. The nauplii and copepodite Stages I–VI are shown separately for each species.

the catch was nauplii and the remaining quarter was fairly evenly divided among Stages I–V. In *Temora* there was no distinct August brood, but in October the distribution was much the same as in *Centropages*, nearly 70 % of the stock being nauplii. This is a very different distribution from that found at the end of the winter, and it is possible that breeding can go on later in the year. Otten (1913), however, mentions that in his catches (in Kiel Bay) there were at the end of September and in November large numbers of *Centropages* nauplii with no corresponding copepodites. The nauplius seems an unlikely stage in which to pass the winter (cf., however, *Microcalanus*), and it is possible that adults survived in small numbers, living so near the bottom that the vertical tow-net did not catch them, and producing a small number of eggs and nauplii throughout the winter. Another possibility is that some sort of resting egg is produced which can survive for long periods (see Fish & Johnson, 1937, p. 307).

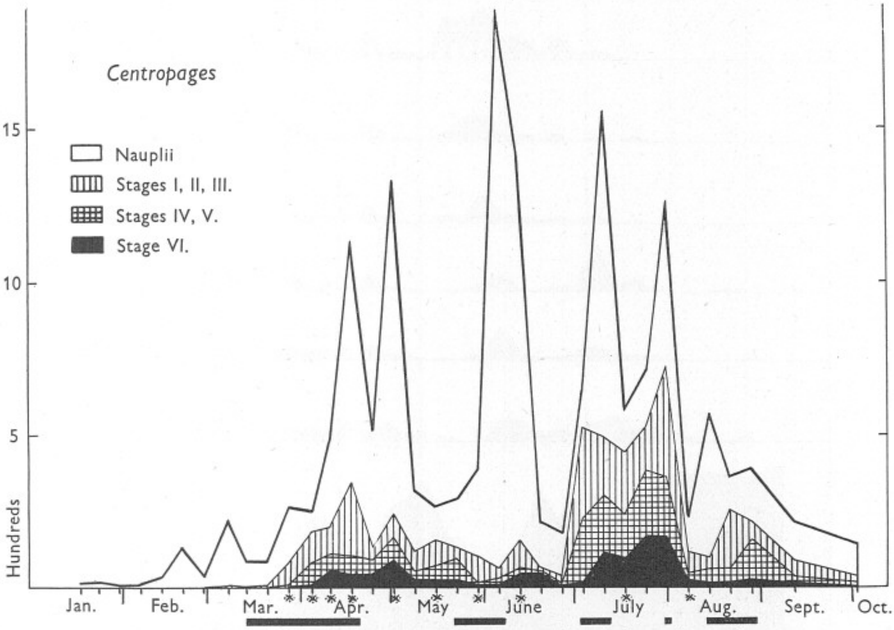


Fig. 8. *Centropages hamatus*. Total number per haul throughout the year.

Otten (1913) mentions *Temora* as carrying an egg-sac with four to eight eggs and says the sac breaks up readily. No sign of a sac was ever seen on the female *Temora* in Loch Striven.

Nauplii were responsible for most of the peaks in numbers during the summer (Figs. 8, 10), since they often formed over 70 % of the catch of *Centropages* and even more in *Temora*. In both species there were maxima of copepodites and adults in April at the time of the first brood and in July with the third or fourth. In *Centropages* the numbers in July were the higher (700 copepodites and adults per haul on 31 July) and in *Temora* the April to May numbers (500 per haul on 1 May).

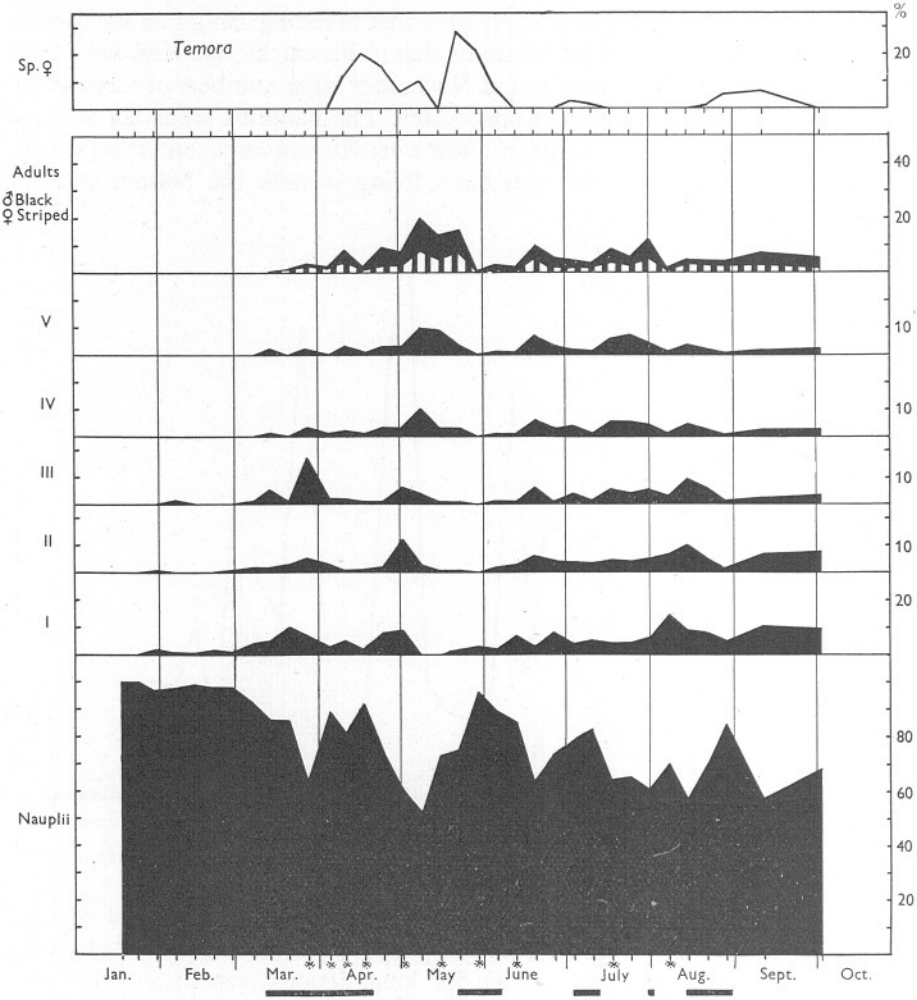


Fig. 9. *Temora longicornis*. Diagram showing the percentage of development stages during the year. The percentage of adult females with spermatophores is shown at the top.

Centropages and *Temora* differ from the other species of copepod examined in that males are more abundant than females throughout the year (Table I, p. 57). This was true also in the Nordåsvatn Fjord near Bergen (Wiborg, 1944). Even in Stage V there was a slight tendency for males to be more numerous. Taking the average over the year males formed 64 % of the *Centropages* adults and 58 % of the *Temora* adults. In Stage V they formed 56 % in both species. In spite of this the number of females carrying spermatophores, although higher than in *Pseudocalanus* and *Microcalanus*, was lower than in *Acartia*, where the sexes were about equal, or in *Oithona* where males formed only 13 %. The number of spermatophore-bearing females is shown at the top of Figs. 7 and 9, and it is on the whole highest on the appearance of the first brood and varies irregularly throughout the summer. The peak in *Centropages* on 26 June means little, for only two females were caught, one with a spermatophore.

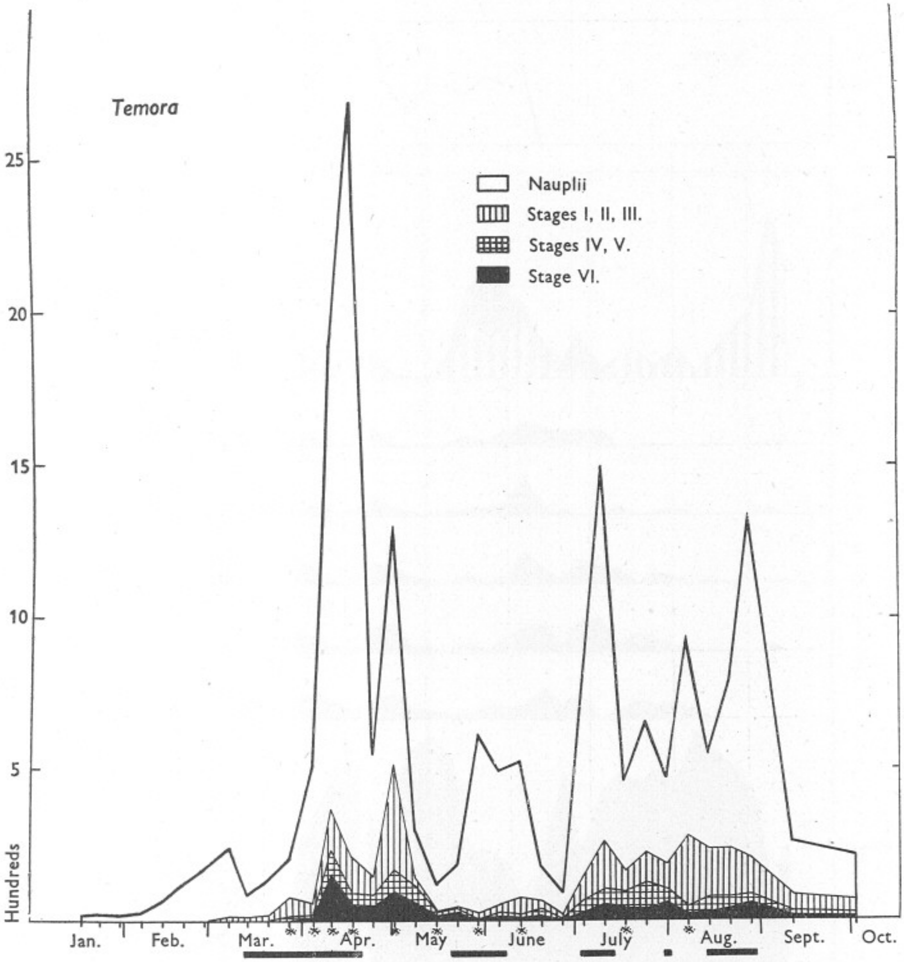


Fig. 10. *Temora longicornis*. Total number per haul throughout the year.

Acartia clausi Giesbrecht

(Table VIII, Figs. 11 and 12)

The stock of *Acartia* in January, unlike the other species examined, consisted almost entirely of adult females and nauplii. In February and March nauplii predominated, and in the latter half of March (along with the spring diatoms) the first brood grew up. The period of reproduction was rather spread out, or else there were two broods in close succession, of which the second

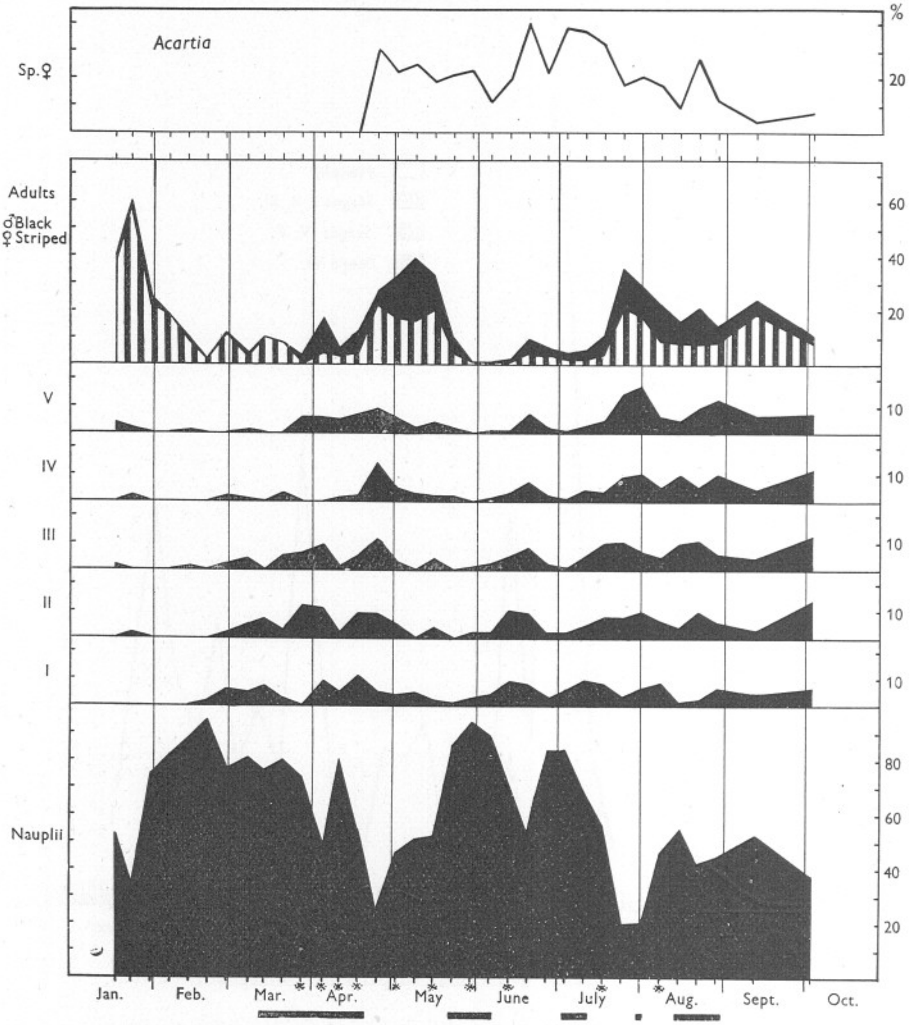


Fig. 11. *Acartia clausi*. Diagram showing the percentage of developmental stages during the year. The percentage of adult females with spermatophores is shown at the top.

came to maturity at the beginning of May. The numbers at this time were, however, very small and hardly show in Fig. 12.

Another peak in nauplius production came with the diatom increase at the end of May, and this brood began to grow up during June. It is difficult to follow it to maturity, however, because of the sudden change (already mentioned) on 19 June in the proportions of nauplii and late copepodites.

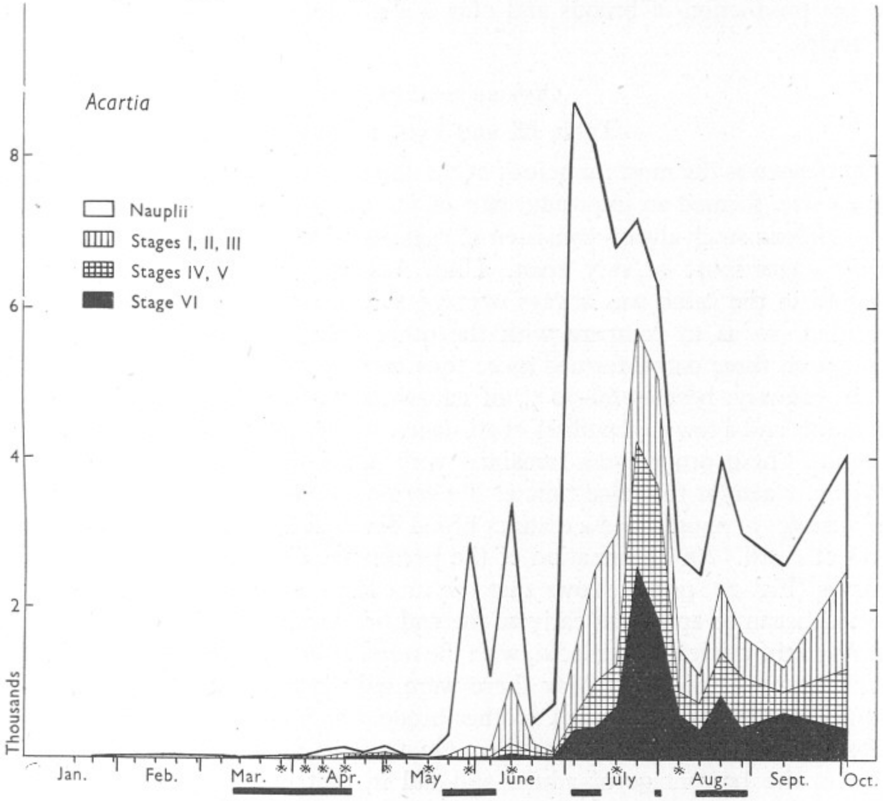


Fig. 12. *Acartia clausi*. Total number per haul throughout the year.

The peak in nauplius production at the beginning of July coincided with a diatom increase, and a brood, the third or fourth, developed during the month and reached the adult stage at the end of July and beginning of August. After this, breeding seemed to be continuous and the number of copepodites and adults remained high. When observations stopped in October there were less than 40 % of nauplii and the other 60 % was fairly evenly distributed among the different copepodite stages, so that in *Acartia*, too, it is possible that breeding may go on well into the winter.

The maximum number for the year occurred in July, as nauplii at the beginning of the month and as copepodites and adults (5000 per haul) at the end.

Taken over the year the sexes were almost equal in number in all stages where they are distinguishable (Table I, p. 57). Although among adults females predominated up to April and after August, during the summer months males often outnumbered females. There were no females carrying spermatophores in January and February, but from the end of April the number was high, especially during June and July, but it seemed to have no relation to the production of broods and only a slight relation to the predominance of males.

Oithona similis Claus

(Table IX and Figs. 13 and 14)

Oithona was the most numerous of the small copepods, and so, in spite of its small size, formed an important part of the plankton. A large proportion of the *Oithona* stock always consisted of eggs and nauplii; the mortality in these early stages must be very great. Until August the percentage of eggs and nauplii in the catch was always over 75 and often over 90. When eggs are omitted (so as to compare with the other copepods studied) the nauplii, except on three dates, formed more than half the catch.

In January, besides 60–70 % of nauplii the stock contained nearly 20 % of adults and a few copepodites of all stages, so that breeding may already have begun. These proportions remained very much the same until the end of March, when (at the same time as the spring diatoms) there was a rise in the percentage of nauplii and a distinct brood developed, reaching maturity at the end of April. An examination of the percentage size-frequency distribution curves (Fig. 29, p. 81) shows that the first large adult females of the spring brood began to appear as early as the end of March. From then till the end of April the curves are bimodal, with the number at the larger mode increasing until on 24 April and 1 May there were only large females present. These adults immediately produced another brood which grew up during May, but after this breeding was continuous. On 19 June there was the same abrupt rise in the percentage of adults and fall in that of nauplii as occurred in *Temora*, *Centropages* and *Acartia*. From July onwards the proportion of nauplii was lower than during the earlier part of the year. When observations stopped, adults and copepodites formed 60 % of the stock, and breeding may have continued throughout the winter.

Although *Oithona* was numerous throughout the year the numbers rose sharply only at the beginning of July, and the total stock (excluding eggs) on 3 July was 18,000 per haul. Numbers fell again to the beginning of August and then rose to the maximum for the year on 21 and 28 August when there were about 30,000 copepodites and nauplii, with 13,000 and 6000 eggs in successive weeks.

Males were always much scarcer than females, the discrepancy being most marked in early spring (Table I, p. 57). In January and March the males numbered only 2 % of the adults, for the whole year 13 %. The number of females with spermatophores was about 10 % or less until April, but after this, with the higher proportion of males, it remained consistently high. The figure probably means little, however, for among the females carrying egg-sacs some had spermatophores and some had not (see p. 69).

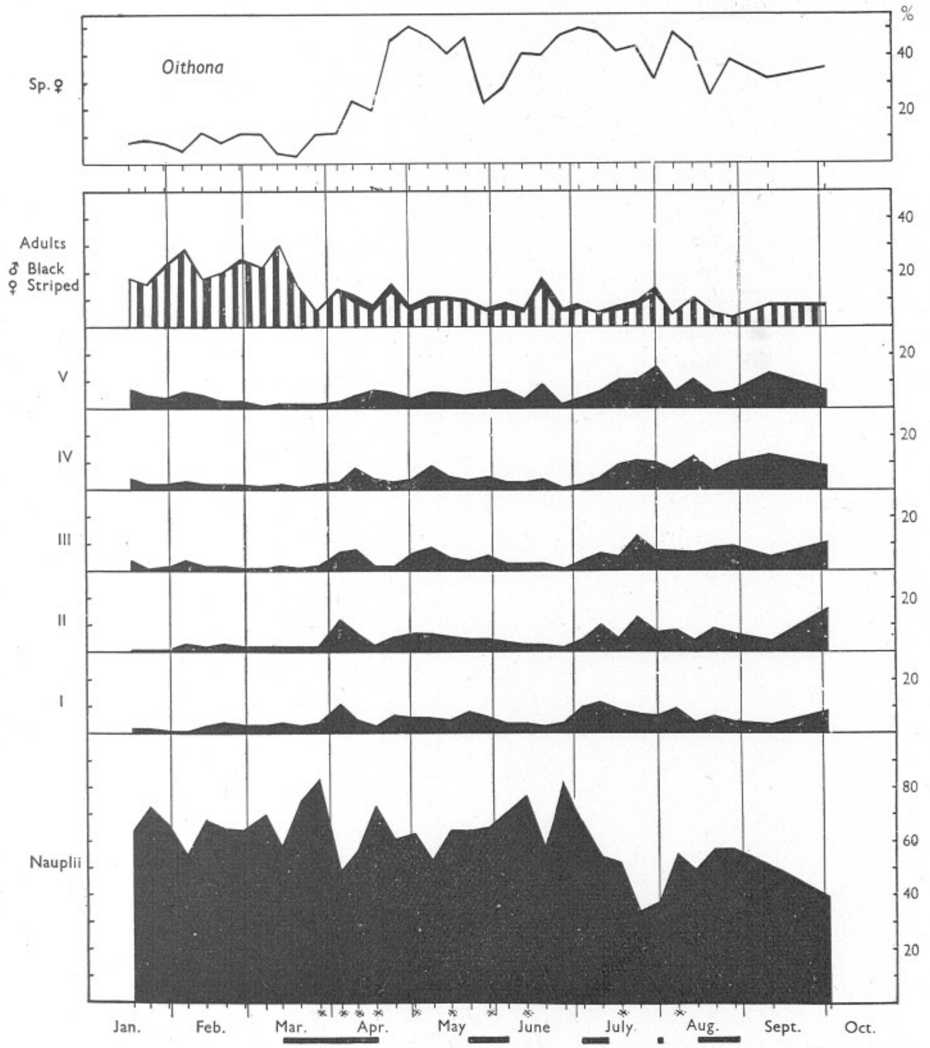


Fig. 13. *Oithona similis*. Diagram showing the percentage of developmental stages during the year. The percentage of adult females with spermatophores is shown at the top.

The eggs are carried by the female in a pair of egg-sacs attached to the genital segment, so it is possible to count the number of eggs per sac and per

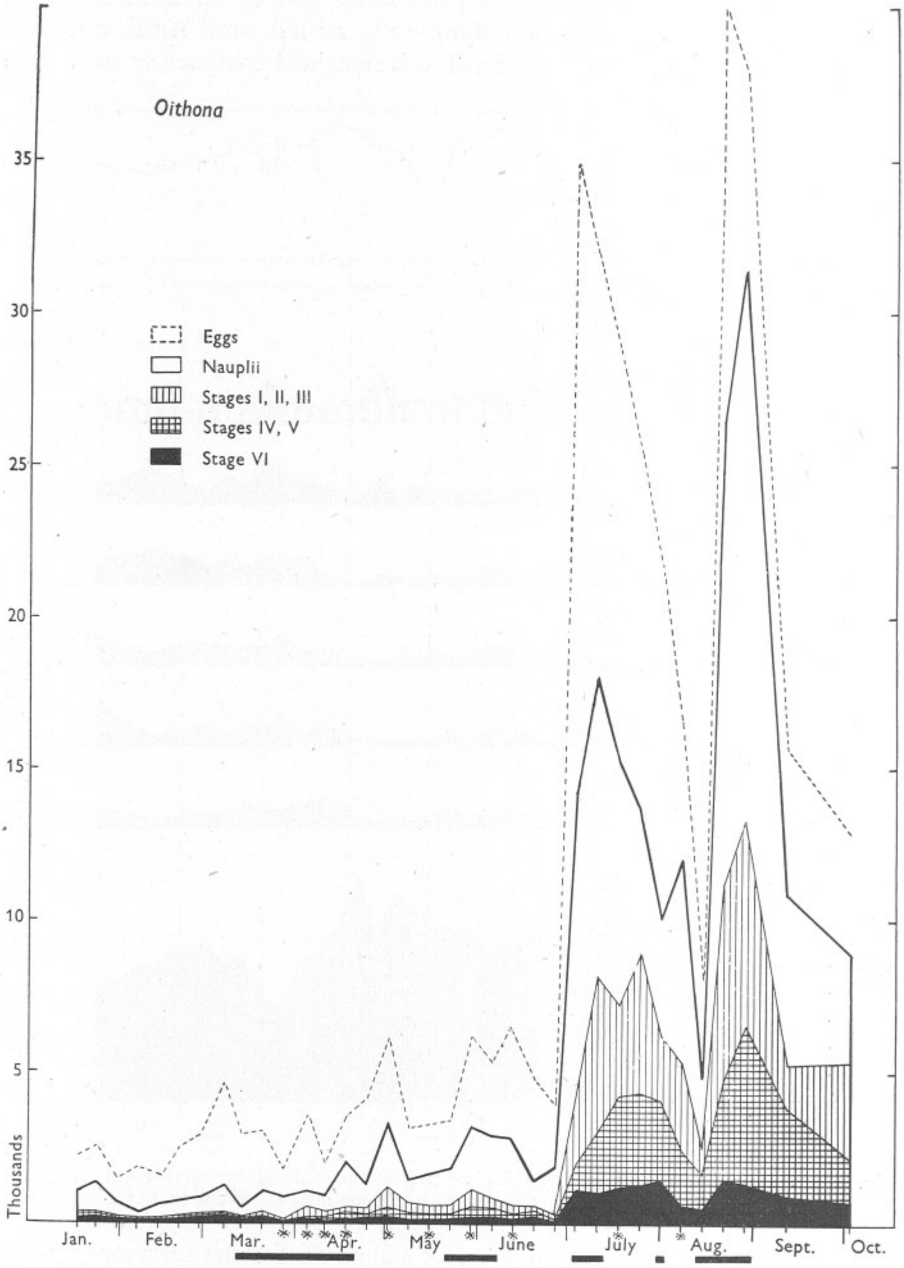


Fig. 14. *Oithona similis.* Total number per haul throughout the year.

female, and the latter is shown in Fig. 3 (p. 53). As in *Pseudocalanus* the number increased gradually to a maximum at the end of April, at the end of the spring diatom increase, when females were about their maximum size. There was then a rapid decrease in number until the middle of May, but from then till 5 June, unlike *Pseudocalanus*, there was a sharp rise to a second maximum. Thereafter numbers decreased gradually till the autumn, although there were two slight checks on the curve on the same dates as those found in *Pseudocalanus*.

The paired sacs did not always contain the same number of eggs, although they were usually nearly the same. The number per egg-sac varied from four to thirty-four, and almost the whole range might be covered in one catch. Over 100 egg-sacs were usually counted.

The curves indicate that the relation between number of eggs and size of female is less close than in *Pseudocalanus*, although the correlation coefficient is still highly significant (0·75, 35 pairs of observations). An examination of Figs. 3 and 28 shows that whereas egg numbers rose to a well-marked peak on 5 June the size of females showed only a slight rise at that time. Diatoms were abundant while the egg numbers were rising, and were scarce after 5 June, so that it is probable that the food supply has an effect on egg production. Diatoms were abundant also on the dates in July and August when the downward trend of egg number is checked, but the differences in egg number are not significant. Otten (1913) counted the number of eggs per sac and found that this varied throughout the year, being, like the nauplii, highest in April and October and lowest in August.

In considering the reproduction of the copepods as a whole, we can see that there are two types of breeding. In one the broods are distinctly separated by periods when eggs and nauplii are scarce. To this type belong *Calanus* and *Microcalanus*. In all the other copepods examined the broods were less distinctly separated and in the second half of the year were indistinguishable. In the second type there seems to be a shorter time between the appearance of adult females and the production of eggs and nauplii. In *Calanus* (Fish, 1936*a*; Marshall *et al.*, 1934) the maturing of the eggs is supposed to take about 3–4 weeks, and the same seems to be true of *Microcalanus*. In the other copepods a peak in nauplius numbers followed more closely (in two or three weeks) upon the appearance of adults, and two broods might appear in quick succession. In the late summer when breeding was continuous, no gap could be distinguished (see, however, Fish, 1936*b*, on *Pseudocalanus*).

In *Calanus* the time occupied in development from egg to adult was estimated, partly from the data from the Loch Striven hauls and partly from laboratory experiments, at about a month. There are no laboratory data for the small copepods, and since visits to the loch were made only weekly, estimates must be uncertain, but the time seems to be little shorter than in

Calanas. In most species the time from a peak in nauplius production to a peak of adults is 3–4 weeks. The great differences between spring and summer mentioned by Fish (1936*c*) do not occur here.

In all species the spring diatom increase seems to have had an important effect on reproduction. Although *Microcalanus* and possibly *Oithona* were breeding before it, yet during or at the end of the diatom-rich period (which in 1933 was long-drawn out—13 March to 17 April), every species showed an increase, in most of nauplii, and in all a successive development of early and late copepodites and adults. The date varied from one species to another between the middle of March and the middle of April. In *Pseudocalanus* and *Acartia* the actual numbers of the first brood were very small; in *Microcalanus*, *Centropages* and *Temora* they were considerable, especially when compared with the numbers occurring later in the year. In all species nauplii form a large proportion of almost every catch, and the greatest mortality must take place at this early stage. Fish (1936*a*, *b*) suggests that another dangerous period in the life of a copepod is during the maturing of the eggs, and that in *Calanus* the mortality is actually greatest at that stage, and is important also in *Pseudocalanus*.

The maximum number of all species of copepod except *Temora*, and sometimes *Calanus* (Nicholls, 1933), came during the summer, in July or August, but the date varied from species to species. This was true for the maximum numbers both of nauplii, and of copepodites and adults, which in *Microcalanus* and *Oithona* occurred on the same date. Besides this summer maximum there was usually a secondary maximum earlier in the year, in April or May, but this was smaller and more variable. In *Acartia* and *Oithona* it was small, in *Temora* it was more important than the summer maximum.

The proportion of the sexes varied among the different species, and it varies also from place to place. Otten (1913) gives figures for seven copepods (Table I, p. 57), mostly the same species as those in Loch Striven, but in his samples males were much scarcer. In both places, however, *Oithona* had the smallest, and *Centropages* and *Temora* the highest, proportion.

In Loch Striven (Table I) the percentage of males in *Calanus*, *Pseudocalanus*, *Acartia* and *Oithona* was lowest from January to March. In *Calanus* and *Pseudocalanus* it was highest from April to June, but in *Acartia* and *Oithona* the proportion did not vary much from April onwards. *Centropages* and *Temora* were too scarce before April for the number of males to be reliable, and after April the proportion remained fairly constant. In *Microcalanus*, on the other hand, their percentage was highest in April and was very low after June.

If, as seems most probable, these very varying proportions indicate the length of life of the adult, then in some species the female is the longer lived, in others the male. The length of life also varies at different times of the year, and this we already know to be true of some of the earlier stages such as Stages IV and V of the autumn stock of *Calanus*, *Pseudocalanus* and *Paracalanus*.

In *Calanus* (Marshall *et al.*, 1934) the percentage of adult females carrying spermatophores was highest before the production of each brood of eggs, and it was observed that the spermatophore was usually lost before the eggs were ripe for spawning. No such relation was made out in the small copepods. In one species (*Oithona similis*) the spermatophore was often retained even after the eggs had been spawned, and this may be so in other species also. It is curious, too, that the very varying proportion of males seems to have little influence on the number of females carrying spermatophores.

Vertical Distribution

From 27 March to 21 August one of the five hauls was taken in two parts, from the bottom (60–70 m.) to 10 m., and from 10 m. to the surface. It must, however, be remembered (see p. 46) that there may have been a considerable and variable loss from the bottom haul which means that the proportion of copepods below 10 m. may be greater than appears from the figures. It is felt that despite this disadvantage the results obtained are substantially true.

In Fig. 15 is shown for all stages of each species the percentage above and below 10 m. No allowance has been made for the much greater depth of water sampled below 10 m. It is felt that the copepods are very unlikely to be evenly distributed throughout the column, and there are in fact indications that they may have been confined to the top 20 or 30 m. A series of samples taken at 10 m. intervals from top to bottom would give a truer picture of their distribution.

It will be seen that from the end of March till the middle of June the great majority of all stages of all species except *Microcalanus* was above 10 m. There was then a rapid descent, and in July most stages of all species were wholly or largely below 10 m. In August there was a gradual rise again in most species, more marked in the younger stages, but when observations stopped on 21 August the distribution had not yet returned to the state shown at the end of March.

Although this gives a general picture of the copepod distribution, there was considerable variation in detail between the different species and the different stages of the same species. *Microcalanus* was unlike any of the others, since during almost the whole year all stages remained consistently below 10 m. On 22 and 29 May the proportion of Stages II and III above 10 m. increased, but the numbers then present were too small to be significant, and on the last two dates in August Stages I and II were absent altogether. The rise of the nauplii in August, however, was based on considerable numbers and seems to be real. On the first two dates, 27 March and 4 April, a considerable proportion of all stages except males and nauplii was found above 10 m., and this may mean that there is a period during the winter when *Microcalanus*, like the other copepods, lives mostly near the surface. Further observations are needed to

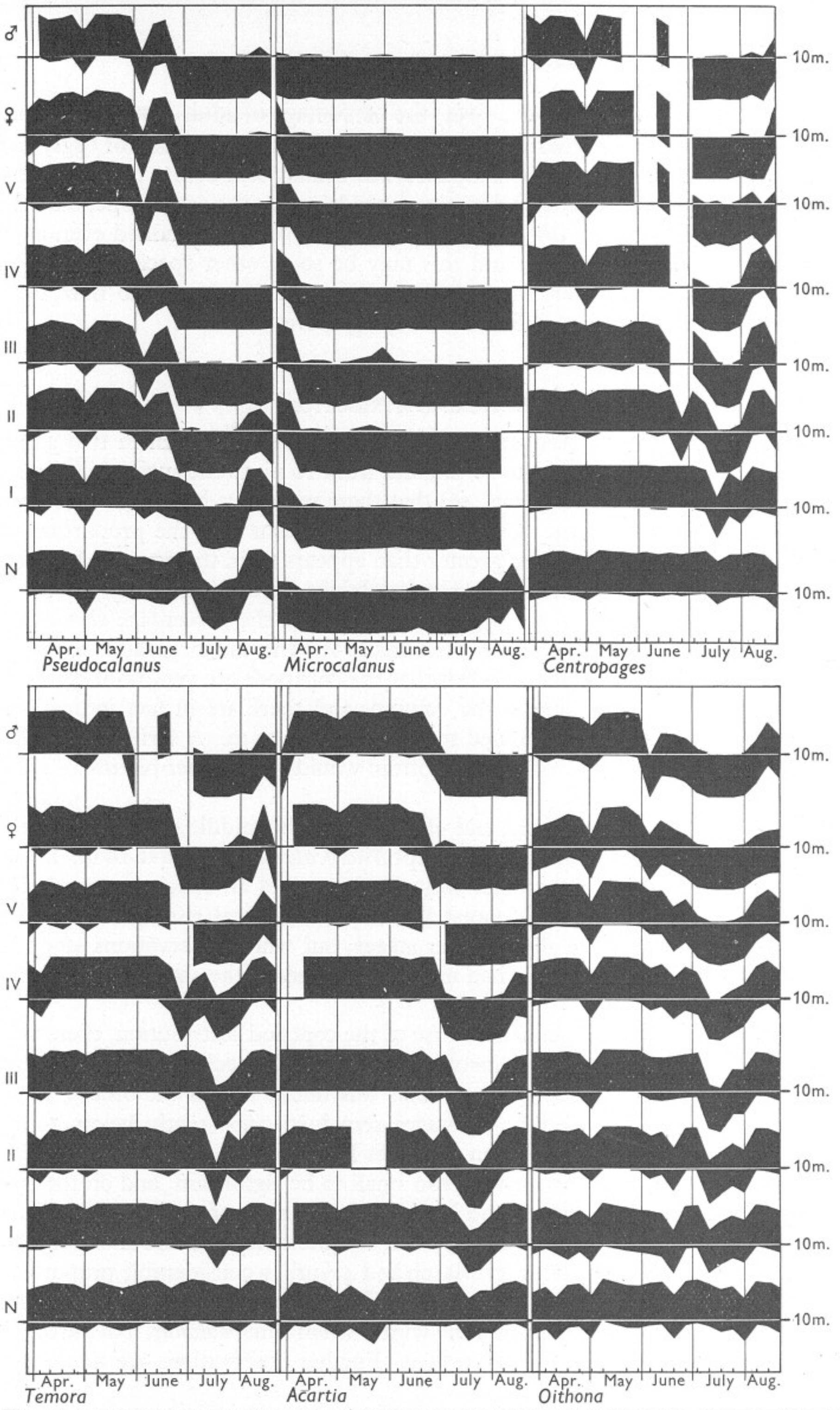


Fig. 15. Diagram showing the percentage of copepods above and below 10 m. from 27 March to 21 August. The nauplii and copepodite Stages I–VI are shown separately for each species.

decide the point, but it may be noted that off East Greenland (Ussing, 1938) *Microcalanus*, like most other species, is found near the surface in winter and in deep water in summer.

In *Calanus* (Marshall *et al.* 1934) the adults and Stage V went below 10 m. in the beginning of June, and the earlier copepodites not till the beginning of July. In the adults and Stage V of this species it was therefore those of the first brood only which were found above 10 m. All stages stayed mainly below 10 m. until observations ended on 21 August.

In *Pseudocalanus* and *Acartia* the return to the surface in August did not take place in the older stages. In *Pseudocalanus* all stages from adults down to Stage III, and in *Acartia* adults and Stage V remained below 10 m. until observations stopped. In the younger stages the descent in July lasted for a shorter time, and there was a gradual rise again during August. The nauplii of *Acartia*, indeed, remained largely above 10 m. all the time.

Centropages and *Temora* resembled each other closely, and although the course of events was the same the descent in July was in general less marked than in the other copepods. Numbers in June were too low to give a reliable estimate for the adults and older copepodites, but all were below 10 m. by the beginning of July. The younger stages went down later and rose earlier and the nauplii showed little change at all. A considerable proportion even of adults had risen to the surface again in August.

Oithona showed the same changes, but in even less degree. There were few dates on which copepodite Stages I and II were mostly below 10 m., and in August the adults and older copepodites were again mainly above 10 m.

All copepods but *Microcalanus*, then, showed the same series of changes, but the younger the stage the less marked the descent into deeper water and the more rapid the subsequent rise. Among nauplii only *Pseudocalanus* showed a clear migration downwards, and in *Temora* and *Oithona* the descent was little marked even in Stages I and II. The time of descent did not correspond to the presence of any particular brood except in *Calanus*.

Since this summer migration occurs in so many species of copepod there is probably some environmental factor causing it. Fish (1936*b*) says that in the Gulf of Maine *Pseudocalanus* disappears from the inshore waters in June and July when the temperature rises above 15 or 20°C., and is found in colder bottom water during the summer. In Loch Striven the temperature never rose much above 15° C. and that not till the end of July, but it is possible that the downward migration may have been caused by increasing warmth. Ussing (1938) attributes the migration to light, and this, too, may have been a factor in Loch Striven.

Apart from this seasonal retreat into deeper water there were several days on which there was a sudden increase of the copepods below 10 m. Such dates were 1 May, 5 June and possibly 21 August. The sudden dip is not seen in the curves for all species or all stages, but it is apparent in many, most clearly in *Pseudocalanus* and *Oithona*, so that these descents also had probably some common environmental cause. They cannot be accounted for by the weather on these particular days, for although 1 May was bright with high cloud, 5 June and 21 August were overcast and rainy.

It is possible that water movement caused by wind was responsible. Such movements may go on for several days after the wind which caused them has died away. The abrupt temperature fluctuations shown in May and June (Marshall *et al.*, 1934, Fig. 5, p. 804) at the surface, and occasionally even at 30 m. (the only depths where temperatures were measured), support this suggestion, and the fact that such migrations are shown in almost all stages of development, even when the temperature change does not go as deep as 30 m., suggests that the population was living above this depth. In the marked disturbance of distribution shown on 5 June the nauplii and young copepodites were less affected than the old, perhaps because they were living nearer the surface.

SIZE

The size of the six species of copepod from copepodite Stage III upwards was measured every week when available. When possible samples of about 100 were used, but the number was often lower, especially in *Centropages* and *Temora*. The measurement used was that of the cephalothorax except in *Oithona*, where it was taken from the tip of the cephalothorax to the end of the first abdominal segment. This was to make the measurement comparable with that of the other copepods, since in Cyclopidae the 'joint' comes between the first and second abdominal segments. The results are shown in Tables X–XVII and Figs. 16–29. Figs. 16, 18, 20, 22, 24, 26 and 28 show the median length throughout the year, Figs. 17, 19, 21, 23, 25, 27 and 29 the percentage size-frequency distribution. For economy of space the latter is not shown for every week but only for a selected number of dates.

All measurements were made with an ocular micrometer whose divisions equalled 17·4 μ. Those between two divisions were taken at the lower figure. In Tables X–XVII the measurements have, for economy in space, been grouped either in twos (for the smaller copepods *Microcalanus*, *Paracalanus* and *Oithona*) or in threes (for *Pseudocalanus*, *Centropages*, *Temora* and *Acartia*), so that each column corresponds to a size difference of 35 or of 52 μ. Figs. 16–29 have, however, been prepared from the extended series of measurements.

Sex differences. The size relationship between the sexes differs considerably in the different species of copepod. Normally the female is the larger, both when adult and in those copepodite stages where the sexes can be distinguished, although in Stage IV the difference is often negligible. This is so in *Calanus* and *Oithona* (where the sex can be distinguished only in the adult), and also in *Centropages*, *Temora* and *Acartia*.

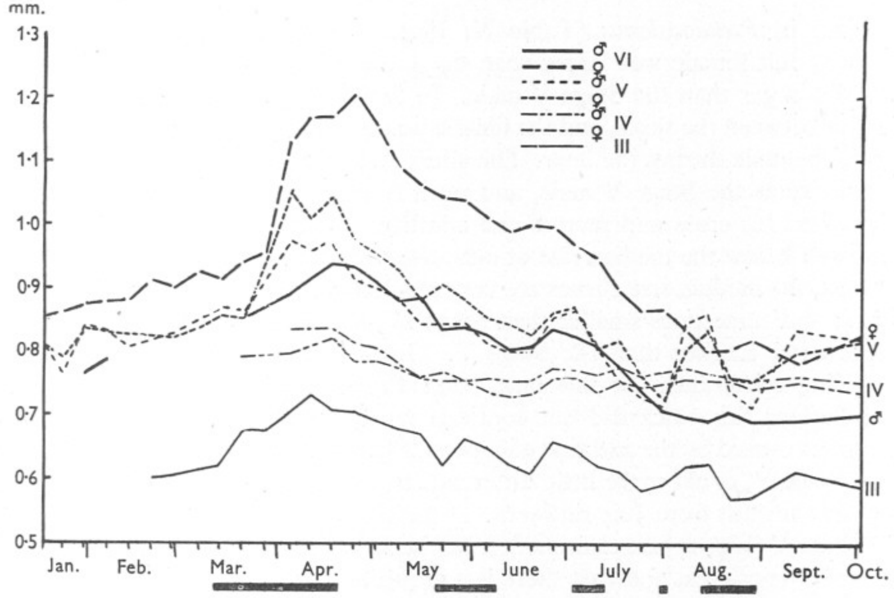


Fig. 16. *Pseudocalanus minutus*. Median size of copepodite Stages III–VI throughout the year

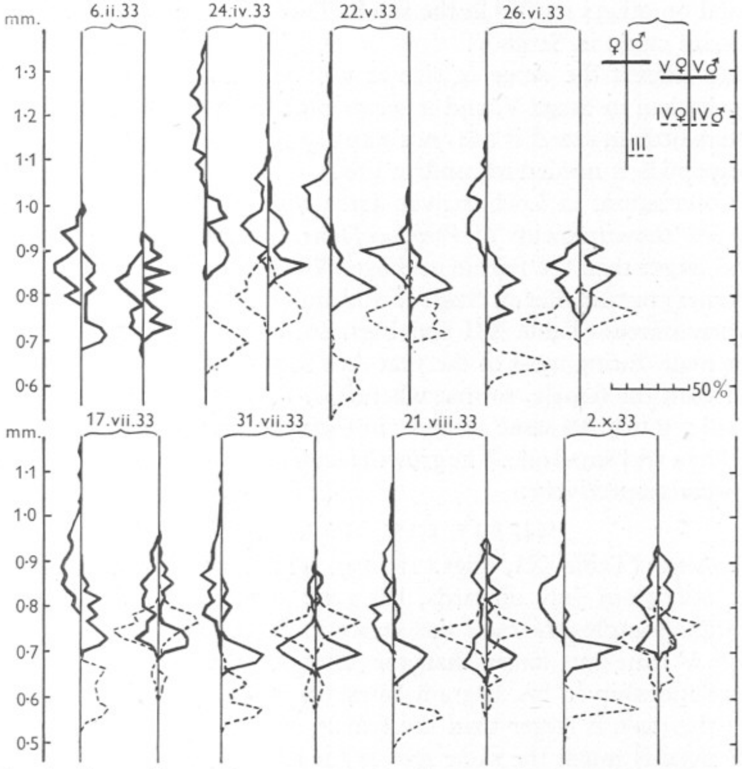


Fig. 17. *Pseudocalanus minutus*. Percentage size distribution of Stages III–VI on selected dates.

Sizes in *Pseudocalanus* (Table X, Figs. 16, 17) were normal in so far as the adult female was larger than the adult male, and the Stage V female usually larger than the Stage V male. In Stage IV there was little difference in size between the sexes, and the female was larger during the early part of the year, the male during the later. The adult male was, however, only about the same size as the Stage V male, and until August the two curves for median size (Fig. 16) cross and recross one another. After August it is smaller still and well below the median size of even the Stage IV. From August onwards, indeed, the median size curves are very much mixed up; Stage V is sometimes larger and sometimes smaller than Stage IV, and even the adult female is on some dates smaller than the Stage V. This can be partly explained by the breeding conditions. At this time Stage IV made up 40–60 % of the total population; this stock did not continue its development, and any small alterations caused by the addition of copepods from Stage III, or loss by moulting into Stage V, could make little difference to the median size, which remained almost constant from July onwards. If the size-frequency distribution curves for Stage V (Fig. 17) are examined, it can be seen that in August the total range in size is very great and that there is a group of large and of small Stage V in both male and female. On some dates most of the Stage V are in the large group and on others mostly in the small. This accounts for the very irregular median-size curve in Stage V.

During August the range of size as well as the mode was smaller in the adult male than in Stage V, and it seems probable that in the final moult the male alters little in size if it does not actually decrease. Experimental work on living copepods is needed to confirm this.

The observations in Loch Striven agree with those of Kraefft (1910), who made a few measurements of *Pseudocalanus* in Kiel Bay and found that the male was larger than the female in Stage IV (like the Loch Striven samples in late summer) but smaller in Stage V and much smaller in the adult.

In *Microcalanus* (Table XII and Figs. 20, 21) the adult female was larger than the male during most of the year, but in both Stages V and IV the male is larger than the female, so that whereas in its three final moults the female increases by much the same amount, in the male there are two large increases followed by a very small one. The growth factors (ratio of the size before and after moult) were respectively:

1·14, 1·17, 1·15; 1·22, 1·20, 1·04.

Paracalanus (Table XI, Figs. 18, 19), which was numerous enough to measure only from July onwards, has gone even further from the normal, and in these samples the male was larger in Stages IV, V and VI, and even the Stage V male was larger than the adult female. Kraefft (1910) shows a similar relationship in his diagram based on measurements in February and August; the male is larger than the female in Stages IV, V and VI, but the Stage V male is much the same size as the adult female.

Seasonal change. Apart from these minor sex differences the size of all the copepods showed a seasonal change. Comparatively small in winter, the size of all stages, especially the adults, underwent a great and rapid increase in spring to a maximum sometime in April, and there was then a gradual decline until August. After this there was in most species little further change, and the sizes were much the same as those found in January.

Since *Paracalanus* copepodites (Table XI and Figs. 18, 19) did not appear in numbers till July, it cannot be known whether it conformed to this normal type early in the year. From July to October the curves for median size are very regular with a slight tendency to rise. The curves for *Microcalanus* are also very regular and show only minor variations. In all copepodite stages they rise gently to a maximum, which lasts most of April, and then decline gently during the rest of the year.

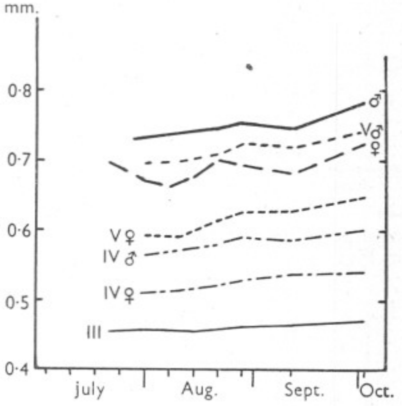


Fig. 18.

Fig. 18. *Paracalanus parvus.* Median size of copepodite Stages III–VI from July to October. Lines as in Fig. 16.

Fig. 19. *Paracalanus parvus.* Percentage size distribution of Stages III–VI on selected dates.

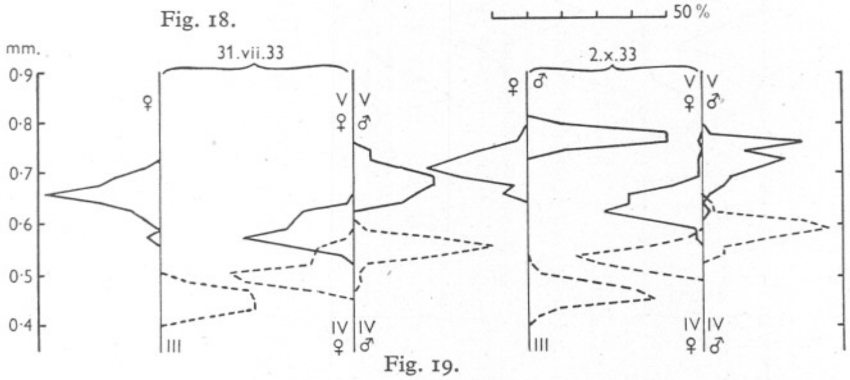


Fig. 19.

In *Pseudocalanus* (Table X and Figs. 16, 17) the increase in size in spring was much more abrupt, and there is a well-marked maximum occurring on 10 April in Stage III and on 24 April in females. After April there was a more gradual decrease till the autumn, with only minor, and probably not significant, fluctuations. One of the most striking features was the wide range in

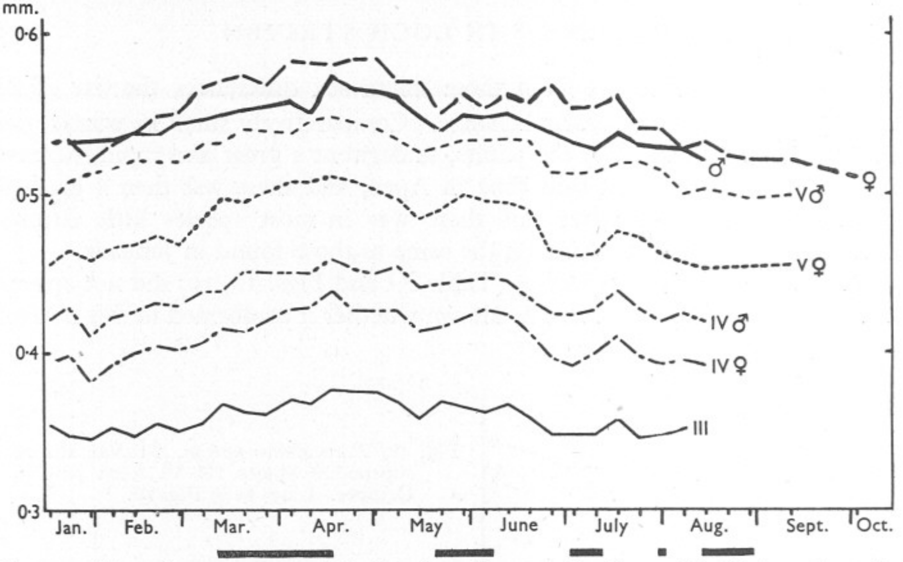


Fig. 20. *Microcalanus pygmaeus*. Median sizes of copepodite Stages III–VI throughout the year. Lines as in Fig. 16.

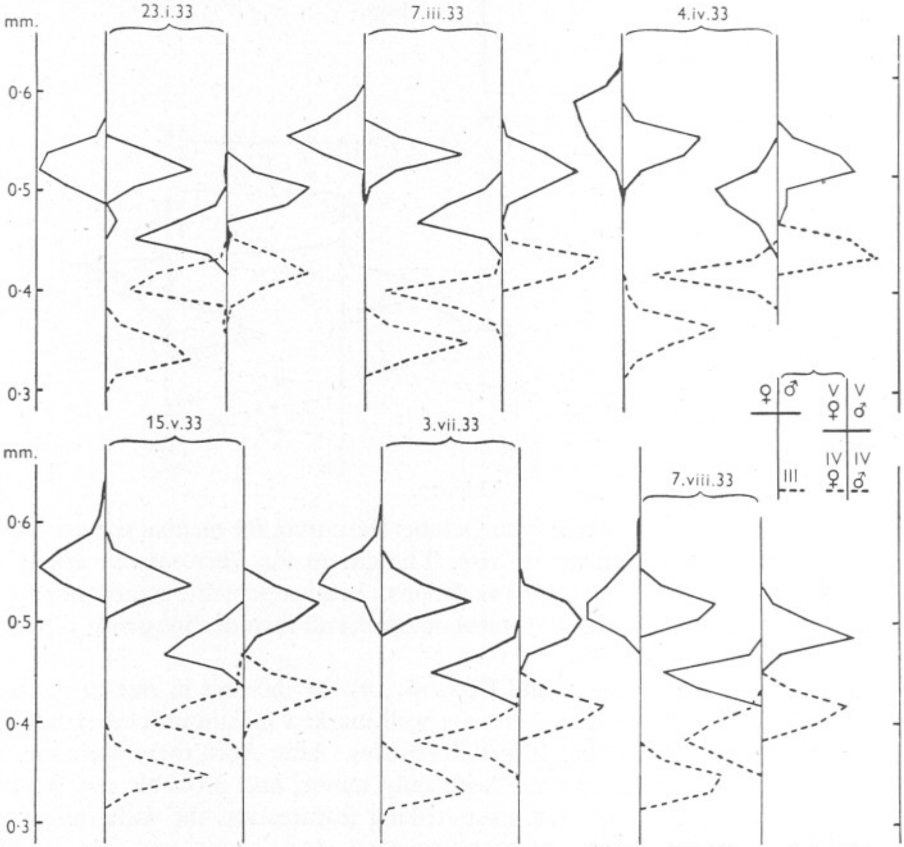


Fig. 21. *Microcalanus pygmaeus*. Percentage size distribution of Stages III–VI on selected dates.

size, so that each stage overlapped the next, sometimes to a considerable extent. Except in Stage III the curves of Fig. 17 are rarely unimodal, and for the older stages are multimodal or very irregular. The two modes seen in Stage III curves do not correspond to the differences in size between male and female Stage IV. Störmer (1929) refers to the great range in size of *Pseudocalanus*, and the samples of Adler & Jespersen (1920) show a maximum size range very much the same as that of the females in Loch Striven.

In *Calanus* with the appearance of a new brood, the size-distribution curves usually became more compact and unimodal as if a large number of similar individuals had moulted together; the median size often showed a rise also (Marshall *et al.*, 1934). In *Pseudocalanus*, however, with its more continuous breeding, this was not obvious. Stage III showed a clearly unimodal curve on its first appearance with the first brood at the end of February, and again at the end of April, May, June and August, perhaps corresponding to broods, but the later stages did not do so regularly. From July onwards, as might be expected from the building up of a large stock which did not develop beyond Stage IV, the curves for Stage IV became more uniform, showing one distinct mode (a little smaller in the female than in the male), with occasionally a smaller size group, perhaps of later-moulting animals.

In *Centropages* and *Temora* (Tables XIII, XIV and Figs. 22–25) there were not enough copepods to measure in the early part of the year, but there was a very well-marked size maximum in the later stages of both species on 24 April. The subsequent decline to a minimum in August was interrupted in both species by a smaller increase in size on 19 June, marked only in adults in *Temora*, but also in Stage V in *Centropages*. *Temora* females, although few in number, also showed a decided increase on 15 May, which was the approximate date of appearance of the adults of the second brood. On 19 June, however, there is nothing obvious in either species to account for an increase in size. The numbers of all stages measured (except males) were small, and the change was perhaps not significant. The size of all stages reached a minimum in the end of July or beginning of August and thereafter began to rise again gradually. After 11 September there were too few to measure. An autumn size-maximum has been described for *Temora* by Adler & Jespersen (1920). In both *Centropages* and *Temora* the range in size of the different stages, distinct during the early part of the year, came to overlap more and more in late summer (Figs. 23, 25).

Apart from a few females in January and February, *Acartia* (Table XV and Figs. 26, 27) was too scarce to measure until 24 April or later, but it seems fair to assume that during March and April the size was gradually increasing and that it reached its maximum about 24 April, a date which marked the first appearance of the spring brood. There was a steady decline from then till the beginning of August, after which the size remained pretty constant or rose a little. Stages V and III were present only in very small numbers at the

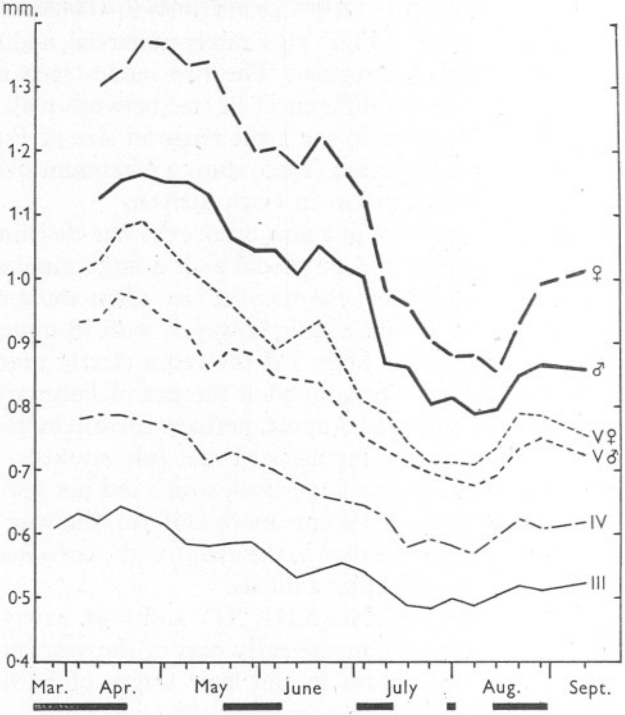


Fig. 22. *Centropages hamatus*. Median size of copepodite Stages III–VI throughout the year. Lines as in Fig. 16.

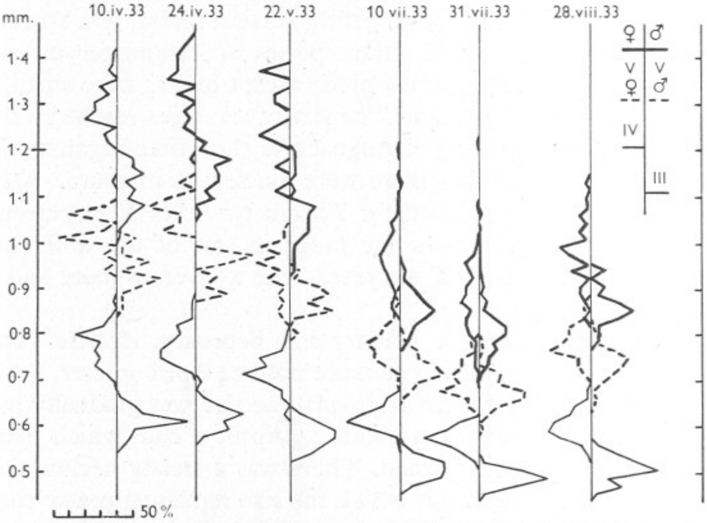


Fig. 23. *Centropages hamatus*. Percentage size distribution of Stages III–VI on selected dates.

end of April, and their maximum size is therefore unknown. *Acartia* differs very much from the other copepods in its size-frequency distribution curves (Fig. 27), for these are almost always clearly unimodal, and the range of size of one stage, apart from a few exceptional individuals, scarcely overlaps that of the next.

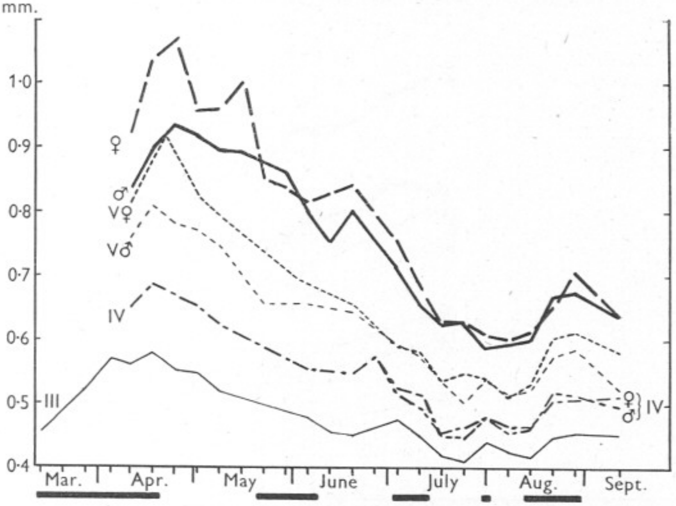


Fig. 24. *Temora longicornis*. Median size of copepodite Stages III–VI throughout the year. Lines as in Fig. 16.

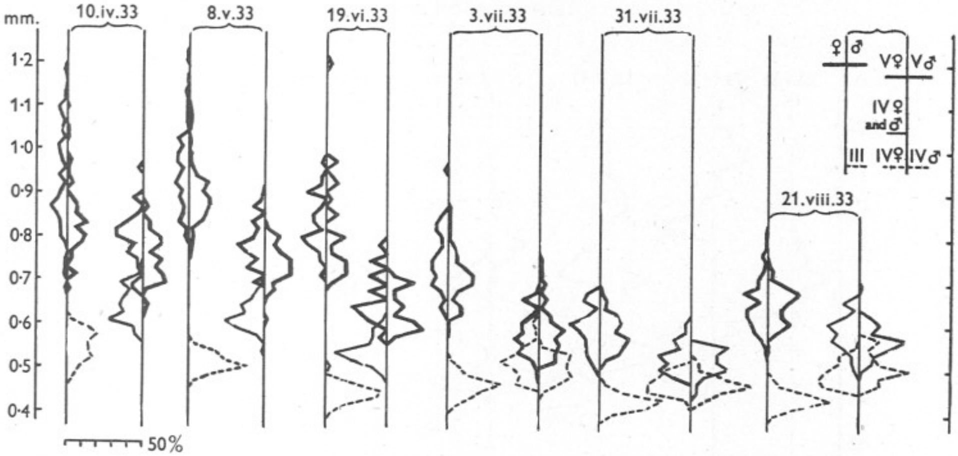


Fig. 25. *Temora longicornis*. Percentage size distribution of Stages III–VI on selected dates.

Oithona (Table XVI and Figs. 28, 29) varied less in size than the other copepods, although there was a gentle rise till the end of April and a subsequent decline. It resembles *Microcalanus* in its lack of a well-marked maximum in spring. There was a slight rise again from 29 May to 19 June which coincided with a diatom increase and also with an increase in the number of eggs produced. After this the size decreased gradually, and by the beginning of August had reached that found in January, where it remained. From January to mid-April the size range of Stage V overlapped almost completely those for both males and females (Fig. 29). For several weeks the median size of males was larger than that of females (Fig. 28) and for 2 weeks Stage V was larger also. If Fig. 29 is examined, however, it will be seen that this is because the

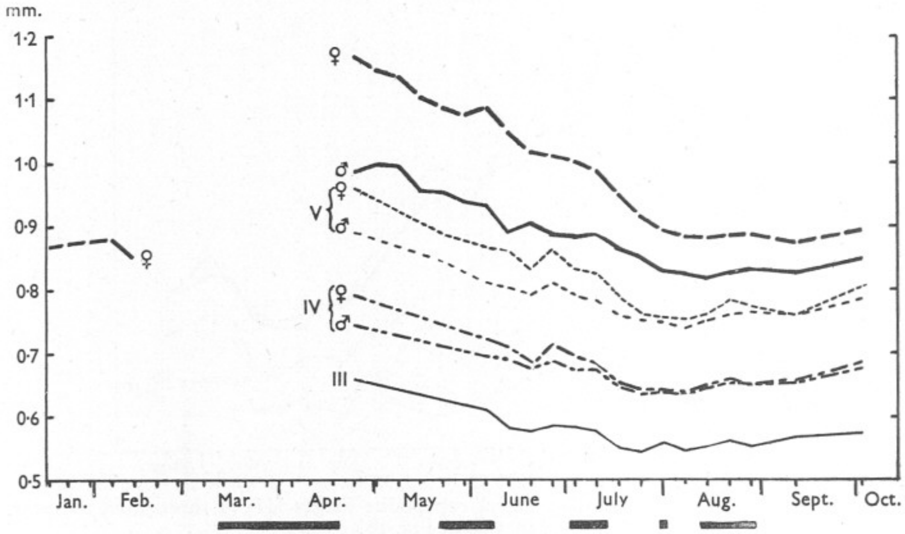


Fig. 26. *Acartia clausi*. Median size of copepodite Stages III–VI throughout the year. Lines as in Fig. 16.

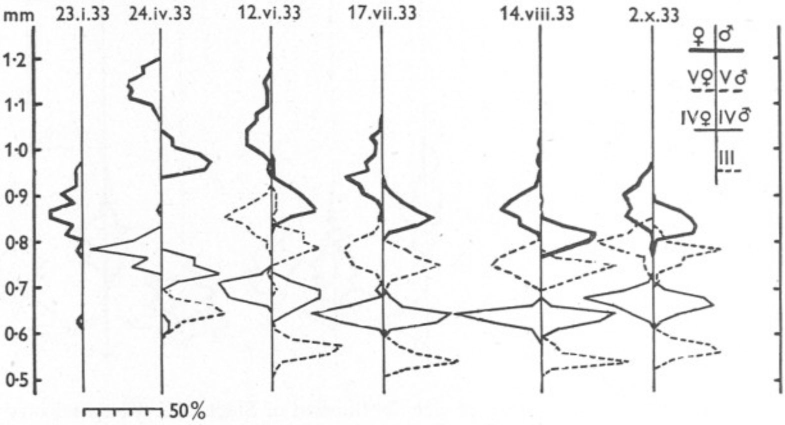


Fig. 27. *Acartia clausi*. Percentage size distribution of Stages III–VI on selected dates.

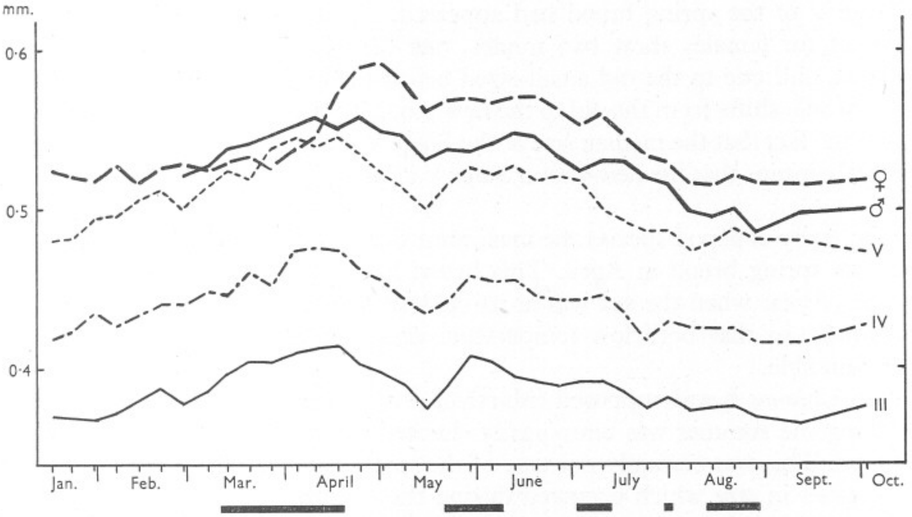


Fig. 28. *Oithona similis*. Median size of copepodite Stages III–VI throughout the year. Lines as in Fig. 16.

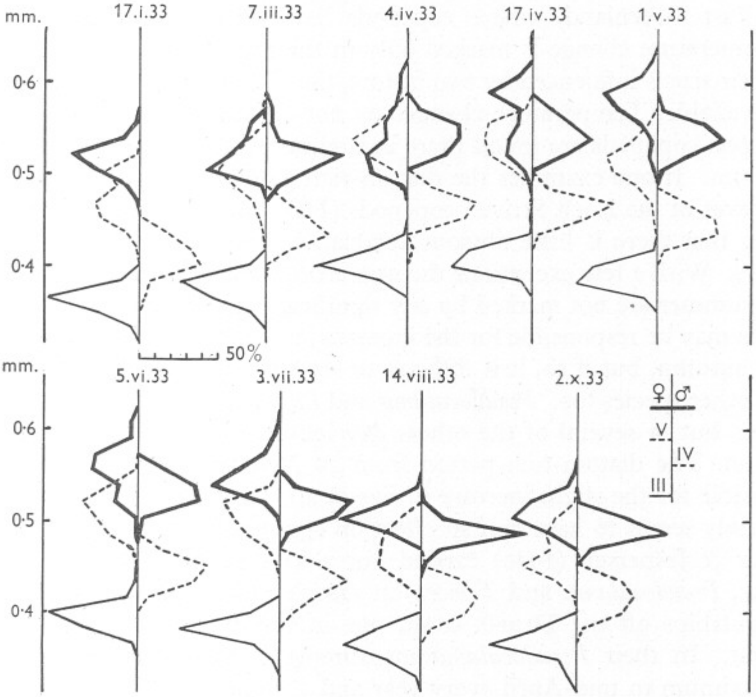


Fig. 29. *Oithona similis*. Percentage size distribution of Stages III–VI on selected dates.

Stage V of the spring brood had appeared. At this time the size-frequency curves for females show two modes, one belonging to the new large-sized brood, and one to the old small-sized brood (Table XVI). The female stock as a whole shifts from the old to the new mode during 27 March to 24 April, so that the fact that the median size of the Stage V is larger than that of the female merely means that the new-brood Stage V is larger than the old-brood females.

In every copepod species the maximum size was reached on the appearance of the spring brood in April. This brood hatched and grew up during that time of year when the sea was at its coldest. It was also a time of abundant diatoms, so that both low temperature and rich food supply may be held accountable.

In *Calanus* it was supposed (Marshall *et al.*, 1934) that the decrease in size during the summer was temporarily checked on the appearance of each new brood. This was certainly not true of the small copepods. In them the slight increases in size which occurred during the summer were hardly significant and bore no relation to broods. Even *Microcalanus*, which in its reproduction resembled *Calanus* closely, showed no comparable size changes. Only in the *Temora* females of the second brood on 15 May was there an increase in size, but this was based on the measurement of ten specimens only.

In East Greenland, where copepods have only one brood a year and the temperature change is marked only in the top 10 m., Ussing (1938) says that their size is influenced by two factors, the size at moult and the amount of food available. Temperature changes do not explain the size differences, for the largest copepods are found there in summer when the temperature is at its maximum. If one examines the diatom-rich periods along with the median-size curves of the Loch Striven copepods (Figs. 16, 18, 20, 22, 26, 28), it will be seen that there is little obvious correlation apart from the spring diatom increase. With a few exceptions the numerous diatom increases in the course of the summer are not marked by any significant changes in size. The August diatoms may be responsible for the increase in size of *Centropages* and *Temora* in late autumn, but if so, it is difficult to see why they did not have an effect on the other species too. *Pseudocalanus* and *Paracalanus* had stopped breeding by then, but in several of the others development seemed to have been still going on. The diatom-rich period from 29 May to 5 June may have been responsible for the slight increase in size of all stages of *Oithona* at that time; it certainly seems to have had an effect on egg production.

Adler & Jespersen (1920) carried out a long series of measurements of *Calanus*, *Pseudocalanus* and *Temora* on samples taken for several years from two lightships off the Danish coast, one in the North Sea and one in the Kattegat. In their *Pseudocalanus* measurements there was a very marked size maximum in mid-April every year and a more gradual decline, showing numerous irregularities, to a minimum in August. In the North Sea this minimum size was retained all winter and there was no increase till the following March. In the Kattegat, however, in two of the three autumns the size increased sharply again in October and November and rose more or less steadily till April. It seems possible that breeding there continued later into the winter and that the lower temperatures then had an effect on the size of the developing copepods, but there is no obvious reason for a late brood. On the whole, however, the size changes agree very well with those found in Loch Striven except that in their samples the male is always about 0·1 mm. smaller than the female, and this difference is maintained throughout the year.

In *Temora* (adults only were measured) they found two maxima in the year, one in spring and the other in winter, usually December. This second maximum was sometimes even larger than the spring one, and perhaps indicated breeding during the winter. The measurement of the Loch Striven samples was not carried on far enough into the winter to see whether the size increase shown in the end of August continued. The actual sizes of the copepods were much the same in all three places, those from the North Sea being on an average rather larger than those from the Kattegat, and those from the Kattegat in turn rather larger than those from Loch Striven.

Food and Feeding

In examining the samples for measurement a note was kept of any copepods with food pellets in the gut. The copepods had been in preservative for up to 10 or 12 years, and the body was often opaque, making the gut difficult or impossible to see. No great reliance can be put therefore on the figures for the percentage feeding, and it seemed to have very little relation to the times of diatom increase. The greatest differences were found between one species of copepod and another. Thus *Temora* and *Centropages* always had a much larger percentage feeding than any of the other species, a fact which confirms observations made on living specimens (Lebour, 1922; Marshall, 1924). On the whole fewer males were seen with food than any of the other stages, and this is what might be expected from their shorter life and specialized function. In some copepods, e.g. *Euchaeta norvegica* (Sars, 1903; Nicholls, 1934), the male has much reduced mouthparts.

The results of some examinations of the gut contents of living copepods, taken from near the Marine Station, Millport, is shown in Table II. Most of these observations were made in autumn and winter, few in spring or summer. It will be noted that *Centropages* and *Temora* have again a larger proportion feeding than *Pseudocalanus* and *Acartia*.

As with *Calanus*, the food actually observed does not seem enough to meet the requirements, and the question remains whether or not the copepods depend largely on the minute naked flagellates about whose abundance and variations in the sea so little is known. Minute flagellates were counted in the

1933 centrifuged water samples (Marshall *et al.*, 1934, p. 824), but centrifuging is not a reliable method for these very small forms, and the figures given may bear little relation to their real abundance. It is perhaps not surprising, therefore, that no relation can be seen between their numbers and copepod size or breeding.

TABLE II

Species	No. examined	Empty or food indistinguishable	Diatoms	Radiolarians	Flagellates	Crustacea
Pseudocalanus	102	73	18	4	1	10
Microcalanus	16	15	1	0	0	0
Centropages	8	2	3	0	2	6
Temora	43	5	28	9	7	18
Acartia	88	59	18	3	1	9

Sixteen *Oithona* females were examined, but they contained only indistinguishable debris.

PARASITES

Pseudocalanus was the only copepod in which parasites were observed, and it seems to be less subject to them than *Calanus*. A trematode has occasionally been seen in its body cavity (although not in the Loch Striven samples), but the internal dinoflagellate parasites so common in *Calanus* (Jepps, 1937) are rare. Ten specimens were seen carrying *Ellobiopsis* and, as usual, most of these were on females (4 on Stage V female, 1 on Stage V male, and 5 on adult female). A *Microniscus* sp. was found on one female.

COMPARISON WITH OBSERVATIONS ELSEWHERE

Pseudocalanus. Among the pelagic copepods, *Pseudocalanus minutus*, because of its large numbers, is perhaps the most important species after *Calanus*, and its breeding and size variations have been studied in numerous places in the North Atlantic. The general course of its growth and development there is remarkably uniform. In Loch Striven, off the Norwegian coast (Oslo Fjord, Wiborg, 1940; Herdla and Hjelte Fjords, Runnström, 1932; off Möre, Ruud, 1929), and in the seas between Norway and Iceland (Störmer, 1929), reproduction begins in early spring, usually at the time of the phytoplankton increase, and goes on throughout the summer. The maximum numbers occur, not with the first brood, but during the summer, and by July or August the stock is mainly in the late copepodite stages and will pass the winter thus. In Nordåsvatn, however, Stage III is the most abundant stage from August to December (Wiborg, 1944). In the most southerly area investigated, the Gulf of Maine, much the same holds good (Fish, 1936*b*); reproduction begins with the spring increase and there are three or four broods during the summer and autumn, of which the second is the largest, but the copepod almost disappears from inshore waters from July to October. Fish supposes that rising temperature is the cause of this and that they move into deeper water offshore.

In the most northerly part of the area, East Greenland, conditions are rather different (Ussing, 1938). Most of the stock spends the winter in deep water (below 50 m.) and rises above this only from June to August. Reproduction begins soon after, but in the cold water there development is slow and there is only one brood a year, although a few individuals may possibly grow fast enough to reproduce in the same summer that they are hatched. Early copepodite stages are found throughout the winter, and even Stage II does not entirely disappear till March of the year following that in which it is hatched. The temperature below 50 m. differs little from that above except near the surface during the summer, and Ussing ascribes the seasonal vertical migrations to the influence of light.

Pseudocalanus is found at all depths, but as a rule is more abundant near the surface, i.e. above 50 m., and even above 20 m. (Ruud, 1929). According to Runnström (1932) it avoids the layers above 10 m., but this was not so in Loch Striven. Ruud records that in 1927 at two Stations it was more numerous below than above 50 m. in May, June and July. Where vertical hauls have been taken in sections the division has commonly been made much deeper than 10 m., so that the seasonal migration above and below 10 m. found in Loch Striven cannot be confirmed from elsewhere. In Nordåsvatn, a land-locked fjord near Bergen, *Pseudocalanus* was often found above 15 m., and there were considerable alterations in vertical distribution from time to time (Wiborg, 1944). Hydrographical conditions were, however, so different (well-marked layering, and lack of oxygen in deep water) that the two areas can hardly be compared.

In the Barents Sea (Bogorov, 1932) the depth distribution was peculiar in that there were maxima at 10–25 and 100–160 m., with an intervening minimum. The upper maximum is composed of Stages I–V, the lower of Stages III–VI.

Paracalanus. In Norwegian waters (Runnström, 1932; Wiborg, 1940) *Paracalanus* is scarce throughout the winter and has a maximum in late summer as in Loch Striven.

Microcalanus. This copepod, owing to its small size, will slip through the meshes of most nets and has not been taken into account in most plankton hauls. There are, however, some data on its occurrence off the Norwegian coast (Ruud, 1929; Runnström, 1932; Wiborg, 1940), and from the *Michael Sars* expedition (Störmer, 1929). It is generally agreed to be a deep-water form living mainly below 50 m. Runnström states that in autumn and winter (in the Herdla and Hjelte Fjords) it is numerous also from 10 to 50 m., and that from May to August it is found mainly below 100 m. Störmer mentions the possibility that it may make diurnal vertical migrations. The dates of spawning, which they judged mainly from the presence of males or of females carrying spermatophores, agree well with those in Loch Striven, March (off Möre), or February to April (Oslo Fjord), May (Herdla and Hjelte Fjords), May to June (off Möre), or June (Oslo Fjord), October to November (Oslo Fjord). Wiborg remarks on the periodicity of the spawning, and his late autumn date is perhaps an indication that spawning can go on during the winter. There was in the Loch Striven samples, however, no clear development from the nauplii even as early as August.

In the fjords of East Greenland (Ussing, 1938) *Microcalanus* was found above 50 m. only in winter (November to May). It spawned in the early months of the year (January to March), but this was probably not the main spawning time. Owing to its withdrawal into deep water during the summer, its complete life history there could not be ascertained.

Centropages hamatus. This is a coastal form living near the surface and there are few observations on it in the literature. Wiborg (1940), working in the Oslo Fjord, says that the chief spawning is in March or April, but that there is some also in summer. The maximum numbers are in June and July when adults and copepodites predominate. On the whole this agrees fairly well with Loch Striven. Otten (1913) says that in Kiel Bay its numbers increase gradually till June, decrease, and then increase again in September. As already mentioned (p. 59) he found a large number of nauplii but no copepodites in the end of September and even in November.

In the zooplankton of the Gulf of Maine (Fish & Johnson, 1937) *C. hamatus* was not present but *C. typicus* occurred, and they mention the possibility of its having a 'winter egg' since the species is sparse or absent most of the year.

Temora. Like *Centropages*, *Temora* is a neritic form, living near the surface, abundant as a rule only in summer. In the Oslo Fjord (Wiborg, 1940) it was scarce during the winter and numerous from April till July. The maximum numbers in the outer fjord were found in April and July, and the main spawning was (as in Loch Striven) in April. Nauplii were found all the year round, and adults were more numerous from June to October. This was not so in Loch Striven, nor was the proportion of adults higher than in the other species. Males outnumber females in the Oslo Fjord but not, according to Otten (1913) in Kiel Bay (see Table I). There reproduction probably went on late into the winter, since maxima of copepodites were found in June, September and also December.

Acartia. In the Oslo Fjord (Wiborg, 1940), as in Loch Striven, *Acartia* had a late summer maximum in numbers and decreased very much from December to June. In other areas, however, such as the Herdla and Hjelte Fjords (Runnström, 1932) and off Möre (Ruud, 1929), there were two maxima, the first in April to May or May to June and the second in July or August to November. Off Möre there were several broods in the year beginning in March to April. *Acartia* has usually been found between 0 and 100 m., but in autumn was found also down to 200 m.

On the east coast of America this species occurs as an inshore form. South of Cape Cod (Fish & Johnson, 1937) it forms an important part of the neritic community in winter, but to the north it has its maximum in late summer and usually spawns then. It is occasionally found to spawn in early spring there also, but this may be an extension of the winter breeding centred to the south of Cape Cod.

Oithona similis. This is a very widely distributed species, and its seasonal variation in numbers has been studied in the Gulf of Maine (Fish, 1936*c*) as well as in the North Atlantic and on the Norwegian coast.

In Norwegian waters the species is found down to 400 m., although it is commonest near the surface. It occurs all the year round and has two maxima in numbers, one in March to May, the other July to August, the date varying from year to year.

Otten (1913), working in Kiel Bay, finds rather different conditions, for he states that maximum numbers occur in April and in October with a minimum in August. This indicates a condition very different from Loch Striven where the maximum comes in August.

Fish (1936*c*) finds that in the Gulf of Maine, as in Loch Striven, eggs and nauplii make up a large proportion of the total catch throughout the year, indicating a heavy mortality in these stages. He suggests, however, that development takes as long as 2 months in winter and 6 weeks in summer, which seems decidedly too long for the Loch Striven *Oithona.* Breeding in the Gulf of Maine as in Loch Striven begins in March, and three or four broods are produced from then till September. The maximum number occurs in August.

DISCUSSION

The importance of a copepod in the ecology of the plankton cannot be judged from its numbers alone; its size must also be taken into account. Very little is known about the weights of the small copepods. Bogorov and Preobraijenskaya (1934) have published a few data for *Pseudocalanus elongatus* (Stages V and VI), *Centropages hamatus* (Stage VI) and *Acartia longiremis* (Stage VI), giving the average dry weights as 0·07–0·09, 0·11 and 0·012 mg. respectively. Lohmann (1908) has given calculated volumes in cubic microns for most of the common species, but his relative values (which are rough averages from nauplius as well as copepodite stages) do not agree very well with the Loch Striven sizes. His volumes for the different species in cubic millimetres are as follows: *Temora*, 0·026; *Centropages hamatus*, 0·025; *Pseudocalanus*, 0·0235; *Acartia*, 0·014; *Paracalanus parvus*, 0·006; *Oithona similis*, 0·003. In this series *Temora* seems too large and *Acartia* too small; *Microcalanus* would presumably be slightly larger than *Oithona.* He does not give *Calanus* either, and it is probably at least ten times the volume of *Pseudocalanus.* Fig. 30 shows the numbers of the seven species of copepod in Loch Striven throughout the year, all drawn on the same scale. Taking Lohmann's values for volume it is found that (apart from *Calanus*) *Pseudocalanus*, because of its size and abundance, is by

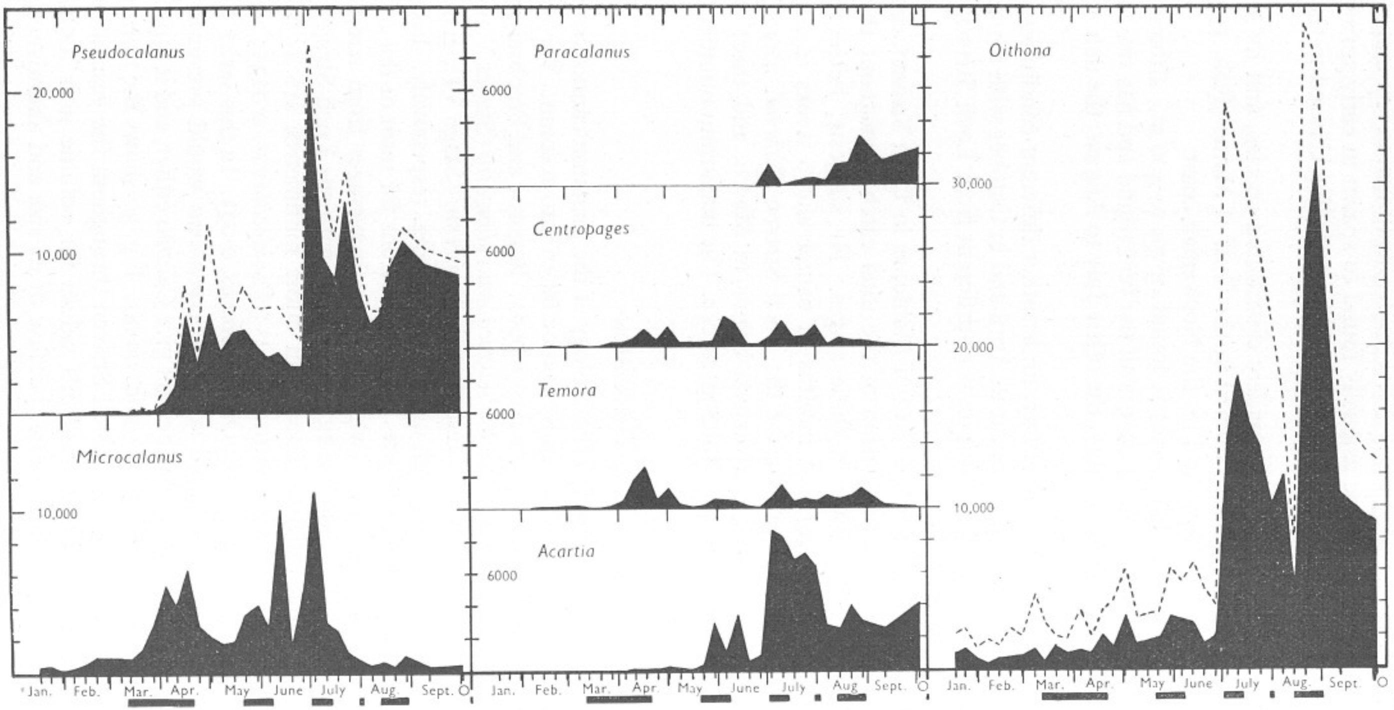


Fig. 30. Total numbers of the seven copepods throughout the year all shown on the same scale. Solid black, nauplii and copepodites, dotted line (*Pseudocalanus* and *Oithona*), total including eggs.

far the most important, *Acartia* (even at Lohmann's low assessment) comes next, and *Oithona*, because of its high numbers, third. *Microcalanus*, *Temora* and *Centropages* are all much the same and considerably less than *Oithona*. This gives a rough idea of the amount of animal food each copepod species can provide. *Paracalanus* is omitted, since it did not become common till July and may have been more important after observations stopped in October. The different stages and species of copepod are, however, eaten by different sizes of fish, the smallest stages providing food for the larvae and the largest for post-larval or even adult fish. Some of this food is available all the year round, but it is most abundant from April on throughout the summer when most young fish are growing.

The life histories of all the copepods so far examined resemble one another in their general features and differ only in detail. Each shows a succession of broods throughout the summer, sometimes distinct but more often running into one another. The dates on which breeding begins and stops vary from year to year and from place to place. The usual number of broods is three or four, but in the cold waters of the far north this may be reduced to one. Since work in Loch Striven stopped in October it is not possible to say for every species whether breeding continued after this date or not. In *Calanus*, *Pseudocalanus* and *Paracalanus* it certainly did not, for by that time a large stock (40–80 % of the total catch of each) of Stages IV or V had been built up, and further development had obviously stopped. In the other copepods a much larger proportion of nauplii was present in October (about 75 % in *Microcalanus*, *Centropages* and *Temora*), and although breeding did not seem to be going on it was still a possibility. In *Acartia* and *Oithona* the percentage of nauplii in October was about 40 %, much lower than was found in January to March. Here, too, further breeding was still possible. The stage in which the winter is passed may therefore vary in different species of copepod, and further work is needed to elucidate this.

The sequence of events described, although true for 1933, may not be followed every year. It is known from unpublished observations in Loch Striven and at Millport that, for instance, *Microcalanus* is not always one of the common copepods, and that the order of appearance and relative abundance of the different species is not always the same. It would therefore be very interesting to have detailed studies of the copepods, not only from different areas, but from the same area in different years.

The vertical distribution of the copepods in Loch Striven was rather different from that described elsewhere, mainly perhaps because the loch is, comparatively speaking, shallow, and the great depths at which they are sometimes found do not occur there. In Loch Striven all but *Microcalanus* followed the same pattern; they were all near the surface till July, and then the older stages were mainly in deeper water for at least a few weeks and in some species a few months.

The seasonal size variations, too, resembled each other closely in all species examined and agreed with what has been found elsewhere. The different species do not all grow at the same rate. Fig. 31 shows the median size of all the copepodite stages of all the copepods on 3 July (see also Table XVII), a date when they were numerous enough to measure, and Fig. 32 shows the maximum and minimum sizes reached during the year by each stage. It can be seen from Figs. 31 and 32 that whereas *Oithona* doubles its length from Stage I to the largest Stage VI, *Pseudocalanus*, *Microcalanus*, *Temora* and *Acartia* about treble it and *Centropages* quadruples it. From Stage I to Stage V (Fig. 31) *Pseudocalanus* and *Acartia* are about the same size as *Centropages*, but in the adult, *Centropages* is the largest.

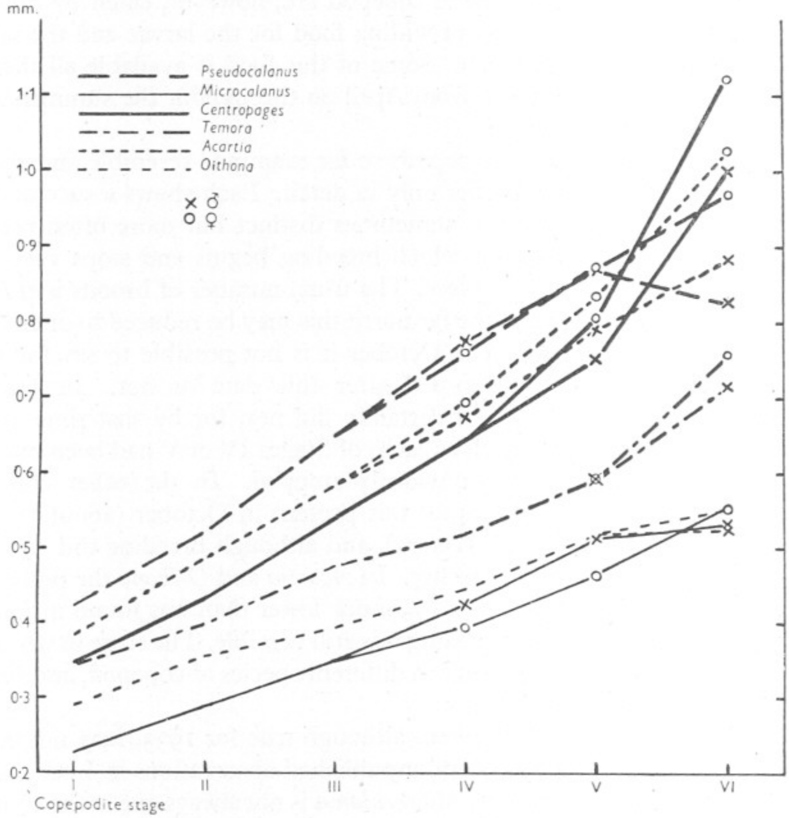


Fig. 31. Median size of copepodite Stages I–VI of six copepod species on 3 July.

The points for the median lengths of the stages in each copepod lie on a more or less straight line up to Stage V, but beyond this the different species vary. In *Centropages* there is a marked, and in *Temora* and *Acartia* a slight, rise in the curve from Stages V to VI, in each case greater in the female than

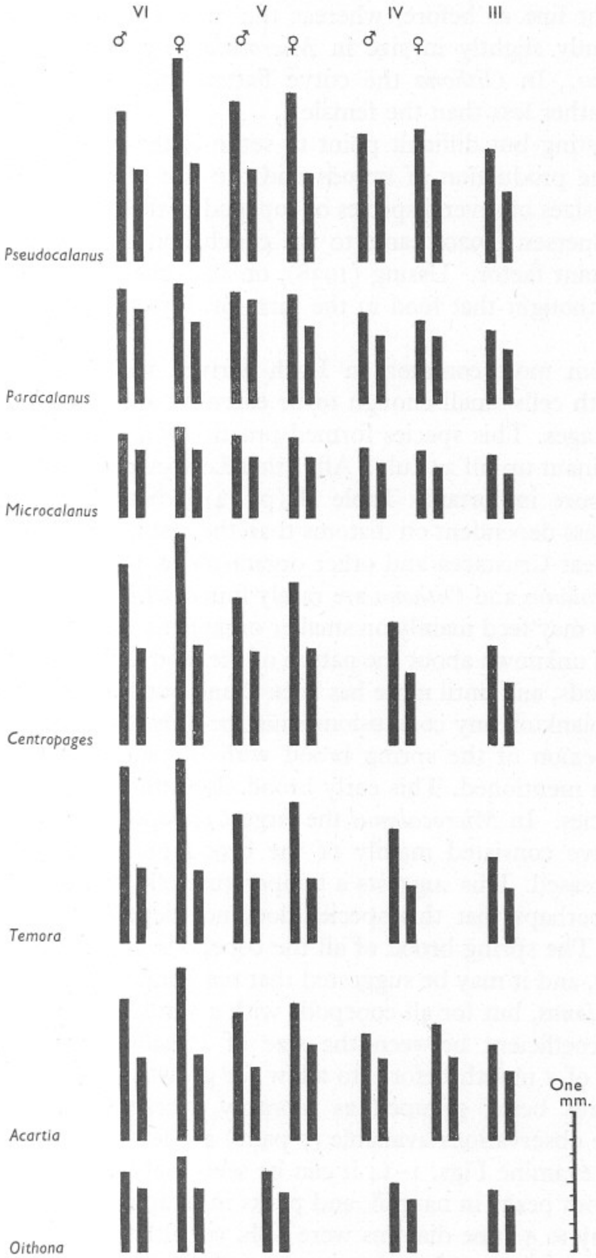


Fig. 32. Maximum and minimum sizes of copepodite Stages III–VI in seven species.

in the male. In *Pseudocalanus* and *Microcalanus* the female continues on the same straight line as before, whereas the male curve flattens off, the male increasing only slightly in size in *Microcalanus* and actually decreasing in *Pseudocalanus*. In *Oithona* the curve flattens off in both sexes, the male increasing rather less than the female.

An interesting but difficult point to settle is the relation between diatom increases, the production of broods and the size of the copepods. In their study of the sizes of several species of copepod in the North Sea and Kattegat, Adler & Jespersen (1920) came to the conclusion that temperature was the most important factor. Ussing (1938), on the other hand, working off East Greenland, thought that food in the form of phytoplankton was much more important.

The diatom most common in Loch Striven was *Skeletonema costatum*, a species with cells small enough to be eaten by all the copepods at least in their later stages. This species formed practically all the spring increase and was predominant up till 24 July. After that *Leptocylindrus* sp. and *Chaetoceros* spp. were more important. Table II (p. 84) indicates that *Centropages* and *Temora* are less dependent on diatoms than the rest because they are voracious feeders and eat Crustacea and other organisms as well as diatoms, and that, since *Microcalanus* and *Oithona* are rarely found with recognizable remains in the gut, they may feed mainly on smaller organisms such as minute flagellates. Much is still unknown about the nature of the food and the food requirements of the copepods, and until more has been found out about the relation of these to the nanoplankton any conclusions must be only tentative.

The connexion of the spring brood with the spring diatom increase has already been mentioned. This early brood also attained the largest size in all but one species. In *Microcalanus* the largest copepods occurred during April and may have consisted mainly of the brood produced before the spring diatoms increased. This suggests a temperature effect rather than a rich food supply, or perhaps that this species does not depend on diatoms for food (see above). The spring brood of all the copepods grew up when the sea was at its coldest, and it may be suggested that temperature is important, not only for *Pseudocalanus*, but for all copepods with a similar size curve. Indeed, the correlation coefficient between the size of *Pseudocalanus* females and the temperature of a month before (to allow for growth from egg to adult), both sets of figures being grouped as monthly averages, is significant (0·88), although the observations available (7 pairs) are few.

When we examine Figs. 1–14 it can be seen that there are both diatom increases without peaks in nauplii, and peaks in nauplii when diatoms are poor. From 22 May to 5 June diatoms were rich, yet although there were increases both in the proportion and in the actual number of nauplii (*Pseudocalanus* was an exception), no brood grew up. The diatom increase on 3 to 10 July, on the other hand, was accompanied in almost every copepod by an increase in nauplii from which a brood grew up. The very short-lived diatom increase on 31 July (164 cells/ml. at the surface only) had no effect except a possible increase of nauplii in *Centropages*. The larger and more prolonged increase from 14 to 28 August was again accompanied by an increase in nauplii in every copepod, but since breeding at that time was more or less continuous it is doubtful whether an increase in the number of older stages resulted.

On the other hand, on 1 May, when diatoms were poor, there was a peak of nauplii followed by a brood in *Centropages*, *Temora* and possibly *Oithona*. These are, however, three of the copepods which may be less dependent on diatoms for food than are the others (Table II, p. 84).

On the whole, then, it does seem that the presence of diatoms increases the production of eggs and nauplii and helps the development of the later stages.

SUMMARY

The seven species of small copepod common in Loch Striven have been studied from vertical tow-net hauls taken there throughout the year 1933. These copepods were *Pseudocalanus minutus*, *Paracalanus parvus*, *Microcalanus pygmaeus*, *Centropages hamatus*, *Temora longicornis*, *Acartia clausi* and *Oithona similis*.

In general, the copepods began to reproduce about the time of the spring diatom increase in March or April, and produced a succession of broods throughout the summer; apart from the first these broods were not as a rule so clearly marked as in *Calanus*. *Microcalanus* begins to breed before the spring increase and has clearly marked broods like *Calanus*.

The numbers of males and females were about equal until the adult stage, when the proportions varied greatly between one species and another.

The number of eggs laid per female was counted in *Pseudocalanus* and *Oithona* and it varied throughout the year. The number is closely correlated with the size of the female and may bear some relation to the amount of phytoplankton present.

With the exception of *Microcalanus* all the copepods showed a seasonal vertical migration. From April till the beginning of July they were found mainly above 10 m. and in July and August mainly below. The migration was more marked in some species than in others and, as in *Calanus*, the younger stages showed it less than the older. *Microcalanus* stayed below 10 m. almost entirely from April to August.

The size of copepodite Stages III–VI was measured throughout the year. In most species there was a well-marked maximum in spring and a gradual decrease till the autumn. The relative size of male and female in copepodite Stages IV–VI is different in different species.

Observations in Loch Striven are compared with those made on the same copepods elsewhere.

The relationship between reproduction, size and phytoplankton is discussed.

REFERENCES

ADLER, G. & JESPERSEN, P., 1920. Variations saisonnières chez quelques copépodes planctoniques marins. *Medd. Komm. Danmarks Fisk. Havund., København, Ser. Plankton,* Bd. II, No. 1, 46 pp.

BOGOROV, B. G., 1932. Materials on the biology of the copepodes of the Barents and the White Seas. *Bull. State Oceanog. Inst. Moscow,* Vol. 4, pp. 1–16.

BOGOROV, B. G. & PREOBRAIJENSKAYA, E., 1934. On the weight characteristics of the plankton organisms of the Barents Sea. II. Copepoda. *All-union Sci. Res. Inst. Mar. Fisheries and Oceanography,* Bull. No. 2, pp. 1–29.

FISH, C. J., 1936*a*. The biology of *Calanus finmarchicus* in the Gulf of Maine and Bay of Fundy. *Biol. Bull., Wood's Hole,* Vol. LXX, pp. 118–41.

FISH, C. J., 1936*b*. The biology of *Pseudocalanus minutus* in the Gulf of Maine and Bay of Fundy. *Biol. Bull., Wood's Hole,* Vol. LXX, pp. 193–216.

FISH, C. J., 1936*c*. The biology of *Oithona similis* in the Gulf of Maine and Bay of Fundy. *Biol. Bull. Wood's Hole,* Vol. LXXI, pp. 168–87.

FISH, C. J. & JOHNSON, M., 1937. The biology of the zooplankton population in the Bay of Fundy and Gulf of Maine with special reference to production and distribution. *Journ. Biol. Board Canada,* Vol. III, pp. 189–322.

JEPPS, M. W., 1937. On the protozoan parasites of *Calanus finmarchicus* in the Clyde Sea Area. *Quart. J. Micr. Sci.,* Vol. 79, pp. 589–658.

KRAEFFT, F., 1910. Über das Plankton in Ost- und Nordsee und den Verbindungsgebieten mit besonderer Berücksichtigung der Copepoden. *Wiss. Meeresunters. Komm. wiss. Unters. deutsch. Meere Kiel* u. *Biol. Anst. Helgoland, Abt. Kiel,* Bd. XI, pp. 29–99.

LEBOUR, M. V., 1922. The food of plankton organisms. *Journ. Mar. Biol. Assoc.,* Vol. XII, pp. 644–77.

LOHMANN, H., 1908. Untersuchungen zur Feststellung des vollständigen Gehaltes des Meeres an Plankton. *Wiss. Meeresunters. Komm. wiss. Unters. deutsch. Meere Kiel. u. Biol. Anst. Helgoland, Abt. Kiel,* Bd. X, pp. 129–370.

MARSHALL, S., 1924. The food of *Calanus finmarchicus* during 1923. *Journ. Mar. Biol. Assoc.,* Vol. XIII, pp. 473–79.

MARSHALL, S., 1933. On the biology of *Calanus finmarchicus*. II. Seasonal variations in the size of *Calanus finmarchicus* in the Clyde Sea-Area. *Journ. Mar. Biol. Assoc.,* Vol. XIX, pp. 111–38.

MARSHALL, S. M., NICHOLLS, A. G. & ORR, A. P., 1934. On the biology of *Calanus finmarchicus*. V. Seasonal distribution, size, weight and chemical composition in Loch Striven in 1933, and their relation to the phytoplankton. *Journ. Mar. Biol. Assoc.,* Vol. XIX, pp. 793–828.

NICHOLLS, A. G , 1933. On the biology of *Calanus finmarchicus*. I. Reproduction and seasonal distribution in the Clyde Sea-Area during 1932. *Journ. Mar. Biol. Assoc.,* Vol. XIX, pp. 83–110.

NICHOLLS, A. G., 1934. The developmental stages of *Euchaeta norvegica*, Boeck. *Proc. Roy. Soc. Edin.,* Vol. LIV, pp. 31–50.

OBERG, M., 1906. Die Metamorphose der Plankton-Copepoden der Kieler Bucht. *Wiss. Meeresunters. Komm. wiss. Unters. deutsch. Meere Kiel u. Biol. Anst. Helgoland, Abt. Kiel,* Bd. IX. pp. 37–175.

OTTEN, P., 1913. Quantitative Untersuchungen über die Copepoden des Fehmarnbeltes und ihre Entwicklungsstadien. *Wiss. Meeresunters. Komm. wiss. Unters. deutsch. Meere Kiel u. Biol. Anst. Helgoland, Abt. Kiel,* Bd. XV, pp. 249–302.

ROSENDORN, I., 1927. (Copepoda I): Die Gattung *Oithona*. *Wiss. Ergeb. deutsch. Tiefsee Exp. Dampf.* '*Valdivia*' 1898–1899, Bd. XXIII, pp. 1–58.

RUNNSTRÖM, S., 1932. Eine Uebersicht über das Zooplankton des Herdla- und Hjeltefjordes. *Bergens Museums Årbok*, 1931, No 7, 67 pp.

RUUD, J. T., 1929. On the biology of copepods off Møre 1925–27. *Cons. Perm. Internat. Explor. Mer: Rapp. Proc. Verb.* Vol. LVI, 84 pp.

SARS, G. O., 1903. *An account of the Crustacea of Norway*. IV. *Copepoda Calanoida*. Bergen.

SARS, G. O., 1918. *An account of the Crustacea of Norway*. VI. *Copepoda Cyclopoida*. Bergen.

STÖRMER, L., 1929. Copepods from the 'Michael Sars' expedition, 1924. *Cons. Perm. Internat. Explor. Mer: Rapp. Proc. Verb.*, Vol. LVI, 57 pp.

USSING, H. H., 1938. The biology of some important plankton animals in the fjords of East Greenland. *Medd. om Grønland*, Bd. 100, pp. 1–108.

WIBORG, K. F., 1940. The production of zooplankton in the Oslo Fjord in 1933–34 with special reference to the copepods. *Hvalrådets Skrifter*, Nr. 21, 87 pp.

WIBORG, K. F., 1944. The production of zooplankton in a land-locked fjord the Nordåsvatn near Bergen, in 1941–42 with special reference to the copepods. *Rep. Norwegian Fishery Mar. Investigations*, Vol. VII, No. 7, 83 pp.

WILSON, C. B., 1932. The copepods of the Woods Hole region Massachusetts. *Smiths. Inst. U.S. Nat. Mus. Bull.*, Vol. 158, pp. 1–635.

WINSOR, C. P. & WALFORD, L. A., 1936. Sampling variations in the use of plankton nets. *Journ. Conseil Internat. Explor. Mer.*, Vol. XI, pp. 190–204.

WITH, C., 1915. Copepoda I. Calanoida Amphascandria. *Danish Ingolf Exp.*, Vol. III, No. 4, 260 pp.

APPENDIX

TABLE III. *PSEUDOCALANUS MINUTUS*. NUMBER PER HAUL

(For meaning of symbols see end of table)

Date	Haul, depth in m.	♂	♀	V	IV	III	II	I	N	Eggs	No. eggs per sac	Total*	
17. i	‖B–0	1	8	30	2	1	1	..	16	V. few	..		59
23. i	‖B–0	1	11	27	1	1	1	3	46	16	..		91
30. i	‖B–0	3	9	17	1	1	1	2	28	9	..		62
6. ii	‖B–0	5	15	12	1	..	1	1	43	39	..		78
13. ii	‖B–0	1	12	4	1	1	..	4	61	27	9·5		84
20. ii	‖B–0	..	7	2	1	3	9	17	178	26	10·6		217
27. ii	‖B–0	..	8	4	2	9	12	15	112	29	10·0		162
7. iii	‖B–0	..	15	7	3	5	5	14	154	61	11·8		203
13. iii	‖B–0	..	10	6	1	2	3	13	95	16	12·6		130
20. iii	§B–0	3	15	9	8	19	25	21	214	79	15·3		314
27. iii	B–10	..	1	..	..	2	4	3	19	..	32·5	29	237
	10–0	..	1	10	13	11	13	38	122	26		208	
4. iv	B–10	..	13	17	1	3	1	2	23	206	32·3	60	671
	10–0	20	53	85	45	29	14	7	358	657		611	
10. iv	B–10	3	12	2	1	..	..	1	95	129	37·1	114	1691
	10–0	24	34	20	11	11	17	90	1370	580		1577	
17. iv	B–10	4	8	6	1	6	1	7	276	85	38·4	309	6078
	10–0	57	118	90	101	143	230	540	4490	1878		5769	
24. iv	B–10	..	3	5	1	3	1	8	330	61	36·4	351	3471
	10–0	83	116	158	175	259	192	167	1970	712		3120	
24. iv	§U.H. B–0	53	153	138	188	200	163	193	2175	1583	36·9		3263
1. v	B–0	74	50	20	66	90	118	136	2270	924	33·3	2824	6248
	10–0	115	256	288	236	222	212	165	1930	4545		3424	
8. v	B–10	1	2	2	1	3	4	17	240	25	28·8	270	8863
	10–0	188	630	810	445	425	555	750	4790	6015		8593	
8. v	§U.H. B–0	133	300	308	235	148	245	388	2150	3037	29·3		3907
15. v	‡B–0	90	97	152	208	230	243	136	3920	1108	24·5		5076
22. v	B–10	1	6	12	2	5	1	8	418	91	23·8	453	7099
	10–0	72	152	318	306	248	304	326	4920	1220		6646	
22. v	§U.H. B–0	148	298	466	350	308	270	512	2875	2679	23·1		5227
29. v	B–10	7	52	27	46	22	14	5	532	920	24·1	705	4338
	10–0	200	190	322	278	134	93	106	2310	1354		3633	
5. vi	B–10	9	33	14	24	24	17	38	555	437	21·8	714	3220
	10–0	1	1	3	6	3	20	102	2370	27		2506	
5. vi	§U.H. B–0	113	288	330	286	244	222	196	1952	2924	20·9		3631

12. vi	B–10	24	45	52	165	87	37	25	645	1052	20·4	1080	3766
	10–0	79	177	222	131	187	204	176	1510	1888		2686	
19. vi	B–10	8	16	24	90	21	10	8	214	53	19·6	391	1432
	10–0	50	84	85	123	148	85	24	442	666		1041	
19. vi	†U.H. B–0 1	166	346	194	302	158	184	48	1768	2681	19·8		3166
19. vi	†U.H. B–0 2	116	276	202	388	216	154	47	1648	2793	19·9		3047
19. vi	†U.H. B–0 3	112	280	152	424	248	138	41	1328	2466	19·9		2723
26. vi	B–10	1	24	23	114	35	4	10	222	256	17·4	433	2496
	10–0	..	1	..	1	..	..	21	2040	22		2063	
26. vi	†U.H. B–0 1	22	310	113	374	135	20	77	1440	2646	19·1		2491
26. vi	†U.H. B–0 2	28	216	115	565	175	32	107	2180	1863	19·8		3418
26. vi	†U.H. B–0 3	21	138	85	466	136	40	104	1850	1198	18·6		2840
26. vi	†U.H. B–0 4	13	144	105	590	149	19	127	1610	1263	18·6		2757
3. vii	B–10	68	358	402	4050	740	264	162	492	2052	15·6	6536	15,370
	10–0	..	3	2	19	8	18	184	8600	82		8834	
3. vii	§U.H. B–0	94	635	610	5080	1140	810	1310	10,680	2408	15·3		20,359
10. vii	B–10	92	450	990	2180	1050	605	328	610	2656	14·1	6305	6580
	10–0	..	2	5	8	5	3	12	240	..	..	275	
10. vii	§U.H. B–0	104	563	619	2498	1136	906	900	3116	3563	14·0		9842
17. vii	B–10	205	527	712	3595	499	437	793	1480	2589	15·4	8248	8379
	10–0	..	4	1	16	8	5	6	91	6	..	131	
24. vii	B–10	107	374	855	4720	1260	490	82	825	1819	11·4	8713	9002
	10–0	..	1	1	20	6	5	5	251	..	..	289	
24. vii	§U.H. B–0	200	575	1420	6900	1770	750	268	1220	1898	11·6		13,103
31. vii	B–10	61	242	575	2460	795	510	204	590	1347	9·8	5437	5755
	10–0	1	1	3	12	7	24	10	260	..	..	318	
31. vii	§U.H. B–0	107	510	990	3760	785	448	284	1020	1474	10·9		7904
7. viii	B–10	30	224	250	2900	185	59	13	57	992	10·1	3718	5494
	10–0	1	..	3	31	12	42	87	1600	..	..	1776	
14. viii	B–10	4	11	62	1800	38	9	3	29	6	6·0	1956	3467
	10–0	1	1	1	27	..	10	31	1440	..	..	1511	
14. viii	§U.H. B–0	27	67	232	4310	212	234	165	990	88	9·2		6237
21. viii	B–10	46	121	312	3030	675	740	324	344	415	9·8	5592	7275
	10–0	..	..	12	53	98	200	310	1010	..	..	1683	
21. viii	§U.H. B–0	37	155	385	3760	1050	1370	795	1710	605	10·5		9262
28. viii	‡B–0	102	520	735	5090	1160	1000	550	1580	745	9·8		10,737
11. ix	‖B–0	80	505	495	5600	910	126	181	1350	922	8·0		9247
2. x	†B–0	44	410	730	4590	414	220	174	1890	972	10·0		8472

U.H. Undivided hauls.
* Excluding eggs.
† One undivided haul.

‡ Average of two undivided hauls.
‖ Average of five undivided hauls.
§ Average of four undivided hauls.

TABLE IV. *PARACALANUS PARVUS*. NUMBER PER HAUL

(For meaning of symbols see end of table)

Date	Haul, depth in m.	♂	♀	V	IV	III	II	I	N		Total
3. vii	B–0	..	..	..	..	..	..	..	1362		1362
10. vii	B–10	..	..	..	1	..	..	..	90*		94
	10–0	..	..	..	..	..	..	3			
10. vii	U.H. B–0			Not counted							
17. vii	B–10	..	..	1	2	6	2	1	169*		206
	10–0	..	..	1	1	3	6	14			
24. vii	B–10	..	5	1	3	..	..	7	348*		423
	10–0	..	2	1	1	9	7	38			
24. vii	U.H. B–0	1	18	20	5	15	10	3			
31. vii	B–10	2	8	14	26	20	5	..	245*		480
	10–0	1	1	7	9	14	23	79			
31. vii	U.H. B–0	2	13	38	72	57	28	58			
7. viii	B–10	..	9	6	..	..	1	1	159*		289
	10–0	1	1	9	15	44	24	19			
14. viii	B–10	..	2	2	..	..	..	8	679*		892
	10–0	..	1	2	5	22	70	168			
14. viii	U.H. B–0	2	21	15	3	8	29	64			
21. viii	B–10	2	11	43	53	28	7	4	148	296	1275
	10–0	..	5	20	118	181	92	38	525	979	
21. viii	U.H. B–0	6	40	120	205	205	85	105	650		1416
28. viii	‡B–0	40	240	196	170	154	212	304	1750		3066
11. ix	§B–0	18	100	192	308	234	202	128	450		1632
2. x	†B–0	11	72	315	575	390	272	212	405		2252

* The nauplii were picked out after the hauls had been mixed and the figure is therefore an average only.

† One undivided haul.

‡ Average of two undivided hauls.

§ Average of five undivided hauls.

TABLE V. *MICROCALANUS PYGMAEUS*. NUMBER PER HAUL

(For meaning of symbols see end of table)

Date	Haul, depth in m.	♂	♀	V	IV	III	II	I	N		Total
7. i	§B–0	1	7	7	16	16	22	16	180		265
23. iii	§B–0	4	14	35	25	7	9	23	322		439
30. iii	§B–0	1	5	8	7	5	21	40	136		223
6. ii	§B–0	6	41	54	17	14	17	44	153		346
13. ii	§B–0	8	30	37	35	71	85	61	209		536
20. ii	§B–0	23	40	70	118	129	125	96	324		925
27. ii	§B–0	3	45	82	58	67	66	38	495		854
7. iii	§B–0	50	139	109	43	11	10	6	488		856
13. iii	§B–0	59	91	116	42	10	4	25	441		788
20. iii	‡B–0	78	135	94	7	6	24	30	1058		1432
27. iii	B–10	9	8	6	1	4	7	94	1894	2023	2865
	10–0	1	24	5	11	63	41	125	572	842	
4. iv	B–10	45	73	22	23	28	60	210	3621	4082	5447
	10–0	..	4	18	34	111	140	152	906	1365	
10. iv	B–10	33	51	31	32	59	85	147	3451	3889	4061
	10–0	..	3	1	4	3	1	1	159	172	
17. iv	B–10	21	83	73	56	76	91	101	5712	6213	6405
	10–0	1	3	4	3	7	6	9	159	192	

TABLE V (*cont.*)

Date	Haul, depth in m.	♂	♀	V	IV	III	II	I	N	Total	
24. iv	B–10	13	81	33	56	80	111	150	292	816	835
	10–0	..	1	1	2	5	2	2	6	19	
24. iv	‡U.H. B–0	85	517	308	338	304	379	366	544		2841
1. v	B–10	41	292	384	294	302	183	95	36	2227	2233
	10–0	..	..	1	..	1	..	..	4	6	
8. v	B–10	16	105	104	47	19	8	9	876	1184	1189
	10–0	..	2	1	..	1	..	..	1	5	
8. v	‡U.H. B–0	48	685	545	193	72	18	22	176		1759
15. v	†B–0	186	305	410	152	32	12	24	772		1893
22. v	B–10	47	238	149	19	5	6	31	3933	4428	4464
	10–0	..	5	2	..	1	1	1	26	36	
22. v	‡U.H. B–0	106	505	336	29	26	35	70	2538		3645
29. v	B–10	53	264	57	15	5	25	102	3523	4044	4149
	10–0	1	7	..	..	3	1	3	90	105	
5. vi	B–10	18	112	10	12	13	34	35	2920	3154	3243
	10–0	..	4	..	..	1	1	2	81	89	
5. vi	‡U.H. B–0	43	464	26	16	29	46	89	1957		2670
12. vi	B–10	6	585	34	35	64	69	79	8870	9742	10,146
	10–0	..	8	2	1	2	2	3	386	404	
19. vi	B–10	1	105	10	14	4	5	11	1080	1230	1409
	10–0	..	..	..	..	..	..	..	179	179	
19. vi	*U.H. B–0	..	240	22	26	21	20	18	1600		1947
19. vi	*U.H. B–0	3	344	35	31	8	12	19	1064		1516
19. vi	*U.H. B–0	3	158	20	15	13	7	11	186		1043
26. vi	B–10	7	132	14	16	23	22	59	7240	7513	7587
	10–0	..	..	..	..	..	..	..	74	74	
26. vi	*U.H. B–0	15	520	91	78	26	25	67	1750		2572
26. vi	*U.H. B–0	14	358	81	56	43	35	95	4740		5422
26. vi	*U.H. B–0	15	384	79	55	33	21	92	4950		5629
26. vi	*U.H. B–0	16	334	76	56	25	25	77	5670		6279
3. vii	B–10	39	1060	224	83	71	82	69	4265	5893	5935
	10–0	..	2	..	..	..	..	..	40	42	
3. vii	‡U.H. B–0	90	2280	386	190	130	258	352	7402		11,088
10. vii	B–10	45	690	144	122	128	80	37	753	1999	2017
	10–0	..	..	..	1	..	..	1	16	18	
10. vii	‡U.H. B–0	46	968	225	151	180	165	106	1122		2963
17. vii	B–10	39	1120	190	122	62	39	15	937	2524	2546
	10–0	1	1	1	..	1	..	..	18	22	
24. vii	B–10	12	625	141	37	12	11	11	553	1402	1489
	10–0	..	..	..	1	..	..	..	86	87	
24. vii	‡U.H. B–0	30	525	183	105	28	15	13	345		1244
31. vii	B–10	13	268	86	32	18	12	5	199	633	771
	10–0	..	..	..	..	..	..	..	138	138	
31. vii	‡U.H. B–0	9	262	90	28	21	9	16	256		691
7. viii	B–10	3	93	34	12	10	6	1	208	367	434
	10–0	..	..	2	..	..	..	..	65	67	
14. viii	B–10	2	31	9	1	..	..	..	199	242	624
	10–0	..	..	..	..	..	..	..	382	382	
14. viii	‡U.H. B–0	7	75	22	6	2	2	2	458		574
21. viii	B–10	1	41	4	..	2	..	..	256	304	339
	10–0	..	..	..	..	..	..	..	35	35	
21. viii	‡U.H. B–0	1	33	4	..	2	1	1	260		302
28. viii	†B–0	3	76	16	16	2	3	3	890		1009
11. ix	§B–0	..	30	5	2	1	3	2	240		283
2. x	*B–0	4	40	12	9	3	15	8	310		401

* One undivided haul.
† Average of two undivided hauls.
‡ Average of four undivided hauls.
§ Average of five undivided hauls.

TABLE VI. *CENTROPAGES HAMATUS.* NUMBER PER HAUL

(For meaning of symbols see end of table)

Date	Haul, depth in m.	♂	♀	V	IV	III	II	I	N	Total	
17. i	‡B–0	..	..	..	..	..	..	..	15		15
23. i	‡B–0	..	..	..	..	..	..	+	17		17
30. i	‡B–0	..	..	+	..	..	..	..	8		8
6. ii	‡B–0	..	..	..	..	..	..	..	10		10
13. ii	‡B–0	..	..	..	..	..	..	..	32		32
20. ii	‡B–0	..	..	..	..	..	..	..	132		132
27. ii	‡B–0	..	..	..	..	..	..	+	39		39
7. iii	‡B–0	+	..	..	..	+	1	+	224		225
13. iii	‡B–0	..	..	..	..	..	..	+	87		87
20. iii	‖B–0	+	+	..	..	1	1	3	82		88
27. iii	B–10	..	..	1	..	2	1	4	36	44	265
	10–0	4	..	1	2	15	23	31	145	221	
4. iv	B–10	1	1	2	1	..	1	2	9	17	256
	10–0	3	5	48	21	20	52	29	61	239	
10. iv	B–10	1	1	1	..	..	1	..	15	19	491
	10–0	31	21	22	32	33	33	24	276	472	
17. iv	B–10	1	..	..	..	2	3	1	22	29	1132
	10–0	27	15	35	26	35	57	143	765	1103	
24. iv	B–10	2	..	..	1	1	1	..	45	50	741
	10–0	21	15	20	52	79	51	18	435	691	
24. iv	‖U.H. B–0	13	33	13	33	18	18	10	388		526
1. v	B–10	35	17	16	14	1	4	..	188	275	1337
	10–0	19	19	35	15	9	24	37	905	1062	
8. v	B–10	..	..	..	1	..	1	..	14	16	1278
	10–0	12	3	15	18	31	54	119	1010	1262	
8. v	‖U.H. B–0	22	8	15	10	9	17	39	201		321
15. v	†B–0	17	10	11	34	52	25	8	113		270
22. v	B–10	1	..	1	..	1	..	..	12	15	396
	10–0	11	5	33	26	6	9	19	272	381	
22. v	‖U.H. B–0	20	6	47	23	9	9	19	160		293
29. v	B–10	..	..	..	..	..	..	..	23	23	388
	10–0	..	2	2	3	14	26	60	258	365	
5. vi	B–10	..	..	..	..	..	..	..	302	302	5598
	10–0	..	..	..	3	6	20	27	5240	5296	
5. vi	‖U.H. B–0	4	5	8	14	17	8	9	1824		1889
12. vi	B–10	3	..	..	..	1	2	1	112	119	1408
	10–0	33	10	11	6	10	20	59	1140	1289	
19. vi	B–10	4	1	1	..	1	..	..	13	20	271
	10–0	12	3	3	1	1	1	2	228	251	
19. vi	*B–0	28	11	2	1	1	1	2	192		238
19. vi	*B–0	35	6	5	3	5	6	3	160		223
19. vi	*B–0	46	19	3	6	3	4	4	106		191
26. vi	B–10	..	..	..	..	..	2	..	24	26	305
	10–0	..	..	..	..	..	1	16	262	279	
26. vi	*B–0	20	2	4	3	1	7	12	80		129
26. vi	*B–0	4	..	5	2	7	8	22	100		148
26. vi	*B–0	2	..	..	1	4	9	16	123		155
26. vi	*B–0	5	..	5	2	9	13	15	128		177
3. vii	B–10	4	2	14	28	8	1	..	6	63	419
	10–0	..	..	4	8	29	45	56	214	356	
3. vii	‖U.H. B–0	13	1	45	170	151	94	51	114		639
10. vii	B–10	82	45	216	74	15	9	6	7	454	1111
	10–0	..	..	1	5	14	22	70	545	657	
10. vii	‖U.H. B–0	79	36	125	64	36	50	105	1058		1553
17. vii	B–10	48	50	63	74	87	66	34	35	457	590
	10–0	1	..	4	..	6	4	10	108	133	
24. vii	B–10	64	42	62	42	22	18	1	22	273	488
	10–0	..	..	..	..	..	1	5	209	215	

TABLE VI (*cont.*)

Date	Haul, depth in m.	♂	♀	V	IV	III	II	I	N	Total	
24. vii	‖U.H. B–0	100	70	135	80	68	48	25	188		714
31. vii	B–10	76	46	62	106	189	112	33	48	672	1434
	10–0	1	4	6	15	24	30	57	625	762	
31. vii	‖U.H. B–0	106	60	93	103	173	124	69	535		1263
7. viii	B–10	13	8	5	3	2	1	..	4	36	236
	10–0	2	..	2	14	13	31	23	115	200	
14. viii	B–10	1	..	2	..	..	..	1	56	60	669
	10–0	..	..	..	1	1	1	11	595	609	
14. viii	‖U.H. B–0	9	6	21	26	14	13	10	475		574
21. viii	B–10	1	3	3	6	23	11	3	15	65	157
	10–0	1	5	3	6	15	17	17	28	92	
21. viii	‖U.H. B–0	6	11	16	27	54	90	50	110		364
28. viii	†B–0	12	15	98	34	19	18	19	177		392
11. ix	‡B–0	8	6	9	11	8	15	32	126		215
2. x	*B–0	..	..	5	9	5	10	8	108		145

* One undivided haul.
† Average of two undivided hauls.
‖ Average of four undivided hauls.
‡ Average of five undivided hauls.
\+ Present, but less than 0·5 per haul.

TABLE VII. *TEMORA LONGICORNIS*. NUMBER PER HAUL

(For meaning of symbols see end of table)

Date	Haul, depth in m.	♂	♀	V	IV	III	II	I	N	Total	
17. i	§B–0	..	..	..	..	..	..	..	20		20
23. i	§B–0	..	..	..	..	..	..	..	22		22
31. i	§B–0	..	..	..	..	..	+	+	18		19
7. ii	§B–0	..	..	..	..	+	..	+	26		27
13. ii	§B–0	..	..	..	..	+	..	1	65		66
20. ii	§B–0	..	..	..	..	+	+	2	122		125
27. ii	§B–0	..	+	..	1	..	1	1	167		171
7. iii	§B–0	+	+	+	1	2	4	9	222		238
13. iii	§B–0	..	..	1	1	4	2	4	74		86
20. iii	‡B–0	..	1	+	+	1	4	13	117		136
27. iii	B–10	..	..	1	1	3	1	1	29	36	206
	10–0	2	4	2	6	32	9	13	102	170	
4. iv	B–10	..	2	..	2	2	4	1	70	81	510
	10–0	3	7	1	3	10	9	14	382	429	
10. iv	B–10	..	2	2	..	..	1	..	135	140	1894
	10–0	85	68	45	28	28	22	88	1390	1754	
17. iv	B–10	..	1	3	..	1	4	1	238	248	2682
	10–0	26	27	18	15	27	34	47	2240	2434	
24. iv	B–10	2	2	..	..	..	..	..	67	71	696
	10–0	9	10	11	17	23	20	50	485	625	
24. iv	‡U.H. B–0	38	13	18	15	8	10	43	408		553
1. v	B–10	21	6	1	3	9	24	16	187	267	1300
	10–0	43	27	35	31	64	138	95	600	1033	
8. v	B–10	..	..	..	..	..	..	..	46	46	986
	10–0	71	53	60	42	26	12	16	660	940	
8. v	‡U.H. B–0	37	23	29	30	13	10	1	156		299
15. v	†B–0	11	6	11	3	1	1	..	88		121
22. v	B–10	..	1	..	..	..	..	..	60	61	384
	10–0	52	12	14	1	1	1	6	236	323	
22. v	‡U.H. B–0	15	14	7	5	1	1	4	140		187
29. v	B–10	1	..	..	..	..	..	..	83	84	615
	10–0	..	1	2	1	2	2	19	504	531	
5. vi	B–10	..	..	..	..	..	..	..	11	11	392
	10–0	..	2	4	11	9	10	27	318	381	

Table VII (*cont.*)

Date	Haul, depth in m.	♂	♀	V	IV	III	II	I	N	Total	
5. vi	‡U.H. B–0	11	3	7	7	4	12	10	440		494
12. vi	B–10	1	..	..	..	..	1	1	13	16	525
	10–0	9	2	4	5	7	15	33	434	509	
19. vi	B–10	..	..	1	4	3	2	..	17	27	154
	10–0	4	4	6	11	19	10	6	67	127	
19. vi	*B–0	2	8	6	1	6	4	3	162		192
19. vi	*B–0	8	8	12	13	9	10	5	77		142
19. vi	*B–0	13	12	17	18	16	19	9	103		207
26. vi	B–10	..	1	..	1	..	..	1	11	14	172
	10–0	..	..	..	..	1	2	11	144	158	
26. vi	*B–0	4	2	6	2	..	..	5	60		79
26. vi	*B–0	3	2	2	1	1	5	11	57		82
26. vi	*B–0	4	1	1	5	2	3	10	67		93
26. vi	*B–0	1	1	2	2	2	6	1	58		73
3. vii	B–10	6	3	2	5	..	..	1	8	25	723
	10–0	1	..	..	4	2	15	26	650	698	
3. vii	‡U.H. B–0	16	12	14	26	24	26	25	520		663
10. vii	B–10	33	32	20	3	2	1	2	9	102	461
	10–0	..	..	2	5	10	20	32	290	359	
10. vii	‡U.H. B–0	31	24	28	19	28	54	79	1238		1501
17. vii	B–10	23	17	27	24	23	20	11	37	182	466
	10–0	..	..	1	2	4	3	10	264	284	
24. vii	B–10	24	19	14	14	14	2	3	23	113	410
	10–0	..	1	1	4	6	24	27	234	297	
24. vii	‡U.H. B–0	21	18	48	38	28	35	38	428		654
31. vii	B–10	22	10	24	14	10	12	9	92	193	596
	10–0	2	4	1	12	18	23	49	294	403	
31. vii	‡U.H. B–0	36	23	22	22	28	26	30	292		479
7. viii	B–10	14	5	9	1	1	1	2	13	46	938
	10–0	1	1	5	12	30	65	133	645	892	
14. viii	B–10	1	..	2	..	1	2	1	38	45	1200
	10–0	1	1	6	26	69	79	103	870	1155	
14. viii	‡U.H. B–0	13	15	22	27	54	56	51	320		558
21. viii	B–10	7	6	6	7	4	5	7	109	151	858
	10–0	2	..	5	18	32	64	66	520	707	
21. viii	‡U.H. B–0	16	21	19	23	49	45	65	545		783
28. viii	†B–0	27	32	14	14	23	27	71	1130		1338
11. ix	§B–0	12	7	5	7	7	18	28	175		259
2. x	*B–0	9	3	5	6	8	17	20	146		214

\+ Present, but less than 0·5 per haul.
* One undivided haul.
† Average of two undivided hauls.
‡ Average of four undivided hauls.
§ Average of five undivided hauls.

Table VIII. *Acartia clausi.* Number per haul

(For meaning of symbols see end of table)

Date	Haul, depth in m.	♂	♀	V	IV	III	II	I	N	Total	
17. i	§B–0	1	4	..	..	+	..	..	5		10
23. i	§B–0	+	6	+	+	..	+	..	4		11
30. i	§B–0	+	3	..	..	..	..	..	9		12
6. ii	§B–0	..	3	..	..	..	..	..	16		19
13. ii	§B–0	+	3	+	..	+	..	..	26		29
20. ii	§B–0	..	1	..	..	..	..	1	32		34
27. ii	§B–0	+	2	..	+	+	+	1	17		22
7. iii	§B–0	+	1	+	+	1	2	2	30		37
13. iii	§B–0	..	1	..	..	..	1	1	6		9
20. iii	‡B–0	..	1	..	+	1	+	+	8		10
27. iii	B–10	1	..	..	..	..	1	..	11	13	34
	10–0	..	..	2	..	2	3	..	14	21	

TABLE VIII (*cont.*)

Date	Haul, depth in m.	♂	♀	V	IV	III	II	I	N	Total	
4. iv	B–10	..	..	..	..	..	..	..	2	2	47
	10–0	6	2	3	..	4	5	4	21	45	
10. iv	B–10	..	..	..	..	..	..	..	10	10	101
	10–0	3	3	5	1	1	2	5	71	91	
17. iv	B–10	..	..	..	..	..	1	..	4	5	149
	10–0	12	6	10	3	8	12	17	76	144	
24. iv	B–10	2	1	1	..	..	..	..	8	12	172
	10–0	22	31	15	25	11	12	6	38	160	
24. iv	‡U.H. B–0	5	20	8	13	10	8	5	23		92
1. v	B–10	5	5	..	..	..	..	1	26	37	161
	10–0	20	22	9	8	4	8	5	48	124	
8. v	B–10	..	..	..	..	..	..	1	21	22	205
	10–0	25	19	5	2	5	5	15	107	183	
8. v	‡U.H. B–0	14	10	1	2	..	..	3	31		61
15. v	†B–0	7	11	2	1	2	2	1	28		54
22. v	B–10	1	..	..	..	..	..	..	274	275	590
	10–0	26	13	24	6	3	..	9	234	315	
22. v	‡U.H. B–0	20	12	5	6	1	1	4	278		327
29. v	B–10	..	..	..	..	..	1	..	220	221	2866
	10–0	6	13	6	3	13	46	98	2460	2645	
5. vi	B–10	..	..	..	..	..	..	2	168	170	2354
	10–0	1	2	3	11	18	53	66	2030	2184	
5. vi	‡U.H. B–0	4	7	10	14	20	23	46	1016		1140
12. vi	B–10	2	6	3	4	22	43	48	164	292	3434
	10–0	32	31	43	81	151	300	264	2240	3142	
19. vi	B–10	..	3	2	..	1	1	1	36	44	478
	10–0	4	12	8	15	33	23	19	320	434	
19. vi	*B–0	23	22	28	29	38	44	44	258		486
19. vi	*B–0	19	7	20	26	41	35	30	258		436
19. vi	*B–0	35	29	45	40	40	48	39	240		516
26. vi	B–10	2	3	..	..	1	1	2	132	141	1213
	10–0	2	..	..	1	3	2	24	1040	1072	
26. vi	*B–0	9	19	7	9	10	10	21	525		610
26. vi	*B–0	25	34	22	18	13	19	26	555		712
26. vi	*B–0	41	32	24	15	22	19	20	830		1003
26. vi	*B–0	13	19	12	12	8	22	13	670		769
3. vii	B–10	63	36	36	15	8	4	12	730	904	6888
	10–0	1	7	1	3	64	200	318	5390	5984	
3. vii	‡U.H. B–0	222	174	99	83	106	210	510	7320		8724
10. vii	B–10	248	198	152	181	127	102	73	342	1423	6382
	10–0	..	3	2	4	22	124	264	4540	4959	
10. vii	‡U.H. B–0	286	149	244	340	333	392	776	5636		8156
17. vii	B–10	456	251	334	214	627	480	365	1795	4522	6808
	10–0	2	2	1	11	13	60	187	2010	2286	
24. vii	B–10	564	490	478	416	402	224	72	520	3166	4549
	10–0	3	3	2	4	4	18	54	1295	1383	
24. vii	‡U.H. B–0	1110	1450	1020	640	720	535	253	1430		7158
31. vii	B–10	485	510	800	590	362	208	114	560	3629	5719
	10–0	10	15	22	40	77	238	298	1390	2090	
31. vii	‡U.H. B–0	750	1130	1100	640	408	600	415	1280		6323
7. viii	B–10	368	238	162	120	46	12	5	111	1062	2715
	10–0	3	1	5	18	87	165	234	1140	1653	
14. viii	B–10	42	27	10	3	10	..	2	144	238	2945
	10–0	1	..	1	5	44	92	154	2410	2707	
14. viii	‡U.H. B–0	212	186	113	246	232	100	36	1350		2475
21. viii	B–10	280	262	163	86	37	18	11	212	1069	2905
	10–0	3	4	18	118	254	362	77	1000	1836	
21. viii	‡U.H. B–0	565	290	375	205	420	385	90	1700		4030
28. viii	†B–0	202	242	376	294	177	177	198	1360		3026
11. ix	§B–0	152	478	171	124	112	79	123	1370		2609
2. x	*B–0	114	324	296	480	500	565	264	1540		4083

+ Present, but less than 0·5 per haul.
* One undivided haul.
† Average of two undivided hauls.
‡ Average of four undivided hauls.
§ Average of five undivided hauls.

TABLE IX. *OITHONA SIMILIS*. NUMBER PER HAUL

(For meaning of symbols see end of table)

Date	Haul, depth in m.	♂	♀	V	IV	III	II	I	N	Eggs	No. eggs per sac	Total*	
17. i	‖B–0	2	192	69	37	44	15	20	662	1150	5·9		1041
23. i	‖B–0	4	210	64	22	16	19	24	956	1210	5·6		1315
30. i	‖B–0	6	149	29	17	16	8	7	438	736	6·1		670
6. ii	‖B–0	3	100	14	10	12	10	2	188	1472	6·7		339
13. ii	‖B–0	3	113	31	9	9	12	12	418	926	7·1		607
20. ii	‖B–0	2	152	25	14	12	19	25	486	1751	8·3		735
27. iii	‖B–0	6	204	24	14	8	13	12	554	2038	8·8		835
7. iii	‖B–0	5	268	25	14	14	17	25	864	3406	9·1		1232
13. iii	‖B–0	2	164	8	8	10	8	15	320	2386	9·4		535
20. iii	§B–0	4	205	26	14	15	23	32	1030	2450	11·8		1349
27. iii	B–10	..	26	5	2	1	..	7	237	545	13·1	278	893
	10–0	4	21	12	11	11	9	27	520	329		615	
4. iv	B–10	2	60	4	2	5	15	10	104	1672	14·6	202	1029
	10–0	10	72	31	28	64	107	97	418	820		827	
10. iv	B–10	2	29	3	2	5	5	7	233	462	14·0	286	911
	10–0	22	55	39	67	62	55	33	292	593		625	
17. iv	B–10	4	26	12	2	2	7	21	236	602	16·8	310	2026
	10–0	33	91	130	86	36	47	43	1250	892		1716	
24. iv	B–10	5	32	7	1	2	4	6	146	888	17·4	203	1667
	10–0	32	79	79	45	36	70	73	1050	821		1464	
24. iv	§U.H. B–0	43	173	75	33	30	73	93	819	3883	17·6		1339
1. v	B–10	24	141	62	63	89	68	78	845	2475	13·6	1370	3319
	10–0	48	52	63	82	144	174	126	1260	303		1949	
8. v	B–10	1	5	1	1	1	2	..	51	152	12·2	62	5090
	10–0	36	66	144	258	236	180	208	3900	413		5028	
8. v	§U.H. B–0	29	135	89	128	127	102	92	780	1675	12·6		1482
15. v	‡B–0	13	160	94	84	78	93	87	1070	1599	9·2		1683
22. v	B–10	..	4	2	1	1	..	11	185	61	10·7	204	1669
	10–0	4	85	67	42	55	75	87	1050	798		1465	
22. v	§U.H. B–0	13	165	100	69	71	99	149	1200	1573	11·1		1866
29. v	B–10	2	47	9	6	3	3	30	360	894	15·5	460	3225
	10–0	36	144	175	141	202	171	155	1740	2088		2765	
5. vi	B–10	8	34	7	10	10	16	13	236	691	17·2	334	2706
	10–0	..	11	21	29	50	60	51	2150	16		2372	
5. vi	§U.H. B–0	44	196	196	101	91	132	106	2104	2406	18·4		2970
12. vi	B–10	19	61	25	13	14	9	30	170	1461	17·2	341	2844
	10–0	20	94	82	65	58	68	86	2030	2230		2503	

19. vi	B–10	10	42	34	12	2	10	10	252	818	15·1	372	830
	10–0	9	34	19	14	11	10	5	356	550		458	
19. vi	†U.H. B–0	42	174	70	36	53	40	51	1040	2872	14·6		1506
19. vi	†U.H. B–0	63	304	206	85	56	67	45	960	3915	14·3		1786
19. vi	†U.H. B–0	38	192	127	56	41	36	28	540	3132	14·4		1058
26. vi	B–10	17	23	6	3	4	3	10	228	537	13·3	294	3310
	10–0	10	10	8	9	31	53	135	2760	50		3016	
26. vi	†U.H. B–0	45	88	33	14	18	27	64	1160	1621	13·8		1449
26. vi	†U.H. B–0	34	114	41	17	26	50	88	1410	2129	13·2		1780
26. vi	†U.H. B–0	29	107	46	25	12	33	71	2120	1990	12·8		2443
26. vi	†U.H. B–0	36	126	65	23	18	40	79	1790	2194	12·9		2177
3. vii	B–10	71	442	216	68	38	14	48	344	7980	13·9	1241	11,156
	10–0	10	37	53	129	326	420	780	8160	52		9915	
3. vii	§U.H. B–0	204	970	525	335	595	675	1360	9560	20,680	13·3		14,224
10. vii	B–10	104	690	462	314	195	150	227	725	13,550	13·0	2867	8427
	10–0	..	12	23	14	38	33	120	5320	24		5560	
10. vii	§U.H. B–0	141	934	1159	827	1226	1789	2104	9889	13,961	12·3		18,069
17. vii	B–10	258	950	1585	1425	765	475	603	2080	13,650	14·2	8142	15,267
	10–0	..	2	10	29	70	324	780	5910	12		7125	
24. vii	B–10	208	920	830	700	400	414	171	915	12,130	10·7	4558	10,086
	10–0	1	10	65	169	419	640	404	3820	59		5528	
24. vii	§U.H. B–0	310	1010	1520	1510	1790	1800	1010	4740	11,990	10·6		13,690
31. vii	B–10	480	990	1300	535	340	368	220	2510	12,790	9·9	6743	11,092
	10–0	26	61	295	273	356	312	336	2690	108		4349	
31. vii	§U.H. B–0	290	1190	1590	1030	770	740	670	3810	11,840	9·7		10,090
7. viii	B–10	34	438	328	212	69	48	35	515	4080	7·6	1679	12,012
	10–0	17	168	488	730	800	930	1070	6130	589		10,333	
14. viii	B–10	4	57	66	29	20	12	23	364	491	7·2	575	4682
	10–0	12	37	256	290	191	193	258	2870	49		4107	
14. viii	§U.H. B–0	31	490	545	595	350	224	212	2450	3158	7·8		4897
21. viii	B–10	83	510	455	505	390	360	404	4240	6490	8·7	6947	25,703
	10–0	67	382	627	1120	1480	2150	1810	11,120	4885		18,756	
21. viii	§U.H. B–0	225	1270	1430	1830	2330	2360	1780	15,350	13,450	8·9		26,575
28. viii	‡B–0	133	1240	2000	3160	3010	2260	1500	18,100	6425	7·1		31,403
11. ix	‖B–0	83	860	1470	1410	575	498	386	5580	4760	7·1		10,862
2. x	†B–0	85	665	620	805	980	1450	770	3580	3940	8·0		8958

* Excluding eggs.
† One undivided haul.
‡ Average of two undivided hauls.
§ Average of four undivided hauls.
‖ Average of five undivided hauls.

TABLE X. SIZE OF *PSEUDOCALANUS MINUTUS* IN MM.

Stage	Date	No.	0·487–0·539	0·539–0·592	0·592–0·644	0·644–0·696	0·696–0·748	0·748–0·800	0·800–0·853	0·853–0·905	0·905–0·957	0·957–1·009	1·009–1·061	1·061–1·114	1·114–1·166	1·166–1·218	1·218–1·270	1·270–1·322	1·322–1·375	1·375–1·427	Median size
♂	17. i	6	..	..	..	2	2	2	..	..	..	..	..	..	..	..	..	..	..	..	..
	23. i	8	..	..	..	..	2	1	4	1	..	..	..	..	..	..	..	..	..	..	..
	30. i	13	..	..	..	..	5	4	..	3	..	1	..	..	..	..	..	..	..	..	0·765
	6. ii	23	..	..	..	..	10	3	4	5	..	1	..	..	..	..	..	..	..	..	0·783
	20. iii	9	..	..	..	..	1	2	2	3	..	1	..	..	..	..	..	..	..	..	0·852
	4. iv	19	..	..	..	..	..	..	2	10	2	3	2	..	..	..	..	..	..	..	0·893
	10. iv	65	..	..	..	..	..	1	5	19	23	13	4	..	..	..	..	..	..	..	0·915
	17. iv	61	..	..	..	..	..	1	3	18	13	20	6	..	..	..	..	..	..	..	0·939
	24. iv	98	..	..	..	..	..	..	..	29	31	27	11	..	..	..	..	..	..	..	0·935
	1. v	133	..	..	..	..	..	..	11	51	43	25	3	..	..	..	..	..	..	..	0·909
	8. v	99	..	..	..	..	..	..	26	40	26	6	1	..	..	..	..	..	..	..	0·882
	15. v	76	..	..	..	..	..	1	20	38	13	4	..	..	..	..	..	..	..	..	0·886
	22. v	119	..	..	..	..	..	6	77	28	8	..	..	..	..	..	..	..	..	..	0·836
	29. v	89	..	..	..	..	..	11	60	18	..	..	..	..	..	..	..	..	..	..	0·839
	5. vi	110	..	..	..	..	..	16	65	27	2	..	..	..	..	..	..	..	..	..	0·830
	12. vi	97	..	..	..	..	2	40	49	6	..	..	..	..	..	..	..	..	..	..	0·806
	19. vi	126	..	..	..	1	1	50	49	22	3	..	..	..	..	..	..	..	..	..	0·808
	26. vi	72	..	..	..	..	1	20	29	21	1	..	..	..	..	..	..	..	..	..	0·837
	3. vii	133	..	..	..	..	5	35	70	23	..	..	..	..	..	..	..	..	..	..	0·826
	10. vii	117	..	..	..	..	12	40	50	14	1	..	..	..	..	..	..	..	..	..	0·809
	17. vii	99	..	..	..	1	33	30	25	9	1	..	..	..	..	..	..	..	..	..	0·778
	24. vii	113	..	..	..	9	56	23	21	4	..	..	..	..	..	..	..	..	..	..	0·741
	31. vii	111	..	..	..	33	53	7	15	3	..	..	..	..	..	..	..	..	..	..	0·708
	7. viii	30	..	..	..	15	5	..	7	3	..	..	..	..	..	..	..	..	..	..	0·698
	14. viii	96	..	..	2	52	15	9	13	5	..	..	..	..	..	..	..	..	..	..	0·692
	21. viii	113	..	..	..	44	46	10	11	2	..	..	..	..	..	..	..	..	..	..	0·705
	28. viii	89	..	..	1	51	26	10	..	1	..	..	..	..	..	..	..	..	..	..	0·690
	11. ix	78	..	..	1	46	23	2	4	2	..	..	..	..	..	..	..	..	..	..	0·692
	2. x	39	..	..	..	11	26	2	..	..	..	..	..	..	..	..	..	..	..	..	0·713
♀	17. i	39	..	..	..	..	..	2	17	17	3	..	..	..	..	..	..	..	..	..	0·855
	23. i	52	..	..	..	..	..	2	20	21	5	4	..	..	..	..	..	..	..	..	0·862
	30. i	38	..	..	..	..	..	1	11	16	6	3	1	..	..	..	..	..	..	..	0·874
	6. ii	71	..	..	..	..	..	..	18	32	17	4	..	..	..	..	..	..	..	..	0·878
	13. ii	41	..	..	..	..	..	..	12	13	10	5	1	..	..	..	..	..	..	..	0·880
	20. ii	29	..	..	..	..	..	..	4	10	8	6	1	..	..	..	..	..	..	..	0·911
	27. ii	38	..	..	..	..	..	2	9	9	13	4	1	..	..	..	..	..	..	..	0·901
	7. iii	66	..	..	..	..	..	..	9	14	21	20	1	..	..	1	..	..	..	..	0·926
	13. iii	44	..	..	..	..	..	..	10	9	16	6	3	..	..	..	..	..	..	..	0·915
	20. iii	57	..	..	..	..	..	1	9	10	16	15	5	1	..	..	..	..	..	..	0·942
	27. iii	21	..	..	..	..	..	..	..	3	8	7	4	2	2	..	1	..	..	..	0·957
	4. iv	59	..	..	..	..	..	2	2	1	6	2	6	8	14	11	3	5	..	..	1·131
	10. iv	108	..	..	..	..	..	..	..	3	9	4	3	14	20	25	10	12	7	1	1·168
	17. iv	112	..	..	..	..	..	..	..	3	5	1	4	7	35	26	15	10	6	..	1·170
	24. iv	153	..	..	..	..	..	..	..	2	2	4	5	21	26	29	30	23	11	..	1·203
	1. v	141	..	..	..	..	..	..	1	..	2	1	10	24	38	26	25	10	3	1	1·157
	8. v	127	..	..	..	..	..	..	..	1	1	7	29	46	26	8	3	5	1	..	1·091
	15. v	82	..	..	..	..	..	..	1	..	3	15	22	19	12	6	3	1	..	..	1·062
	22. v	125	..	..	..	..	..	..	..	..	1	28	60	19	6	4	3	4	..	..	1·042
	29. v	99	..	..	..	..	..	..	..	1	1	23	41	24	8	..	1	..	..	..	1·039
	5. vi	102	..	..	..	..	..	..	..	1	8	38	44	8	..	1	2	..	..	..	1·012

Stage	Date	No.	0·487–0·539	0·539–0·592	0·592–0·644	0·644–0·696	0·696–0·748	0·748–0·800	0·800–0·853	0·853–0·905	0·905–0·957	0·957–1·009	1·009–1·061	1·061–1·114	1·114–1·166	1·166–1·218	1·218–1·270	1·270–1·322	1·322–1·375	1·375–1·427	Median size
♀	12. vi	130	..	..	..	..	..	..	..	4	32	50	37	6	..	1	..	..	..	..	0·989
	19. vi	104	..	..	..	..	..	..	2	6	23	30	28	14	1	..	..	..	..	..	0·999
	26. vi	110	..	..	..	..	..	..	..	3	24	35	30	14	3	1	..	..	..	..	0·997
	3. vii	116	..	..	..	..	..	..	..	9	39	34	21	10	3	..	..	..	..	..	0·970
	10. vii	137	..	..	..	..	..	1	3	22	52	41	14	3	1	..	..	..	..	..	0·951
	17. vii	98	..	..	..	..	..	..	18	34	23	17	4	1	1	..	..	..	..	..	0·901
	24. vii	134	..	..	..	..	1	20	35	31	20	19	5	3	..	..	..	..	..	..	0·866
	31. vii	113	..	..	..	..	2	22	28	30	20	7	2	2	..	..	..	..	..	..	0·868
	7. viii	102	..	..	..	1	3	26	31	13	18	9	1	..	..	..	..	..	..	..	0·839
	14. viii	125	..	..	..	..	7	53	28	8	12	10	6	1	..	..	..	..	..	..	0·803
	21. viii	127	..	..	..	..	14	43	28	16	15	6	4	1	..	..	..	..	..	..	0·806
	28. viii	102	..	..	..	..	2	31	39	14	9	4	3	..	..	..	..	..	..	..	0·820
	11. ix	82	..	..	..	..	7	48	19	5	3	..	..	..	..	..	..	..	..	..	0·784
	2. x	167	..	..	..	..	2	40	77	40	5	2	1	..	..	..	..	..	..	..	0·829
♂ V	17. i	42	..	..	..	..	8	12	15	6	1	..	..	..	..	..	..	..	..	..	0·809
	23. i	33	..	..	..	1	7	15	4	3	3	..	..	..	..	..	..	..	..	..	0·765
	30. i	25	..	..	..	..	2	7	6	10	..	..	..	..	..	..	..	..	..	..	0·841
	6. ii	17	..	..	..	..	4	4	2	5	2	..	..	..	..	..	..	..	..	..	0·827
	13. ii	8	..	..	..	..	2	2	3	1	..	..	..	..	..	..	..	..	..	..	0·809
	27. ii	11	..	..	..	..	1	2	5	3	..	..	..	..	..	..	..	..	..	..	0·827
	13. iii	9	..	..	..	..	..	1	2	5	1	..	..	..	..	..	..	..	..	..	0·870
	20. iii	18	..	..	..	..	..	2	5	8	2	1	..	..	..	..	..	..	..	..	0·864
	4. iv	45	..	..	..	..	..	..	..	11	11	15	8	..	..	..	..	..	..	..	0·974
	10. iv	23	..	..	..	..	..	..	..	7	5	10	1	..	..	..	..	..	..	..	0·957
	17. iv	50	..	..	..	..	..	..	1	7	9	26	7	..	..	..	..	..	..	..	0·975
	24. iv	51	..	..	..	..	..	..	2	23	13	9	3	..	1	..	..	..	..	..	0·914
	1. v	73	..	..	..	..	..	..	9	31	20	10	2	1	..	..	..	..	..	..	0·900
	8. v	62	..	..	..	..	..	1	10	29	21	1	..	..	..	..	..	..	..	..	0·885
	15. v	65	..	..	..	..	..	3	39	16	4	2	1	..	..	..	..	..	..	..	0·843
	22. v	87	..	..	..	..	1	5	50	26	4	1	..	..	..	..	..	..	..	..	0·842
	29. v	53	..	..	..	..	..	3	28	19	2	..	1	..	..	..	..	..	..	..	0·846
	5. vi	80	..	..	..	..	1	32	25	14	5	2	..	1	..	..	..	..	..	..	0·816
	12. vi	91	..	..	..	..	2	44	36	7	1	1	..	..	..	..	..	..	..	..	0·800
	19. vi	103	..	..	..	..	7	45	22	27	2	..	..	..	..	..	..	..	..	..	0·800
	26. vi	83	..	..	..	..	..	12	27	27	17	..	..	..	..	..	..	..	..	..	0·856
	3. vii	97	..	..	..	..	..	5	30	42	19	1	..	..	..	..	..	..	..	..	0·868
	10. vii	106	..	..	..	..	8	38	34	22	4	..	..	..	..	..	..	..	..	..	0·811
	17. vii	67	..	..	..	..	29	14	6	14	3	1	..	..	..	..	..	..	..	..	0·757
	24. vii	103	..	..	..	8	65	8	6	10	4	2	..	..	..	..	..	..	..	..	0·730
	31. vii	103	..	..	..	17	62	5	7	10	2	..	..	..	..	..	..	..	..	..	0·716
	7. viii	73	..	..	..	10	11	4	14	19	14	1	..	..	..	..	..	..	..	..	0·847
	14. viii	84	..	..	..	6	18	3	10	30	17	..	..	..	..	..	..	..	..	..	0·862
	21. viii	115	..	..	..	23	36	7	19	12	18	..	..	..	..	..	..	..	..	..	0·740
	28. viii	74	..	..	..	12	44	3	2	7	5	1	..	..	..	..	..	..	..	..	0·714
	11. ix	58	..	..	..	7	10	3	19	13	5	1	..	..	..	..	..	..	..	..	0·837
	2. x	60	..	..	..	..	16	8	17	14	5	..	..	..	..	..	..	..	..	..	0·822
♀ V	17. i	88	..	..	..	1	18	20	31	18	..	..	..	..	..	..	..	..	..	..	0·808
	23. i	79	..	..	..	..	11	32	22	11	3	..	..	..	..	..	..	..	..	..	0·790
	30. i	44	..	..	..	..	2	6	22	14	..	..	..	..	..	..	..	..	..	..	0·836
	6. ii	44	..	..	..	1	5	8	18	11	1	..	..	..	..	..	..	..	..	..	0·831
	13. ii	9	..	..	..	..	1	2	3	3	..	..	..	..	..	..	..	..	..	..	0·827
	27. ii	10	..	..	..	..	..	5	5	..	..	..	..	..	..	..	..	..	..	..	0·822

TABLE X (*contd.*)

Stage	Date	No.	0·487–0·539	0·539–0·592	0·592–0·644	0·644–0·696	0·696–0·748	0·748–0·800	0·800–0·853	0·853–0·905	0·905–0·957	0·957–1·009	1·009–1·061	1·061–1·114	1·114–1·166	1·166–1·218	1·218–1·270	1·270–1·322	1·322–1·375	1·375–1·427	Median size
♀ V	7. iii	21	..	..	..	..	..	3	13	4	..	1	..	..	..	..	..	..	..	..	0·838
	13. iii	18	..	..	..	..	..	3	6	5	3	1	..	..	..	..	..	..	..	..	0·857
	20. iii	16	..	..	..	..	..	2	7	4	2	1	..	..	..	..	..	..	..	..	0·850
	4. iv	38	..	..	..	..	..	..	1	1	5	8	7	14	2	..	..	..	..	..	1·053
	10. iv	23	..	..	..	..	..	..	2	2	2	6	5	4	2	..	..	..	..	..	1·009
	17. iv	35	..	..	..	..	..	..	1	..	1	9	12	11	1	..	..	..	..	..	1·042
	24. iv	55	..	..	..	..	..	..	..	5	14	20	7	8	..	1	..	..	..	..	0·973
	1. v	63	..	..	..	..	..	..	..	10	23	21	6	1	2	..	..	..	..	..	0·956
	8. v	60	..	..	..	..	..	..	..	15	35	9	..	..	1	..	..	..	..	..	0·927
	15. v	56	..	..	..	..	..	..	6	37	11	..	2	..	..	..	..	..	..	..	0·881
	22. v	81	..	..	..	..	..	..	3	36	34	4	4	..	..	..	..	..	..	..	0·906
	29. v	71	..	..	..	..	..	2	8	42	14	3	..	1	1	..	..	..	..	..	0·882
	5. vi	78	..	..	..	..	..	6	32	32	4	3	1	..	..	..	..	..	..	..	0·855
	12. vi	93	..	..	..	..	..	9	49	31	3	..	..	1	..	..	..	..	..	..	0·843
	19. vi	95	..	..	..	..	3	25	36	27	3	..	1	..	..	..	..	..	..	..	0·827
	26. vi	81	..	..	..	..	..	7	30	34	8	2	..	..	..	..	..	..	..	..	0·862
	3. vii	62	..	..	..	..	..	2	17	33	8	1	..	..	1	..	..	..	..	..	0·871
	10. vii	84	..	..	..	..	10	30	29	9	6	..	..	..	..	..	..	..	..	..	0·805
	17. vii	62	..	..	..	..	13	12	17	13	7	..	..	..	..	..	..	..	..	..	0·819
	24. vii	75	..	..	..	..	32	16	18	8	1	..	..	..	..	..	..	..	..	..	0·763
	31. vii	90	..	..	..	12	54	9	8	7	..	..	..	..	..	..	..	..	..	..	0·725
	7. viii	45	..	..	..	12	8	2	13	7	2	1	..	..	..	..	..	..	..	..	0·806
	14. viii	75	..	..	..	5	18	3	25	19	5	..	..	..	..	..	..	..	..	..	0·835
	21. viii	101	..	..	..	22	27	10	11	23	8	..	..	..	..	..	..	..	..	..	0·760
	28. viii	55	..	..	1	7	18	9	6	10	4	..	..	..	..	..	..	..	..	..	0·755
	11. ix	79	..	..	..	14	16	10	18	16	4	..	1	..	..	..	..	..	..	..	0·800
	2. x	58	..	..	..	..	14	10	21	10	3	..	..	..	..	..	..	..	..	..	0·816
♂ IV	20. iii	12	..	..	..	..	2	5	5	..	..	..	..	..	..	..	..	..	..	..	0·789
	4. iv	24	..	..	..	..	2	14	3	5	..	..	..	..	..	..	..	..	..	..	0·792
	17. iv	52	..	..	..	..	..	20	24	8	..	..	..	..	..	..	..	..	..	..	0·820
	24. iv	57	..	..	..	..	5	34	15	3	..	..	..	..	..	..	..	..	..	..	0·785
	1. v	65	..	..	..	..	6	34	23	2	..	..	..	..	..	..	..	..	..	..	0·785
	8. v	79	..	..	..	..	20	39	19	1	..	..	..	..	..	..	..	..	..	..	0·775
	15. v	57	..	..	..	1	19	35	2	..	..	..	..	..	..	..	..	..	..	..	0·760
	22. v	66	..	..	..	..	28	35	2	1	..	..	..	..	..	..	..	..	..	..	0·756
	29. v	49	..	..	..	3	20	23	3	..	..	..	..	..	..	..	..	..	..	..	0·755
	5. vi	78	..	..	1	10	23	31	11	2	..	..	..	..	..	..	..	..	..	..	0·758
	12. vi	90	..	..	..	28	9	47	5	1	..	..	..	..	..	..	..	..	..	..	0·755
	19. vi	99	..	1	2	26	15	47	8	..	..	..	..	..	..	..	..	..	..	..	0·756
	26. vi	85	..	..	..	..	8	68	9	..	..	..	..	..	..	..	..	..	..	..	0·775
	3. vii	133	..	..	..	3	24	97	9	..	..	..	..	..	..	..	..	..	..	..	0·774
	10. vii	97	..	..	..	11	9	70	7	..	..	..	..	..	..	..	..	..	..	..	0·770
	17. vii	64	..	..	3	3	8	41	9	..	..	..	..	..	..	..	..	..	..	..	0·775
	24. vii	117	..	..	14	8	14	72	9	..	..	..	..	..	..	..	..	..	..	..	0·763
	31. vii	89	..	..	11	5	9	56	8	..	..	..	..	..	..	..	..	..	..	..	0·770
	7. viii	52	..	..	1	1	4	39	7	..	..	..	..	..	..	..	..	..	..	..	0·776
	14. viii	82	..	..	..	1	10	66	5	..	..	..	..	..	..	..	..	..	..	..	0·768
	21. viii	79	..	..	6	7	12	48	6	..	..	..	..	..	..	..	..	..	..	..	0·759
	28. viii	92	..	..	14	6	20	48	4	..	..	..	..	..	..	..	..	..	..	..	0·753
	11. ix	81	..	..	2	..	19	57	3	..	..	..	..	..	..	..	..	..	..	..	0·762
	2. x	89	..	..	2	19	20	46	2	..	..	..	..	..	..	..	..	..	..	..	0·752

Stage	Date	No.	0·487– 0·539	0·539– 0·592	0·592– 0·644	0·644– 0·696	0·696– 0·748	0·748– 0·800	0·800– 0·853	0·853– 0·905	0·905– 0·957	0·957– 1·009	1·009– 1·061	1·061– 1·114	1·114– 1·166	1·166– 1·218	1·218– 1·270	1·270– 1·322	1·322– 1·375	1·375– 1·427	Median size
♀ IV	4. iv	17	..	..	..	..	..	4	6	4	3	..	..	..	..	..	..	..	..	..	0·835
	17. iv	47	..	..	..	..	..	9	20	14	4	..	..	..	..	..	..	..	..	..	0·835
	24. iv	87	..	..	..	..	1	26	43	17	..	..	..	..	..	..	..	..	..	..	0·816
	1. v	71	..	..	..	..	2	30	34	5	..	..	..	..	..	..	..	..	..	..	0·806
	8. v	70	..	..	..	..	9	40	19	2	..	..	..	..	..	..	..	..	..	..	0·783
	15. v	71	..	..	..	..	17	48	5	1	..	..	..	..	..	..	..	..	..	..	0·762
	22. v	59	..	..	..	..	13	39	7	..	..	..	..	..	..	..	..	..	..	..	0·768
	29. v	77	..	..	..	1	34	40	2	..	..	..	..	..	..	..	..	..	..	..	0·753
	5. vi	71	..	..	..	11	34	23	3	..	..	..	..	..	..	..	..	..	..	..	0·739
	12. vi	82	..	..	..	17	31	33	1	..	..	..	..	..	..	..	..	..	..	..	0·732
	19. vi	89	..	..	..	21	31	37	..	..	..	..	..	..	..	..	..	..	..	..	0·735
	26. vi	84	..	..	..	..	21	59	4	..	..	..	..	..	..	..	..	..	..	..	0·760
	3. vii	116	..	..	..	2	37	74	3	..	..	..	..	..	..	..	..	..	..	..	0·760
	10. vii	98	..	..	..	27	33	32	6	..	..	..	..	..	..	..	..	..	..	..	0·738
	17. vii	77	..	..	1	6	24	44	2	..	..	..	..	..	..	..	..	..	..	..	0·754
	24. vii	131	..	..	15	9	47	58	2	..	..	..	..	..	..	..	..	..	..	..	0·746
	31. vii	108	..	..	13	5	31	55	4	..	..	..	..	..	..	..	..	..	..	..	0·770
	7. viii	83	..	..	3	..	21	57	2	..	..	..	..	..	..	..	..	..	..	..	0·757
	14. viii	88	..	..	..	..	30	55	3	..	..	..	..	..	..	..	..	..	..	..	0·756
	21. viii	99	..	1	7	1	35	52	3	..	..	..	..	..	..	..	..	..	..	..	0·756
	28. viii	113	..	..	15	8	42	45	3	..	..	..	..	..	..	..	..	..	..	..	0·743
	11. ix	95	..	..	2	2	40	50	1	..	..	..	..	..	..	..	..	..	..	..	0·751
	2. x	97	..	..	4	14	47	30	2	..	..	..	..	..	..	..	..	..	..	..	0·737
III	20. ii	12	..	5	6	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·601
	27. ii	41	..	10	21	10	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·605
	7. iii	22	..	5	13	2	2	..	..	..	..	..	..	..	..	..	..	..	..	..	0·614
	13. iii	11	..	..	10	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	0·622
	20. iii	72	..	..	19	27	25	1	..	..	..	..	..	..	..	..	..	..	..	..	0·677
	27. iii	10	..	..	..	8	2	..	..	..	..	..	..	..	..	..	..	..	..	..	0·677
	4. iv	31	..	..	1	13	11	6	..	..	..	..	..	..	..	..	..	..	..	..	0·703
	10. iv	20	..	..	..	5	12	3	..	..	..	..	..	..	..	..	..	..	..	..	0·732
	17. iv	133	..	..	..	48	70	15	..	..	..	..	..	..	..	..	..	..	..	..	0·709
	24. iv	82	..	..	..	29	49	4	..	..	..	..	..	..	..	..	..	..	..	..	0·706
	1. v	106	..	..	2	58	44	2	..	..	..	..	..	..	..	..	..	..	..	..	0·692
	8. v	81	..	..	2	54	25	..	..	..	..	..	..	..	..	..	..	..	..	..	0·678
	15. v	79	..	..	14	56	9	..	..	..	..	..	..	..	..	..	..	..	..	..	0·670
	22. v	93	..	19	47	24	3	..	..	..	..	..	..	..	..	..	..	..	..	..	0·621
	29. v	138	..	1	33	89	15	..	..	..	..	..	..	..	..	..	..	..	..	..	0·664
	5. vi	109	..	4	45	55	5	..	..	..	..	..	..	..	..	..	..	..	..	..	0·649
	12. vi	113	..	16	55	39	3	..	..	..	..	..	..	..	..	..	..	..	..	..	0·622
	19. vi	76	..	22	31	23	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·608
	26. vi	157	..	..	27	128	2	..	..	..	..	..	..	..	..	..	..	..	..	..	0·659
	3. vii	82	..	4	31	46	1	..	..	..	..	..	..	..	..	..	..	..	..	..	0·648
	10. vii	105	..	10	59	36	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·622
	17. vii	104	..	37	34	32	1	..	..	..	..	..	..	..	..	..	..	..	..	..	0·613
	24. vii	89	1	55	22	11	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·583
	31. vii	121	..	62	35	24	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·591
	7. viii	78	..	31	34	13	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·620
	14. viii	92	1	34	30	27	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·622
	21. viii	73	8	56	7	1	1	..	..	..	..	..	..	..	..	..	..	..	..	..	0·569
	28. viii	98	4	74	13	7	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·571
	11. ix	70	..	29	32	9	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·613
	2. x	85	1	47	36	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·590

TABLE XI. SIZE OF *PARACALANUS PARVUS* IN MM.

Stage	Date	No.	0·383–0·418	0·418–0·452	0·452–0·487	0·487–0·522	0·522–0·557	0·557–0·592	0·592–0·626	0·626–0·661	0·661–0·696	0·696–0·731	0·731–0·766	0·766–0·800	0·800–0·835	0·835–0·887	Median size
♂	17. vii–14. viii	13	..	..	..	..	..	..	..	..	1	6	6	..	..	..	0·730
	21. viii	21	..	..	..	..	..	..	..	..	1	6	11	2	1	..	0·745
	28. viii	75	..	..	..	..	..	..	..	..	..	17	33	24	1	..	0·753
	11. ix	84	..	..	..	..	..	..	..	..	2	21	49	12	..	..	0·747
	2. x	10	..	..	..	..	..	..	..	..	..	..	1	8	1	..	0·785
♀	17 and 24. vii	13	..	..	..	..	..	..	1	..	6	2	3	1	..	..	0·696
	31. vii	24	..	..	..	..	..	1	3	12	7	1	..	..	..	..	0·671
	7. viii	24	..	..	..	..	..	..	1	10	10	3	..	..	..	..	0·664
	14. viii	19	..	..	..	..	..	..	1	4	7	5	2	..	..	..	0·678
	21. viii	21	..	..	..	..	..	..	..	4	6	10	..	1	..	..	0·700
	28. viii	113	..	..	..	..	..	..	..	11	49	39	9	1	2	2	0·694
	11. ix	93	..	..	..	..	..	..	5	21	40	23	1	2	1	..	0·683
	2. x	70	..	..	..	..	..	..	..	..	8	34	25	3	..	..	0·725
♂ V	31. vii	22	..	..	..	..	..	..	..	3	9	8	2	..	..	..	0·695
	7 and 14. viii	16	..	..	..	..	..	..	..	2	6	7	1	..	..	..	0·698
	21. viii	29	..	..	..	..	..	..	..	..	7	14	8	..	..	..	0·710
	28. viii	50	..	..	..	..	..	..	..	..	3	26	20	1	..	..	0·726
	11. ix	30	..	..	..	..	..	..	..	1	3	19	7	..	..	..	0·720
	2. x	50	..	..	..	..	..	..	..	1	4	12	18	15	..	..	0·743
♀ V	17 and 24. vii	7	..	..	..	..	1	4	2	..	..	..	..	..	..	..	..
	31. vii	36	..	..	..	..	1	17	13	5	..	..	..	..	..	..	0·593
	7 and 14. viii	13	..	..	..	..	1	6	6	..	..	..	..	..	..	..	0·591
	21. viii	52	..	..	..	..	1	9	29	12	1	..	..	..	..	..	0·615
	28. viii	37	..	..	..	..	..	3	17	12	4	1	..	..	..	..	0·625
	11. ix	52	..	..	..	..	..	4	20	22	5	..	1	..	..	..	0·629
	2. x	90	..	..	..	..	..	2	14	44	26	2	1	1	..	..	0·648
♂ IV	31. vii	53	..	..	..	2	15	34	2	..	..	..	..	..	..	..	0·565
	7 and 14. viii	7	..	..	..	1	2	4	..	..	..	..	..	..	..	..	..
	21. viii	51	..	..	..	..	5	32	14	..	..	..	..	..	..	..	0·581
	28. viii	40	..	..	..	..	1	20	19	..	..	..	..	..	..	..	0·591
	11. ix	50	..	..	..	1	4	25	20	..	..	..	..	..	..	..	0·587
	2. x	36	..	..	..	..	2	9	23	2	..	..	..	..	..	..	0·602
♀ IV	17 and 24. vii	8	..	..	2	4	2	..	..	..	..	..	..	..	..	..	..
	31. vii	51	..	..	5	34	11	1	..	..	..	..	..	..	..	..	0·510
	7 and 14. viii	15	..	..	1	11	3	..	..	..	..	..	..	..	..	..	0·514
	21. viii	50	..	..	..	25	24	1	..	..	..	..	..	..	..	..	0·523
	28. viii	40	..	..	1	14	21	3	1	..	..	..	..	..	..	..	0·530
	11. ix	85	..	..	..	15	56	14	..	..	..	..	..	..	..	..	0·538
	2. x	53	..	..	..	8	35	10	..	..	..	..	..	..	..	..	0·542
III	17 and 24. vii	13	1	5	7	..	..	..	..	..	..	..	..	..	..	..	0·455
	31. vii	90	..	37	47	6	..	..	..	..	..	..	..	..	..	..	0·458
	7. viii	39	..	17	22	..	..	..	..	..	..	..	..	..	..	..	0·456
	14. viii	29	..	13	16	..	..	..	..	..	..	..	..	..	..	..	0·455
	21. viii	78	1	33	39	5	..	..	..	..	..	..	..	..	..	..	0·458
	28. viii	69	1	21	35	11	1	..	..	..	..	..	..	..	..	..	0·462
	11. ix	105	1	37	54	13	..	..	..	..	..	..	..	..	..	..	0·464
	2. x	78	..	9	52	16	1	..	..	..	..	..	..	..	..	..	0·472

TABLE XII. SIZE OF *MICROCALANUS PYGMAEUS* IN MM.

Stage	Date	No.	0·313–0·348	0·348–0·383	0·383–0·418	0·418–0·452	0·452–0·487	0·487–0·522	0·522–0·557	0·557–0·592	0·592–0·626	0·626–0·661	Median size
♂	23. i	18	..	..	..	..	1	3	14	..	..	..	0·533
	6. ii	29	..	..	..	..	..	4	25	..	..	..	0·535
	13. ii	30	..	..	..	..	..	7	21	2	..	..	0·540
	20. ii	110	..	..	..	..	..	10	85	15	..	..	0·538
	27. ii	13	..	..	..	..	..	..	10	3	..	..	0·546
	7. iii	67	..	..	..	..	..	2	51	14	..	..	0·548
	13. iii	81	..	..	..	..	..	1	56	24	..	..	0·551
	20. iii	90	..	..	..	..	..	2	48	40	..	..	0·554
	4. iv	42	..	..	..	..	..	1	19	22	..	..	0·558
	10. iv	85	..	..	..	..	..	5	47	32	1	..	0·552
	17. iv	19	..	..	..	..	..	..	5	14	..	..	0·574
	24. iv	43	..	..	..	..	..	..	12	29	2	..	0·566
	1. v	37	..	..	..	..	..	..	12	23	2	..	0·564
	8. v	55	..	..	..	..	..	..	23	31	1	..	0·561
	15. v	78	..	..	..	..	..	1	53	24	..	..	0·550
	22. v	109	..	..	..	..	..	7	93	9	..	..	0·541
	29. v	42	..	..	..	..	..	1	26	15	..	..	0·551
	5. vi	54	..	..	..	..	..	..	39	15	..	..	0·549
	12. vi	27	..	..	..	..	..	1	17	9	..	..	0·552
	26. vi	56	..	..	..	..	..	5	44	7	..	..	0·540
	3. vii	95	..	..	..	..	..	17	72	6	..	..	0·533
	10. vii	75	..	..	..	..	..	23	52	..	..	..	0·529
	17. vii	47	..	..	..	..	..	8	31	8	..	..	0·539
	24. vii	22	..	..	..	..	..	4	18	..	..	..	0·531
	31. vii	20	..	..	..	..	..	6	14	..	..	..	0·530
	7. viii	27	..	..	..	..	..	9	18	..	..	..	0·529
	14. viii	28	..	..	..	..	..	15	13	..	..	..	0·522
♀	17. i	35	..	..	..	..	..	9	24	2	..	..	0·533
	23. i	64	..	..	..	..	..	15	46	3	..	..	0·535
	30. i	26	..	..	..	..	..	14	11	1	..	..	0·521
	6. ii	93	..	..	..	..	..	26	60	7	..	..	0·532
	13. ii	67	..	..	..	..	..	6	54	7	..	..	0·539
	20. ii	59	..	..	..	..	..	4	33	21	1	..	0·550
	27. ii	105	..	..	..	..	..	6	53	45	1	..	0·552
	7. iii	71	..	..	..	..	..	1	18	47	5	..	0·566
	13. iii	74	..	..	..	..	..	..	15	50	9	..	0·571
	20. iii	76	..	..	..	..	..	2	14	46	14	..	0·574
	27. iii	27	..	..	..	..	..	..	9	16	2	..	0·568
	4. iv	69	..	..	..	..	..	1	11	31	25	1	0·583
	10. iv	122	..	..	..	..	..	1	16	72	32	1	0·581
	17. iv	78	..	..	..	..	..	..	12	49	17	..	0·580
	24. iv	89	..	..	..	..	..	..	9	50	30	..	0·584
	1. v	88	..	..	..	..	..	..	7	52	28	1	0·584
	8. v	102	..	..	..	..	..	2	23	65	11	1	0·570
	15. v	105	..	..	..	..	..	..	26	67	11	1	0·569
	22. v	103	..	..	..	..	..	1	63	36	3	..	0·551
	29. v	157	..	..	..	..	..	1	61	79	16	..	0·562
	5. vi	126	..	..	..	..	..	3	64	49	10	..	0·555
	12. vi	88	..	..	..	..	..	3	33	43	9	..	0·562
	19. vi	118	..	..	..	..	..	..	58	49	11	..	0·558
	26. vi	115	..	..	..	..	..	2	33	65	15	..	0·567
	3. vii	129	..	..	..	..	..	8	61	55	5	..	0·555
	10. vii	101	..	..	..	..	..	7	47	41	5	1	0·555
	17. vii	112	..	..	..	..	..	5	42	58	6	1	0·561
	24. vii	62	..	..	..	..	..	8	39	14	1	..	0·542
	31. vii	92	..	..	..	..	..	16	59	17	..	..	0·541
	7. viii	81	..	..	..	..	..	31	40	9	1	..	0·529
	14. viii	82	..	..	..	..	..	26	45	10	1	..	0·533
	21. viii	97	..	..	..	..	1	43	44	9	..	..	0·525
	28. viii	63	..	..	..	..	2	31	26	3	1	..	0·522
	11. ix	78	..	..	..	..	1	38	37	2	..	..	0·522
	2. x	29	..	..	..	..	1	22	6	..	..	..	0·511
♂ V	17. i	20	..	..	..	..	4	15	1	..	..	..	0·497
	23. i	71	..	..	..	..	1	59	11	..	..	..	0·508
	30. i	20	..	..	..	..	2	14	4	..	..	..	0·513
	6. ii	57	..	..	..	..	2	38	16	1	..	..	0·516
	13. ii	42	..	..	..	..	..	22	20	..	..	..	0·522
	20. ii	42	..	..	..	..	..	23	19	..	..	..	0·521
	27. ii	72	..	..	..	..	1	38	33	..	..	..	0·521
	7. iii	61	..	..	..	..	..	16	43	2	..	..	0·532
	13. iii	43	..	..	..	..	..	7	32	4	..	..	0·433
	20. iii	53	..	..	..	..	..	5	41	7	..	..	0·541
	4. iv	22	..	..	..	..	..	2	18	2	..	..	0·539
	10. iv	58	..	..	..	..	..	3	45	10	..	..	0·546
	17. iv	36	..	..	..	..	..	2	25	9	..	..	0·549
	24. iv	56	..	..	..	..	..	4	44	8	..	..	0·546
	1. v	75	..	..	..	..	..	9	57	9	..	..	0·542
	8 v.	69	..	..	..	..	..	11	54	4	..	..	0·535
	15. v	73	..	..	..	..	..	27	46	..	..	..	0·527

TABLE XII (*cont.*)

Stage	Date	No.	0·313–0·348	0·348–0·383	0·383–0·418	0·418–0·452	0·452–0·487	0·487–0·522	0·522–0·557	0·557–0·592	0·592–0·626	0·626–0·661	Median size
♂ V	22. v	48	..	..	..	..	..	15	32	1	..	..	0·530
	29. v	33	..	..	..	..	..	5	26	2	..	..	0·534
	5. vi	13	..	..	..	..	..	..	10	3	..	..	0·534
	12. vi	56	..	..	..	..	..	6	48	2	..	..	0·535
	19. vi	28	..	..	..	..	..	5	23	..	..	..	0·534
	26. vi	66	..	..	..	1	4	42	19	..	..	..	0·514
	3. vii	66	..	..	..	..	3	43	20	..	..	..	0·513
	10. vii	79	..	..	..	..	3	53	23	..	..	..	0·514
	17. vii	62	..	..	..	..	..	37	25	..	..	..	0·519
	24. vii	53	..	..	..	..	..	29	24	..	..	..	0·520
	31. vii	69	..	..	..	..	..	51	18	..	..	..	0·515
	7. viii	26	..	..	..	..	3	21	2	..	..	..	0·500
	14. viii	31	..	..	..	1	4	24	2	..	..	..	0·503
	28. viii	15	..	..	..	..	4	11	..	..	..	..	0·497
	11. ix	13	..	..	..	..	3	10	..	..	..	..	0·499
♀ V	17. i	10	..	..	..	4	6	..	..	..	..	..	0·456
	23. i	79	..	..	..	9	64	5	1	..	..	..	0·465
	30. i	15	..	..	..	5	9	1	..	..	..	..	0·459
	6. ii	46	..	..	..	5	36	5	..	..	..	..	0·467
	13. ii	35	..	..	..	4	28	3	..	..	..	..	0·468
	20. ii	57	..	..	..	6	41	10	..	..	..	..	0·474
	27. ii	27	..	..	..	2	23	2	..	..	..	..	0·469
	7. iii	52	..	..	..	..	30	22	..	..	..	..	0·485
	13. iii	42	..	..	..	1	9	30	1	1	..	..	0·497
	20. iii	31	..	..	..	..	9	20	2	..	..	..	0·495
	4. iv	17	..	..	..	..	3	11	3	..	..	..	0·508
	10. iv	38	..	..	..	..	2	33	3	..	..	..	0·508
	17. iv	29	..	..	..	..	1	24	4	..	..	..	0·511
	24. iv	36	..	..	..	..	1	31	4	..	..	..	0·509
	1. v	50	..	..	..	..	6	38	6	..	..	..	0·503
	8. v	40	..	..	..	..	9	28	3	..	..	..	0·497
	15. v	59	..	..	..	..	34	25	..	..	..	..	0·485
	22. v	86	..	..	..	1	35	48	2	..	..	..	0·490
	29. v	12	..	..	..	..	1	8	3	..	..	..	0·499
	5. vi	22	..	..	..	1	4	17	..	..	..	..	0·496
	12. vi	56	..	..	..	..	16	38	2	..	..	..	0·495
	19. vi	41	..	..	..	1	17	20	3	..	..	..	0·490
	26. vi	87	..	..	..	17	62	8	..	..	..	..	0·464
	3. vii	53	..	..	..	13	39	1	..	..	..	..	0·461
	10. vii	69	..	..	..	13	56	..	..	..	..	..	0·462
	17. vii	60	..	..	..	4	44	11	1	..	..	..	0·476
	24. vii	49	..	..	..	1	43	5	..	..	..	..	0·473
	31. vii	82	..	..	..	15	63	4	..	..	..	..	0·462
	7. viii	28	..	..	..	10	18	..	..	..	..	..	0·457
	14. viii	48	..	..	..	23	25	..	..	..	..	..	0·453
	11. ix	11	..	..	..	5	6	..	..	..	..	..	0·455
♂ IV	17. i	34	..	..	14	20	..	..	..	..	..	..	0·422
	23. i	43	..	..	9	33	1	..	..	..	..	..	0·429
	30. i	23	..	..	19	4	..	..	..	..	..	..	0·410
	6. ii	45	..	..	17	28	..	..	..	..	..	..	0·422
	13. ii	38	..	..	9	29	..	..	..	..	..	..	0·426
	20. ii	61	..	..	5	55	1	..	..	..	..	..	0·432
	27. ii	55	..	..	8	46	1	..	..	..	..	..	0·430
	7. iii	32	..	..	..	31	1	..	..	..	..	..	0·438
	13. iii	38	..	..	..	35	3	..	..	..	..	..	0·439
	20. iii	14	..	..	..	8	6	..	..	..	..	..	0·451
	4. iv	23	..	..	..	13	10	..	..	..	..	..	0·451
	10. iv	41	..	..	2	22	17	..	..	..	..	..	0·450
	17. iv	27	..	..	..	8	18	1	..	..	..	..	0·459
	24. iv	60	..	..	..	29	31	..	..	..	..	..	0·453
	1. v	71	..	..	..	41	30	..	..	..	..	..	0·450
	8. v	57	..	..	..	25	32	..	..	..	..	..	0·454
	15. v	56	..	..	2	46	8	..	..	..	..	..	0·441
	22. v	16	..	..	2	12	2	..	..	..	..	..	0·443
	5. vi	13	..	..	..	10	3	..	..	..	..	..	0·447
	12. vi	57	..	..	3	39	15	..	..	..	..	..	0·445
	19. vi	33	..	..	3	26	4	..	..	..	..	..	0·435
	26. vi	38	..	..	9	29	..	..	..	..	..	..	0·425
	3. vii	51	..	..	18	33	..	..	..	..	..	..	0·424
	10. vii	47	..	..	11	36	..	..	..	..	..	..	0·427
	17. vii	45	..	..	1	41	3	..	..	..	..	..	0·439
	24. vii	32	..	..	3	29	..	..	..	..	..	..	0·428
	31. vii	19	..	..	9	10	..	..	..	..	..	..	0·420
	7. viii	12	..	..	4	8	..	..	..	..	..	..	0·425
	14. viii	10	..	..	5	5	..	..	..	..	..	..	0·420

TABLE XII (*cont.*)

Stage	Date	No.	0·313–0·348	0·348–0·383	0·383–0·418	0·418–0·452	0·452–0·487	0·487–0·522	0·522–0·557	0·557–0·592	0·592–0·626	0·626–0·661	Median size
♀ IV	17. i	40	..	7	32	1	..	..	..	..	..	..	0·394
	23. i	68	..	1	65	2	..	..	..	..	..	..	0·398
	30. i	12	..	7	5	..	..	..	..	..	..	..	0·381
	6. ii	32	..	6	26	..	..	..	..	..	..	..	0·393
	13. ii	36	..	2	34	..	..	..	..	..	..	..	0·400
	20. ii	48	..	2	42	4	..	..	..	..	..	..	0·404
	27. ii	35	..	..	30	5	..	..	..	..	..	..	0·402
	7. iii	28	..	1	26	1	..	..	..	..	..	..	0·406
	13. iii	42	..	..	24	18	..	..	..	..	..	..	0·415
	20. iii	11	..	..	7	4	..	..	..	..	..	..	0·413
	4. iv	30	..	..	4	26	..	..	..	..	..	..	0·427
	10. iv	39	..	..	1	38	..	..	..	..	..	..	0·428
	17. iv	23	..	..	4	17	2	..	..	..	..	..	0·438
	24. iv	61	..	..	11	47	3	..	..	..	..	..	0·427
	1. v	63	..	..	15	46	2	..	..	..	..	..	0·427
	8. v	38	..	..	9	28	1	..	..	..	..	..	0·427
	15. v	51	..	..	31	19	1	..	..	..	..	..	0·414
	22. v	25	..	..	14	11	..	..	..	..	..	..	0·416
	5. vi	14	..	..	3	11	..	..	..	..	..	..	0·427
	12. vi	59	..	..	18	41	..	..	..	..	..	..	0·424
	19. vi	41	..	1	24	14	2	..	..	..	..	..	0·414
	26. vi	75	..	5	67	3	..	..	..	..	..	..	0·397
	3. vii	69	..	13	55	1	..	..	..	..	..	..	0·392
	10. vii	70	..	3	62	5	..	..	..	..	..	..	0·399
	17. vii	69	..	1	48	20	..	..	..	..	..	..	0·410
	24. vii	41	..	2	37	2	..	..	..	..	..	..	0·398
	31. vii	37	..	9	27	1	..	..	..	..	..	..	0·393
	7. viii	18	..	4	13	1	..	..	..	..	..	..	0·395
	14. viii	8	..	2	6	..	..	..	..	..	..	..	0·392
III	17. i	71	22	49	..	..	..	..	..	..	..	..	0·354
	23. i	33	18	15	..	..	..	..	..	..	..	..	0·347
	30. i	19	12	7	..	..	..	..	..	..	..	..	0·345
	6. ii	56	22	34	..	..	..	..	..	..	..	..	0·352
	13. ii	137	75	62	..	..	..	..	..	..	..	..	0·347
	20. ii	68	19	48	1	..	..	..	..	..	..	..	0·355
	27. ii	83	39	44	..	..	..	..	..	..	..	..	0·350
	7. iii	50	13	37	..	..	..	..	..	..	..	..	0·355
	13. iii	46	4	38	4	..	..	..	..	..	..	..	0·367
	20. iii	19	1	16	1	1	..	..	..	..	..	..	0·362
	27. iii	59	3	56	..	..	..	..	..	..	..	..	0·361
	4. iv	64	5	52	7	..	..	..	..	..	..	..	0·370
	10. iv	53	5	40	8	..	..	..	..	..	..	..	0·367
	17. iv	72	..	54	17	1	..	..	..	..	..	..	0·376
	24. iv	63	..	49	14	..	..	..	..	..	..	..	0·375
	1. v	79	1	56	22	..	..	..	..	..	..	..	0·375
	8. v	75	4	66	5	..	..	..	..	..	..	..	0·369
	15. v	50	8	40	2	..	..	..	..	..	..	..	0·358
	22. v	24	2	20	2	..	..	..	..	..	..	..	0·369
	5. vi	41	3	35	3	..	..	..	..	..	..	..	0·362
	12. vi	57	4	47	6	..	..	..	..	..	..	..	0·367
	19. vi	36	7	28	1	..	..	..	..	..	..	..	0·359
	26. vi	67	35	32	..	..	..	..	..	..	..	..	0·348
	3. vii	56	29	27	..	..	..	..	..	..	..	..	0·348
	10. vii	82	41	41	..	..	..	..	..	..	..	..	0·348
	17. vii	61	19	40	2	..	..	..	..	..	..	..	0·357
	24. vii	22	13	9	..	..	..	..	..	..	..	..	0·346
	31. vii	35	19	16	..	..	..	..	..	..	..	..	0·347
	7. viii	17	7	10	..	..	..	..	..	..	..	..	0·352

TABLE XIII. SIZE OF *CENTROPAGES HAMATUS* IN MM.

Stage	Date	No.	0·592–0·644	0·644–0·696	0·696–0·748	0·748–0·800	0·800–0·853	0·853–0·905	0·905–0·957	0·957–1·009	1·009–1·061	1·061–1·114	1·114–1·166	1·166–1·218	1·218–1·270	1·270–1·322	1·322–1·375	1·375–1·427	1·427–1·479	1·479–1·531	Median size
♂	10. iv	51	..	..	..	..	..	..	..	..	5	18	18	10	..	..	..	..	..	..	1·123
	17. iv	25	..	..	..	..	..	..	..	..	3	5	8	7	1	1	..	..	..	..	1·152
	24. iv	26	..	..	..	..	..	..	..	..	..	4	10	10	2	..	..	..	..	..	1·163
	1. v	52	..	..	..	..	..	..	..	..	1	7	26	16	1	1	..	..	..	..	1·152
	8. v	30	..	..	..	..	..	..	1	1	2	5	9	8	4	..	..	..	..	..	1·151
	15. v	29	..	..	..	..	..	..	..	..	7	4	10	7	1	..	..	..	..	..	1·131
	22. v	24	..	..	..	..	..	..	1	3	8	7	2	3	..	..	..	..	..	..	1·064
	29. v	22	..	..	..	..	..	..	1	5	9	3	4	..	..	..	..	..	..	..	1·046
	5. vi	36	..	..	..	..	..	2	2	7	13	9	3	..	..	..	..	..	..	..	1·045
	12. vi	46	..	..	..	..	..	..	9	14	16	6	1	1	..	..	..	..	..	..	1·010
	19. vi	112	..	..	..	..	..	1	5	19	36	34	15	2	..	..	..	..	..	..	1·052
	26. vi	26	..	..	..	..	..	..	3	9	6	6	2	..	..	..	..	..	..	..	1·018
	3. vii	45	..	..	..	..	2	9	7	11	14	2	..	..	..	..	..	..	..	..	1·002
	10. vii	138	..	..	..	7	43	63	21	3	..	..	1	..	..	..	..	..	..	..	0·867
	17. vii	61	..	..	2	9	13	25	9	2	1	..	..	..	..	..	..	..	..	..	0·863
	24. vii	90	..	1	8	33	25	14	6	..	2	1	..	..	..	..	..	..	..	..	0·806
	31. vii	175	..	..	11	50	77	19	10	5	2	1	..	..	..	..	..	..	..	..	0·816
	7. viii	103	..	..	12	56	25	6	..	3	1	..	..	..	..	..	..	..	..	..	0·789
	14. viii	33	..	..	1	19	11	2	..	..	..	..	..	..	..	..	..	..	..	..	0·795
	21. viii	23	..	..	..	1	12	6	4	..	..	..	..	..	..	..	..	..	..	..	0·850
	28. viii	22	..	..	..	1	6	11	4	..	..	..	..	..	..	..	..	..	..	..	0·866
	11. ix	40	..	..	..	1	18	17	4	..	..	..	..	..	..	..	..	..	..	..	0·858
♀	10. iv	33	..	..	..	..	..	..	..	..	..	..	1	..	5	17	6	4	..	..	1·302
	17. iv	15	..	..	..	..	..	..	..	..	..	..	..	1	2	4	5	1	1	1	1·326
	24. iv	25	..	..	..	..	..	..	..	..	..	..	..	1	2	3	7	9	3	..	1·374
	1. v	35	..	..	..	..	..	..	..	..	..	..	..	..	1	8	11	14	1	..	1·367
	8. v	8	..	..	..	..	..	..	..	..	..	1	..	1	1	4	1	..	..	..	1·335
	15. v	17	..	..	..	..	..	..	..	..	..	..	..	1	2	2	7	2	3	..	1·339
	22. v	10	..	..	..	..	..	..	..	..	..	..	1	1	4	1	1	2	..	..	1·262
	29. v	14	..	..	..	..	..	..	..	..	..	..	3	6	3	2	..	..	..	..	1·198
	5. vi	14	..	..	..	..	..	..	..	..	1	1	3	4	3	1	1	..	..	..	1·205
	12. vi	14	..	..	..	..	..	..	..	..	..	2	5	3	3	1	..	..	..	..	1·175
	19. vi	34	..	..	..	..	..	..	..	..	..	3	9	5	8	4	3	2	..	..	1·222
	3. vii	18	..	..	..	..	..	..	2	1	3	3	5	2	1	1	..	..	..	..	1·123
	10. vii	83	..	..	..	..	1	9	19	29	15	6	3	1	..	..	..	..	..	..	0·979
	17. vii	57	..	..	..	1	2	6	18	19	7	2	2	..	..	..	..	..	..	..	0·958
	24. vii	65	..	..	2	6	9	14	16	7	7	1	1	1	1	..	..	..	..	..	0·909
	31. vii	103	..	..	4	8	22	28	22	16	1	1	..	..	1	..	..	..	..	..	0·881
	7. viii	48	..	..	..	3	12	15	9	5	2	..	1	1	..	..	..	..	..	..	0·881
	14. viii	20	..	..	..	3	7	6	4	..	..	..	..	..	..	..	..	..	..	..	0·855
	21. viii	46	..	..	..	..	7	10	13	10	6	..	..	..	..	..	..	..	..	..	0·931
	28. viii	30	..	..	..	..	1	3	7	10	4	4	1	..	..	..	..	..	..	..	0·993
	11. ix	23	..	..	..	..	..	4	7	5	7	..	..	..	..	..	..	..	..	..	0·963
♂ V	4. iv	26	..	..	..	..	1	4	14	7	..	..	..	..	..	..	..	..	..	..	0·933
	10. iv	25	..	..	..	..	..	3	12	7	3	..	..	..	..	..	..	..	..	..	0·937
	17. iv	22	..	..	..	..	..	1	8	10	3	..	..	..	..	..	..	..	..	..	0·977
	24. iv	14	..	..	..	..	..	3	3	8	..	..	..	..	..	..	..	..	..	..	0·966
	1. v	30	..	..	..	..	..	5	15	9	1	..	..	..	..	..	..	..	..	..	0·934
	8. v	14	..	..	..	..	..	4	7	2	1	..	..	..	..	..	..	..	..	..	0·920
	15. v	14	..	..	..	1	6	7	..	..	..	..	..	..	..	..	..	..	..	..	0·856
	22. v	36	..	..	..	..	3	23	10	..	..	..	..	..	..	..	..	..	..	..	0·890
	29. v	11	..	..	..	..	3	5	2	..	1	..	..	..	..	..	..	..	..	..	0·879
	5 .vi	26	..	..	1	3	11	11	..	..	..	..	..	..	..	..	..	..	..	..	0·848
	12. vi	9	..	..	..	1	6	1	1	..	..	..	..	..	..	..	..	..	..	..	0·837
	19. vi	7	..	..	..	1	2	4	..	..	..	..	..	..	..	..	..	..	..	..	
	26. vi	8	..	..	..	2	4	2	..	..	..	..	..	..	..	..	..	..	..	..	
	3. vii	98	..	2	44	38	13	1	..	..	..	..	..	..	..	..	..	..	..	..	0·753
	10. vii	185	..	17	115	52	1	..	..	..	..	..	..	..	..	..	..	..	..	..	0·733
	17. vii	33	1	11	16	4	1	..	..	..	..	..	..	..	..	..	..	..	..	..	0·713
	24. vii	61	3	29	24	4	1	..	..	..	..	..	..	..	..	..	..	..	..	..	0·695
	31. vii	83	2	57	22	2	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·684
	7. viii	39	5	28	6	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·675
	14. viii	42	1	24	16	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·691
	21. viii	42	..	5	26	11	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·735
	28. viii	50	..	4	21	22	3	..	..	..	..	..	..	..	..	..	..	..	..	..	0·749
	11. ix	31	..	3	22	6	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·724

♀ V	4. iv	21	..	..	..	..	..	..	4	7	6	4	..	..	..	..	..	..	..	..	1·009
	10. iv	13	..	..	..	..	..	..	1	1	6	5	..	..	..	..	..	..	..	..	1·026
	17. iv	11	..	..	..	..	..	..	..	2	3	4	2	..	..	..	..	..	..	..	1·078
	24. iv	10	..	..	..	..	..	..	..	..	3	6	1	..	..	..	..	..	..	..	1·088
	1. v	16	..	..	..	..	..	..	..	3	7	3	3	..	..	..	..	..	..	..	1·053
	8. v	12	..	..	..	..	..	1	1	4	5	1	..	..	..	..	..	..	..	..	1·018
	15. v	9	..	..	..	..	..	1	6	2	..	..	..	..	..	..	..	..	..	..	0·931
	22. v	28	..	..	..	..	1	5	7	13	2	..	..	..	..	..	..	..	..	..	0·961
	5. vi	24	..	..	..	..	6	9	8	1	..	..	..	..	..	..	..	..	..	..	0·890
	12–26. vi	15	..	..	..	..	1	5	6	3	..	..	..	..	..	..	..	..	..	..	0·934
	3. vii	67	..	2	7	23	20	11	3	1	..	..	..	..	..	..	..	..	..	..	0·806
	10. vii	136	..	..	15	73	37	10	1	..	..	..	..	..	..	..	..	..	..	..	0·788
	17. vii	49	..	6	20	18	5	..	..	..	..	..	..	..	..	..	..	..	..	..	0·744
	24. vii	53	3	17	23	7	2	..	1	..	..	..	..	..	..	..	..	..	..	..	0·711
	31. vii	55	..	22	22	11	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·711
	7. viii	43	..	16	22	4	1	..	..	..	..	..	..	..	..	..	..	..	..	..	0·708
	14. viii	31	..	6	15	8	2	..	..	..	..	..	..	..	..	..	..	..	..	..	0·734
	21. viii	36	..	..	4	21	8	2	1	..	..	..	..	..	..	..	..	..	..	..	0·789
	28. viii	38	..	..	5	20	11	2	..	..	..	..	..	..	..	..	..	..	..	..	0·787
	11. ix	12	..	..	6	4	2	..	..	..	..	..	..	..	..	..	..	..	..	..	0·752
IV	4. iv	24	..	..	..	..	..	3	15	5	1	..	..	..	..	..	..	..	..	..	0·781
	10. iv	65	..	..	..	..	..	15	23	26	1	..	..	..	..	..	..	..	..	..	0·788
	17. iv	27	..	..	..	..	..	..	19	6	2	..	..	..	..	..	..	..	..	..	0·786
	24. iv	60	..	..	..	..	..	9	35	14	2	..	..	..	..	..	..	..	..	..	0·777
	1. v	34	..	..	..	..	..	7	19	7	1	..	..	..	..	..	..	..	..	..	0·771
	8. v	28	..	..	..	..	..	12	15	1	..	..	..	..	..	..	..	..	..	..	0·753
	15. v	62	..	..	..	..	15	43	4	..	..	..	..	..	..	..	..	..	..	..	0·712
	22. v	40	..	..	..	1	4	24	10	1	..	..	..	..	..	..	..	..	..	..	0·727
	5. vi	39	..	..	..	4	14	18	3	..	..	..	..	..	..	..	..	..	..	..	0·700
	12. vi	6	..	..	..	3	3	..	..	..	..	..	..	..	..	..	..	..	..	..	0·661
	19. vi	9	..	..	..	2	6	1	..	..	..	..	..	..	..	..	..	..	..	..	
	26. vi	6	..	..	..	2	3	1	..	..	..	..	..	..	..	..	..	..	..	..	
	3. vii	97	..	..	4	44	41	8	..	..	..	..	..	..	..	..	..	..	..	..	0·645
	10. vii	122	..	..	3	92	26	1	..	..	..	..	..	..	..	..	..	..	..	..	0·624
	17. vii	73	..	3	44	25	1	..	..	..	..	..	..	..	..	..	..	..	..	..	0·581
	24. vii	70	..	3	33	31	3	..	..	..	..	..	..	..	..	..	..	..	..	..	0·591
	31. vii	80	..	2	50	28	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·584
	7. viii	81	..	5	62	14	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·570
	14. viii	89	..	..	41	46	2	..	..	..	..	..	..	..	..	..	..	..	..	..	0·595
	21. viii	63	..	..	9	34	19	1	..	..	..	..	..	..	..	..	..	..	..	..	0·624
	28. viii	62	..	..	15	39	8	..	..	..	..	..	..	..	..	..	..	..	..	..	0·609
	11. ix	52	..	..	8	35	7	2	..	..	..	..	..	..	..	..	..	..	..	..	0·619
III	27. iii	13	..	..	1	12	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·607
	4. iv	15	..	..	..	11	4	..	..	..	..	..	..	..	..	..	..	..	..	..	0·630
	10. iv	44	..	..	6	32	6	..	..	..	..	..	..	..	..	..	..	..	..	..	0·619
	17. iv	34	..	..	..	19	15	..	..	..	..	..	..	..	..	..	..	..	..	..	0·641
	24. iv	77	..	..	4	53	17	3	..	..	..	..	..	..	..	..	..	..	..	..	0·630
	1. v	10	..	..	1	8	1	..	..	..	..	..	..	..	..	..	..	..	..	..	0·616
	8. v	35	..	2	20	12	1	..	..	..	..	..	..	..	..	..	..	..	..	..	0·585
	15. v	91	..	1	58	32	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·581
	22. v	14	..	..	9	5	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·585
	29. v	23	..	..	14	9	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·586
	5. vi	63	..	14	41	8	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·559
	12. vi	22	..	15	7	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·532
	19. vi	10	..	5	5	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·543
	26. vi	22	..	8	13	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·554
	3. vii	64	1	30	28	5	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·541
	10. vii	47	4	38	5	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·516
	17. vii	87	41	45	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·489
	24. vii	43	25	18	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·484
	31. vii	91	24	67	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·497
	7. viii	33	17	16	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·487
	14. viii	45	12	33	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·502
	21. viii	83	1	64	18	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·517
	28. viii	35	8	25	2	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·512
	11. ix	32	2	22	8	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·523

TABLE XIV. SIZE OF *TEMORA LONGICORNIS* IN MM.

Stage	Date	No.	0·383–0·435	0·435–0·487	0·487–0·539	0·539–0·592	0·592–0·644	0·644–0·696	0·696–0·748	0·748–0·800	0·800–0·853	0·853–0·905	0·905–0·957	0·957–1·009	1·009–1·061	1·061–1·114	1·114–1·166	1·166–1·218	1·218–1·270	1·270–1·322	Median size
♂	10. iv	92	..	..	..	..	..	2	8	17	31	17	7	6	3	1	..	..	..	..	0·837
	17. iv	24	..	..	..	..	..	1	..	2	1	10	6	2	1	1	..	..	..	..	0·898
	24. iv	24	..	..	..	..	..	..	..	2	2	6	3	6	3	1	1	..	..	..	0·937
	1. v	59	..	..	..	..	..	..	2	6	9	9	18	5	8	2	..	..	..	..	0·919
	8. v	88	..	..	..	..	..	..	..	3	14	34	25	6	1	4	..	..	1	..	0·895
	15. v	21	..	..	..	..	..	..	..	1	8	5	4	1	..	1	1	..	..	..	0·887
	22. v	61	..	..	..	..	..	..	2	13	18	13	9	4	..	..	1	1	..	..	0·847
	29. v	14	..	..	..	..	..	..	1	3	3	3	2	..	2	..	..	..	..	..	0·862
	5. vi	29	..	..	..	..	..	1	6	7	11	4	..	..	..	..	..	..	..	..	0·803
	12. vi	15	..	..	..	..	..	..	7	6	2	..	..	..	..	..	..	..	..	..	0·754
	19. vi	24	..	..	..	..	..	..	7	5	3	3	3	2	..	..	..	1	..	..	0·803
	26. vi	8	..	..	..	..	..	..	3	5	..	..	..	..	..	..	..	..	..	..	..
	3. vii	69	..	..	..	..	8	14	31	11	3	2	..	..	..	..	..	..	..	..	0·716
	10. vii	72	..	..	..	2	20	37	7	5	..	..	1	..	..	..	..	..	..	..	0·657
	17. vii	26	..	..	..	6	14	6	..	..	..	..	..	..	..	..	..	..	..	..	0·625
	24. vii	41	..	..	..	12	12	7	6	2	2	..	..	..	..	..	..	..	..	..	0·630
	31. vii	56	..	..	2	27	21	6	..	..	..	..	..	..	..	..	..	..	..	..	0·591
	7. viii	77	..	..	1	33	32	9	1	1	..	..	..	..	..	..	..	..	..	..	0·597
	14. viii	44	..	..	1	14	26	3	..	..	..	..	..	..	..	..	..	..	..	..	0·601
	21. viii	68	..	..	..	1	22	31	13	1	..	..	..	..	..	..	..	..	..	..	0·669
	28. viii	51	..	..	..	..	11	23	12	3	2	..	..	..	..	..	..	..	..	..	0·678
	11. ix	54	..	..	..	9	23	15	7	..	..	..	..	..	..	..	..	..	..	..	0·635
♀	10. iv	85	..	..	..	..	..	1	3	2	12	21	11	9	10	10	3	3	..	..	0·922
	17. iv	25	..	..	..	..	..	..	..	..	..	3	1	6	4	3	5	2	1	..	1·036
	24. iv	13	..	..	..	..	..	..	..	..	..	1	1	1	3	3	3	1	..	..	1·067
	1. v	33	..	..	..	..	..	..	..	..	5	3	9	5	3	5	1	1	..	1	0·957
	8. v	60	..	..	..	..	..	..	..	..	7	10	13	13	8	3	3	2	1	..	0·960
	15. v	10	..	..	..	..	..	..	1	..	..	1	..	4	2	1	1	..	..	..	1·001
	22. v	21	..	..	..	..	..	..	..	5	6	5	2	1	..	1	1	..	..	..	0·852
	29. v	14	..	..	..	..	..	..	1	2	6	..	3	2	..	..	..	..	..	..	0·839
	5. vi	13	..	..	..	..	..	1	1	4	3	..	4	..	..	..	..	..	..	..	0·817
	19. vi	23	..	..	..	..	..	..	1	5	7	3	5	1	..	..	..	..	..	..	0·844
	3. vii	37	..	..	..	..	1	5	11	9	8	2	..	1	..	..	..	..	..	..	0·757
	10. vii	57	..	..	..	2	7	22	17	5	2	2	..	..	..	..	..	..	..	..	0·693
	17. vii	13	..	..	..	1	8	4	..	..	..	..	..	..	..	..	..	..	..	..	0·632
	24. vii	26	..	..	2	3	10	7	1	3	..	..	..	..	..	..	..	..	..	..	0·630
	31. vii	35	..	..	3	9	15	8	..	..	..	..	..	..	..	..	..	..	..	..	0·611
	7. viii	64	..	..	1	22	29	10	1	1	..	..	..	..	..	..	..	..	..	..	0·604
	14. viii	56	..	..	1	18	27	9	1	..	..	..	..	..	..	..	..	..	..	..	0·615
	21. viii	80	..	..	..	5	27	29	12	5	2	..	..	..	..	..	..	..	..	..	0·657
	28. viii	58	..	..	..	..	1	22	18	15	2	..	..	..	..	..	..	..	..	..	0·709
	11. ix	32	..	..	..	6	12	9	5	..	..	..	..	..	..	..	..	..	..	..	0·638
♂ V	10. iv	55	..	..	..	..	1	3	20	17	12	2	..	..	..	..	..	..	..	..	0·758
	17. iv	12	..	..	..	..	..	..	1	4	6	..	1	..	..	..	..	..	..	..	0·809
	24. iv	10	..	..	..	..	..	..	..	7	1	2	..	..	..	..	..	..	..	..	0·781
	1. v	25	..	..	..	..	..	1	6	11	7	..	..	..	..	..	..	..	..	..	0·772
	8. v	41	..	..	..	..	1	4	17	14	5	..	..	..	..	..	..	..	..	..	0·746
	22. v	13	..	..	..	..	4	8	1	..	..	..	..	..	..	..	..	..	..	..	0·657
	5. vi	16	..	..	..	3	4	7	2	..	..	..	..	..	..	..	..	..	..	..	0·657
	19. vi	17	..	..	..	1	8	4	4	..	..	..	..	..	..	..	..	..	..	..	0·643
	3. vii	66	..	..	7	25	21	7	5	1	..	..	..	..	..	..	..	..	..	..	0·594
	10. vii	26	..	..	5	10	10	1	..	..	..	..	..	..	..	..	..	..	..	..	0·578
	17. vii	24	..	2	11	11	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·537
	24. vii	15	..	5	7	2	1	..	..	..	..	..	..	..	..	..	..	..	..	..	0·504
	31. vii	24	..	2	12	10	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·533
	7. viii	60	..	1	48	11	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·516
	14. viii	47	..	2	32	13	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·522
	21. viii	40	..	..	4	24	11	..	1	..	..	..	..	..	..	..	..	..	..	..	0·575
	28. viii	13	..	..	..	8	4	1	..	..	..	..	..	..	..	..	..	..	..	..	0·586
	11. ix	13	..	2	7	4	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·522

♀ V	10. iv	28	..	..	..	..	..	2	3	6	13	3	..	1	..	..	..	..	..	..	0·812
	17. and 24. iv	13	..	..	..	..	..	..	1	..	2	3	3	4	..	..	..	..	..	..	0·922
	1. v	15	..	..	..	..	..	1	1	4	6	3	..	..	..	..	..	..	..	..	0·825
	8. v	32	..	..	..	..	..	..	7	12	8	4	1	..	..	..	..	..	..	..	0·793
	5 and 12. vi	13	..	..	..	..	3	4	3	2	1	..	..	..	..	..	..	..	..	..	0·696
	19. vi	17	..	..	..	1	5	6	2	3	..	..	..	..	..	..	..	..	..	..	0·657
	3. vii	41	..	..	4	17	13	7	..	..	..	..	..	..	..	..	..	..	..	..	0·591
	10. vii	32	..	..	6	13	13	..	..	..	..	..	..	..	..	..	..	..	..	..	0·583
	17. vii	17	..	2	8	5	2	..	..	..	..	..	..	..	..	..	..	..	..	..	0·536
	24. vii	14	..	2	5	5	2	..	..	..	..	..	..	..	..	..	..	..	..	..	0·548
	31. vii	24	..	..	12	10	2	..	..	..	..	..	..	..	..	..	..	..	..	..	0·541
	7. viii	64	..	10	38	16	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·512
	14. viii	38	..	3	20	11	3	1	..	..	..	..	..	..	..	..	..	..	..	..	0·531
	21. viii	39	..	..	3	13	18	5	..	..	..	..	..	..	..	..	..	..	..	..	0·604
	28. viii	14	..	..	..	5	7	2	..	..	..	..	..	..	..	..	..	..	..	..	0·613
	11. ix	10	..	..	2	6	2	..	..	..	..	..	..	..	..	..	..	..	..	..	0·581
IV	10. iv	40	..	..	..	2	16	15	7	..	..	..	..	..	..	..	..	..	..	..	0·657
	17. iv	14	..	..	..	..	2	6	3	2	1	..	..	..	..	..	..	..	..	..	0·688
	24. iv	19	..	..	..	1	4	9	4	1	..	..	..	..	..	..	..	..	..	..	0·670
	1. v	33	..	..	..	1	13	19	..	..	..	..	..	..	..	..	..	..	..	..	0·653
	8. v	57	..	..	..	4	33	17	3	..	..	..	..	..	..	..	..	..	..	..	0·626
	5. vi	29	..	..	6	18	4	1	..	..	..	..	..	..	..	..	..	..	..	..	0·555
	12. vi	8	..	..	4	1	3	..	..	..	..	..	..	..	..	..	..	..	..	..	..
	19. vi	35	..	..	12	19	4	..	..	..	..	..	..	..	..	..	..	..	..	..	0·548
	26. vi	10	..	1	3	4	2	..	..	..	..	..	..	..	..	..	..	..	..	..	0·577
♂ IV	3. vii	47	..	8	28	11	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·517
	10. vii	23	..	9	13	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·493
	17. vii	13	2	10	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·458
	24. vii	18	4	12	2	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·449
	31. vii	20	..	14	6	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·480
	7. viii	51	1	48	2	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·458
	14. viii	58	5	44	9	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·465
	21. viii	31	..	4	18	9	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·519
	28. viii	19	..	5	10	3	1	..	..	..	..	..	..	..	..	..	..	..	..	..	0·515
	11. ix	17	..	6	11	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·497
♀ IV	3. vii	53	..	8	29	13	3	..	..	..	..	..	..	..	..	..	..	..	..	..	0·526
	10. vii	11	..	3	5	3	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·514
	17. vii	23	5	15	3	..	..	..	..	..	..	..	..		..	..	..	..	..	..	0·455
	24. vii	14	1	8	4	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·465
	31. vii	24	..	15	9	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·481
	7. viii	44	1	36	7	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·466
	14. viii	56	3	45	8	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·467
	21. viii	38	..	9	23	6	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·506
	28. viii	8	..	..	6	2	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
	11. ix	15	..	3	10	2	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·514
III	13. iii	19	2	16	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·456
	27. iii	27	..	4	16	6	1	..	..	..	..	..	..	..	..	..	..	..	..	..	0·522
	4. iv	11	..	..	..	8	3	..	..	..	..	..	..	..	..	..	..	..	..	..	0·570
	10. iv	35	..	1	11	17	6	..	..	..	..	..	..	..	..	..	..	..	..	..	0·560
	17. iv	25	..	..	1	17	7	..	..	..	..	..	..	..	..	..	..	..	..	..	0·579
	24. iv	18	..	..	8	8	2	..	..	..	..	..	..	..	..	..	..	..	..	..	0·552
	1. v	67	..	..	25	39	3	..	..	..	..	..	..	..	..	..	..	..	..	..	0·548
	8. v	39	..	1	30	8	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·520
	5. vi	31	2	20	7	2	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·478
	12. vi	15	5	9	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·456
	19. vi	39	5	33	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·455
	26. vi	6	1	4	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
	3. vii	65	3	47	15	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·475
	10. vii	36	10	23	3	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·450
	17. vii	31	28	3	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·419
	24. vii	27	24	3	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·410
	31. vii	48	19	29	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·440
	7. viii	59	48	11	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·425
	14. viii	102	84	18	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·419
	21. viii	75	13	59	3	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·449
	28. viii	36	4	32	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·456
	11. ix	30	3	26	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0·453

TABLE XV. SIZE OF *ACARTIA CLAUSI* IN MM.

Stage	Date	No.	0·487– 0·539	0·539– 0·592	0·592– 0·644	0·644– 0·696	0·696– 0·748	0·748– 0·800	0·800– 0·853	0·853– 0·905	0·905– 0·957	0·957– 1·009	1·009– 1·061	1·061– 1·114	1·114– 1·166	1·166– 1·218	1·218– 1·270	Median size
♂	24. iv	25	..	..	..	..	..	..	..	..	..	21	4	..	..	..	..	0·987
	1. v	24	..	..	..	..	..	..	..	..	2	15	7	..	..	..	..	0·998
	8. v	35	..	..	..	..	..	..	..	..	7	18	10	..	..	..	..	0·994
	15. v	10	..	..	..	..	..	1	..	..	4	5	..	..	..	..	..	0·959
	22. v	41	..	..	..	..	..	..	..	1	21	18	1	..	..	..	..	0·955
	29. v	13	..	..	..	..	..	..	..	..	10	2	1	..	..	..	..	0·939
	5. vi	15	..	..	..	..	..	..	..	3	9	3	..	..	..	..	..	0·934
	12. vi	51	..	..	..	..	..	..	1	33	15	2	..	..	..	..	..	0·893
	19. vi	68	..	..	..	..	..	..	1	31	33	3	..	..	..	..	..	0·907
	26. vi	80	..	..	..	..	..	..	2	63	14	1	..	..	..	..	..	0·889
	3. vii	164	..	..	..	..	..	..	12	132	20	..	..	..	..	..	..	0·885
	10. vii	134	..	..	..	..	..	..	6	98	29	1	..	..	..	..	..	0·887
	17. vii	139	..	..	..	..	..	..	37	90	12	..	..	..	..	..	..	0·866
	24. vii	104	..	..	..	..	..	2	50	48	4	..	..	..	..	..	..	0·853
	31. vii	131	..	..	..	..	..	4	95	29	3	..	..	..	..	..	..	0·833
	7. viii	101	..	..	..	..	..	10	79	11	1	..	..	..	..	..	..	0·827
	14. viii	77	..	..	..	..	..	13	62	2	..	..	..	..	..	..	..	0·819
	21. viii	89	..	..	1	..	..	9	71	8	..	..	..	..	..	..	..	0·828
	28. viii	84	..	..	..	..	..	3	72	9	..	..	..	..	..	..	..	0·833
	11. ix	80	..	..	..	..	..	4	70	6	..	..	..	..	..	..	..	0·828
	2. x	103	..	..	..	..	..	1	58	44	..	..	..	..	..	..	..	0·848
♀	17. i	17	..	..	..	..	..	1	3	7	6	..	..	..	..	..	..	0·870
	23. i	28	..	..	1	..	..	1	5	14	6	1	..	..	..	..	..	0·874
	30. i	13	..	..	..	..	..	..	3	9	1	..	..	..	..	..	..	0·879
	6. ii	25	..	..	..	..	..	..	5	15	4	1	..	..	..	..	..	0·882
	13. ii	13	..	..	..	1	..	..	6	5	..	1	..	..	..	..	..	0·853
	24. iv	33	..	..	..	..	..	..	..	1	..	..	..	1	15	16	..	1·168
	1. v	27	..	..	..	..	..	..	..	..	1	1	..	6	9	9	1	1·148
	8. v	28	..	..	..	..	..	..	..	..	..	..	3	8	9	8	..	1·138
	15. v	21	..	..	..	..	..	..	..	..	..	..	7	5	7	2	..	1·105
	22. v	19	..	..	..	..	..	..	..	1	..	..	3	10	4	1	..	1·089
	29. v	35	..	..	..	..	..	..	..	..	..	2	11	9	7	6	..	1·076
	5. vi	17	..	..	..	..	..	..	..	..	..	3	2	9	3	..	..	1·088
	12. vi	61	..	..	..	..	..	..	..	..	..	8	30	14	7	2	..	1·049
	19. vi	60	..	..	..	..	..	..	..	..	..	25	30	4	1	..	..	1·018
	26. vi	86	..	..	..	..	..	..	..	..	4	38	37	6	..	1	..	1·011
	3. vii	121	..	..	..	..	..	..	..	..	12	59	48	1	1	..	..	1·004
	10. vii	126	..	..	..	..	..	..	..	..	27	62	32	5	..	..	..	0·989
	17. vii	110	..	..	..	..	..	..	..	7	57	29	16	1	..	..	..	0·952
	24. vii	119	..	..	..	..	..	..	4	38	52	20	5	..	..	..	..	0·919
	31. vii	93	..	..	..	..	..	..	11	50	25	7	..	..	..	..	..	0·895
	7. viii	108	..	..	..	..	..	..	10	71	24	3	..	..	..	..	..	0·885
	14. viii	103	..	..	..	..	..	..	17	63	19	3	1	..	..	..	..	0·883
	21. viii	94	..	..	..	..	..	1	29	60	3	1	..	..	..	..	..	0·887
	28. viii	111	..	..	..	..	..	..	16	68	25	2	..	..	..	..	..	0·888
	11. ix	91	..	..	..	..	..	2	15	53	21	..	..	..	..	..	..	0·875
	2. x	79	..	..	..	..	..	1	8	39	29	2	..	..	..	..	..	0·894
♂ V	24. iv	9	..	..	..	..	..	..	1	8	..	..	..	..	..	..	..	0·891
	22. v	9	..	..	..	..	..	..	7	2	..	..	..	..	..	..	..	0·845
	5. vi	30	..	..	..	..	..	7	23	..	..	..	..	..	..	..	..	0·811
	12. vi	35	..	..	..	..	1	16	15	2	1	..	..	..	..	..	..	0·803
	19. vi	40	..	..	..	..	1	28	11	..	..	..	..	..	..	..	..	0·792
	26. vi	22	..	..	..	..	..	7	15	..	..	..	..	..	..	..	..	0·810
	3. vii	48	..	..	..	..	1	31	16	..	..	..	..	..	..	..	..	0·792
	10. vii	124	..	..	..	..	3	98	23	..	..	..	..	..	..	..	..	0·783
	17. vii	79	..	..	..	..	21	55	3	..	..	..	..	..	..	..	..	0·760
	24. vii	72	..	..	..	..	31	39	2	..	..	..	..	..	..	..	..	0·752
	31. vii	73	..	..	..	..	38	35	..	..	..	..	..	..	..	..	..	0·748
	7. viii	61	1	..	..	..	40	20	..	..	..	..	..	..	..	..	..	0·738
	14. viii	51	..	..	..	..	23	28	..	..	..	..	..	..	..	..	..	0·750
	21. viii	40	..	..	..	..	10	30	..	..	..	..	..	..	..	..	..	0·760
	28. viii	87	..	..	..	..	20	66	1	..	..	..	..	..	..	..	..	0·764
	11. ix	60	..	..	..	..	16	44	..	..	..	..	..	..	..	..	..	0·759
	2. x	66	..	..	..	..	4	52	10	..	..	..	..	..	..	..	..	0·786

♀ V	24. iv	8	..	..	..	..	..	..	..	1	3	4	..	..	..	..	..	0·960
	22. v	18	..	..	..	..	..	..	1	12	5	..	..	..	..	..	..	0·889
	5. vi	18	..	..	..	..	4	..	2	7	5	..	..	..	..	..	..	0·868
	12. vi	37	..	..	..	..	1	1	11	23	1	..	..	..	..	..	..	0·862
	19. vi	45	..	..	..	..	1	4	28	12	..	..	..	..	..	..	..	0·833
	26. vi	34	..	..	..	..	..	1	9	24	..	..	..	..	..	..	..	0·864
	3. vii	67	..	..	..	..	..	7	41	19	..	..	..	..	..	..	..	0·833
	10. vii	126	..	..	..	..	..	14	106	6	..	..	..	..	..	..	..	0·825
	17. vii	72	..	..	..	..	4	45	21	2	..	..	..	..	..	..	..	0·788
	24. vii	107	..	..	..	..	31	60	16	..	..	..	..	..	..	..	..	0·762
	31. vii	72	..	..	..	1	27	43	1	..	..	..	..	..	..	..	..	0·756
	7. viii	89	..	..	..	1	33	54	1	..	..	..	..	..	..	..	..	0·753
	14. viii	58	..	..	..	..	17	41	..	..	..	..	..	..	..	..	..	0·760
	21. viii	67	..	..	..	..	12	40	15	..	..	..	..	..	..	..	..	0·782
	28. viii	87	..	..	..	1	17	60	9	..	..	..	..	..	..	..	..	0·773
	11. ix	91	..	..	..	..	28	62	1	..	..	..	..	..	..	..	..	0·760
	2. x	62	..	..	..	..	2	21	39	..	..	..	..	..	..	..	..	0·807
♂ IV	24. iv	19	..	..	2	..	9	8	..	..	..	..	..	..	..	..	..	0·746
	5. vi	43	..	..	..	21	21	1	..	..	..	..	..	..	..	..	..	0·697
	12. vi	57	..	..	..	34	23	..	..	..	..	..	..	..	..	..	..	0·691
	19. vi	41	..	..	1	36	6	..	..	..	..	..	..	..	..	..	..	0·677
	26. vi	20	..	..	..	15	5	..	..	..	..	..	..	..	..	..	..	0·688
	3. vii	23	..	..	..	19	4	..	..	..	..	..	..	..	..	..	..	0·674
	10. vii	70	..	..	..	64	6	..	..	..	..	..	..	..	..	..	..	0·673
	17. vii	65	..	..	25	39	1	..	..	..	..	..	..	..	..	..	..	0·649
	24. vii	50	..	..	36	13	1	..	..	..	..	..	..	..	..	..	..	0·635
	31. vii	49	..	..	31	17	1	..	..	..	..	..	..	..	..	..	..	0·638
	7. viii	46	..	..	33	13	..	..	..	..	..	..	..	..	..	..	..	0·636
	14. viii	28	..	..	13	15	..	..	..	..	..	..	..	..	..	..	..	0·646
	21. viii	55	..	1	16	38	..	..	..	..	..	..	..	..	..	..	..	0·652
	28. viii	53	..	..	15	38	..	..	..	..	..	..	..	..	..	..	..	0·652
	11. ix	49	..	..	11	38	..	..	..	..	..	..	..	..	..	..	..	0·653
	2. x	37	..	..	2	32	3	..	..	..	..	..	..	..	..	..	..	0·675
♀ IV	24. iv	11	..	..	..	..	..	8	3	..	..	..	..	..	..	..	..	0·793
	5. vi	26	..	..	..	..	26	..	..	..	..	..	..	..	..	..	..	0·721
	12. vi	56	..	..	..	16	40	..	..	..	..	..	..	..	..	..	..	0·709
	19. vi	47	..	..	1	31	15	..	..	..	..	..	..	..	..	..	..	0·686
	26. vi	22	..	..	..	2	20	..	..	..	..	..	..	..	..	..	..	0·713
	3. vii	46	..	..	1	23	21	1	..	..	..	..	..	..	..	..	..	0·696
	10. vii	74	..	..	..	57	17	..	..	..	..	..	..	..	..	..	..	0·685
	17. vii	42	..	..	12	28	2	..	..	..	..	..	..	..	..	..	..	0·653
	24. vii	62	..	..	34	27	1	..	..	..	..	..	..	..	..	..	..	0·642
	31. vii	77	..	..	44	33	..	..	..	..	..	..	..	..	..	..	..	0·641
	7. viii	69	..	..	44	25	..	..	..	..	..	..	..	..	..	..	..	0·638
	14. viii	34	..	..	13	21	..	..	..	..	..	..	..	..	..	..	..	0·648
	21. viii	56	..	..	14	39	3	..	..	..	..	..	..	..	..	..	..	0·660
	28. viii	75	..	..	29	45	1	..	..	..	..	..	..	..	..	..	..	0·650
	11. ix	56	..	..	21	34	2	..	..	..	..	..	..	..	..	..	..	0·656
	2. x	53	..	..	1	42	10	..	..	..	..	..	..	..	..	..	..	0·685
III	24. iv	15	..	..	3	12	..	..	..	..	..	..	..	..	..	..	..	0·659
	29. v	24	..	1	23	..	..	..	..	..	..	..	..	..	..	..	..	0·619
	5. vi	75	..	12	63	..	..	..	..	..	..	..	..	..	..	..	..	0·610
	12. vi	108	..	80	28	..	..	..	..	..	..	..	..	..	..	..	..	0·583
	19. vi	123	2	105	16	..	..	..	..	..	..	..	..	..	..	..	..	0·577
	26. vi	50	..	34	16	..	..	..	..	..	..	..	..	..	..	..	..	0·585
	3. vii	81	..	55	26	..	..	..	..	..	..	..	..	..	..		..	0·584
	10. vii	69	1	59	9	..	..	..	..	..	..	..	..	..	..	..	..	0·577
	17. vii	125	16	107	2	..	..	..	..	..	..	..	..	..	..	..	..	0·551
	24. vii	73	27	46	..	..	..	..	..	..	..	..	..	..	..	..	..	0·544
	31. vii	72	8	64	..	..	..	..	..	..	..	..	..	..	..	..	..	0·559
	7. viii	45	13	32	..	..	..	..	..	..	..	..	..	..	..	..	..	0·546
	14. viii	65	4	61	..	..	..	..	..	..	..	..	..	..	..	..	..	0·553
	21. viii	60	2	58	..	..	..	..	..	..	..	..	..	..	..	..	..	0·562
	28. viii	66	11	54	1	..	..	..	..	..	..	..	..	..	..	..	..	0·552
	1. ix	59	3	53	3	..	..	..	..	..	..	..	..	..	..	..	..	0·568
	2. x	57	..	50	7	..	..	..	..	..	..	..	..	..	..	..	..	0·574

TABLE XVI. SIZE OF *OITHONA SIMILIS* IN MM.

Stage	Date	No.	0·313– 0·348	0·348– 0·383	0·383– 0·418	0·418– 0·452	0·452– 0·487	0·487– 0·522	0·522– 0·557	0·557– 0·592	0·592– 0·626	0·626– 0·661	Median size
♂	20. ii	8	..	..	..	..	..	5	3	..	..	..	..
	27. ii	23	..	..	..	..	..	12	11	..	..	..	0·522
	7. iii	26	..	..	..	..	..	9	15	2	..	..	0·528
	13. iii	9	..	..	..	..	..	1	8	..	..	..	0·539
	20. iii	15	..	..	..	..	..	4	9	2	..	..	0·542
	4. iv	12	..	..	..	..	..	..	7	5	..	..	0·554
	10. iv	37	..	..	..	..	..	1	17	19	..	..	0·559
	17. iv	34	..	..	..	..	..	1	20	13	..	..	0·552
	24. iv	46	..	..	..	..	..	..	21	25	..	..	0·559
	1. v	65	..	..	..	..	..	2	41	22	..	..	0·550
	8. v	57	..	..	..	..	..	3	44	10	..	..	0·548
	15. v	19	..	..	..	..	..	4	10	5	..	..	0·532
	22. v	14	..	..	..	..	..	1	13	..	..	..	0·538
	29. v	32	..	..	..	..	..	4	27	1	..	..	0·537
	5. vi	49	..	..	..	..	..	3	37	9	..	..	0·542
	12. vi	94	..	..	..	..	..	5	65	24	..	..	0·548
	19. vi	82	..	..	..	..	..	3	67	12	..	..	0·546
	26. vi	90	..	..	..	..	..	14	75	1	..	..	0·534
	3. vii	85	..	..	..	..	..	36	49	..	..	..	0·525
	10. vii	91	..	..	..	..	..	21	70	..	..	..	0·531
	17. vii	115	..	..	..	..	..	22	92	1	..	..	0·530
	24. vii	88	..	..	..	..	..	50	38	..	..	..	0·520
	31. vii	95	..	..	..	..	..	72	23	..	..	..	0·516
	7. viii	46	..	..	..	..	5	40	1	..	..	..	0·499
	14. viii	40	..	..	..	..	6	33	1	..	..	..	0·496
	21. viii	68	..	..	..	..	6	61	1	..	..	..	0·500
	28. viii	67	..	..	..	..	37	30	..	..	..	..	0·486
	11. ix	71	..	..	..	..	11	60	..	..	..	..	0·498
	2. x	72	..	..	..	..	6	65	1	..	..	..	0·500
♀	17. i	123	..	..	..	..	3	49	67	4	..	..	0·525
	23. i	194	..	..	..	..	2	105	83	3	1	..	0·521
	30. i	126	..	..	..	..	4	66	55	1	..	..	0·518
	6. ii	97	..	..	..	..	..	35	60	2	..	..	0·528
	13. ii	83	..	..	..	..	2	54	23	4	..	..	0·517
	20. ii	67	..	..	..	..	1	26	34	6	..	..	0·526
	27. ii	88	..	..	..	..	..	32	50	6	..	..	0·529
	7. iii	71	..	..	..	..	..	30	34	7	..	..	0·526
	13. iii	73	..	..	..	..	..	23	40	10	..	..	0·530
	20. iii	69	..	..	..	..	..	21	37	8	3	..	0·534
	27. iii	39	..	..	..	..	..	16	16	7	..	..	0·528
	4. iv	126	..	..	..	..	..	31	52	30	13	..	0·539
	10. iv	69	..	..	..	..	1	12	29	12	15	..	0·546
	17. iv	105	..	..	..	..	1	7	35	21	40	1	0·574
	24. iv	82	..	..	..	..	..	3	6	34	38	1	0·590
	1. v	97	..	..	..	..	..	2	10	36	45	4	0·593
	8. v	85	..	..	..	..	1	3	15	35	30	1	0·581
	15. v	69	..	..	..	..	..	2	26	33	8	..	0·563
	22. v	77	..	..	..	..	..	4	23	32	16	2	0·569
	29. v	85	..	..	..	..	..	2	19	49	12	3	0·570
	5. vi	95	..	..	..	..	..	4	26	54	10	1	0·568
	12. vi	103	..	..	..	..	..	1	28	62	12	..	0·571
	19. vi	112	..	..	..	..	..	1	27	73	10	1	0·571
	26. vi	91	..	..	..	..	..	2	34	50	5	..	0·563
	3. vii	98	..	..	..	..	..	1	54	37	6	..	0·554
	10. vii	91	..	..	..	..	..	..	41	46	4	..	0·560
	17. vii	94	..	..	..	..	..	4	61	25	4	..	0·547
	24. vii	74	..	..	..	..	..	17	48	9	..	..	0·535
	31. vii	91	..	..	..	..	..	27	58	6	..	..	0·530
	7. viii	78	..	..	..	..	..	52	25	1	..	..	0·517
	14. viii	61	..	..	..	..	..	45	16	..	..	..	0·515
	21. viii	95	..	..	..	..	2	46	47	..	..	..	0·522
	28. viii	65	..	..	..	..	2	41	22	..	..	..	0·517
	11. ix	60	..	..	..	..	..	44	16	..	..	..	0·516
	2. x	65	..	..	..	..	..	39	25	1	..	..	0·519
V	17. i	53	..	..	..	5	28	19	1	..	..	..	0·480
	23. i	49	..	..	..	..	30	18	1	..	..	..	0·482
	30. i	27	..	..	..	1	11	13	2	..	..	..	0·494
	6. ii	12	..	..	..	..	4	6	2	..	..	..	0·496
	13. ii	18	..	..	..	1	5	10	2	..	..	..	0·506
	20. ii	54	..	..	..	..	8	23	23	..	..	..	0·512
	27. ii	88	..	..	..	3	22	42	21	..	..	..	0·501
	7. iii	95	..	..	..	1	12	48	32	2	..	..	0·515
	13. iii	39	..	..	..	..	8	11	19	1	..	..	0·524
	20. iii	93	..	..	..	..	9	43	37	4	..	..	0·519
	27. iii	13	..	..	..	..	3	3	6	1	..	..	0·539
	4. iv	26	..	..	..	..	..	3	16	7	..	..	0·546
	10. iv	36	..	..	..	..	1	10	18	7	..	..	0·540
	17. iv	132	..	..	..	..	1	14	75	42	..	..	0·546
	24. iv	66	..	..	..	..	4	34	27	1	..	..	0·536
	1. v	107	..	..	..	..	6	44	51	6	..	..	0·524
	8. v	87	..	..	..	..	20	34	32	1	..	..	0·514
	15. v	81	..	..	..	1	22	39	19	..	..	..	0·501

TABLE XVI (*cont.*)

Stage	Date	No.	0·313–0·348	0·348–0·383	0·383–0·418	0·418–0·452	0·452–0·487	0·487–0·522	0·522–0·557	0·557–0·592	0·592–0·626	0·626–0·661	Median size
V	22. v	80	..	..	..	..	14	33	33	..	..	..	0·516
	29. v	109	..	..	..	..	2	40	67	..	..	..	0·527
	5. vi	101	..	..	..	..	3	46	51	1	..	..	0·523
	12. vi	97	..	..	..	..	1	35	60	1	..	..	0·528
	19. vi	113	..	..	..	..	12	51	50	..	..	..	0·519
	26. vi	72	..	..	..	..	5	33	34	..	..	..	0·521
	3. vii	82	..	..	..	..	7	41	34	..	..	..	0·518
	10. vii	98	..	..	..	..	30	42	26	..	..	..	0·501
	17. vii	94	..	..	..	..	42	42	10	..	..	..	0·494
	24. vii	101	..	..	..	7	44	48	2	..	..	..	0·487
	31. vii	108	..	..	..	2	53	49	4	..	..	..	0·487
	7. viii	75	..	..	..	6	42	27	..	..	..	..	0·474
	14. viii	68	..	..	..	8	35	25	..	..	..	..	0·479
	21. viii	107	..	..	..	6	47	52	2	..	..	..	0·488
	28. viii	64	..	..	..	11	24	29	..	..	..	..	0·481
	11. ix	60	..	..	..	7	27	26	..	..	..	..	0·480
	2. x	78	..	..	..	10	40	26	2	..	..	..	0·473
IV	17. i	28	..	1	13	14	..	..	..	..	..	..	0·419
	23. i	21	..	..	8	12	1	..	..	..	..	..	0·424
	30. i	15	..	..	3	10	2	..	..	..	..	..	0·435
	6. ii	10	..	..	4	4	2	..	..	..	..	..	0·427
	13. ii	8	..	..	1	4	3	..	..	..	..	..	..
	20. ii	68	..	..	4	43	21	..	..	..	..	..	0·441
	27. ii	67	..	..	2	49	16	..	..	..	..	..	0·441
	7. iii	67	..	..	1	38	28	..	..	..	..	..	0·449
	13. iii	36	..	..	1	24	11	..	..	..	..	..	0·446
	20. iii	56	..	..	2	16	37	1	..	..	..	..	0·461
	27. iii	11	..	..	..	6	5	..	..	..	..	..	0·452
	4. iv	27	..	..	..	1	22	4	..	..	..	..	0·474
	10. iv	57	..	..	..	3	44	10	..	..	..	..	0·476
	17. iv	77	..	..	..	3	66	8	..	..	..	..	0·474
	24. iv	54	..	..	..	17	35	2	..	..	..	..	0·462
	1. v	89	..	..	..	38	51	..	..	..	..	..	0·456
	8. v	68	..	..	6	43	19	..	..	..	..	..	0·444
	15. v	72	..	..	15	47	10	..	..	..	..	..	0·435
	22. v	84	..	..	10	49	25	..	..	..	..	..	0·443
	29. v	79	..	..	..	29	50	..	..	..	..	..	0·458
	5. vi	73	..	..	..	31	42	..	..	..	..	..	0·455
	12. vi	62	..	..	..	26	36	..	..	..	..	..	0·456
	19. vi	72	..	..	..	51	21	..	..	..	..	..	0·445
	26. vi	81	..	..	5	54	22	..	..	..	..	..	0·443
	3. vii	70	..	..	6	46	18	..	..	..	..	..	0·443
	10. vii	81	..	..	2	50	29	..	..	..	..	..	0·446
	17. vii	74	..	..	10	54	10	..	..	..	..	..	0·435
	24. vii	57	..	..	30	27	..	..	..	..	..	..	0·417
	31. vii	66	..	1	21	42	2	..	..	..	..	..	0·429
	7. viii	49	..	..	19	30	..	..	..	..	..	..	0·425
	14. viii	75	..	..	27	47	1	..	..	..	..	..	0·425
	21. viii	82	..	..	28	51	3	..	..	..	..	..	0·425
	28. viii	88	..	1	46	40	1	..	..	..	..	..	0·416
	11. ix	61	..	..	33	27	1	..	..	..	..	..	0·416
	2. x	77	..	..	25	50	2	..	..	..	..	..	0·427
III	17. i	19	1	16	2	..	..	..	..	..	..	..	0·371
	30. i	16	1	13	2	..	..	..	..	..	..	..	0·369
	6. ii	13	1	11	1	..	..	..	..	..	..	..	0·373
	20. ii	53	..	19	34	..	..	..	..	..	..	..	0·388
	27. ii	32	2	19	11	..	..	..	..	..	..	..	0·378
	7. iii	58	..	24	34	..	..	..	..	..	..	..	0·386
	13. iii	44	..	5	38	1	..	..	..	..	..	..	0·397
	20. iii	56	..	3	47	6	..	..	..	..	..	..	0·405
	27. iii	9	..	..	8	1	..	..	..	..	..	..	0·404
	4. iv	64	..	..	48	16	..	..	..	..	..	..	0·410
	10. iv	55	..	..	35	20	..	..	..	..	..	..	0·413
	17. iv	45	..	..	26	19	..	..	..	..	..	..	0·415
	24. iv	36	..	4	29	3	..	..	..	..	..	..	0·403
	1. v	65	..	5	59	1	..	..	..	..	..	..	0·398
	8. v	73	..	21	52	..	..	..	..	..	..	..	0·390
	15. v	65	..	45	20	..	..	..	..	..	..	..	0·376
	22. v	36	..	8	28	..	..	..	..	..	..	..	0·391
	29. v	104	..	2	85	17	..	..	..	..	..	..	0·408
	5. vi	88	..	3	78	7	..	..	..	..	..	..	0·404
	12. vi	63	..	6	56	1	..	..	..	..	..	..	0·395
	19. vi	75	..	21	53	1	..	..	..	..	..	..	0·392
	26. vi	86	..	28	58	..	..	..	..	..	..	..	0·389
	3. vii	57	..	11	46	..	..	..	..	..	..	..	0·392
	10. vii	71	..	14	57	..	..	..	..	..	..	..	0·392
	17. vii	66	..	29	37	..	..	..	..	..	..	..	0·385
	24. vii	87	1	61	25	..	..	..	..	..	..	..	0·377
	31. vii	64	..	33	31	..	..	..	..	..	..	..	0·382
	7. viii	65	..	54	11	..	..	..	..	..	..	..	0·373
	14. viii	59	1	41	17	..	..	..	..	..	..	..	0·375
	21. viii	68	..	50	18	..	..	..	..	..	..	..	0·376
	28. viii	54	1	47	6	..	..	..	..	..	..	..	0·369
	11. ix	52	2	48	2	..	..	..	..	..	..	..	0·365
	2. x	50	3	34	13	..	..	..	..	..	..	..	0·375

TABLE XVII. SIZE OF STAGES I AND II IN MM. ON 3 JULY

Species	Stage	No.	0·209–0·244	0·244–0·278	0·278–0·313	0·313–0·348	0·348–0·383	0·383–0·418	0·418–0·452	0·452–0·487	0·487–0·522	0·522–0·557	0·557–0·592	0·592–0·626	Median size
Pseudocalanus	I	83	..	..	..	..	1	35	40	7	..	..	..	..	0·422
,,	II	61	..	..	..	..	..	..	..	3	32	21	4	1	0·519
Microcalanus	I	28	26	2	..	..	..	..	..	..	..	..	..	..	0·226
,,	II	44	..	6	36	2	..	..	..	..	..	..	..	..	0·289
Centropages	I	39	..	..	3	19	17	..	..	..	..	..	..	..	0·346
,,	II	41	..	..	..	..	1	7	29	4	..	..	..	..	0·431
Temora	I	40	..	..	1	25	13	1	..	..	..	..	..	..	0·342
,,	II	36	..	..	..	..	9	24	2	1	..	..	..	..	0·398
Acartia	I	47	..	..	..	..	24	23	..	..	..	..	..	..	0·382
,,	II	45	..	..	..	..	..	3	24	16	2	..	..	..	0·483
Oithona	I	49	..	3	46	..	..	..	..	..	..	..	..	..	0·289
,,	II	32	..	..	..	11	21	..	..	..	..	..	..	..	0·353

THE THIXOTROPY AND DILATANCY OF A MARINE SOIL

By Garth Chapman, M.A.

From the Department of Zoology, Queen Mary College, London

(Text-figs. 1–6)

CONTENTS

INTRODUCTION AND HISTORICAL

In a previous paper (Chapman & Newell, 1947) attention was called to the importance to their inhabitants of the thixotropic* and dilatant properties of marine soils. It will be recalled that the property of dilatancy, shown by the whitening of wet sand under the footstep, was first described by Osborne Reynolds (1885), and has subsequently been investigated chiefly by Freundlich and his collaborators (Freundlich, 1935; Freundlich & Jones, 1936; Freundlich & Röder, 1938). Reynolds considered that the close packing of particles in a liquid medium was altered by an applied force so that the interstitial volume was increased and more liquid was drawn from the periphery into the dilatant mixture. By these changes the dilatant mass becomes harder and more resistant to shear. Freundlich & Röder described the relation between thixotropy and dilatancy. They considered that thixotropy could be described as a reduction in resistance with increased rate of shear as opposed to dilatancy, in which increased shearing force brings about an increased resistance. Thixo-

---

* The term *thixotropy* was originally used by Peterfi and Freundlich for the isothermal reversible sol-gel transformation shown by some colloidal solutions, but it has now come to be applied more generally and is used to denote a system which shows a decrease in viscosity upon agitation or a decreased resistance to shear when the rate of shear increases. For example, a suspension of fullers' earth in water liquefies on being shaken or on being stirred, but sets in a few seconds when the agitation stops. Many paints are thixotropic and flow easily and smoothly when they are being applied (whilst they are subject to shearing forces) but their viscosity increases enough when brushing stops for them not to 'run'. Some interesting aspects of the subject are dealt with in articles by Pryce-Jones (1946) and Boswell (1948).

tropic properties are shown by a variety of substances among which are clays whose particles are anisotropic, being rod-like or plate-like in shape. The range of concentration of solid particles to liquid is also important in influencing the behaviour of the suspension to shearing forces, and in their work on quartz particles (1–5 μ in diameter) in water Freundlich & Röder stated that dilatancy occurred only in the range 42–45 % by volume of the solid. Below 42 % the mixture remained fluid however rapidly it was stirred, whereas above 45 % it remained compact. They described a dilatancy viscometer for use with solid suspensions by means of which they investigated the thixotropic and dilatant properties of a number of mixtures. It was admitted, however, that the machine was difficult to use with suspensions of particles above 50 μ (0·05 mm.) in diameter. The dilatancy viscometer was described in detail by Röder (1939) in a paper in which is also set out the relation between particles and dispersion medium. Röder's apparatus and results have been criticized on technical grounds by Van Selms & Kruyt (1943), and another machine for the measurement of the consistency of plastic suspensions has been described by them in their investigation of the effect of a third phase on the rheology of suspensions of quartz particles and glass spheres in carbon tetrachloride (Kruyt & Van Selms, 1943*a*, *b*). It is not suitable for use with marine soils.

Freundlich & Juliusburger (1935) described an investigation into the thixotropy of quicksands and came to the conclusion that, whereas some quicksands have a larger clay content than neighbouring ordinary sands, this cannot be taken as a generalization and that other factors must be taken into account.

The soil of the Whitstable Flats. Clays, in general, are notably thixotropic, and it may be that even a small amount of clay is sufficient to alter the properties of suspensions of particles of larger size. Sand from the Flats at Whitstable in which *Arenicola marina* is so abundant can be said to possess quicksand or thixotropic properties, although to a much lesser extent than those soils which are recognized as true quicksands. The soil of the Flats is reasonably uniform for a distance of about 400 yd. between tidemarks and is characterized by having a sandy-coloured upper layer of about 1 in. in depth and a deeper layer of 6–12 in. in depth, black in colour but similar in particle-size composition. On exposure to the air this black sand becomes identical in appearance with that of the uppermost layer, the two layers being similar in all features except in the chemical composition of the iron compounds which they contain. A preliminary investigation showed that the soil consists largely of 'fine sand', as defined by Robinson (1932), of particle size between 0·2 and 0·02 mm. diameter with an admixture of 1–3 % of 'silt and clay' of particle size less than 0·02 mm. diameter. Eighty per cent. of the sand passes a 100-mesh sieve and therefore has a particle diameter of less than 0·12 mm. which, although above the upper limit of 0·05 mm. diameter given by Freundlich & Röder as suitable for use in the dilatancy viscometer, is not so widely different from their figure as to suggest that useful results might not be obtained by the use of their machine.

The interest in the present inquiry lies in the relation of the physical properties of marine soils to the habits of the animals which inhabit them. Some of the properties which appear to be of importance and which have been studied are the resistance to penetration, the thixotropic properties and their variations with changes of composition of the soil.

I am grateful for help at various times to Professor P. G. H. Boswell, F.R.S., Professor A. J. Grove, Dr G. E. Newell and Dr G. W. Scott-Blair.

The Measurement of Resistance to Penetration

For the easy testing of marine soils *in situ* the apparatus described by Chapman & Newell (1947) was used. This penetrometer was modified by the provision of a scale by which readings in the field were made easier to take. A diagram of the modified instrument is given in Fig. 1, from which it can be seen that when the slider or collar (*C*) is held in the hand, and the disk (*D*) placed upon the sand, pressures varying from zero upwards can be obtained. By calibrating the penetrometer against weights counterpoised on a balance the thrust exerted on the sand by the disk can be measured. A series of springs of different gauge steel wire give the instrument a considerable range. A graph of weight counterpoised against scale reading was made for each spring. This rather crude method of calibration had the advantage that the instrument was manipulated in the way in which it was used in the field when measurements were being made.

In use the instrument was held as nearly vertical as possible and was pressed gently into the soil, the reading on the scale being then noted. Ten or more readings were always made and a mean calculated, the pressure equivalent to the scale reading being then read off from the graph. The hardness of the soil is here expressed as grams per square centimetre necessary for penetration. It was fairly easy, with practice, to obtain a 'good' or close set of figures for any particular locality, but in order to do so it was necessary on occasions to discard readings, for example, when it was clear that the penetrating disk had struck a larger stone or had penetrated a worm burrow.

The measurements made with the penetrometer are correlated in this paper with other features of the soil such as water content or the burrowing speed of *Arenicola*. Accordingly, the results are set out in conjunction with details of the features with which a connexion was being sought and the results of the tests (expressed always as g./cm.^{2} necessary for the penetration of a disk of area 0·125 cm.^{2} to a depth of 3 cm.) will be found in the section dealing with the burrowing speed of the lugworm (p. 136). But, to anticipate briefly, both the hardness of the soil and the time taken by the lugworms to burrow was found to increase as the water content decreased.

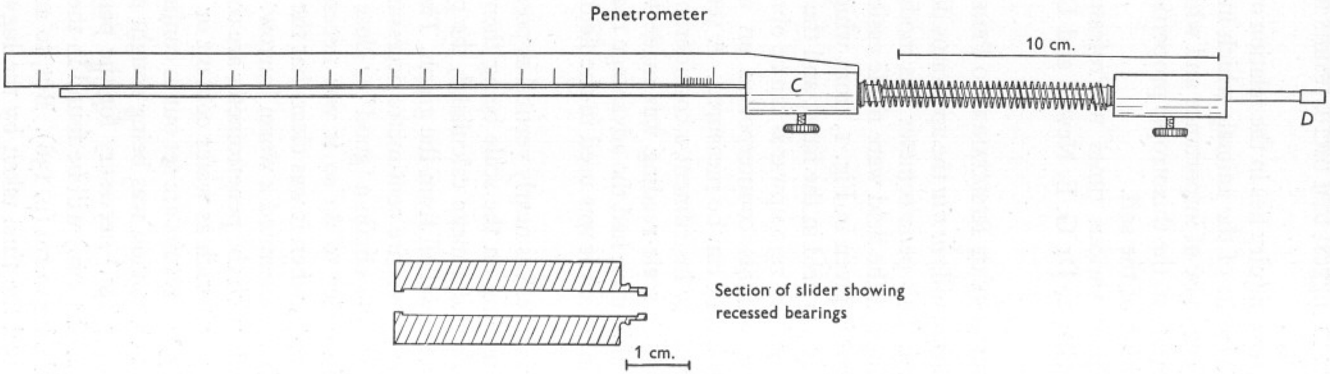


Fig. 1. The modified penetrometer. *C*, slider or collar. *D*, penetrating disk.

THE THIXOTROPY AND DILATANCY OF MUDDY SAND

One striking feature of the soil of the Flats is the difference between its physical properties when wet and when dry. For example, if water is slowly added to a sample of dry sand it becomes a darker brown as it is wetted. It is hard when touched with a glass rod. Small portions, made up of adhering particles, can be broken off. It does not appear to flow when it is tapped. In fact, it behaves almost as a friable solid.

As more water is added the material 'settles' when the vessel containing it is agitated so that it has a level, shiny but not plane, surface. There is, therefore, sufficient water to appear at the interstices of the superficial particles. When the mass is prodded with a glass rod the colour becomes lighter and the appearance no longer shiny but dull or matt. Its resistance to penetration increases as the rod is pushed in.

The addition of still more water causes the surface to become plane; there is a layer of water unbroken by particles. No lightening of the colour occurs when the mass is prodded nor does the surface become matt in appearance. Its resistance to prodding is smaller and does not increase as distortion occurs.

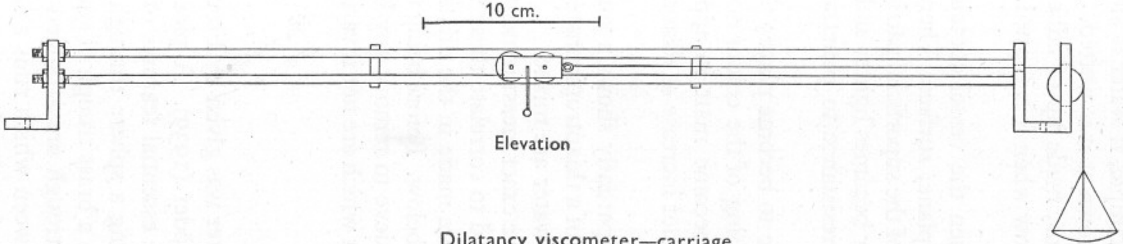
In other words, the mixture of sand and water apparently shows a variety of properties ranging from those of a dilatant to those of a thixotropic material, according to the proportions in which the sand and water are mixed.

An attempt was therefore made to obtain some more exact measurements of the thixotropic and dilatant properties of the sand and to correlate these with the mechanical analysis and water content. Tests were made in the dilatancy viscometer of Freundlich & Röder which is described below. Before being used the sand was passed through a 2 mm. round-holed sieve to remove any large particles such as shells which are found in the soil but which are not invariable constituents.

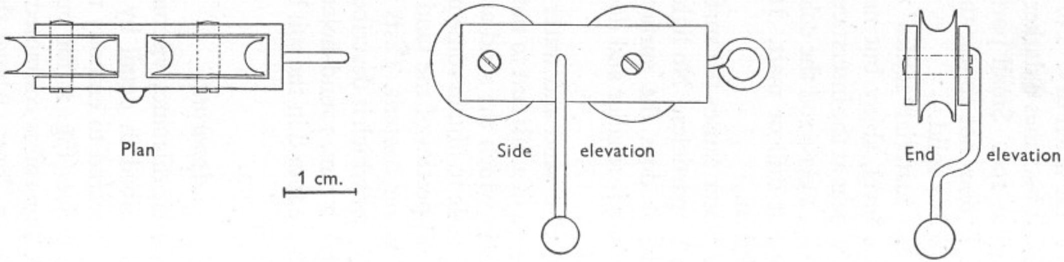
Apparatus

No detailed description of their dilatancy viscometer was given by Freundlich & Röder, but it was described in detail by Röder (1939). A piece of apparatus was made which appeared to embody the essential features of the machine described. It is a device (Fig. 2) for pulling a sphere through the substance to be investigated. The soil is contained in a brass trough of square section 1·6 cm. deep and 50 cm. long. Above the trough are arranged two brass guide rails, one vertically above the other, between which runs a small carriage. Fixed to this is a narrow shaft ending in a phosphor-bronze sphere of diameter 5 mm. which can thereby travel along the locus of the long axis of the trough. The construction of the carriage is also shown in Fig. 2. It is attached by a thread, running over a pulley at one end of the guide rails, to a pan for holding weights. The pulley, carriage wheels and guide rails are of

Dilatancy viscometer



Dilatancy viscometer—carriage



Dilatancy viscometer—trough

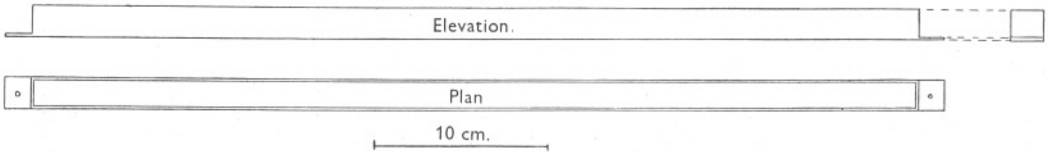


Fig. 2.

a high finish and are polished each time before use with household metal polish.

The time taken for the sphere to travel through a distance of 30 cm. was measured by a stop-watch to the nearest $\frac{1}{5}$th sec. Prior to making each run the soil was treated in a standard way, being tapped forty times on the bench and being left for 60 sec. before the test was begun. Even after using this standard preliminary treatment it was difficult to ensure that the soil was always in a 'natural' packing similar to that found in the sand of the undisturbed shore.

Results

The results obtained with this machine were plotted graphically as speed (ordinate) against weights placed in the pan. Ignoring the friction forces in the apparatus, the curve given by a Newtonian liquid (glycerol) is a straight line passing through the origin. According to Freundlich & Röder a thixotropic substance also gives a straight-line graph, but instead of passing through the origin it cuts the abscissa some distance to the right. They obtained this result using a suspension of quartz particles in carbon tetrachloride, a non-polar liquid, instead of water in which their quartz was dilatant. When once movement of the sphere begins in a thixotropic system its speed is proportional to weight as for a Newtonian liquid, but a minimum force is necessary before movement can begin, whereas with a perfect liquid the smallest applied force causes movement. (It would appear, however, that this 'ideal' curve for a thixotropic substance is not fully in accordance with the definition of thixotropy as decreased resistance to increased rate of shear.) Freundlich and Röder point out that dilatant substances do not give a straight-line graph but one which is a straight line only over the first part of the range of applied weights. Above a certain weight it flattens out so that no further increase in weight gives any increase in speed. In other words, when slow movement is taking place in dilatant systems—with small applied weights—their behaviour is nearly that of Newtonian liquids, but at a certain speed no further increase is possible without an incommensurate increase in applied weight. The form of the curves as they should appear according to Freundlich & Röder is shown in Fig. 3. 'A horizontal part of the curve,' they say, 'implying solid behaviour, occurs in thixotropic systems at zero rate of shear, i.e. at rest....Liquid behaviour is represented in both cases by a steep part of the curve; in thixotropic systems at a sufficiently high rate of shear..., in dilatant systems at rest and at small rates of shear.'

Preliminary tests showed that the behaviour of the soil was complex. For example, in a mixture of sand and water with a small amount of superfluous water on top and with a weight of 20 g. applied to the sphere, its speed through the soil was 0·05 cm./sec. on the first test after the trough was filled. After giving the trough forty taps and allowing the contents to settle for 60 sec., the speed rose to 3·0 cm./sec. After prodding the soil, as well as tapping it, the speed fell to 0·3 cm./sec., whereas on the fourth test, preceded only by the standard tapping procedure, the speed had risen to 0·6 cm./sec. Further tests along these lines confirmed these results which showed that it was essential for the soil to be treated in a standard way before each test because the 'particle structure' of the soil was altered by the passage of the sphere, the alteration being at a maximum in rather dry sand, in which a clear channel was left. With dry sand the channel did not disappear even after the standard tapping procedure. The results of some of the preliminary tests, using sand saturated with sea water, are shown graphically in Fig. 4. It will be seen that there is no hint of a break in the curve such as Freundlich & Röder say occurs with a dilatant material.

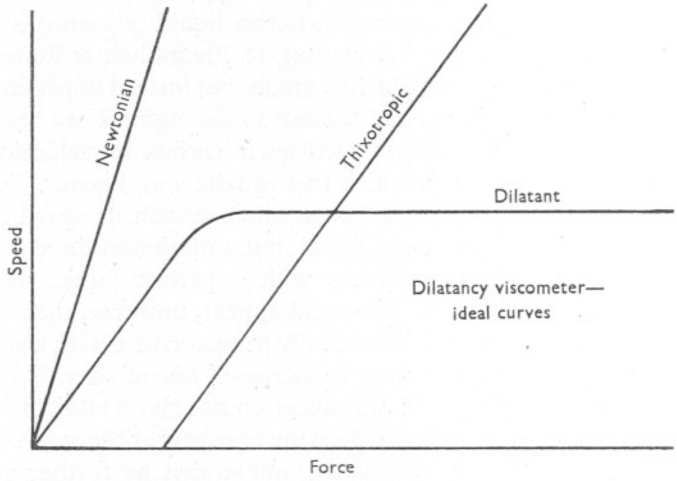


Fig. 3. Graph showing 'ideal' curves obtained by the use of the dilatancy viscometer.

The standard tapping procedure adopted may depend for its efficacy in standardizing the structure of the soil on the property described by Freundlich & Jones as *rheopexy*. Suspensions showing this property solidify more quickly when subjected to moderate agitation.

The effect of variations of water content

If the soil behaved as a thixotropic substance when excess of water was present, might it not become dilatant when the water content was reduced? In order to test this possibility runs were made in the dilatancy viscometer using soil containing a different amount of water. The samples of sand and water were prepared by filling the trough with damp soil and adding sufficient water to cover it completely. Water was then drained off until the appearance of the soil was considered suitable. After the tests had been made the soil was scraped into a weighed beaker and dried in an oven at 105° C. until of constant weight;

from these weighings the water content was calculated. The results are given in Table I and are also shown plotted graphically in Fig. 5.

As can be seen from the table the results are not clear-cut. It is apparently true to say that the speed of the sphere is greater when the water content is higher, but over the range of weights applied the effects of dilatancy do not appear in the graphical result. The results agree with a thixotropic behaviour of the substratum in that the graphs cut the abscissa to the right of the origin. Against that, however, must be set the appearance of the sand. Especially when its water content is low its appearance is clearly of the dilatant type whilst the sphere is travelling through it. In front of the sphere the surface layer of the soil is shiny but not plane, the water surface being broken by sand

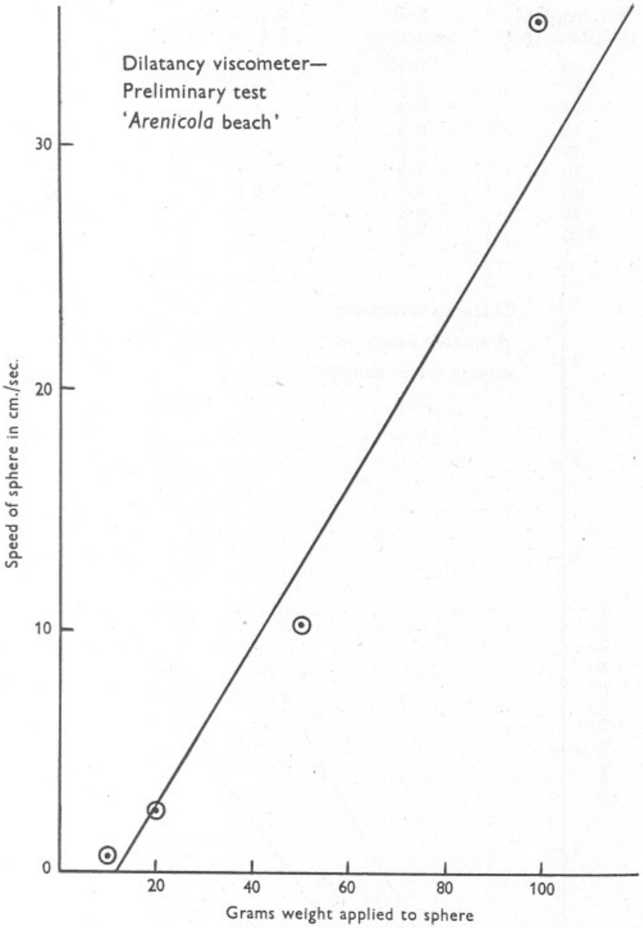


Fig. 4. Preliminary results of dilatancy viscometer tests.

TABLE I. THE EFFECT OF WATER CONTENT ON THE SPEED OF A SPHERE PASSING THROUGH MUDDY SAND FROM THE *ARENICOLA* REGION OF THE WHITSTABLE FLATS

Speed of sphere in cm./sec. Water content expressed as percentage wet weight of mixture. Almost all the figures for the speed of the sphere represent a mean of not less than three readings.

Wt. applied to sphere (g.)	Soil saturated	Soil with 28 % water	Soil with 21 % water
9	0·16	—	—
10	—	—	0·04
11	0·4	—	—
15	0·9	—	—
20	0·9	0·25	0·15
30	1·5	—	—
40	—	0·9	—
50	3·8	2·7	1·25
100	8·6	6·0	3·8

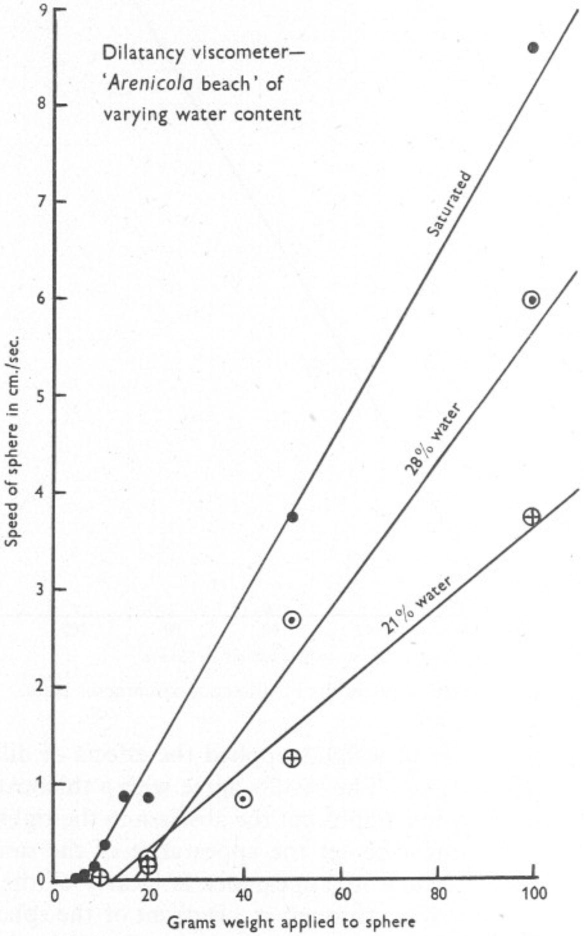


Fig. 5. Results of dilatancy viscometer tests on sand with varying water content.

particles. Alongside and behind the sphere the surface appears dull or matt, the water now being insufficient to fill the enlarged interstices. This behaviour is characteristic of dilatant substances, as is the behaviour of the sand when the trough is being emptied. The sand becomes quite hard and firm so that it cannot be induced to flow but has to be scraped out.

It appears then as if the sand exhibits both dilatant and thixotropic properties in one sample and that, although its pore space may increase with the application of an external force, the resistance to shear does not reach a maximum at any particular rate of shear tested. It is possible, but unlikely, that this phenomenon was not shown over the range of forces which were applied. It is also possible that the amount of silt and clay present in the mixture was sufficient to render the mutual slipping of the particles easy enough to avoid any great increase in resistance to the applied shear force while yet not completely masking the fact that increase in pore space *is* effected by the shear force.

The effect of the removal of silt and clay

To see if a small amount of silt and clay might affect the physical properties of the soil, tests were made with the dilatancy viscometer, using sand which had been repeatedly washed in such a way that all the silt and clay were removed and all the fine sand left. This was done, as in the estimation of the various soil fractions by the method of Robinson, by the decantation of the supernatant liquid to a depth of 10 cm. at a time of 4 min. 48 sec. after the sample was dispersed by agitation. After repeated washings the sea water no longer appeared turbid and it was clear that all the silt and clay had been removed, unless there was any still adhering to the sand particles which could not be removed by washing but which might yet affect the physical properties.

Two tests were made with the washed sand, one in which there was a superfluity of water and the other in which the water content was found by subsequent analysis to be 21 % by weight. The results are given in Table II and are plotted graphically in Fig. 6.

There was no very noticeable difference in behaviour between the washed and the unwashed sand during the course of the tests, and this was borne out by the graph which again showed that there was no clear indication, by a break in the straight line, of any marked dilatant behaviour of the sample of soil.

Discussion

Indeed, as Freundlich & Röder remarked, the dilatancy viscometer is difficult to use with large particle systems, and it may be that therein lies the reason for the absence of any clear sign of dilatancy in the numerical results in spite of the clear signs of dilatancy given by qualitative tests. The only thing that does emerge clearly is that it takes longer for the ball to travel through drier sand than through wetter sand under a given weight, and that this is

Table II. The Effect of Water Content on the Speed of a Sphere Passing through Washed, Silt-Free Sand from the *Arenicola* Region of the Whitstable Flats

Wt. applied to sphere (g.)	Soil saturated	Soil with 21 % water
10	0·3	—
20	1·0	—
30	1·8	—
40	2·5	—
50	3·5	<0·2
100	7·5	<0·3
200	20·0	0·7

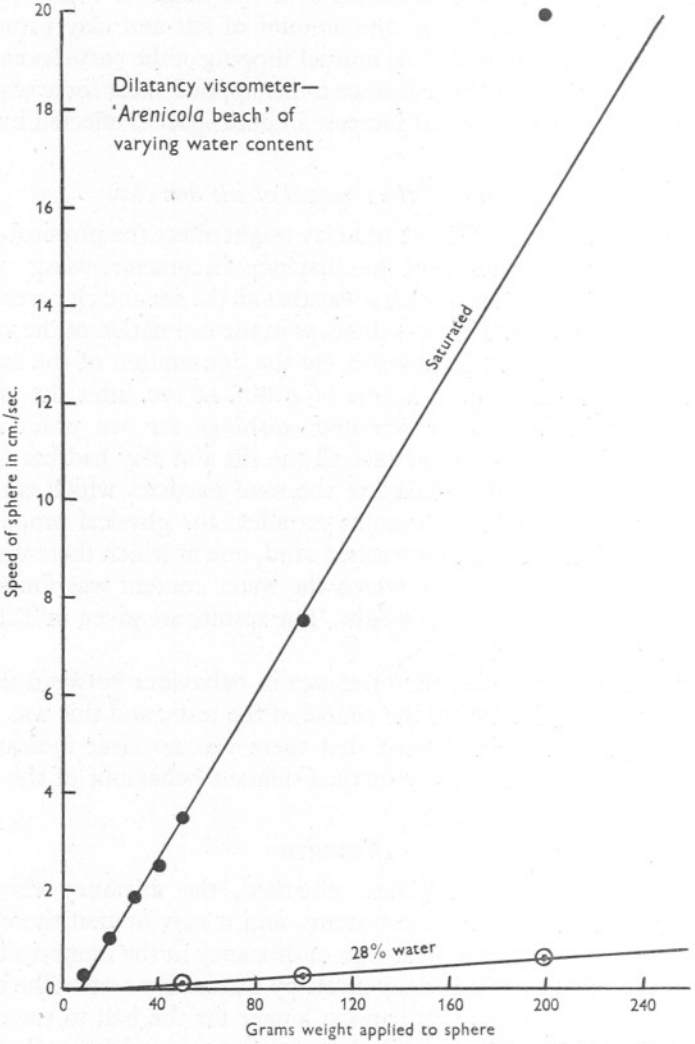


Fig. 6. Results of dilatancy viscometer tests with washed sand

supported by the hardness measurements made with the penetrometer. Clearly the water content is important in the determination of the resistance of the sand to gross penetration and equally clearly the presence of excess water is necessary for the sand to become almost fluid as it may do when agitated. What is suggested, perhaps, by the straight-line graph of speed against force (which is characteristic of Newtonian liquids as well as of thixotropic substances) is that the limiting factor in the passage of the sphere through the system is the viscosity of the water. It can easily be seen in suspensions with only a small quantity of superfluous water above the sand that there is a visible flow of liquid from in front of to behind the sphere as it passes through the mass. If it can be shown that the sphere in its passage through the suspension leaves behind it a clear, fluid-filled channel (as it can be seen to do in relatively dry suspensions), then the liquid filling the channel has had to flow into its new position from elsewhere in the suspension. Clearly then, if there is a superfluity of liquid, more than enough completely to fill the interstices between the particles, liquid can flow in from all directions and will not have to come from very far away from the point at which the clear channel is being made. If, on the other hand, there is not a great superfluity of water, liquid will have to come from a greater distance away in order to fill the channel which is being made. Since it comes from a greater distance the time taken for it to accumulate will be greater and hence the speed of the sphere through the suspension slower.

If these suggestions are correct, then they would account for the straight-line graph obtained, because the relations of speed and force depend on the viscosity and density of the water which is a Newtonian liquid. Owing to turbulence of flow through the interstices between the particles the effect of viscosity is partly lost. But the hypothesis can be roughly checked by the substitution for water of other liquids with higher or lower viscosities and densities, the substitution of liquids with a higher viscosity and density should result in a slower rate of travel, and of liquids with a lower viscosity and density in a greater rate of travel for the same applied force.

Tests were accordingly made with dry sand to which was added one of the three polar liquids glycerol, water and ether, the viscosities of which are in the approximate ratio of 5000:5:1 and the densities in the approximate ratio of 1·6:1·3:1. With the same weight in the scale-pan the speed of the sphere through sand-glycerol, sand-water and sand-ether mixtures was in the approximate ratio of 50:5:1. Had the viscosity factor alone been operative the ratio of speeds should have approached more nearly to 5000:5:1, and had the density factor alone been operative the ratio of speeds should have been nearer to 1·6:1·3:1. In a general way the results of this test confirm the suggestion that the viscosity and density of the interstitial liquid may be one of the main factors influencing the movement of marine soil. It is not suggested that this has been proved but merely that the absence of any kind of dilatant behaviour revealed by the viscometer and the rough correspondence of speeds and viscosities and densities suggests that the physical properties of the liquid determine the behaviour of marine soils *as well as* the size of the component particles.

SOIL HARDNESS AND BURROWING SPEED OF *ARENICOLA*

Since the purely physical method of the dilatancy viscometer did not show clearly any very striking difference between washed and unwashed sand, or between saturated and drier sand, a biological method was tried for testing the properties of the soil. The speed of burrowing of *Arenicola marina* L. was used for this purpose, since a certain amount is already known about this activity (Chapman & Newell, 1947). The usefulness of the animal as a biological tool is due to the fixity of its behaviour. When placed upon the surface of the substratum it at once begins to burrow in, whether its ventral or its dorsal surface is in contact with the soil. It seldom attempts to 'right itself' first. If the first attempt with its proboscis should fail to find a suitable spot it may try other places, but equally, it may persist for some time in attempting to force its way into an unsuitable place. Its behaviour seems quite unchanging although the environment may vary. This fixity does not leave scope for any kind of crawling or seeking behaviour. Hence, when the creature is placed on a soil into which it is not prevented from burrowing by large stones, the time which it takes to enter the soil, from the instant at which it is placed on the surface, can be taken as an indication of the difficulty which it has in the penetration of the soil.

The time taken by samples of worms to burrow into sands of different water content was measured and the sands subsequently sampled and analysed. The sampling was done with a cork borer which removed, with very little disturbance, a cylinder of soil of 1 cm. diameter; the analysis was done by drying a sample of some 15 g. to constant weight at 105° C. The samples of sand of different water content, in which the exercises were carried out, were arranged by making small mounds of different heights on the Flats. Water then drained from the upper parts of these leaving them drier than the surrounding shore. Alternatively, a circular moat was dug round a central 'island' which again became drier by the draining of water into the moat. This latter method had the advantage of not disturbing the natural structure of the sand. But even in the other method an attempt was made to preserve this structure as far as possible by being careful to construct the mound of clean spits of sand, in which the natural upper surface was left uppermost.

In the first set of experiments three batches, each of ten worms, were used. The first batch constituted a control and were allowed to burrow into undisturbed sand, the second batch were set to burrow into a low mound and the third batch into a higher mound. In the first set of experiments the water content of the mounds was not estimated. A second set of experiments was made in a similar fashion and the water content of the soil was estimated. A selection of the detailed results of these tests is set out in Table III. They are quite clear-cut and from them it can be seen that the worms were quite unable to burrow into the high mound from which the water appeared to have drained. Some of them could burrow into the low mound, but those which succeeded in doing this took longer than the worms which burrowed into the undisturbed sand. Worms which had been trying to burrow into the high mound were put on to the surface of undisturbed beach, into which they burrowed at about the normal rate.

Although the weighing error in estimating the water content of the sand samples did not exceed ± 0·1 % it would seem that the accuracy of sampling, even if not the accuracy of estimation of the water content, was not sufficiently accurate to yield useful results. It may be that the method of taking the sample, disturbing the sand as little as it did, was yet unsuitable for the estimation of very small differences in the water content. It was, however, very striking that the animal was quite unable to cope with the drier sand which, of course, was distinctly harder to feel and apparently dilatant when disturbed. It would appear that another method of estimating the effect which diminution of its water content had on the sand was necessary, so that hardness tests were made with the penetrometer.

TABLE III. THE EFFECT OF THE WATER CONTENT OF THE SAND ON THE BURROWING SPEED OF *ARENICOLA*

	Time to burrow to end of branchial region in min.		
Worm no.	Control, undisturbed sand	Mound of height 10 cm.	Mound of height 25 cm.
1	2·25	2·75	Unsuccessful
2	2·5	4·0	..
3	3·0	5·25	..
4	3·5	5·5	..
5	3·5	10·0	..
6	4·0	Unsuccessful	..
7	4·0	..	..
8	4·5	..	..
9	Damaged	..	..
10	..	..	..

After 10 min. the worms from the high mound were placed on undisturbed sand when they burrowed in the following times: 2·5, 2·75, 3·5, 4·0, 4·25, 4·5, 5·0, 5·25, 5·5, 5·75.

In the third set of experiments the same methods as before were used to produce small areas of soil in which the water content differed from that of the surrounding shore, but the water content of the soil was not estimated. Instead the hardness of the soil was measured with the penetrometer. The results are given in Table IV from which it can be seen that they agree with the first two sets of tests. As the height of the mound increases so the hardness of the soil increases and the ability of the worms to burrow into it decreases.

A synopsis of the experiments on the correlation of soil hardness and burrowing times is set out in Table V.

CONCLUSIONS

The aim of the work which has been set out in this paper is ultimately to determine to what extent the physical properties of the substratum determine the kind and number of its inhabitants, particularly in the intertidal zone. It is well known that some worms prefer fine soil, others a coarser medium, but it is not known precisely how these changes in composition affect the properties of the soil which are important to the animals. In the intertidal zone, from which the soil used in the experiments was obtained, even an apparently uniform environment may be subject to small local variations of silt or water content which are sufficient to bring about marked changes in the properties of the soil. The Flats at Whitstable are uncovered for about 10 out of the 24 hr., so that the time during which the animals may be subjected to varying physical conditions is an appreciable part of their life. The slope of the shore, which is

TABLE IV. THE EFFECT OF WATER CONTENT ON THE HARDNESS OF THE SOIL AND THE BURROWING SPEED OF *ARENICOLA*

Burrows made into mounds of varying height above water level. Time to burrow in min. and sec. Hardness in g./cm.^{2} required for penetration. (Each figure represents a mean of not less than twelve readings.)

Worm no.	Mound height zero. Hardness 1088	Mound height 5 cm. Hardness 1616	Mound height 7·5 cm. Hardness 1961	Mound height 13 cm. Hardness 2272
1	2.30	4.20	8.00	6.00
2	3.15	4.35	16.00+	10.00
3	4.00	4.45	16.00+	10.00
4	4.10	4.50	16.00+	Unsuccessful
5	4.20	5.15	Unsuccessful	..
6	5.00	5.50	..	..
7	5.05	7.20	..	..
8	5.05	8.00	..	..
9	5.10	8.10	..	..
10	5.15	8.30	..	..

TABLE V. SYNOPSIS OF HARDNESS AND BURROWING EXPERIMENTS

Hardness of soil (g./cm.^{2})	Burrowing time or percentage of animals burrowing	Height of mound (cm.)
1088	4·38 min.	Zero
1616	6·17 min.	5·0
1961	40 %	7·5
2272	30 %	13·0

here very gradual; the nature of the underlying stratum, whether porous or impervious; small local variations in elevation; shelter from wind or sea scour; all these may serve to alter the physical properties which have been studied.

An attempt has been made to show that the properties of thixotropy and dilatancy, which are of importance to burrowing animals, are affected by water content, that the hardness of the soil varies with water content and that the burrowing speed of lugworms is also affected. It is disappointing to find that the physical method of investigation using the dilatancy viscometer of Freundlich & Röder did not give clear-cut results, and did not show that there was any marked difference in properties between wet and dry sands, nor between those containing silt and clay and those which had been washed free from small particles. But the results obtained from the machine suggest that it is the density, viscosity and amount of water which determines to a large extent the fluidity of the sand on agitation. This conclusion was supported by tests which were made using liquids having viscosities and densities different from that of water.

Changes in the amount of water mixed with the sand of the Flats caused a marked change in its hardness and the speed with which lugworms could burrow into it. This is clearly a property which may be of great importance in the distribution of *Arenicola*. At Whitstable the sand is underlain by impervious clay and does not dry out at low water. It is possible that the worms can 'work' the headshafts of their burrows (Wells, 1945) at all states of the tide. But if there were no clay to retain the water, then at low tide the drained soil would become too hard for them to 'work', their feeding time would be limited to the time during which they were covered by the water and their distribution might well be limited also. The Flats appear too uniform in water content and worm population for the correlation of these features to be very striking, and it is hoped that some more suitable site will be investigated. But it is clear that there are considerable differences in the density of population of small local areas, the arrangement of the burrows in straight lines being one of the most striking (Newell & Chapman, 1948).

The effect of the clay content on the physical properties of the soil, for which it was not easy to obtain numerical data from the dilatancy viscometer, may also prove more susceptible of investigation by a biological method. The burrowing speed of *Arenicola* which has been correlated with the hardness of the soils would clearly be suitable for this purpose.

SUMMARY

Modifications are described to the penetrometer originally designed by Chapman & Newell (1947) for the measurement of the resistance to penetration of marine soils.

An account is given of qualitative and quantitative tests made during the study of the thixotropy and dilatancy of the muddy sand of the *Arenicola* region of the shore at Whitstable. The results of tests made with the dilatancy viscometer originally used by Freundlich & Röder are shown not to be in clear agreement with the observed behaviour of the soil.

It is suggested that the fluidity or otherwise of a marine soil is a function of the viscosity and density of the liquid filling the interstices between the particles.

It is shown that the resistance to penetration of the soil and the burrowing speed of *Arenicola* are dependent upon the water content.

REFERENCES

Boswell, P. G. H., 1948. The thixotropy of certain sedimentary rocks. *Science Progress*, No. 143, pp. 412–22.

Chapman, G. & Newell, G. E., 1947. The role of the body-fluid in relation to movement in soft-bodied invertebrates. I. The burrowing of *Arenicola*. *Proc. Roy. Soc.*, B, Vol. cxxxiv, pp. 431–55.

Freundlich, H., 1935. *Thixotropy*. Paris: Hermann.

Freundlich, H. & Jones, A. D., 1936. Sedimentation volume, dilatancy, thixotropy and plastic properties of concentrated suspensions. *Journ. Phys. Chem.*, Vol. xl, pp. 1217–36.

Freundlich, H. & Juliusburger, F., 1935. Quicksand as a thixotropic system. *Trans. Faraday Soc.*, Vol. xxxi, pp. 769–74.

Freundlich, H. & Röder, H. L., 1938. Dilatancy and its relation to thixotropy. *Trans. Faraday Soc.*, Vol. xxxiv, pp. 308–16.

Kruyt, H. R. & Van Selms, F. G., 1943*a*. The influence of traces of water on the plasticity of starch and quartz suspensions in organic media. *Rec. Trav. Chim. Pays-Bas*, Vol. lxii, pp. 407–14.

—— —— 1943*b*. The influence of a third phase on the rheology of suspensions. *Rec. Trav. Chim. Pays-Bas*, Vol. lxii, pp. 415–26.

Newell, G. E. & Chapman, G., 1948. Distribution of lugworms. *Nature*, Vol. clxii, p. 75.

Pryce-Jones, J., 1946. The flow of suspensions—thixotropy and dilatancy. *Proc. Univ. Durham Philos. Soc.*, Vol. x, pp. 427–67.

Reynolds, O., 1885. On the dilatancy of media composed of rigid particles in contact. With experimental illustrations. *Phil. Mag.*, Vol. xx, pp. 469–81.

Robinson, G. W., 1932. *Soils, their Origin, Constitution and Classification*. London.

Röder, H. L., 1939. *Rheology of Suspensions*. Amsterdam: Paris.

Van Selms, F. G. & Kruyt, H. R., 1943. Apparatus for measuring the consistency of plastic suspensions. *Rec. Trav. Chim. Pays-Bas*, Vol. lxii, pp. 398–406.

Wells, G. P., 1945. The mode of life of *Arenicola marina* L. *Journ. Mar. Biol. Assoc.*, Vol. xxvi, pp. 170–207.

THE USE OF PROBABILITY PAPER FOR THE GRAPHICAL ANALYSIS OF POLYMODAL FREQUENCY DISTRIBUTIONS

By J. P. Harding, Ph.D.

British Museum, Natural History

(Text-figs. 1–6)

The mathematical analysis of bimodal distributions is very complex. Karl Pearson (1894) investigated the problem and developed equations for the purpose; but found them unsolvable as the 'majority [of the relations] lead to exponential equations the solution of which seems more beyond the wit of man than that of a numerical equation even of the ninth order'. He did indeed evolve an equation of this order and used it to analyse a few bimodal distributions, but the arithmetic involved was very laborious. Later he (Pearson, 1914) gives a table for 'Constants of normal curve from moments of tail about stump' which, as he describes in the introduction, occasionally permits a rough analysis of a distribution which is known to be bimodal. This method is much more rapid than the solution of the nonic equation, but 'owing to the paucity of material in tails and corresponding irregularity there will be large probable errors'. Gottschalk (1948) discusses the question and shows that in the special case where the bimodal distribution is symmetrical comparatively simple solutions can be found.

The purpose of this paper is to describe by a series of examples a straightforward graphical method which enables one to analyse not only bimodal distributions, both symmetrical and asymmetrical; but also more complex distributions. The last example will show how a distribution comprising three unequal and overlapping populations can be analysed, an estimate being obtained of each separate mean, each separate standard distribution, and the relative proportions in which the three populations are mixed.

The method makes use of probability graph paper[1] devised by Hazen (1913) for the analysis of the flow of water in rivers. The use of this and other probability papers for various engineering and industrial purposes has been described by Rissik (1941), Doust & Josephs (1941–42), Levi (1946) and others; but I know of no description of its use for the analysis of bimodal or polymodal distributions. Perhaps the methods I am describing are so obvious to mathematicians familiar with probability graph paper, that for them description is superfluous. To the biologist, however, the simplicity of this

---

[1] Obtainable from Messrs Wightman Mountain, London, as 'Data sheet No. 37. Arithmetic Probability'. A similar paper is also stocked by H.M. Stationery Office.

powerful tool is perhaps its greatest attraction. He has long been aware that the mean and standard deviation of populations he is confronted with are often of little biological significance; because these populations are compounded of individuals belonging to the two sexes, to different species, or to different age-groups, and are therefore necessarily bimodal or polymodal in character.

Hazen's probability graph paper (Fig. 1) has along the bottom a scale of percentages reading from 0·01 % on the left to 99·99 % on the right (Fig. 4 shows the complete ruling). Along the top of the paper the same scale reads from right to left. The scales are not evenly spaced; but are much more crowded in the middle than at the sides, being specially arranged so that when any normally distributed population is plotted, in a manner which will shortly be described, the points all fall on a straight line. The position of this line is determined by the mean and its slope by the standard deviation, and these statistics may be estimated without laborious calculations. If a bimodal or polymodal distribution is compounded of distributions which are themselves normally distributed, and with biological data this is generally true enough for practical purposes, it will give a curve when plotted which is the resultant of two or more straight lines.[1] These lines are usually not difficult to find and the irrespective positions and slopes give the means and standard deviations of the component populations.

Fig. 1 shows the analysis of 1572 cuckoos' eggs each measured to the nearest half millimetre. The histogram to the left of the figure gives the size distribution; there are for example 156 eggs between 20·75 and 21·25 mm. in length. The histogram is not part of the method, but is included to facilitate description.

The data are plotted as cumulative percentages. Take, for example, the point P indicated by a small circle: here 4·7 % (scale along the bottom) of the sample is less than 20·75 mm. in length, for there are $1+3+30+39=73$ eggs or 4·7 % of 1572 eggs shorter than this. Alternatively, 95·3 % (scale along the top) of the sample of eggs exceed 20·75 mm. in length. When all the points are plotted it is found that they lie approximately in a straight line AB. This line represents a normal distribution whose mean length is the length corresponding to the point M at which the line cuts the vertical for 50 %. i.e. 22·35 mm. The standard deviation is estimated from the points S_1 and S_2 where the line AB cuts the verticals for 15·87 and 84·13 % respectively, S_1 corresponds to a length of 21·35 mm. and S_2 to 23·4 mm. and the standard deviation is half the difference $(23·4-21·35)/2=1·025$ mm. This is because 15·87 % of any normally distributed population is less than the mean by an amount equal to the standard deviation or more, and another 15·87 % exceeds the mean by this amount. The vertical lines for 15·87 and 84·13 % are not

---

[1] Apart from 'Normal' distributions the ones most frequently encountered with biological data are 'log-normal' and Poisson distributions. Log-normal distributions may be handled either by plotting the logarithm of the measurement instead of the actual measurement, or by the use of logarithmic probability paper, and Doust & Josephs (1941–42) describe a probability paper which is specially designed for Poisson distributions.

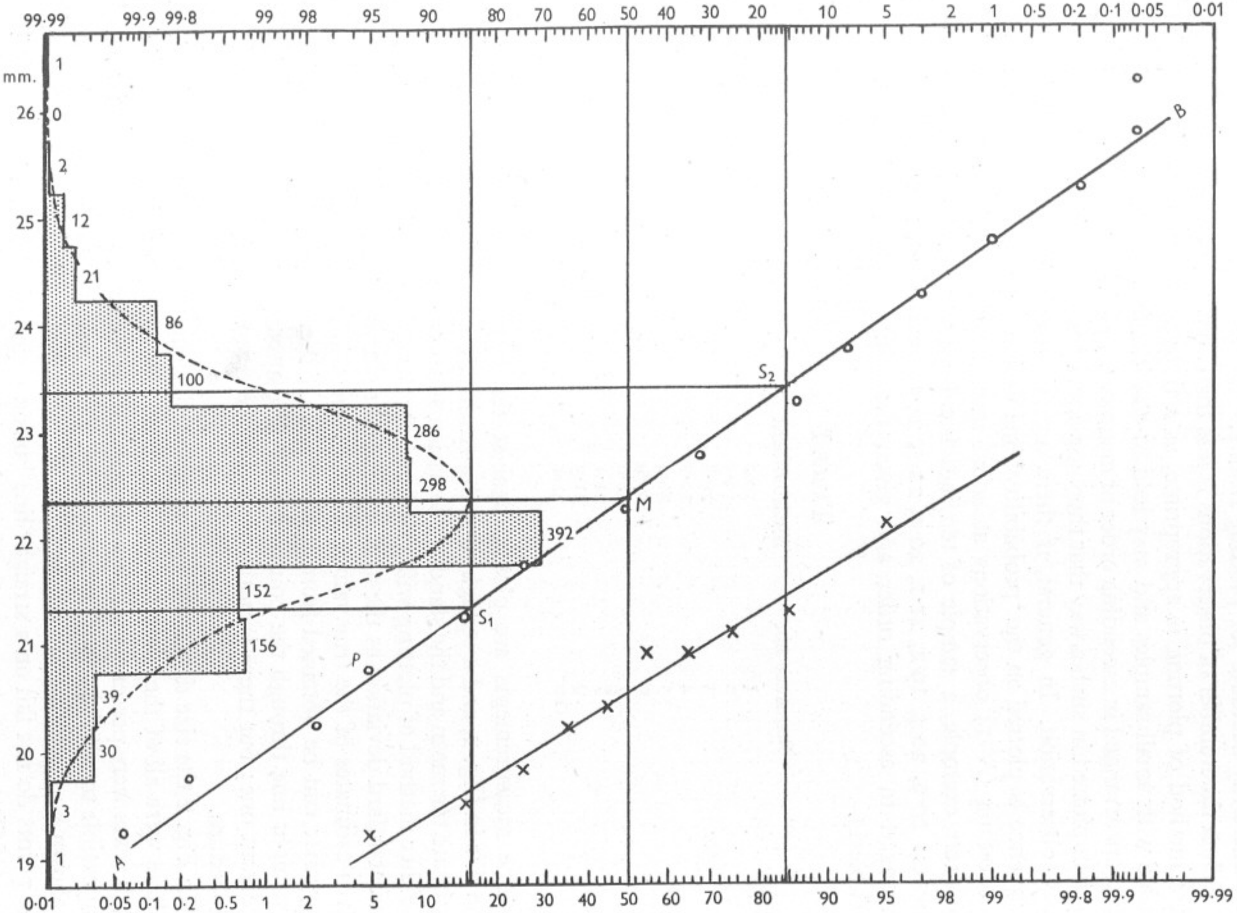

99·99 99·9 99·8 99 98 95 90 80 70 60 50 40 30 20 10 5 2 1 0·5 0·2 0·1 0·05 0·01
mm.
26
25
24
23
22
21
20
19
1
0
2
12
21
86
100
286
298
392
152
156
39
30
3
1
S_2
M
S_1
P
A
B
0·01 0·05 0·1 0·2 0·5 1 2 5 10 20 30 40 50 60 70 80 90 95 98 99 99·8 99·9 99·99

Fig. 1.

marked on the paper as supplied; but are easily put in. A 10 in. slide-rule is sufficiently accurate for plotting results.

When the number of observations is less than about twenty-five an alternative method of plotting is appropriate, as a frequency tabulation is of little value with small samples and may lead to considerable grouping errors. The data are arranged in ascending order of magnitude, each individual observation is then plotted in such a way that there are equal percentage intervals between each observation. In general, if there are N observations, the first in the sequence is plotted on the 'probability' line whose value is $50/N$ %, and the succeeding (N–1) observations at equal intervals of $100/N$ %. To give a concrete example, a sample of ten individuals gave the following measurements: 20·9, 20·4, 19·2, 21·1, 20·9, 22·1, 21·3, 19·8, 19·5, 20·2. These are arranged in ascending order and given the appropriate percentage value (Table I).

TABLE I

Sequence no.	Measurement	Percentage
1	19·2	5
2	19·5	15
3	19·8	25
4	20·2	35
5	20·4	45
6	20·9	55
7	20·9	65
8	21·1	75
9	21·3	85
10	22·1	95

The measurements are plotted against the percentages as indicated by the X's in Fig. 1, and a straight line drawn through the points enables one to estimate the mean and the standard deviation as 20·5 and 0·9 mm. respectively. Neither method of plotting will give precisely the same estimates of the mean and standard deviation as the arithmetical method; but the graphical solution gives estimates of the true values for the population which are as reliable as any that can be obtained from the sample. If there is difficulty in placing a straight line through the points, it is at once apparent that the sample is an aberrant one; but there is nothing to indicate this with the usual arithmetic procedure.

In Fig. 2 the size distribution of forty-one immature copepods is analysed. These were all of the same species and all in the same developmental stage; both sexes were present, probably in approximately equal numbers, but it was impossible to tell the sex of any individual. The size distribution of the sample is shown by the histogram on the left. When plotted on the probability paper the points do not fall on a straight line but on a sigmoidal curve. The dotted line GLH was not drawn to fit the points plotted from the data, but is the resultant of the two straight lines CD and EF. The lines CD and EF were found by assuming that the distribution was a bimodal one due to the

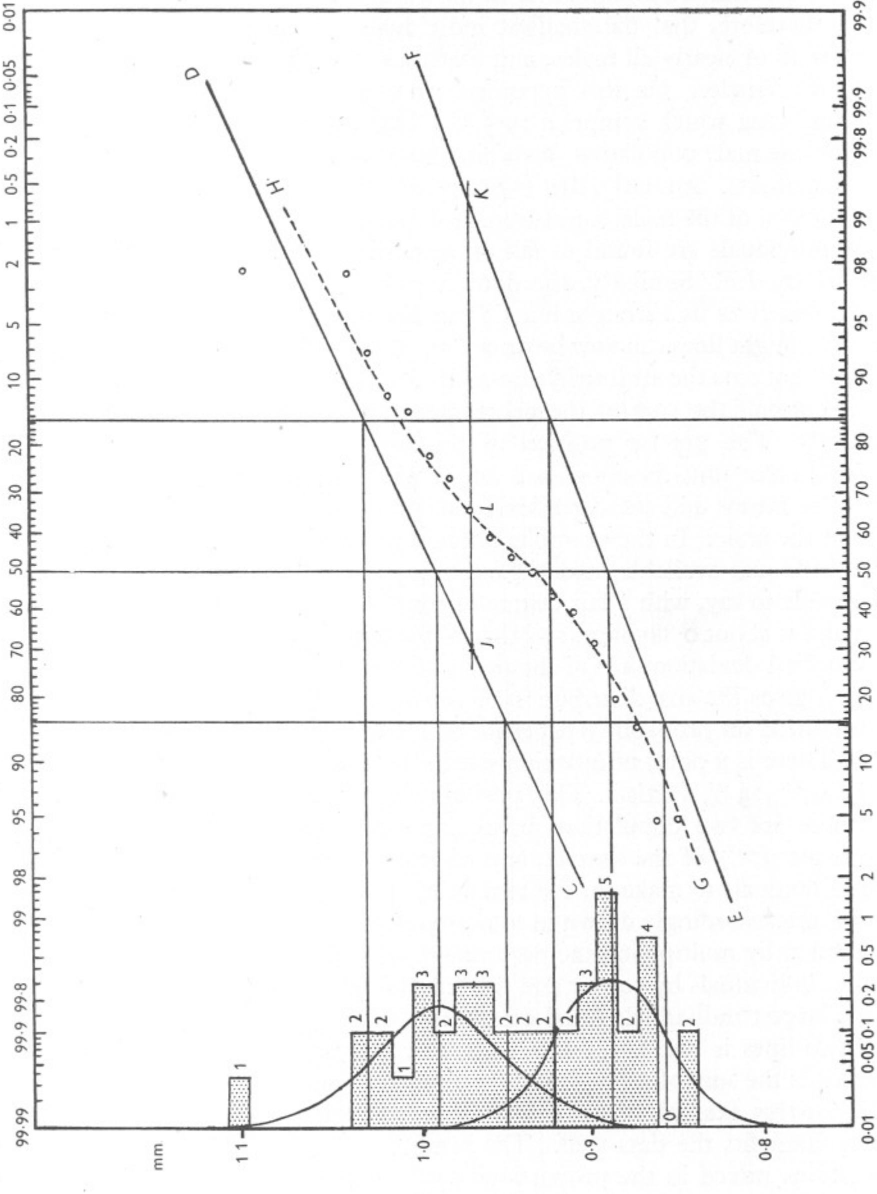

0·01
0·05
0·1
0·2
0·5
1
2
5
10
20
30
40
50
60
70
80
90
95
98
99
99·8
99·9
99·99
D
F
H
K
L
J
C
G
E
mm
1·1
1·0
0·9
0·8
1
2
2
1
3
2
3
3
2
2
2
2
3
5
2
4
0
2

Fig. 2.

difference in the average lengths of the males and females. It is known that the adult females are distinctly larger than the adult males and it is reasonable to assume a similar sex difference in the immature specimens measured. It is likely, therefore, that the smallest individuals, say those less than 0·9 mm. long are all or nearly all males, and that those longer than about 1·0 mm. are nearly all females. On this hypothesis the eight male individuals less than 0·88 mm. long which comprise 19·5 % of the total population will comprise 39 % of the male population (assuming that males and females are present in equal numbers). Similarly, the six males less than 0·72 mm. long are estimated to be 29·3 % of the male population. A few points plotted in this way for the small individuals are found to fall on a straight line which is approximately that drawn, *EF*. Similarly, the doubling of the percentages for the largest size groups gives us a straight line *CD* or thereabouts. The resultant, *GLH*, of the two straight lines can now be drawn in. For example, the position *L*, where the resultant cuts the arbitrarily chosen horizontal line *JK*, is placed at 64·7 %; this being half the sum of the percentages for *J* and *K*, 30 and 99·4 % respectively. The precise position of the two lines should be adjusted by trial and error until positions are found whose resultant curve best fits the data. The means and standard deviations of the two populations can then be read off the scale. In the example, although only a small sample of forty-one individuals was available, and although no single individual could be sexed we are able to say, with a fair degree of confidence, that the average length of the males is about 0·885 mm. and that of the females about 0·99 mm. and that the standard deviations are of the order of 0·375 mm.

Fig. 3 gives the size distribution of 360 adult female copepods. The points when plotted on probability paper lie on an asymmetrically placed sigmoidal curve. There is a point of inflexion where the direction of curvature changes, on the 97 %:3 % vertical. This position for the point of inflexion suggests that there are two populations involved: a population of small individuals comprising 97 % of the sample, and mixed with them a small population of large individuals to make up the remaining 3 % of the sample. The lines *ST* and *QR* are accordingly drawn in to represent these two populations. The line *ST* is fitted by multiplying the percentages (read on the bottom scale) for the smallest individuals by 100/97 and the line *QR* by multiplying the percentages for the largest individuals (read on the top scale) by 100/3. The resultant of these two lines is the dotted line *UV*. The percentage at *Z* on this line, for example, is the sum of 3 % of the percentage at *X* and 97 % of the percentage at *Y*. In this example adjustment of the position of *QR* is unnecessary as the resultant fits the data well. The sample is analysed as representing two populations mixed in the proportions 97:3, with mean lengths of 1·223 and 1·477 mm. respectively, the standard deviations of both populations being about 50 μ.

Before leaving Fig. 3 I should like to draw attention to the abnormally small-size group for 1·26 mm. where there are only nine individuals although there are twenty-four in the groups on either side. This is probably a sampling error due to the groupings being too small, there may have been some unconscious bias against the number for this group, in the units used for measurement. This irregularity is not apparent when the data are plotted on the probability paper.

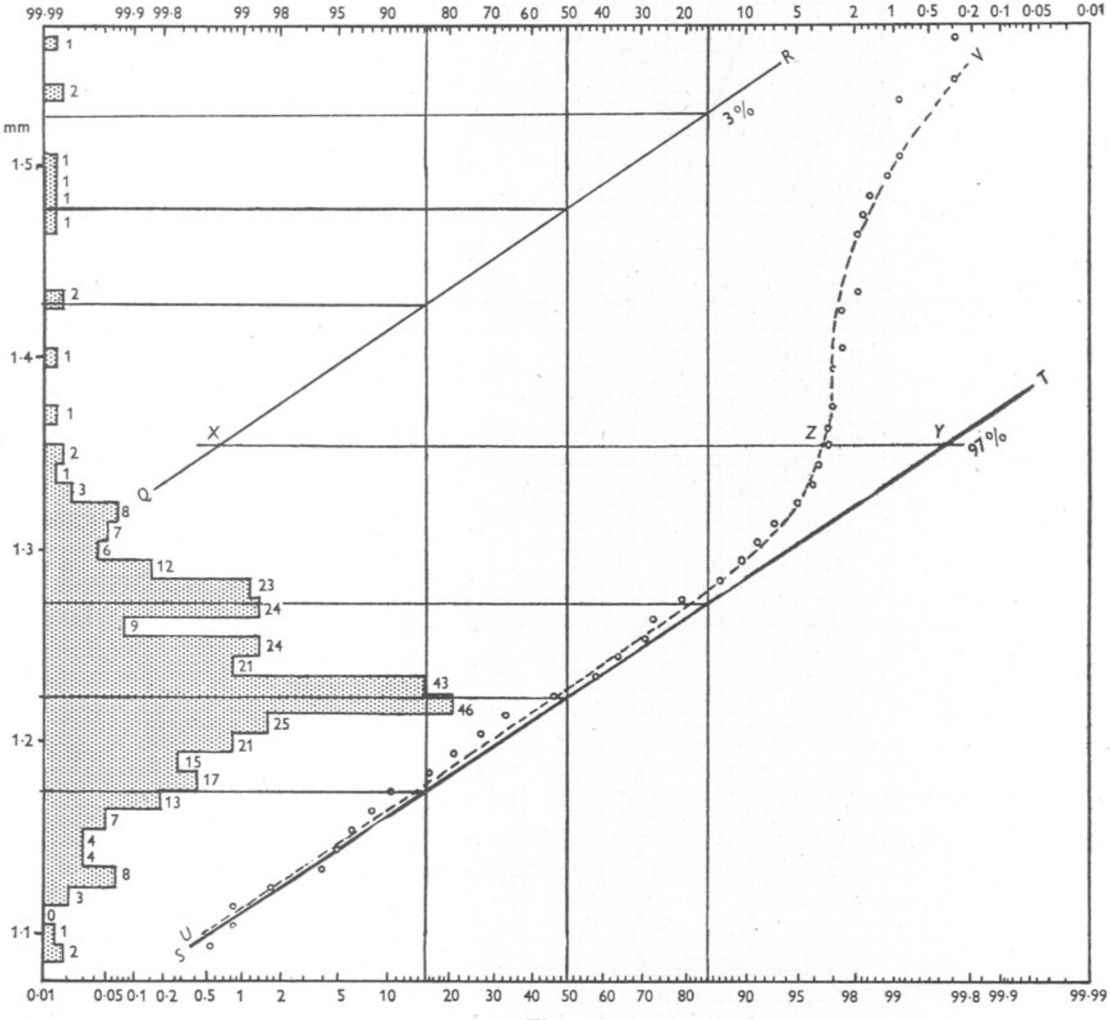


Fig. 3.

Polymodal curves are not difficult to analyse if the sample is large enough and the component populations do not overlap each other too much. Fig. 4 is drawn to show the effect of mixing three hypothetical populations in the

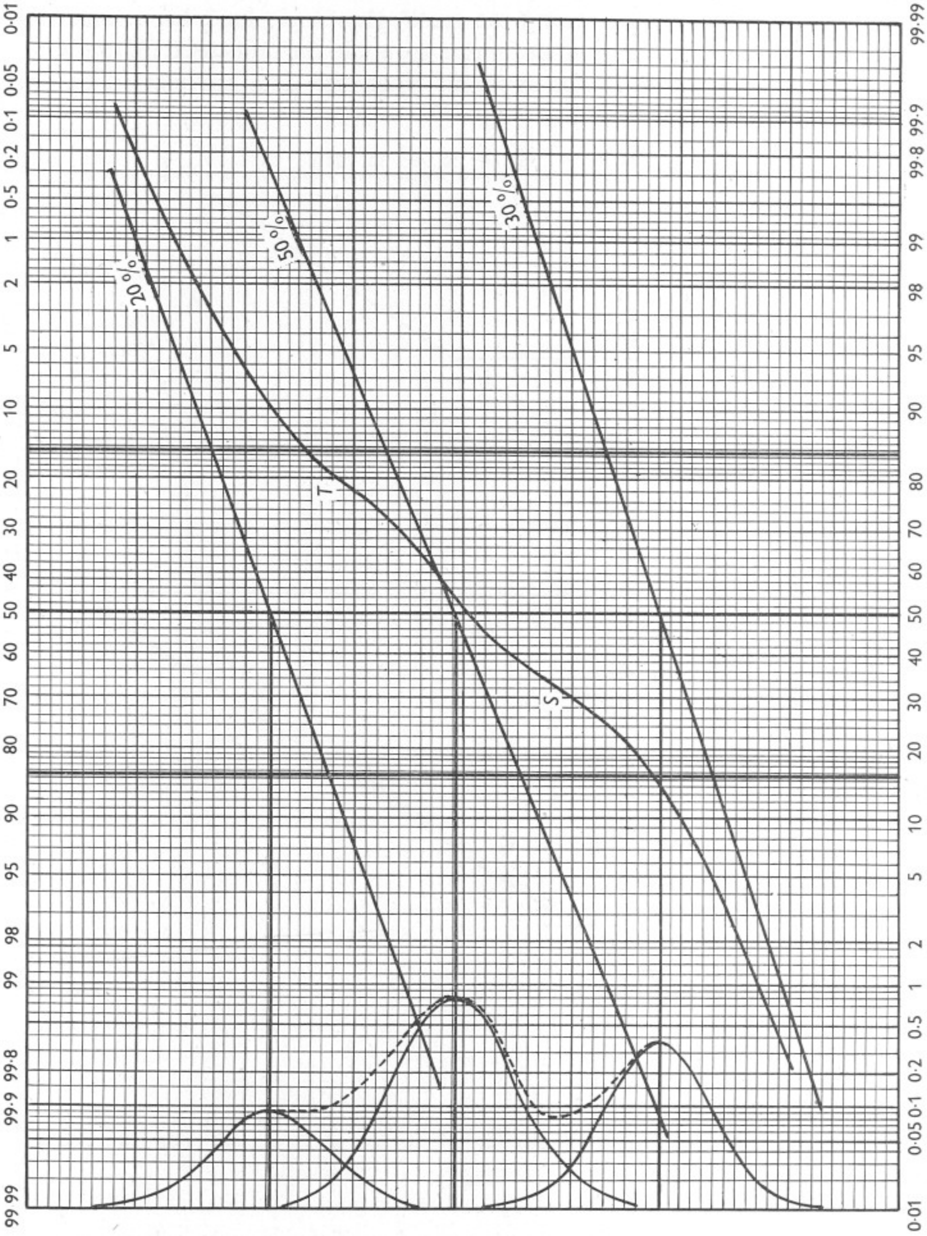

0·01
0·05
0·1
0·2
0·5
1
2
5
10
20
30
40
50
60
70
80
90
95
98
99
99·8
99·9
99·99
99·99
99·9
99·8
99
98
95
90
80
70
60
50
40
30
20
10
5
2
1
0·5
0·2
0·1
0·05
0·01
20%
50%
30%
T
S

Fig. 4.

proportions 2:5:3. There are two points of inflexion at S and T, and these give the approximate proportions in which the populations are mixed, S occurring on the 30 % and T on the 80 % vertical, the difference between the two being 50 %. It is sometimes possible to analyse a polymodal curve even though there is considerable overlapping of the populations and there are no points of inflexion to guide one. Figs. 5 and 6 show two possible ways of analysing such a sample. The data analysed are the lengths of 1122 fish calculated by Ford (1928, p. 294), from the measurements of scales. Hodgson (Buchanan-Wollaston & Hodgson, 1929) considered that this population of fish 'certainly contains two modes at 12 cm. and about 15 cm.' He had reason to believe from experience with other samples that there was a third mode, he thought concealed between the two. We shall see that analysis by probability paper indicates a third, small population with a smaller mean length than either of the main populations. The sigmoidal shape of the distribution when plotted on probability paper is very similar in appearance to that of Fig. 1 and the data can be analysed as a symmetrical bimodal curve in the same way as Fig. 1 was. The resultant of the two lines shown fits the lengths of the fish above 13 cm. long very well and the fish below this length not quite so well. A better fit is shown in Fig. 6 where the upper tail of the distribution is fitted by a 20 % line. This leaves 30 % of the sample of fish to be fitted in between. By trial and error one finds that the only way of placing this line is at an angle to the other two as shown in Fig. 6. The resultant of these three lines is shown by the small x's, while the circles are plotted from Ford's data. The agreement between the two is remarkable. The summation of the three distributions, shown as a dotted line superimposed on the histogram, also shows much better agreement with the sample than does the cruder analysis of Fig. 5. Table II gives the expected frequencies calculated from the results of Figs. 5 and 6 with the help of either Sheppard's tables or of tables of probits.

A χ^2 test for goodness of fit applied to these shows that the analysis of Fig. 5 is very unlikely to be true; but that the data are quite consistent with the analysis of Fig. 6, the probability of a χ^2 of 4·65 being about 0·2. In the calculations of χ^2 the classes for the 6·5 and 18·5 cm. have been bracketed together. A degree of freedom has to be subtracted for each mean, for each standard deviation, for all but one of the component populations and for the total. It is not claimed that the analysis of Fig. 5 gives the only possible, or even the best solution, indeed an attractive solution is the following:

50 % of the population with a mean 14·5 cm. and S.D. 1·3
40 % of the population with a mean 11·85 cm. and S.D. 1·1
10 % of the population with a mean 9·15 cm. and S.D. 0·9

The χ^2 summation for this solution is 7·95 which gives a value for $p = 0{\cdot}048$. The goodness of fit is therefore not quite so good; but the ratio of the standard deviation to the mean for each population remains constant and this might be

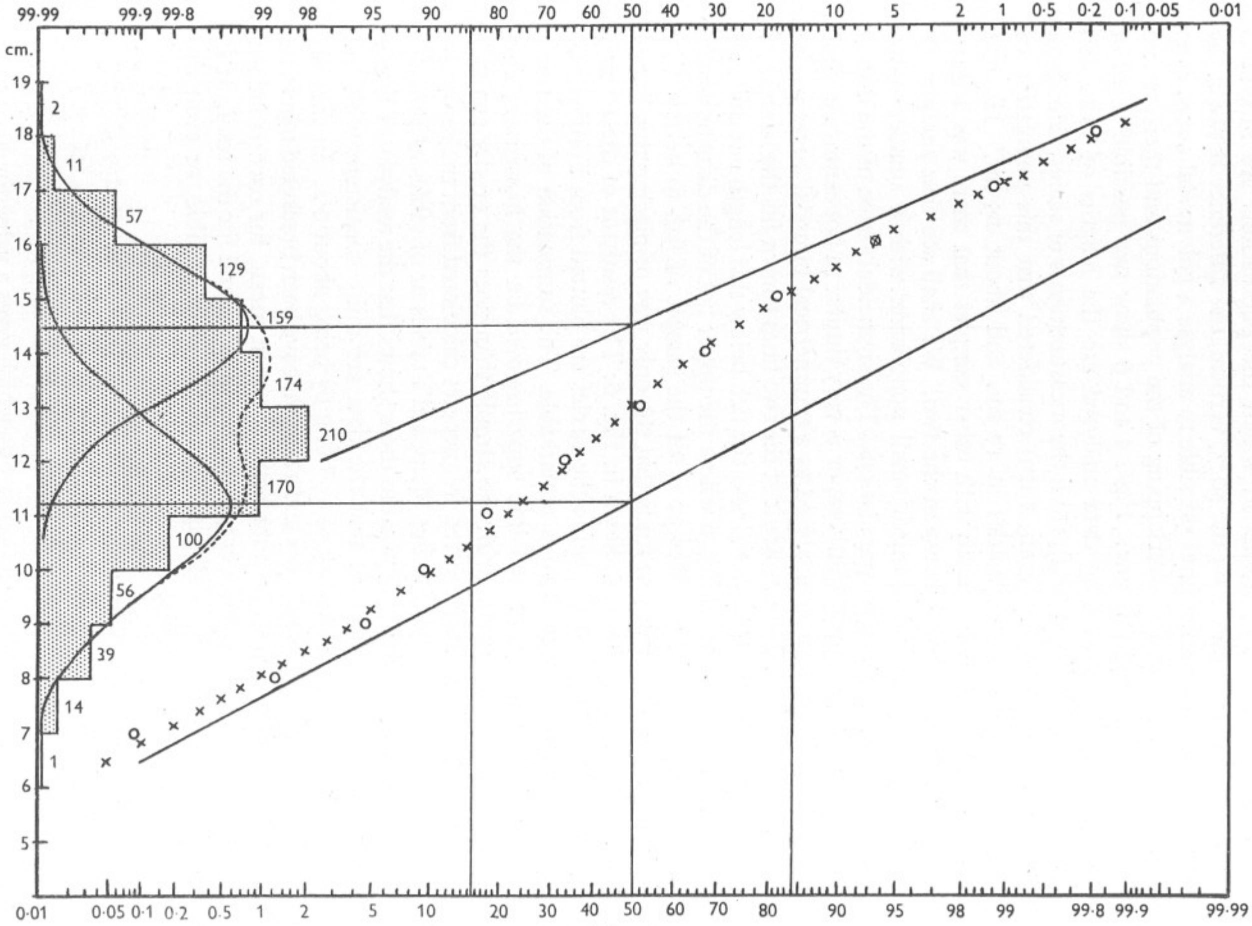

99·99
99·9
99·8
99
98
95
90
80
70
60
50
40
30
20
10
5
2
1
0·5
0·2
0·1
0·05
0·01
cm.
19
18
17
16
15
14
13
12
11
10
9
8
7
6
5
2
11
57
129
159
174
210
170
100
56
39
14
1
0·01
0·05
0·1
0·2
0·5
1
2
5
10
20
30
40
50
60
70
80
90
95
98
99
99·8
99·9
99·99

Fig. 5.

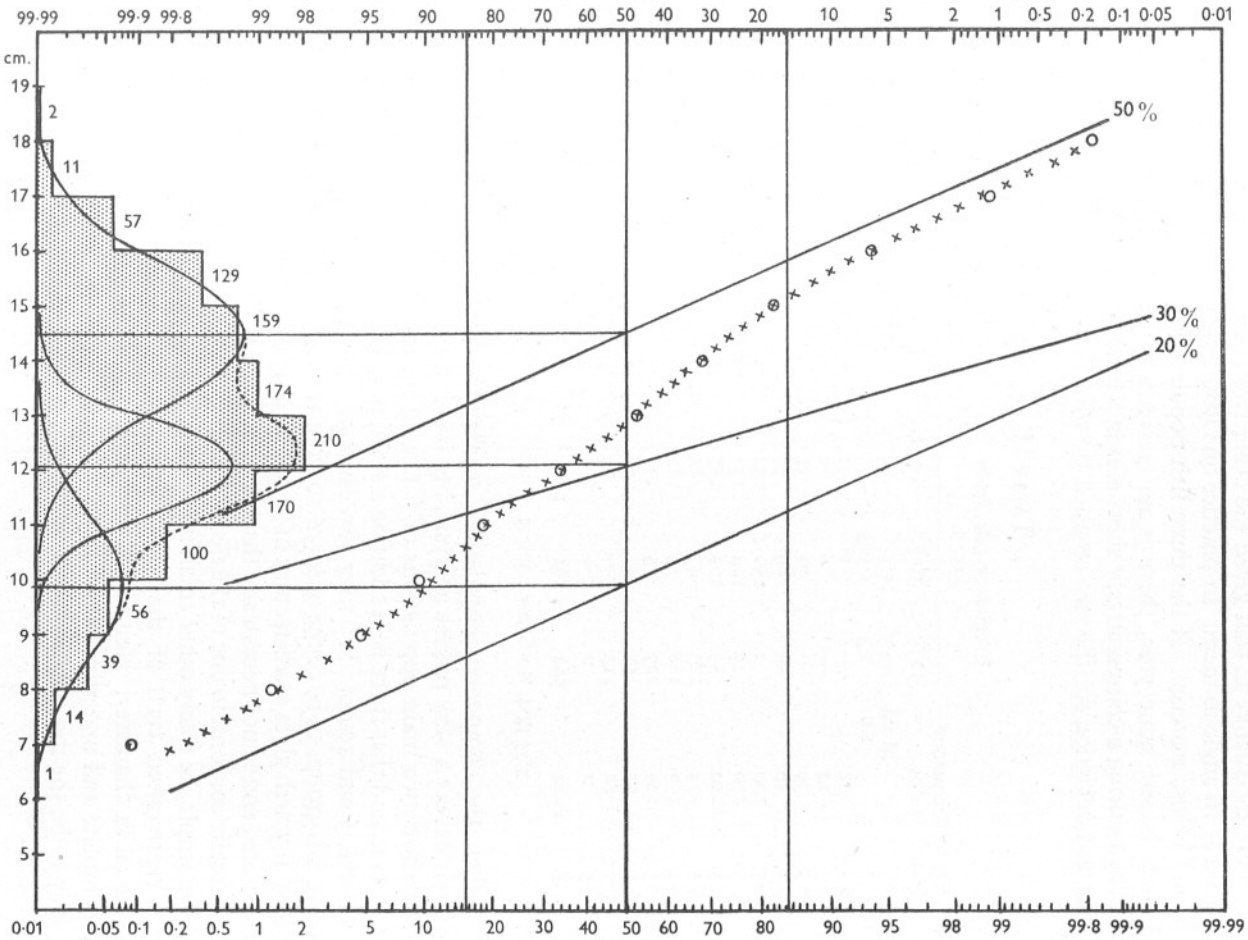

99·99
99·9 99·8
99 98
95
90
80 70 60 50 40 30 20
10
5
2 1 0·5 0·2 0·1 0·05 0·01
cm.
19
18
17
16
15
14
13
12
11
10
9
8
7
6
5
2
11
57
129
159
174
210
170
100
56
39
14
1
50 %
30 %
20 %
0·01
0·05 0·1 0·2 0·5 1 2
5
10
20 30 40 50 60 70 80
90
95
98
99
99·8 99·9
99·99

Fig. 6.

in its favour. I have chosen the solution of Fig. 5 for illustration because it is the more instructive in that given the other two lines the 30 % line has to be placed at an angle to them. In practice one would be guided by the biological nature of the material. If the three fish populations, for example, are three broods of the same year, there is no reason why one brood may not have hatched during a comparatively short season which might account for a small standard deviation for the size attained by winter.

TABLE II

		Frequency calc. from Fig. 5			Frequency calc. from Fig. 6			
Class (cm.)	Frequency obs.	50 %	50 %	Total	50 %	30 %	20 %	Total
	Mean ...	14·5	11·2		14·5	12·1	9·9	
	S.D. ...	1·3	1·505		1·3	0·8	1·3	
6·5	1	—	1	1	—	—	3	3
7·5	14	—	8	8	—	—	13	13
8·5	39	—	31	31	—	—	39	39
9·5	56	—	79	79	—	1	64	65
10·5	100	2	132	134	2	27	61	90
11·5	170	13	144	157	13	123	32	168
12·5	210	55	102	157	55	141	10	206
13·5	174	127	47	174	127	41	2	170
14·5	159	168	14	182	168	3	—	171
15·5	129	127	3	130	127	—	—	127
16·5	57	55	—	55	55	—	—	55
17·5	11	13	—	13	13	—	—	13
18·5	2	2	—	2	2	—	—	2
Total	1122	562	561	1123	562	336	224	1122

$\chi^2 = 43{\cdot}4,\ n = 6,\ p = < 0{\cdot}001$ $\chi^2 = 4{\cdot}65,\ n = 3,\ p = 0{\cdot}2$

When the component populations overlap as much as they do here one cannot expect a very precise analysis, but one is justified in saying that Ford's data show two main populations of fish with mean lengths of about 12 and 14·5 cm., and that there is in addition a small population whose mean length is between 9 and 10 cm. We may also estimate the standard deviations of the three fish groups to be of the order of 10 % of the respective mean lengths. An analysis which gives a satisfactory fit (Fig. 6) is only one of the simplest possible solutions, and is not necessarily the most complete picture of the facts, which may really conform to one of the many possible complex solutions. There may, for example, be many other small fish groups in the sample, and if both sexes are represented each of the three main groups are probably themselves bimodal in character. Neither the graphical method nor any other will give a complete and unequivocal solution; but fortunately the simplest solution is likely to be the most significant biologically, as well as statistically.

ACKNOWLEDGEMENTS

I am indebted to Dr G. A. Barnard, University of London, for bringing probability paper and its possibilities to my notice, and also to Mr W. F. Adams, Ministry of Transport, and Mr H. J. Joseph, Post Office Engineering Research Station, for their interest and help with the literature quoted.

REFERENCES

BUCHANAN-WOLLASTON, H. J. & HODGSON, W. C., 1929. A new method of treating frequency curves in fishery statistics, with some results. *Journ. Conseil Int. Explor. Mer*, Copenhagen, Vol. 4, pp. 207–25.

DOUST, J. F. & JOSEPHS, H. J., 1941–42. A simple introduction to the use of statistics in telecommunications engineering. *Post Office Eng. Journ.*, Vol 34, pp. 36–41, 79–84, 139–44 and 173–8.

FORD, E., 1928. Herring investigations at Plymouth. III. The Plymouth winter fishery during the seasons 1924–25, 1925–6 and 1926–7. *Journ. Mar. Biol. Assoc.*, Vol. 15, pp. 279–304.

GOTTSCHALK, V. H., 1948. Symmetrical bi-modal frequency curves. *Journ. Franklin Inst. Philadelphia*, Vol. 245, pp. 245–52.

HAZEN, A., 1913. Storage to be provided in impounding reservoirs for municipal water supply. *Proc. Amer. Soc. Civil Eng.*, Vol. 39, pp. 1943–2044.

LEVI, F., 1946. Graphical solutions for statistical problems. *The Engineer*, *London*, Vol. 182, pp. 338–40 and 362–4.

PEARSON, K., 1894. Contribution to the mathematical theory of evolution. *Phil. Trans. Roy. Soc.*, A, Vol. 185, pp. 71–110.

—— 1914. *Tables for statisticians and biometricians*, Part I. Cambridge.

RISSIK, H., 1941. Probability graph paper and its engineering applications. *The Engineer*, *London*, Vol. 172, pp. 276–82 and 296–8.

ON MANGANESE IN SEA AND FRESH WATERS

By H. W. Harvey, Sc.D., F.R.S.

Hydrologist at the Plymouth Laboratory

(Text-figs. 1–4)

Chemical and spectrographic analyses have shown that the sea contains a variable quantity of manganese, ranging between 1 and 10 mg./m.^{3} (Thompson & Wilson, 1935; Noddack & Noddack, 1940), while river waters contain some 500 to 1000 mg./m.^{3} (Twenhofel, 1938). These estimates include manganese in solution and that present as particulate or colloidal oxides soluble in concentrated hydrochloric acid.

In the deep waters of the oceans there is a continuous rain of manganese oxides falling on the ocean floor. Pettersson (1945) estimates that some 10 mg. of manganese may fall on each square metre annually.

In a previous communication it was shown that the sea off Plymouth contained, in 1946, insufficient manganese for the continued growth of several species of flagellates (Harvey, 1947). The experimental data, considered as a biological estimation of manganese in the water, indicated that the water contained only a fraction of 1 mg./m.^{3} in a form available to plant life.

These various observations indicate that the state of manganese in the sea—ionic, colloidal or particulate—and its distribution, are a pertinent subject for inquiry. Manganese is necessary for marine life. Sea waters obtained from different localities and depths are known to differ, the one from the other, in their capacity to support marine plant life irrespective of their content of available nitrogen, phosphorus and iron. It is not known what part, if any, varying concentrations of manganese *in an available form* may play in affecting the biological environment provided by the sea from place to place.

ESTIMATION OF MANGANESE SOLUBLE IN DILUTE ACIDS

The oxidation of tetramethyldiaminodiphenylmethane (*tetrabase*) in solutions containing periodate, to form a transient blue compound, is catalysed by traces of manganese. This reaction has been used by Nicholas (1946) to estimate this element in plant tissues. It was found possible to develop the method so that it could be used to estimate manganese in sea water to within a small fraction of a milligram per cubic metre of water.

The oxidation does not allow the estimation of manganese in solution in water at pH 8, since it can only be carried out in dilute acid, the tetrabase being insoluble in neutral solution. It is thought that the concentration of manganese in the sea, present both in the ionic form and as colloidal or particulate oxides soluble at pH 4·7, should provide a fair index of the maximum concentration of manganese likely to be available to plants. Any colloidal micelles or particles which dissolve at a pH one or two units lower than that of natural sea water are likely to be available to plants, as is iron oxide (Harvey, 1937), the pH at the plant-water interface being lower than in the surrounding water (Danielli, 1944). On the other hand, particles which are insoluble in dilute acid are unlikely to be available, unless conditions at the plant-water interface are tantamount to a reducing medium, for which there is no evidence. (Particles of manganese oxides insoluble in dilute acid are readily soluble in an acidic reducing medium.)

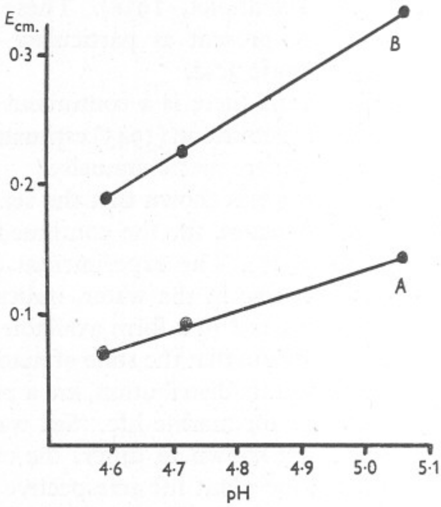


Fig. 1. Relation between pH and the extinction coefficient (*E*) in yellow light of the transient blue formed in sea water (*A*) and in the same sea water to which 3 mg. Mn/m.³ had been added (*B*). Waters buffered with hydrochloric acid and ammonium acetate, and containing 50 mg. potassium periodate and 35 mg. tetrabase per litre.

When tetrabase is added to a solution containing periodate and manganese ions, oxidized to high valency by the periodate, a blue colour develops and quickly fades. In strongly acid solution the coloured oxidation product is unstable and is not formed. The intensity of blue colour formed depends upon the following factors:

(i) *The concentration of tetrabase in solution.* This is very insoluble in neutral solution, its solubility increasing with increasing acidity.

(ii) *The hydrogen-ion concentration.* With increasing acidity and the same concentration of tetrabase, less blue is formed (Fig. 1).

(iii) *The concentration of periodate present.* It was also observed that less blue is formed when using a freshly made solution of periodate than with a solution of the same concentration which has aged and started to smell of ozone. Ozone or ozonides play a part either in the oxidation of manganous-manganese or of the tetrabase.

Thus, of the reagents used, the periodate solution becomes more effective on aging, while the solution of tetrabase in acetone becomes less effective.

(iv) *The oxidation period*, or time during which the periodate has been mixed with the buffered sea water before mixing with tetrabase. Some evidence indicated that the oxidation of manganese ions to higher valency, having catalytic activity, is not quantitative but that an equilibrium mixture of polyvalent states is set up. This equilibrium mixture is unstable in buffered sea water, slowly reverting after an interval of time.

(v) *Salts in solution.* At the same pH and with the same concentration of periodate and tetrabase, the increase in blue developed due to unit addition of manganous salt was greater in water than in sea water, or in $3\frac{1}{2}\%$ sodium chloride solution.

(vi) *The nature and quantity of organic solvent in which the tetrabase has been dissolved.* The most satisfactory results have been obtained by adding the water and buffer and periodate to tetrabase dissolved in acetone, so that sufficient tetrabase is present to saturate fully the resulting mixture. If an excess of acetone is used, thereby increasing the solvency of the final mixture, no colour develops.

(vii) *Manganese present.* With solutions of a manganous salt in distilled water, containing up to 3 mg. Mn/m.^{3}, and buffered with ammonium acetate and hydrochloric acid, a linear relation was found between the blue developed and the quantity of manganese present. An experiment such as is shown in Fig. 2 allows the 'reagent blank' to be calculated.

With lesser concentrations of tetrabase, the colour developed did not bear a linear relation to the quantity of manganese present, being proportionately less for greater than for smaller additions. From this observation it is concluded that there is a linear relation between the quantity of catalyst and the quantity of tetrabase transformed only when the concentration of the latter is at least 40,000 times that of the catalyst—about 10,000 times more molecules of tetrabase than of the catalytic manganese ions.

With sea water or sodium chloride, buffered at pH 4·6, to which manganese in quantity not exceeding 3 mg./m.^{3} had been added, the relation between blue formed and manganese present was not strictly linear with 130 mg./l. of tetrabase present (Fig. 3). This lack of linearity was found with 130 mg./l. of tetrabase at acidities varying between 4·5 and 5·0 pH and with a wide range of periodate concentrations.

This lack of linearity suggested that the salts in solution in the sea water affected the oxidation of the tetrabase by lowering its effective concentration relative to that of the active manganese. It was possible to increase the concentration of tetrabase to 200 mg./l. without causing turbidity by precipitation in sea water, and probably to decrease the concentration of active manganese by adding less periodate.

Under these conditions the transient blue formed showed a linear relation to the quantity of added manganese salt (Fig. 4).

The procedure adopted in this experiment was as follows. There were added to 50 c.c. of sea water, from which most of the particulate matter had settled during storage in a glass carboy, (i) 1·5 c.c. of hydrochloric acid *c.* 1·75 N, and 3 days later (ii) 1·5 c.c. of a solution of 100 g. ammonium acetate in 200 c.c. of water, and (iii) 3·7 c.c. of a solution containing 0·85 mg. potassium periodate (as found by titration in alkaline solution with sodium arsenite after adding potassium iodide). The oxidation of the manganous ions present was allowed to proceed for exactly 10 min. when the liquid was poured quickly into 4·5 c.c. of a 0·25% solution of tetrabase in acetone

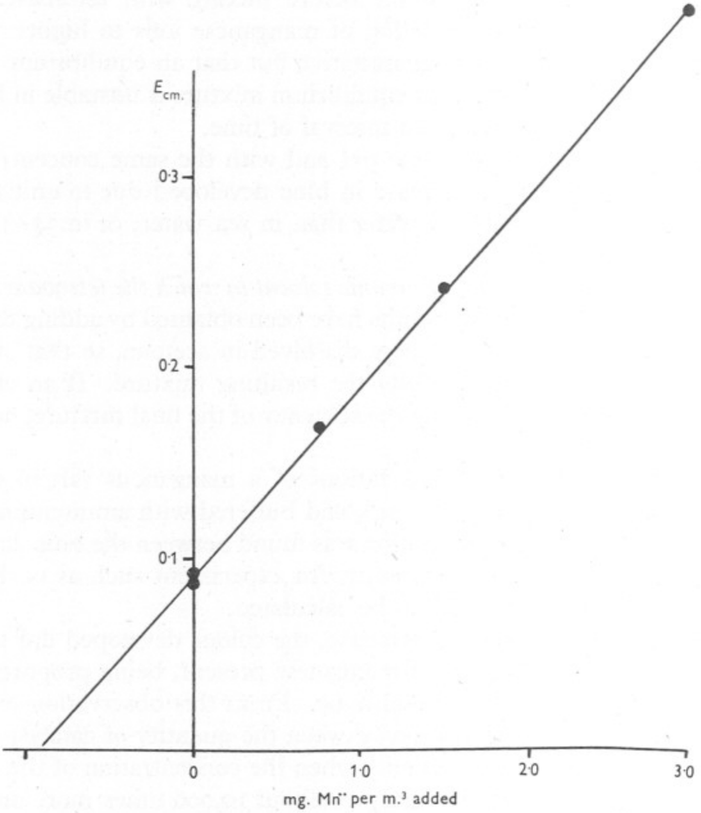


Fig. 2. The relation between the blue colour developed in distilled water, buffered at pH 4·8, and the quantity of manganese added. The extinction coefficients are of yellow light passing 'Ilford Spectrum 606' filters. Concentration of tetrabase, 130 mg./l.; of potassium periodate, 30 mg./l. Reagent blank deduced = 0·9 mg. Mn/m.^{3}

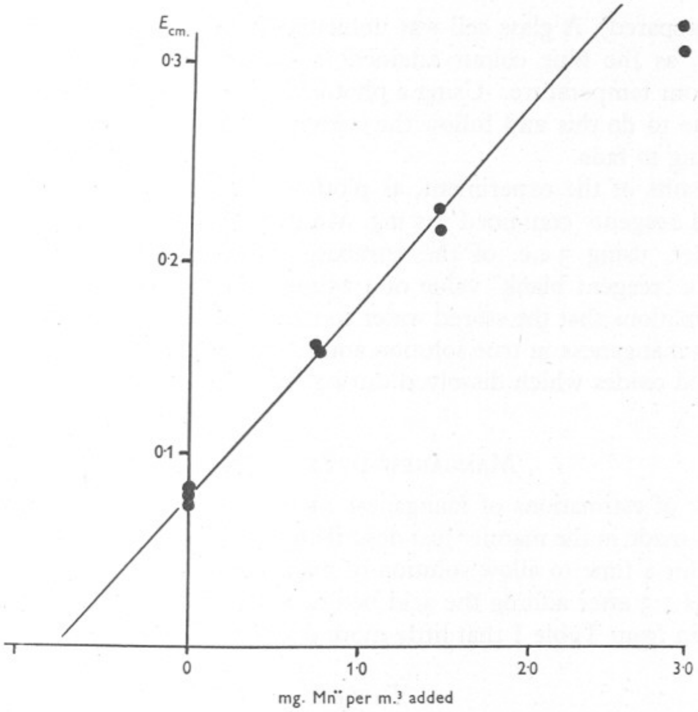


Fig. 3. Relation between colour formed and quantity of manganous salt added to sea water buffered at pH 4·6. Concentration of tetrabase, 130 mg./l.; of potassium periodate, 42 mg./l.

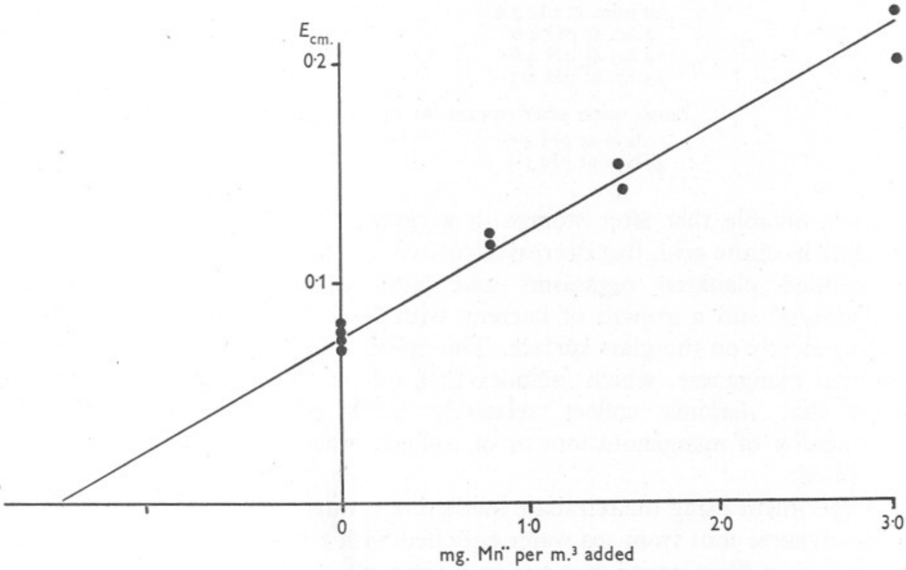


Fig. 4. Relation between colour formed and quantity of manganese salt added to stored sea water. Concentration of tetrabase, 200 mg./l.; of potassium periodate, 14 mg./l.

(freshly prepared). A glass cell was immediately filled and its optical density measured, as the blue colour attained its maximum some 40 sec. later at winter room temperature. Using a photoelectric absorption meter there was ample time to do this and follow the colour attaining its maximum, pausing and starting to fade.

The results of the experiment, as plotted in Fig. 4, indicate that the sea water and reagents contained 1·5 mg. Mn/m.^{3} Similar procedure with distilled water, using 3 c.c. of the tetrabase solution and the same buffers, provided a 'reagent blank' value of 1·25 mg. Mn/m^3. It is concluded from these estimations that the stored water contained 0·25 mg. Mn/m.^{3}, originally present as manganese in true solution and as any colloidal or minute particles of hydrated oxides which dissolved during the 3 days at pH 1·3.

MANGANESE IN SEA WATER

A number of estimations of manganese in sea water collected off Plymouth have been made in the manner just described. The waters were either buffered and kept for a time to allow solution of manganese oxides at pH 4·6–4·75 or kept at pH 1·3 after adding the acid before adding the acetate.

It is seen from Table I that little more dissolves at pH 1·3 than at pH 4·6.

TABLE I

Time allowed for solution of manganese oxides before adding periodate	Estimated concentration of manganese in solution (mg. Mn/m.^{3})
10 min. at pH 4·6	0·8
2 hr. at pH 4·6	0·9
24 hr. at pH 4·6	0·9
24 hr. at pH 1·3	1·0
Same water after storage for 14 days in a carboy	
4 days at pH 4·6	0·0
4 days at pH 1·3	0·2

It is notable that after storage in a carboy for 14 days the manganese, soluble in dilute acid, had decreased to a very low value. During this period, suspended plankton organisms and particles of organic detritus had sedimented and a growth of bacteria with some neritic diatoms had taken place, mostly on the glass surface. Thompson & Wilson's (1935) estimations of total manganese, which includes that soluble in hot concentrated acid, show that diatoms collect relatively large quantities of manganese. Adsorption of manganous ions or of colloidal micelles of hydrated oxides is indicated.

Experiment using the tetrabase method of estimation has shown adsorption of manganese ions from sea water enriched with a manganous salt on protein and even on filter-paper, but not on a clean glass surface.

The deposition of colloidal iron hydroxide on aquatic plants is a common phenomenon. Presumably colloidal and minute particles of oxide of manganese will tend to deposit on organisms in a similar manner.

The next series of estimations show a similar decrease in concentration of soluble manganese after 8 days' storage in a bottle, and further indicate that the adsorbed fraction is wholly eluted by acid at pH 1·3.

TABLE II. SEA WATER COLLECTED FROM A DEPTH OF 2 M. ABOUT 8 MILES OFF PLYMOUTH, 5 APRIL 1948

Time allowed for solution of manganese after adding acid at pH 1·3	Estimated mg. Mn/m.³
20 hr.	0·85
8 days	0·8
Stored 8 days in bottle, then acid added to bottle	
3 hr.	0·9
Poured out of bottle after 8 days' storage before adding acid	
3 hr.	0·05, 0·7, 0·15

In subsequent estimations a buffer mixture was used, consisting of: 117 c.c. glacial acetic acid, 56 c.c. concentrated hydrochloric acid, 113 c.c. 0·880 ammonium hydroxide, 490 c.c. distilled water; and 3 c.c. were added to 50 c.c. of water.

This buffered sea water gave a lower 'reagent blank' value than the ammonium acetate mixture used previously.

In order to determine whether there was any marked difference in concentration of soluble manganese with depth of the water, the series of estimations shown in Table III was made.

TABLE III. WATER COLLECTED 20 MILES SEAWARD FROM PLYMOUTH ON 8 JUNE 1948, DEPTH 72 M.

Sample from (m.)	Time allowed for solution of manganese after adding buffer at pH4·76	Estimated mg. Mn/m.³
0·5	30 min.	1·1
5		0·9
25		1·0
50		1·1
70		1·1
Water collected from same position 30 June 1948		
5	20 hr.	0·75
50		0·3
Water collected 50° 00′ N. 7° 10′ W., 30 June 1948, depth 110 m.		
5	20 hr.	0·45
75		0·25, 0·3

The water occupying the area off Plymouth on 30 June contained less soluble manganese than samples collected earlier in the year. This water differed in other characteristics from that collected in the area during the previous and subsequent months, and in common with the water collected from 7° 10′ W. it contained a considerably larger quantity of organic phosphorus.

I am indebted to Dr M. Parke for the information that the waters of Port Erin Bay, in the Isle of Man, usually contain a rich flora of flagellates during the summer months. In consequence, it was interesting to find whether these waters were richer in soluble manganese than those sampled in the mouth of the English Channel where the water contains fewer flagellates, since the growth of these plants is much affected by shortage of available manganese.

Mr J. R. Bruce kindly collected samples from the former locality, which on analysis gave the following estimates:

Collected from Port Erin Bay	mg. Mn/m.^{3} after 24 hr. at pH 4·7
Sample *a*	2·2
Sample *b*	2·6
Sample *c*	2·0

In this usually flagellate-rich locality the water contained more than twice as much soluble manganese as the waters sampled in the English Channel.

MANGANESE IN FRESH WATERS

River waters are known to contain relatively large quantities of manganese. Twenhofel (1938) writes of 500–5000 mg./m.^{3} in streams, ‘in which it is probable that the prevalent method of transportation of manganese is as oxide hydrosols stabilized by organic colloids’.

It was of interest to find how much of this total was in the form of manganese soluble in dilute acid, and how this varied with the nature of the stream.

Samples of natural waters were collected in June 1948, those from the Lake District by Mr F. J. Mackereth who also kindly supplied the appended particulars relating to the usual planktonic life in the six waters. The results of examining these samples are given in Table IV.

It is noteworthy that the readily acid-soluble manganese varies in the waters from the Lake District in roughly the same order as their productivity. It seems improbable that the manganese content in any way controls the productivity, but more likely that it is affected by those factors which themselves control plant and animal growth. Heintze & Mann (1946) find that more manganese can be washed out from agricultural soils containing greater quantities of organic matter than from soils containing less organic matter. Moreover, addition of organic compounds to the water increased the manganese in the leachate.

TABLE IV. MANGANESE IN SAMPLES OF RIVER AND LAKE WATER

Locality	mg. Mn/m.^{3} soluble after 24 hr. at pH 4·7
Devonshire:	
River Yealm at Wisdome on leaving moorland	1·15
River Yealm at Yealm Bridge after passing through some 7 miles of agricultural country	10
Plymouth tap water (moorland reservoir)	1·8
Lake District:	
Esthwaite. 'A very productive lake' surrounded by agricultural land	>40
Bellham Tarn. 'A small lake containing a good supply of nutrients but not so productive as Esthwaite'	20
Black Beck. Stream feeding Esthwaite and bringing in most of the nutrients	12
Windermere (North Basin). Of fairly high productivity for diatoms, but few blue-green algae	10
Loweswater. A lowland lake lying in agricultural land and usually fairly productive	11 (after 44 hr. 11, 7·5)
Ennerdale. Usually very poor in planktonic organisms and has low concentrations of nutrients	6·5, 8 (after 44 hr. 8, 8·5)

SUMMARY

A method of estimating the maximum quantity of manganese available to plants in sea and fresh waters is described.

Samples of sea water collected off Plymouth in 1948 contained 0·7–1·0 mg. Mn/m.^{3} in solution plus any particles soluble at pH 4·6. After storage and sedimentation of particulate matter, the quantity decreased to 0·0–0·25 mg./m.^{3}

Samples collected off the Isle of Man, an area with a rich summer population of flagellates, contained 2·0–2·6 mg./m.^{3}

The river Yealm, south Devon, on leaving Dartmoor contained 1 mg., and after passing through agricultural land 10 mg./m.^{3}

Lakes and streams in the English Lake District contained 6–40 mg./m.^{3} The least fertile waters contained the least soluble manganese.

REFERENCES

Danielli, J. F., 1944. The biological action of ions and the concentration of ions at surfaces. *Journ. Exp. Biol.*, Vol. 20, pp. 167–76.

Harvey, H. W., 1937. The supply of iron to diatoms. *Journ. Mar. Biol. Assoc.*, Vol. 22, pp. 205–19.

—— 1947. Manganese and the growth of phytoplankton. *Journ. Mar. Biol. Assoc.*, Vol. 26, pp. 562–79.

Heintze, S. G. & Mann, P. J., 1946. Divalent manganese in soil extracts. *Nature*, Vol. 158, p. 791.

Nicholas, D. J., 1946. Detection of manganese deficiency in plants by tissue tests, using tetramethyldiaminodiphenylmethane. *Nature*, Vol. 157, p. 695.

Noddack, I. & Noddack, W., 1940. Die Häufigkeiten der Schwermetalle in Meerestieren. *Arch. Zool.*, Bd. 32, No. 1, p. 1.

Pettersson, H., 1945. Iron and manganese on the ocean floor. *Göteborgs Kungl. Vetensk. Vitterh. Sam. Handl.*, Ser. B, Bd. 3, No. 8, 37 pp.

Thompson, T. G. & Wilson, T., 1935. The occurrence and determination of manganese in sea water. *Journ. Amer. Chem. Soc.*, Vol. lvii, pp. 233–6.

Twenhofel, W. H., 1938. *Principles of Sedimentation.* New York and London.

THE BIOLOGY OF *ASTERIAS RUBENS* L.: GROWTH AND REPRODUCTION

By H. G. Vevers, M.A.

Zoologist at the Plymouth Laboratory

(Text-figs. 1–5)

CONTENTS

INTRODUCTION

The morphology and embryology of the common starfish, *Asterias rubens* L., have been extensively studied, but its general biology and, in particular, the details of its sexual maturity and spawning, have hitherto been largely neglected. This is the more surprising since the species is one of considerable negative economic importance, being a voracious consumer of marketable lamellibranchs and a competitor for food with many bottom-feeding fishes.

In the present work an attempt has been made to follow the cycle of gonad changes which occur throughout the year in populations of *A. rubens* occurring in the English Channel off Plymouth, and also to obtain data on its rate of growth, the relation between size and maturity and the factors influencing the onset of sexual maturity.

DISTRIBUTION, HABITAT AND FOOD

A. rubens is distributed throughout the north-east Atlantic from high water to a depth of 400 m., sometimes to 650 m. The geographical limits of its distribution are to the north, the White Sea and Iceland; to the east, the Baltic; and to the south, the coast of Senegal. It is not found off Greenland and only accidentally in the Mediterranean (Mortensen, 1927).

In his survey of the bottom fauna near the 30-fathom line from Eddystone to Start Point in south Devon, Allen (1899) found that it occurred on nearly all the grounds, varying from mud to coarse and shelly gravel and rock, although there were considerable differences in its abundance on the various substrata. He also observed that in this area its distribution was closely correlated with that of *Chlamys opercularis* (L.) which provides a large part of its food.

While still in a young stage it eats barnacles and small lamellibranchs. As an adult it feeds chiefly on worms, crustaceans, other echinoderms and many lamellibranchs, in particular *C. opercularis* and *Mytilus edulis*. In fact, it would appear to be omnivorous, eating any living or dead animal material on which it can get a firm hold.

POPULATIONS OF *ASTERIAS RUBENS* OFF PLYMOUTH

As is usual with asteroids, size is expressed in the following study in terms of radius length, measured from the anus to the tip of the longest arm. The starfishes were all measured living, out of water, on a flat bench, so that each arm could be flattened out and straightened before measurement. Arm measurements (denoted as R = radius length) were taken to the nearest millimetre, except those of starfishes with R greater than 20 cm., where arm contraction and expansion made the readings only accurate to the nearest 0·5 cm.

Records were also kept of the length of the gonad in each measured arm. These measurements were taken from the central point of the blunt proximal end of the gonad to the tip of the most distal tubule. At the same time smears of each gonad measured were examined microscopically, and sections were cut of a number of gonads in each sample.

The difference in size composition of populations living under different conditions is clearly brought out by a comparison of the two main populations of *A. rubens* studied. The first population occurs on the Rame-Eddystone Grounds on a mixed substratum of sand and rough ground at a depth of 25–30 fathoms. The second population, which will be termed the Outer Grounds population, occurs some miles away to the south and south-west of Eddystone. The sea bottom in this area is largely composed of sand with patches of gravel, and it shelves gradually from a depth of 64 m. 3 miles south of Eddystone to 70 m. at 6 miles south. The routine hauls for starfishes were all taken with an otter trawl.

The Rame-Eddystone Grounds Population

The means and ranges of the starfish samples taken in this area are shown in Table I. It will be seen that there are certain differences between one catch and another not always consistent with the period at which they were taken; for instance, the catch for 24 June 1947 has a lower size range and mean than that for 13 June 1947. This is to be expected in a species where growth is so directly dependent upon available food, and where it may cease altogether in places where the food supply is poor. It would not be possible with present bottom-sampling techniques to obtain periodic representative samples from any one small section of the main area, nor was such attempted.

TABLE I. ANALYSIS OF HAULS OF *ASTERIAS RUBENS* ON RAME-EDDYSTONE GROUNDS

	Total in catch	Males			Females			Sex not known
Date		No.	Range	Mean σ_M	No.	Range	Mean σ_M	
1. i. 47	58	27	4·0–15·9	9·24 ± 0·56	28	4·0–13·9	9·43 ± 0·48	3
4. ii. 47	30	15	4·0–12·9	8·70 ± 0·67	12	4·0–14·9	9·75 ± 1·06	3
27. iii. 47	44	16	3·0–13·9	8·50 ± 0·74	19	3·0–14·9	8·66 ± 0·63	9
16. iv. 47	41	10	5·0–15·9	8·30 ± 1·11	18	5·0–14·9	9·33 ± 0·61	13
28. iv. 47	87	34	3·0–14·9	8·79 ± 0·38	42	5·0–13·9	9·45 ± 0·33	11
13. vi. 47	33	14	8·0–13·9	11·15 ± 0·32	16	6·0–15·9	11·13 ± 0·68	3
24. vi. 47	35	11	5·0–14·9	9·60 ± 0·91	23	7·0–16·9	11·02 ± 0·52	1
2. vii. 47	78	33	5·0–22·0	13·40 ± 0·57	38	7·0–17·9	12·66 ± 0·42	7
3. vii. 47	50	18	6·0–21·0	11·00 ± 0·77	22	7·0–15·9	11·77 ± 0·45	10
24. vii. 47	42	15	3·0–16·9	9·70 ± 0·82	19	5·0–15·9	10·13 ± 0·69	8
25. vii. 47	40	19	3·0–16·9	9·66 ± 0·84	12	5·0–17·9	9·83 ± 0·96	9
7. viii. 47	68	30	7·0–16·9	11·27 ± 0·39	35	5·0–15·9	11·30 ± 0·47	3
19. viii. 47	78	27	3·0–16·9	10·98 ± 0·59	44	6·0–24·0	12·05 ± 0·51	7
11. ix. 47	77	28	3·0–17·9	10·43 ± 0·64	45	3·0–14·9	9·66 ± 0·42	4
28. x. 47	38	12	6·0–15·9	11.32 ± 0·82	18	8·0–15·9	11·28 ± 0·45	8
17. xi. 47	38	19	5·0–18·9	11·08 ± 0·81	18	5·0–16·9	10·56 ± 0·79	1
16. i. 48	49	23	4·0–14·9	9·98 ± 0·61	26	4·0–15·9	10·35 ± 0·61	0
10. ii. 48	41	21	4·0–15·9	9·74 ± 0·64	13	4·0–13·9	8·35 ± 0·79	7
23/24. iii. 48	61	23	4·0–15·9	10·14 ± 0·70	32	4·0–18·9	10·47 ± 0·54	6
11. v. 48	68	28	4·0–18·9	11·46 ± 0·57	38	5·0–17·9	10·50 ± 0·50	2
7. vi. 48	50	25	6·0–17·9	10·78 ± 0·53	25	6·0–17·9	11·30 ± 0·55	0
21. vi. 48	110	58	5·0–16·9	11·57 ± 0·36	52	5·0–19·9	11·13 ± 0·40	0
	1216	506			595			115

TABLE II. ANALYSIS OF HAULS OF *ASTERIAS RUBENS* ON OUTER GROUNDS

	Total in catch	Males			Females			Sex not known
Date		No.	Range	Mean σ_M	No.	Range	Mean σ_M	
20. iii. 47	33	12	6·0–16·9	12·50 ± 0·90	21	9·0–21·9	14·60 ± 0·61	0
9. iv. 47	29	11	8·0–18·9	12·68 ± 1·02	13	7·0–19·9	13·27 ± 0·85	5
18. iv. 47	50	25	11·0–19·9	14·86 ± 0·43	25	9·0–21·9	15·66 ± 0·52	0
25. iv. 47	175	66	5·0–18·9	14·21 ± 0·32	105	6·0–18·9	15·05 ± 0·21	4
23. v. 47	57	17	9·0–15·9	12·26 ± 0·47	39	8·0–16·9	12·35 ± 0·33	1
16. vi. 47	101	44	10·0–22·9	15·84 ± 0·43	57	11·0–23·9	16·45 ± 0·33	0
4. vii. 47	213	83	8·0–19·9	14·79 ± 0·27	127	8·0–21·9	15·49 ± 0·25	3
16. vii. 47	172	89	7·0–21·9	16·56 ± 0·28	79	8·0–22·9	16·92 ± 0·36	4
27. viii. 47	151	63	9·0–19·9	14·29 ± 0·30	85	8·0–22·9	14·88 ± 0·28	3
21. x. 47	71	36	6·0–22·9	14·72 ± 0·51	34	10·0–21·9	15·88 ± 0·48	1
13. xi. 47	39	19	13·0–26·9	18·55 ± 0·93	20	12·0–33·9	17·95 ± 1·02	0
15. i. 48	29	15	5·0–22·0	14·03 ± 1·19	14	10·0–21·8	15·36 ± 0·95	0
4. ii. 48	15	7	9·0–21·5	13·64 ± 1·53	8	7·1–16·1	12·0 ± 1·03	0
12. iii. 48	38	15	5·9–16·6	12·23 ± 0·76	20	8·9–18·8	14·35 ± 0·61	3
14. iv. 48	103	50	8·0–20·0	14·34 ± 0·38	53	7·6–20·5	15·88 ± 0·43	0
13. v. 48	231	87	10·5–23·8	16·89 ± 0·32	144	8·8–25·5	18·51 ± 0·25	0
11. vi. 48	148	64	7·5–17·8	13·48 ± 0·32	84	6·2–23·5	13·44 ± 0·32	0
6. vii. 48	90	38	8·4–21·5	14·24 ± 0·52	52	7·6–21·5	14·98 ± 0·42	0
11. viii. 48	50	20	11·1–22·2	15·00 ± 0·66	30	9·6–27·5	15·6 ± 0·73	0
	1795	761			1010			24

The Outer Grounds Population

The means and ranges of the starfish samples taken in this area are shown in Table II. This shows clearly the overall larger sizes of the starfishes in this area, compared with those in the Rame-Eddystone Grounds.

The Population near E 1

A smaller number of samples was taken by trawling in the grounds near International Station E 1 (10 miles S.W. of Eddystone). The means and sizes of these samples are shown in Table III. The starfishes taken in this area are still larger than those on the Outer Grounds.

TABLE III. ANALYSIS OF HAULS OF *ASTERIAS RUBENS* NEAR E 1

	Total in	Males			Females		
Date	catch	No.	Range	Mean σ_M	No.	Range	Mean σ_M
3. vi. 47	168	44	11·0–23·9	17·98 ± 0·42	124	11·0–30·9	20·36 ± 0·31
10. vi. 47	19	7	16·0–20·9	18·64 ± 0·49	12	18·0–23·9	20·75 ± 0·40
17. vi. 47	39	9	14·0–21·9	19·38 ± 0·77	30	15·0–27·9	21·37 ± 0·57
15. ix. 47	50	21	14·0–27·9	20·16 ± 0·72	29	15·0–28·9	21·43 ± 0·69
	276	81			195		

The Cawsand Bay Population

A single haul was obtained from this area on 23 May 1947, and it consisted of 18 small starfishes. The means and range of the starfishes in this haul were:

	No.	Range	Mean (cm.)
Males	8	3·0–4·0	3·7
Females	10	3·0–8·4	4·3

The Plymouth Sound Population

In spring 1948 a new and very large population of *A. rubens* was found on Asia Grounds in Plymouth Sound, 800 m. W.S.W. of the Plymouth Laboratory. A small sample was obtained on 10 February 1948 and a larger one on 16 April 1948, both of which were examined for size and gonad maturity. The means and size ranges of these samples are shown in Table IV.

TABLE IV. ANALYSIS OF HAULS OF *ASTERIAS RUBENS* ON ASIA GROUNDS IN PLYMOUTH SOUND

	Total in	Males			Females		
Date	catch	No.	Range	Mean σ_M	No.	Range	Mean σ_M
10. ii. 48	25	11	8·3–11·0	9·50 ± 0·08	14	6·6–10·1	8·79 ± 0·28
16. iv. 48	100	52	5·9–18·4	9·30 ± 0·28	48	6·0–11·8	9·54 ± 0·21
	125	63			62		

In addition to these samples, hauls were also made on 3 and 4 March 1948. On 3 March three 40-min. trawl hauls were made and the total catch was

595 *A. rubens*. On 4 March four 40-min. trawl hauls yielded a total catch of 1259 *A. rubens*.

This population was undoubtedly the most homogeneous of those examined, and it was found to be feeding entirely on very rich beds of mussels (*Mytilus edulis*). In contrast with the starfishes caught outside Plymouth Sound, which were red-brown or more rarely pale yellowish brown in colour, the starfishes from Asia Grounds were, without exception, a bright red colour. In addition, there was a marked difference in body shape. Starfishes from the Rame-Eddystone and Outer Grounds had thin, gradually tapering arms, whereas the Asia Grounds population had thick robust arms which tapered only in the distal part. These very distinct differences may be correlated with the differences in food supply of the starfishes from the two areas.

The Rame Mud Population

A single haul was taken with an Agassiz trawl on the Rame mud, 2 miles W.S.W. of Rame Head in 26 fathoms. Although the catch with this trawl is not strictly comparable with those taken with the otter trawl, it is interesting to note that no medium or large starfishes were taken, although these sizes have often been taken with an Agassiz trawl working on the Outer Grounds. The starfishes taken on the mud were all small or very small, with thin arms, coloured dark red-brown. The mean and range for the starfishes in this haul were:

Date	Total in catch	Range (cm.)	Mean (cm.)
7. iv. 48	95	1·0–6·4	2·52

The above data are for both sexes, as the specimens in this catch were mostly too small and underdeveloped to allow the sex to be determined accurately.

Comparison of the Size Compositions of the Populations

The means and ranges have been used only to characterize the starfish populations of the different grounds, and it will be seen from Fig. 1 that the differences are marked. This graphical representation of the samples shows that, apart from the marked difference between the means, there was in the Outer Grounds a complete lack of the size classes *R* 3–5 cm. and a scarcity of the size classes 7–10 cm.; and this in spite of the large number of individuals taken in many of the Outer Grounds hauls. These size classes are all present in reasonable numbers in the Rame-Eddystone samples. This difference between the two sets of samples cannot be due to selective fishing by the trawl. It is unlikely that the same fishing gear used over similar substrata would select large and medium starfishes in the Outer Grounds and small and medium ones on the Rame-Eddystone Grounds if all three size groups were present in each area. It is considered that the trawl brings up from each ground a random sample of all those sizes which are present, with the exception of the smallest sizes (*R* under 3 cm.). These smaller sizes were, in fact, present on the Rame-Eddystone Grounds in the spring and summer of the year, when they were caught in a few dredge hauls. They were not found on the Outer Grounds until about October, when a few small (*R ca.* 3–6 cm.) starfishes were taken.

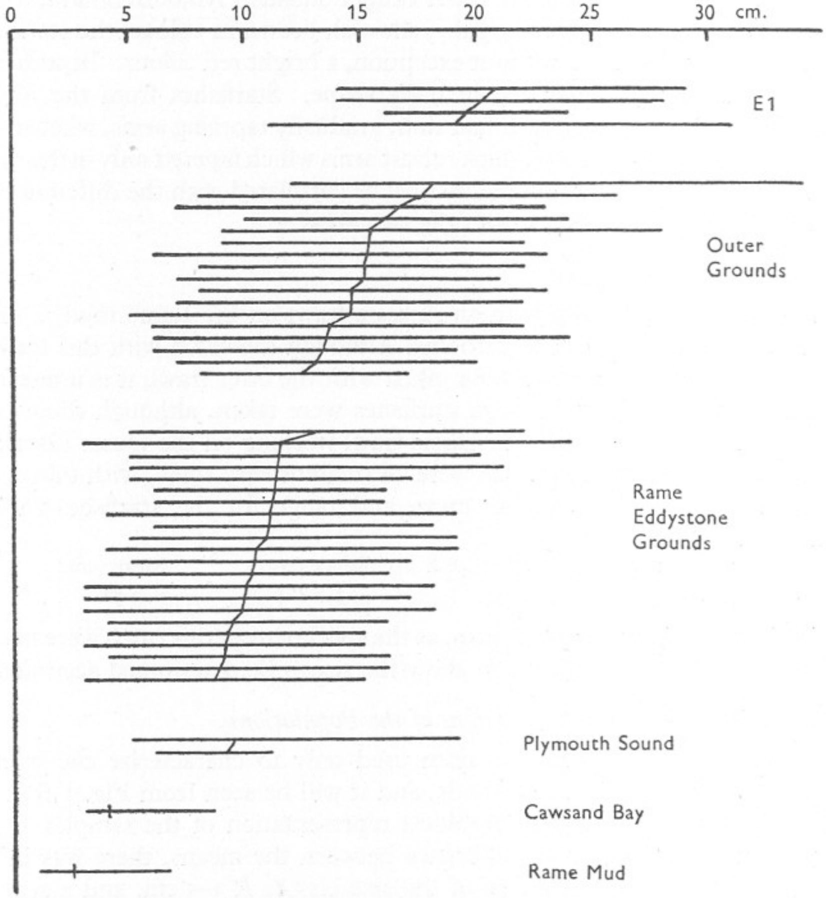


Fig. 1. Size ranges and means (in cm.) of six starfish populations off Plymouth. (Means joined by vertical lines.)

There are two possible explanations for the absence from the Outer Grounds of the small (*R* 3–6 cm.) sizes. First, the 1946 starfish spat might have failed to settle in the Outer Grounds. This is very unlikely in view of the large breeding population on these grounds. But secondly, a proportion of the 1946 brood may have settled successfully in the Outer Grounds and prospered so well on the rich food there that by March–April 1947 they had already reached and passed the 6 cm. size class. This would mean that by April 1947 there would be few, if any, starfishes with a radius length of less than 6 cm.

remaining on the Outer Grounds, and the chances of catching them in trawl or dredge would be slight. On this view it would be necessary to postulate a radial growth of a least 6 cm. (and probably more) in the 9 months between metamorphosis in July 1946 and April 1947; that is, an average monthly increment of rather less than one centimetre. That this is quite possible is shown by the laboratory observations on rate of growth in *Asterias rubens* recorded below.

The Plymouth Sound starfishes caught in 1948 could not have been younger than the 1947 brood, and they show means of $R=9{\cdot}4$ cm. for the males and $R=9{\cdot}2$ cm. for the females. This very homogeneous population was almost certainly made up of one year-group only, and, again on the basis of laboratory observations, it is considered that they did, in fact, belong to the 1947 brood. A large concentrated starfish population such as this, feeding on an abundant fixed food supply, will tend to remain localized in space and its individuals will be likely to grow at approximately similar growth rates so long as the food lasts. When the food is depleted the population will disperse and the growth rate of the individual starfishes will then become variable, leading to a population which is heterogeneous in size composition.

In contrast, the Rame Mud population with a mean $R=2{\cdot}5$ must also have been at least 10 or 11 months old, and probably represented the remains of one or more spatfalls which had fallen on a bottom poor in available starfish food.

GROWTH RATE

During 1947 a number of starfishes taken on the Rame-Eddystone Grounds or from weed collected in Plymouth Sound were kept in laboratory tanks with an excess supply of graded sizes of *Mytilus edulis*, *Tellina crassa* and *Chlamys opercularis*. After about a week the starfishes became acclimatized to aquarium conditions and started feeding voraciously. Measurements of radius length were taken at intervals, and results are shown in Table V. (No attempt was made in these preliminary experiments to record the quantity of food consumed by each individual starfish, although further work on this subject is now in progress.) The data in Table V are shown graphically in the form of growth curves in Fig. 2. Growth is fastest during the summer, when the monthly increment may exceed 1 cm. Even during the winter growth continues, although at a reduced rate, and a further increase in rate occurs in spring.

Most of these observations were made on starfishes which were caught inshore in summer 1947 at sizes between 4 and 8 cm. radius. Assuming that these belonged to the 1946 brood, they must have been growing at an average rate of 0·5 cm. per month since metamorphosis 11 or 12 months before. When fed with unrestricted supplies they grew at a somewhat faster rate. Thus starfish B 11, caught and measured as 4·4 cm. *R* on 10 August, had reached 9·2 cm. *R* by 30 November. This is an increment of 4·8 cm. in $3\frac{3}{4}$ months, or an average of 1·2 cm. per month. This was a fast summer rate and growth decreased from November onwards. The curves show that growth in this starfish and in other similar ones was not steady, but that it appears to have proceeded in a number of steps. This may, of course, have been due to slight errors in measurement.

TABLE V. GROWTH MEASUREMENTS FOR WELL-FED INDIVIDUALS OF *ASTERIAS RUBENS* IN CM.

	B 1	B2	B 3	B 4	B 5	B 6	B 7	B 8	B 9	B 10	B 11	B12	B13	B14	B15	BB 9
26. i. 47	5·9	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
2. ii. 47	6·0	3·5	—	—	—	—	—	—	—	—	—	—	—	—	—	—
16. ii. 47	6·2	3·6	4·4	—	—	—	—	—	—	—	—	—	—	—	—	—
2. iii. 47	6·4	3·7	4·7	3·0	—	—	—	—	—	—	—	—	—	—	—	—
6. iv. 47	7·2	4·3	5·5	4·1	—	—	—	—	—	—	—	—	—	—	—	—
13. iv. 47	7·6	4·3	5·5	—	—	—	—	—	—	—	—	—	—	—	—	—
27. iv. 47	—	4·5	5·9	—	7·2	—	—	—	—	—	—	—	—	—	—	—
4. v. 47	—	4·8	6·1	—	7·4	—	—	—	—	—	—	—	—	—	—	—
25. v. 47	—	5·4	7·1	—	8·0	6·0	—	—	—	—	—	—	—	—	—	—
1. vi. 47	—	—	7·4	—	8·0	6·4	4·8	—	—	—	—	—	—	—	—	—
29. vi. 47	—	—	8·3	—	9·4	7·3	5·7	—	—	—	—	—	—	—	—	—
6. vii. 47	—	—	8·6	—	—	7·7	6·1	1·3	—	—	—	—	—	—	—	—
20. vii. 47	—	—	8·8	—	—	8·3	6·7	1·8	1·0	—	—	—	—	—	—	—
10. viii. 47	—	—	9·7	—	—	9·0	7·6	2·3	1·4	8·6	4·4	4·2	—	—	—	—
17. viii. 47	—	—	9·8	—	—	9·6	8·3	2·8	1·6	8·7	4·5	4·2	7·8	5·8	—	—
24. viii. 47	—	—	9·8	—	—	10·1	—	3·0	2·0	8·9	4·9	4·6	8·0	6·1	—	—
7. ix. 47	—	—	—	—	—	10·5	—	3·1	2·2	10·2	5·6	5·1	8·6	7·0	—	—
21. ix. 47	—	—	—	—	—	11·2	—	3·9	2·7	11·0	6·6	5·3	9·2	8·1	—	—
28. ix. 47	—	—	—	—	—	11·3	—	—	2·8	11·7	7·3	—	9·4	8·8	—	—
26. x. 47	—	—	—	—	—	11·9	—	—	3·2	12·4	8·7	—	—	10·3	6·3	—
2. xi. 47	—	—	—	—	—	11·9	—	—	3·4	—	8·8	—	—	10·4	6·3	—
30. xi. 47	—	—	—	—	—	—	—	—	4·5	—	9·2	—	—	10·7	6·9	—
7. xii. 47	—	—	—	—	—	—	—	—	4·8	—	9·3	—	—	—	7·0	—
14. xii. 47	—	—	—	—	—	—	—	—	5·0	—	9·3	—	—	—	7·0	—
4. i. 48	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	9·8
1. ii. 48	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	10·7
7. iii. 48	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	11·3
14. iii. 48	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	11·3

A few growth curves were obtained for starfishes almost certainly belonging to the 1947 brood. Starfish B 9 was caught on 20 July 1947 on a clump of *Mytilus edulis* and it then measured 1 cm. *R*. By 7 December 1947 it measured 4·8 cm., an increment of 3·8 cm. in $3\frac{2}{3}$ months, or about 1 cm. (average) per month. Some idea of the size likely to have been reached by starfish B 9 by April 1948 may be obtained by referring to the growth curve of another well-fed starfish B 1 which measured 5·9 cm. *R* on 26 January 1947. By 13 April 1947 this starfish had grown to 7·6 cm. *R*, an increment of 1·7 cm. in $2\frac{1}{2}$ months, or an average (winter) monthly increment of 0·7 cm.

From the present observations on growth rate it is clear that small and very small starfishes (up to at least 6 cm. *R*) can grow at a monthly rate of rather more than 1 cm. in summer and autumn and of rather less than 0·5 cm. in winter. These rates are only attained when the food supply is abundant.

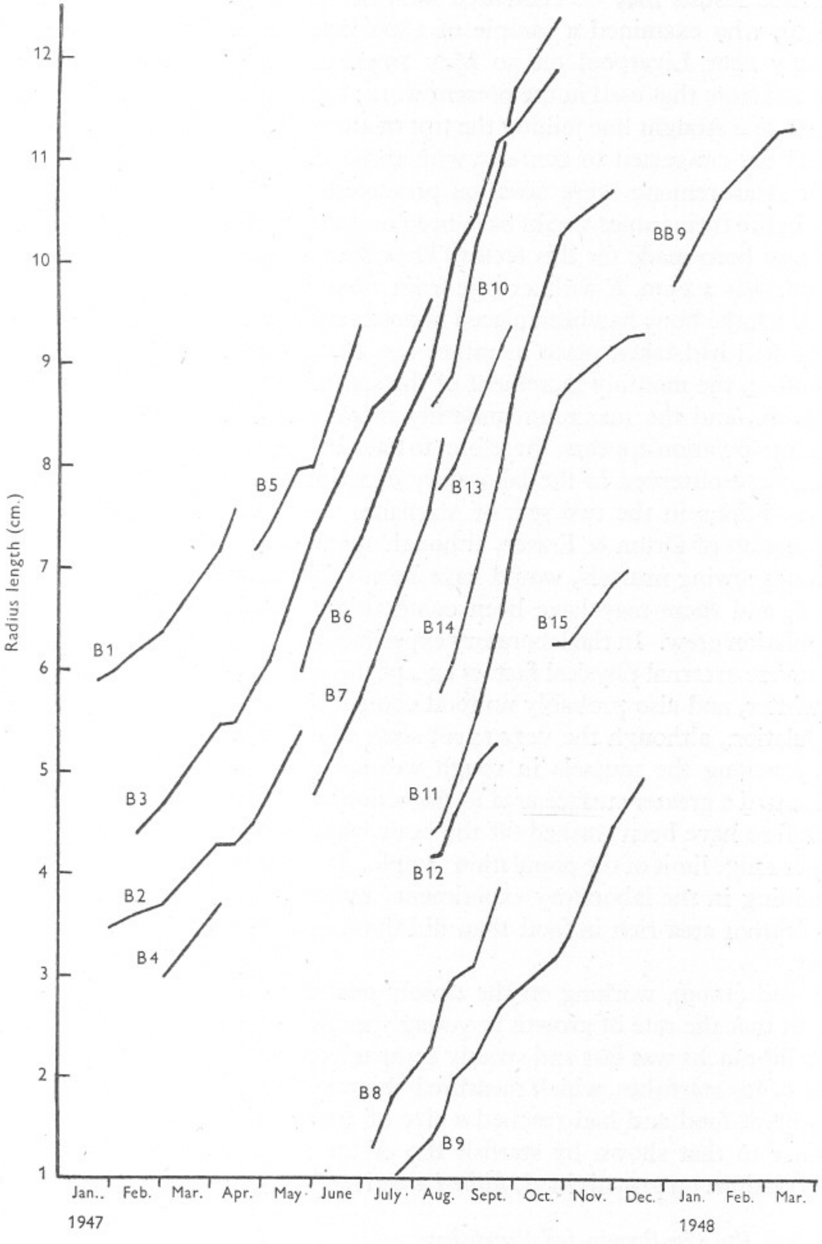


Fig. 2. Growth curves of well-fed *A. rubens* plotted from Table V.

These results may be compared with the observations of Orton & Fraser (1930), who examined a sample of 1800 young *Asterias rubens* taken from a buoy near Liverpool on 30 May 1930. Their method of measurement differed from that used in the present work; they expressed size in terms of the length of a straight line joining the tips of alternate arms. Their values for size have been converted to conform with those used in this study. In addition, their measurements were taken on preserved specimens, and they suggested that in life their values would have been on an average 5 mm. larger; allowance has also been made for this factor. They found that the modal value of their sample was 2·2 cm. *R* with a range from 0·6 to 5·2 cm., and, knowing the date on which the buoy had been placed in position, they reckoned that this amount of growth had taken place in rather less than a year. On this information, therefore, the monthly increment of the starfishes round the mode was about 0·25 cm., and the maximum monthly increment a little more than 0·5 cm. Their population appears, therefore, to have been growing considerably slower than those observed in the laboratory experiments. However, the total sum of conditions in the two sets of starfishes is not strictly comparable. The population of Orton & Fraser, although surrounded by a plentiful supply of young growing mussels, would have been subject to the action of waves and wind, and there may have been competition for suitably sized food as the population grew. In the laboratory experiments, on the other hand, there were no severe external physical factors except the seasonal decrease in temperature in winter, and also probably no food competition. Furthermore, in the buoy population, although the very small sizes would have no difficulty in hiding away among the mussels in rough weather, the larger starfishes will have presented a greater surface area to the action of the waves. Some of them may therefore have been washed off the buoy, thus reducing the modal value and upper range limit of the population sample. It is considered that the conditions obtaining in the laboratory experiments more closely resembled those on a sea bottom area rich in food than did those in the population on the floating buoy.

Mead (1899), working on the closely related species *A. forbesi* Desor, also found that the rate of growth in young specimens fed on plentiful supplies of lamellibranchs was fast and strictly comparable with the present observations. One of his starfishes, which measured about 1·8 cm. on 18 August, was fed on abundant food and had reached a size of 3·5 cm. *R* by 26 September, a rate similar to that shown by starfish B 9 of the present observations. Further observations on growth in *A. forbesi* are given by Galtsoff & Loosanoff (1939).

Growth Rate in Poorly-fed Starfishes

As control to these experiments a number of starfishes were kept in a separate tank with a minimum of food (a few small barnacles only). They were measured periodically and it was found that no measurable growth occurred, and in a few the length of the radius actually decreased, although the amount of reduction was within the limits of accuracy of the method of measurement.

As a further control experiment, starfishes of known size were placed in three boxes on a raft in Plymouth Sound on 13 December 1946.

Six *A. rubens* were placed in box R together with six *Tellina crassa*, three *Paphia rhomboides* and one *Venus casina*. Each starfish measured $R = 6$ cm. ± 0·1. No further food was added and the box was left undisturbed until 21 May 1948 when it contained: three *Asterias rubens* ($R = 6{\cdot}4$, 6·2, and 6·2 cm.), eight *Ciona intestinalis*, four *Ascidiella aspersa*, two *Polycirrus caliendrum*, and numerous *Jassa falcata*, as well as the empty shells of the original molluscs. Besides the latter, it is probable that the three surviving starfishes had eaten the remains of the three which had died, as well as possible spatfalls of barnacles.

Boxes L and C each started with six *Asterias rubens* of the same size as in box R, but without any food. When opened on 21 May 1948 they contained:

Box L	Box C
Three *A. rubens* ($R = 5{\cdot}8$, 5·7, 5·0 cm.)	Three *A. rubens* ($R = 6{\cdot}1$, 5·1, 3·8 cm.)
Two colonies *Leucosolenia* sp.	Four *Molgula tubifera*
Numerous *Jassa falcata*	Three *Sycon coronatum*
	Three colonies *Leucosolenia* sp.
	Two colonies *Halichondria panicea*
	Numerous *Jassa falcata* and one empty *Mytilus edulis* shell (2·3 cm. long)

In these boxes the surviving starfishes would again have had the remains of the dead starfishes to feed on, as well as possible spatfalls. In box C the *Mytilus* had also almost certainly been eaten by one of the starfishes.

In all three boxes the amount of food available was infinitesimal in comparison with the long period of the experiment ($17\frac{1}{4}$ months). The starfishes were, therefore, to all intents without food during the greater part of this period and, as the measurements show, there was no significant growth. All the starfishes which survived were emaciated and darker in colour than at the outset of the experiment. In the three individuals which showed a significant decrease in size the arrangement of the spines on the aboral side and of the ambulacral plates suggested a marked contraction of the muscles between the various skeletal plates. This apparent contraction may have been due to actual resorption of muscle tissue, and further observations are being made to check this explanation.

Lack of food therefore stops growth, as would be expected, but this cessation of growth is not necessarily followed by the death of the animal, since it has been shown that starfishes will live for at least 17 months with practically no food. This means that it is not possible to tell the age of a starfish from its size, and a starfish 1 year old may, in fact, measure anything between about 1 and 9 cm. in radius.

REPRODUCTION

Criteria of Breeding

Three main phases may be recognized in the reproduction of a marine invertebrate:

(*a*) Maturing of the gametes in the parent gonad.

(*b*) Spawning of the gametes, usually directly into the sea, and fertilization.

(*c*) Development of the fertilized egg into the adult, usually with an intermediate free-swimming larval stage.

With *Asterias rubens* reliable observations on the reproductive period have been largely based on records of larvae in different localities. Examination of these records shows that there is considerable variation from year to year in the period at which larvae were taken, even in the same locality. There is, however, no certain way of knowing from which local population the larvae have been derived, as they may be carried away from the area in which they were spawned by the action of currents. Collections of larvae have often been taken sporadically and not regularly throughout the year, so that the absence of a record during any period may only mean that no collections were made. As an exception to this criticism mention should be made of the valuable observations on the occurrence of *A. rubens* and other echinoderm larvae in the Sound between Denmark and Sweden recorded by Thorson (1946).

The mechanism of spawning (phase *b*) has been studied in echinoids by Fox (1924) and Palmer (1937). In *A. rubens* Gemmill (1914) found that spawning may be induced by the presence of sperms and ova, but he did not separate ova from sperm when they were used as stimuli to spawning.

The present work is primarily concerned with phase *a*, the process of gonad ripening within wild populations, as distinct from the cytology of gamete maturation—which has been described for *A. rubens* by Gemmill (1914). Data on this process in a number of separated populations may give information on the factors controlling the differences in productivity of the bottom fauna of different areas. Regular examinations were made of the state of the gonads in the parent starfishes.

The relation between body size in *A. rubens* and the size of the gonads varies greatly according to the time of the year. After the breeding season the gonads are thin, short and shrunken caeca, almost never exceeding 2–3 cm. in length, even in the largest starfish. During the period of maturity, on the other hand, the gonads are very large and may extend from their origin near the interradial angle almost to the tip of the arm.

Although this increase is very largely one of volume, the coelomic cavity of the arms in which the maturing gonads are at liberty to grow is essentially elongated, and it has been found most practicable to denote gonad size by length measurements. This method of gonad measurement also allows a direct comparison to be made between gonad size and the size of the parent animal expressed in terms of radius length.

Stages of Ovarian Maturity

The gonads of all the starfishes taken in the hauls were examined living, and records were kept of the state of sexual maturity. To allow comparison of the gonad states between one catch and the next an arbitrary scheme of stages of ovarian maturity was used. This was not attempted in the male, where any separation of stages beyond 'unripe', 'ripe' and 'spawned' was found to be unreliable. For the ovaries six stages of maturity were defined, primarily in terms of the sizes of the oocytes and eggs, but account was also taken of the outer appearance and length of each ovary. Examination of the colour and texture only does not provide a reliable criterion of the stage of sexual maturity reached.

The six stages of ovarian maturity were defined as follows:

1. *Very immature.* Ovary transparent and thin, with a length usually between 0·1 and 0·5 cm. Few early transparent oocytes, with no trace of yolk, up to 40 μ in diameter. Most ovaries in this stage were probably virgin.

2. *Immature.* Ovary opaque; length usually between 0·5 and 1·5 cm. Oocytes still transparent, without yolk, but more numerous and up to 80 μ in diameter. This stage included many virgin starfishes, but also probably a few which had bred before.

3. *Ripening.* Ovary always opaque, white to yellowish, and more than 1 cm. in length. Distinguished at once from stage 2 by the very numerous oocytes, all yolky, and varying in diameter between 200 μ and the diameter of the ripe eggs.

4. *Ripe.* Ovary almost translucent and greatly enlarged with swollen caeca, and nearly always longer than 1·5 cm. The maximum length of the ripe ovary varies considerably, but is commonly between one-tenth and two-fifths of the radius length, sometimes up to seven-eighths of this length. Containing 90% or over of ripe eggs.

5. *Spawned.* Ovary opaque and yellow with shrunken caeca. Usually between 1 and 4 cm. in length, according to the size of the animal. A few oocytes appear in a smear, but the distinguishing character is the residue of a few ripe but unspawned eggs which are in process of breaking up, their yolky material being ingested by amoebocytes.

6. *Spawned and Re-ripening.* Ovary similar in shape and size to that in stage 5, but no unspawned eggs remain, and a fresh generation of yolky oocytes has appeared. This stage occurs in late summer and can be recognized with some certainty up to September. After this it is not distinguishable from stage 3 and so from 1 October all records of this type of ovary with yolky oocytes are recorded as stage 3.

The sequence of stages in the life of an individual starfish appears, therefore, to be

$$\overset{\text{Breeding year}}{\overbrace{1\quad 2\quad 3\quad 4\ {}_{\star}\ 5\quad 6}^{\text{1st}}\qquad \overbrace{3\quad 4\ {}_{\star}\ 5\quad 6}^{\text{2nd}}\qquad \overbrace{3\quad 4\ {}_{\star}\ 5\quad 6\quad 3}^{\text{3rd}},\ \text{etc.}}$$

In each year spawning is indicated by an asterisk. Starfishes which have once bred never appear to pass through stage 1 again, although it is possible that a few may return to stage 2. The available evidence shows, however, that after spawning a population never shows any significant increase in the number of individuals in ovarian stage 2. In a few individual starfish the ovaries may show signs of complete atrophy as opposed to the normal seasonal regression.

Analysis of Reproductive Cycles

Rame-Eddystone Grounds. The percentages in each stage of ovarian maturity in 1947 are plotted graphically against time in Fig. 3A. Although each point in this graph is based on a relatively small number of females (owing to the small catches in this area), it is quite evident that the number of females which actually reached sexual maturity (stage 4) during 1947 was surprisingly small. Ripe ovaries were, in fact, only found in the two April catches of this year, and then only in 17 and 19% of the females. This small proportion of ripe females is reflected later in the season in the small percentages of stage 5 recorded. Fig. 3A also shows the large and steady percentages of stages 1 and 2 during 1947. The peak values for stages 1 and 2 in June and July 1947 are probably due to the arrival in the catches of young starfishes which the trawl had previously failed to capture but which had by then reached a catchable size. It is unlikely that these young starfishes had bred before, but they would probably have done so in the following year (1948), that is when they were 2 years old. As their ovaries start to mature in preparation for this breeding the values for stages 1 and 2 should fall off and stage 3 should increase. This is beginning to happen in September and October 1947.

During 1947, therefore, less than 20% of the total female population of starfishes (over $R=3$ cm.) on these grounds produced ripe eggs.

In 1948 comparable samples from the same grounds showed a similar breeding cycle, but with important modifications (Fig. 4A). The most noticeable difference was the greater length of time during which ripe eggs were recorded in 1948, namely February till the beginning of June, with peak egg production in April and May. In 1948, however, the percentage of definitely non-breeding starfishes (stages 1 and 2) was still high, being approximately 40% compared with 50–70% in 1947.

The Outer Grounds. On these grounds the observations on state of maturity showed an entirely different picture. The percentages in each stage of ovarian maturity in 1947 and 1948 are plotted graphically against time in Figs. 3B and 4B. Nearly all the catches from this area were large, the majority totalling over fifty individuals and some over 100. Furthermore, the proportion of females in these catches was nearly always above 50% and so the samples on which Figs. 3B and 4B are based are relatively larger than those which form the basis of Figs. 3A and 4A. Fig. 3B shows that ripe females were already present (11%) in the population on 7 March, the date of the first catch from this area. The percentage of ripe females increased from then onwards to a peak in the second half of April. On 23 May 1947 there were no

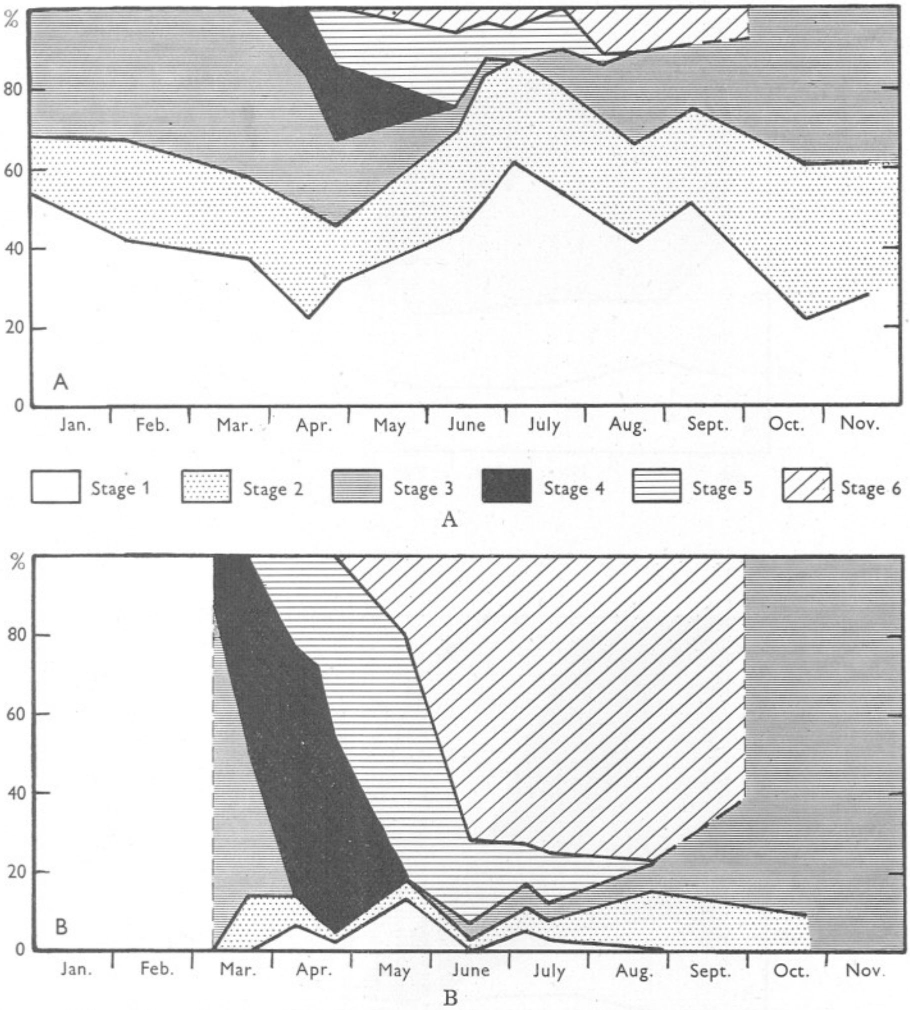


Fig. 3. Ovarian maturity. Percentages in each stage during 1947. A, Rame-Eddystone Grounds; B, Outer Grounds.

ripe females in the population sample. Stage 5 females were dominant in the population in May and the first half of June. After this 'recently spawned' ovaries were again scarce, as they gave place to those in stage 6.

In this area the proportions of stages 1 and 2 combined are remarkably constant and never exceeded 15% of the total population of females.

During 1948 the reproductive cycle (Fig. 4*b*) was essentially similar to that of 1947. Data are, however, available for the early part of 1948, and they show that ripe eggs were produced from February till the end of May with a peak in March and April.

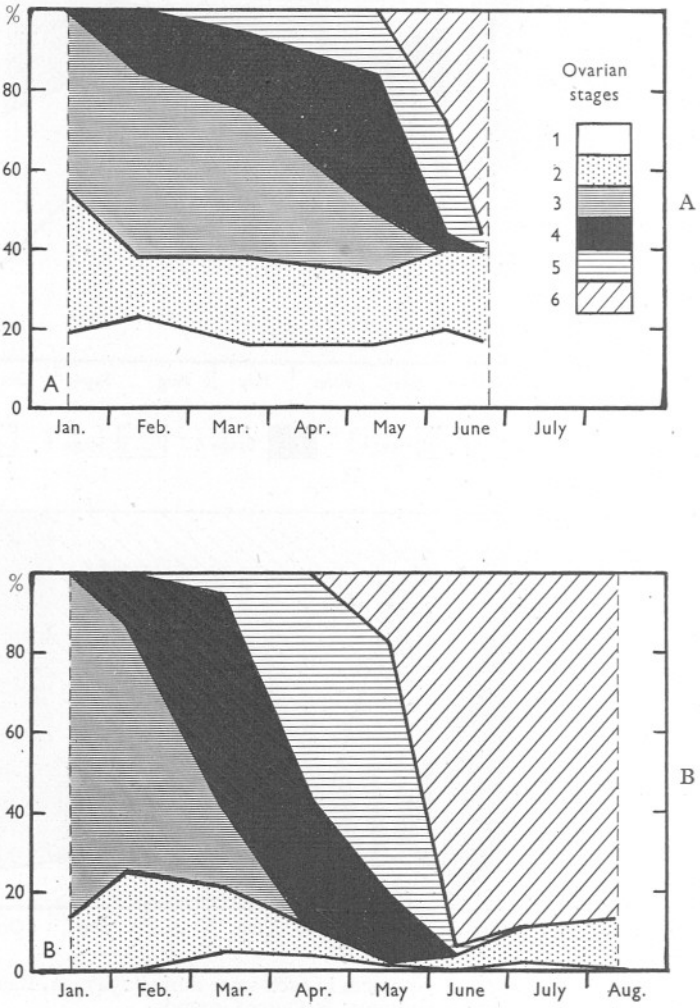


Fig. 4. Ovarian maturity. Percentages in each stage during 1948. A, Rame-Eddystone Grounds; B, Outer Grounds.

On the Outer Grounds the data for both 1947 and 1948 show that the proportions of stages 1 and 2 combined are very constant and only once (early 1948) exceeded 20% of the total population of ovaries.

The Population near E 1. By the time samples were obtained in the area the majority of individuals had already spawned; this is clear from Table VI, which suggests that the peak of the spawning period in 1947 had taken place in May, and so probably a little later than in the Outer Grounds population.

The Cawsand Bay Population. Only one haul was obtained from this area (on 23 May 1947), and as already mentioned the starfishes were all very small and almost certainly belonged to the 1946 brood. In spite of their small size eight of the ten females had already spawned (stage 5), with ripe eggs still present in some tubules. Also two of the eight males were still ripe with motile sperms, and two others showed signs of having spawned recently.

The Plymouth Sound Population. The characteristics of the reproductive cycle in this population were as homogeneous as the size composition. On 10 February 1948 fourteen females were taken, of which one had ovaries in stage 2 and thirteen in stage 3. On 16 April forty-eight females were caught and all were ripe (stage 4).

The Rame Mud Population. In the single sample of ninety-five starfishes from this area only seventeen could be sexed, and of these only five were females, all with ripe gonads. Breeding in this area was evidently very intermittent.

RELATION BETWEEN OVARIAN MATURITY AND BODY SIZE

The criterion of ovarian maturity has been used as an index of the potential breeding efficiency of a number of populations and certain conclusions may now be drawn. Of the two populations most extensively studied that on the Outer Grounds showed a significantly higher percentage of ripe ovaries than the Rame-Eddystone Grounds population. At first sight it might appear that this difference in percentage of females matured between the Rame-Eddystone and the Outer Grounds populations was related to body size, namely that the larger individuals matured and the smaller ones did not. This might explain the differences in maturing between the large-sized and the medium-sized populations, but it would not account for the high percentage of maturity in the small-sized Cawsand Bay population. Nor would it account for the difference in maturity between the Rame-Eddystone population and the somewhat smaller-sized Plymouth Sound population. On 16 April 1948 the Plymouth Sound female starfishes had a mean radius length of 9·5 cm. and 100% of the females had ripe ovaries. In the Rame-Eddystone population at the peak of the breeding season (as determined by the percentage ovarian maturity, 11 May 1948) only 34% of the females were ripe, and yet the starfishes in this sample were somewhat larger (mean $R = 10{\cdot}5$ cm.) than those in Plymouth Sound.

Furthermore, analysis of the sizes of the mature females in the Rame-Eddystone and Outer Grounds populations provides interesting data. The size distributions of the female starfishes in stages 4 and 5 from the Rame-

Eddystone sample for 28 April 1947 and from the Outer Grounds sample for 25 April 1947 are shown in Table VI. This shows that the size classes $R=6$ cm. and $R=9$–13 cm. were represented in both samples.

TABLE VI. NUMBER OF FEMALES IN STAGES 4 OR 5 IN EQUAL-SIZED STARFISHES FROM TWO POPULATIONS

		Size class in cm.													
Grounds and date		5	6	7	8	9	10	11	12	13	14	15	16	17	18
Rame-Eddystone (28. iv. 47)	Total ♀♀	1	4	6	10	6	4	5	2	4	0	0	0	0	0
	♀♀ in stages 4 or 5	1	1	0	1	3	2	2	2	2	0	0	0	0	0
Outer Grounds (25. iv. 47)	Total ♀♀	0	1	0	0	1	2	5	8	16	13	16	25	12	6
	♀♀ in stages 4 or 5	0	0	0	0	1	1	5	7	15	11	14	23	11	6

Analysis of the numbers of stages 4 and 5 in these common size classes shows that: Rame-Eddystone Grounds had twelve in breeding condition out of twenty-five (48%); Outer Grounds had twenty-nine in breeding condition out of thirty-three (88%).

Similarly, comparison of the common size classes in the other pair of contemporaneous breeding-season samples shows that: Rame-Eddystone Grounds (16 April 1947) had two in breeding condition out of seven; and Outer Grounds (18 April 1947) had ten in breeding condition out of eleven.

It appears, therefore, from a comparison of the Outer Grounds and the Rame-Eddystone Grounds populations, that there was a marked difference in the incidence of ripe and spawned ovaries among equal-sized starfishes on these grounds, over 85% of the Outer Grounds female starfishes having reached breeding condition, while on the Rame-Eddystone Grounds under 50% had reached this stage.

The length of the season during which ripe eggs were present was no longer in the Rame Eddystone Grounds than in the Outer Grounds, so that there is no lengthening of the breeding season to account for the low percentage of ripe females on the dates on which samples were taken. Indeed, during 1947, the ripe-egg season in the Rame-Eddystone Grounds was considerably shorter than in the Outer Grounds.

OVARY LENGTHS AND RELATIVE EGG PRODUCTION

The previous analysis gives an index of the number of individuals reaching stages 4–5, but gives no indication of any difference in the scale of gamete production between equal-staged starfishes in different populations. A further analysis of the lengths of the ripe ovaries (stage 4) in equal-sized starfishes from contemporaneous samples is shown graphically in Fig. 5. This shows that in equal-sized starfishes in April 1947 ripe ovaries were longer in the Outer Grounds than they were in the Rame-Eddystone Grounds and, similarly, they were significantly longer in April 1948 in the Plymouth Sound population than in the early May 1948 sample from the Rame-Eddystone

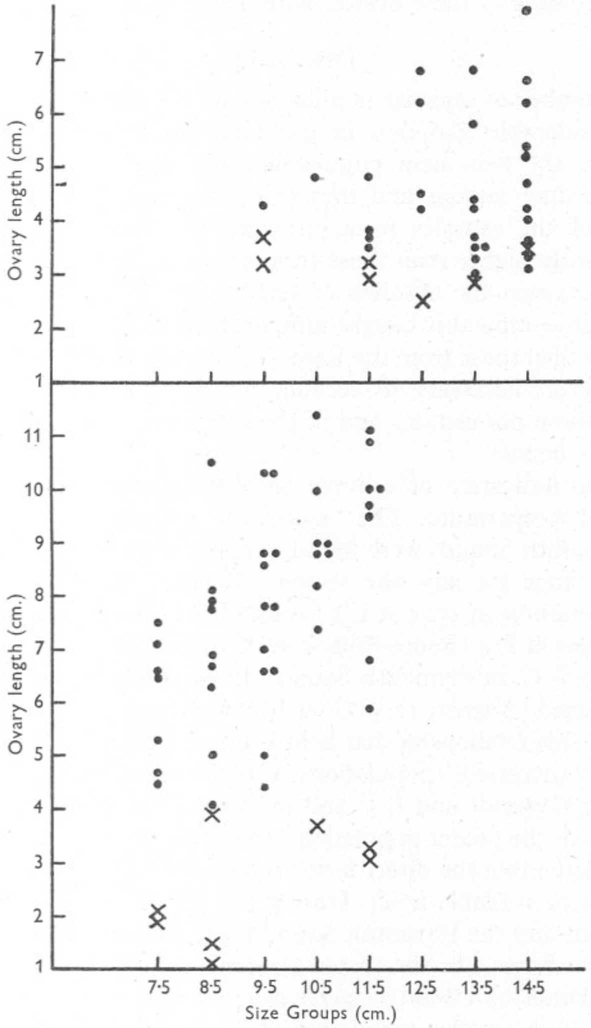


Fig. 5. Lengths of ovaries in stage-4 starfishes in different populations. Above: ×, Rame-Eddystone Grounds on 16 and 28 April 1947; ●, Outer Grounds on 9, 18 and 25 April 1947. Below: ×, Rame-Eddystone Grounds on 11 May 1948; ●, Plymouth Sound on 16 April 1948.

Grounds. The production of eggs in the Outer Grounds and Plymouth Sound populations must therefore have been considerably greater than in the Rame-Eddystone Grounds population.

It is interesting to note that in April 1948 the ovaries from the Plymouth Sound sample were sometimes longer, when dissected out, than the starfish arms in which they had been growing. This was due to a certain amount of longitudinal folding of these ovaries within the coelomic cavity of the arms.

DISCUSSION

Study of a number of separate populations of *Asterias rubens* has shown that there is considerable variation in the total productivity on the different grounds. For the two main populations investigated, data were collected over two breeding seasons and they show conclusively that the size means and ranges of the samples from one area and their percentage matured were significantly higher than those from the other area. No attempt has yet been made to assess the absolute or relative numbers of starfishes in these areas, although comparably caught samples from the Outer Grounds were in general larger than those from the Rame-Eddystone Grounds. Some explanation is, however, necessary to account for the differences in growth and maturing of these populations and of those from the other areas which were studied in less detail.

There is no indication of a direct correlation between good growth and maturing and temperature. The 'successful' populations (Outer Grounds, E 1, and Plymouth Sound) were found at opposite extremes of the very small temperature range for any one season. Harvey (1928) found that winter bottom temperatures in 1924 at E 1 (south of the Outer Grounds) were about 10° C., whereas at L 4 (Rame-Eddystone Grounds) they were approximately 9·8° C., and 9·0° C. in Plymouth Sound. In summer, however, this relationship was reversed (August, 12·5° C. at E 1, and 13·5° C. at L 4). With minor modifications this relationship has held good in subsequent years. Similarly, with salinity, 'successful' populations were found in both the least polluted waters (Outer Grounds and E 1) and in the most polluted waters (Plymouth Sound), whereas the poorer populations were living in the intermediate waters.

It is considered that the direct factor responsible for the differences noticed is the amount of available food. During the period of the investigations the Outer Grounds and the Plymouth Sound area were very rich in food animals suitable for starfishes. In the Outer Grounds the flat sandy bottom carried a large population of *Chlamys opercularis*, which formed the chief starfish food, as well as a smaller population of *Cyprina islandica*, which is eaten by large specimens of *Asterias* sp. (Hunt, 1925). In the Asia Grounds where the rich Plymouth Sound starfish population was found, the trawl brought up many medium and large *Mytilus edulis*. On the other hand, in the Rame-Eddystone Grounds it is difficult to name any one main food source for the starfishes living there. Trawl and dredge hauls brought up a few *Chlamys opercularis*, and a few tubicolous worms, as well as large clusters of hydroids and bryozoans. In these clusters there were small crabs, lamellibranchs and other starfishes, but little that could serve as a main food supply for medium and large starfishes. The same may be said of the Rame Mud area, where the epifauna is even poorer, although the infauna, which is largely inaccessible to *Asterias*, is relatively abundant.

The abundance of the supply of *Mytilus* in Plymouth Sound in 1948 was probably the result of an exceptionally good spatfall correlated with the presence of detritus brought down by the rivers Plym, Tamar and Tavy and by the Plymouth City effluents, all of which flow into the Sound; in addition plankton would be brought in from the open sea. A heavy spatfall of *Mytilus* coinciding in time and space with a rich settlement of *Asterias rubens* will provide ideal conditions for the growth of a large starfish population, such as that investigated in Plymouth Sound in 1948. On the other hand, large numbers of young starfishes settling on a bed of adult mussels would not thrive, since their size would be out of phase with that of the food animal. There must, therefore, be a rather limited optimum mean size and total concentration of the food animal before a large homogeneous population of starfishes can be produced. These conditions have been fulfilled on Asia Grounds, but not on the Rame-Eddystone Grounds or on the Rame Mud.

For the Outer Grounds population a different food animal is involved, and whereas a heavy spatfall of *Mytilus* in Plymouth Sound is apparently rare, it is probable that good spatfalls of *Chlamys* are quite usual in the waters of the English Channel. The ultimate factors responsible for the distribution of *Chlamys* are not known, although it is possible that, as they are active swimmers, they may move away from areas poor in food and congregate in more favourable waters. At the same time they are known actively to avoid concentrations of *Asterias rubens*, which will in their turn follow the *Chlamys*. The distribution of *Chlamys* on the sea bottom is, therefore, probably a resultant of both these biological factors. Whereas the Plymouth Sound population, feeding on an abundant fixed food animal, was itself strictly localized in distribution, the Outer Grounds population feeding on a mobile food animal was probably moving to and fro on the sea bottom in pursuit of *Chlamys*. Furthermore, as the *Chlamys* move about, neighbouring groups of *Asterias* will be attracted to the fringes of the Outer Grounds. If this type of dilution of the population occurs, it would account for the wide size ranges of some of the Outer Grounds samples and the dispersion of their means (Fig. 1). There is no evidence for regarding these movements of *Asterias* and *Chlamys* as large-scale migrations involving long distances.

There is no sharp limiting boundary between the Rame-Eddystone and the Outer Grounds populations, although, in practice, the 30-fathom line has been regarded as a convenient line of demarcation, and it is probable that starfishes from the Rame-Eddystone Grounds play a part in the dilution of the Outer Grounds population. On the basis of the growth-rate observations it is likely that many Outer Grounds starfishes had metamorphosed there and had reached medium size ($R = ca.$ 6–10 cm.) and breeding condition in one year. On the other hand, other starfishes of similar sizes caught on the same grounds were probably immigrants, aged 2 or even 3 years, from the Rame-Eddystone Grounds and other neighbouring areas.

There is, unfortunately, no method of determining age in *Asterias*. However, investigation of different wild populations coupled with growth-rate observations have shown that the productivity of a starfish population, as measured by the percentage of matured gonads and by the sizes of these gonads, is not primarily correlated with age. Poorly fed populations will survive and show minimum growth and little or no gonad maturing, whereas well fed populations will grow fast and reach breeding condition within one year from metamorphosis.

SUMMARY

Considerable differences were found in the size compositions of populations of *Asterias rubens* off Plymouth. These differences were not correlated with age.

Laboratory observations on rate of growth showed that well fed starfishes grow fast during summer and autumn and somewhat slower in winter. Poorly fed starfishes did not increase in size, but were able to survive for long periods with a minimum of food.

In favourable conditions *A. rubens* may grow to a radius size of 8–9 cm. in one year and may also reach breeding condition during this time.

Investigation of breeding cycles by determination of the percentage of females in different stages of ovarian maturity showed further differences between populations. Starfish populations with a high percentage of large and ripe ovaries during the breeding season were not necessarily those with large body-size means.

It is considered that the differences in size composition and production of ripe eggs were primarily correlated with food, and observations are given on the food animals in the areas supporting 'successful' starfish populations.

For the production of a large homogeneous starfish population it is necessary for spat to fall on an area rich in suitable food animals. There is an optimum relationship between size of starfish and size of food animal which must be maintained if the starfish population is to remain large and homogeneous and show maximum productivity during the breeding season.

REFERENCES

ALLEN, E. J., 1899. On the fauna and bottom-deposits near the thirty-fathom line from the Eddystone Grounds to Start Point. *Journ. Mar. Biol. Assoc.*, Vol. v, pp. 365–542.

FOX, H. M., 1924. The spawning of echinoids. *Proc. Camb. Phil. Soc.* (*Biol. Sci.*), Vol. 1, pp. 71–4.

GALTSOFF, P. S. & LOOSANOFF, V. L., 1939. Natural History and method of controlling the starfish (*Asterias forbesi* Desor). *Bull. U.S. Bur. Fisheries*, No. 49, pp. 75–132.

GEMMILL, J. F., 1914. The development and certain points in the adult structure of the starfish *Asterias rubens* L. *Phil. Trans. Roy. Soc.*, B, Vol. 205, pp. 213–94.

HARVEY, H. W., 1928. *Biological Chemistry and Physics of Sea Water*. Cambridge University Press.

HUNT, O. D., 1925. The food of the bottom fauna of the Plymouth fishing grounds. *Journ. Mar. Biol. Assoc.*, Vol. XIII, pp. 560–98.

MEAD, A. D., 1899. Special Report on the Starfish. *29th Ann. Rep. Comm. Inland Fisheries, Rhode Island*, pp. 37–76.

MORTENSEN, TH., 1927. *Handbook of the Echinoderms of the British Isles*. Oxford University Press.

ORTON, J. H. & FRASER, J. H., 1930. Rate of growth of the common starfish, *Asterias rubens*. *Nature*, Vol. 126, p. 567.

PALMER, L., 1937. The shedding reaction in *Arbacia punctulata*. *Physiol. Zool.*, Vol. 10, pp. 352–67.

THORSON, G., 1946. Reproduction and larval development of Danish marine bottom invertebrates, with special reference to the planktonic larvae in the Sound (Øresund). *Medd. Komm. Danmarks Fisk. Havund., København, Ser. Plankton*, Bd. 4, No. 1, 523 pp.

THE FAUNA OF SAND AND MUD BANKS NEAR THE MOUTH OF THE EXE ESTUARY

By N. A. Holme, B.A.

From the Plymouth Laboratory

(Plates I and II and Text-figs. 1–11)

CONTENTS

INTRODUCTION

In 1901 Allen & Todd (1902) made a survey of the fauna of the Exe Estuary consisting of collections of the macrofauna of the intertidal sand and mud-banks, and some trawling and dredging. An account of the Foraminifera of the estuary is given by Worth (1902). Since 1901, considerable changes have occurred in the physiography of the lower part of the estuary, and the present paper records some observations made on the fauna in the area most affected by these changes.

The papers by Allen & Todd (1900, 1902) on the Salcombe and Exe Estuaries are almost the first comprehensive estuarine surveys. Since about

1928 a number of more detailed surveys have been published, some of which deal with the quantitative aspects of populations in sand- and mud-banks. One of the most recent of these is that by Spooner & Moore (1940) on the macrofauna of the intertidal muds of the Tamar estuary. Serventy's (1934) survey of the Scolt Head Island fauna and Beanland's (1940) work on the Dovey estuary are accounts of the fauna of sand- and mud-banks in sheltered and near-marine conditions, comparable to those described in this paper.

Populations on sandy and muddy shores have been described by Stephen (1929*a*), Elmhirst (1931), Pirrie, Bruce & Moore (1932), Rees (1939), Watkin (1942), and Brady (1943). Besides these general surveys, there have been more intensive studies of certain species, such as those of Stephen (1928, 1929*a*, *b*, 1931, 1932) on the biology of *Tellina tenuis* and certain other lamellibranchs.

Most surveys have necessarily been restricted to collections made during a limited period, and little is known of changes in the populations from season to season or from year to year. Fischer-Piette (1931) found a correlation between salinity changes in the estuary of La Rance and the up-river penetration of certain animals in successive seasons and years, but his observations were primarily on non-burrowing species.

It is well known that both salinity and the type of soil influence the distribution of species within an estuary; but the exact role of each and the influence of other factors is still virtually unknown. Some light on the causes of distribution is revealed from the work of Day & Wilson (1934) and Wilson (1937, 1948), on the influence of particular grades of sand on the metamorphosis of certain polychaete larvae. The larvae show a tendency to settle on soil characteristic of the adult habitat, and, as *Ophelia bicornis* from the Exe, may postpone metamorphosis until a suitable grade of sand has been reached.

As a result of erosion of Dawlish Warren an area of sand has come to lie in close proximity to, and grading into, the original mud-banks. Thus it was possible to study the fauna over a wide range of soils, without the complications which usually occur due to differences in salinity, currents or wave action.

Acknowledgements

I am indebted to the Trustees of the Balfour Fund for a grant to meet collecting expenses, and to the Deputy Provincial Director of the Ministry of Agriculture and Fisheries at Starcross for the provision of accommodation while collecting was in progress. I am also grateful to the Soils Department of the above establishment for their help with the pH readings, and in other ways. Much of the collecting equipment was kindly lent by the Director of the Plymouth Laboratory.

I am especially indebted to Dr C. F. A. Pantin, F.R.S., for his help, both as Administrator of the Balfour Fund, and for his encouragement and advice in planning the course of the work. The collecting and the sorting of specimens at Starcross was only made possible by the generous help of the following: Miss U. M. Grigg, Miss S. M. Davies, and Messrs B. O. C. Gardiner, D. Langridge, R. M. Laws, A. J. Lee, A. W. Mansfield and H. Swift. Mr and Mrs G. M. Spooner were also of great assistance for a few days at the beginning of the summer. Mr A. J. Lee, who was surveying the Warren, has kindly provided an up-to-date map of the area which is reproduced, with modifications, in this paper.

The following have been of great assistance in the techniques of measuring physical conditions: Dr H. W. Harvey, F.R.S., Dr C. H. Mortimer and Dr J. A. Ramsay.

The later stages of this work and the writing of this paper were made during the term of a D.S.I.R. training grant at the Plymouth Laboratory. I am indebted to the Director and Staff of the Plymouth Laboratory for advice and assistance during this period.

Certain salinity readings were kindly supplied by the Ministry of Agriculture and Fisheries, Fisheries Experimental Station, Castle Bank, Conway.

The following have been kind enough to identify or check certain groups: *Nemertinea*—Dr J. E. Smith; *Annelida*—Mr D. P. Wilson; *Mollusca*—Dr V. Fretter, Miss S. M. Davies, Miss U. M. Grigg, Mr R. Winckworth; *Crustacea*—Dr E. E. Watkin, Mr G. M. Spooner, Mrs W. M. Tattersall; *Pisces* (*Ammodytes*)—Mr P. G. Corbin; *Zostera* spp.—Mr T. G. Tutin; *Algae*—Dr M. Parke.

I am indebted to Mr F. S. Russell, F.R.S. and Dr T. J. Hart for helpful criticism of the manuscript.

THE EXE ESTUARY

The River Exe is tidal up to Countess Wear, 9 miles from the mouth, but between Countess Wear and Topsham the channel is fairly narrow and the water is almost fresh. Between Topsham and Exmouth the estuary is about a mile wide and is 6 miles long. A small river, the Clyst, enters the estuary near Topsham and a few streams flow into the estuary at various points. At high tide the estuary is almost completely covered by water, but at low tide extensive sand- and mud-banks are uncovered through which a shallow main channel winds. Near Exmouth the estuary narrows, being diverted at right angles to the east by a sand spit on the western shore, called Dawlish Warren. The channel runs parallel to Exmouth shore for 2 miles, being separated from the sea at low tide by a large sand-bank known as Pole Sands. The banks in the upper part of the estuary are of mud, but nearer Exmouth they become more sandy. Two banks of clean sand occur near the mouth: Bull Hill Bank and Pole Sands. The river channel is well scoured and has a bed of stones in the lower part of the estuary.

Tidal streams are very swift, particularly near the mouth. Opposite Exmouth Dock a speed of 5 knots (9·25 km./hr.) may be reached on spring tides. The scour produced by the currents causes banks opposite the main channel to slope down steeply near low-water mark. Thus most of the banks are at high- and mid-tide levels, and very little additional area is uncovered at low spring as compared with low neap tides. The tidal range is 12·2 ft. (3·72 m.) at spring tides, and 4·8 ft. (1·46 m.) at neap tides.

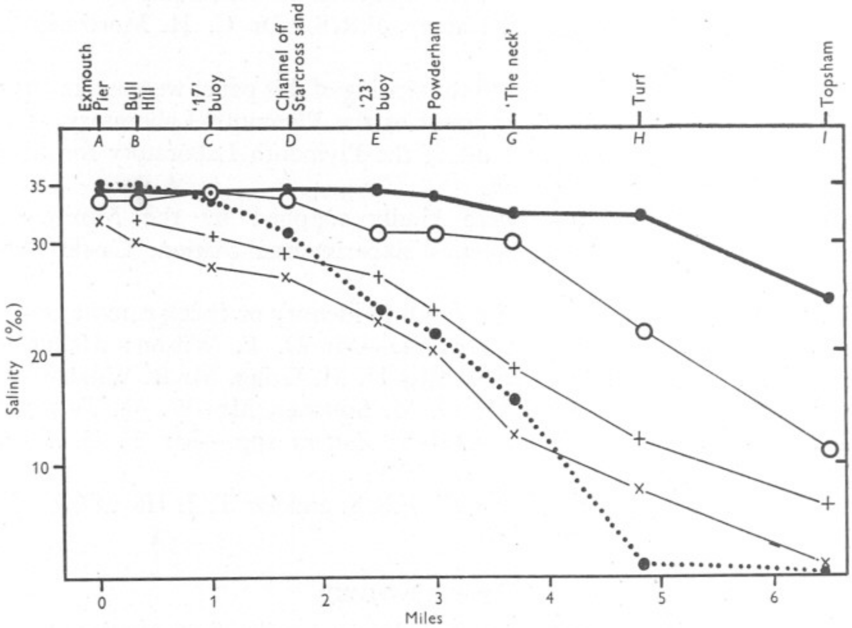


Fig. 1. Surface salinities in the Exe Estuary. Distances are measured up the main channel from Exmouth Pier. The area studied in this paper is opposite the station marked 'Bull Hill'. Samples were taken on the following occasions: —●—, high spring tide (12 ft. 5 in.), 3. ix. 47; —○—, high neap tide (9 ft. 6 in.), 27. vii. 47; —+—, low neap tide (10 ft. 2 in.), 28. viii. 47; —×—, low spring tide (12 ft. 2 in.), 18. vii. 47; ··●··, high neap tide (10 ft. 2 in.), 2. iii. 48.

A certain amount of sand is mixed with all the deposits; and in dry windy weather sand may be blown up the estuary from Dawlish Warren, so adding to the sand-content of the banks.

The considerable width of the estuary enables small waves to be formed within it, and in addition swell from the sea may be felt as far up as Starcross at high tide. During a recent south-east gale the sea was sufficiently rough inside the estuary to damage severely the railway embankment below Starcross.

Sewage from Exeter is discharged into the river near Countess Wear, and sewers empty into the estuary opposite the villages and towns on its shores. There is no chemical pollution.

The extent of the fresh-water inflow was discussed by Allen & Todd (1902). The watershed area of the Exe is 584 square miles (1512 km.^{2}) and it was found that conditions at Exmouth were almost marine, whereas at Topsham fresh water was recorded at low tide after heavy rain. Some additional salinity records are given in this paper. They were made by running a motor-boat at top speed up the estuary, taking surface water samples at intervals. Starting about half an hour before high or low tide it was possible to take most of the samples during the period of slack water. Samples were taken at high and low spring and neap tides in the summer of 1947, and one set of samples was taken in March 1948. The results are summarized in Table IX and Fig. 1. In the lower part of the estuary conditions are marine at high tide, but salinity drops to about 30 °/₀₀ at low tide. The greatest range of salinity occurs at about Turf, 1½ miles below Topsham, and the river is evidently brackish for a short distance above Topsham.

It seems likely, however, that few estuarine species are subjected to such extremes of salinity. At low tide the greater part of each bank is uncovered, and so not exposed to the lowest salinities. In addition, Reid (1930) has shown that a stream of fresh water flowing over intertidal sand has little effect on the salinity of the water retained in the sand, which presumably is of about the mean of the various salinities to which the bank is subjected. Species with an 'open' burrow, such as *Arenicola* will, however, be exposed to the salinity of the overlying water rather than to that of the surrounding sand.

The fauna of buoys is exposed to the surrounding water at all times, but Milne (1940) has shown that mussels close their valves when the salinity drops below 25 °/₀₀, the water retained in the shell at low tide being of higher salinity than that of the water outside.

The main channel is shallow for the greater part of its length. This, and the ease with which the water may be disturbed by waves and currents, renders it unlikely that any marked stratification of water layers of different salinities would occur. Some records made in connexion with the Ministry of Agriculture and Fisheries' Mussel-Washing Station at Lympstone show, however, that stratification may occur under certain conditions:

(*a*) *In calm weather* (25 September 1917)

Neap tides. High water 12 noon. Wind S., light. Samples in channel off Powderham Boathouse (half-way up the estuary).

5.12 p.m.	Density at surface	1·009
5.15 p.m.	Density at bottom (9 ft.)	1·023
5.20 p.m.	Density at bottom (9 ft.)	1·021
5.25 p.m.	Density at surface	1·005

(*b*) *During floods* (18 January 1918)

High tide 10.19 a.m. Water very high, due to floods and melting snow. Winds S.W., fresh. In channel between Starcross and Lympstone.

12.15 p.m.	Density at surface	1·002
12.15 p.m.	Density at 6 ft. depth	1·015
12.20 p.m.	Density at 8 ft. depth	1·021
12.20 p.m.	Density at 5 ft. depth	1·004
12.23 p.m.	Density at 6 ft. depth	1·017
12.25 p.m.	Density at 7 ft. depth	1·020
12.27 p.m.	Density at surface	1·002

Clearly fresh water was flowing out over the denser salt water, the line dividing the two water masses being at a depth of 5–6 ft. The surface samples were muddy, while the bottom water samples were clear.

Dawlish Warren

The Warren is a spit jutting out across the mouth of the Exe, and formerly narrowing it to a channel a quarter of a mile wide between Warren Point and Exmouth (see Fig. 2). It consists of two separate spits: the Outer and Inner Warren. The Outer Warren is a line of sand-dunes on the seaward side of the Inner Warren; it was (in 1939) about 1½ miles long, its north-eastern end forming an area known as Warren Point, on which were a number of bungalows. The Outer Warren has been subject to considerable erosion in recent years, and Warren Point has now disappeared.

Between the Inner and Outer Warren is a low area with little vegetation known as Greenland Lake. This was formerly flooded at high spring tides, but its connexion with the sea has now been closed by a barricade. It is, however, still liable to occasional flooding, and this presumably prevents the establishment of permanent vegetation.

The Inner Warren is an established spit, with a heath-like appearance, and a few small trees. The soil is sandy, and it is used as a golf course. This spit was rather shorter than the Outer Warren and has until recently been completely protected by the latter on its seaward side.

A survey of the Warren made by Mr A. J. Lee showed that the Inner Warren is founded upon a bed of clay rising above high-water mark. On the seaward side the clay dips down steeply and has not been found under the Outer Warren. On the northern shore of the Warren the clay is visible on the surface in places, and forms a gently sloping layer under the mud flats for some distance from it.

These observations confirm the suggestion made by Worth (1902) that the western end of the Warren is a genuine spit of land, whereas the eastern end and the Pole Sands are due to littoral drift.

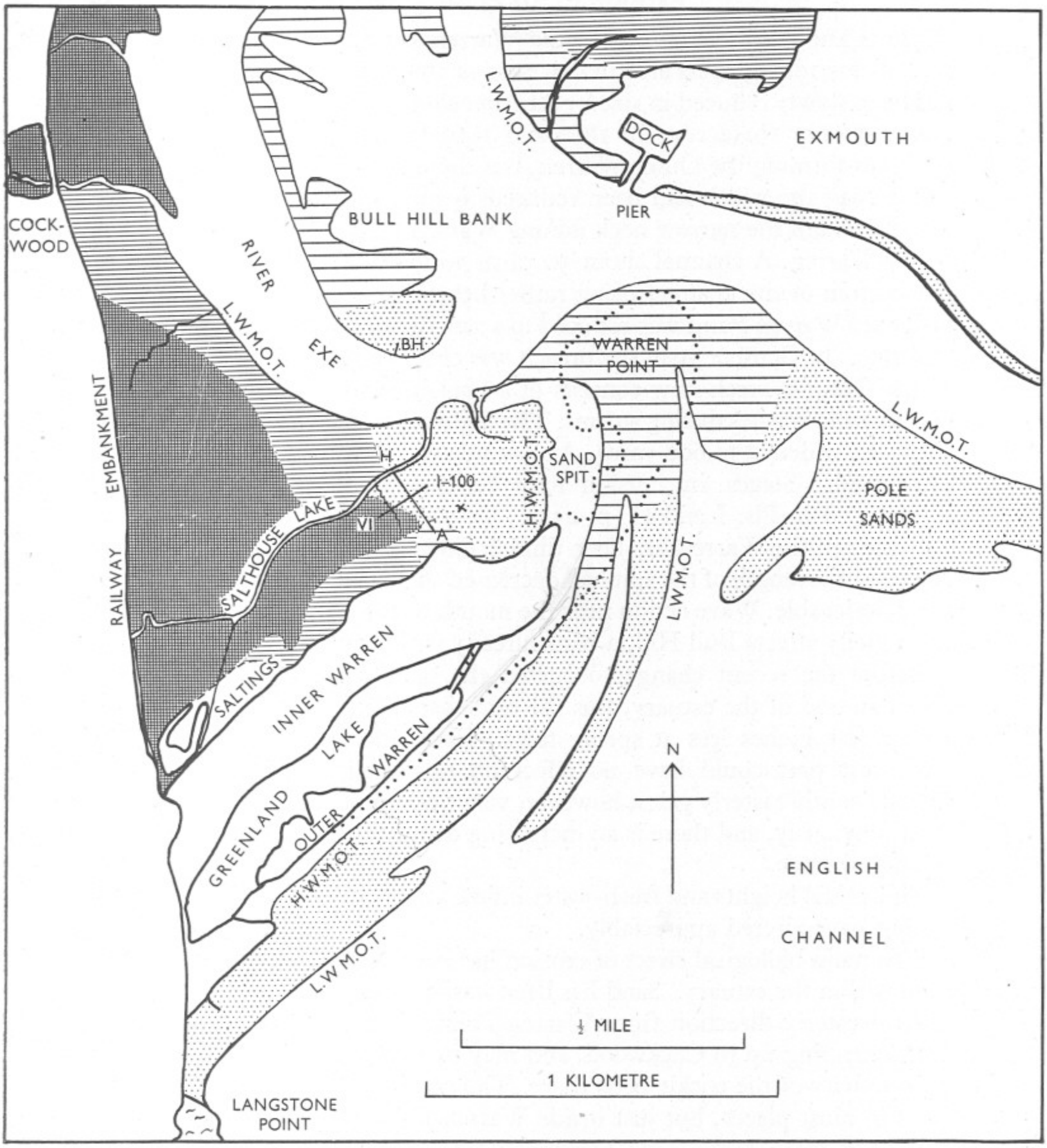


Fig. 2. Map of the lower part of the Exe Estuary, from a survey by A. J. Lee, July 1947. The position of the traverses is indicated. Note that erosion has nearly doubled the high-tide channel opposite Exmouth.

▦ Mud. ▤ Muddy sand. ░ Sand. ☰ Gravel.

...... Outline of Warren Point in 1935

EROSION OF DAWLISH WARREN

Little is known of the extent of the Warren before the eighteenth century; records for 1723 give its area in that year as 398 acres. Since then the Warren has been slowly reduced in size by attrition along its seaward face. In 1888 the area was only 191 acres. In 1859 and 1869 breaches were made in the line of dunes forming the Outer Warren, but these were subsequently closed. By about 1943 the width had been reduced to such an extent that a breach was made through the narrow neck joining Warren Point to the remainder of the Outer Warren. A channel about 50 yards wide was formed through the spit, the bottom of the channel being rather below half-tide mark. Between 1943 and 1946 Warren Point was reduced to a sand bank by the action of waves and currents. In October 1946 the breach was closed by littoral drift, and the end of the Outer Warren now consists of a hooked sand spit over which the sea occasionally washes during storms. The high-water channel opposite Exmouth has been widened to 600 yards. At low tide the remains of Warren Point are uncovered. Stages in erosion may be seen in the aerial photographs reproduced in Pls. I and II (p. 232).

Although the Warren has been diminishing in width for a long time, it was not until the length of the spit had decreased that any effects within the estuary were noticeable. Wave action near the mouth of the estuary has increased, but this chiefly affects Bull Hill, a bank already well scoured by currents.

Before the recent changes occurred the tidal range at Topsham, at the northern end of the estuary, was the same as at Exmouth at neap tides, and only a few inches less at spring tides. Hence the increase in width at its narrowest part could have no effect on tidal heights within the estuary. During south-easterly gales, however, water accumulates in the estuary more than previously, and there is an increasing danger to the railway embankment in consequence.

Since tidal heights and fresh-water inflow are unchanged, salinity conditions cannot have altered appreciably.

The main biological effect of erosion has been through the redistribution of sand within the estuary. Sand has been washed and blown up the estuary in a north-westerly direction from Warren Point. The sand has come to lie in a belt extending up to Cockwood, and may be responsible for a decline in the productivity of the cockle beds there. The sand has become mingled with the mud in most places, but just inside Warren Point there is a stretch of newly deposited clean sand. Two hundred yards to the west is an area of mud covered with *Zostera*. In the intermediate zone a range of soil types, from sand to mud, is found.

SCOPE OF THE SURVEY

Since 1902 there has been little published work on the estuary. Crawford (1937*c*) recorded certain Crustacea from the estuary; and Beanland (1940) considered that the absence of *Corophium volutator* from an area in which it had been found by Allen & Todd was due to decreasing shelter resulting from erosion of the Warren.

The area selected for study lies between Dawlish Warren and a small stream running parallel to it through the mud flats, known as Salthouse Lake. Allen & Todd (1902) did not collect here, but they gave a list of species from a similar ground at a slightly lower level to the north of the stream.

In all, collections were made on three traverses: (i) along a traverse passing from sand to mud, stations all being at about half-tide level; (ii) on an intertidal traverse in the same region, passing from high- to low-water marks, in which most stations were on sand; (iii) a short traverse across the top and edge of Bull Hill Bank.

METHODS

Faunistic collections

Collections were made of a $\frac{1}{4}$ m.^{2} surface area dug to a depth of about 10 in. The area to be dug was marked out by a square metal frame of side half a metre and depth 6 in., which was driven into the ground. This prevented collapse of soil into the hole during digging.

The soil was sieved through a gauze sieve with holes 1 mm. square. A 'souping' technique, as used by Spooner & Moore (1940), was adopted in the muddier areas. Practically all the soil passed through the sieve at most stations, but *Zostera* and other plant remains were often abundant in the sievings. Now and then a sieve with round holes 0·8 mm. across was also used, but never on the top 2–3 in. of soil where small individuals chiefly congregate. Occasionally, mainly in the *Zostera* areas, sub-sampling was resorted to after the larger specimens had been picked out.

'Sievings' were taken back to Starcross, where they were sorted and preserved, with preliminary identifications. All specimens were kept and have been identified and size-grouped by the author while at Plymouth.

The collecting technique seems adequate for all the larger specimens, but it is likely that only a fraction of the smaller worms, etc., were retained by the sieve. With animals of a definite shape and size, such as the Gastropod *Hydrobia ulvae*, a constant lowest size of animal is retained by the sieve; but the proportion of other small specimens must largely depend on the duration and violence of sieving: in time all would pass through. At least one moderate-sized worm (*Scoloplos armiger*?) has a habit of actively crawling through the meshes of the sieve and so tends to be lost.

In so far as no animals below 1 mm. were included, this survey of the populations is incomplete. But the study of the micro- and meio-benthos requires special techniques outside the scope of this work. A sieve with mesh of 1 mm. is about the smallest that can conveniently be used for sieving a large bulk of sand, and for subsequent sorting without resorting to a lens.

Along each traverse stations were at 100 ft. (30·48 m.) intervals; at each two collections were made 3 ft. on either side of the station along the line of the traverse. These were designated as +3 and −3 ft. from each station.

Intermediate stations were also worked and are designated by the distance in feet from the preceding station. Thus Station II+33 was 33 ft. from Station II and 67 ft. from Station III. Stations were I−100, I, II, III, IV, V and VI on the main traverse, and A, B, C, D, E, F, G and H on the intertidal traverse. These traverses cross at Stations II and E, which are therefore identical. Stations on Bull Hill were measured in feet from a point 'BH' at the top of the steep slope of the bank.

Population figures from adjacent collections at each main station are given separately to emphasize the variation to be expected due to patchy distribution of certain species.

Physical conditions

Salinity was measured in two ways:

(i) Titration with silver nitrate solution using potassium dichromate as indicator. Comparison was made by titration of a sea-water sample taken at sea outside the estuary. This was assumed to have a salinity of 35·0 ‰ as no accurate salinity determinations were made.

(ii) Using a brass and also a glass hydrometer with density ranges from fresh to salt water. These instruments give an approximate reading only, to which a temperature correction must be applied.

pH. The pH of marine soils seems to be chiefly related to the carbon dioxide concentration (Dr H. W. Harvey: personal communication), and since determinations were not made in the field it is difficult to assess the importance of this factor. The pH of the water in the soil was determined by comparing samples, obtained by digging a small hole in the soil and allowing it to fill with water, with standard buffer tubes, using cresol red as indicator.

pH was also measured electrically. A glass jar was filled full of soil, and from the middle of this sample a small quantity was taken out for pH measurement, which was determined within 24 hr. of collection. The soil was mixed to a smooth paste with the minimum quantity of sea water, and the pH of the mixture measured.

Temperature. Readings of soil temperatures were made by inserting a thermometer into a small hole in the ground made with a stick. Temperatures were recorded with the bulb at $\frac{1}{2}$ in. and at 3 in. depths below the surface.

Water table. A small hole dug in the soil was allowed to fill with water. The top of the water is approximately equal to the level of the water table.

Tidal levels. A number of stations were levelled to Ordnance Datum by means of a 'Dumpy Level' and a bench-mark on Dawlish Warren. Tidal heights are given relative to Chart Datum, which is 0·2 ft. below M.L.W.M.S.T.

Soil analysis. Grade analysis was carried out by means of the standard method used in agriculture. This method has been applied with success to soils on the shore by Beanland (1940) and Watkin (1942). It is not in itself sufficiently precise to distinguish the slight differences in soil grade which seem to affect the distribution of certain species. If material retained on the standard 0·2 mm. sieve is passed through a series of sieves of slightly coarser mesh a more exact grading of the sand can be achieved.

Owing to difficulty in obtaining a Standard 70 I.M.M. (0·2 mm.) sieve, a sieve of 80 meshes to the inch was substituted. This had openings 0·22 mm. across. Results obtained with this sieve have been compared with those made with a standard sieve (Table X). Many of the grains were about 0·2 mm. in size so that there is some divergence in results from those made with the standard sieve. In the present investigation the following grades were distinguished:

Stones and fine gravel	Retained on 2 mm. sieve
Very coarse sand	Retained on 0·5 mm. sieve
Coarse sand	Retained on 0·256 mm. sieve
Medium sand	Retained on 0·22 mm. sieve
Fine sand	0·22–0·02 mm.; passing 0·22 mm. sieve and settling in 5 min.
Silt and clay	Less than 0·02 mm.; still in suspension after 5 min.

The method used is based on that described by Piper (1942):

Samples were taken from the top 4 in. of soil and were air-dried.

The soil was graded through a 2 mm. sieve, all retained on the sieve being rejected.

10 g. of soil were weighed out and were treated with hydrogen peroxide in the cold, and subsequently at 100° C.

Hydrochloric acid was added to dissolve carbonates.

Water was added until the depth in the beaker was 10 cm.; this was allowed to stand and the liquid decanted off. This was repeated.

The small quantity of silt decanted off was allowed to settle, and was dried and weighed.

The soil was dispersed by rubbing with a rubber pestle, and was washed through a 0·22 mm. sieve.

The sand retained on the sieve was dried and rubbed on the sieve until no more passed. Sand passing through was added to that in the beaker.

The residue on the sieve was graded through 0·5 and 0·256 mm. sieves.

The material in the beaker was filled up to 10 cm. depth with water and caustic soda solution was added. After stirring it was allowed to settle for 5 min. (at 18° C.). The silt was decanted off.

Successive decantations were made, a small quantity of concentrated ammonia solution being added each time. This was repeated until the liquid was clear after 5 min.

The silt was allowed to settle in a large jar, and was dried and weighed. To this weight was added that obtained from decantation from acid solution.

The residue after decantation was fine sand.

Soil grades have been expressed as percentages of their total weight, not of the original 10 g. of soil. There is a small loss in weight during analysis, mainly due to solution of carbonates. For brevity the silt-plus-clay content of a soil has here been referred to as its silt content.

It is suggested that for marine soils the solution of carbonates is unnecessary, and may give a misleading result where large quantities of shell-fragments are present; but in most of these samples the calcium carbonate content was fairly low.

Nomenclature

Nomenclature is that of the Plymouth Marine Fauna (Marine Biological Assoc., 1931), but with the following alterations and additions:

Eteone longa (Fabricius). See Fauvel (1923).
Ophelia bicornis Savigny. See Fauvel (1927).
Spiophanes bombyx (Claparède). See Fauvel (1927).
Bathyporeia pilosa Lindström, and *B. sarsi* Watkin. See Watkin (1938).
Urothöe grimaldii Chevreux. See Chevreux & Fage (1925).
Corophium arenarium Crawford. See Crawford (1937*a*).

Algae. Nomenclature in accordance with *A Handbook of the British Seaweeds* by Newton (1931).

Flowering plants are named in accordance with the *Handbook of the British Flora* by G. Bentham, revised by Sir J. D. Hooker, seventh edition, 1924. The reference to *Zostera hornemanniana* Tutin is in Tutin (1936).

The spelling of place-names follows the Ordnance Survey: the names 'Bull Hill' and 'Pole Sands' being used in preference to Allen & Todd's 'Bullhill' and 'Polesands'.

DESCRIPTION OF THE TRAVERSES

The Main Traverse

Conditions

Seven main stations at 100 ft. intervals were worked; at each two collections were made from $\frac{1}{4}$ m.^{2} Some collections at intermediate positions were also made.

The general appearance of the traverse may be summarized as:

I−100 → I	Well-drained clean sand
I → I +70	Moist clean sand
I+70 → III−10	Muddy sand with small pools. *Arenicola* casts numerous
III−10 → III+11½	Shallow stream running over sand
III+11½ → III+57	Sand becoming muddier
III+57 → III+88	Soft mud with some sand
III+88 → IV+12	Soft mud with patches of *Enteromorpha*
IV+12 → IV+87	Clayey mud
IV+63 → IV+67	Narrow stream
IV+87 → VI	Mud with *Zostera* spp.

(All descriptions are of the conditions at low tide.)

Analyses of the soil grades are given in Table I. The silt content rose gradually from 0·7% at I−100 to 2·2% at II+67. Beyond Station III there was a sharp rise, with a maximum of 22·6% at Station V. The small quantity of silt at Station III was probably due to the stream over the sand at this point. The proportions of the coarser grades are constant along the traverse; in all but one or two samples the greatest proportion consisted of 'fine sand' (0·22–0·02 mm.). Over 95 % of the total was made up of grades below 0·5 mm.

TABLE I. SOIL GRADES ON THE MAIN TRAVERSE, EXPRESSED AS PERCENTAGES BY WEIGHT

The dimensions are those of the sieves used.

Station	>2 mm.	2–0·5 mm.	0·5–0·256 mm.	0·256–0·22 mm.	0·22–0·02 mm.	Silt and clay
I–100	Few stones	4·6	26·6	23·9	44·2	0·7
I–40	Very few stones	0·5	9·3	12·3	77·5	0·3
I	Nil	2·8	22·2	23·2	51·7	0·05
I+8	Nil	1·4	17·2	25·3	56·0	0·35
I+33	Nil	1·6	17·8	25·0	55·0	0·7
I+67	Nil	1·2	19·9	29·1	49·2	0·7
II	Nil	1·1	13·9	21·2	62·2	1·6
II+33	Nil	0·7	9·4	15·9	72·6	1·35
II+67	Nil	0·8	10·8	16·5	69·7	2·2
III	Nil	1·7	10·4	15·8	70·7	1·5
III+33	Nil	1·1	3·2	6·0	82·7	6·9
III+67	Nil	0·7	6·2	7·9	76·8	8·4
IV	Nil	0·2	2·7	3·3	77·3	16·6
IV+33	Nil	0·6	7·5	8·9	73·6	9·4
IV+67	Nil	0·6	5·5	5·1	73·8	15·0
V	Nil	0·8	4·7	3·0	68·9	22·6
VI	Few shell fragments	6·8	18·0	10·4	53·8	11·2

The traverse was situated at about half-tide mark, but sloped upwards towards Stations I and I–100 which were a little below mean high-water mark of neap tides. These stations were not covered at extreme neap tides. Stations III, IV, V and VI were at about the same level (Fig. 3).

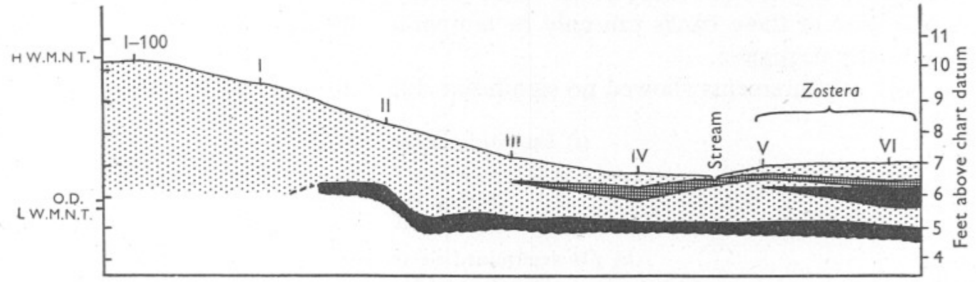


Fig. 3. Profile of the main traverse. The distance between stations is 100 ft., and the vertical scale is greatly exaggerated. The white area is below the depth investigated.

▒ Mud or sand. ▦ Shell-layer. ■ Clay.

Much of the traverse lay on top of a bed of clay, which was quite near the surface at Stations V and VI. In addition, Stations III–VI inclusive overlay a bed of shell remains at a depth of about a foot. The shells were of the same species as those now living in this area, consisting mainly of *Hydrobia*, *Cardium*, *Scrobicularia* and *Macoma*.

The greater height of the bank at Stations I and I-100 was presumably due to deposition of sand from Warren Point in this area. It was not possible to find any trace of the original surface of the bank, and it was presumed that the new sand had become mingled with the old layer. The depth to which the bank had been inundated was, however, determined by the discovery of a wood post in the sand. (Position marked by a cross in Fig. 2.) This post had been driven into a bed of clay on the original bank and was half covered by sand. On it were found empty shells of *Balanus* sp. and *Chthalmus stellatus* at a maximum depth of 26 in. below the surface of the sand. The post appeared fairly new and had probably been erected within the past 10 years. The lower end of the post was embedded in clay, and it seemed unlikely that it had been disturbed since its original erection. Thus sand had probably accumulated here to a depth of about 30 in. The traverse area is clearly at the edge of the region covered by sand, and Station I-100 had probably been covered by about 2 ft. of sand, and Station I and possibly also Station II, to a lesser depth.

The nature of the banks before the recent changes is uncertain. The Ordnance Survey Map of 1903–4 marks the area inside Warren Point as 'mud', whereas that of 1935 marks it as 'sand and mud'. It had probably become more sandy as the Outer Warren narrowed, being finally inundated by clean sand about 1943 when the breach occurred.

Currents in the Salthouse Lake area were slight, but there was some scour in the bed of the stream at low tide. There seemed to be no significant differences in current action along the traverse. Mud stirred up by waves and currents may tend to settle in the sandy areas of the traverse, and the present condition of these banks can only be temporary. Wave action in this area is normally negligible.

pH measurements showed no significant differences along the traverse.

		pH
(i) Interstitial water		
12. vii. 47, low tide	Station I	7·8
	Station II	7·8–8·0
	Station III	8·0
(ii) pH determined electrically		
6. viii. 47, low tide	Station II	7·3
	Station IV	8·3
	Station VI	7·8
14. viii. 47, low tide	Station I	7·5
	Station II	7·5
	Station III	7·9
	Station IV	7·9
	Station V	7·5

Salinity and temperature. Miscellaneous salinity records showed that the salinity in the area was near-marine, there being no differences along the traverse (except, perhaps, during rain). On 11 July 1947 (high tide 11.15 a.m., height 9 ft. 6 in.) the surface salinity of water covering certain stations was measured:

Station	Salinity ($^{\circ}/_{\circ\circ}$)	Depth of water (in.)	Time (p.m.)
I	34	4	12.20
III	34	24	1.00
VI	34	15	1.15

On 2 days, at spring and neap tides, all-day readings of conditions were made:

19 August 1947. High tide: 8.37 a.m. 13 ft. 2 in. (spring tide); 8.45 p.m. 13 ft. 2 in. A fine sunny day, but with some haze. Calm sea. Gentle breeze. There had been no rain for the previous fortnight and the River Exe was very low. Records were made of:

(i) The temperature in the soil at each station at depths of $\frac{1}{2}$ and 3 in., when uncovered by the tide.

(ii) The temperature and salinity at Station III, taken in the overlying water at high tide, and in a small pool at low tide.

(iii) Temperature and salinity of the surface water in the main channel by Bull Hill Bank.

(iv) Duration of exposure of each station at low tide.

(v) Depth of the water-table in the soil.

(vi) Air temperature.

The results are summarized in Tables II, III, IV, XI, XII and Figs. 4 and 5. The readings show:

The surface ($\frac{1}{2}$ in.) soil rose to a high temperature, 26·5° C. being the maximum recorded. The temperatures attained by the different types of soil were very similar. Thus at 4.15 p.m. the maximum soil temperature was 26° C. and the minimum 25° C.

A temperature gradient is set up in the soil during the day, the temperature at 3 in. depth being about 2° C. lower than in the surface soil. In the evening the soil cools and the gradient is reversed. At Station III the temperature ranged from 19° C. at high tide to 27·25° C. in a pool at low tide. The temperature changes occurring when the tide covered this station again in the evening were not as sudden as might be expected, as the water had already been warmed as it flowed over banks in the vicinity. At low tide the salinity rose from 34·5 to 38 $^{\circ}/_{\circ\circ}$ as a result of evaporation.

Station I was uncovered for over $7\frac{1}{2}$ hr., whereas Stations II–VI were each uncovered for about 6 hr. On a neap tide the relative differences in the periods of emergence would be much greater.

Observations on the water-table showed that it was at the surface at all stations except I–100, I and II. Drainage at Station I was very much more thorough than at II. The better drainage at this end of the traverse may be due to the nature of the soil, the greater height of these stations, or to the absence of a clay layer at any significant depth.

In the main channel the temperature ranged from 18·75 to 22·5°; the highest temperature being at low tide. The salinity showed a corresponding fluctuation, being 35 $^{\circ}/_{\circ\circ}$ at high tide, and 32·5 $^{\circ}/_{\circ\circ}$ at low tide. For most of the tidal cycle the salinity was over 34 $^{\circ}/_{\circ\circ}$, there being a marked drop for an hour or two each side of low water.

A set of readings was also taken on 12 August 1947 on a neap tide, results being similar to those above. In addition it was noted that:

The salinity of the water in Salthouse Lake was found to drop to about 19 $^{\circ}/_{\circ\circ}$ for about an hour at low water. The fresh-water inflow of this stream is small, and does not appear to exert any local influence on the fauna.

At Station I the water-table dropped to 13 in. depth, as compared with 11 in. on a spring tide. This increased drainage was probably due to the absence of water flowing down the beach from regions above high neap-tide level. Thus on spring tides the quantity of water draining down from these areas prevents the water-table from dropping as much as on neap tides.

TABLE II. TEMPERATURE READINGS ON THE MAIN TRAVERSE, 19 AUGUST 1947

Temperatures (°C) were recorded at depths of ½ and 3 in. below the soil surface. A dash indicates that the station was covered by water.

		I		II		III		IV		V		VI	
Time	Air (°)	½ in.	3 in.	½ in.	3 in.	½ in.	3 in.	½ in.	3 in.	½ in.	3 in.	½ in.	3 in.
7.30 a.m.	22	—	—	—	—	—	—	—	—	—	—	—	—
8.00	20·25	—	—	—	—	—	—	—	—	—	—	—	—
9.30	20·25	—	—	—	—	—	—	—	—	—	—	—	—
10.00	23	—	—	—	—	—	—	—	—	—	—	—	—
11.00	22·25	—	—	—	—	—	—	—	—	—	—	—	—
12 noon	23·25	24·75	22	24	21·75	—	—	—	—	21·75	20·5	22·25	21
1.05 p.m.	22·5	26	24	25	23	25·5	23·5	25	22·5	25	22·5	25·5	22·5
2.10	22·25	26·5	24·5	26	24	26	24	26	24	26	24	26·25	24
3.15	21·5	25·75	24·75	26	24·5	26·5	25	26·25	25	26	24·5	26·25	24·5
4.15	21·5	25·25	24·5	26	24·75	25·5	25·5	25·5	24·5	25	24	25	24
5.15	21·5	23·5	24	23	23·5	23·5	24	23·5	24	23·25	23·5	23·5	24
6.10	—	23	23	22·5	23	—	—	—	—	—	—	23	23·5
6.35	20	—	—	—	—	—	—	—	—	—	—	—	—

TABLE III. DEPTH OF THE WATER-TABLE BELOW THE SOIL SURFACE, 19 AUGUST 1947

At Stations II+33 to VI the water-table was at the surface at all times. Station I was uncovered at about 11 a.m. and Station II at 11.50 a.m. S, water-table at surface.

Time	I (in.)	I+50 (in.)	II (in.)
11.20 a.m.	S	—	—
11.40	—	S	—
12 noon	S	S	S
1.05 p.m.	S	S	½
2.20	5	¼	1
3.15	8	1	1
4.10	10	¾	1½
5.15	10	6½	1
6.05	11	6½	1

TABLE IV. DURATION OF EXPOSURE AT LOW TIDE OF STATIONS ON MAIN TRAVERSE, 19 AUGUST 1947

Station	Time
I	7½ hr.+
II	6 hr. 24 min.
III	*c.* 6 hr.
IV	5 hr. 50 min.
V	6 hr. 15 min.
VI	6 hr. 17 min.

There are a number of other factors, not readily measurable, which may affect distribution. The oxygen content of the soil cannot be easily determined in the field; the degree of aeration of the soil can, however, be measured by the depth of the 'black-layer'. Bruce (1928) has shown that the black-layer is produced by ferrous sulphide, which is oxidizable to ferric oxide. The top of the black-layer is a level at which there is equilibrium between sulphide production at a depth in the soil and oxidation in the more superficial layers.

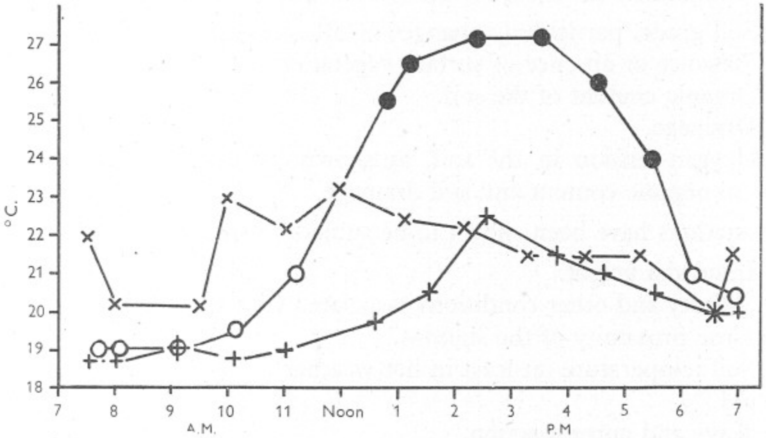


Fig. 4. Temperatures at Station III, and in the channel near Bull Hill, 19. viii. 47. —○—, water covering III; —●—, pool at III (low tide); —×—, air temperature; —+—, main channel.

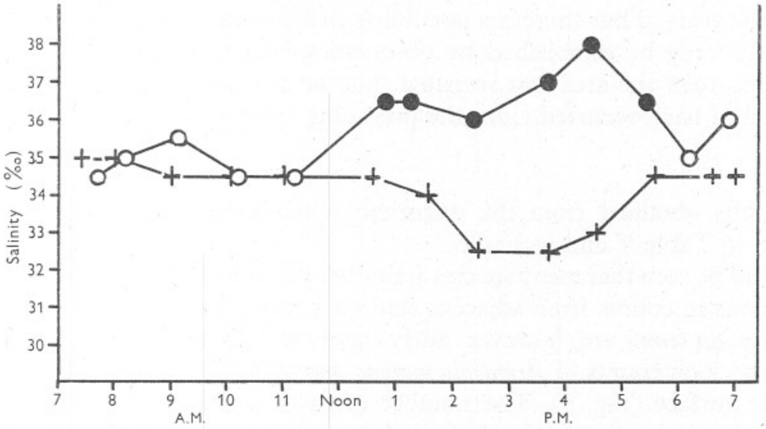


Fig. 5. Salinities at Station III, and in the channel, 19. viii. 47. —○—, water covering III; —●—, pool at III (low tide); —+—, main channel.

The black-layer tends to occur where there is little circulation (of water) through the sand, or where much organic matter occurs. The black-layer was within an inch or so of the surface from Stations II to VI, but was at a greater depth in the well-drained areas. The smell of hydrogen sulphide was not noticeable when any of the muds were disturbed, so that it is unlikely that extremely anaerobic conditions occurred anywhere on the traverse.

There seems to be no satisfactory method of estimating the organic content of marine soils, but it can be assumed that the organic content of the mud covered by *Zostera* was very much higher than elsewhere.

To summarize—the main factors which differed along the traverse were:

(1) Soil grade, particularly changes in silt content.

(2) Presence or absence of surface vegetation.

(3) Organic content of the soil.

(4) Drainage.

(5) Oxygen-tension in the soil, as shown by the 'black-layer'. This is related to organic content and soil drainage.

The stations have been shown to be subject to similar conditions of:

(1) Intertidal height.

(2) Salinity and other conditions associated with the overlying water—due to the close proximity of the stations.

(3) Soil temperature (at least in hot weather).

(4) pH.

(5) Wave and current action.

Another factor to be considered is the age of the various banks. Stations III–VI inclusive are evidently long established, but sand has recently accumulated at the other stations, and the communities must have developed in the past few years. Thus there is a possibility that succession may be taking place; this can only be established by observations over a number of years. In October 1948 the area was revisited, but no marked changes in the fauna seemed to have occurred since the preceding summer.

Fauna

Results obtained from the quantitative sampling along the traverse are shown in Table V and in Fig. 6.

It will be seen that many species are rather patchily distributed, considerable variations in counts from adjacent stations being experienced. A few species, e.g. *Tellina tenuis* are, however, fairly evenly distributed.

A check on counts of *Arenicola marina* was provided by the density of casts on the surface (Fig. 7). The number of casts of this species per m.^{2} were counted at intervals of 6 ft. along the traverse, corrections being made where one worm appeared to have produced more than one cast. The area was sufficiently calm for casts to persist for several days, and the numbers agreed well with those found in the digging. It would appear that a $\frac{1}{4}$ m.^{2} sample is adequate for assessing the numbers of a comparatively sparse animal such as *Arenicola*.

Collections were made over a period of 2 months (July and August 1947) so that it is possible that some differences were due to seasonal changes. No very great differences are shown, however, between, for example, the fauna

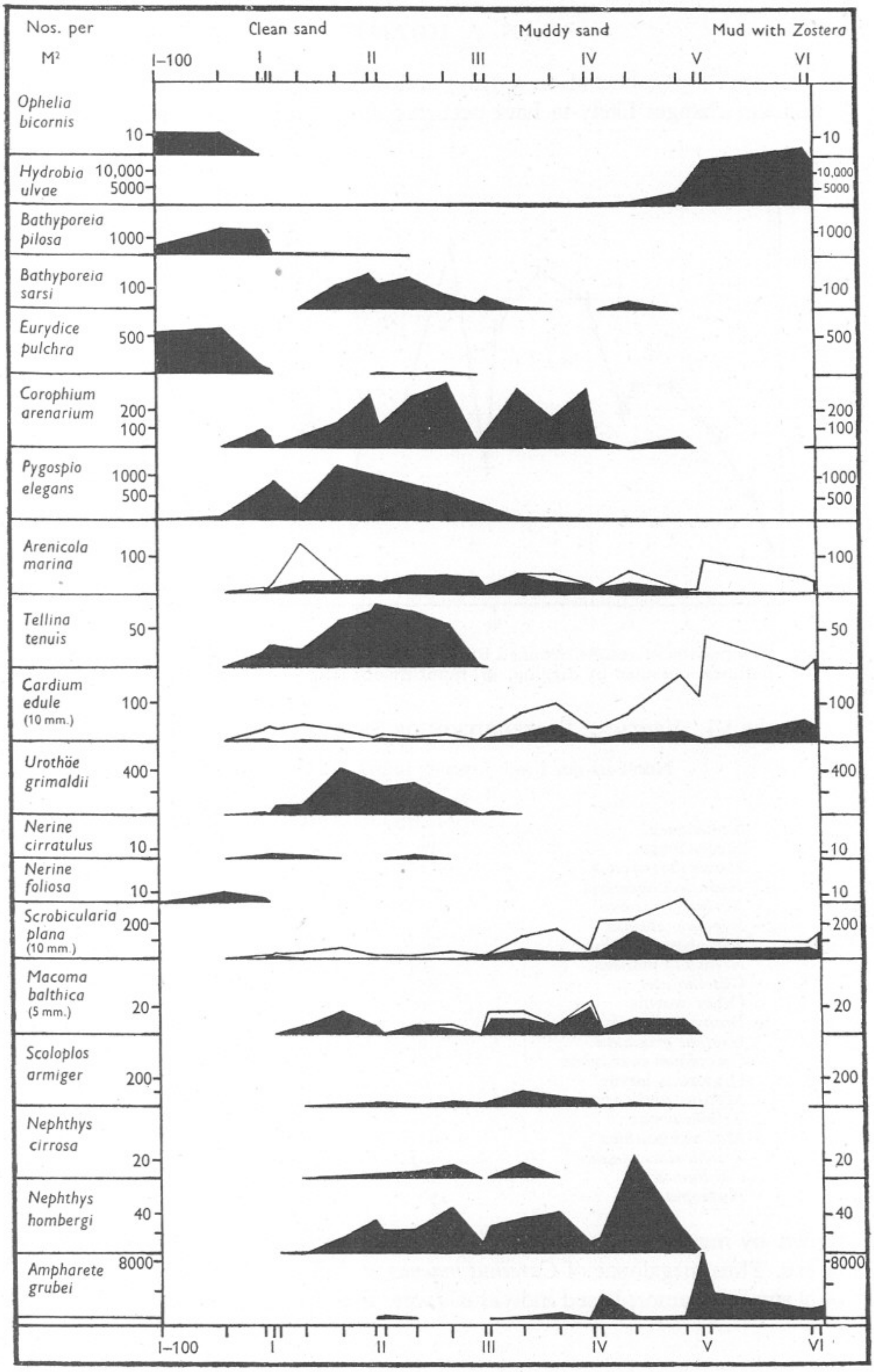


Fig. 6. The distribution of certain species on the main traverse. Small individuals are indicated by the outlined areas; adults by the solid black areas. The figures in brackets under the names of lamellibranchs indicate the length measurement dividing small individuals from adults.

at Station I+3 (collected on 3 July) and of I+8 (collected on 22 August). The main changes likely to have occurred are in the sizes of the animals, as shown by measurements of the shells of molluscs and in the settlement of larvae. Thus megalopae of *Carcinus maenas* were found in early July, whereas only small metamorphosed individuals were found in late July and in August.

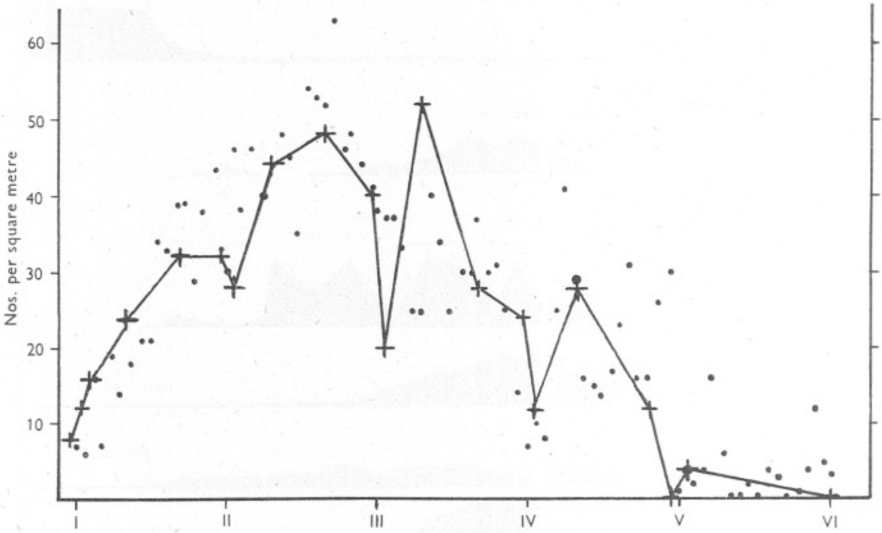


Fig. 7. Comparison of results obtained by counts of casts of adult *Arenicola marina*, and of numbers obtained by digging. ●, numbers of casts; —+—, worms dug up.

TABLE VI. VERTICAL DISTRIBUTION OF SPECIES IN THE SAND AT I+30

Numbers per ¼ m.^{2} *j*, young individuals; +, present.

	0–4 in.	4–8 in.	8–12 in.
Nemertinea	7	1	—
Eteone longa	10	—	—
Nereis diversicolor	1	—	—
Nephthys hombergi	—	1	—
Nerine cirratulus	—	1	—
Pygospio elegans	+	—	1
Spiophanes bombyx	—	2	1
Arenicola marina	26*j*	2*j*+5	1
Clitellio ater	85	2	—
Other worms	—	1	—
Bathyporeia pilosa	6	1	—
Urothöe grimaldii	2	20	1
Corophium arenarium	16	—	1
Dipterous larvae	6	—	—
Mytilus edulis spat.	1	—	—
Tellina tenuis	6	—	—
Macoma balthica	2	—	—
Scrobicularia plana	10*j*	—	—
Cardium edule	11	—	—
Hydrobia ulvae	136	—	—

TABLE V. THE FAUNA OF THE MAIN AND INTERTIDAL TRAVERSES

Populations per ¼ m.^{2} Stations I-3A and B are adjacent. 'Other worms' includes various small polychaets and oligochaets which were not identifiable from the preserved material.

Station	Date (1947)	Depth (in.)	Soil	Small anemone	*Nemertinea*†	*Phyllodoce maculata?*	*Eteone longa?*	*Nereis diversicolor*	*Nephthys hombergi*	*Nephthys cirrosa*	*Glycera convoluta*	*Scoloplos armiger*	*Nerine foliosa*	*Nerine cirratulus*	*Pygospio elegans*	*Spiophanes bombyx*	*Heterocirrus* sp.	*Cirratulidae*	*Ophelia bicornis*
I-100	22. vii.	10	S.	—	(20)	—	—	—	—	—	—	—	—	—	—	—	—	—	3
I-40	11. viii.	12½	S.	—	6	—	—	—	—	—	—	—	3	—	50	—	—	—	3
I-3B	2. vii	10	S.	—	11	—	2	—	—	—	—	—	—	2	+	—	—	—	—
I-3A	2. vii.	10	S.	—	1	—	—	—	—	—	—	—	1	—	+	—	—	—	—
I+3	3. vii.	12	S.	—	2	—	6	—	—	—	—	—	—	1	375	1	—	—	—
I+8	22. viii.	10	S.	—	9	—	2	2	—	—	—	—	—	2	440	—	—	—	—
I+30	4. vii.	12	S.	—	8	—	10	1	1	—	—	—	—	1	180	3	—	—	—
I+67	14. vii.	10	S.	—	2	—	—	—	4	—	—	2	—	—	635	—	—	—	—
II-3	7. vii.	12	S.	—	2	—	9	—	9	1	—	5	—	—	+	3	—	—	—
II+3	4. vii.	9	S.	—	—	—	7	—	6	1	—	8	—	—	+	—	—	—	—
II+33	15. vii.	9	S.	—	6	—	10	—	6	2	1	3	—	1	+	—	1	—	—
II+67	23. vii.	9	S.	—	1	—	4	—	12	4	1	10	—	—	320	—	7	—	—
III-3	7. vii.	12	S.	—	—	—	—	—	2	—	—	5	—	—	+	—	—	—	—
III+3	8. vii.	6	S.	—	1	—	—	—	7	—	—	10	—	—	+	—	5	—	—
III+33	24. vii.	6½	M.S.	—	1	—	—	—	9	4	—	27	—	—	52	—	—	—	—
III+67	28. vii.	8½	M.S.	—	—	5	7	—	11	—	—	17	—	—	+	—	50	—	—
IV-3	14. vii.	10	M.	—	1	2	(8)	—	2	—	2	12	—	—	+	—	4	—	—
IV+3	15. vii.	10	M.	—	6	1	15	—	4	—	5	—	—	—	+	—	8	—	—
IV+33	21. viii.	9	M	—	—	5	—	—	26	—	2	4	—	—	24	—	27	—	—
IV+80	22. viii.	7	M.	—	1	—	3	1	5	—	—	1	—	—	+	—	4	—	—
V-3	17. vii.	6	M.	—	2	—	18	—	—	—	—	—	—	—	+	—	—	—	—
V+3	17. vii.	6	M.	—	—	5	(4)	—	—	—	—	—	—	—	+	—	9	289	—
VI-3	4. viii.	5	M.	1	—	7	—	—	—	—	—	—	—	—	+	—	6	—	—
VI+3	7. viii.	5	M.	1	5	7	2	—	—	—	—	1	—	—	+	—	16	—	—
A-3	9. viii.	6	ST.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
B-3	9. viii.	9	ST.	—	—	—	4	—	—	—	—	—	2	—	+	—	—	—	—
C-3	2. viii.	2½	M.S.	—	—	—	—	5	2	—	—	—	—	—	+	—	—	—	—
C+3	2. viii.	3	M.S.	—	4	—	1	3	—	—	—	—	—	—	+	—	1	—	—
C+15	1. ix.	5	M.S.	—	1	—	5	33	1	1	—	79	—	—	+	—	1	—	—
D-3	30. vii.	8½	S.	—	2	1	14	—	4	—	1	68	—	—	+	—	1	—	—
D+3	1. viii.	7	S.	—	4	—	4	—	4	—	1	57	—	—	+	—	1	—	—
II-3	7. vii.	12	S.	—	2	—	9	—	9	1	—	5	—	—	+	3	—	—	—
II+3	4. vii.	9	S.	—	—	—	7	—	6	1	—	8	—	—	+	—	—	—	—
F-3	15. viii.	9½	S.	—	—	—	1	—	6	1	—	1	—	—	+	—	—	—	—
F+3	15. viii.	11	S.	—	5	—	1	—	11	—	—	2	—	—	+	2	—	—	—
G-3	21. viii.	8½	S.	—	—	—	—	—	4	3	—	3	—	—	+	—	—	—	—
G+3	21. viii.	8½	S.	—	—	—	1	—	5	5	—	3	—	—	+	—	—	—	—
H-3	14. viii.	10	S.	—	—	—	—	—	1	8	1	2	—	—	—	—	—	—	—
H+3	14. viii.	7½	S.	—	—	—	—	—	2	2	—	1	—	—	+	—	—	—	—
H+15	22. viii.	4	S.	—	—	—	—	—	4	3	—	—	—	—	—	—	—	—	—

Station	*Arenicola marina*		*Ampharete grubei*	*Melinna palmata*	*Clitellio ater*	*Hirudinea*	Other worms	*Eurydice pulchra*	*Idotea viridis*	*Bathyporeia pilosa*	*Bathyporeia sarsi*	*Haustorius arenarius*	*Urothoë grimaldii*	*Melita* sp.	*Amphipod* indet.	*Gammarus locusta*	*Corophium arenarium*	*Praunus flexuosus*	*Schistomysis ornata*	*Paramysis helleri*	*Crangon vulgaris*
	Juv.	Ad.																			
I-100	—	—	—	—	—	—	—	140	—	140	—	—	—	—	—	—	—	—	—	—	—
I-40	—	—	—	—	2	—	—	153	—	362	—	—	—	—	—	—	4	—	—	—	—
I-3B	2	3	—	—	3	—	3	35	—	545	—	—	9	—	—	—	37	—	—	—	—
I-3A	—	1	—	—	4	—	—	12	—	194	—	—	2	—	—	—	12	—	—	—	—
I+3	—	3	—	—	12	—	4	15	—	210	—	—	14	—	—	4	16	—	—	—	—
I+8	3	4	—	—	26+	—	8	—	—	5	—	—	21	—	—	—	2	—	—	1	—
I+30	28	6	—	—	87+	—	1	—	—	7	—	—	23	—	—	—	17	—	—	—	—
I+67	—	8	—	—	3	—	2	—	—	6	28	—	106	—	—	—	36	—	—	—	1
II-3	—	8	—	—	—	—	2	—	—	2	43	—	75	—	—	—	73	—	—	—	26
II+3	—	7	1	—	—	—	1	1	—	3	33	—	59	—	—	—	31	—	—	—	3
II+33	—	11	4	—	—	—	2	1	—	—	41	—	67	—	—	—	70	—	—	—	5
II+67	—	12	—	—	+	—	2	5	—	—	19	—	30	—	—	—	90	—	—	—	—
III-3	—	10	—	—	—	—	—	—	—	—	6	—	—	—	—	—	4	—	—	—	—
III+3	—	5	—	—	1	—	1	—	—	—	13	—	3	—	—	1	21	1	1	1	10
III+33	—	13	127+	4	2	—	—	—	—	—	2	—	—	—	—	—	84	—	—	1	22
III+67	(4)	7	234+	—	+	—	18	—	—	—	—	—	—	—	—	9	40	—	—	—	15
IV-3	—	6	93	—	+	—	20	—	—	—	—	—	—	—	—	—	81	—	—	—	16
IV+3	—	3	888	2	+	—	6	—	1	—	—	—	—	—	—	—	11	—	—	—	—
IV+33	(8)	7	192	3	+	—	11	—	—	—	(8)	—	—	—	1	(15)	1	—	—	—	—
IV+80	—	3	120	—	+ +	—	2	—	—	—	—	—	—	—	—	—	13	—	—	—	—
V-3	2	—	2300	(6)	+	—	14	—	—	—	—	—	—	—	—	—	—	(6)	—	—	—
V+3	22	1	996	—	2	—	7	—	—	—	—	—	—	—	—	—	—	—	—	—	—
VI-3	(18)	—	393	—	—	—	106	—	—	—	—	—	—	—	—	—	—	—	—	—	1
VI+3	8	—	439	(8)	+	—	9	—	4	—	—	—	—	—	—	1	1	—	—	—	11
A-3	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—
B-3	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	20	—	—	—	—
C-3	—	—	—	—	—	—	4	—	—	—	1	—	—	—	—	—	6	—	—	—	—
C+3	—	—	—	—	+	—	40	—	—	—	—	—	—	—	—	—	4	—	—	—	—
C+15	25	1	3	—	+	1	3	—	—	—	—	—	—	—	—	—	78	—	—	—	—
D-3	1	7	—	1	+	—	15	—	—	—	17	—	—	—	—	—	71	—	—	—	1
D+3	—	5	—	—	+	—	10	—	1	1	—	—	1	1	—	3	126	—	—	—	—
II-3	—	8	—	—	—	—	2	—	—	2	43	—	75	—	—	—	73	—	—	—	26
II+3	—	7	1	—	—	—	1	1	—	3	33	—	59	—	—	—	31	—	—	—	3
F-3	—	15	—	—	—	—	3	2	—	—	88	—	20	—	—	—	—	—	—	—	—
F+3	—	7	—	—	—	—	2	—	—	—	41	1	16	—	—	—	—	—	—	—	—
G-3	—	6	—	—	—	—	—	—	—	—	20	—	5	—	—	—	—	—	—	—	27
G+3	—	5	—	—	—	—	—	—	—	—	52	—	10	—	—	1	—	—	—	—	3
H-3	—	1	—	—	—	—	—	—	—	—	13	—	1	—	—	—	—	—	—	—	4
H+3	—	1	—	—	—	—	—	—	—	—	17	—	2	—	—	—	—	—	—	—	1
H+15	—	—	—	—	4	—	—	—	—	—	8	2	—	—	—	—	—	1	—	—	1

Station	*Carcinus maenas*			Dipterous larvae	*Lepidochiton cinereus*	*Mytilus edulis*	*Tellina tenuis*	*Macoma balthica*		*Scrobicularia plana*		*Paphia decussata*	*Cardium edule*		*Littorina rudis*	*Littorina littorea*	*Hydrobia ulvae*	*Ammodytes tobianus*	Station
	Meg.	Juv.	Sm.					Juv.	Ad.	Juv.	Ad.		Juv.	Ad.					
I-100	—	—	—	1	—	10	—	—	—	—	—	—	—	—	—	—	30	—	I-100
I-40	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	8	—	I-40
I-3B	1	—	—	1	—	—	5	—	—	—	—	—	8	—	—	—	30	—	I-3B
I-3A	1	—	—	1	—	—	4	—	—	4	—	—	12	1	—	—	10	—	I-3A
I+3	—	1	—	1	—	—	7	—	—	2	—	—	10	—	—	—	42	—	I+3
I+8	—	—	—	1	—	—	7	—	—	6	2	—	8	—	—	—	148	—	I+8
I+30	—	—	—	6	—	1	6	—	2	10	—	—	10	1	—	—	136	—	I+30
I+67	2	1	—	—	—	—	16	—	5	16	—	—	7	1	—	—	101	—	I+67
II-3	—	—	—	—	—	—	19	—	2	4	—	—	2	—	—	—	51	—	II-3
II+3	—	—	—	—	—	—	22	—	—	4	—	—	2	2	—	—	39	—	II+3
II+33	—	3	1	—	—	1	19	—	2	5	—	—	2	—	—	—	112	—	II+33
II+67	—	8	—	—	—	3	15	1	1	10	—	1	5	—	—	5	40	—	II+67
III-3	2	2	—	—	—	—	1	—	—	—	3	—	1	—	—	—	2	—	III-3
III+3	2	10	—	—	—	—	—	2	4	5	5	—	4	2	—	—	42	—	III+3
III+33	—	4	2	—	—	1	—	2	4	16	16	—	13	5	1	3	76	—	III+33
III+67	—	36	—	—	—	4	—	—	2	30	13	—	15	11	—	2	250	—	III+67
IV-3	—	3	1	—	—	—	—	1	6	(6)	8	—	(8)	2	—	—	91	—	IV-3
IV+3	—	13	1	—	—	—	—	—	1	45	10	—	2	7	—	—	155	—	IV+3
IV+33	—	19	2	—	—	—	—	—	4	(18)	39	—	14	6	—	4	422	—	IV+33
IV+80	—	12	1	1	—	—	—	—	4	(79)	8	—	(38)	7	—	7	1126	—	IV+80
V-3	—	106	5	2	—	1	—	—	—	(39)	15	—	27	3	(19)	3	2862	—	V-3
V+3	—	34	6	—	—	—	—	—	—	12	15	—	71	1	(5)	(21)	3320	—	V+3
VI-3	—	(79)	—	—	1	1	—	—	—	(6)	19	—	34	15	26	(64)	4120	—	VI-3
VI+3	—	76	—	—	1	6	—	—	—	(28)	10	—	43	12	26	32	3332	—	VI+3
A-3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	16	—	A-3
B-3	—	—	—	—	—	—	—	—	—	—	—	—	—	1	2	30	1700	—	B-3
C-3	—	—	—	11	—	—	—	—	—	(4)	—	—	2	3	1	9	617	—	C-3
C+3	—	2	—	11	—	—	—	—	—	16	—	—	22	7	2	—	1770	—	C+3
C+15	—	—	4	—	—	23*	—	—	8	(93)	8	—	56	13	—	—	1250	—	C+15
D-3	—	4	—	1	—	—	3	—	9	4	—	—	12	5	—	—	260	—	D-3
D+3	—	2	—	—	—	—	3	—	8	13	1	—	15	5	—	—	197	—	D+3
II-3	—	—	—	—	—	—	19	—	2	4	—	—	2	—	—	—	51	—	II-3
II+3	—	—	—	—	—	—	22	—	—	4	—	—	4	2	—	—	39	—	II+3
F-3	1	—	—	—	—	—	45	—	1	—	—	—	4	2	—	—	10	—	F-3
F+3	—	—	—	—	—	—	46	—	—	—	—	—	3	1	—	—	12	—	F+3
G-3	—	—	—	—	—	—	47	—	—	—	—	—	—	—	—	—	3	—	G-3
G+3	—	1	—	—	—	—	47	—	—	—	—	—	1	—	—	—	3	—	G+3
H-3	—	1	—	1	—	—	42	—	—	—	—	—	—	—	—	—	2	—	H-3
H+3	—	—	—	—	—	—	45	—	—	—	—	—	1	—	—	—	—	—	H+3
H+15	—	—	—	—	—	—	48	—	2	—	—	—	1	3	—	—	—	1	H+15

S.	Sand.
M.	Mud.
M.S.	Muddy sand.
ST.	Stones.

Juv.	Young specimens (i.e. *Macoma* less than 5 mm., and *Cardium* and *Scrobicularia* less than 10 mm. long).
Ad.	Adult.
Meg.	Megalopa stage } of *Carcinus*.
Sm.	Half-grown } of *Carcinus*.

*	At C+15 there were 6 young and 17 adult *Mytilus*. Elsewhere only young individuals were found.
†	Probably *Cephalothrix linearis* Rathke.

( )	Unreliable figures owing to subsampling error.
+	Present, but not counted.

The vertical distribution of species at Station I + 30 is shown in Table VI; it will be seen that practically all species occur in the top 4 in., notable exceptions being *Arenicola marina* and *Urothöe grimaldii*.

The close proximity of the various types of ground may also affect the distribution of certain species. Individuals may stray from their typical habitat (perhaps as a result of 'population pressure') so that in time a species will come to colonize all suitable grounds. This spreading tendency presumably operates continually and will result in a fringing zone where individuals may occur on quite atypical grounds. The extent of this zone will vary with the migratory ability of the species and the degree of unsuitability of the ground to be traversed. The outstanding example here was *Hydrobia ulvae*, normally inhabiting the mud, particularly the *Zostera* beds, but which is continually endeavouring to extend its range so that specimens occur even on the sandy grounds. They would not occur there but for the contiguity of their normal habitat.

The fauna of the main traverse may be arbitrarily divided into a number of zones:

(1) *Fauna of clean loose sand*. Stations I − 100 and I − 40. The silt content was less than 1 % and the grade of sand was coarser than at other stations on this traverse. The sand was very well drained, there being no black-layer near the surface.

Typical species were (Station I − 40):

	Per m.²		Per m.²
Ophelia bicornis	12	*Bathyporeia pilosa*	1448
Nerine foliosa	12	*Corophium arenarium*	16
Pygospio elegans	A few	*Hydrobia ulvae*	32
Eurydice pulchra	612		

(2) *Fauna of firm moist sand*. Stations I–III. The sand was rather finer than at the previous stations. The silt content rose from 0·05 % to a maximum of 2·2 % at II + 67. The bank sloped down gently, so that while Stations I to I + 67 were fairly well drained, the subsequent stations had standing water on the surface. A black layer usually occurred within a few inches of the surface.

Typical species were (Station II + 33):

	Per m.²		Per m.²
Nephthys hombergi	24	*Urothöe grimaldii*	268
N. cirrosa	8	*Corophium arenarium*	280
Scoloplos armiger	12	*Tellina tenuis*	76
Pygospio elegans	Common	*Macoma balthica*	8
Arenicola marina	44	*Cardium edule*	8 young
Bathyporeia sarsi	164	*Hydrobia ulvae*	448

Ophelia bicornis and *Nerine foliosa* were no longer present, and *Eurydice* was much less frequent. *Bathyporeia pilosa* had been replaced by *B. sarsi*, probably due to the fall in height. According to Watkin (1938) *B. pilosa* is restricted to a narrow zone at about H.W.M.N.T., whereas *B. sarsi* has a wider range extending down to below low-water mark. A number of species appeared at about Station I and extended almost the length of the traverse; e.g. *Nephthys hombergi*, *Scoloplos armiger*, *Scrobicularia plana* and *Cardium edule*. But *Bathyporeia sarsi*, *Tellina*, *Urothöe* and *Nerine cirratulus* were restricted to the clean sand of this zone.

(3) *Muddy sand.* Stations III + 33 to IV + 80. This was a transitional zone from sand to mud. At Station III + 33 the silt content was 6·9 %, and a maximum of 16·6 % silt occurred at Station IV. The other grades of soil were in very similar proportions to that found elsewhere in the traverse. The rise in silt content seems to be the cause of the absence of *Bathyporeia*, *Tellina*, *Urothöe* and *Nerine*; but the species extending into this zone usually show a higher density than on the clean sand.

Typical species were (Station IV + 3):

	Per m.²		Per m.²
Nephthys hombergi	16	*Corophium arenarium*	44
Glycera convoluta	20	*Macoma balthica*	4
Pygospio elegans	Present	*Scrobicularia plana*	180 young and 40 adult
Arenicola marina	12	*Cardium edule*	8 young and 28 adult
Ampharete grubei	3552	*Hydrobia ulvae*	620
Melinna palmata	8		

Large numbers of *Ampharete* occur; this species being most abundant where the silt content is high. *Pygospio* occurred in small numbers, and thus inhabits a wide range of soils.

(4) *Mud with* Zostera. Stations V and VI. The soil contained about 10–20 % of silt, and was of a rather clayey consistency. When walking over it, one's feet sunk in only a few inches. Holes dug in the mud persisted for months after digging. The surface of the mud was covered by a dense growth of *Z. hornemanniana* Tutin and *Z. nana* Roth, which provided a refuge for numerous small *Carcinus maenas* and *Hydrobia ulvae*. Small specimens of *Arenicola marina* were abundant. The burrowing fauna was, if anything, a little less dense than on the muddy sand. *Macoma*, *Scoloplos* and *Nephthys hombergi* were absent.

Typical species were (Station V + 3):

	Per m.²		Per m.²
Arenicola marina	88 small and 4 adult	*Cardium edule*	284 young and 4 adult
Ampharete grubei	3984	*Littorina rudis*	20
Carcinus maenas	160	*L. littorea*	84
Scrobicularia plana	48 young and 60 adult	*Hydrobia ulvae*	13,280

The intertidal traverse

Conditions

This was at right angles to the main traverse, crossing it at Station II, which is identical with Station E. Stations were at 100 ft. intervals and were designated A, B, C ... H. 'A' was near high-water mark, and 'H' at low-water mark. Stations A, B and C were on gravel, with some admixture of sand. The fauna at these stations was imperfectly sampled owing to difficulties in sieving. From C+12 to H the soil was fairly clean moist sand, overlying the bed of clay. Grade analyses showed a silt content of under 1% for stations from D downwards (Table VII).

TABLE VII. SOIL GRADES ON THE INTERTIDAL TRAVERSE, EXPRESSED AS PERCENTAGES BY WEIGHT

Station	>2 mm.	2–0·5 mm.	0·5–0·256 mm.	0·256–0·22 mm.	0·22–0·02 mm.	Silt and clay
A	Many stones	24·3	44·5	19·6	11·1	0·5
B	Few stones	5·7	38·7	29·7	24·0	2·0
C	Few stones	2·5	9·3	10·0	73·8	4·4
D	Nil	1·6	19·5	25·0	53·0	1·0
E	Nil	1·1	13·9	21·2	62·2	1·6
F	Nil	0·8	13·9	26·1	58·7	0·6
G	Nil	0·4	8·4	28·9	61·3	0·9
H	Nil	0·2	4·5	16·5	77·7	1·0

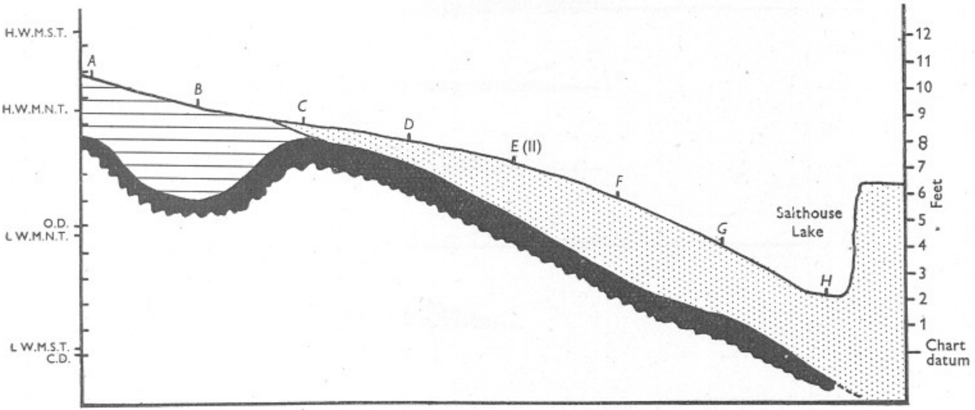


Fig. 8. Profile of the intertidal traverse. Vertical scale greatly exaggerated. Interval between stations is 100 ft. The white area is below the depth investigated.

░ Sand. ▤ Gravel. ■ Clay.

The profile of the traverse is shown in Fig. 8. The bank sloped down to Salthouse Lake, so that there was little scouring of the banks near low water. This is in contrast to banks adjacent to the main channel which are exposed to a considerable tidal stream. The water-table was at or near the surface at all stations, and a black-layer was usually present at a depth of a few inches. Other conditions were similar to those to which the main traverse was exposed.

pH was determined electrically from samples taken at low tide on 21 August 1947:

	pH		pH
A	7·9	E	7·5
B	7·9	F	7·8
C	7·7	G	7·8
D	7·8	H	8·0

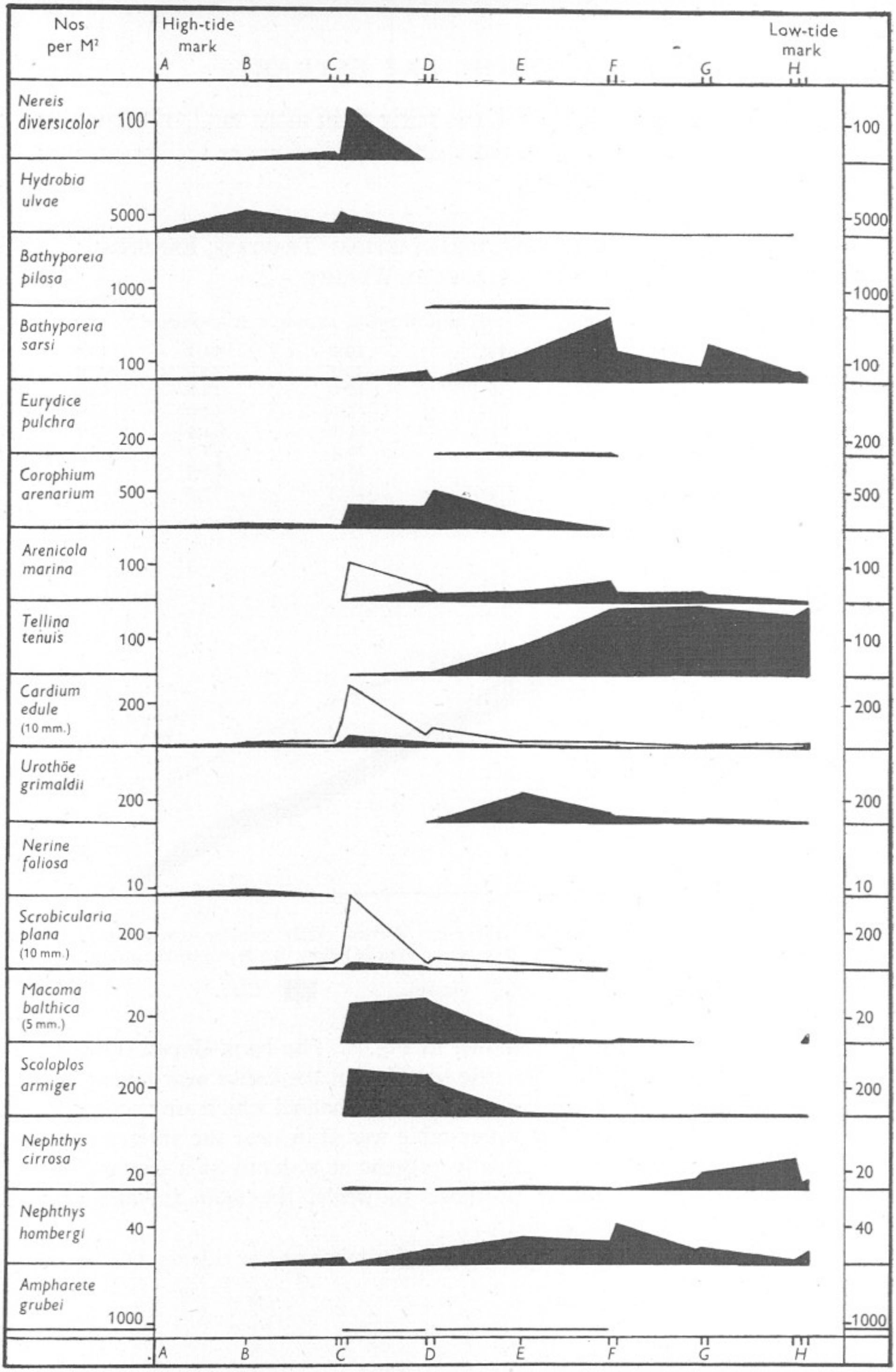


Fig. 9. Distribution of certain species on the intertidal traverse. For explanations see Fig. 6. Station 'E' is the average of numbers from Stations II−3 and II+3.

Fauna

The results obtained from quantitative sampling are shown in Table V and in Fig. 9. Only one collection was made at Stations A and B; and additional collections were made at C + 15 and H + 15, the latter being in the bed of Salthouse Lake. No other intermediate stations were worked.

The stations are too few to give a detailed picture of the distribution of the fauna, the object of these collections being to determine the intertidal distribution of species occurring in the main traverse. At Stations A, B and C the fauna was poor, especially in burrowing species. At C − 3 typical species were:

	Per m.^{2}		Per m.^{2}
Nereis diversicolor	20	*Cardium edule*	8 young and 12 adult
Nephthys hombergi	8	*Littorina rudis*	4
Corophium arenarium	24	*L. littorea*	36
Larval Diptera	44	*Hydrobia ulvae*	2468
Scrobicularia plana	16 young		

At Station C + 15, off the edge of the gravel, many species were abundant. The silt content was probably about 3%, but was not determined. Small individuals of *Arenicola*, *Cardium* and *Scrobicularia* were very abundant. Typical species included:

	Per m.^{2}
Nereis diversicolor	132
Nephthys hombergi	4
Scoloplos armiger	316
Arenicola marina	100 small and 4 adult
Corophium arenarium	312
Mytilus edulis	24 young and 68 adult
Macoma balthica	32
Scrobicularia plana	372 young and 32 adult
Cardium edule	224 young and 52 adult
Hydrobia ulvae	5000

The intertidal distribution of species is discussed on pp. 218–28. It is apparent that most of the species encountered have a fairly wide intertidal range, so that the small differences in height occurring along the main traverse would have little effect on their distribution.

The distribution of the following species may, however, be affected by small changes in height: *Nereis diversicolor* occurred at about H.W.M.N.T., and was consequently scarce on the main traverse, which was at a slightly lower level. *Bathyporeia pilosa*, *Eurydice pulchra* and *Nerine foliosa* occurred only at about half-tide mark, and this may account for their occurrence only at the higher stations on the main traverse. Drainage may also be an important factor in determining their distribution.

Bull Hill Bank

This was a bank of clean sand in the middle of the estuary near Dawlish Warren. The bank was scoured by strong currents, and to a lesser extent by waves; the surface of the sand being consequently furrowed, and the edge facing the main channel sloped away steeply. The top was at about half-tide mark, and was fairly level.

The sand was rather coarser than that from Salthouse Lake. A sample from the top of the bank (from Station BH + 100) giving on analysis:

(mm.)	(%)	(mm.)	(%)
>2	—	0·256–0·22	30·1
2–0·5	5·1	0·22–0·02	10·3
0·5–0·256	54·0	Silt and clay	0·5

Independent analyses of the sand from Bull Hill Bank and Salthouse Lake are given by Wilson (1948).

There was no black-layer in the soil, which was very well drained, except near low-water mark, where it remained saturated at low tide.

Salinity and temperature conditions were similar to those in Salthouse Lake.

The fauna was investigated by a single traverse passing through the steep edge of the bank, and for a short distance across the top. A single collection from $\frac{1}{4}$ m.^{2} was made at each station.

TABLE VIII. FAUNA OF BULL HILL BANK

Clean sand at all stations. Numbers per $\frac{1}{4}$ m.^{2}; *j*, young individuals; '−' stations are on top, and '+' stations down the slope of the bank.

Station	Date	Depth (in.)	*Nemertinea*	*Nephthys cirrosa*	*Nerine cirratulus*	*Ophelia bicornis*	Other worms	*Eurydice pulchra*	*Bathyporeia sarsi*	*Haustorius arenarius*	*Urothöe grimaldii*	Dipterous larvae	*Mytilus edulis*	*Tellina tenuis*	*Hydrobia ulvae*
BH − 100	23. viii.	6	.	.	6	67	.	24	6	.	.	.	.	.	.
BH − 50	23. viii.	7	.	.	6	25	.	42	2	.	.	1	.	1	.
BH + 4	25. vii.	6	.	.	4	19	1	10	1	.	.	.	.	.	.
BH + 9	25. vii.	6	.	.	2	53	.	29	.	.	.	1	.	.	.
BH + 14	25. vii.	6	1	.	8	43	.	27	2	.	.	.	.	.	.
BH + 19	25. vii.	6	2	1	7	14	.	32	2	1	.	.	1*j*	3	4
BH + 24	25. vii.	6	.	3	8	.	1	3	24	1	19	.	.	13	.

The fauna (Table VIII and Fig. 10) was very poor, this being perhaps due to:

(i) Strong currents, which prevent the establishment of an epifauna.

(ii) The coarse and loose texture of the soil. Watkin (1942) found that coarser grades of sand usually supported a poorer fauna than was found in finer grades.

(iii) Drainage. This would seem to be an important factor in restricting typically intertidal species to low-water mark.

On top of the bank typical species were (Station BH − 100):

	Per m.^{2}		Per m.^{2}
Nerine cirratulus	24	*Eurydice pulchra*	96
Ophelia bicornis	268	*Bathyporeia sarsi*	25

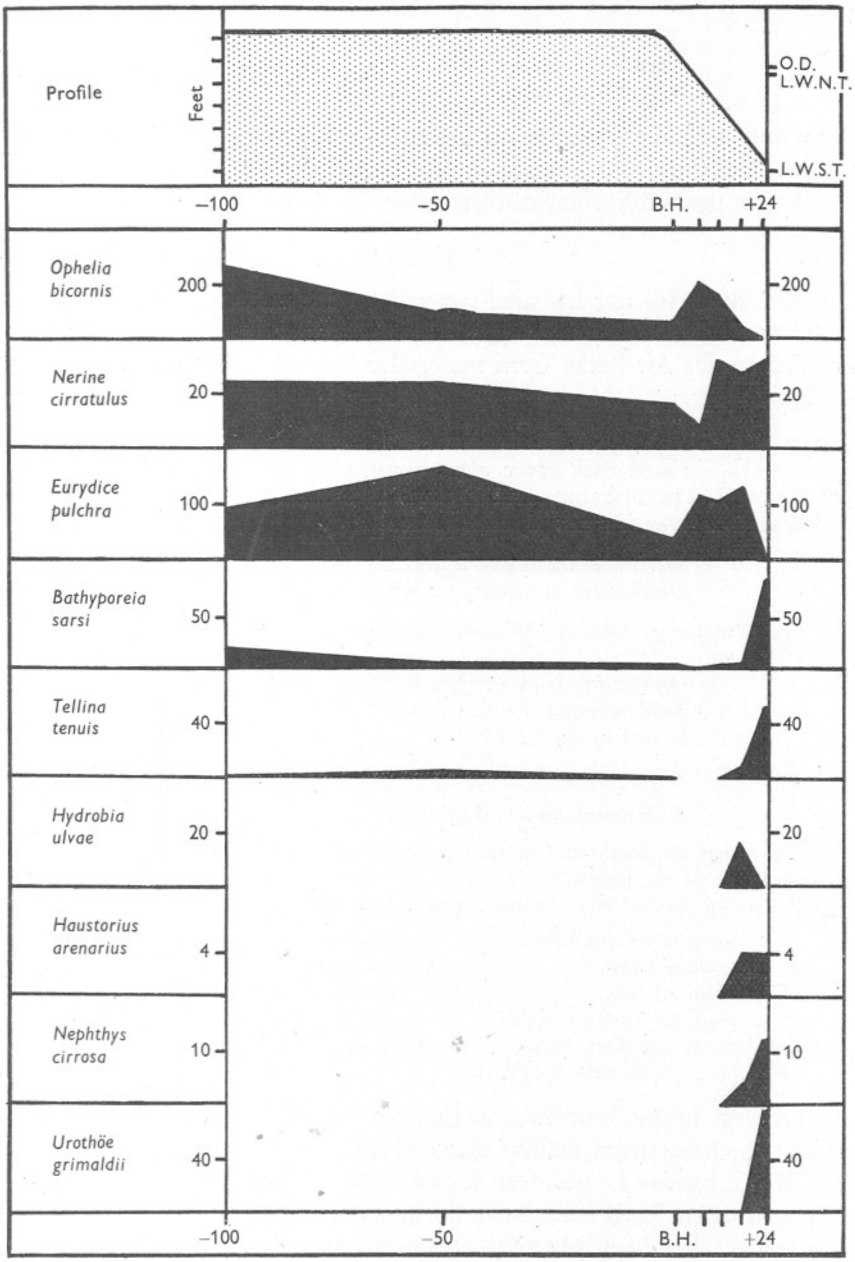


Fig. 10. Profile and fauna on Bull Hill Bank. Note that many typically intertidal species are here restricted to low-water mark. Numbers per m.²

At low-water mark *Ophelia* was absent, but certain other species appeared:

Nephthys cirrosa
Haustorius arenarius
Urothöe grimaldii
Tellina tenuis
Hydrobia ulvae

The only abundant species on the bank was *Ophelia*, which occurred all over the top, buried to a depth of about 4 in. in the sand. It seemed to be most abundant in the valleys between the ridges in the sand.

Flora

Neither Bull Hill nor the area covered by the intertidal traverse had any significant growth of surface algae. The following species have kindly been identified by Dr M. Parke from material collected on the main traverse on 29 August 1947:

I – 100. Algae absent.

I – 78 → III. Minute dark green algae occurred, with a maximum abundance at about Station I. The algae increased in abundance during the summer and tended to bind the surface layer of sand. Species recorded:

Merismopedia glauca Kütz
Oscillatoria margaritifera Kütz

III + 15. Patches of *Enteromorpha crinita* J.Ag.

IV → IV + 33.
Oscillatoria margaritifera Kütz
Enteromorpha crinita J.Ag.
E. intestinalis Link.

IV + 75 → VI. *Zostera nana* Roth

Z. Hornemanniana Tutin

Drifting algae, or fragments of them, stranded by the receding tide, add to the organic content of the banks.

The following species were found deposited on the traverse:

Enteromorpha crinita J.Ag.
E. intestinalis Link.
Ulva lactuca Linn.
Chaetomorpha litorea Cooke
Lomentaria clavellosa Gaill.
Gracilaria confervoides Grev.
Ceramium rubrum Ag.
Callithamnion corymbosum Lyngb.
Ectocarpus confervoides Le Jol.
Isthmoplea sphaerophoia Kjellm.
Fucus vesiculosus L.

Large areas of the mud-flats in this part of the estuary were covered by *Zostera*, which occurred mainly between high- and low-water mark of neap tides. No *Z. marina* L. has been found in the estuary.

Spartina stricta Roth. is native in the area north of the Warren, but *S. Townsendii* Groves has been planted. 1000 setts of the latter were planted o near the Warren in November 1935 to stabilize the mud-flats. *S. Townsen* is spreading slowly along the edge of the Warren, and a careful examinati revealed small clumps along the whole of the northern side of the In

Warren. In the traverse area, about 200 yards square, twenty-three plants or small clumps were found. These occurred on the sand or among the *Zostera*, mostly at about H.W.M.N.T.

BIOMASS AND SOURCES OF FOOD

The 'rough weight' of the principal species at certain stations was determined by weighing preserved specimens after removal of surface moisture. The shells of lamellibranchs were removed before weighing. The species comprising the 'epifauna' were not included. Details of biomasses are in Table XII.

On sand at Station I – 100 the biomass was 4·6 g./m.^{2}, this being by far the poorest area. On Bull Hill Bank, however, where *Ophelia* was abundant, a total of 36·9 g./m.^{2} was reached, this being almost entirely made up of these worms. At Stations II, IV and VI, the biomasses were 69·3, 101·7 and 45·4 g. respectively. The greatest weight at these stations was made up by only four species, *Arenicola*, *Scrobicularia*, *Cardium* and *Ampharete*. It would seem that 'soil-swallowers' such as *Ophelia* and *Arenicola* have a very efficient mode of feeding, as they outweigh all other species combined at their zone of maximum abundance. Carnivores (*Nephthys*, *Glycera*, *Eurydice*, etc.) are nowhere abundant, comprising about 5–10% of the total weight.

MacGinitie (1935), discussing food relations in a Californian estuary, found that carnivores comprised about 5% by weight of the total population of a mud-flat. Detritus-feeders made up the greatest weight of the population, probably on account of their longevity. MacGinitie considered that the main sources of food were *Zostera*, *Enteromorpha*, *Polysiphonia* and pieces of algae which floated in with the tide. Very few animals lived directly on these plants, the filter-feeders subsisting mainly on plants in various stages of decay, and on bacteria. *Zostera* appeared to be of use not only as a source of detritus, but also for its part in the accumulation of detritus which becomes caught around its roots. Hence it was in and near the *Zostera* regions that the greatest abundance and variety of life was found. At low tide plant tissue tended to become dried up and killed; dead leaves started decomposing into detritus, and meanwhile would be distributed by the action of animals and by water movements, so becoming available to all the bottom animals in the neighbourhood.

Although no attempt has been made to assess the relative roles of detritus, bacteria and plankton as the food supply of animals in the Exe Estuary, it is clear that conditions are not unlike those in the Californian estuary. The settling of drifting algae on the banks has already been referred to, and the importance of *Zostera* as a source of food for areas outside its habitat was emphasized by some observations made in August 1947. During the neap tides of that month some parts of the *Zostera* beds were left uncovered for several days during hot sunny weather. When again covered by the tide some of the leaves, which had become dry and black, became detached and floated away. At this time leaves of *Zostera* were quite abundant floating up and down the estuary with the tide, being deposited on the banks as the tide receded.

NOTES ON CERTAIN SPECIES

The distribution of certain estuarine species is discussed by Spooner & Moore (1940), and of sand-living species by Watkin (1942). The following notes are intended to supplement these in the light of subsequent work and the results obtained in the present survey.

POLYCHAETA

Phyllodoce maculata (L.)

Fauvel (1923) regards *P. maculata* (L.) and *P. teres* Malmgren as one and the same species, although they were recorded separately by Allen & Todd (1902). In 1901, *P. teres* was found in clean sand above Starcross, in sand west of the mouth of Salthouse Lake, and from gravel between Powderham and Starcross. A specimen doubtfully assigned to *P. maculata* was taken on the sandy ground between Starcross and Cockwood.

The specimens found in 1947 were probably of the same species as those previously taken, but identification was difficult as many of the specimens were fragmented. *Phyllodoce* was found on the more muddy part of the main traverse, from Stations III + 67 to VI + 3. It was not found on Bull Hill.

Eteone longa (Fabricius)

In 1901 Allen & Todd found specimens identified as *E. pusilla* Örsted (*nec* Malmgren) in clean sand; and it seems likely that the 1947 specimens were of the same species as found in 1901, but there is some doubt as to their identity. Those found in 1947 had a head approaching that described by Malmgren (1865) for *E. pusilla*, but the anal cirri are not '*lineare-fusiformes elongati*', but of the type described by Örsted (1843) as '*papillis caudalibus subglobosis*'. The head does not correspond with Örsted's description, however. Fauvel (1923) does not refer to *E. pusilla* Örsted, and *E. pusilla* Malmgren is now *E. lactea* Claparède.

The specimens correspond most closely to *Eteone longa* (Fabricius), both in the shape of the head and of the anal cirri, and it is to this species that they have been provisionally assigned.

Eteone extended from sand to mud on the main traverse. Intertidally it ranged from about H.W.M.N.T. to about L.W.M.N.T., with a maximum near the upper part of its range. It was absent from Bull Hill.

Nephthys hombergi Lamarck

This species was recorded by Allen & Todd from sand and muddy sand all over the estuary, but not in very muddy ground.

In 1947 it was collected at stations ranging from sand to mud. Its maximum density was at IV + 33: 104 per m.^{2}; with a silt content of 9·4%. It was less abundant, *c.* 12 per m.^{2}, at IV, where the silt content was 16·6%, and was absent on muddy stations with *Zostera*, where the silt percentage ranged from 11·2 to 22·6. At the other end of the traverse it did not extend beyond I + 30, possibly being limited by the better drainage at this end. Intertidally it ranged throughout the tidal zone, with no distinct maximum. It was not found on Bull Hill.

This species is not confined to the shore, being common on sandy and muddy bottoms at sea. Spooner & Moore (1940) and Alexander, Southgate & Bassindale (1935) have found it plentiful towards the mouth of the estuaries of the Tamar and Tees respectively. On the Tamar its normal density was between 100 and 300 per m.^{2}, rather higher than that met with on the Exe. Brady (1943), however, found the maximum density of this species at Black Middens on the Northumberland coast to be only 60 per m.^{2}

Nephthys cirrosa Ehlers

Found by Allen & Todd only in fine, clean sand, where it was quite plentiful. In 1947 this species was found in wet sand at stations between II and III + 33, the silt content ranging from 1·35 to 6·9%. Intertidally, it occurred at most stations, with its greatest density, 32 per m.^{2}, near low-water mark. On Bull Hill it was restricted to two stations near low-water mark. The intertidal range of this species thus seems to be dependent on drainage conditions in the sand.

There are few other records of this species. In the Plymouth Marine Fauna (Marine Biological Assoc., 1931) it is recorded from sand between tide-marks on Drakes Island and the Yealm Estuary. Bassindale (1938) found single specimens in sand near the mouth of the Mersey Estuary. Rees (1939) found it on a number of traverses on sandy shores in North Donegal; the species extended up the beach to half-tide mark, maximum numbers occurring at low-water mark.

Scoloplos armiger (O. F. Müller)

In 1901 this species was found in sand or muddy sand within the estuary, but not on the Pole Sands. In the 1947 survey it was found on soils ranging from 0·7 to 16·6% silt, but was absent at the muddiest stations. Its highest density was in muddy sand at III + 33: 108 per m.^{2}, the silt content being 6·9%. It did not occur on the well-drained sand, and was absent from Bull Hill. Intertidally it showed a maximum just below H.W.M.N.T.

The distribution of *Scoloplos* on the main traverse resembles that of *Macoma* and *Nephthys hombergi*, being typical of species with an optimum density in muddy sand, and being intolerant of 'pure' mud. It is recorded from muddy sand in a number of areas, but not from clean, sandy beaches, and it is usually less abundant in mud. Spooner & Moore (1940) found it in moderate numbers, up to 152 per m.^{2}, on St John's Lake, where it seemed to be restricted to the upper tidal levels in the *Zostera* zone.

Brady (1943) found *Scoloplos* at Budle Bay on the Northumberland coast. It was widely distributed in slightly muddy sand, its density seeming to be inversely related to that of *Macoma balthica*. The author considered that the two species were in competition for detritus as food, but that since *Macoma* also fed on suspended detrital and planktonic matter, it tended to become the dominant species. Thus *Scoloplos* could only become really abundant where *Macoma* was for some reason scarce.

The density of *Macoma* on the Salthouse Lake traverse was nowhere great, so that competition for food between the two species was probably not very intense. On the whole, *Macoma* and *Scoloplos* show similar distribution and densities, so failing to agree with Brady's observations.

Nerine foliosa (Audouin & Edwards)

This species was recorded as *N. coniocephala* Johnston by Allen & Todd, several specimens being obtained in sand west of the mouth of Salthouse Lake and in the hard clayey mud to the north of it.

In 1947 small numbers were found on clean sand at Stations I–40 and I–3A, also among gravel above H.W.M.N.T. at B–3. None was found on Bull Hill.

There are few records of this species: Percival (1929) records it from the River Tamar, in mud; in the Plymouth Marine Fauna it is also recorded from Wembury, Drakes Island, east side of the Sound, Kingsand Beach, and the River Yealm sand bank. Brady (1943) found it in Budle Bay, a few occurring at about low-water mark in firm clayey sand.

Nerine cirratulus (Della Chiaje)

In 1901 specimens were found on Bull Hill Bank and Cocklesand.

In 1947 it was found in small numbers on the main traverse chiefly in clean, fairly well-drained sand near Station I. It did not occur in company with *Ophelia* on this traverse. On Bull Hill, however, it was more abundant, occurring at all stations, and was therefore occurring with *Ophelia*.

The distribution of this species is discussed by Watkin (1942), who finds it to have a wide intertidal range, with maximum densities about half-tide mark. Pirrie, Bruce & Moore (1932) describe a similar zonation on the sandy beach at Port Erin. It is recorded from muddy sand at Salcombe by Allen & Todd (1900), and in the Mersey Estuary by Bassindale (1938).

Pygospio elegans Claparède

Allen & Todd record this species in clean hard sand inside the estuary, but not on the Pole Sands.

Pygospio was found at nearly all stations on the main traverse, the maximum

The vertical distribution of species at Station I + 30 is shown in Table VI; it will be seen that practically all species occur in the top 4 in., notable exceptions being *Arenicola marina* and *Urothöe grimaldii*.

The close proximity of the various types of ground may also affect the distribution of certain species. Individuals may stray from their typical habitat (perhaps as a result of 'population pressure') so that in time a species will come to colonize all suitable grounds. This spreading tendency presumably operates continually and will result in a fringing zone where individuals may occur on quite atypical grounds. The extent of this zone will vary with the migratory ability of the species and the degree of unsuitability of the ground to be traversed. The outstanding example here was *Hydrobia ulvae*, normally inhabiting the mud, particularly the *Zostera* beds, but which is continually endeavouring to extend its range so that specimens occur even on the sandy grounds. They would not occur there but for the contiguity of their normal habitat.

The fauna of the main traverse may be arbitrarily divided into a number of zones:

(1) *Fauna of clean loose sand*. Stations I − 100 and I − 40. The silt content was less than 1 % and the grade of sand was coarser than at other stations on this traverse. The sand was very well drained, there being no black-layer near the surface.

Typical species were (Station I − 40):

	Per m.^{2}		Per m.^{2}
Ophelia bicornis	12	*Bathyporeia pilosa*	1448
Nerine foliosa	12	*Corophium arenarium*	16
Pygospio elegans	A few	*Hydrobia ulvae*	32
Eurydice pulchra	612		

(2) *Fauna of firm moist sand*. Stations I–III. The sand was rather finer than at the previous stations. The silt content rose from 0·05 % to a maximum of 2·2 % at II + 67. The bank sloped down gently, so that while Stations I to I + 67 were fairly well drained, the subsequent stations had standing water on the surface. A black layer usually occurred within a few inches of the surface.

Typical species were (Station II + 33):

	Per m.^{2}		Per m.^{2}
Nephthys hombergi	24	*Urothöe grimaldii*	268
N. cirrosa	8	*Corophium arenarium*	280
Scoloplos armiger	12	*Tellina tenuis*	76
Pygospio elegans	Common	*Macoma balthica*	8
Arenicola marina	44	*Cardium edule*	8 young
Bathyporeia sarsi	164	*Hydrobia ulvae*	448

Ophelia bicornis and *Nerine foliosa* were no longer present, and *Eurydice* was much less frequent. *Bathyporeia pilosa* had been replaced by *B. sarsi*, probably due to the fall in height. According to Watkin (1938) *B. pilosa* is restricted to a narrow zone at about H.W.M.N.T., whereas *B. sarsi* has a wider range extending down to below low-water mark. A number of species appeared at about Station I and extended almost the length of the traverse; e.g. *Nephthys hombergi*, *Scoloplos armiger*, *Scrobicularia plana* and *Cardium edule*. But *Bathyporeia sarsi*, *Tellina*, *Urothöe* and *Nerine cirratulus* were restricted to the clean sand of this zone.

(3) *Muddy sand.* Stations III + 33 to IV + 80. This was a transitional zone from sand to mud. At Station III + 33 the silt content was 6·9%, and a maximum of 16·6% silt occurred at Station IV. The other grades of soil were in very similar proportions to that found elsewhere in the traverse. The rise in silt content seems to be the cause of the absence of *Bathyporeia*, *Tellina*, *Urothöe* and *Nerine*; but the species extending into this zone usually show a higher density than on the clean sand.

Typical species were (Station IV + 3):

	Per m.^{2}		Per m.^{2}
Nephthys hombergi	16	*Corophium arenarium*	44
Glycera convoluta	20	*Macoma balthica*	4
Pygospio elegans	Present	*Scrobicularia plana*	180 young and 40 adult
Arenicola marina	12	*Cardium edule*	8 young and 28 adult
Ampharete grubei	3552	*Hydrobia ulvae*	620
Melinna palmata	8		

Large numbers of *Ampharete* occur; this species being most abundant where the silt content is high. *Pygospio* occurred in small numbers, and thus inhabits a wide range of soils.

(4) *Mud with* Zostera. Stations V and VI. The soil contained about 10–20% of silt, and was of a rather clayey consistency. When walking over it, one's feet sunk in only a few inches. Holes dug in the mud persisted for months after digging. The surface of the mud was covered by a dense growth of *Z. hornemanniana* Tutin and *Z. nana* Roth, which provided a refuge for numerous small *Carcinus maenas* and *Hydrobia ulvae*. Small specimens of *Arenicola marina* were abundant. The burrowing fauna was, if anything, a little less dense than on the muddy sand. *Macoma*, *Scoloplos* and *Nephthys hombergi* were absent.

Typical species were (Station V + 3):

	Per m.^{2}		Per m.^{2}
Arenicola marina	88 small and 4 adult	*Cardium edule*	284 young and 4 adult
Ampharete grubei	3984	*Littorina rudis*	20
Carcinus maenas	160	*L. littorea*	84
Scrobicularia plana	48 young and 60 adult	*Hydrobia ulvae*	13,280

The intertidal traverse

Conditions

This was at right angles to the main traverse, crossing it at Station II, which is identical with Station E. Stations were at 100 ft. intervals and were designated A, B, C ... H. 'A' was near high-water mark, and 'H' at low-water mark. Stations A, B and C were on gravel, with some admixture of sand. The fauna at these stations was imperfectly sampled owing to difficulties in sieving. From C + 12 to H the soil was fairly clean moist sand, overlying the bed of clay. Grade analyses showed a silt content of under 1% for stations from D downwards (Table VII).

TABLE VII. SOIL GRADES ON THE INTERTIDAL TRAVERSE, EXPRESSED AS PERCENTAGES BY WEIGHT

Station	>2 mm.	2–0·5 mm.	0·5–0·256 mm.	0·256–0·22 mm.	0·22–0·02 mm.	Silt and clay
A	Many stones	24·3	44·5	19·6	11·1	0·5
B	Few stones	5·7	38·7	29·7	24·0	2·0
C	Few stones	2·5	9·3	10·0	73·8	4·4
D	Nil	1·6	19·5	25·0	53·0	1·0
E	Nil	1·1	13·9	21·2	62·2	1·6
F	Nil	0·8	13·9	26·1	58·7	0·6
G	Nil	0·4	8·4	28·9	61·3	0·9
H	Nil	0·2	4·5	16·5	77·7	1·0

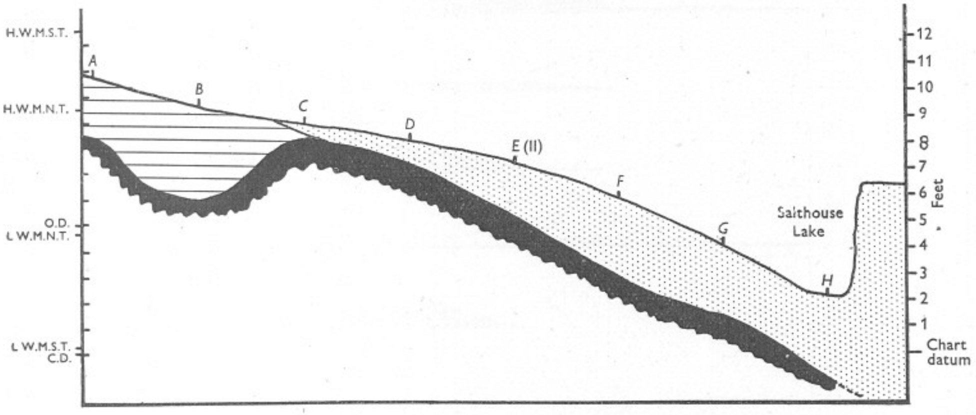


Fig. 8. Profile of the intertidal traverse. Vertical scale greatly exaggerated. Interval between stations is 100 ft. The white area is below the depth investigated.

▒ Sand. ☐ Gravel. ■ Clay.

The profile of the traverse is shown in Fig. 8. The bank sloped down to Salthouse Lake, so that there was little scouring of the banks near low water. This is in contrast to banks adjacent to the main channel which are exposed to a considerable tidal stream. The water-table was at or near the surface at all stations, and a black-layer was usually present at a depth of a few inches. Other conditions were similar to those to which the main traverse was exposed.

pH was determined electrically from samples taken at low tide on 21 August 1947:

	pH		pH
A	7·9	E	7·5
B	7·9	F	7·8
C	7·7	G	7·8
D	7·8	H	8·0

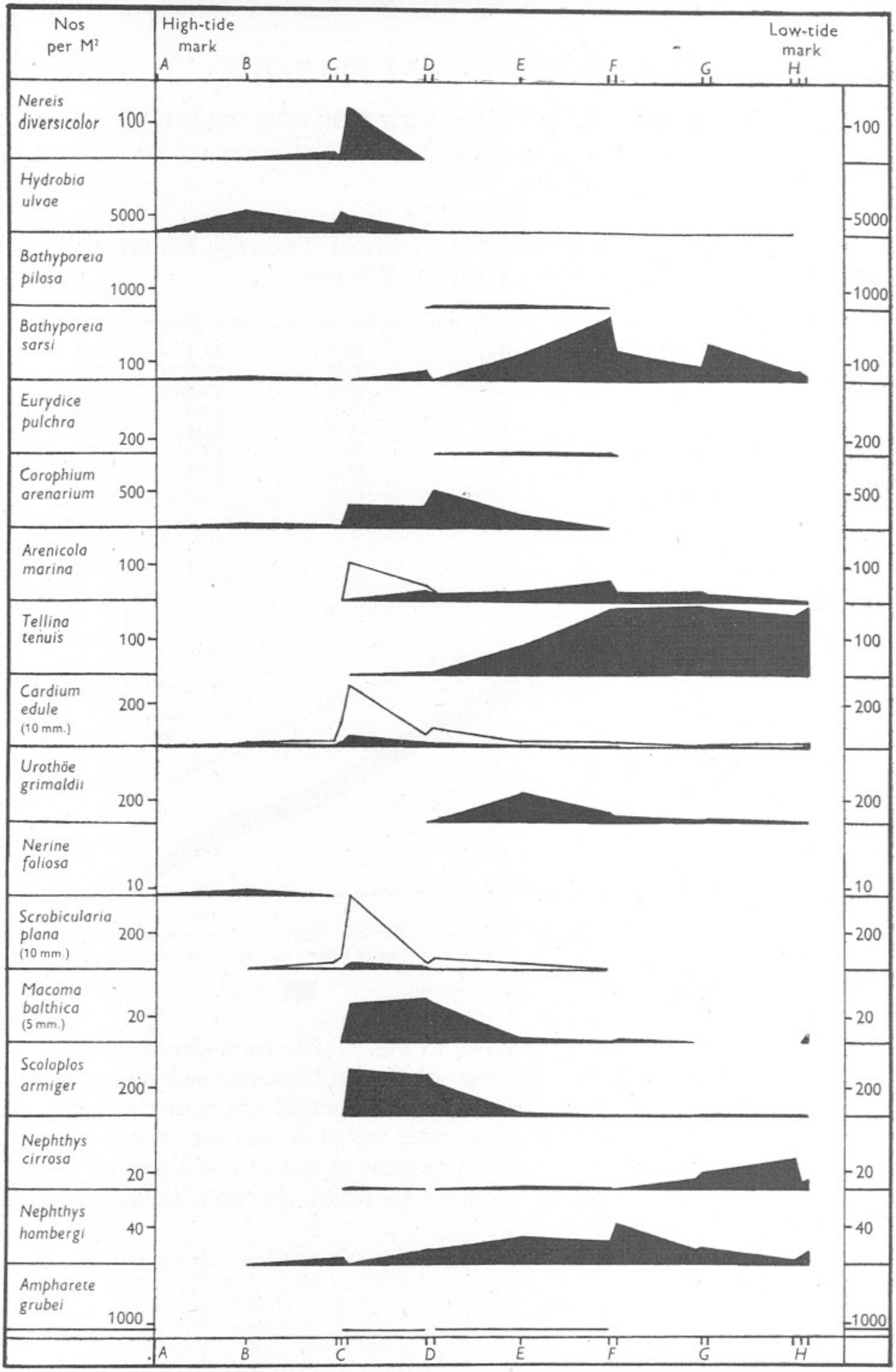


Fig. 9. Distribution of certain species on the intertidal traverse. For explanations see Fig. 6. Station 'E' is the average of numbers from Stations II−3 and II+3.

Fauna

The results obtained from quantitative sampling are shown in Table V and in Fig. 9. Only one collection was made at Stations A and B; and additional collections were made at C+15 and H+15, the latter being in the bed of Salthouse Lake. No other intermediate stations were worked.

The stations are too few to give a detailed picture of the distribution of the fauna, the object of these collections being to determine the intertidal distribution of species occurring in the main traverse. At Stations A, B and C the fauna was poor, especially in burrowing species. At C−3 typical species were:

	Per m.^{2}		Per m.^{2}
Nereis diversicolor	20	*Cardium edule*	8 young and 12 adult
Nephthys hombergi	8	*Littorina rudis*	4
Corophium arenarium	24	*L. littorea*	36
Larval Diptera	44	*Hydrobia ulvae*	2468
Scrobicularia plana	16 young		

At Station C+15, off the edge of the gravel, many species were abundant. The silt content was probably about 3%, but was not determined. Small individuals of *Arenicola*, *Cardium* and *Scrobicularia* were very abundant. Typical species included:

	Per m.^{2}
Nereis diversicolor	132
Nephthys hombergi	4
Scoloplos armiger	316
Arenicola marina	100 small and 4 adult
Corophium arenarium	312
Mytilus edulis	24 young and 68 adult
Macoma balthica	32
Scrobicularia plana	372 young and 32 adult
Cardium edule	224 young and 52 adult
Hydrobia ulvae	5000

The intertidal distribution of species is discussed on pp. 218–28. It is apparent that most of the species encountered have a fairly wide intertidal range, so that the small differences in height occurring along the main traverse would have little effect on their distribution.

The distribution of the following species may, however, be affected by small changes in height: *Nereis diversicolor* occurred at about H.W.M.N.T., and was consequently scarce on the main traverse, which was at a slightly lower level. *Bathyporeia pilosa*, *Eurydice pulchra* and *Nerine foliosa* occurred only at about half-tide mark, and this may account for their occurrence only at the higher stations on the main traverse. Drainage may also be an important factor in determining their distribution.

Bull Hill Bank

This was a bank of clean sand in the middle of the estuary near Dawlish Warren. The bank was scoured by strong currents, and to a lesser extent by waves; the surface of the sand being consequently furrowed, and the edge facing the main channel sloped away steeply. The top was at about half-tide mark, and was fairly level.

The sand was rather coarser than that from Salthouse Lake. A sample from the top of the bank (from Station BH + 100) giving on analysis:

(mm.)	(%)	(mm.)	(%)
> 2	—	0·256–0·22	30·1
2–0·5	5·1	0·22–0·02	10·3
0·5–0·256	54·0	Silt and clay	0·5

Independent analyses of the sand from Bull Hill Bank and Salthouse Lake are given by Wilson (1948).

There was no black-layer in the soil, which was very well drained, except near low-water mark, where it remained saturated at low tide.

Salinity and temperature conditions were similar to those in Salthouse Lake.

The fauna was investigated by a single traverse passing through the steep edge of the bank, and for a short distance across the top. A single collection from $\frac{1}{4}$ m.^{2} was made at each station.

TABLE VIII. FAUNA OF BULL HILL BANK

Clean sand at all stations. Numbers per $\frac{1}{4}$ m.^{2}; *j*, young individuals; ' − ' stations are on top, and ' + ' stations down the slope of the bank.

Station	Date	Depth (in.)	*Nemertinea*	*Nephthys cirrosa*	*Nerine cirratulus*	*Ophelia bicornis*	Other worms	*Eurydice pulchra*	*Bathyporeia sarsi*	*Haustorius arenarius*	*Urothöe grimaldii*	Dipterous larvae	*Mytilus edulis*	*Tellina tenuis*	*Hydrobia ulvae*
BH − 100	23. viii.	6	.	.	6	67	.	24	6	.	.	.	.	.	.
BH − 50	23. viii.	7	.	.	6	25	.	42	2	.	.	1	.	1	.
BH + 4	25. vii.	6	.	.	4	19	1	10	1	.	.	.	.	.	.
BH + 9	25. vii.	6	.	.	2	53	.	29	.	.	.	1	.	.	.
BH + 14	25. vii.	6	1	.	8	43	.	27	2	.	.	.	.	.	.
BH + 19	25. vii.	6	2	1	7	14	.	32	2	1	.	.	1*j*	3	4
BH + 24	25. vii.	6	.	3	8	.	1	3	24	1	19	.	.	13	.

The fauna (Table VIII and Fig. 10) was very poor, this being perhaps due to:

(i) Strong currents, which prevent the establishment of an epifauna.

(ii) The coarse and loose texture of the soil. Watkin (1942) found that coarser grades of sand usually supported a poorer fauna than was found in finer grades.

(iii) Drainage. This would seem to be an important factor in restricting typically intertidal species to low-water mark.

On top of the bank typical species were (Station BH − 100):

	Per m.^{2}		Per m.^{2}
Nerine cirratulus	24	*Eurydice pulchra*	96
Ophelia bicornis	268	*Bathyporeia sarsi*	25

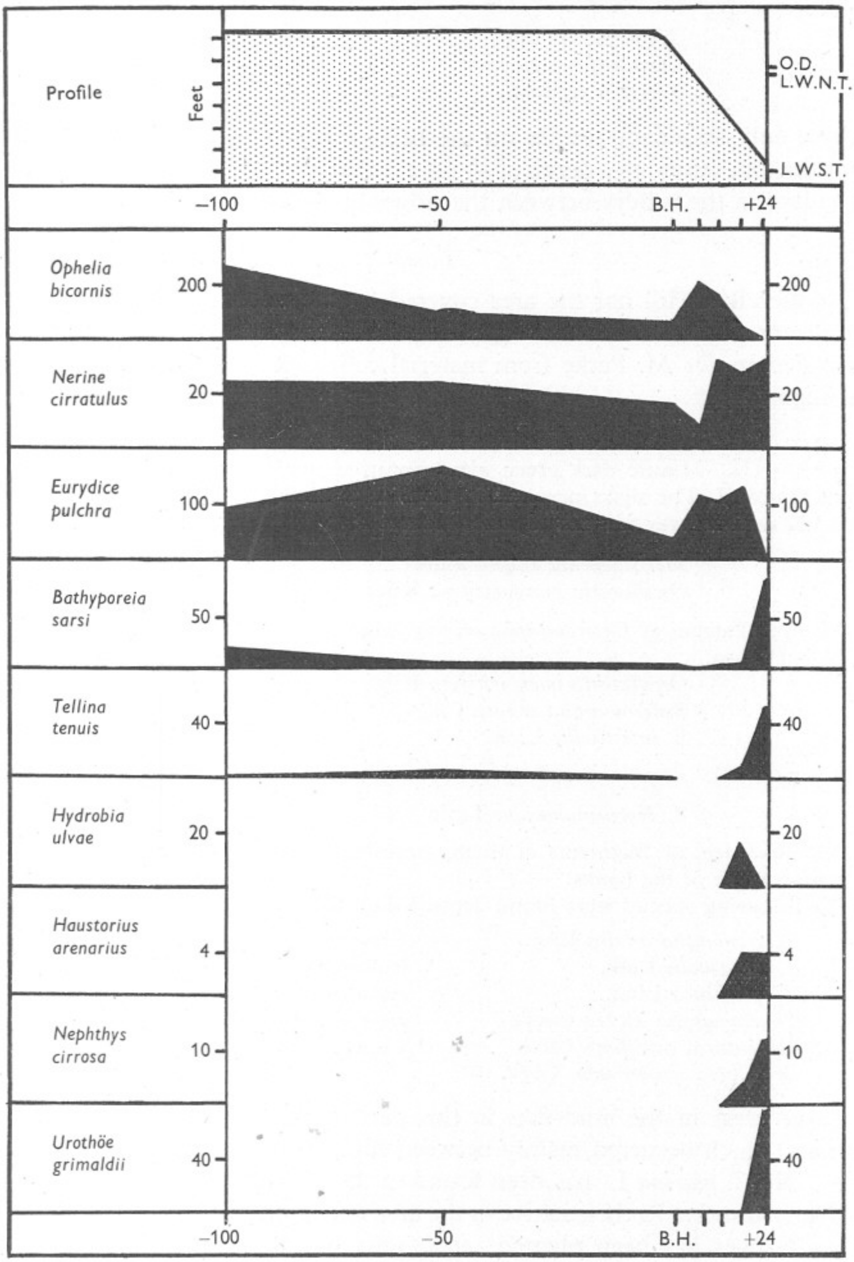


Fig. 10. Profile and fauna on Bull Hill Bank. Note that many typically intertidal species are here restricted to low-water mark. Numbers per m.^{2}

At low-water mark *Ophelia* was absent, but certain other species appeared:

Nephthys cirrosa
Haustorius arenarius
Urothöe grimaldii
Tellina tenuis
Hydrobia ulvae

The only abundant species on the bank was *Ophelia*, which occurred all over the top, buried to a depth of about 4 in. in the sand. It seemed to be most abundant in the valleys between the ridges in the sand.

Flora

Neither Bull Hill nor the area covered by the intertidal traverse had any significant growth of surface algae. The following species have kindly been identified by Dr M. Parke from material collected on the main traverse on 29 August 1947:

I – 100. Algae absent.

I – 78 → III. Minute dark green algae occurred, with a maximum abundance at about Station I. The algae increased in abundance during the summer and tended to bind the surface layer of sand. Species recorded:

Merismopedia glauca Kütz
Oscillatoria margaritifera Kütz

III + 15. Patches of *Enteromorpha crinita* J.Ag.

IV → IV + 33.
Oscillatoria margaritifera Kütz
Enteromorpha crinita J.Ag.
E. intestinalis Link.

IV + 75 → VI. *Zostera nana* Roth

Z. Hornemanniana Tutin

Drifting algae, or fragments of them, stranded by the receding tide, add to the organic content of the banks.

The following species were found deposited on the traverse:

Enteromorpha crinita J.Ag.
E. intestinalis Link.
Ulva lactuca Linn.
Chaetomorpha litorea Cooke
Lomentaria clavellosa Gaill.
Gracilaria confervoides Grev.
Ceramium rubrum Ag.
Callithamnion corymbosum Lyngb.
Ectocarpus confervoides Le Jol.
Isthmoplea sphaerophoia Kjellm.
Fucus vesiculosus L.

Large areas of the mud-flats in this part of the estuary were covered by *Zostera*, which occurred mainly between high- and low-water mark of neap tides. No *Z. marina* L. has been found in the estuary.

Spartina stricta Roth. is native in the area north of the Warren, but *S. Town sendii* Groves has been planted. 1000 setts of the latter were planted o near the Warren in November 1935 to stabilize the mud-flats. *S. Townsen* is spreading slowly along the edge of the Warren, and a careful examinati revealed small clumps along the whole of the northern side of the In

Warren. In the traverse area, about 200 yards square, twenty-three plants or small clumps were found. These occurred on the sand or among the *Zostera*, mostly at about H.W.M.N.T.

BIOMASS AND SOURCES OF FOOD

The 'rough weight' of the principal species at certain stations was determined by weighing preserved specimens after removal of surface moisture. The shells of lamellibranchs were removed before weighing. The species comprising the 'epifauna' were not included. Details of biomasses are in Table XII.

On sand at Station I–100 the biomass was 4·6 g./m.^{2}, this being by far the poorest area. On Bull Hill Bank, however, where *Ophelia* was abundant, a total of 36·9 g./m.^{2} was reached, this being almost entirely made up of these worms. At Stations II, IV and VI, the biomasses were 69·3, 101·7 and 45·4 g. respectively. The greatest weight at these stations was made up by only four species, *Arenicola*, *Scrobicularia*, *Cardium* and *Ampharete*. It would seem that 'soil-swallowers' such as *Ophelia* and *Arenicola* have a very efficient mode of feeding, as they outweigh all other species combined at their zone of maximum abundance. Carnivores (*Nephthys*, *Glycera*, *Eurydice*, etc.) are nowhere abundant, comprising about 5–10% of the total weight.

MacGinitie (1935), discussing food relations in a Californian estuary, found that carnivores comprised about 5% by weight of the total population of a mud-flat. Detritus-feeders made up the greatest weight of the population, probably on account of their longevity. MacGinitie considered that the main sources of food were *Zostera*, *Enteromorpha*, *Polysiphonia* and pieces of algae which floated in with the tide. Very few animals lived directly on these plants, the filter-feeders subsisting mainly on plants in various stages of decay, and on bacteria. *Zostera* appeared to be of use not only as a source of detritus, but also for its part in the accumulation of detritus which becomes caught around its roots. Hence it was in and near the *Zostera* regions that the greatest abundance and variety of life was found. At low tide plant tissue tended to become dried up and killed; dead leaves started decomposing into detritus, and meanwhile would be distributed by the action of animals and by water movements, so becoming available to all the bottom animals in the neighbourhood.

Although no attempt has been made to assess the relative roles of detritus, bacteria and plankton as the food supply of animals in the Exe Estuary, it is clear that conditions are not unlike those in the Californian estuary. The settling of drifting algae on the banks has already been referred to, and the importance of *Zostera* as a source of food for areas outside its habitat was emphasized by some observations made in August 1947. During the neap tides of that month some parts of the *Zostera* beds were left uncovered for several days during hot sunny weather. When again covered by the tide some of the leaves, which had become dry and black, became detached and floated away. At this time leaves of *Zostera* were quite abundant floating up and down the estuary with the tide, being deposited on the banks as the tide receded.

NOTES ON CERTAIN SPECIES

The distribution of certain estuarine species is discussed by Spooner & Moore (1940), and of sand-living species by Watkin (1942). The following notes are intended to supplement these in the light of subsequent work and the results obtained in the present survey.

POLYCHAETA

Phyllodoce maculata (L.)

Fauvel (1923) regards *P. maculata* (L.) and *P. teres* Malmgren as one and the same species, although they were recorded separately by Allen & Todd (1902). In 1901, *P. teres* was found in clean sand above Starcross, in sand west of the mouth of Salthouse Lake, and from gravel between Powderham and Starcross. A specimen doubtfully assigned to *P. maculata* was taken on the sandy ground between Starcross and Cockwood.

The specimens found in 1947 were probably of the same species as those previously taken, but identification was difficult as many of the specimens were fragmented. *Phyllodoce* was found on the more muddy part of the main traverse, from Stations III+67 to VI+3. It was not found on Bull Hill.

Eteone longa (Fabricius)

In 1901 Allen & Todd found specimens identified as *E. pusilla* Örsted (*nec* Malmgren) in clean sand; and it seems likely that the 1947 specimens were of the same species as found in 1901, but there is some doubt as to their identity. Those found in 1947 had a head approaching that described by Malmgren (1865) for *E. pusilla*, but the anal cirri are not '*lineare-fusiformes elongati*', but of the type described by Örsted (1843) as '*papillis caudalibus subglobosis*'. The head does not correspond with Örsted's description, however. Fauvel (1923) does not refer to *E. pusilla* Örsted, and *E. pusilla* Malmgren is now *E. lactea* Claparède.

The specimens correspond most closely to *Eteone longa* (Fabricius), both in the shape of the head and of the anal cirri, and it is to this species that they have been provisionally assigned.

Eteone extended from sand to mud on the main traverse. Intertidally it ranged from about H.W.M.N.T. to about L.W.M.N.T., with a maximum near the upper part of its range. It was absent from Bull Hill.

Nephthys hombergi Lamarck

This species was recorded by Allen & Todd from sand and muddy sand all over the estuary, but not in very muddy ground.

In 1947 it was collected at stations ranging from sand to mud. Its maximum density was at IV + 33: 104 per m.^{2}; with a silt content of 9·4%. It was less abundant, *c.* 12 per m.^{2}, at IV, where the silt content was 16·6%, and was absent on muddy stations with *Zostera*, where the silt percentage ranged from 11·2 to 22·6. At the other end of the traverse it did not extend beyond I + 30, possibly being limited by the better drainage at this end. Intertidally it ranged throughout the tidal zone, with no distinct maximum. It was not found on Bull Hill.

This species is not confined to the shore, being common on sandy and muddy bottoms at sea. Spooner & Moore (1940) and Alexander, Southgate & Bassindale (1935) have found it plentiful towards the mouth of the estuaries of the Tamar and Tees respectively. On the Tamar its normal density was between 100 and 300 per m.^{2}, rather higher than that met with on the Exe. Brady (1943), however, found the maximum density of this species at Black Middens on the Northumberland coast to be only 60 per m.^{2}

Nephthys cirrosa Ehlers

Found by Allen & Todd only in fine, clean sand, where it was quite plentiful.

In 1947 this species was found in wet sand at stations between II and III + 33, the silt content ranging from 1·35 to 6·9%. Intertidally, it occurred at most stations, with its greatest density, 32 per m.^{2}, near low-water mark. On Bull Hill it was restricted to two stations near low-water mark. The intertidal range of this species thus seems to be dependent on drainage conditions in the sand.

There are few other records of this species. In the Plymouth Marine Fauna (Marine Biological Assoc., 1931) it is recorded from sand between tide-marks on Drakes Island and the Yealm Estuary. Bassindale (1938) found single specimens in sand near the mouth of the Mersey Estuary. Rees (1939) found it on a number of traverses on sandy shores in North Donegal; the species extended up the beach to half-tide mark, maximum numbers occurring at low-water mark.

Scoloplos armiger (O. F. Müller)

In 1901 this species was found in sand or muddy sand within the estuary, but not on the Pole Sands. In the 1947 survey it was found on soils ranging from 0·7 to 16·6% silt, but was absent at the muddiest stations. Its highest density was in muddy sand at III + 33: 108 per m.^{2}, the silt content being 6·9%. It did not occur on the well-drained sand, and was absent from Bull Hill. Intertidally it showed a maximum just below H.W.M.N.T.

The distribution of *Scoloplos* on the main traverse resembles that of *Macoma* and *Nephthys hombergi*, being typical of species with an optimum density in muddy sand, and being intolerant of 'pure' mud. It is recorded from muddy sand in a number of areas, but not from clean, sandy beaches, and it is usually less abundant in mud. Spooner & Moore (1940) found it in moderate numbers, up to 152 per m.^{2}, on St John's Lake, where it seemed to be restricted to the upper tidal levels in the *Zostera* zone.

Brady (1943) found *Scoloplos* at Budle Bay on the Northumberland coast. It was widely distributed in slightly muddy sand, its density seeming to be inversely related to that of *Macoma balthica*. The author considered that the two species were in competition for detritus as food, but that since *Macoma* also fed on suspended detrital and planktonic matter, it tended to become the dominant species. Thus *Scoloplos* could only become really abundant where *Macoma* was for some reason scarce.

The density of *Macoma* on the Salthouse Lake traverse was nowhere great, so that competition for food between the two species was probably not very intense. On the whole, *Macoma* and *Scoloplos* show similar distribution and densities, so failing to agree with Brady's observations.

Nerine foliosa (Audouin & Edwards)

This species was recorded as *N. coniocephala* Johnston by Allen & Todd, several specimens being obtained in sand west of the mouth of Salthouse Lake and in the hard clayey mud to the north of it.

In 1947 small numbers were found on clean sand at Stations I–40 and I–3A, also among gravel above H.W.M.N.T. at B–3. None was found on Bull Hill.

There are few records of this species: Percival (1929) records it from the River Tamar, in mud; in the Plymouth Marine Fauna it is also recorded from Wembury, Drakes Island, east side of the Sound, Kingsand Beach, and the River Yealm sand bank. Brady (1943) found it in Budle Bay, a few occurring at about low-water mark in firm clayey sand.

Nerine cirratulus (Della Chiaje)

In 1901 specimens were found on Bull Hill Bank and Cocklesand.

In 1947 it was found in small numbers on the main traverse chiefly in clean, fairly well-drained sand near Station I. It did not occur in company with *Ophelia* on this traverse. On Bull Hill, however, it was more abundant, occurring at all stations, and was therefore occurring with *Ophelia*.

The distribution of this species is discussed by Watkin (1942), who finds it to have a wide intertidal range, with maximum densities about half-tide mark. Pirrie, Bruce & Moore (1932) describe a similar zonation on the sandy beach at Port Erin. It is recorded from muddy sand at Salcombe by Allen & Todd (1900), and in the Mersey Estuary by Bassindale (1938).

Pygospio elegans Claparède

Allen & Todd record this species in clean hard sand inside the estuary, but not on the Pole Sands.

Pygospio was found at nearly all stations on the main traverse, the maximum density being at about Station I + 67. It was rare or absent in loose sand, and was not therefore found on Bull Hill. In small numbers it ranged on to the muddy stations of the traverse, its requirements seeming to be merely the presence of a firm substratum and of sufficient sand-grains with which to construct its tube.

In the sorting dish a number of the worms emerge from their tubes a day or two after collection, but many more probably remain within their tubes. A rough estimate of numbers was made by determining the dry weight of sandy tubes at certain stations. (Sometimes the tubes were sorted out from the general collections, at other times a special collection was made by carefully sieving the top 2–3 in. of soil from an area close to the original station.)

There are few records of this species in Britain: if present in small numbers it might easily be overlooked. It has been found in various grades of soil near the mouth of certain estuaries. Percival (1929) records it from the River Lynher near Ince Castle, Bassindale (1938) found it in the upper estuary of the Mersey, and Allen & Todd (1900) found it in muddy gravel under the Marine Hotel at Salcombe. Beanland (1940) records it from banks near the mouth of the Dovey Estuary, where it occurred on soils ranging from 0 to 20·3% of silt-plus-clay.

Ophelia bicornis Savigny

Allen & Todd found *Ophelia* to be abundant on the north-eastern side of Pole Sands and on Bull Hill. Single specimens were found at three other stations in the estuary.

In 1947 it was found in small numbers (12 per $m.^2$) on clean well-drained sand at Stations I – 100 and I – 40. On Bull Hill it was abundant at all stations except at low-water mark where it was absent. Its distribution was rather patchy, but a varying number could be dug up anywhere on top of the bank. The maximum density was 268 per $m.^2$

The occurrence of *Ophelia* is clearly related to the degree of drainage of the sand, but Wilson (1948) has shown that the grade of soil may also affect distribution. Experiments with larvae of *Ophelia* show that they 'metamorphose most readily in sand from their natural habitat and with hesitancy or not at all in sands from other sources'. It is shown that the size and shape of the sand grains, or perhaps of the interstices, determines the readiness with which metamorphosis occurs. Wilson has found that sand from the Salthouse Lake area is less effective in bringing about metamorphosis than the coarser sand from Bull Hill Bank. Although the Salthouse Lake sand used in the experiments was probably not from the region where *Ophelia* occurs, it appears to be of a similar grade to that in which small numbers of *Ophelia* were found.

Thus the relative numbers of *Ophelia* in the two localities is explicable in terms of the soil grade.

> ...If this be so, we have a reasonable explanation of the observed distribution of *Ophelia* in the Exe estuary, a heavy concentration in the metamorphosis-stimulating sand of the Bullhill Bank and the Polesands, with a much lower concentration in the less stimulating Salthouse Lake area. As the larvae in the later pelagic stages drift over the banks the majority of these coming into contact with the Bullhill sand will enter it and stay there, but of those washed over the Salthouse Lake only a small proportion will settle, the majority will leave the sand after testing it and, continuing pelagic life, may later on eventually reach the Bullhill Bank or the almost equally suitable Polesands nearer the open sea. This explanation is at least as reasonable as supposing that there is an even settlement over the whole area followed by greater destruction of the young worms in the unfavourable soils, and the results of these experiments support it [from Wilson, 1948].

Arenicola marina L.

Allen & Todd recorded this species as abundant on most of the banks of the estuary, being scarce on Pole Sands and on a mud-bank near the top of the estuary.

In 1947 *Arenicola* was found at nearly all stations in the Salthouse Lake area. It was absent from the well-drained area where *Ophelia* occurred, from gravel near high-water mark, and from the bed of Salthouse Lake (H+15). None was found on Bull Hill.

A comparison of numbers found by digging and by counts of casts has already been described (p. 206). On the main traverse the maximum density was 52 adults per m.^{2}, at Station III+33, where the silt content was 6·9%. *Arenicola* was found in soils with 0·05–22·6% silt.

Intertidally it ranged from the edge of the gravel, at about H.W.M.N.T. down to low-water mark. At F−3 (half-tide mark) a density of 60 per m.^{2} was recorded, there being only 0·6% of silt. Serventy (1934), describing the fauna of Scolt Head Island, found that *Arenicola* was scarce in soft muds with *Zostera*, in hard compact mud, and in clean sand. It did, however, occasionally occur on the open beach with *Ensis* and *Spisula*. Spooner & Moore (1940) found *Arenicola* to be scarce on the Tamar Estuary, where the soil contains very little sand, being almost entirely silt. Wells (1945) noticed that it was most abundant on sand where drainage was poor: where a stretch of sand dried out soon after the tide had receded, only small specimens were found.

Newell (1948) has recently investigated the life history of *Arenicola*. Fertilized eggs appear to be carried up the beach on the incoming tide and become lodged among pebbles or sand, where larval development probably takes place. The maximum spawning intensity at Whitstable is at neap tides (in October) so that the eggs tend to be deposited at high-neap-tide mark rather than in unfavourable environments higher up the beach. The larvae metamorphose in the following spring.

Casual observations in the Salthouse Lake area indicated that large numbers of small *Arenicola* did occur high up the beach (many well above high water of neap tides, however), suggesting that conditions are similar to those at

Whitstable. On the traverses numbers of small specimens occurred among *Zostera*, below the pebble zone at C+15, and on clean sand near Station I. Perhaps the pebble zone and the *Zostera* beds are 'nursery areas' where the larvae develop, subsequently migrating to the regions where the adults occur.

Ampharete grubei Malmgren

This species was not recorded by Allen & Todd. In Salthouse Lake it was abundant in the more muddy stations of the main traverse, reaching a maximum density of about 9200 per m.^{2} at V−3, where the silt content was the highest on the traverse (22·6%). Its distribution was patchy, as only 4000 per m.^{2} were found at the adjacent Station, V+3. *Ampharete* was abundant over a range of soils with silt concentrations of 6·9–22·6%. It was absent from Bull Hill.

There are few other records of this species: Serventy (1934) found a large colony in very soft mud at Scolt Head Island, while Spooner & Moore (1940) record up to 4000 per m.^{2} at St John's Lake, from about mid-tide downwards. It did not penetrate far up the Tamar Estuary. Perhaps the scarcity of records of *Ampharete* is due to the few intertidal mud banks which are exposed to marine conditions; the species evidently having little tolerance of reduced salinity. The mud-flats at Salcombe would seem to provide a suitable habitat for this species, but none were found there by Allen & Todd (1900), although it is possible that *Ampharete* was overlooked among collections of *Melinna*.

Melinna palmata Grube

Allen & Todd found this species (recorded as *M. adriatica* von Marenzeller) in small numbers in the lower part of the estuary. In 1947 a few specimens were found on the more muddy parts of the Salthouse Lake traverse.

Like *Ampharete*, *Melinna* is absent from many muddy localities, but occurs in the Tamar and at Salcombe. Spooner & Moore (1940) found it together with *Ampharete* in the Tamar, but penetrating farther up-river than the latter; it was most abundant at low water at the edge of West Muds, where the density was 189 per m.^{2}

CRUSTACEA

Eurydice pulchra Leach

This species seems to have been overlooked by Allen & Todd, perhaps on account of its small size.

In 1947 it was found on the main traverse in clean sand just below H.W.M.N.T., with a maximum density of 612 per m.^{2} It was rare on the intertidal traverse. On Bull Hill it was quite plentiful, occurring at all stations, with a maximum density of 168 per m.^{2} On this bank it thus ranges from half-tide down to nearly L.W.M.S.T.

This species has been recorded from clean sand above half-tide mark by Brady (1943), Watkin (1942), Rees (1939), Pirrie *et al.* (1932) and by Elmhirst (1931). Crawford (1937*b*), however, records it from sand about half-tide mark downwards. Its intertidal distribution is perhaps related to the degree of drainage of the sand.

Elmhirst (1931) has shown that it has a pelagic phase; in winter it seeks shelter in the shallow water beyond low-water springs, and in summer it may swim in large numbers, following the flotsam at the edge of the tide. Watkin (1941 *b*), however, states that they 'rise out of the sand with the inflowing tide, proceed to feed immediately and sink again into the sand with the retreating tide'.

Bathyporeia pilosa Lindström

The systematics of the genus *Bathyporeia* were somewhat confused before the publication of a paper by Watkin (1938), and records before 1938 are consequently unreliable.

Allen & Todd recorded *B. pelagica* Sp. Bate from collections with a mosquito-net trawl in the estuary, but the few available specimens are of *B. sarsi* (see notes under the latter species).

On the Salthouse Lake traverse *B. pilosa* occurred from Stations I − 100 to II on clean sand. It was most abundant on the loose well-drained sand just below H.W.M.N.T., which was not covered by extreme neap tides. The maximum density was 2180 per $m.^2$ This species was absent from Bull Hill.

Beanland (1940) found it at several stations on the Dovey, the soil having a silt content of under 1%. The maximum density was 298 per sq.ft. At Kames Bay Watkin (1942) records a density of *c.* 17,000 per $m.^2$

Species of this genus have a pelagic phase. Watkin (1939) found that in Kames Bay *B. pilosa* occupied a definite belt across the shore at a level above H.W.M.N.T. Tow-nettings made at high tide showed that the different species became pelagic, but each more or less retained its zonation, returning to its own area at low tide. Watkin (1938) gives a list of localities for this species.

Bathyporeia sarsi Watkin

This species is distinguished from *B. pilosa* by several minor characters, the most conspicuous being the shape of the basal joint of the antennule (which is relatively broader in *B. sarsi*) and by the number of groups of spines on the third epimeral plate. Specimens in the museum of the Plymouth Laboratory show that some of the specimens recorded by Allen & Todd (1902) as *B. pelagica* Sp. Bate were in fact what is now *B. sarsi* Watkin. The specimens in question were caught on 8 July 1901 between Cockwood and Bull Hill Bank.

On the Salthouse Lake traverse it occurred in moist sand from Station I + 67 to Station III + 33, thus slightly overlapping the *B. pilosa* zone. Intertidally it extended from about high-neap-tide mark downwards. The maximum density was at F − 3 (half-tide mark) where there were 352 per $m.^2$ On Bull Hill it occurred at all but one station, the greatest density, 96 per $m.^2$, being at low-water mark.

A short list of localities is given by Watkin (1938); it is an intertidal or shallow water form.

Haustorius arenarius (Slabber)

Haustorius was found by Allen & Todd in Pole Sands, Shaggles Sand, and in sand north of the Warren.

In 1947 only five specimens were found; three in wet sand below half tide on the intertidal traverse, and two on Bull Hill near low-water mark.

This seems to be nowhere an abundant species; Watkin (1942) records 21 per sq.ft. near high-neap-tide mark in Kames Bay. Its intertidal distribution, which is variable, is discussed by Watkin.

Corophium arenarium Crawford

This species was created by Crawford (1937*a*) to distinguish a form closely resembling *C. volutator* (Pallas), but which occurs in sandy habitats. It is possible, and indeed likely, that *C. arenarium* was found in the 1901 survey but was included with *C. grossipes* L. (=*volutator*). *C. volutator* also occurs in this area (Crawford, 1937*c*).

On the Salthouse Lake traverses *C. arenarium* was found on a wide range of substrata, being scarce, however, on loose sand and on mud with *Zostera*. Its maximum abundance was at II+67: 360 per m.^{2}, where the silt content of the soil was 2·2%. Intertidally it ranged from above H.W.M.N.T. to about half-tide mark. It was absent from Bull Hill.

Crawford (1937*a*) found it in firm but slightly muddy sand from half tide to L.W.M.N.T. It is recorded from the Dovey Estuary by Beanland (1940) and by Watkin (1941*a*). Watkin states that 'away from the influence of the streams and above the high-water mark of neap tides *Corophium volutator* is replaced by *C. arenarium*, which is the dominant species in the estuary. The two species may overlap at their limits of distribution; but at their centres of density, which in all cases are well marked, they remain unmixed'.

The occurrence of the two species in the same area seems to confirm the validity of *C. arenarium* as a separate species. Furthermore, Mr Spooner informs me he has observed additional morphological differences between them.

MOLLUSCA

Tellina tenuis da Costa

In 1901 *Tellina* was common on the west side of Pole Sands at low-water mark, and between Cocklesand and Lympstone mussel beds; a few were taken on Bull Hill, the Warren and Shaggles Sand.

In 1947 this species was found in moderate numbers on moist clean sand. The maximum density on the main traverse being 88 per m.^{2} at II+3. Intertidally it occurred up to nearly H.W.M.N.T., and extended down to low-water mark. Population densities in the lower half of the tidal zone were remarkably constant, averaging 184 per m.^{2} On Bull Hill the species is restricted to a zone near low-tide mark, but one individual was found on top of the bank. The length of shell of each specimen was measured to the nearest mm. 'above', the results being shown in Table XIII.

Tellina has been studied by Stephen (1928, 1929*a*, *b*, 1931). Populations in Kames Bay reached 1897 per $\frac{1}{4}$ m.^{2}, but elsewhere lower densities, averaging 250 per $\frac{1}{4}$ m.^{2}, are recorded by Stephen. In Kames Bay densities decreased from low- to high-water mark; large individuals occurring mainly at the higher levels, whereas many small animals were found at low-water mark.

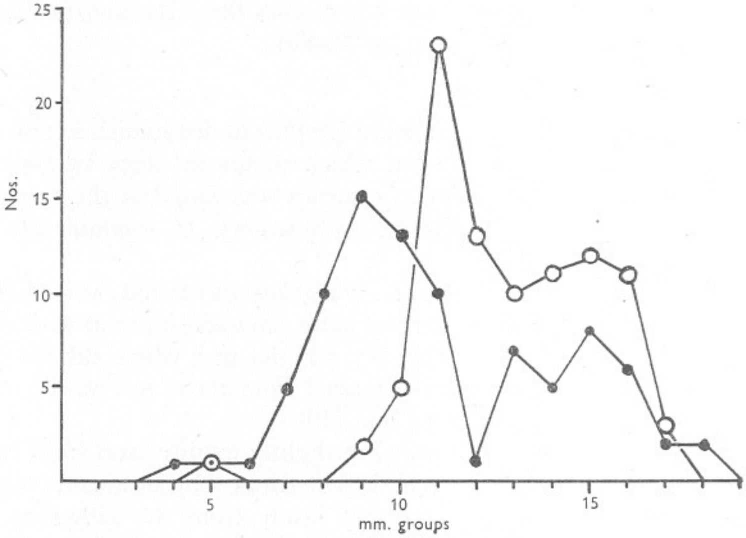


Fig. 11. Length-frequency distribution graphs for *Tellina tenuis* at Stations F (half-tide mark) and H (low-tide mark); 14 and 15 August 1947. Based on ninety-one individuals from F and eighty-seven from H. —○—, Station F; —●—, Station H.

The density of *Tellina* on Salthouse Lake was very much less than in areas studied by Stephen, numbers not being large enough to give statistically significant results after size-grouping. Comparison with Stephen's results, however, shows the following features:

(i) Population density decreased at higher levels on the beach; but up to about half-tide mark densities were uniform.

(ii) Measurements of shell length show that on the whole a greater proportion of the smaller size-groups occurred near low water. This is shown in Fig. 11. The maxima for what may be a year group occur at 9 mm. length at low-tide mark, but at 11 mm. length for individuals from half-tide mark, suggesting a greater growth rate in the latter position.

(iii) Stations at the same level on the main traverse showed little difference in the numerical proportions of the different size-groups, although the population density was variable.

The species has been found on a number of sandy estuaries and shores where there is some shelter from wave action. Rees (1939) found that the extent of its range up the beach from low-water mark was variable. This is probably related to drainage, as *Tellina* is restricted to low-water mark on Bull Hill where the drainage is very thorough.

Macoma balthica (L.)

In 1901 this was recorded (as *Tellina balthica* L.) from the mud flats between Cocklesand and Exmouth railway station, on mud, south of Lympstone mussel-bed, and on the west side of the estuary.

In the Salthouse Lake area it occurred on the main traverse on soils ranging from moist sand to mud. The maximum density was 24 per m.^{2} at IV−3, where the silt content was 16·6%. On the intertidal traverse it was restricted to a zone at about half-tide mark, but two were found in the bed of Salthouse Lake. It was absent from Bull Hill.

Comparable densities, up to 36 per m.^{2}, were recorded by Spooner & Moore (1940) from St John's Lake, where it was fairly evenly distributed through the tidal zone. As on the Exe, few spat were found. Population figures for other areas, quoted by Spooner & Moore, show that very much higher densities may occur. Beanland (1940) found populations up to 657 per sq.ft. on the Dovey, over a soil range from 0-32·4% silt, with maximum densities where there was 2·5–4·3% silt. Brady (1943) showed an inverse relation between densities of *Macoma* and of *Scoloplos*, which is discussed in the notes on the latter species.

Scrobicularia plana (da Costa)

This was recorded by Allen & Todd (as *S. piperata* (L.)) as one of the commonest bivalves of the estuary.

On the main traverse it occurred at all stations from III to VI, on mud and muddy sand; and small individuals (under 10 mm. long) also occurred on wet sand from I to III. It reached its maximum abundance at IV+33, where there were 156 'adults' and 72 'young' per m.^{2} Intertidally it occurred over a fairly narrow range at about half tide, and was absent from Bull Hill. Measurements of shell-length are shown in Table XIV.

Spooner & Moore (1940) state that this species is characteristic of estuaries in the south and east of England, but is scarce and more local in the north. On the Tamar conditions for settlement of spat seemed to be most favourable at the seaward end of the estuary, while growth conditions were at an optimum much higher up the estuary. The great majority of spat settling on St John's Lake, near the mouth of the estuary, die off at an early age.

Cardium edule L.

Cockles are plentiful in the estuary: Allen & Todd recorded them in profusion from Cocklesand, Bull Hill Bank, and along the west side of the estuary.

In the Salthouse Lake area *Cardium* occurred on a wide range of soils, from clean sand to mud, and from high-water mark of neap tides down to the bed of Salthouse Lake. It was absent from well-drained sand at one end of the main traverse, and from Bull Hill Bank (the cockle bed is farther to the north, on the gravelly part of this bank).

Its maximum abundance was in mud at Station VI–3, where there were 136 small and 60 adults per $m.^2$ The length of the shells of individuals at each station is given in Table XVI.

A limited amount of cockle gathering occurs in the Salthouse Lake area.

Hydrobia ulvae (Pennant)

In 1901 this was recorded from nearly all grounds in the estuary.

Its distribution on the main traverse is clearly related to the presence of *Zostera*, which provides shelter and may be a source of food. Its maximum abundance was 16,000 per $m.^2$. Outside the *Zostera* beds it was much less abundant, and it was absent from areas scoured by currents, such as the bed of Salthouse Lake and the top of Bull Hill. Intertidally, it was mainly concentrated towards H.W.M.N.T. *Hydrobia* has the habit of floating upside down from the surface film, and may in this way be dispersed away from the *Zostera* beds to the sandy areas, which are not its normal habitat.

The distribution of this common estuarine species is discussed at length by Spooner & Moore (1940).

Discussion

A study of the fauna of the main traverse on Salthouse Lake has shown that the distribution of burrowing species is closely linked with the nature of the soil. Drainage may be of importance at one end of the traverse, but most of the stations had standing water on the surface at low tide.

Although conclusions as to the role of the soil as a limiting factor can only be applied with confidence to the area investigated, they should also apply (modified by divergencies in other factors) to the fauna of other areas. The great value of the Salthouse Lake traverse lay in the opportunity it offered for a study of the influence of soil grade on distribution, the effect of other factors being eliminated owing to the peculiar local conditions.

A striking example of the influence of silt on distribution is exhibited by the difference in the fauna on either side of Station III. On one side was an area with a silt content of under 2·5%, and on the other side there was over 6·5% silt. This difference is clearly shown in the distribution of certain species. Thus *Bathyporeia sarsi*, *Urothöe grimaldii* and *Tellina tenuis* were restricted to the former area, whereas *Ampharete grubei* and *Melinna palmata* occurred only in the latter area. Some species, more tolerant of variable silt concentrations, ranged across the two areas, but these often showed a marked change in density.

The apparent correlation between distribution of animals and silt content, however, can establish neither the degree to which silt can be regarded as a limiting factor, nor its method of operation. The observed distribution of species may be related to: (i) a direct effect of silt on distribution; (ii) an indirect effect of silt, through its effects on the type of vegetation, consistency of the soil, drainage, or some chemical or physical factor in the soil; (iii) some other factor of which silt may merely be an indicator. With regard to the last, the organic content of a soil is probably closely related to the quantity of silt, since both fine organic matter and silt tend to settle in the more sheltered parts of an estuary. In grade analysis much of this organic matter will be represented in the silt fraction, though it would appear that in the samples dealt with here much of the silt was of inorganic origin.

It would seem possible that silt as such limits the inhabitants of clean sand to their normal habitat, whereas the mud-living species are restricted to the muddy areas on account of the abundant food supply in the form of detritus.

As yet very little is known of the action of the factors limiting the distribution of intertidal animals, but they presumably operate in one of three ways: by their influence on the settling reactions of planktonic larvae, by their effect on the migration of adults, or by affecting mortality after metamorphosis. *Ophelia* has already been cited as an example of a species whose distribution and density is partly determined by the settling reactions of the larvae. Lamellibranchs probably move about to a considerable extent after metamorphosis, and their distribution may be related to a choice of the more favourable grounds during the course of their wanderings.

Chapman & Newell (1947) have emphasized the possible importance of the 'thixotropic' properties of a soil in relation to the burrowing of *Arenicola*. The ease with which a burrower can penetrate the soil is enhanced by the capacity of thixotropic soils to decrease their resistance to penetration immediately after agitation. The thixotropic properties of a soil depend upon a high water content and also upon the presence of small quantities of colloidal substances. At Whitstable, as on Salthouse Lake, a layer of clay occurs beneath the surface, and this is believed to supply these colloidal substances to the soil. Thus the presence of small quantities of silt or clay may profoundly alter the properties of a sand and hence its suitability for burrowing species.

At one end of the main traverse there is a marked change in the fauna of the clean sand, which is almost certainly due to the better drainage conditions in this area. Most of the species common on the rest of the traverse are absent, but *Ophelia* occurs here and nowhere else on Salthouse Lake. Thus the distribution of *Ophelia* and intertidal species such as *Tellina* would appear to be complementary, the one depending on a well-drained, the other on a water-saturated soil. This is emphasized by the distribution of these species in the extremely well-drained sand on Bull Hill Bank. Here *Ophelia* extends almost to low-water mark, but wherever the soil is wet, *Ophelia* is absent and *Tellina* appears.

The intertidal distribution of many species cannot, however, be explained in terms of drainage conditions. Thus *Bathyporeia pilosa* occurs only in a zone at high-neap-tide mark, although *Eurydice*, which exhibits a similar zonation on Salthouse Lake, ranges down to low-water mark on Bull Hill.

SUMMARY

Erosion of Dawlish Warren, at the mouth of the Exe Estuary has resulted in a redistribution of sand, which has come to lie in close proximity to certain of the original mud banks.

Quantitative collections of the macrofauna were made along a traverse passing from the newly deposited sand to the old mud bank, stations all being at about half-tide level.

Measurements of salinity, temperature, pH, currents and wave action show that these are similar for all stations. Thus it has been possible to observe the distribution of the fauna in relation to the type of soil without the usual complications due to differences in other factors.

The occurrence and density of many species is shown to be correlated with the silt content of the soil, or some factor related to it. A traverse extending from high- to low-tide marks was worked in the same area. This provides information on the intertidal distribution of species occurring in the main traverse.

An additional traverse was worked on Bull Hill Bank, a sand bank which is much scoured by currents. The distribution of the fauna on this bank emphasizes the importance of soil drainage on distribution.

The distribution of certain species is discussed in the light of data obtained from other areas. No marked changes in the fauna of the estuary seem to have occurred since a survey of the estuary was made by Allen & Todd in 1901.

The possible mode of action of limiting factors is briefly discussed.

REFERENCES

ALEXANDER, W. B., SOUTHGATE, B. A. & BASSINDALE, R., 1935. Survey of the River Tees. Part II. The Estuary—chemical and biological. *D.S.I.R. Water Pollution Research*, Tech. Paper No. 5. H.M. Stationery Office.

ALLEN, E. J. & TODD, R. A., 1900. The fauna of the Salcombe Estuary. *Journ. Mar. Biol. Assoc.*, Vol. VI, pp. 151–217.

—— —— 1902. The Fauna of the Exe Estuary. *Journ. Mar. Biol. Assoc.*, Vol. VI, pp. 295–335.

BASSINDALE, R., 1938. The Intertidal fauna of the Mersey Estuary. *Journ. Mar. Biol. Assoc.*, Vol. XXIII, pp. 83–98.

BEANLAND, F. L., 1940. Sand and mud communities in the Dovey Estuary. *Journ. Mar. Biol. Assoc.*, Vol. XXIV, pp. 589–611.

BRADY, F., 1943. The distribution of the fauna of some intertidal sands and muds on the Northumberland Coast. *J. Anim. Ecol.*, Vol. 12, pp. 27–41.

BRUCE, J. R., 1928. Physical factors on the sandy beach. Part II. Chemical changes—carbon dioxide concentration and sulphides. *Journ. Mar. Biol. Assoc.*, Vol. XV, pp. 553–65.

CHAPMAN, G. & NEWELL, G. E., 1947. The role of the body fluid in relation to movement in soft-bodied invertebrates. I. The burrowing of *Arenicola. Proc. Roy. Soc.* B., Vol. 134, pp. 431–55.

CHEVREUX, E. & FAGE, L., 1925. Amphipodes. *Faune de France*, Vol. IX. 488 pp. Paris.

CRAWFORD, G. I., 1937*a*. A review of the Amphipod genus *Corophium*, with notes on the British species. *Journ. Mar. Biol. Assoc.*, Vol. XXI, pp. 589–630.

—— 1937*b*. Notes on the distribution of burrowing *Isopoda* and *Amphipoda* in various soils on the sea-bottom near Plymouth. *Journ. Mar. Biol. Assoc.*, Vol. XXI, pp. 631–46.

—— 1937*c*. The Fauna of certain estuaries in West England and South Wales, with special reference to the *Tanaidacea*, *Isopoda* and *Amphipoda*. *Journ. Mar. Biol. Assoc.*, Vol. XXI, pp. 647–62.

DAY, J. H. & WILSON, D. P., 1934. On the relationship of the substratum to the metamorphosis of *Scolecolepis fuliginosa* (Claparède). *Journ. Mar. Biol. Assoc.*, Vol. XIX, pp. 655–62.

ELMHIRST, R., 1931. Studies in the Scottish Marine Fauna. The Crustacea of the Sandy and Muddy Areas of the Tidal Zone. *Proc. Roy. Soc. Edin.*, Vol. LI, pp. 169–75.

FAUVEL, P., 1923. Polychètes errantes. *Faune de France*, Vol. V, 488 pp. Paris.

—— 1927. Polychètes sédentaires. *Faune de France*, Vol. XVI. 494 pp. Paris.

FISCHER-PIETTE, E., 1931. Sur la pénétration des diverses espèces marines sessiles dans les estuaires et sa limitation par l'eau douce. *Ann. Inst. Oceanogr.*, Tome X, fasc. 8, pp. 217–43.

MACGINITIE, G. E., 1935. Ecological aspects of a California marine estuary. *Amer. Midl. Nat.*, Vol. 16, pp. 629–765.

MALMGREN, A. J., 1865. Nordiska Hafs-Annulater. *K. Vet. Akad. Forhandlingar*, 1865, No. 1, pp. 51–110.

MARINE BIOLOGICAL ASSOCIATION, 1931. *Plymouth Marine Fauna.* (2nd ed.)

MILNE, A., 1940. Some ecological aspects of the intertidal area of the Aberdeenshire Dee. *Trans. Roy. Soc. Edin.*, Vol. LX, pp. 107–40.

NEWELL, G. E., 1948. A contribution to our knowledge of the life history of *Arenicola marina* L. *Journ. Mar. Biol. Assoc.*, Vol. XXVII, pp. 554–80.

NEWTON, L., 1931. *A handbook of the British Seaweeds.* 478 pp. British Museum, London.

ÖRSTED, A. S., 1843. *Annulatorum Danicorum Conspectus.* Fasc. 1. *Maricolae.* pp. 1–32.

PERCIVAL, E., 1929. A report on the fauna of the estuaries of the River Tamar and the River Lynher. *Journ. Mar. Biol. Assoc.*, Vol. XVI, pp. 81–108.

PIPER, C. S., 1942. *Soil and plant analysis.* A Monograph from the Waite Agricultural Research Institute, 368 pp. Adelaide: University of Adelaide.

PIRRIE, M. E., BRUCE, J. R. & MOORE, H. B., 1932. A quantitative study of the fauna of the sandy beach at Port Erin. *Journ. Mar. Biol. Assoc.*, Vol. XVIII, pp. 279–96.

REES, C. B., 1939. Notes on the ecology of the sandy beaches of North Donegal. *Proc. Roy. Irish Acad.*, Vol. XLV, pp. 215–29.

Reid, D. M., 1930. Salinity interchange between sea water in sand and overflowing fresh water at low tide. *Journ. Mar. Biol. Assoc.*, Vol. xvi, pp. 609–14.

Serventy, D. L., 1934. The Marine Invertebrate Fauna. In '*Scolt Head Island*', edited by J. A. Steers, Cambridge, 1934, pp. 196–213.

Spooner, G. M. & Moore, H. B., 1940. The ecology of the Tamar Estuary. VI. An account of the macrofauna of the intertidal muds. *Journ. Mar. Biol. Assoc.*, Vol. xxiv, pp. 283–330.

Stephen, A. C., 1928. Notes on the biology of *Tellina tenuis* da Costa. *Journ. Mar. Biol. Assoc.*, Vol. xv, pp. 683–702.

—— 1929*a*. Studies on the Scottish marine fauna: the fauna of the sandy and muddy areas of the tidal zone. *Trans. Roy. Soc. Edin.*, Vol. lvi, pp. 291–306.

—— 1929*b*. Notes on the rate of growth of *Tellina tenuis* da Costa in the Firth of Clyde. *Journ. Mar. Biol. Assoc.*, Vol. xvi, pp. 117–29.

—— 1931. Notes on the biology of certain lamellibranchs on the Scottish Coast. *Journ. Mar. Biol. Assoc.*, Vol. xvii, pp. 277–300.

—— 1932. Notes on the biology of some lamellibranchs in the Clyde Area. *Journ. Mar. Biol. Assoc.*, Vol. xviii, pp. 51–68.

Tutin, T. G., 1936. New species of *Zostera* from Britain. *Journ. Botany*, Vol. lxxiv, pp. 227–30.

Watkin, E. E., 1938. A revision of the Amphipod genus *Bathyporeia* Lindström. *Journ. Mar. Biol. Assoc.*, Vol. xxiii, pp. 211–36.

—— 1939. The pelagic phase in the life-history of the amphipod genus *Bathyporeia*. *Journ. Mar. Biol. Assoc.*, Vol. xxiii, pp. 467–81.

—— 1941*a*. The yearly life-cycle of the amphipod, *Corophium volutator*. *Journ. Anim. Ecol.*, Vol. 10, pp. 79–93.

—— 1941*b*. Observations on the night tidal migrant Crustacea of Kames Bay. *Journ. Mar. Biol. Assoc.*, Vol. xxv, pp. 81–96.

—— 1942. The macrofauna of the intertidal sand of Kames Bay, Millport, Buteshire. *Trans. Roy. Soc. Edin.*, Vol. lx, pp. 543–61.

Wells, G. P., 1945. The mode of life of *Arenicola marina* L. *Journ. Mar. Biol. Assoc.*, Vol. xxvi, pp. 170–207.

Wilson, D. P., 1937. The influence of the substratum on the metamorphosis of *Notomastus* larvae. *Journ. Mar. Biol. Assoc.*, Vol. xxii, pp. 227–43.

—— 1948. The relation of the substratum to the metamorphosis of *Ophelia* larvae. *Journ. Mar. Biol. Assoc.*, Vol. xxvii, pp. 723–60.

Worth, R. H., 1902. The Foraminifera of the Exe Estuary. *Journ. Mar. Biol. Assoc.*, Vol. vi, pp. 336–43.

EXPLANATION OF PLATES

Plate I

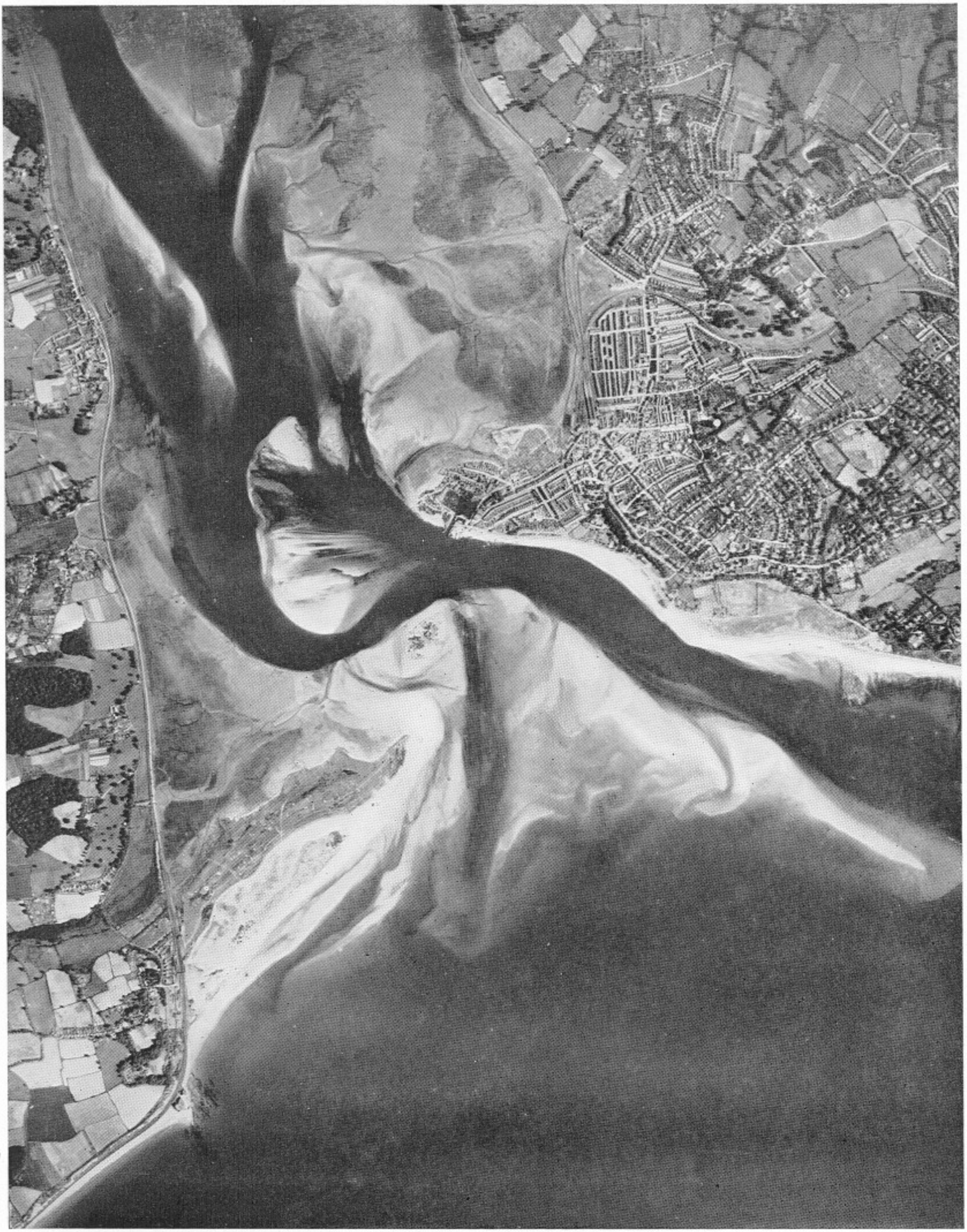
(*By kind permission of the Under Secretary of State for Air*)

Aerial photograph of the lower part of the Exe Estuary, taken at low tide, 3 August 1945. Submerged parts of some of the sand-banks are visible under water. Langstone Point: bottom left; Exmouth: centre right. Bull Hill is slightly to the left of the centre, and Dawlish Warren is below it. The remains of Warren Point are seen separated by a narrow channel from the rest of the spit.

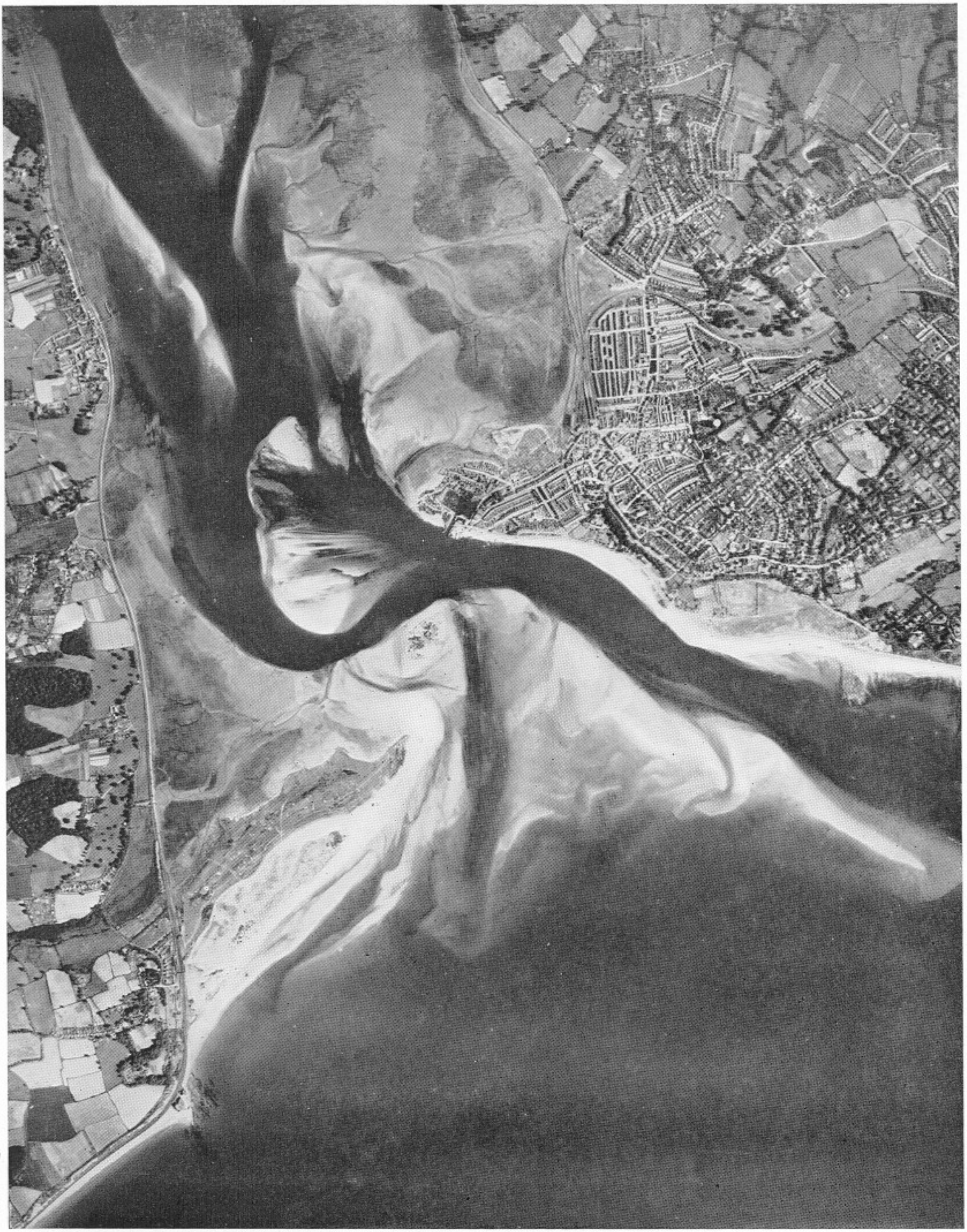
Plate II

(*By kind permission of the Under Secretary of State for Air*)

Aerial photograph of Dawlish Warren, 13 April 1946. Warren Point has been almost completely washed away. Note the sand distributed in a north-westerly direction from the breach. Photograph taken with water at about high-neap-tide mark. Bull Hill Bank is seen top-centre; note the ridges on its surface.



[*Air Ministry Copyright*



[*Air Ministry Copyright*

Air Ministry Copyright

APPENDIX

Table IX. Surface Salinities (per Mille) in the Exe Estuary (see also Fig. 1)

The stations 'A' to 'I' are those indicated on the top of Fig. 1. The column marked 'position' gives the distance of each station from Exmouth Pier, in miles. The readings taken in 1947 were taken during a period of drought when the River Exe was very low: those taken in the spring of 1948 when the river was at about normal level. The time each reading was taken, relative to the time of high or low tide, is indicated in italics under the salinity readings. Thus *−15* is 15 min. before, and *+45* is 45 min. after high or low water. The time and height of high tide are also given. (The readings made on 5 July 1947 are not given in Fig. 1.)

Date ...		5. vii. 47	18. vii. 47	27. vii. 47	28. viii. 47	3. ix. 47	3. iii. 48
Time of high tide		7.47 a.m.	6.31 a.m.	1.42 p.m.	4.23 p.m.	8.03 a.m.	11.30 a.m.
Height ...		11 ft. 2 in.	12 ft. 2 in.	9 ft. 6 in.	10 ft. 2 in.	12 ft. 5 in.	10 ft. 2 in.
State of tide ...		Low	Low	High	Low	High	High
Station	Position (miles)						
A	0	27 *−15*	32 *−50*	34 *−52*	—	34·5 *−23*	35 *−15*
B	0·35	27 *−10*	30 *−45*	34 *−13*	32 *−25*	34·5 *−18*	35 *−8*
C	1·0	24·5 *0*	28 *−30*	34·5 *−23*	30·5 *−15*	34·5 *−3*	34 *+1*
D	1·7	24·5 *+10*	27 *−17*	34 −17	29 *−5*	34·5 *+2*	31 *+8*
E	2·5	20 *+20*	23 *−6*	31 *−9*	27 *+3*	34·5 *+12*	24 *+18*
F	3·0	20 *+30*	20·5 *+2*	31 *−3*	24 *+9*	34 *+17*	22 *+24*
G	3·7	16 *+45*	13 *+30*	30 *+8*	18·5 +25	32·5 +30	16 *+37*
H	4·85	12 *+60*	8 *+48*	22 *+22*	12·5 *+34*	32·5 *+42*	1·5 *+51*
I	6·5	1·5 *+75*	1·5 *+68*	11·5 *+39*	6·5 *+50*	25 *+57*	0 *+75*

Table X. Comparison of Soil Analyses as Made here with Results Obtained, Using a 70 I.M.M. Sieve (0·2 mm. Mesh)

Samples from Station II. Percentages by weight.

Grade (mm.)	Percentage	Grade (mm.)	Percentage
Over 2	—	Over 2	—
2–0·5	1·1	2–0·5	1·1
0·5–0·256	13·9	0·5–0·2	53·6
0·256–0·22	21·2		—
0·22–0·02	62·2	0·2–0·02	44·2
<0·02	1·6	<0·02	1·2

Table XI. Temperature and Salinity Readings at Station III, 19 August 1947 (see also Figs. 4 and 5)

C., station covered—sample from overlying water; U., station uncovered—sample from small pool.

Time	State	°C.	Salinity	Time	State	°C.	Salinity
7.40 a.m.	C.	19	34·5	2.20 p.m.	U.	27·25	36
8.05	C.	19	35·0	3.30	U.	27·25	37
9.05	C.	19	35·5	4.25	U.	26	38
10.10	C.	19·5	34·5	5.25	U.	24	36·5
11.10	C.	21	34·5	6.10	C.	21	35
12.45 p.m.	U.	25·5	36·5	6.55	C.	20·5	36
1.10	U.	26·5	36·5				

Table XII. Temperature and Salinity in the Main Channel, near Bull Hill Bank, 19 August 1947 (see also Figs. 4 and 5)

Time	°C.	Salinity	Time	°C.	Salinity
7.30 a.m.	18·75	35	2.30 p.m.	22·5	32·5
8.00	18·75	35	3.45	21·5	32·5
9.00	19	34·5	4.35	21	33
10.05	18·75	34·5	5.35	20·5	34·5
11.00	19	34·5	6.35	20	34·5
12.35 p.m.	19·75	34·5	7.00	20	34·5
1.35	20·5	34			

TABLE XIII. 'BIOMASS' OF THE FAUNA, IN G. PER M.^{2} DETERMINED FROM WEIGHTS OF PRESERVED SPECIMENS

Station I−100

	No.	Weight (g.)
Ophelia bicornis	12	2·04
Eurydice pulchra	560	1·84
Bathyporeia pilosa	560	0·74
Total		4·62

Station II+3

	No.	Weight (g.)
Nephthys spp.	24	4·68
Scoloplos armiger	32	0·96
Arenicola marina	28	47·84
Ampharete grubei	4	0·02
Eurydice pulchra	4	0·01
Bathyporeia pilosa	12	0·02
B. sarsi	132	0·58
Urothöe grimaldii	236	0·92
Corophium arenarium	124	0·29
Tellina tenuis	88	9·80
Scrobicularia plana	12	0·08
Cardium edule	16	4·12
Total		69·32

Station IV+3

	No.	Weight (g.)
Nephthys hombergi	12	4·12
Glycera convoluta	20	2·88
Arenicola marina	12	12·64
Ampharete grubei	3536	18·36
Melinna palmata	8	0·36
Corophium arenarium	44	1·04
Macoma balthica	4	0·16
Scrobicularia plana	112	39·48
Cardium edule	36	22·68
Total		101·72

Station VI+3

	No.	Weight (g.)
Scoloplos armiger	4	0·12
Arenicola marina	32	1·92
Ampharete grubei	1680	8·72
Melinna palmata	32	1·44
Scrobicularia plana	152	20·72
Cardium edule	180	12·52
Total		45·44

Station BH+9

	No.	Weight (g.)
Ophelia bicornis	212	36·04
Nerine fragments	—	0·44
Eurydice pulchra	116	0·40
Total		36·88

TABLE XIV. *TELLINA TENUIS*. NUMBERS OF INDIVIDUALS IN EACH MM. LENGTH GROUP

Length of shell taken to nearest mm. 'above'.

Length (mm.)	I−100	I−40	I−3B	I−3A	I+3	I+8	I+30	I+67	II−3	II+3	II+33	II+67	III−3	III+3	D−3	D+3	F−3	F+3	G−3	G+3	H−3	H+3	H+15	BH−50	BH+19	BH+24
2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	2	1	.	.	.	.	.
5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	2	.	1	1	.	.	1
6	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	1	.	2	.	.	.
7	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	1	.	.	.	.
8	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	6	4	6	.	.	2
9	.	.	.	.	.	.	.	.	1	.	.	2	.	.	.	.	.	2	1	2	6	9	9	1	.	1
10	.	.	.	.	.	.	.	1	.	.	.	1	.	.	.	.	2	3	2	2	8	5	11	.	.	1
11	.	.	.	.	1	.	.	2	.	2	.	3	.	.	.	.	12	11	3	3	4	6	4	.	.	3
12	.	.	.	.	.	1	.	1	1	.	1	.	.	.	1	1	7	6	3	4	.	1	4	.	2	1
13	.	.	2	.	1	.	1	4	2	1	1	7	.	.	.	.	6	4	2	3	4	3	5	.	.	2
14	.	.		2	3	4	3	.	.	2	6	2	.	.	1	1	5	6	6	5	4	1	1	.	1	.
15	.	.		.	1	.	2	3	7	10	.	.	.	.	1	.	8	4	6	10	3	5	5	.	.	1
16	.	.	3	2	.	.	.	3	5	5	6	.	1	.	.	1	5	6	14	6	1	5	.	.	.	.
17	.	.		.	.	1	.	1	1	2	4	.	.	.	.	.	.	3	4	6	.	2	.	.	.	.
18	.	.		.	.	.	.	1	2	.	.	.	.	.	.	.	.	.	4	1	.	2	.	.	.	.

TABLE XV. *SCROBICULARIA PLANA*. NUMBER OF INDIVIDUALS IN EACH MM. LENGTH GROUP

Figures in italics unreliable owing to subsampling error.

Length (mm.)	I−100	I−40	I−3B	I−3A	I+3	I+8	I+30	I+67	II−3	II+3	II+33	II+67	III−3	III+3	III+33	III+67	IV−3	IV+3	IV+33	IV+80	V−3	V+3	VI−3	VI+3	C−3	C+3	C+15	D−3	D+3
2	.	.	.	.	.	.	.	1	.	1	.	.	.	.	1		.	.	.			.	.	*27*	.			.	1
3	.	.	.	.	.	1	2	1	3	2	.		.	.	4	29	.	42			*36*		.		.			1	2
4	.	.	.	2	1	2	1	3	1	.	1	10	.	.	4		*6*		9	*78*		12	.	.	.	16	92	2	6
5	.	.	.	2	1	3	4	7	.	.	.		.	.	2		.	.			.		.	.	.			.	1
6	.	.	.	.	.	.	2	3	.	.	2		.	.	4	.	.	.	*8*		.		.	.	*4*			.	1
7	.	.	.	.	.	.	1	.	.	.	1	.	.	2	.	1	.	2	.	.	1	.	.	.	.			.	1
8	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	1	.	*6*	.	.	.	1	1	1
9	.	.	.	.	.	.	.	.	.	1	1	.	.	3	1	.	.	1	1	1	1	.	.	1	.	.	.	.	.
10	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.	2	.	.	1	.	.	.	1	.	.
11	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	1	.	.	.	1	.	.	.	.	.	.	.	.	.
12	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
13	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	1	.	.	.	.	.	.	.	.	.
14	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	1	.	.	.	3	.	.	.	.	.
15	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	1	.	6	1	.	.	.	.	.	.	.	.	.
16	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	1	.	.
17	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1	.	.	.	.	.	1
18	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	1	.	.	.	.	.	.	.	.
19	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1	.	.	2	.	.
20	.	.	.	.	.	1	.	.	.	.	.	.	.	1	.	.	.	.	3	.	1	*4*	6	.	.	.	.	.	.
21	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1	1	1	*4*	.	1	.	.	3	.	.
22	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	2	.	.	.	.	2	.	1	.	.	.	.	.	.
23	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	1	.	1	.	1	.	.	.	1	.	.
24	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.
25	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1	.	1	1	.	2	1	.	.	.	.	.	.	.
26	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1	1	.	.	.	.	.	.	.
27	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	2	.	.	.	.	.	.
28	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.	1	.	1	.	.	.	.	.	.	.	.
29	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1	1	1	.	.	2	.	.	.	.	.	.	.
30	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1	.	.	1	.	1	2	.	.	.	.	.
31–35	.	.	.	.	.	.	.	.	.	.	.	.	2	1	2	.	.	2	4	.	3	1	5	3	.	.	.	.	.
36–40	.	.	.	.	.	.	.	.	.	.	.	.	1	.	5	6	4	3	10	.	.	1	.	.	.	.	.	.	.
41–45	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	1	2	.	.	.	.	.	.	.	.	.	.

TABLE XVI. *CARDIUM EDULE.* NUMBER OF INDIVIDUALS IN EACH MM. LENGTH GROUP

Figures in italics unreliable owing to subsampling error.

Length (mm.)	I−100	I−40	I−3B	I−3A	I+3	I+8	I+30	I+67	II−3	II+3	II+33	II+67	III−3	III+3	III+33	III+67	IV−3	IV+3	IV+33	IV+80	V−3	V+3	VI−3	VI+3	A−3	B−3	C−3	C+3	C+15	D−3	D+3	F−3	F+3	G−3	G+3	H−3	H+3	H+15
2	.	.	1	.	2	2	4	2	1	.	1	5	.	3	5	15	.	.	.	37	.	1	2	23	.	.	.	3	.	10	13	2	2	.	.	.	.	.
3	.	.	2	3	5	2	2	2	.	.	.		.	.	3		.	.	.		.	*8*	2		.	.	.	.	45			1	.	.	.	.	1	.
4	.	.	1	6	.	.	3	2	.	.	.	.	.	.	1	.	*2*	.	.		*27*	*5*	1		.	.	.	5				.	1	.	1	.	.	.
5	.	.	.	.	2	.	.	1	.	1	.	.	.	.	.	.	*6*	.	9	.		*21*	1	3	.	.	.	5		.	.	.	.	.	.	.	.	1
6	.	.	.	3	.	.	.	.	.	1	.	.	1	1	3	.	.	1	3	.		*16*	4	7	.	.	1	5		.	.	.	.	.	.	.	.	.
7	.	.	.	.	1	1	.	.	.	.	.	.	.	.	1	.	.	.	.	1		*9*	*11*	2	.	.	1	1		1	1	.	.	.	.	.	.	.
8	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	*10*	3	4	.	.	.	2	3	.	.	.	.	.	.	.	.	.
9	.	.	.	.	.	2	1	.	1	.	.	.	.	.	.	.	.	1	1	.	.	1	*10*	4	.	.	.	1	6	1	1	1	1	.	.	.	.	.
10	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	1	.	.	2	3	.	.	.	1	2	.	.	.	.	.	.	.	.	.
11	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	1	1	2	.	.	.	1	3	.	.	.	.	5	1	1	.	.	.	.	.	.	.
12	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	1	.	1	.	.	1	1	.	.	.	1	2	.	.	.	.	.	.	.	.	.
13	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.
14	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	4	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.	.	.
15	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	1	.	.	.	.	.	1	1	.	.	.	.	.	.	.	.
16	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	1	.	.	1	.	.	.	.	.	.
17	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.
18	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	2	.	.	.	1	.	.	.	.	.	.	.
19	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.	.	.
20	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
21	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	2	1	.	.	1	1	1	2	1	.	.	.	.	.	.	.
22	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
23	.	.	.	.	.	.	1	.	.	.	.	.	.	.	1	.	.	.	.	1	.	.	1	.	.	.	.	1	.	1	.	.	.	.	.	.	.	.
24	.	.	.	1	.	.	.	.	.	.	.	.	.	1	1	.	.	1	.	.	.	.	.	.	.	.	.	.	1	.	2	.	.	.	.	.	.	.
25	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	1	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	1
26	.	.	.	.	.	.	.	.	.	1	.	.	.	.	1	.	.	.	1	.	.	.	.	1	.	.	.	.	1	.	.	.	.	.	.	.	.	.
27	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
28	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
29	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
30	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
31–35	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	1	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1

A PRELIMINARY REPORT ON THE PLYMOUTH MARINE AND BRACKISH-WATER ROTIFERA

By E. D. Hollowday, F.R.M.S.

(Text-figs. 1–2)

CONTENTS

INTRODUCTION

Throughout the sixty odd years during which the Plymouth Laboratory has been the centre of the scientific investigation of British marine life, especially that of Plymouth Sound and neighbouring areas, there has only been one species of rotifer recorded,[1] namely *Synchaeta gyrina* Hood (Marine Biological Association, 1931, p. 149), but some doubt is cast on the accuracy of this identification by the mention of it occurring 'with eggs'. It is a well-established fact that *S. gyrina* does not carry its eggs after extrusion, but drops them immediately, although several closely related species are known to carry the eggs attached to the cloaca until they hatch. On the other hand, 'with eggs' may possibly mean that specimens were observed with the egg developing within the ovisac, in which event there is no objection to the identification. Anyhow, it is highly probable that *S. gyrina* actually occurs either in the Sound or the Hamoaze, although it was not observed during the writer's survey.

The dearth of information on the Plymouth brackish and marine Rotifera is probably not so surprising as it may at first appear, as none of the pelagic

---

[1] Shortly after completing this report, two unpublished records by the late David Bryce were forwarded to the writer from the Plymouth Laboratory. These relate to the occurrence of *Synchaeta vorax* and *S. triophthalma* in the Sound during April 1934, and there is a doubtful record of *S. cecilia* Rousselet occurring beyond the Plymouth breakwater in March of the same year. Although this species was not refound by the writer, it is common in the Liverpool area (per A. L. Galliford) and it is highly probable that it does occur at Plymouth.

species found by the writer (with the possible exception of *S. vorax* Rousselet) ever become really numerous in the plankton, and, furthermore, there have been no serious students of the rotifers round our coasts since the death of Charles Rousselet, and very few before him. It is quite likely that workers at the laboratory specializing in plankton studies occasionally come upon rotifers in tow-net samples, but, being occupied with other forms, pay little attention to them. If this is so, the writer would gladly welcome rough sketches of any species noticed by workers on other phyla during their studies.

The writer wishes to emphasize that, although a considerable number of fine plankton samples have been examined at all times of the year, not to mention scrapings of algae from rocks and rock pools, at Jenny Cliff, Rum Bay, Barn Pool, and various locations in the Hamoaze, etc., the investigations carried out have only been of a preliminary nature. The Yealm, Cattewater, and upper reaches of the Tamar have not been looked into at all, and the apparent poverty of the brackish rotatorian fauna at Plymouth may be due to insufficient investigation.

The writer wishes to place on record his very deep gratitude to those who have been of great assistance in the compilation of this preliminary survey; to Mr F. S. Russell, F.R.S., for his kindness in allowing the writer unrestricted facilities at the Plymouth Laboratory; to Dr M. V. Lebour for a tube of preserved *Synchaeta* from Plymouth Sound plankton samples; to Mr S. M. Nunn for setting aside plankton samples from the laboratory's boats as required; and to Mr A. L. Galliford of Liverpool to whom the writer is indebted for general information on many aspects of the study of rotifers, for placing at his disposal information concerning the coastal Rotifera of the Liverpool area, for advice, and also for checking and criticizing the present report.

Historical Survey

Our knowledge of marine and brackish-water Rotifera dates back to the first half of the nineteenth century. In 1830, a certain Dr Michaelis collected a species of *Synchaeta* (which has more marine and brackish representatives than any other known genus of rotifers) in Kiel harbour. This discovery, and its subsequent publication as *Synchaeta baltica* by C. von Ehrenberg (1834, p. 220), led to a great deal of confusion regarding the identity of several other species of *Synchaeta* found in coastal waters during the next sixty years, and the matter was not really cleared up until Charles Rousselet (1902) published his monograph on the genus. The writer has not had access to the original description of *S. baltica*. In his *Die Infusionsthierchen* of 1838 (p. 439; Pl. 53, fig. 5), Ehrenberg is mainly concerned with the rotifer's supposed luminosity, originally suggested by Michaelis, but finds little support for the theory. The luminosity was doubtless due to the presence in the same water of phosphorescent dinoflagellates, which, Ehrenberg states, were collected with the rotifers. Even so, P. H. Gosse (1856, p. 274, pl. xiv), and several other workers, apparently clung to the idea of *Synchaeta* spp. being responsible for luminous phenomena in coastal waters. Rousselet (1902) states, however, that 'there is no valid reason for the statement that this *Synchaeta*, or any other rotifer, is connected with the luminosity of the sea'.

During the period 1838–60, little work appears to have been done, apart from the occasional papers of P. H. Gosse and Dujardin, but in 1886, Hudson & Gosse published their monograph *The Rotifera or Wheel Animalcules*, and the supplement issued in 1889 contains drawings and descriptions of several species which Gosse had found in tidal pools along the Devon coast. Some of these are also known from fresh-water habitats. The publication of *The Rotifera* stimulated a great interest on the part of amateurs and professionals alike during the closing years of the nineteenth century. On the continent Dr Karl Zelinka, Dr Plate, and Zacharias, not to mention K. M. Levander and Robert Lauterborn, considerably advanced rotatorian anatomy, physiology, ecology and taxonomy; while John Hood, Charles Rousselet, and David Bryce extended our knowledge of the British fauna. Nearly all the above-mentioned workers described coastal forms, and in the report of the German plankton expedition of 1895 (Zelinka, 1907) is published a description and figure of a new species of *Synchaeta*, namely *S. atlantica*, which was collected at several stations in mid-Atlantic.

The years 1859, 1868, and 1876 are important milestones in the study of coastal Rotifera. In 1859, A. E. Grube published a description of a peculiar rotifer, *Seison nebaliae*, found as an ecto-parasite (probably only commensal) on the malacostracous crustacean *Nebalia*. In 1876, Claus described another species of this genus. In 1868, E. Ray Lankester described a rotifer, now known as *Zelinkiella* (*Discopus*) *synaptae*, from the alimentary canal of a sea cucumber. These two genera, along with the genus *Paraseison*, are the only exclusively marine rotatorian genera. The above-mentioned rotifers are highly specialized, and it is likely that careful examination of macroscopic marine animals may reveal further parasitic and commensal rotifers.

The published work on the Rotifera since the first years of the present century has been mainly devoted to the physiology, ecology and systematics of fresh-water forms, the only marine studies being those of Remane (1929) at Kiel, Wulfert (1942) in Germany and Italy, and Galliford (1945, 1946) in Liverpool Bay and along the Cheshire coast. A preliminary survey of rotifers from tidal pools at Millport was made by the late David Bryce in 1927 (Scottish Marine Biological Association, 1928).

Collecting and other Methods

As with most other forms of life, the methods and apparatus used in collecting rotifers have to be varied according to the habitat. The pelagic species were collected by fine bolting-silk tow-nets, either from the laboratory's boat or by the writer from a rowing boat. The former collections were made at various stations in Plymouth Sound, from inshore to beyond the breakwater. The writer's own plankton hauls were made in the mouth of the Tamar, at various points in the Hamoaze, and from Drake's Island to the shore. Scrapings of algae from tidal pools and crevices along the shore at Barn Pool, Cremyl, Rum Bay, Jennycliff Bay, and the Royal William Victualling Yard wharfs, were taken and examined for the weed-haunting littoral forms. Masses of *Fucus* from all the above-mentioned stations were washed and squeezed through bolting silk in order to dislodge browsing forms. Collections were also made with a hand-net of fine bolting silk in the creek known as Stonehouse Lake.

Samples were always examined in fresh condition. It is a great mistake to preserve plankton samples when searching for Rotifera if there is any means of examining them within a reasonable time. This applies not only to marine, but to brackish and fresh-water samples also. Indeed, it is highly probable that many rotifers are overlooked by workers who would otherwise notice them, as a result of specimens being contracted or otherwise distorted through preservation. Furthermore, and this applies especially to the genus *Synchaeta*, it is usually impossible to detemine species from contracted specimens, and often, when the animal is very transparent and lying amongst flocculent debris, etc., it is very difficult to distinguish it as a rotifer at all. When located, however, and after careful note has been taken of external appearances, it is often necessary to kill the animal and dissolve out the jaws or trophi with a solution of sodium or potassium hydroxide. Samples were first examined in a glass dish under the low power of a dissecting microscope, and individual specimens transferred with a fine pipette to a Rousselet compressorium for detailed study. All drawings were made from living specimens while held still in the compressorium, the method of drawing being that described by the writer (Hollowday, 1946).

Synchaeta triophthalma Lauterborn (Fig. 1 A, B).

Lauterborn, R., 1894. *Wiss. Meeresunters. Biol. Anst., Abt. Helgoland*, Bd. pp. 207–13, fig. 1.

S. triophthalma was originally found in 1893 by Dr Lauterborn off the coast of Heligoland, and subsequently by John Hood in the sea off Dundee. A brackish-water species, it has now been recorded from the Bay of Naples, Trieste, the Skagerak, Bergen, Liverpool and the Cheshire coast, where it is found in rock pools on Hilbre Island. It has recently also been recorded from New Zealand, in Oamuru Harbour.

At Plymouth it occurred in Stonehouse Lake, a tidal creek opening on Plymouth Sound between Plymouth and Devonport. It is quite probable that this species is common in brackish situations all round our coasts.

It occurred at Plymouth in April 1946, only female specimens being observed, and most of these carried eggs. As far as the writer is aware, the male is as yet unknown. The eggs carried by these Stonehouse specimens were of the ordinary, parthenogenetic type. According to Rousselet, *S. triophthalma* dies almost immediately if placed in fresh water, but, on the other hand, it never seems to occur in water of a very high salinity, preferring rock pools above the highwater mark, or in the 'splash' or 'spray zone', or the upper reaches of creeks and river estuaries. It was never observed in the Hamoaze or the Sound.

S. triophthalma is fairly easy to recognize, being extremely wide anteriorly, possessing, as a rule, three main pigment spots. A rather unique feature is the asymmetrical left lateral antenna, situated, not in the usual position (the lumbar region), but on a prominent swelling on the left dorso-lateral surface of the foot. According to Rousselet, the right lateral antenna is absent, but the writer has recently been informed by Mr A. L. Galliford that Remane has found what he believes to be the right lateral antenna in the normal position, but very inconspicuous, and without the brush of sensory setae. Nothing was seen of this in the Plymouth specimens.

The foot terminates in a single pointed toe (Fig. 1B).

Synchaeta littoralis Rousselet (Fig. 1C).

Rousselet, C., 1902. *Journ. Micr. Soc.*, p. 398, pl. vii, fig. 15.

While apparently a rare rotifer in Plymouth Sound and the Hamoaze, this species is reported common in brackish water at Leasowe, Cheshire, by Mr Galliford, and the accompanying illustration was drawn from a Leasowe specimen. It has been observed only once or twice at Plymouth, occurring in fine tow-net samples collected by the motor boat *Gammarus* between Drake's Island and the Hoe in May and June 1947.

The size of this species seems rather variable. Rousselet gives the maximum length as 238 μ. The specimen here depicted, and most of the other Leasowe specimens measured 192 μ or thereabouts, and the Plymouth Sound specimens agreed with this.

The body is stouter than in *S. triophthalma*, being more cylindrical in shape. There are two streams of purple granules connecting the frontal eyespots with the occipital. The lateral antennae are placed some three-quarters of the way down towards the foot, at the point where the trunk begins to narrow. No males were observed at Plymouth.

Originally described by Rousselet from specimens collected at Dundee by Hood, it has been found at Great Yarmouth, Margate and Leasowe, Cheshire. There is a doubtful record for Naples.

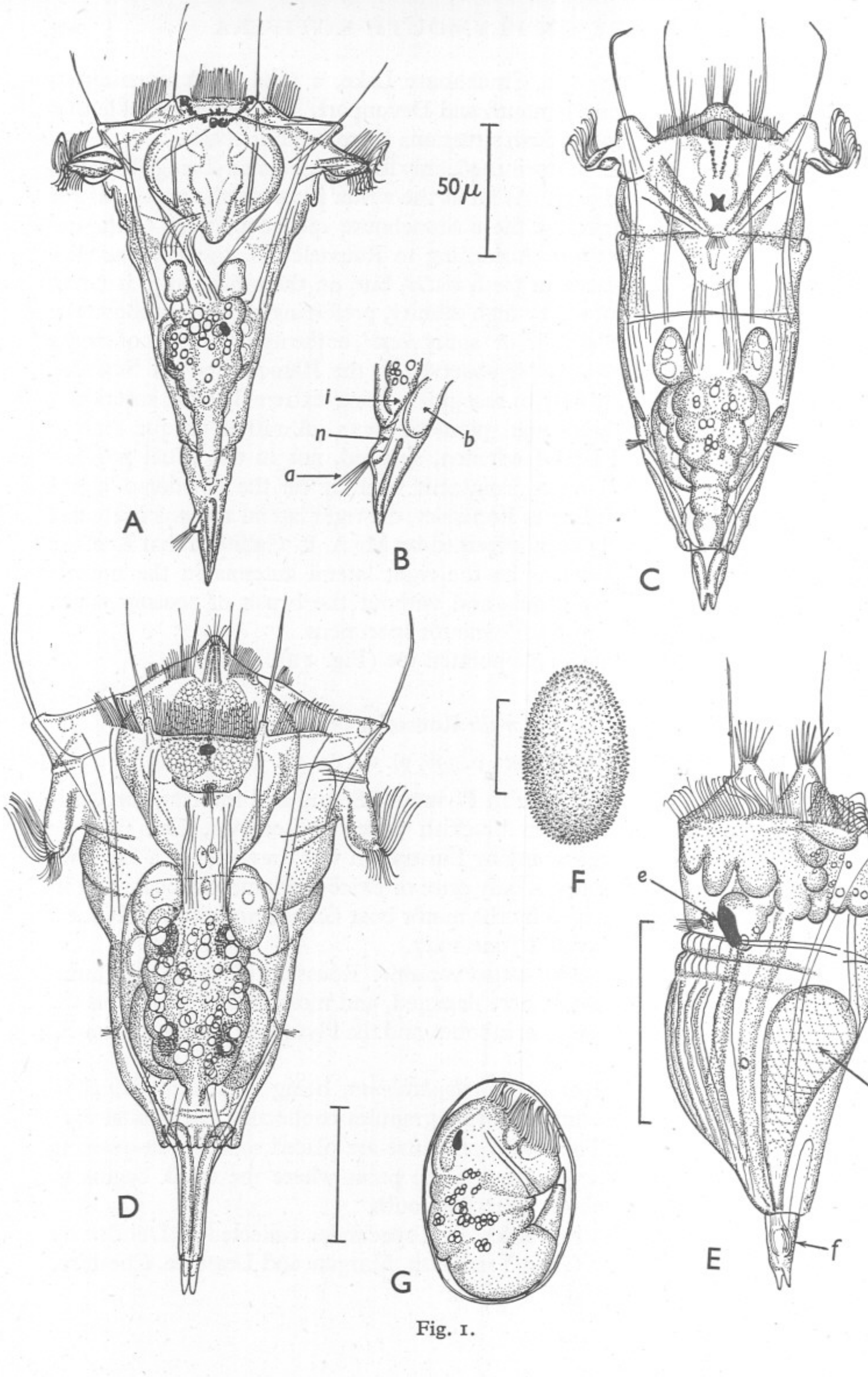


Fig. 1.

Synchaeta vorax Rousselet (Fig. 1 D–G, 2 A).

Rousselet, C., 1902. *Journ. R. Micr. Soc.*, pp. 408–10, pl. viii, fig. 19.

This species has been more thoroughly investigated by the writer at Plymouth than any other rotifer. It is not only common in the inshore waters of the Sound, but occurs also beyond the breakwater for considerable distances. Its presence in large numbers in all fine tow-net collections, during the summer months, must have been noticed by many workers studying fresh plankton samples at Plymouth. It is probably this species which Lebour records 'occasionally in tow-nets from the Sound' (Marine Biological Association, 1931, p. 149).

Occurrence and swarming periods at Plymouth

S. vorax was numerous in the first plankton samples collected by the writer from a rowing boat beyond Drake's Island in April 1946. Fig. 1 D was drawn from a specimen in this first collection. It subsequently occurred in samples collected by the laboratory boat beyond the breakwater, although somewhat sparingly. Owing to the writer's preoccupation with other groups, no further records were made during 1946, but this was doubtless due to the fact that only medium tow-net samples were examined. During 1947, however, the rotifer was closely studied from February until its climax and sudden disappearance in May. Owing to extremely adverse weather conditions early in the year, no collections were made before February, so it is not possible to say exactly when it reappears from the previous summer's resting eggs. It was present in very small numbers during February, increasing steadily throughout March and April, and by the middle of May it was, on several occasions, easily the most numerous member of the zooplankton in fine tow-net collections. Mr P. S. B. Digby informed the writer about this time, that he had recently found it very numerous while studying copepods from the Sound.

About the time that *S. vorax* reached its climax, in the middle of May, there appeared in the Sound great quantities of the alga *Phaeocystis poucheti* Langerh., and it was a common sight to see many *Synchaeta vorax* madly tearing away with their protruded unci at the cells round the outer margins of

---

Fig. 1. A, *Synchaeta triophthalma* Lauterborn; ♀ from Stonehouse Lake, Plymouth; length 190 μ; dorsal aspect. B, the same, enlarged lateral aspect of 'foot'. C, *S. littoralis* Rousselet; ♀ from Leasowe, Cheshire; length 192 μ; dorsal aspect. D, *S. vorax* Rousselet; ♀ from Plymouth Sound, Apr. 1946; length, with foot extended, 250 μ. E, the same; ♂ from Plymouth Sound, May 1947, showing the 'foot' extended; length 129 μ; left dorso-lateral aspect. F, the same, resting egg deposited in *Phaeocystis*, Plymouth Sound, May 1947; length 93 μ. G, the same, developing egg showing ♂ shortly due to hatch, length 84 μ. *a*, antenna; *b*, bladder; *e*, eye spot; *f*, foot; *i*, intestine; *n*, nerve; *s*, sperm sac. Vertical scales all represent lengths of 50 μ.

the colonies. This went on for over a week, and then males appeared in large numbers. It must be noted that the writer never actually witnessed copulation, which is usually a necessary observation before deciding on the identity of most male rotifers, but these males agreed in most respects with the details given by Rousselet; furthermore, there were no females of any other species of *Synchaeta* present at the time, and almost immediately after these males appeared, the *S. vorax* began to lay resting eggs (a result of fertilization), these being deposited in the gelatinous masses of the *Phaeocystis*. The rotifer disappeared with a suddenness quite common in plankton rotifers; samples collected on 23 May 1947 being entirely devoid of a single active specimen, although many resting eggs still remained in the masses of *Phaeocystis*.

For over a year after first collecting this species at Plymouth, the writer was undecided as to its specific identity, and although the final decision was agreed to by Mr Galliford (who has studied the species fairly extensively at Liverpool), after much discussion and detailed study of all available literature, drawings, and Rousselet's own mounted specimens, there are one or two points wherein the Plymouth specimens differ from Rousselet's original published description and the accompanying figures.

First of all, it would appear that there are two distinct forms of *Synchaeta vorax* differing in the size of the whole animal, and in the proportions of the foot. In all other respects, these two forms are identical. The Plymouth specimens all measured an average of 250 μ, being possessed of a long slender foot. This size compares well with the average of 272 μ given in the original description, and the 238 μ which is the greatest length of some specimens mounted by Rousselet himself in 1899 and recently examined by the writer. At Southport and Liverpool, however, Mr Galliford finds a smaller form which has a somewhat stouter foot than those at Plymouth, being more in keeping with the original description and drawing in this respect, but measuring only 200 μ. Another slide mounted by Rousselet, and lodged at the Manchester University, shows specimens with a fairly stout foot and a total length which varies from 196 μ to 216 μ.

Another slight difference in the Plymouth specimens was their apparent 'calmness', which is certainly not in keeping with the wild, voracious habits ascribed to the species by Rousselet, and faithfully exhibited by the specimens from the Lancashire coast. Indeed, Rousselet had good reasons for adopting the specific name *vorax*, and in his original description he says: 'the species swims with such impetuosity through the water that its rush cannot be described otherwise than furious; its course is straight forward, then it dashes suddenly round in another direction, attacking any other *Synchaeta* that may come in its way, and not at all particular as to species. I have seen it seize an unfortunate *S. triophthalma* with its jaws, carry it in its mouth and devour it without a moment's stop in its furious career. No other *Synchaeta* of my aquaintance is so fast in motion and so fierce of temper.'

The Plymouth specimens seemed placid enough, though swimming fairly rapidly in spirals, but were never observed to attack other small organisms, or their own kind. Fierce nibbling attacks were, however, made on the *Phaeocystis* as already mentioned.

The males, which appeared in numbers during the middle of May, were a little smaller than the 149 μ specified by Rousselet, and the majority averaged 125 μ. Like most other male rotifers, the males of this genus are devoid of digestive system, but possess a well-developed genito-urinary system. Most of the body cavity is occupied by the large sperm sac which opens into a small protuberance on the dorsal surface of the foot, forming a rudimentary penis. The movements of the male are even more vigorous and rapid than those of the female.

A final perplexing point regarding this species may be mentioned. Although the two frontal coronal prominences of the male, each with its crown of setae, were plainly visible (these are stated by Rousselet to be peculiar to the male of *Synchaeta vorax*), the three small tubular frontal antennae, also a characteristic feature of this male, could not be found.

The resting egg has an opaque shell, beset with many small pointed protuberances, and measures about 93 μ in length (Fig. 1 G).

S. vorax appears to have a wide distribution, but it is quite probable, in view of the cosmopolitan habits of many rotifers, that further investigation of marine and brackish rotatorian faunas in foreign parts will reveal that many of the rotifers occurring round our coasts have a world-wide distribution. To date, *S. vorax* has been recorded from Dundee, Liverpool, Southport, Bergen, Lake Ladoga (fresh water), and the Suez canal.[1]

As in fresh water, planktonic rotifers in the sea doubtless become the prey of fish fry, but it would appear they also figure in the diet of other pelagic invertebrates, and *S. vorax* has been observed being devoured by Hydromedusae at Plymouth and also at Southport (Hollowday 1947).

Encentrum marinum (Dujardin) (Fig. 2 B, C)

Furcularia marina Dujardin, 1841. *Histoire naturelle des Zoophytes* etc., p. 649, pl. 22, fig. 4.

Distemma marina Gosse, 1887. *Journ. R. Micr. Soc.*, 1887, p. 367. (Not *Distemma marinum* Ehr.)

Distemma platyceps Gosse, P. H., 1887. *Journ. R. Micr. Soc.*, 1887, p. 866, pl. 14, fig. 12.

Pleurotrocha marina Bergendal, D., 1892. *Acta Univ. Lundensis*, Vol. 28, No. 4, p. 50, pl. 1, fig. 13.

Diglena marina N. von Hofsten, 1912. Marine, Litorale Rotatorien etc. *Zool. Bidr. Uppsala*, Vol. 1, p. 203.

---

[1] Since this report was compiled, it has been found in brackish water at West Mersea, Essex, by A. L. Galliford and C. Rudlin.

A strictly littoral-zone species, occurring in masses of algae in rock pools and brackish pools above the high-tide mark. It is also capable of living in fresh water as well as water of oceanic salinity.

The general appearance of the rotifer can be observed in the accompanying drawing, made from a rock pool specimen collected along the shores of Barn Pool and Mount Edgcumbe. It is doubtless common all round the shores of the Sound, although specimens were observed only in the above-mentioned region.

E. marinum has been recorded from Naples, Jacobshaven, Helsingfors, Bergen, Liverpool, and the Firth of Tay, also in salt and brackish water at Atlantic City, New Jersey, and Mount Desert Island, Maine. In fresh water, Royal Botanic Gardens, Regent's Park.

Several members of this genus are known to occur in salt pools and brackish waters.

Proales reinhardti (Ehrenberg) (Fig. 2 D, E)

Furcularia reinhardti Ehrenberg, 1833. *Abh. Akad. wiss. Berlin*, p. 208.

Distemma marinum Ehrenberg, 1838. *Infusionsth.*, p. 450, pl. 56, fig. 4. (Not *Distemma marina* Gosse.)

Mytilia tavina Hudson, C. T. & Gosse, P. H., 1886. *The Rotifera*, Vol. 2, p. 110, pl. 26, fig. 8.

M. teresa Gosse, P. H., 1887. *Journ. R. Micr. Soc.*, p. 3, pl. 1, fig. 7.

Notommata theodora Gosse, 1887. *Journ. R. Micr. Soc.*, p. 862, pl. 14, fig. 2.

Mytilia poecilops Gosse, 1887. *Journ. R. Micr. Soc.*, p. 869, pl. 15, fig. 21.

M. producta Gosse, 1887. *Journ. R. Micr. Soc.*, p. 870, pl. 15, fig. 22.

Notommata reinhardti Hudson & Gosse, 1889. *The Rotifera*. Suppl., p. 22.

Diops marina Bergendal, D., 1892. *Acta. Univ. Lundensis*, Vol. 28, No. 4, p. 83, pls. 4, 5, fig. 27.

Pleurotrocha reinhardti von Hofsten, 1912. *Zool. Bidr. Uppsala*, Vol. 1, p. 187, fig. 1.

Proales reinhardti Harring, H. K. & Myers, F., 1924. Rotifera of Wisconsin. II. *Trans. Wis. Acad. Sci. Arts, Let.*, p. 431, pl. XVI, figs. 6–10.

Few rotifers have been described so many times under different names by the same author as the one now known as *Proales reinhardti* (Ehrenberg).

A littoral, browsing species, *P. reinhardti* is common in rock pools, and in masses of *Fucus*.

All the main characteristics of the rotifer are so clearly shown in the accompanying illustrations drawn from Plymouth specimens, that little comment

---

Fig. 2. A, *Synchaeta vorax* Rousselet; ♂, from Plymouth Sound, May 1947, with foot and penis withdrawn; length 124 μ; left dorso-lateral aspect (cf. Fig. 1 E). B, *Encentrum marinum* (Dujardin); ♀, from rock pool, Mount Edgcumbe, Plymouth, with trophi (*t*) protruded for browsing; length *c.* 165 μ; right lateral aspect. C, the same, enlarged view of the trophi. D, *Proales reinhardti* (Ehrenberg); ♀, from rock pool, Jennycliff, Plymouth; length 260 μ; left lateral aspect. E, the same, ♀ from rock pool, Mount Edgcumbe, Plymouth; dorsal aspect. F, *Trichocerca marina* (Daday), ♀ from the plankton, Plymouth Sound; body length 150 μ; left lateral aspect. *d*, ingested diatoms; *e*, eye spot; *f*, foot; *g*, gastric gland; *r.c.*, renal canal; *r.s.*, retrocerebral sac; *s*, sperm sac; *t*, trophi; *v*, vitellarium. Vertical scales (different for each drawing) all represent lengths of 50 μ.

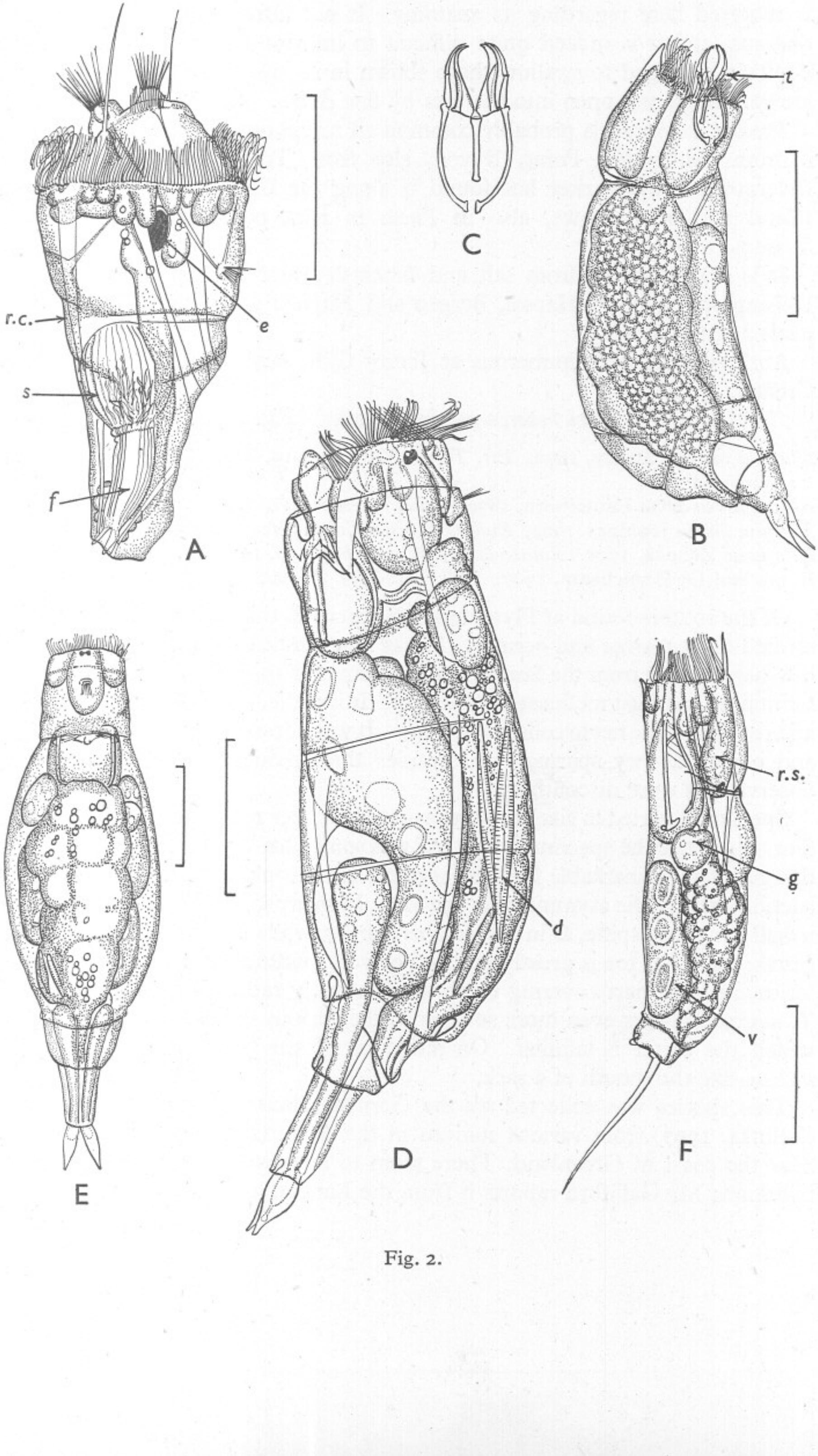


Fig. 2.

is required here regarding its anatomy. It not infrequently swallows large diatoms, and it is indeed quite difficult to imagine how the specimen here depicted managed to swallow those shown in its stomach. The pedal glands are very long, and open into the toes by fine ducts.

Proales reinhardti is probably common all round our coast, Gosse recorded it from Oddicombe Point, Devon, also from Torbay, and tide-pools at Invergowrie. The writer has found it along the Cheshire coast, at Hilbre Island and at Leasowe, also in *Fucus* in rock pools at Bexhill-on-Sea, Sussex.

It is also reported from salt and brackish water at Copenhagen, Reval, Helsingfors, Wiborg, Hapsal, Bergen and Naples, and from brackish tidal pools at Atlantic City.

At Plymouth it is numerous at Jenny Cliff, Rum Bay, Barn Pool and Cremyl.

Trichocerca marina (Daday) (Fig. 2F)

Diurella marina Daday, 1890. *Ert. Termi. Kör.*, Vol. 19, No. 17, p. 16, pl. 1, figs. 2 3, 9 and 10.
Mastigocerca dubia Lauterborn, 1894. *Wiss. Meeresunters.* N.S., Vol. 1, p. 213, fig. 2.
Rattulus dubius Jennings, 1902. *Bull. U.S. Fish. Comm.*, Vol. 22, p. 340, pl. 14, fig. 133.
R. henseni Zelinka, 1907. *Rotatoria Plankton-Expedit.*, p. 19, pl. 2, figs. 1–7.
R. marinus De Beauchamp, 1907. *Bull. Soc. Zool. France*, Vol. 32, p. 148.

Of the rotifers found at Plymouth this species is the only one which can be termed truly marine and oceanic. It was first noticed by the writer in coarse tow-net samples from the Sound in the summer of 1946, when it was observed swimming amongst medusae of *Obelia* sp. It is rather a small rotifer, however, and requires a fine net to collect it as a rule. It was not seen again until May 1947, and occurred very sparingly in samples throughout June, after which all observations were discontinued.

Specimens varied in size; most measured just over 150 μ including the single foot spine, but the specimen depicted was somewhat larger. The members of this genus are remarkable for their asymmetrical trophi, which are adapted for suction, and for the asymmetry of the toes. In many species one toe only is left, usually as a long spine, as in *Trichocerca marina*, while in other members of the genus, the other toe is greatly reduced or very rudimentary. The front of the lorica, i.e. that part covering the head, is usually rather flexible, but that of *T. marina* appears even more so than in the various fresh-water species with which the writer is familiar. On retraction of the head it can be drawn to a close like the mouth of a sack.

This species was collected by the German Plankton Expedition of 1895 (Zelinka, 1907) from various stations in the Atlantic, being most numerous near the coast of Greenland. There seem to be very few records of its distribution; Mr Galliford reports it from the Lancashire coast.

THE PLYMOUTH ROTATORIAN FAUNA COMPARED WITH THAT OF LIVERPOOL

It must be admitted that the writer was somewhat disappointed at the apparent poverty of the Plymouth rotatorian fauna as compared with that of Liverpool and neighbouring stations along the Lancashire and Cheshire Coast, reported by Galliford (1945, 1946), although, as previously remarked, further investigation at Plymouth would probably add several species to the present list. Compared with the six species found at Plymouth, Galliford has recorded no less than thirty-five species as occurring in salt and brackish waters at Liverpool. Although no figures are available for comparison, degree of salinity may be a controlling factor, and it is hoped that further details regarding the comparative salinity of the Plymouth and Liverpool habitats will be assembled in due course, but it is here vitally necessary to stress certain facts regarding the application of the term 'marine' to the rotifers occurring round our coasts, as well as in continental coastal waters in general.

It is probably a little premature at this stage of our knowledge to make broad generalizations on the distribution of coastal Rotifera, for so little collecting has yet been done, but it is noticeable that most of the species referred to by various workers as 'marine rotifers' are in fact confined to estuarine waters of low salinity, being more numerous in the upper reaches of creeks and in 'marine lakes', such as that at Southport, which is occasionally replenished from the sea, but which is constantly having the salinity lowered by rain. Pools above high-water mark which receive spray and rain are also favourite haunts of these brackish rotifers. The extensive analytical details given by Zelinka (1907) are apt to be misleading, for many of his salt-water records are really from brackish habitats, and should be considered with caution. Although *Synchaeta vorax* and *S. littoralis* have been found in the open waters of the Sound, the Sound itself, like Liverpool Bay, and the various other stations at which coastal rotifers have been studied in these islands, has numerous sources of fresh water emptying into it. At Bexhill-on-Sea, Sussex, where there are no rivers close at hand, extensive collecting with hand-net and tow-net, inshore and on the open sea, revealed no rotifers whatsoever, although *Proales reinhardti* occurred in *Fucus* in rock pools. One single specimen of *Synchaeta*, contracted and otherwise unrecognizable, was taken in the incoming tide.

Certain rotifers however, among them *Proales reinhardti* and *Encentrum marinum*, appear to inhabit salt, brackish, and fresh-water habitats, although it is not known whether individuals are capable of withstanding transfer from one habitat to the other. That both species are found in all three situations however, is quite certain. Some of the brackish species seem very susceptible to osmotic changes; thus Rousselet (1902) records that *Synchaeta triophthalma* quickly succumbs on immersion in fresh water. On the other hand, it does not appear to favour waters of high salinity.

As to the seasonal appearances, life histories, and general ecology of these coastal rotifers, little or nothing is known, and the field presents many interesting problems worthy of further investigation.

SUMMARY

Six species of rotifer, including one oceanic species and representing four genera, are recorded for the first time from Plymouth. Remarks are made on various interesting features of their anatomy, details are given of their times of occurrence at Plymouth, with notes on their location and known distribution in other parts of the British Isles, and in foreign waters.

Attention is called to the apparent poverty of the Plymouth marine and brackish-water Rotifera as compared with that of Liverpool, investigated at length by Galliford. It is stressed that no exact conclusions as to the reason for this can be made until after a more exhaustive survey, as some likely habitats adjacent to the Sound were not investigated. Attention is also called to the caution which must be exercised in terming rotifers marine, as most of those collected in coastal waters appear at present to be confined to areas where a considerable amount of fresh water is discharged into the sea. At least two species, one of which occurs in the Sound in May, are known to be truly oceanic, having been found in mid-Atlantic.

It is suggested that 'brackish' and 'estuarine' are the terms most applicable to the majority of coastal rotifers in the present state of our knowledge.

REFERENCES

Claus, C., 1876. Ueber die Organisation und die systematische Stellung der Gattung *Seison* Grube. *Festschr. Zool.-Bot. Ges. Wien*, pp. 74–88, 2 pls.

Ehrenberg, C. G., 1834. Dritter Beitrag zur Erkenntnis grosser Organisation in der Richtung des kleinsten Raumes. *Abh. Akad. Wiss., Berlin* for 1833, p. 220.

—— 1838. *Die Infusionsthierchen als vollkommene Organismen*. Leipzig.

Galliford, A. L., 1945. A contribution to the rotifer fauna of the Liverpool area with a description of a new species. *Proc. Liverpool Naturalists' F.C.*, pp. 11–16, 1 pl.

—— 1946. Additions to the rotifer fauna of the Liverpool area. *Proc. Liverpool Naturalists' F.C.*, pp. 6–9.

Gosse, P. H., 1856. *Tenby: a Sea-Side Holiday*. London.

Grube, A. E., 1859. Neue mikroskopische Thierform. *Jb. Schlesischen Ges. Vaterl. Cultur*, Bd. 37, p. 25.

Hollowday, E. D., 1946. Introduction to the study of the Rotifera. Part IV. Drawing Rotifera. *The Microscope and Entomological Monthly*, Vol. 6, pp. 3–9.

—— 1947. On the capture of marine Rotifera as food by Hydromedusae. *Journ. Quekett Micr. Club*, Ser. 4, Vol. 2, pp. 190–2.

Hudson, C. T., & Gosse, P. H., 1886. *The Rotifera; or wheel-animalcules*. Vols. I and II. 128 and 144 pp. (also plates). London.

—— 1889. *The Rotifera; or wheel-animalcules:* Supplement, 64 pp. London.

Lankester, E. Ray, 1868. Note on the Synaptae of Guernsey and Herm, and a new parasitic rotifer. *Quart. J. Micr. Sci.*, Vol. 8, pp. 53–5.

Marine Biological Association, 1931. *Plymouth Marine Fauna*, 2nd ed.

Remane, A., 1929. Rotatoria. *Die Tierwelt der Nord- und Ostsee.* L. xvi, T. viie. 156 pp. Leipzig.

Rousselet, C. F., 1902. The genus *Synchaeta:* a monographic study, with descriptions of five new species. *Journ. R. Micr. Soc.*, pp. 269–90, 393–411, pls. III–VIII.

Scottish Marine Biological Association, 1928. Annual Report, 1927–28. [Faunistic Notes, pp. 11–13.]

Wulfert, K., 1942. Ueber die Meeres- und Brackwasser-Rotatorien in der Umgebung von Rovigno D'Istria. *Thalassia*, Bd. iv, H. 7, 26 pp., 6 pl.

Zelinka, C., 1907. Die Rotatorien der Plankton-Expedition, *Ergeb. der Plankton-Expedition der Humboldt-Stiftung*, Bd. ii, H.a., 82 pp., 3 pl.

STUDIES ON MARINE FLAGELLATES

By Mary Parke, B.Sc., Ph.D.
Botanist at the Plymouth Laboratory

(Plates I and II, and Text-figs. 1–73)

CONTENTS

INTRODUCTION

During the years 1935 to 1940 experimental work was carried out at the Port Erin Marine Biological Station on the rearing of the larvae of the European flat oyster, *Ostrea edulis* L. At first, algal zooids and the naturally occurring microplankton in the sea water were used as sources of food for the larvae, but later the larvae were fed on pure cultures of flagellates with much more successful results (Bruce, Knight & Parke, 1940).

Six of the flagellates used in the experiments are here described. Three were isolated by Dr F. Gross at the Plymouth Laboratory (temporary labels 'B', 'C' and 'H', Gross) and three were isolated at Port Erin (temporary labels 'D', 'E' and 'I', Parke). Cultures of four of these flagellates are still maintained at the Plymouth Laboratory but the cultures of 'C' and 'H' were lost in 1941 when the laboratory was damaged.

ACKNOWLEDGEMENTS

My most sincere thanks are due to Prof. F. E. Fritsch and Prof. E. G. Pringsheim for their helpful criticism of part of the work. I am most grateful also to Mr W. M. S. Russell, who translated my descriptions of the organisms into Latin and who suggested the name *Dicrateria* for one of the new genera.

CHLOROPHYCEAE

POLYBLEPHARIDACEAE

Pyramimonas Schmarda

P. grossii n.sp. (Flagellate 'H', Gross.)
(Pl. II, figs. 17, 18; Text-figs. 1–12.)

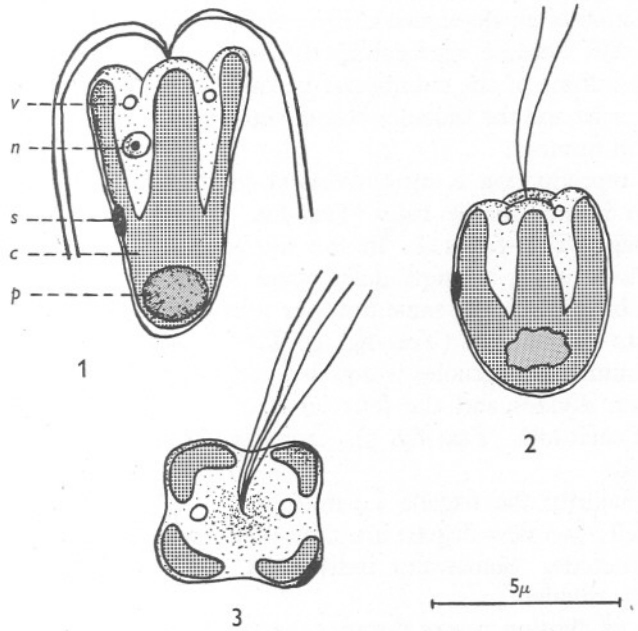
Cellula parva, pyramidiformi plerumque ac 4 lobis distinctis anterioribus praedita; quae transverse secta nisi ad apicem extremum formam praebet circularem; forma mutabili; 4 flagellis longitudine cellulae fere paribus in depressione mediocriter tenui ad apicem insertis; chromatophoro luteo viridi caliciformi cum 4 lobis anterioribus in margine dispositis et magno pyrenoide basali; amyli capsula pyrenoidi circumdata conspicua; stigmate singulo, mediano plerumque, rarius anteriore; nucleo anteriore plerumque ac laterali; 2 vacuolis ad apicem sitis, haud contractiliis; cellula 5·5–8 μ longa, lata 4·5–5·5 μ. Ab nomine Doctoris F. Gross appellata, per quem segregata est.

This species was isolated by Dr F. Gross from a plankton sample taken from the sea water off Plymouth. In his records the first culture of 'H' was dated April 1936.

This species is normally inversely pyramidal, sharply truncate and four-lobed at the anterior end and somewhat tapering towards the posterior region (Text-fig. 1). As the periplast admits of extensive change of shape, transitions to shorter more or less cordate forms are frequent and longer, more subcylindrical forms also occur (Pl. II, figs. 17, 18). The lobes are confined to the anterior end of the cell and are continued backwards as ridges for only a short distance, so that an individual is circular in transverse section except at the extreme apex. Here the swelling of the lobes gives a transverse section the appearance of a square which has had the corners rounded and the sides indented (Text-fig. 3).

The anterior lobes surround a fairly shallow depression, from the centre of which arise four flagella, all originating from one point. The flagella are equal to, or slightly longer than, the length of the cell. No difference in the appearance of the four flagella could be detected when the staining methods of Loeffler (1889) and Fischer (1894) were used. The four are equal in length and thickness, and show no tapering towards the free end, but end quite bluntly. Movement of the organism is spasmodic and extremely rapid, but the organism can remain constant in direction for relatively long periods.

The chloroplast, bright yellowish green in colour, is cup-shaped with the sides deeply cleft into four lobes (Pl. II, figs. 17, 18). The thickened basal part of the chloroplast, behind the lobes, fills the posterior third of the body, occupying the whole periphery of the cell. It has a smooth outline since no posterior lobes or indentations are developed. Each lobe of the chloroplast passes forwards into one of the body lobes and is smooth at the apex, not indented. A large pyrenoid is situated in the thickened posterior portion of the chloroplast below the fusion of the lobes, usually at the extreme posterior end of the cell (Text-fig. 1). The pyrenoid is surrounded by a well-developed starch sheath.



Text-figs. 1–3. (× 5000.) *Pyramimonas grossii* n.sp. 1. Normal shape of young motile stage, side view. *c*, chloroplast; *n*, nucleus; *p*, pyrenoid; *s*, stigma; *v*, vacuole. 2. Biflagellate stage, side view. 3. Young motile stage viewed from anterior end.

A bright red stigma, projecting slightly above the general surface of the organism, is usually median in position (Text-fig. 1), but has frequently been observed at the extreme anterior end on a line with two non-contractile vacuoles which occur in the general cytoplasm within the chloroplast. The nucleus is visible in the living individual and is situated anteriorly in the body in a lateral position (Text-fig. 1).

Approximately 10% of the motile stages in a culture possess only two flagella. These individuals are smaller (4–5 μ) than the individuals with four flagella and practically spheroidal in shape with the anterior lobes less well developed (Text-fig. 2). The nature and function of the biflagellate individuals have not been determined but, as Pascher (1927) has suggested for other genera, they may possibly be the 'basic' form, and the more frequent individuals with four flagella can then be regarded as double cells resulting from the early multiplication of the flagella prior to division. Fusion of the biflagellate individuals was never observed.

The motile individuals are very strongly phototactic and therefore tend to collect on one side of the culture flask. Here they readily assume the 'palmella-state'; the flagella are lost and the cells become spheroidal, developing a thin hyaline gelatinous envelope measuring 6–8 μ in diameter (Text-fig. 11). When numerous cells become aggregated together they become very irregular in shape. The outline of the chloroplast becomes indistinct but the stigma and pyrenoid persist and the vacuoles become more apparent, the latter frequently increasing in number.

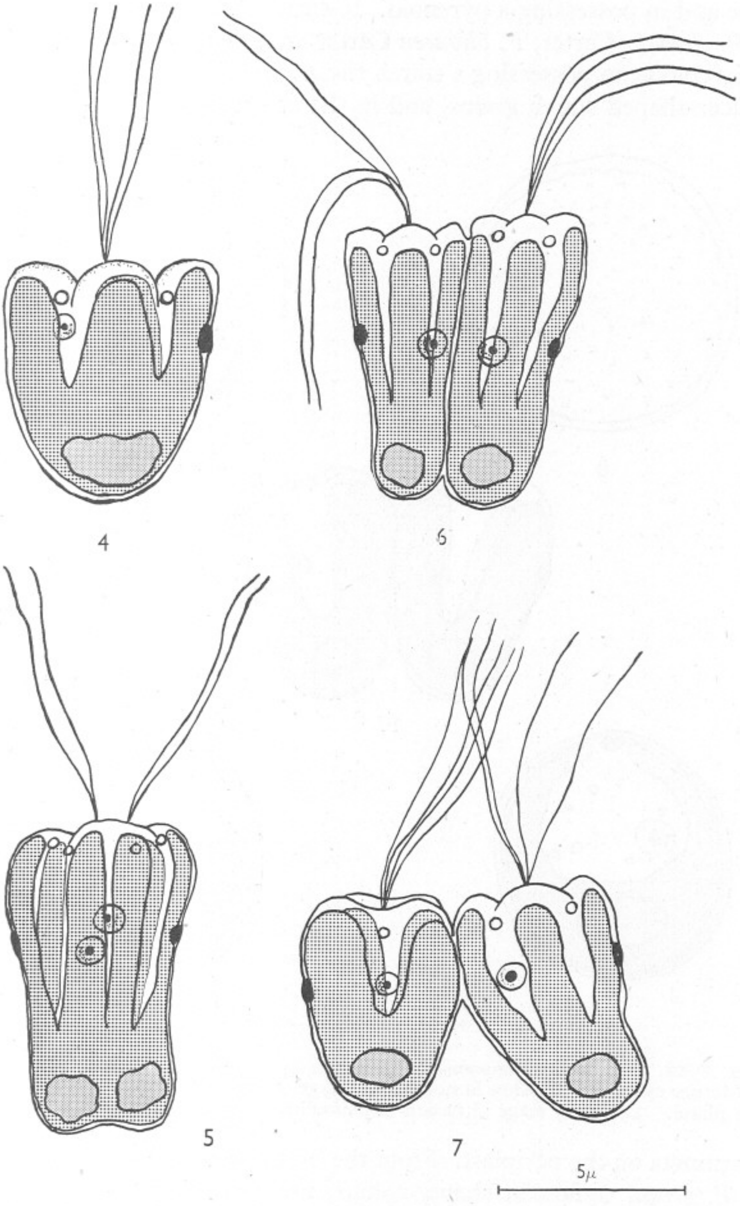
Asexual reproduction is most frequent in the motile individuals, but it occurs also in non-motile cells (Text-fig. 10), and in individuals in the palmella-stage (Text-fig. 12). In the motile individuals it takes place by simple division along a longitudinal plane. When about to divide the cells increase in breadth; at the same time the pyrenoid shows signs of elongation transverse to the cell axis (Text-fig. 4). The pyrenoid then divides into two parts, the number of vacuoles is doubled and a second stigma develops. The nucleus then divides and the four lobes of the chloroplast divide by the splitting of each lobe (Text-fig. 5). Occasionally the nucleus divides before the pyrenoid.

In the majority the flagella separate as the cell broadens, two to each daughter-cell; two new flagella are then developed by each daughter-cell as division proceeds. Sometimes individuals bear eight flagella before the pyrenoid has divided.

The line of division passes through the thickened posterior portion of the chloroplast so that each part has one complete, now divided into two, and two half lobes of the original chloroplast (Text-fig. 6). In *P. delicatulus* Griffiths two complete lobes pass to each daughter-cell. Separation of the two daughter-cells takes place by gradual constriction, starting simultaneously at both the anterior and posterior ends of the individual but advancing more rapidly from the posterior pole (Text-fig. 7). The periplast divides simultaneously with the rest of the protoplast and is gradually completed on adjacent surfaces of the new individuals. The daughter-cells are commonly of unequal size.

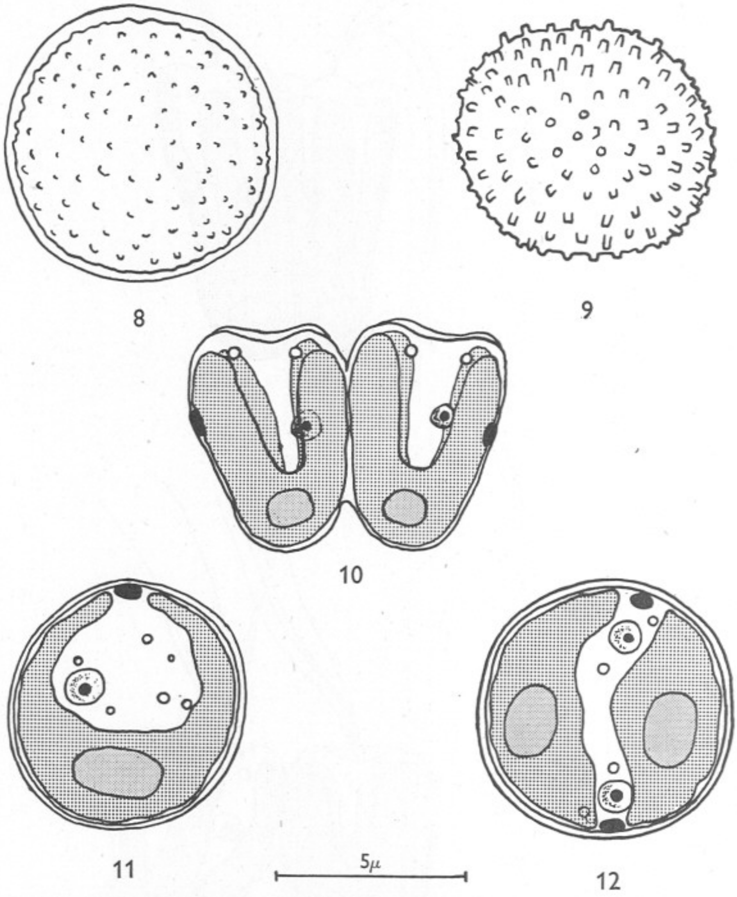
Hypnospores or cysts have been observed in the cultures (Text-figs. 8, 9). They are formed either from ordinary motile cells after the flagella have been withdrawn or from individuals already in the palmelloid phase. The cysts are usually spheroidal in shape, sculptured externally and measure 6–7 μ in diameter. The release of the contents of the cysts has not been observed.

From the marine species so far described, *P. adriaticus* Schiller (1913), *P. oltmannsi* Schiller and *P. impressus* Schiller (1925), *P. grossii* differs both



Text-figs. 4–7. (× 5000.) *Pyramimonas grossii* n.sp. 4. Large motile stage just prior to division, side view. 5. Early division stage of motile individual, side view. 6. Later division stage of motile individual, side view. 7. Two daughter-cells just prior to separation, side view.

in shape and in possessing a pyrenoid. It differs also from the brackish-water forms *P. obovata* Carter, *P. olivacea* Carter and *P. angulata* Carter (1937) in shape, in colour, in possessing a starch sheath around the pyrenoid instead of two saucer-shaped starch grains, and in the absence of longitudinal series of minute puncta on the periplast. From the brackish-water *P. octociliata* Carter (1937) *P. grossii* differs in shape, colour, number of flagella, in possessing a stigma and in lacking puncta on the periplast. *P. grossii* also differs in shape and size from the six species described by Pascher (1932).



Text-figs. 8–12. (× 5000.) *Pyramimonas grossii* n.sp. 8. Early stage in cyst formation. 9. Mature cyst. 10. Fission in non-motile stage, side view. 11. Individual in palmelloid phase. 12. Early stage in fission in palmelloid phase.

It differs also from *P. utrajectina* Bretschneider (1925) and *P. ovalis* Conrad (1930*a*) in size, shape, development of the anterior lobes, and in the size, shape and position of the stigma. *P. botryodes* Jane (1944) is clearly distinguished from *P. grossii* by the rounded prominences on the surface of the cell and by the shape of the chloroplast.

P. grossii is somewhat similar in shape to *P. tetrarhynchus* Schmarda (1850), *P. delicatulus* Griffiths (1909), *P. inconstans* Hodgetts (1920), and *P. montana* Geitler (1925). From all these species, however, it differs in its smaller size. In addition, it differs from *P. tetrarhynchus* in the number of the anterior incisions in the chloroplast, in the position of the stigma and in the absence of stroma starch grains. It lacks also the hollowing at the posterior end that occurs in *P. delicatulus* and possesses a stigma and vacuoles which are lacking in that species. *P. grossii* differs from *P. inconstans* in having a lobed chloroplast and in the degree of development of the body lobes. From *P. montana* it differs in colour, in the absence of stroma starch and also in the development of the apical lobes.

CHRYSOPHYCEAE

CHROMULINACEAE

Chromulina Cienk.

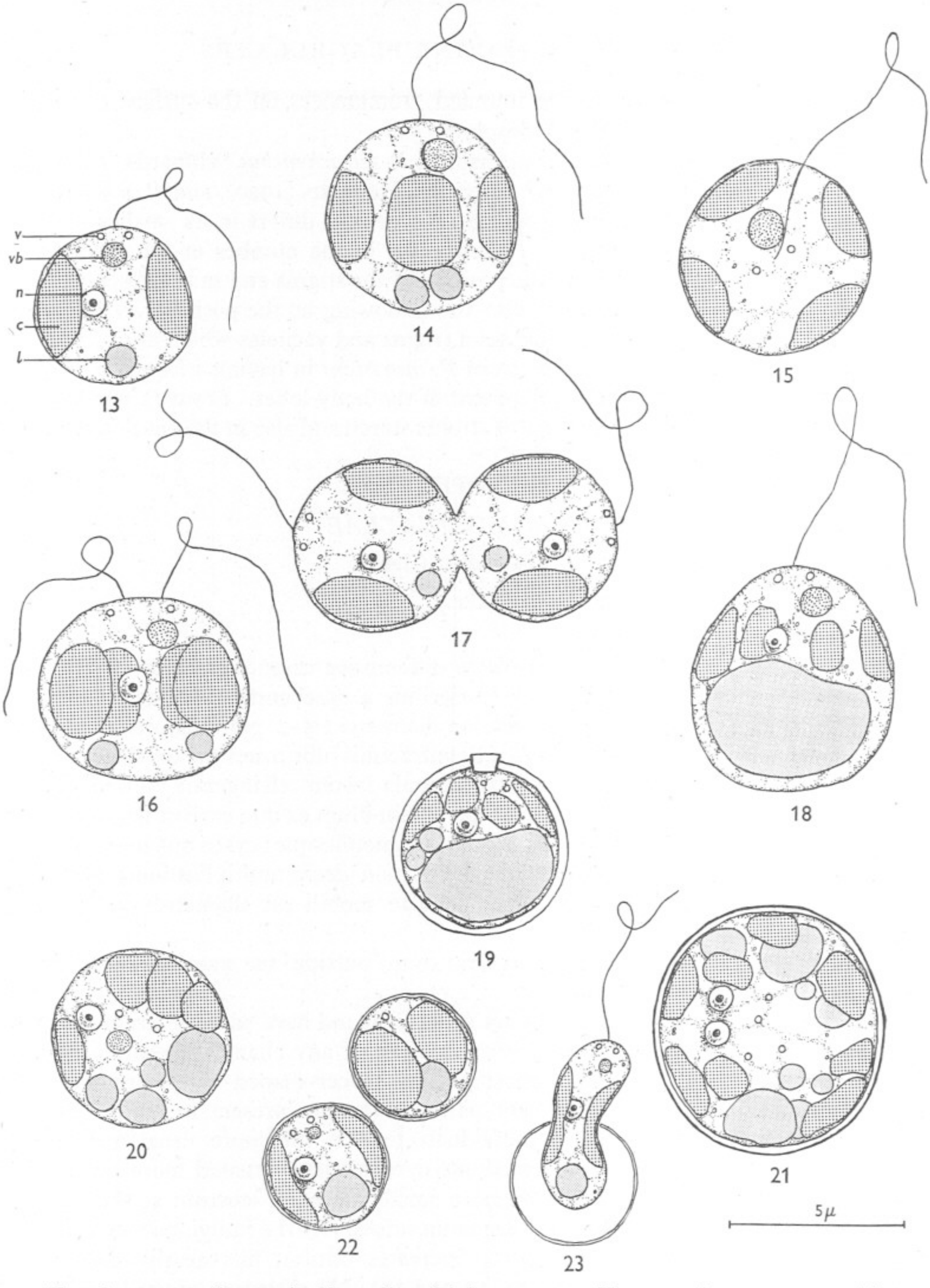
C. pleiades n.sp. (Flagellate 'E', Parke.)
(Pl. I, fig. 2; Text-figs. 13–23.)

Cellula parva, sphaeroidi, periplasto differentiae carente praedita; 2 chromatophoros cellulis recentibus, vetustioribus 4 praebentibus fulvos pallidos crateriformes; flagello singulo cellulae diametro 1·5–2 plo longiore; nucleo fere centrali; 2 vacuolis parvis haud contractiliis ubi insertum est flagellum fere sitis; 'vacuolo' bene definito cui granula insunt refringentia vibrantia in cellula mobili plerumque visendo prope polum illum ex quo exsistit flagellum; sine sexu propagatur per gradus mobiles immobilesque; cystis sphaeroidibus subovatisve cum membrana externa laevi; non deest multiplicationis genus palmelloidem per gradum effectae; cellulae mobili est diametros 3·5–6 μ; cysto diametros 5–6 μ.

This species was isolated at Port Erin from 'outside' sea water in February 1939.

The individuals of this species are spheroidal and have an undifferentiated, smooth, firm periplast, which does not admit of any change of shape; they measure from 3·5 to 6 μ in diameter. The saucer-shaped chromatophores, pale golden-brown in colour, are parietal; two are present in the smaller individuals, but in the larger individuals four is the more usual number (Text-figs. 13, 14). There is a medium-sized nucleus situated more or less centrally in the body and one or more small masses of leucosin at the pole opposite to that from which the flagellum arises. As the individuals increase in size the amount of leucosin also increases until it fills nearly half the volume of the cell (Text-figs. 13, 14 and 18). No extrusion of the leucosin masses has been observed.

The flagellum, one and a half to twice the cell diameter in length, is delicate



Text-figs. 13–23. (×5000.) *Chromulina pleiades* n.sp. 13. Young motile stage, equatorial view. *c*, chromatophore; *l*, leucosin; *n*, nucleus; *v*, vacuole; *vb*, vibrating body. 14. Older motile stage, equatorial view. 15. Older motile stage, viewed from pole at which flagellum is inserted. 16. Early division stage of motile individual. 17. Later division stage of motile individual. 18. Older motile stage containing large leucosin mass. 19. Mature cyst, equatorial view. 20. Reproduction in the palmelloid phase, stage 1. 21. Reproduction in the palmelloid phase, stage 2. 22. Reproduction in the palmelloid phase, stage 5. 23. Reproduction in the palmelloid phase, stage 6.

and difficult to see in the living individuals; stained preparations show that it does not arise from a basal granule and that it tapers very slightly towards the free end. No evidence was obtained of the presence of fine cilia on the flagellum although Vlk (1938) records them in an unnamed species of *Chromulina*. This species moves smoothly and fairly slowly; it swims for comparatively short distances, or round in circles, and then has long periods of quiescence. Strong illumination tends to stop movement in a fairly short time.

Two small non-contractile vacuoles are present near the point of insertion of the flagellum. Another larger 'vacuole', or clearly delimited spheroidal body, is usually developed in the motile individuals near to the two small vacuoles (Text-figs. 13–15, 18). This well-defined structure is sometimes quite large and contains shining vibrating bodies. The movement of these bodies is very similar to that found in Desmids in the terminal vacuoles containing minute crystals of calcium sulphate. In addition to the Brownian movement of crystals, Chifflot & Gautier (1905) have shown that Brownian movement of cytoplasmic granules frequently occurs. They observed its occurrence in many species of *Spirogyra*, in *Haematococcus pluvialis* and in the dense protoplasm at the tips of the root hairs of *Azolla caroliniana*. In the last genus they found Brownian movement also in the vacuoles in the root hairs, but in the vacuoles the motile bodies, more numerous than in the protoplasm, were found to be crystals of calcium oxalate.

Carter (1937) records the presence of large numbers of minute granules in active Brownian movement in individuals of *Prymnesium parvum* and *P. minutum* Carter. In these species, however, the granules are in 'an ill-defined region', not a clearly defined one as in *Chromulina pleiades*, and are therefore most probably cytoplasmic granules. The sharp outline of this body in *C. pleiades* suggests that it is a vacuole and that the 'bodies', showing Brownian movement, are probably of a crystalline nature.

There are records in the literature of the occurrence, in members of the Chrysophyceae, of collections of strongly refractive particles having a crystalline appearance (Scherffel, 1911; Doflein, 1922, 1923). Scherffel (1911) observed them in *C. nebulosa* Cienk., in addition to other genera, and Doflein (1923) records them as being a distinctive feature of *C. minima* Doflein. Neither author refers to movement of the particles nor to their enclosure in a clearly defined 'body'. Korshikov (1929) refers to leucosin masses becoming, under pressure, vacuoles containing suspended particles in Brownian movement; he records, however, that these vacuoles have lost the former refraction power of the leucosin. They are therefore different in nature from the 'vacuoles' in *C. pleiades*.

Asexual reproduction takes place by simple fission, usually of the motile individuals, but sometimes of individuals which have either cast or withdrawn their flagellum. Division of the cells takes place in both the light and the dark, and occurs in the normal way. The individual first broadens and a second flagellum develops close to the original one, usually before the division of the nucleus. Four chromatophores are usually present in the cell before division starts so that two pass to each daughter-cell. One of the small vacuoles passes to each cell and the second arises anew as the two cells start to separate. The vibrating 'vacuole' can be seen in the early division stages but not in the late stages as the two daughter-cells draw apart (Text-figs. 16, 17).

Cysts are produced in cultures which have been left for at least 3 months without subculturing. They develop inside large individuals which are nearly half-filled by leucosin. No gelatinous investment forms round the individuals. The cysts are spheroidal to very slightly ovoid in shape and measure 5–6 μ in diameter (Text-fig. 19). The outer surface of the cyst wall is smooth and the plug, which protrudes only slightly above the surface, has the shape of an inverted truncated cone.

In this species (Text-figs. 20–23), and in the three following species belonging to the Chrysophyceae, a form of reproduction takes place in a palmelloid phase which has so far not been recorded in the literature, unless Lund's description of the production of sporangia in *C. sporangifera* is a somewhat similar process (Lund, 1942). The stages that have been obtained so far in this palmelloid form of reproduction are described and discussed under the next genus, *Isochrysis*.

Chromulina pleiades differs from *C. microplankton* Pascher (1913), *C. parvula* Conrad (1930*b*) and *C. sphaerica* Doflein (1923) in possessing two chromatophores; it differs further from the first two in size and from the last, which is about the same size, in lacking pyrenoids and also in the length of the flagellum. *C. pleiades* resembles most closely *C. sphaeridia* Schiller (1929), but it is smaller in size, has a shorter flagellum and its vacuoles are not contractile. It differs also from all other species of *Chromulina* in possessing a 'vacuole' containing vibrating bodies.

ISOCHRYSIDACEAE

Isochrysis n.gen.

Cellula solitaria, natante, nuda, periplasto differentiae carente praedita; ellipsoidi, ad anteriorem partem truncata, ad posteriorem rotundata; dorsiventraliter paulum depressa; quae transverse secta formam praebet ovatam; forma mutabili; 2 flagellis, longitudine paribus, ad anteriorem partem exsistentibus; 2 chromatophoris magnis lateralibus fulvis; ocello parvo; nucleo parvo mediano; desunt vacuola; cellula pabulum holophytica; nec oleo nec leucosino indigente; sine sexu propagatur fissione in longitudinem effecta per gradus mobiles immobilesque; cysto intra cellulam confecto; cystis sphaeroidibus cum membrana externa paulum sculpta; non deest multiplicationis genus palmelloidem per gradum effectae.

I. galbana n.sp. (Flagellate 'I', Parke.)
(Pl. I, figs. 4–10; Text-figs. 24–45.)

With the characters of the genus.

Motile cell: length, 5–6 μ; breadth, 2–4 μ; thickness, 2·5–3 μ.

Cyst diameter, 5–6 μ.

Isolated from sea water from one of the fish ponds at the Marine Biological Station, Port Erin, in January 1938.

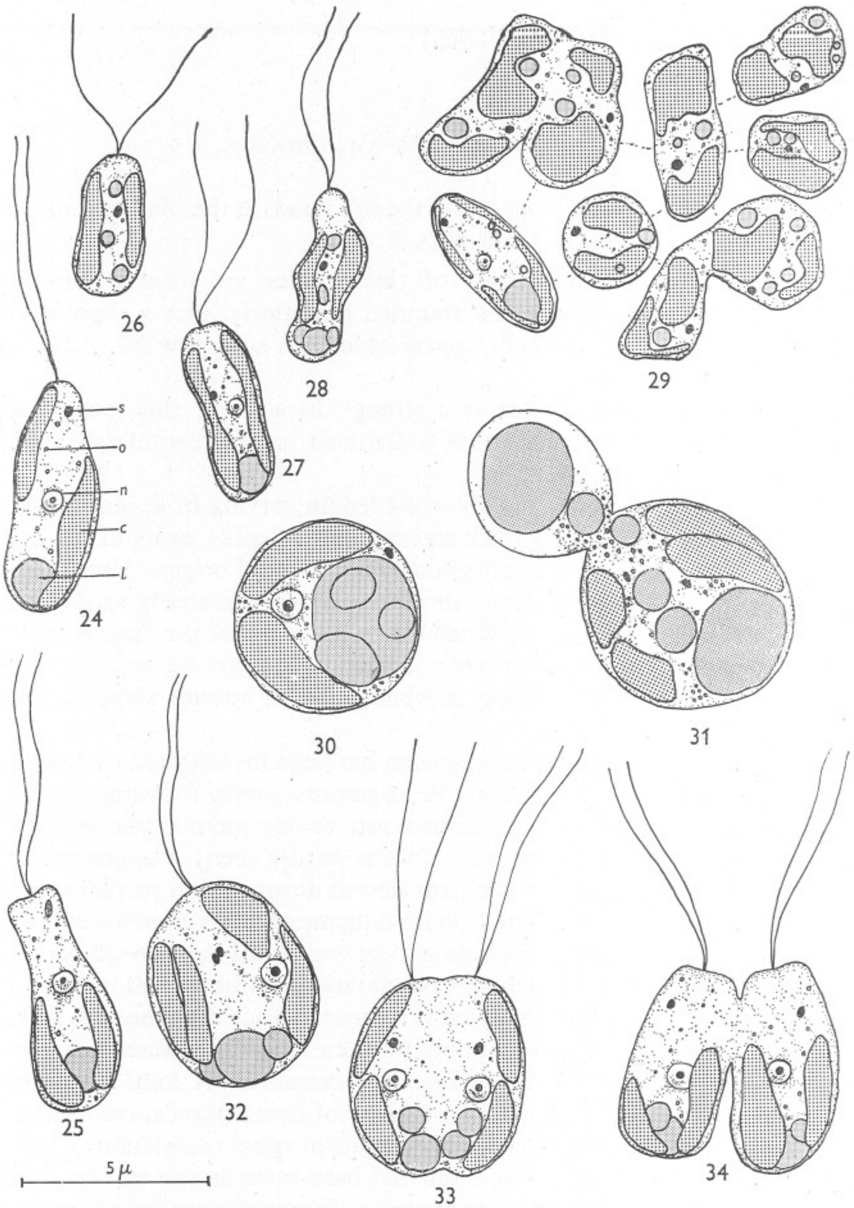
The actively motile individuals of this species are usually somewhat ellipsoidal, flattened anteriorly and rounded posteriorly, with a slight dorso-ventral flattening so that the cells appear oblong in side view (Pl. I, fig. 10), and ovoid in cross-section.

The capacity to change shape is a strong character of this species, and consequently variation in the shape of individuals is quite considerable (Pl. I, figs. 7, 10; Text-figs. 24–28).

Two equal flagella arise anteriorly, their length varying from once to twice that of the cell; they are fairly thick and can be seen quite easily in the living material; no basal granule is developed at their point of origin. Movement of the individuals, usually in a forward direction, is slow and steady with rotation of the body round the long axis. When the cells are at rest the flagella are stiff and lie away from the body, but when in motion they are out in front of the cell and carry out an undulating movement. This species shows a slight phototactic reaction.

The method of swimming of this species has been investigated by Lowndes (1943, pp. 101–2). He found that the organisms swam forward smoothly, rotating and gyrating at the approximate rate of one rotation per sec. When swimming, vibration of the anterior tip was hardly seen; it appeared quite definitely, however, when the organisms slowed down, and in particular when it suddenly changed its direction. 'On investigating these vibrations by means of the stroboscope, the maximum rate of beat was found to be 46–48 per sec., and since this somewhat regular beat or vibration can be looked upon as the rebound from each flagellum, it probably means that each flagellum was making about 24 beats per sec.' The swimming movement of this species was almost identical with that of a *Chlamydomonas* sp. examined by him. Lowndes's work (1936, 1941, 1943, 1947), on the activity of living flagella, confirmed by Brown (1945), has shown that a flagellum beats in spiral undulations with the waves of contraction progressing from the base towards the tip, the waves often increasing in amplitude as they progress. Brown also confirms Lowndes's theory that the rotation and gyration of the body alone may adequately account for the locomotion of many flagellates, without any forward component produced directly by the flagellum.

Fischer (1894), Loeffler (1889), Peterson (1918, 1929), Vlk (1938), and others, using drying and staining techniques, have described two types of



Text-figs. 24–34. (×5000.) *Isochrysis galbana* n.g., n.sp. 24–28. Young motile stage, illustrating the form variation and the variation in the shape and position of the chromatophores. 24. *c*, chromatophore; *l*, leucosin; *n*, nucleus; *o*, oil globule; *s*, stigma. 29. Fission in non-motile stage. 30. Reproduction in palmelloid phase; stage 1, spheroidal cell. 31. Reproduction in palmelloid phase; stage 1, apparent fusion of two of the spheroidal cells; nuclei could not be seen. 32. Early stage in fission of motile individual, front view. 33. Later stage in fission of motile individual, front view. 34. Separation of daughter-cells practically completed, front view.

flagellum: one which is whip-like, and one which bears fine cilia along its whole length. Brown (1945), by means of the electron microscope, investigated the structure of the flagellum of several species. He found that the flagella were of approximately uniform diameter throughout their entire length, and that each flagellum consisted of a denser axial core and a less dense sheath surrounding the core; some of the flagella also bore delicate filaments extending from the sheath. The two flagella of *Isochrysis*, studied from dried and stained preparations, are equal in length and uniform in diameter throughout their entire length; no evidence was obtained of the presence of fine cilia on either flagellum.

Two large, elongate, parietal chromatophores are present; they are usually placed laterally in the body, but their shape and position change with the change in shape of the body (Text-figs. 24–28). The chromatophores are golden-brown in colour; in actively motile individuals they appear to have a faint greenish tinge to the gold, but in older slow-moving individuals, palmelloid-phases and cysts the colour of the chromatophore lacks the slight tinge of green. A small dark red stigma, ovoid in shape, is most frequently in a median position, more rarely at the extreme anterior end. It does not project above the general surface of the cell. The nucleus, just visible in living individuals, is nearly always median; no mouth-band could be distinguished and no vacuoles are developed.

Oil and leucosin are developed as in other members of this class. Small oil drops are distributed through the general cytoplasm of the cell but the leucosin, in actively motile cells, occurs most frequently as a greyish, highly refractile, rounded mass at the extreme posterior end (Pl. I, fig. 7; Text-figs. 24, 25). In some of the smaller motile individuals from two to five small masses of leucosin may be present, and these are not always in a posterior position (Text-figs. 26, 28). The expulsion of leucosin from the body in the form of a droplet has never been observed in this species, although Carter (1937) records its occurrence in *Chromulina lunaris* Carter and *Prymnesium parvum* Carter; she concluded that the expulsion of leucosin was probably a process of excretion.

In this species the amount of leucosin present in the cells varies in different aged cultures; instead of expelling leucosin it seems to build up a large reserve. In actively dividing cultures, 2–4 weeks old, the quantity of leucosin in the cells is fairly small (Pl. I, figs. 7, 10; Text-figs. 24–28); as the cultures increase in age (over 6 weeks old), cell division is greatly reduced and the amount of leucosin in the cells increases. In still older cultures (3–4 months), the leucosin practically fills the posterior part of the cell so that the chromatophores, much reduced in size, and the nucleus, now occupy an anterior position (Pl. I, fig. 4; Text-fig. 35). The shape and size of an individual alters as the amount of leucosin increases; it becomes more pyriform, increasing very considerably in breadth and thickness, so that a cell can be 5–6 μ long, and 4–5 μ broad. These heavily laden individuals are extremely sluggish and exhibit a much slower movement than the younger individuals. The cells packed with leucosin eventually become non-motile and either form cysts or pass into a palmelloid phase in which another form of reproduction occurs.

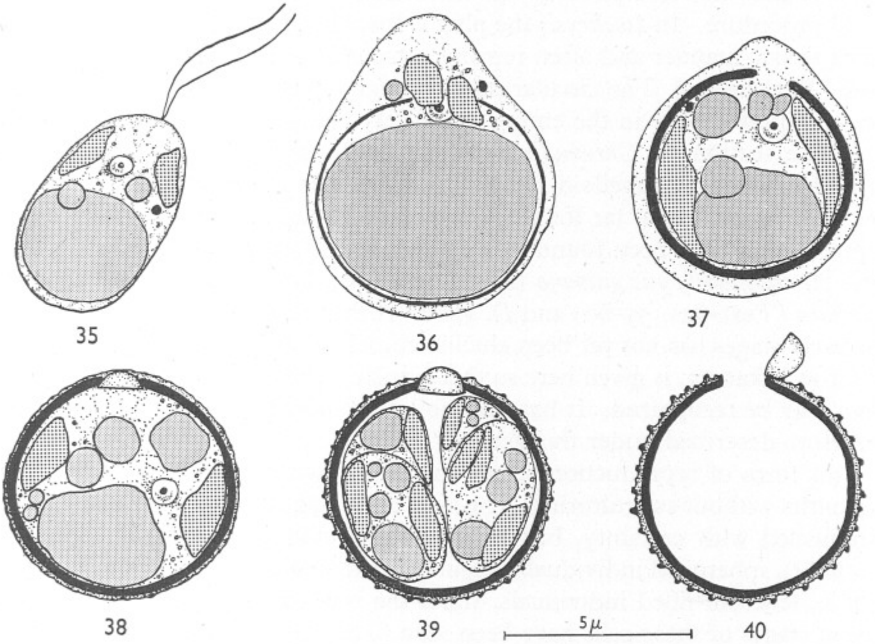
Asexual reproduction in this species occurs by the longitudinal division of both motile and non-motile individuals, and also by cyst formation. In the young motile stages division is most frequent in the early morning. Counts made of the numbers of individuals in both sterilized sea water and culture solution showed that individuals could divide more than once in 5 hr. When an individual is about to divide the body broadens, and division of the chromatophores occurs; one chromatophore, now divided into two, passes to each daughter-cell. A second stigma appears, frequently close to the one already present (Text-fig. 32). The two flagella of the parent pass to one daughter-cell, the other daughter-cell developing two anew; the new flagella arise frequently before the nucleus has divided but sometimes not until after separation of the two cells has already started.

Before the separation of the two daughter-cells begins the leucosin appears to break up into a number of smaller masses, some passing to each daughter-cell (Text-fig. 33). Separation of the two cells is by constriction, mainly from the posterior end (Text-fig. 34). The products of division are, nearly always, of unequal size.

In cultures more than 4 weeks old some individuals lose their flagella before division takes place (Text-fig. 29). These non-motile individuals form quite a thick layer on the bottom of a flask; their shape becomes irregular but they are not surrounded by a mucilaginous investment. Fission takes place as in the motile stage, the products of division developing flagella when the separation of the individual is almost complete or after it has been completed.

Cyst formation in *Isochrysis* takes place in 3- to 6-months-old cultures. The cysts develop inside the large pyriform individuals mentioned earlier and their development follows very closely that already described for many Chrysomonadineae. When the large pyriform cells are about to develop into cysts they cast their flagella, but they do not form any gelatinous envelope around the protoplast; they can measure up to 8 μ in length and 7 μ in breadth. Each individual then secretes near the periphery a spheroidal cellulose membrane, measuring about 6 μ in diameter. The membrane develops around the large posterior mass of leucosin leaving the anterior nucleus, stigma and small chromatophores external to it. It does not enclose the leucosin entirely however, since an opening remains in it; this faces the anterior end of the cell (Text-fig. 36). A great many very early cyst stages have been examined, but no evidence has been obtained to show that the opening in the membrane arises secondarily.

As the cellulose membrane of the cyst thickens and becomes impregnated with silica, the nucleus, stigma, small chromatophores and some of the cytoplasm pass into the cyst through the pore at the anterior end; a certain amount of cytoplasm remains outside the cyst (Text-fig. 37). Once the chromatophores have passed into the cyst they become much larger in size (Text-fig. 37). The cytoplasm, external to the cyst, gradually shrinks, but it persists as a thin layer until after the anterior aperture of the cyst has been closed by a hemispherical plug measuring 1·5 μ across the base (Text-fig. 38). The plug can be seen quite clearly when pressure is exerted on an early cyst stage. The outer surface of the cyst is covered by small protuberances which can be seen quite clearly after the remaining external cytoplasm has disintegrated (Pl. I, fig. 6; Text-figs. 39, 40). In this species, the spheroidal cysts, 5–6 μ in diameter, are not as large as the individuals from which they were produced; the motile individuals themselves increased in size, mainly due to the increase in the amount of leucosin present, before the production of the cysts (Text-figs. 36, 39).

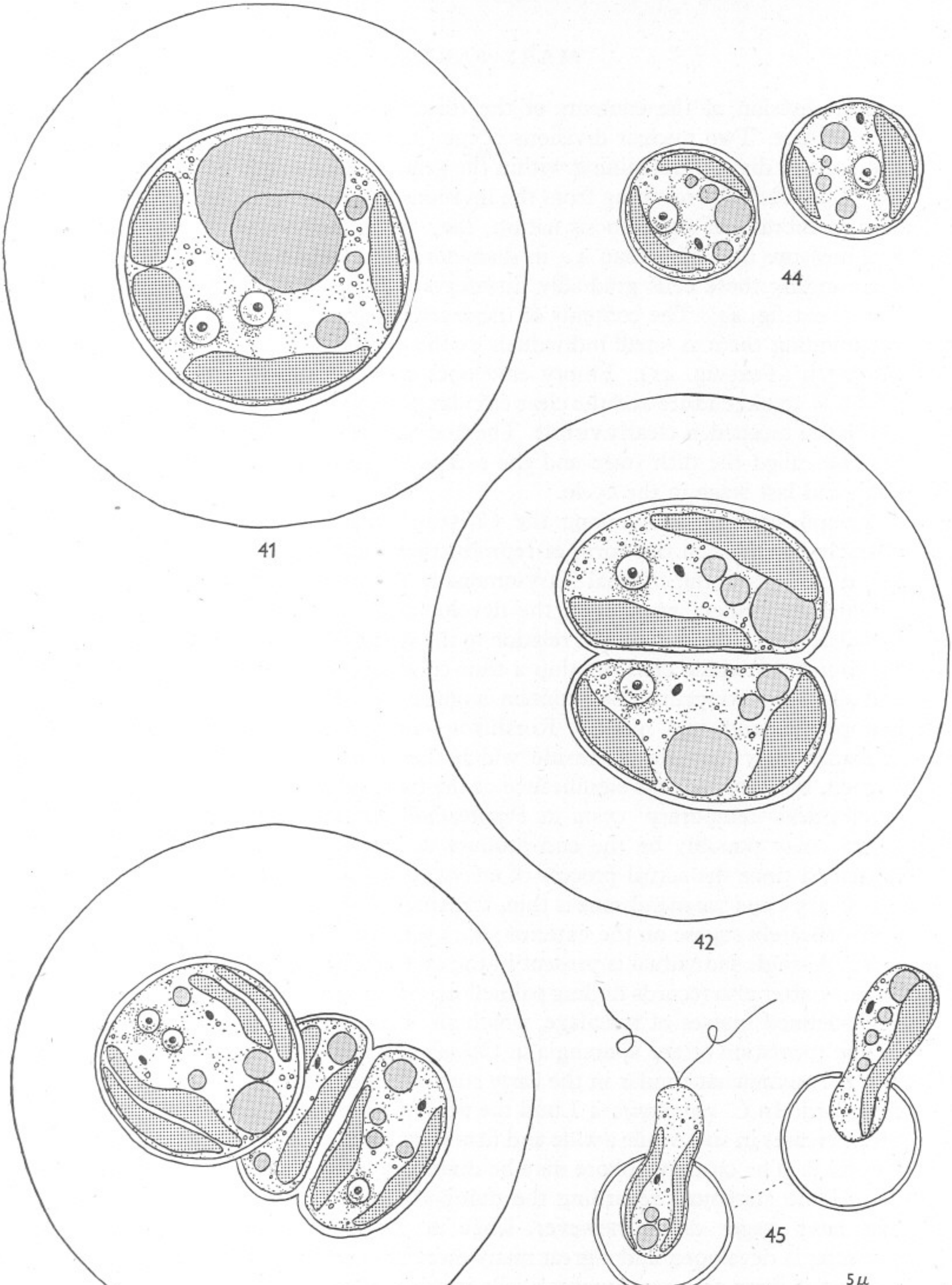


Text-figs. 35–40. (× 5000.) *Isochrysis galbana* n.g., n.sp. 35. Older motile stage containing large mass of leucosin, front view. 36. Start of cyst formation, development of cellulose membrane round leucosin mass, front view. 37. Cyst membrane thickened, cell contents passed into cyst, front view. 38. Fully formed cyst, equatorial view. 39. Early stage in the division of the contents of the cyst, equatorial view. 40. Cyst from which contents have been liberated, plug attached to one side of the pore, equatorial view.

In old cultures, the cyst stage can persist indefinitely without the contents showing any division. If the deposit from the bottom of an old culture (containing many cysts) is added to fresh culture solution, however, the first division stage of the contents of a cyst can be observed within 24 hr. Four divisions take place in the cyst in a line at right angles to the bottom of the plug. Text-fig. 39 shows a cyst in which the first two divisions have been completed. In a cyst in which the contents are fully divided (Pl. I, fig. 6) sixteen naked cells are present; these cells resemble the young motile stages described earlier, possessing two chromatophores, a stigma, a nucleus and one or more small masses of leucosin. The flagella may also be developed, but they could not be seen. The cells are released from the cyst as motile individuals measuring approximately 3 μ in length. The release of the individuals from the cyst does not take place by the dissolving of the plug as seems to be the usual procedure. In *Isochrysis* the plug is forced out of the pore of the cyst in an explosive manner and often remains attached to the cyst at one side of the pore (Text-fig. 40). The circular pore through which the contents escape can be seen quite clearly in the empty cyst (Text-fig. 40).

In the section on *Chromulina pleiades* reference was made to a form of reproduction in a palmelloid phase which seems to differ from any form that has been described so far for the Chrysomonadineae. Stages in this form of reproduction have been found in the four species studied, *C. pleiades* (Text-figs. 20–23), *Isochrysis galbana* (Pl. I, figs. 8, 9; Text-figs. 41–45), *Dicrateria inornata* (Text-figs. 55–60) and *D. gilva.* Although the nuclear behaviour in the early stages has not yet been elucidated, a brief description of the process, as far as is known, is given here so that similar stages in other members of the class may be recognized. It has been followed most fully in *Isochrysis*, and is therefore described under this genus.

This form of reproduction occurs in cultures which have been left at least 2 months without subculturing. The very early stages in the cycle are still not established with certainty, but there is some evidence that fusion of non-motile(?), spheroidal individuals, about 5 μ in diameter, derived from the large motile, leucosin-filled individuals, starts the process (Text-fig. 30). Possible fusion stages of these cells have been seen (Text-fig. 31). The next or second stage is a larger spheroidal individual, measuring 8–9 μ in diameter; it is covered by a thin gelatinous envelope of firm consistency and it possesses two nuclei, two stigmata, four chromatophores and a number of large masses of leucosin (Pl. I, fig. 8). Stage 2 may be the product of the fusion of the large motile individuals which either cast or withdraw their flagella as soon as fusion starts; the non-motile spheroidal stage 1 may be individuals which have not fused. The third stage is figured on Pl. I, fig. 9, and shows that a larger secondary gelatinous envelope, of a less firm consistency than the first, has now developed; it measures about 15 μ in diameter. In this stage one nucleus only is present so that the two nuclei, originally present, have either fused or one has degenerated. The third stage, therefore, may be a zygote. The fusion of motile gametes, and the subsequent reduction during the two nuclear divisions that follow the sexual fusion resulting in the formation of four daughter-cells, are recorded by Schwarz (1932) for *Ochrosphaera neapolitana* Schussnig.



Text-figs. 41–45. (×5000.) *Isochrysis galbana* n.g., n.sp. Stages in reproduction in the palmelloid phase. 41. Early stage 4, nucleus of stage 3 just divided. 42. Stage 4, first division. 43. Stage 4, second division. 44. Stage 5, products of division free from gelatinous envelope. 45. Stage 6, liberation of daughter-cells as young motile stage.

The division of the contents of the third stage may be regarded as the fourth stage. Two nuclear divisions occur (possible reduction division), the products of division remaining within the gelatinous envelope (Text-figs. 41–43). The four cells resulting from the divisions are each surrounded by a thin firm membrane of a gelatinous nature; they are spheroidal or ovoid in shape and measure not more than 4 μ in diameter. The large gelatinous envelope surrounding these cells gradually disintegrates leaving the thin-walled cells free (Text-fig. 44). The contents of these cells escape from the firm envelope surrounding them as small individuals of the motile stage, measuring 3·5–4 μ in length (Text-fig. 45). Empty envelopes are plentiful on the bottom of a flask of an old culture and the clear circular pore, through which the contents of the cell escaped, is clearly visible. The free cells covered by the firm envelope may be called the fifth stage and the escape of the contents of the cells the sixth and last stage in the cycle.

Several stages found among the Chrysophyceae by other workers may possibly be stages in this form of reproduction. Korshikov (1929) describes, in old cultures of the colonial Chrysomonad, *Synochromonas pallida*, after the colonies had fallen into pieces, the development of solitary cells which are balled as if inflated so that their relation to the species is not readily established. He found that these cells develop a thin colourless membrane which is soft and slightly refringent. They contain large masses of leucosin, several chromatophores and two nuclei. Korshikov considers that these stages are probably early cyst stages, inside which the true cysts may eventually be formed, but says that the significance of the two nuclei is obscure. The ovoid or elliptical 'temporary' cysts in *Prymnesium parvum*, described by Carter (1937), may possibly be the end-product of the type of reproduction just described since the actual process of encystment was not observed. In these temporary cysts the membrane is thin, transparent, colourless or brownish and very delicately rugose on the exterior; the cyst lacks a plug as far as could be seen. A single individual is present in the cyst and it is released as the motile stage. Carter also records finding palmelloid groups of naked cells, two to four, in ill-defined masses of mucilage, which she believes belong to *P. parvum*.

The formation of the sporangia in *Chromulina sporangifera* given by Lund (1942) is somewhat similar in the early stages to the type of reproduction just described. In *C. sporangifera* Lund the protoplast assumes a spherical shape and increases in size, while a wide and firm mucilaginous membrane is secreted around it. The chromatophore may be divided into two or four portions, but there is no statement regarding the number of nuclei present at this stage. The later stages differ, however, since no large secondary mucilaginous envelope is developed and a great many more divisions occur so that the final product is forty or more daughter-cells instead of four.

In *C. pleiades* the first stage, the non-motile spheroidal individual (Text-fig. 20), and the second stage, the larger binucleate individual, covered by a thin gelatinous envelope (Text-fig. 21), have been found, but neither the third stage, with the large secondary envelope, nor the fourth stage, the division of the contents of stage 3, has been seen. Although the fifth and sixth stages have been found (Text-figs. 22, 23) there is no proof at present that the large secondary envelope does develop and that two divisions only take place in *C. pleiades* during the fourth stage. The fifth stage does definitely possess, however, a very thin firm envelope from which the contents escape as motile individuals. Lund makes no reference to any thin-walled envelope around the daughter-cells from the sporangium of *C. sporangifera*; he says that when liberated they are spherical, but that they soon become actively motile and assume the ellipsoid shape.

In general form *Isochrysis* agrees rather closely with the two described species of the genus *Wyssotzkia* Lemm., but in the latter genus there appears to be considerable doubt concerning the number of flagella present; Büttner (1911, p. 126, fig. 5*d*, *e*) actually figures a third flagellum in *W. gladociliata* Lemm. Carter (1937) is of the opinion that *W. gladociliata* Lemm. is probably identical with *Prymnesium parvum* Carter and that *Wyssotzkia biciliata* (Wyss.) Lemm. belongs also to the genus *Prymnesium* and possibly also represents *P. parvum*. Conrad (1941), on the other hand, thinks that both species of *Wyssotzkia* belong to the Cryptophyceae.

Dicrateria n.gen.

Cellula natante, solitaria, nuda, periplasto differentiae carente praedita; protoplasto rigidiore, formam praebente immutabilem; cellula sphaeroidi subovatave; deest sulcus; 2 flagellis, longitudine paribus, ex granulo basali distincto exsistentibus in parte cytoplasmatis hyalina sito; 2 chromatophoris magnis parietalibus crateriformibus fulvis contrapositis; nucleo mediocri propius polum illum sito ex quo exsistunt flagella; cellula pabulum holophytica; nec oleo nec leucosino indigente; sine sexu propagatur fissione per gradum mobilem; cysto intra cellulam confecto; cystis sphaeroidibus subovatisque cum membrana externa laevi; non deest multiplicationis genus palmelloidem per gradum effectae.

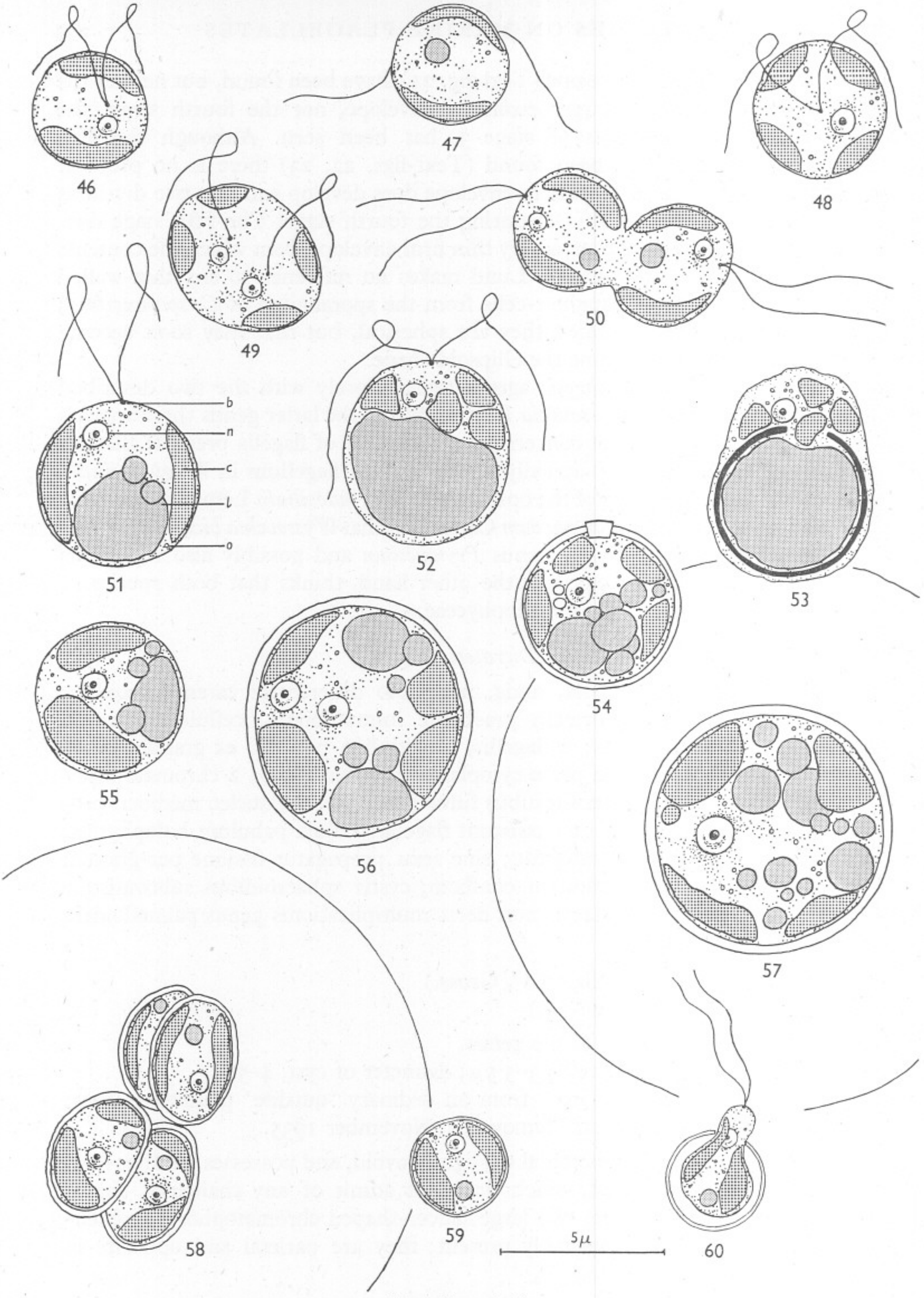
D. inornata n.sp. (Flagellate 'B', Gross.)
(Pl. I, fig. 1; Text-figs. 46–60.)

With the characters of the genus.

Diameter of motile cells, 3–5·5 μ; diameter of cyst, 4–5 μ.

Isolated by Dr F. Gross from an ordinary 'outside' plankton sample which was taken off Plymouth in November 1935.

The motile stage is spheroidal to slightly ovoid, and possesses a rather rigid undifferentiated periplast, which does not admit of any change of shape. In the young motile stage, two large saucer-shaped chromatophores, golden-brown in colour, are normally present; they are parietal and opposite in



Text-figs. 46–60.

position so that a clear zone of cytoplasm lies between them (Pl. I, fig. 1; Text-fig. 51). In the older motile stage four chromatophores are more frequently developed (Text-figs. 48, 52). The medium-sized nucleus is situated near to the pole from which the flagella arise and in the young stage a rather small mass of leucosin is present at the opposite pole (Pl. I, fig. 1). Small oil drops are distributed through the general cytoplasm, but the species lacks both stigmata and vacuoles.

Two equal flagella, one and a half to twice the diameter of the cell in length, arise from a distinct basal granule, or from two placed very close together, situated in the clear part of the cytoplasm (Text-figs 46, 48); they are very delicate, but can just be seen in the living cells. Stained preparations show that both flagella taper very slightly towards the free end, and neither are apparently plumate in structure. When in motion the cells rotate in a slow and steady manner and are constant in direction for relatively long periods. When swimming the flagella lie backwards down the sides of the body and carry out an undulating movement, but when at rest, they lie away from the body. Before the swimming individuals come to rest, however, they exhibit, for a short time, a peculiar dithering movement; they then remain motionless for a fairly long period. This species is slightly phototactic in reaction.

In this organism, as in *Isochrysis*, the quantity of leucosin in the cell varies in cultures of different ages (Pl. I, fig. 1; Text-figs. 51, 52). In the young actively dividing individuals, 3–4 μ in diameter, the quantity is very small (Pl. I, fig. 1), but as the culture increases in age so also does the quantity of leucosin in the cells (Text-fig. 51), until in 4- to 5-month-old cultures the leucosin may occupy from one-third to more than one-half the volume of the cell (Text-fig. 52). In the very slow-moving leucosin-filled cells, 4–5·5 μ in diameter, the chromatophores, usually four, may be so reduced in size that they appear as small disks, situated with the nucleus, at the pole from which the flagella arise (Text-fig. 52). These cells either form endogenous cysts or pass into the first stage of the reproductive cycle that takes place in the palmelloid phase.

Asexual reproduction by division of the motile cells takes place in both the light and the dark. Counts show that more than two divisions can take place within 6 hr. The procedure is similar to that described in *Isochrysis*. When

---

Text-figs. 46–60. (× 5000.) *Dicrateria inornata* n.g., n.sp. 46. Young motile stage, viewed from pole at which flagella are inserted. 47. Young motile stage, viewed from opposite pole to Fig. 46. 48. Older motile stage with four chromatophores, viewed from pole at which flagella are inserted. 49. Early division stage of motile individual. 50. Late division stage of motile individual. 51. Older motile stage with large leucosin mass, equatorial view. *b*, basal granule; *c*, chromatophore; *l*, leucosin; *n*, nucleus; *o*, oil-globule. 52. Older motile stage with four chromatophores and still larger mass of leucosin, equatorial view. 53. Contents of cell passing into cyst, membrane of cyst thickened. 54. Mature cyst. 55–60. Stages in reproduction in the palmelloid phase. 55. Stage 1. 56. Stage 2. 57. Stage 3. 58. Stage 4, second division. 59. Stage 5. 60. Stage 6.

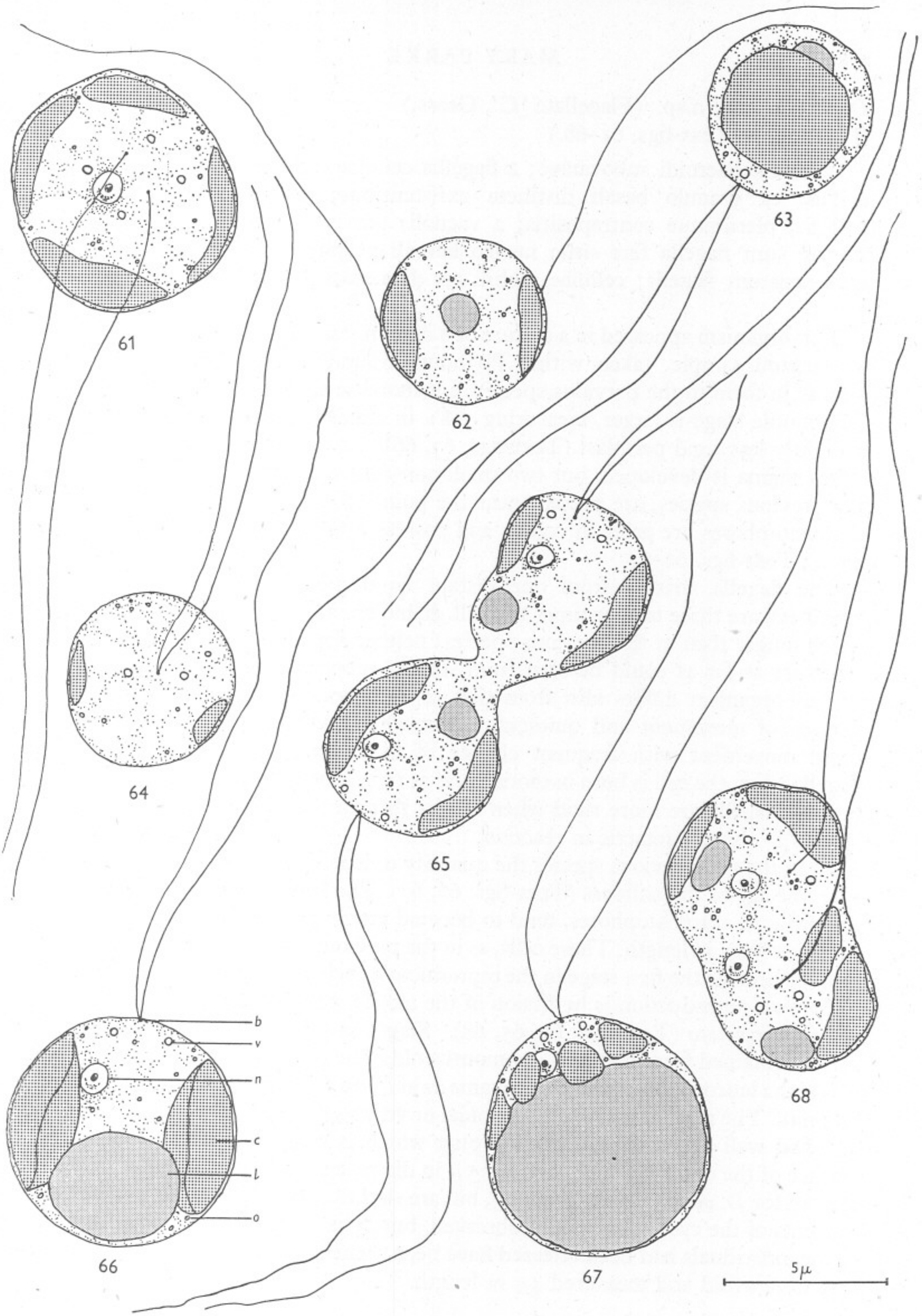
about to divide the cell broadens, the two chromatophores divide, if they have not already divided, and the leucosin breaks up into two or more smaller masses. The nucleus then divides and the two flagella separate, each attached to its basal granule or part of the basal granule (Text-fig. 49). Fission of the cell starts at the pole from which the flagella arise and passes down through the individual until the two cells are connected only at the pole away from the flagella (Text-fig. 50). A second flagellum is developed by each daughter-cell before they finally separate; the cells are usually of equal size. No loss or withdrawal of the flagella before fission has been observed in this species.

Cyst formation occurs in cultures left 5 months without subculturing. The cysts develop inside the leucosin-filled cells (Text-fig. 53) in a manner similar to that described for *Isochrysis*. The mature cysts are spheroidal with a smooth silicified wall and a plug, the shape of a truncated cone, that is raised slightly above the general surface of the cyst (Text-fig. 54).

The form of reproduction in the palmelloid phase found in the genus *Isochrysis* occurs also in this genus. In *Dicrateria inornata* the six stages in the cycle defined earlier have been obtained from old cultures (Text-figs. 55–60). The large spheroidal, leucosin-filled cells of stage 1 measure 4·5–5 μ (Text-fig. 55); stages in the apparent fusion of pairs of these cells have been seen, but the actual fusion of the nuclei of the cells has not yet been observed. Stage 2, the larger binucleate cell covered by a thin gelatinous envelope, has been found frequently (Text-fig. 56); it measures 7–8 μ in diameter. Stage 3, the uninucleate cell (Text-fig. 57), and stage 4, the division of this cell into four daughter-cells (Text-fig. 58), are not uncommon; the large secondary gelatinous envelope surrounding these stages measures 15–17 μ in diameter. In stage 5 the four daughter-cells become free by the disintegration of the large gelatinous envelope: they are spheroidal and are covered by a very thin, smooth, firm wall, measuring about 3 μ in diameter (Text-fig. 59). Stage 6, the liberation of the contents of these cells, has also been seen; the contents escape from a small pore as a single small individual of the motile stage, measuring approximately 3 μ in diameter (Text-fig. 60).

D. inornata shows some resemblance to *Chrysidalis peritaphrena* Schiller, but it is smaller and lacks the decided groove, passing forwards and backwards from the base of the flagella, which is present in that species.

Text-figs. 61–68. (× 5000.) *Dicrateria gilva* n.g., n.sp. 61. Early stage in fission of motile individual, chromatophores and vacuoles doubled, viewed from pole at which flagella are inserted. 62. Young motile stage viewed from pole opposite to that at which flagella are inserted. 63. Young motile stage, equatorial view. 64. Young motile stage, viewed from pole at which flagella are inserted. 65. Late division stage, fission of cell nearly complete. 66. Older motile stage with two chromatophores and large mass of leucosin, equatorial view. *b*, basal granule; *c*, chromatophore; *l*, leucosin; *n*, nucleus; *o*, oil-globule; *v*, vacuole. 67. Older motile stage with four chromatophores, reduced in size, and very large leucosin mass, equatorial view. 68. Division stage of motile individual, nucleus and chromatophores divided, number of vacuoles doubled.



Text-figs. 61–68.

Dicrateria gilva n.sp. (Flagellate 'C', Gross.)
(Pl. I, fig. 3; Text-figs. 61–68.)

Cellula sphaeroidi subovatave; 2 flagellis cellulae diametro 3–4 plo longioribus, ex granulo basali distincto exsistentibus; chromatophoris fulvis pallidis, plerumque contrapositis; 2 vacuolis parvis non trepidantibus ubi inserta sunt flagella fere sitis; nucleo laterali propius polum illum sito ex quo exsistunt flagella; cellulae mobili est diametros 5–8 μ; cysto diametros 7–7·5 μ.

This organism appeared in a culture of a diatom started by Dr F. Gross from a plankton sample, taken within Plymouth Sound in March 1936. It is similar in form to the previous species, but shows several points of difference. The motile stage is larger, measuring 5–8 μ in diameter, and appears to have a slightly less rigid periplast (Text-figs. 63, 66).

No stigma is developed, but two small non-contractile vacuoles, lacking in the previous species, are present near the point of origin of the flagella; the chromatophores are paler in colour and possess a faint greenish tinge (Pl. I, fig. 3; Text-figs. 62–64).

The flagella, arising from one distant basal granule (or two adjacent granules), are three to four times the cell diameter in length and are therefore much longer than in the previous species; neither flagellum shows a plumate structure as far as could be seen from stained preparations. The movement of this organism differs also from that of *D. inornata*; there are alternate periods of movement and quiescence, but when swimming it shows fairly rapid movement with frequent change of direction. The position of the flagella when the cell is both in motion and at rest is the same as in *D. inornata*, but the flagella are more rigid when at rest than in the former species. This species is also phototactic in reaction.

As in the two previous species the quantity of leucosin in the cells increases with the age of the cultures (Text-figs. 66, 67). The leucosin-filled cells, with the reduced chromatophores, tend to become rather pyriform in shape; they measure 7–8 μ in length. These cells, as in the previous species, give rise to the cysts or become the first stage in the reproductive cycle in the palmelloid phase.

Asexual reproduction is by fission of the motile individuals and takes place as in *D. inornata* (Text-figs. 61, 65, 68). Stages in the formation of the cyst can be obtained from cultures 4–5 months old. The development of the cyst, inside the leucosin-filled cells, is the same as in *Isochrysis galbana* and *Dicrateria inornata*. The mature cysts are spheroidal or very slightly ovoid with a smooth silicified wall and a conical hyaline plug which is raised slightly above the surface of the cyst; they measure 7–7·5 μ in diameter. They are similar to that figured for *D. inornata* (Text-fig. 54), but are slightly larger. The release of the contents of the cyst has not been observed, but cysts from which the majority of the individuals had been released have been seen; the cells remaining in the cyst were ovoid and measured 4 μ in length.

Five of the six stages in the palmelloid form of reproduction, described in and figured for the two previous species, have been seen in this species. The first stage, measuring 6–7 μ in diameter, is spheroidal and shows two vacuoles and two or four chromatophores; in stage 2, the cells, covered by a thin gelatinous envelope, have four vacuoles, two nuclei and four or eight chromatophores; they measure 9–10 μ in diameter. The large secondary envelope of stages 3 and 4 is not of such firm consistency as in the two previous species; it measures 18–20 μ in diameter. The free cells of stage 5 measure 4–5 μ, but stage 6, the escape of the contents of these cells, has not been observed.

CRYPTOPHYCEAE

NEPHROSELMIDACEAE

Hemiselmis n.gen.

Cellula solitaria, natante, nuda, phaseliformi, dorsiventraliter depressa; quae transverse secta formam praebet ellipsoidem; periplasto perspicuo differentiam praebente praedita; sulco bene notato a margine anteriore dorsuali trans latus laterale concavum oblique currente, in superficie ventrali evanescente plane mediana sub linea; deest gula; cellulis maioribus forma valde mutabilibus; 2 flagellis disparibus lateris concavi lateralem ad partem exsistentibus plane mediana sub linea; chromatophoro singulo magno, parietali; pyrenoide singulo, amyli capsula circumsaepto, in medio plerumque sito; vacuolo contractilio singulo ubi inserta sunt flagella fere sito; ocello singulo haud conspicuo ad posteriorem partem in superficie ventrali posito; nucleo parvo mediano; cellula pabulum holophytica; cellula amyli genus praebente; sine sexu propagatur fissione obliqua secundum sulcum effecta.

H. rufescens n.sp. (Flagellate 'D', Parke.)
(Pl. II, figs. 11–16; Text-figs. 69–73.)

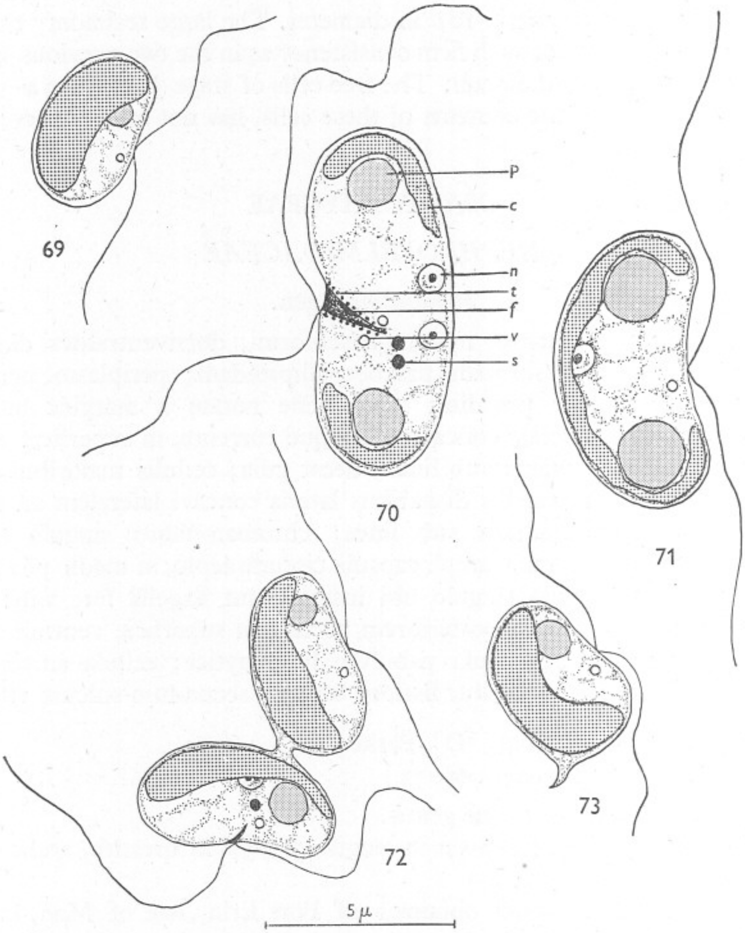
With the characters of the genus.

Motile cells measure 4–8·5 μ in length, 3·5–5 μ in breadth, and 2–3 μ in thickness.

Isolated from sea water obtained off Port Erin, Isle of Man, in April 1937.

In this species the body is bean-shaped and in the larger individuals is very flattened in a dorsiventral plane (Pl. II, figs. 11–14; Text-figs. 69, 71); in the smaller stages, however, the body is not quite so flattened. A furrow, not deepened to form a gullet, arises near the dorsal anterior edge; it runs down obliquely over the lateral edge to die out on the ventral surface just below the median line (Pl. II, figs. 12–14; Text-fig. 70).

Two delicate flagella arise laterally just below the furrow, that is, a little below the middle of the concave surface. The flagella are unequal in length, the one directed anteriorly is about one and a half times the length of the cell and the one directed posteriorly is slightly shorter (Pl. II, figs. 11–16). No difference in the structure of the two flagella could be detected from stained preparations; neither flagellum was plumate.



Text-figs. 69–73. (× 5000.) *Hemiselmis rufescens* n.g., n.sp. 69. Young motile stage, dorsal view. 70. Early division stage of motile individual, ventral view. *c*, chromatophore; *f*, furrow; *n*, nucleus; *p*, pyrenoid; *s*, stigma; *t*, trichocysts?; *v*, contractile vacuole. 71. Older motile individual, dorsal view. 72. Final stage in fission of motile individual, two daughter-cells just separating. 73. Daughter-cell immediately after fission has been completed, dorsal view.

The swimming of this organism has also been studied by Lowndes (1943, p. 102), and the following is his description of its movement. 'It swims rapidly, and with an enormous amount of gyration compared with the previous species (i.e. *Isochrysis galbana*). The individuals progressed in a very characteristic manner traversing a spiral, the diameter of which is many times the length of the organism. It is obvious that the peculiar spiral swimming of the organism is not due to any kind of irregularity in the length or structure of the flagella, but it is dictated solely by the shape of the cell, with its strong dorsoventral flattening, and also by the fact that the flagella are attached laterally.' Movement of the cells, normally in a forward direction, is constant in direction for relatively long periods. All the cells show periods of quiescence, but these are of longer duration, and occur more frequently, in the larger individuals. This species is extremely phototactic in reaction.

The capacity to change shape is well marked in the large and in the dividing individuals, but it is not so obvious in the small stages. The periplast is clear and can be seen easily in all individuals (Pl. II, figs. 11–16). In the young stage there is a single, large, deep crimson parietal chromatophore covering about half the body surface (Pl. II, fig. 11; Text-fig. 69); it covers one lateral side and about half the surface of the ventral and dorsal sides of the body which are away from the lateral side on which the furrow arises. The edge of the chromatophore may be slightly lobed. A highly refractive, large, spheroidal pyrenoid, appearing greenish grey in colour, is present; it is normally surrounded by a sheath of solid material, which gives a blue coloration with iodine and appears therefore to be a form of starch. This organism is, therefore, undoubtedly a member of the Cryptophyceae. The pyrenoid is situated somewhat centrally in the body in most individuals and is frequently partly covered by the chromatophore (Text-fig. 69); it may be found towards either the anterior or posterior end of the body. The nucleus, round or ovoid in shape, is situated medianly or slightly posteriorly in the body, usually nearer to the ventral surface than to the dorsal. One contractile vacuole is developed immediately below the furrow in a median position in the body near the point of insertion of the flagella (Pl. II, figs. 11–13). A stigma is present on the ventral surface, placed usually near to where the furrow dies out; it can, however, be found nearer to the lateral side from which the flagella arise. In some individuals the stigma is dull in colour and difficult to detect, but its presence in this species has been confirmed for the writer by Prof. E. G. Pringsheim.

In nearly all the larger individuals two pyrenoids are present, one situated anteriorly and the other posteriorly (Pl. II, figs. 12, 14; Text-fig. 71). The quantity of starch around them has also increased so that they form large conspicuous bodies in the anterior and posterior regions of the cell. The chromatophore, now covering very little of the dorsal or ventral surface of the body (Pl. II, fig. 12; Text-fig. 71), becomes less intense in colour than in the smaller individuals, usually showing only a faint pink coloration, but occasionally becoming greenish; it may divide into two (Pl. II, fig. 14). The furrow is also more clearly defined in the large individuals. In these cells two rows of minute, highly refractive granules, probably trichocysts, can be seen, one row on either side of the furrow (Pl. II, figs. 12–14; Text-fig. 70).

Asexual reproduction in this species is by division of the cell in the motile stage (Pl. II, figs. 15, 16; Text-figs. 70, 72). Multiplication is very rapid, fission of individuals occurring in both the light and the dark. Division is oblique, the division line passing through the centre of the furrow. The large individuals, which contain two pyrenoids and two chromatophores (Pl. II, fig. 14), are probably early division stages, but the organism is more commonly found in this condition than in the small stage with one pyrenoid and one chromatophore.

When about to divide the cell becomes stretched out lengthwise, the breadth becoming slightly narrower. The nucleus then divides and a second contractile vacuole and second stigma make their appearance, usually close to the vacuole and stigma already present (Text-fig. 70). Fission starts at the anterior dorsal edge, passes down through the centre of the furrow (Pl. II, fig. 15) and continues obliquely, that is in the line of the furrow, across the cell until fission is nearly complete (Pl. II, fig. 16). The anterior chromatophore passes to the individual on the ventral side, and the posterior chromatophore to the one on the dorsal side (Pl. II, fig. 15). The two daughter-individuals, now separated except at a point below the mid-line on the convex lateral side, pull away from each other and are attached only by a very narrow connexion (Text-fig. 72). When the individuals separate, the remains of the connexion can be seen for a short while as a small papilla on the convex side of the cell (Text-fig. 73). The flagella of the dividing cell are retained by one of the daughter-cells (Pl. II, fig. 16), the other develops them anew before fission is completed (Text-fig. 72). Multiplication by fission of the motile stage is the only form of reproduction that has been found so far in this species.

This organism undoubtedly belongs to the Cryptophyceae, and adopting Pringsheim's (1944) suggested subdivision of the class, it belongs to family 5, Nephroselmidaceae Pascher, the characters of which are body bean-shaped and flagella laterally inserted. Pascher placed three genera in this family, *Nephroselmis* Stein (1878), *Protochrysis* Pascher (1911) and *Sennia* Pascher (1912), but their position in it does not yet seem to be definitely established; two species of *Nephroselmis* have been described, but the two other genera are monotypic.

Hemiselmis rufescens resembles *Nephroselmis olivacea* Stein (1878) in general shape, but appears to be more flattened. It differs from this species, however, in the absence of a gullet (as far as could be detected), in the presence of a stigma, and in the development of one contractile vacuole instead of two alternating contracting vacuoles. It is also much smaller in size and if Stein's figures (1878, Taf. XIX, figs. 36, 37) illustrate the method of fission in the motile stage of *N. olivacea*, the type of oblique fission found in *Hemiselmis* is again different. *Nephroselmis marina* Schiller (1925) is about the same size as *Hemiselmis*, but differs in shape, and lacks stigma, pyrenoid, vacuole and trichocysts. From Schiller's illustration (1925, Taf. 3, fig. 13), the flagella of

Nephroselmis marina also appear to be inserted on the convex side of the body.

Hemiselmis is very much more flattened than the genus *Protochrysis*; *Hemiselmis* differs also in its ability to change shape and in possessing a single vacuole. The lobing of the chromatophore is also very much more pronounced in the larger *Protochrysis*. A further difference is in the form of asexual reproduction; in *Hemiselmis* fission takes place in the motile stage, but in *Protochrysis phaeophycearum* Pascher it is recorded as occurring in the palmelloid phase.

The young motile stage of *Hemiselmis* is somewhat similar in shape to *Sennia commutata* Pascher, but it is more flattened. *Sennia*, however, has a fixed shape and it has only a slight indication of a furrow. The position of the nucleus in the two genera also differs.

Hemiselmis differs in colour from the three genera (golden-brown) already placed in the Nephroselmidaceae, but as Pringsheim (1944) points out, the custom of relying solely on colour as a means of generic distinction should be abandoned. There are, however, a sufficient number of differences, without the colour, to warrant the placing of this organism in a new genus.

SUMMARY

Six marine flagellates, used as food in the rearing of the larvae of *Ostrea edulis* L., are described.

One belongs to the Chlorophyceae, *Pyramimonas grossii* n.sp. (Polyblepharidaceae); four belong to the Chrysophyceae, *Chromulina pleiades* n.sp. (Chromulinaceae), *Isochrysis galbana* n.g., n.sp., *Dicrateria inornata* n.g., n.sp., *D. gilva* n.g., n.sp. (Isochrysidaceae); and one belongs to the Cryptophyceae, *Hemiselmis rufescens* n.g., n.sp. (Nephroselmidaceae).

A form of reproduction in a palmelloid phase, not previously described, is recorded for the Isochrysidaceae.

REFERENCES

BRETSCHNEIDER, L. H., 1925. *Pyramimonas utrajectina* n.sp. *Arch. Protistenk.*, Bd. 53, pp. 124–30.

BROWN, H. P., 1945. On the structure and mechanics of the protozoan flagellum. *Ohio Journ. Sci.*, Vol. XLV, pp. 247–301.

BRUCE, J. R., KNIGHT, M. & PARKE, M., 1940. The rearing of oyster larvae on an algal diet. *Journ. Mar. Biol. Assoc.*, Vol. XXIV, pp. 337–74.

BÜTTNER, J., 1911. Die farbigen Flagellaten des Kieler Hafens. *Wiss. Meeresunters. Kiel.*, Bd. 12, pp. 121–33.

CARTER, N., 1937. New and interesting algae from brackish water. *Arch. Protistenk.*, Bd. 90, pp. 1–68.

CHIFFLOT, J. & GAUTIER, C., 1905. Sur le mouvement intraprotoplasmique à forme Brownienne des granulations cytoplasmiques. *Journ. de Bot.*, T. 19, pp. 40–4.

CONRAD, W., 1930*a*. Flagellates nouveaux ou peu connus. I. *Arch. Protistenk.*, Bd. 70, pp. 657–80.

CONRAD, W., 1930*b*. Flagellates nouveaux ou peu connus. II. *Arch. Protistenk.*, Bd. 72, pp. 538–53.

—— 1941. Notes Protistologiques. XXI. Sur les Chrysomonadines à trois fouets. Aperçu synoptique. *Bull. Mus. roy. Hist. nat. Belg.*, T. 17, no. 45, pp. 1–16.

DOFLEIN, F., 1922. Untersuchungen über Chrysomonadinen. *Arch. Protistenk.*, Bd. 44, pp. 149–213.

—— 1923. Untersuchungen über Chrysomonadinen. III. *Arch. Protistenk*, Bd. 46, pp. 267–327.

FISCHER, A., 1894. Über die Geisseln einiger Flagellaten. *Jahrb. Wiss. Bot.*, Bd. 26, pp. 187–235.

GEITLER, L., 1925. Zur Kenntnis der Gattung *Pyramimonas*. *Arch. Protistenk.*, Bd. 52, pp. 356–70.

GRIFFITHS, B. M., 1909. On two new members of the Volvocaceae. *New Phytol.*, Vol. 8, pp. 130–7.

HODGETTS, W. J., 1920. Notes on freshwater algae. I–IV. *New Phytol.*, Vol. 19, pp. 254–63.

JANE, F. W., 1944. Studies on the British Volvocales. *New Phytol.*, Vol. 43, pp. 36–48.

KORSHIKOV, A. A., 1929. Studies on the Chrysomonads. I. *Arch. Protistenk.*, Bd. 67, pp. 253–90.

LOEFFLER, F., 1889. Eine neue Methode zum Färben der Microorganismen. *Bacteriolog. Centralblatt.*, Bd. 6, pp. 209–24.

LOWNDES, A. G., 1936. Flagellar movement. *Nature*, Vol. 138, pp. 210.

—— 1941. On flagellar movement in unicellular organisms. *Proc. Zool. Soc. Lond.*, Ser. A., Vol. 111, pp. 111–34.

—— 1943. The swimming of unicellular flagellates. *Proc. Zool. Soc. Lond.*, Ser. A, Vol. 113, pp. 99–107.

—— 1947. Recent work on flagellar movement. *Science Progress*, Vol. 35, No. 137, pp. 62–8.

LUND, J. W. G., 1942. Contributions to our knowledge of British Chrysophyceae. *New Phytol.*, Vol. 41, pp. 274–92.

PASCHER, A., 1911. Zwei braune Flagellaten. *Ber. Deutsch. Bot. Ges.*, Bd. 29, pp. 190–2.

—— 1912. Braune Flagellaten mit seitlichen Geisseln. *Zeitschr. Wiss. Zool.*, Bd. 100, pp. 177–89.

—— 1913. Chrysomonadinae, Cryptomonadinae, in *Süsswasserfl. Deutschlands, Oesterreichs u.d. Schweiz*, Bd. 2, pp. 7–114.

—— 1927. Volvocales—Phytomonadinae. *Süsswasserfl. Deutschlands, Oesterreichs u.d. Schweiz*, Bd. 4, pp. 1–506.

—— 1929. Beiträge zur allgemeinen Zellehre. 1. Doppelzellige Flagellaten und Parallelentwicklungen zwischen Flagellaten und Algenschwärmern. *Arch. Protistenk.*, Bd. 68, pp. 261–304.

—— 1932. Zur Kenntnis der einzelligen Volvocalen. *Arch. Protistenk.*, Bd. 76, pp. 1–82.

PETERSON, J. B., 1918. Om *Synura Uvella* Stein og nögle andre Chrysomonadiner. *Vidensk. Medd. Dansk Nat. Foren.*, Bd. 69, pp. 345–57.

—— 1929. Beiträge zur Kenntnis der Flagellaten Geisseln. *Bot. Tidsskr.*, Bd. 40, pp. 373–89.

PRINGSHEIM, E. G., 1944. Some aspects of taxonomy in the Cryptophyceae. *New Phytol.*, Vol. 43, pp. 143–50.

SCHERFFEL, A., 1911. Beitrag zur Kenntnis der Chrysomonadineen. *Arch. Protistenk.*, Bd. 22, pp. 299–344.

SCHERFFEL, A., 1912. Zwei neue, trichocystenartige Bildungen führende Flagellaten. *Arch. Protistenk.*, Bd. 27, pp. 94–128.

SCHILLER, J., 1913. Vorläufige Ergebnisse der Phytoplankton-Untersuchungen auf den Fahrten S.M.S. 'Najade' in der Adria 1911/12. *SitzBer. Akad. Wiss. Wien, Math.-Nat. Kl.*, Bd. 122, pp. 621–30.

—— 1925. Die planktonischen Vegetationen des adriatischen Meeres. *Arch. Protistenk.*, Bd. 53, pp. 59–123.

—— 1929. Neue Chryso- und Cryptomonaden aus Altwässern der Donau bei Wien. *Arch. Protistenk.*, Bd. 66, pp. 436–58.

SCHMARDA, L. K., 1850. Neue Formen von Infusorien. *Denkschrift d. Wien Acad.*, Bd. 1, Abt. 2, pp. 9–14.

SCHWARZ, E., 1932. Der Formwechsel von *Ochrosphaera neapolitana*. *Arch. Protistenk.*, Bd. 77, pp. 434–62.

STEIN, F. RITTER VON, 1878. *Der organismus der Infusionsthiere*. Abt. 3, 154 pp. Leipzig.

VLK, W., 1938. Über den Bau der Geissel. *Arch. Protistenk.*, Bd. 90, pp. 449–88.

EXPLANATION OF PLATES I AND II

PLATE I

(Figs. 1–10, ×7000.)

Fig. 1. *Dicrateria inornata* n.g., n.sp., young motile stage, equatorial view.

Fig. 2. *Chromulina pleiades* n.sp., young motile stage, from pole at which flagellum arises.

Fig. 3. *Dicrateria gilva* n.g., n.sp., young motile stage, equatorial view.

Figs. 4–10. *Isochrysis galbana* n.g., n.sp.

Fig. 4. Older motile stage containing large mass of leucosin, front view.

Fig. 5. Immature cyst, plug not yet formed, front view.

Fig. 6. Mature cyst with division of contents completed, front view.

Fig. 7. Young motile stage with lateral chromatophores, front view.

Fig. 8. Reproduction in the palmelloid phase; binucleate stage 2 with narrow gelatinous envelope.

Fig. 9. Reproduction in the palmelloid phase; uninucleate stage 3 with additional large gelatinous envelope, nucleus in early prophase.

Fig. 10. Young motile stage, lateral view.

PLATE II

(Figs. 11–16, ×7000; figs. 17, 18, ×4900.)

Figs. 11–16. *Hemiselmis rufescens* n.g., n.sp.

Fig. 11. Young motile stage with vacuole, stigma and pyrenoid, ventral view.

Fig. 12. Older motile stage with two pyrenoids, ventral view.

Fig. 13. Older motile stage, lateral view.

Fig. 14. Older motile stage with two chromatophores, ventral view.

Fig. 15. Early division stage in motile individual showing the oblique line of fission, ventral view.

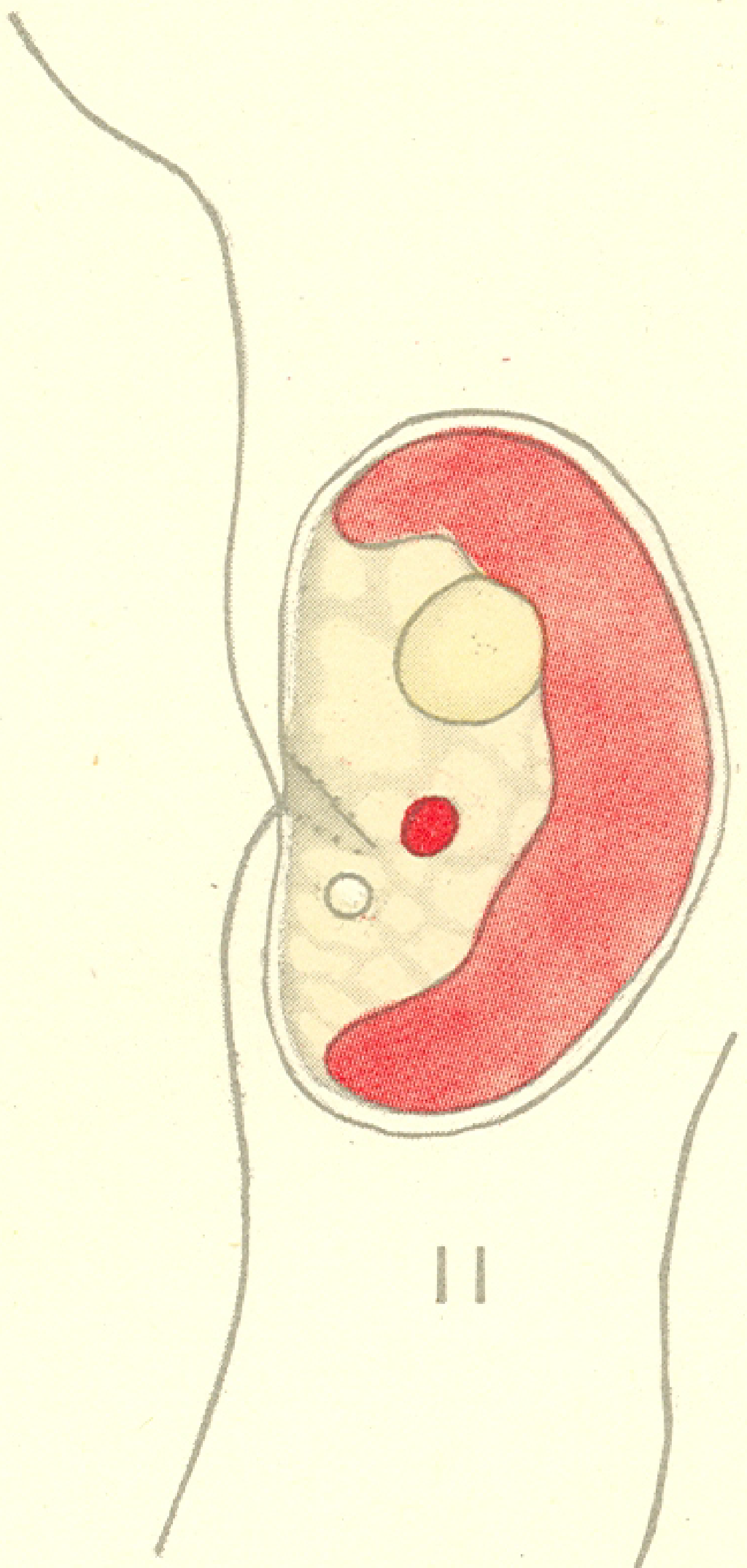
Fig. 16. Later division stage with fission nearly completed.

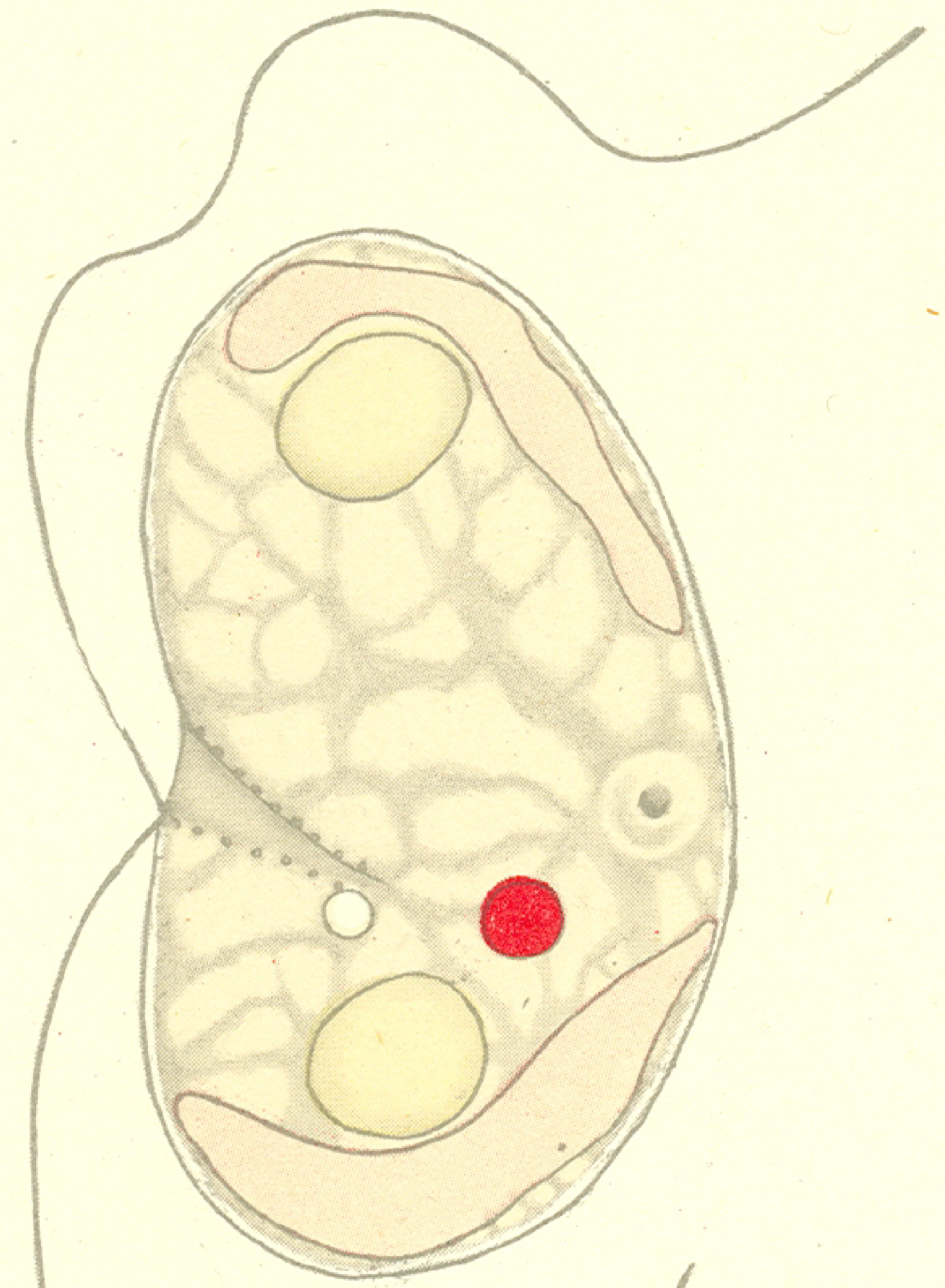
Figs. 17, 18. *Pyramimonas grossii* n.sp.

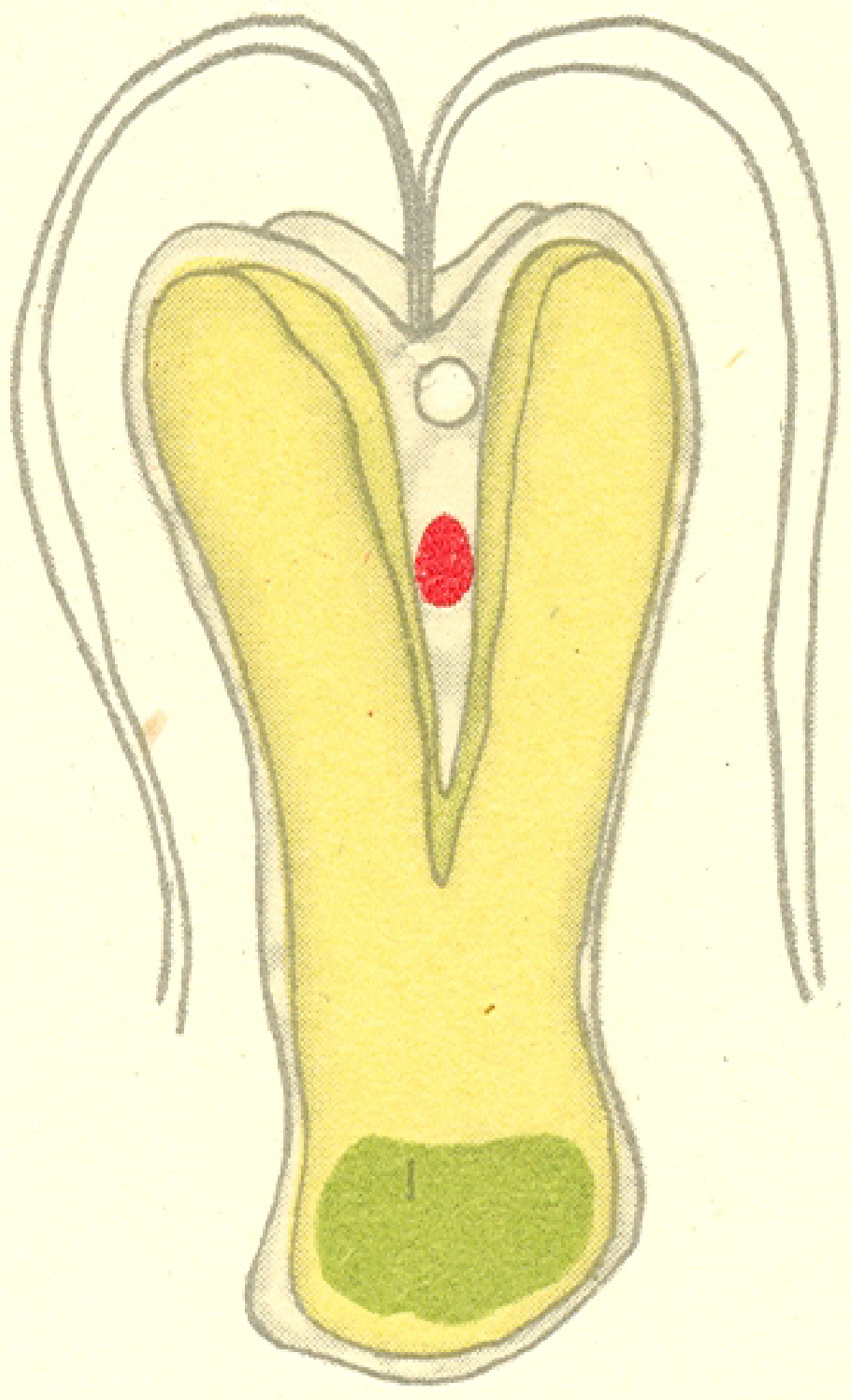
Fig. 17. Young motile stage, showing the position of the flagella when the organism is swimming, side view.

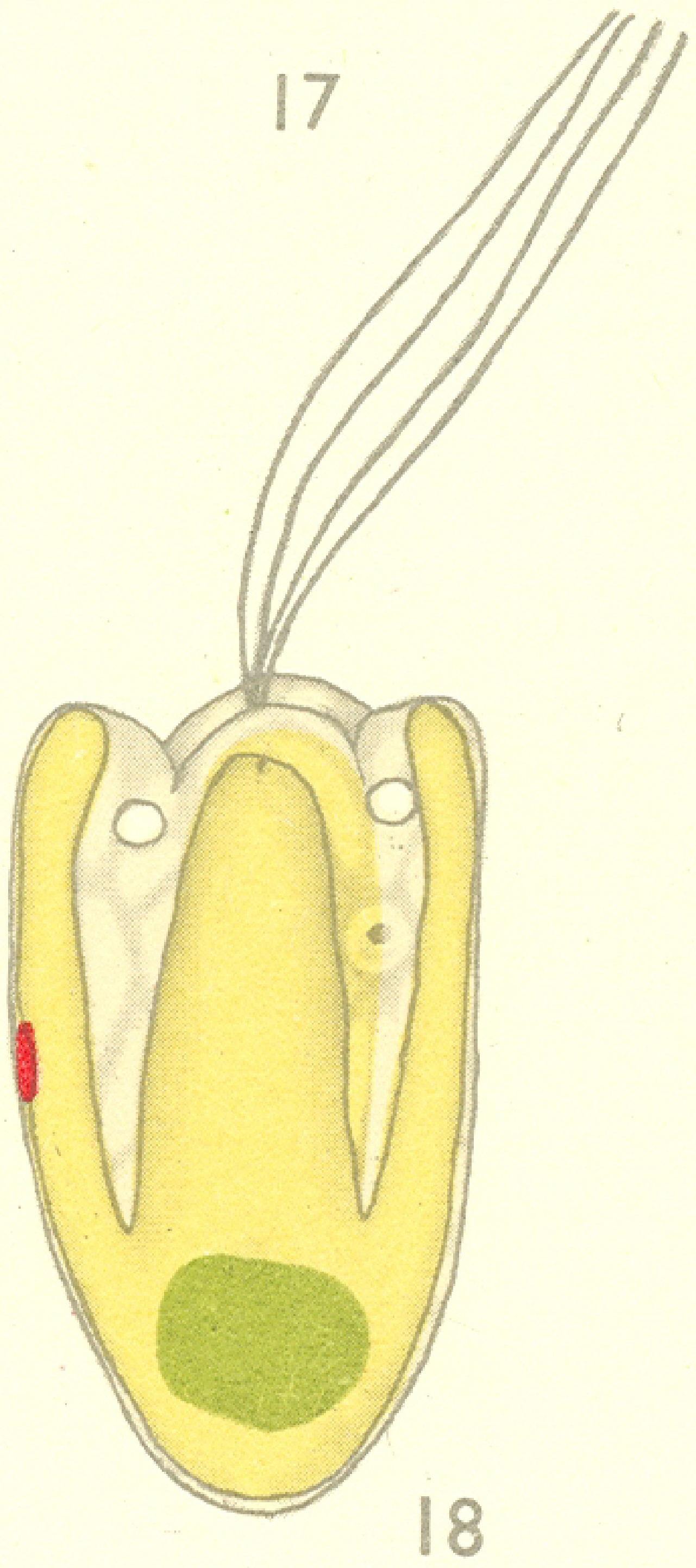
Fig. 18. Young motile stage, showing the position of the flagella when the organism is quiescent, side view.

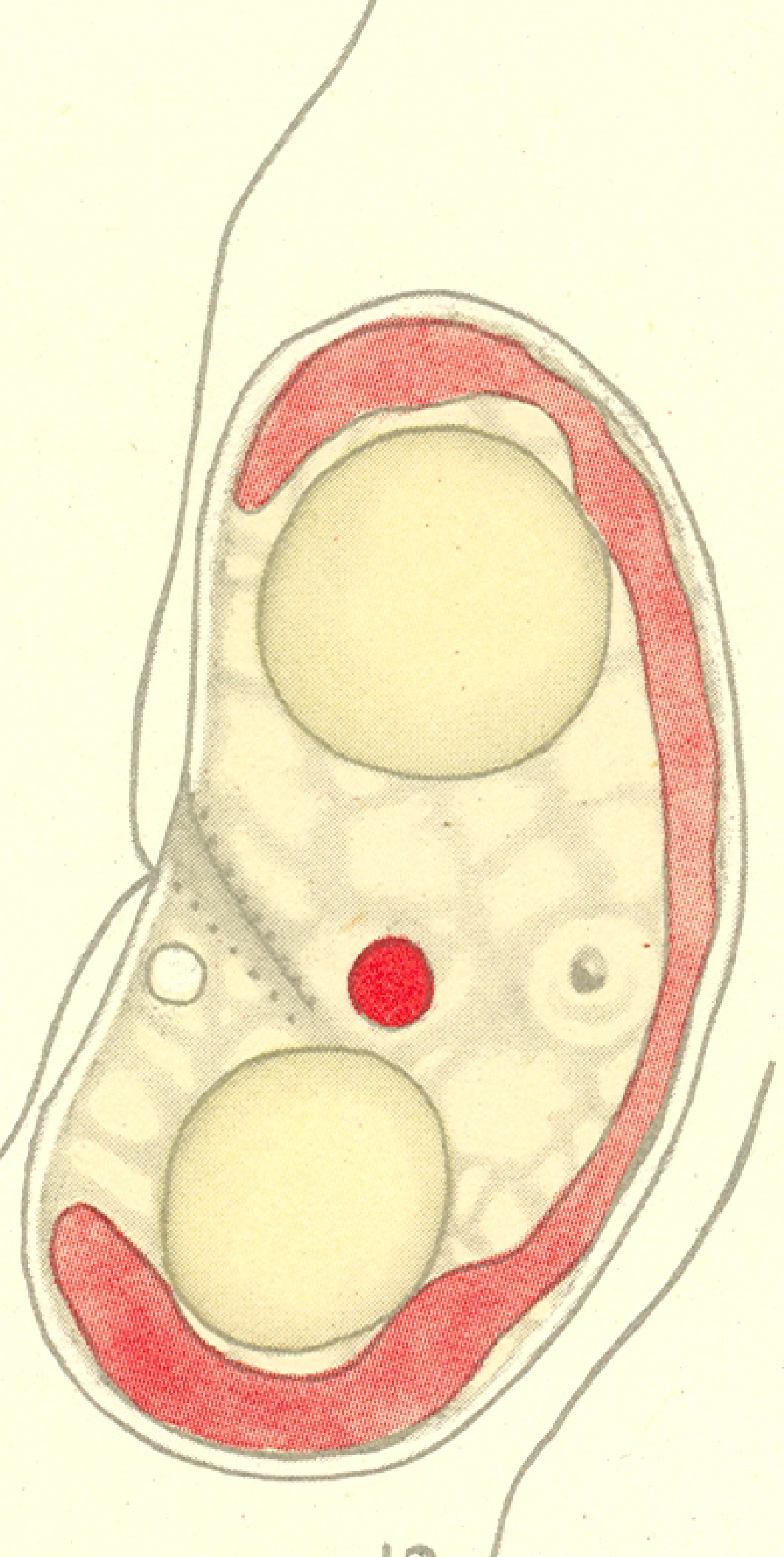

1
2
3
4
5
6
7
8
9
10


11

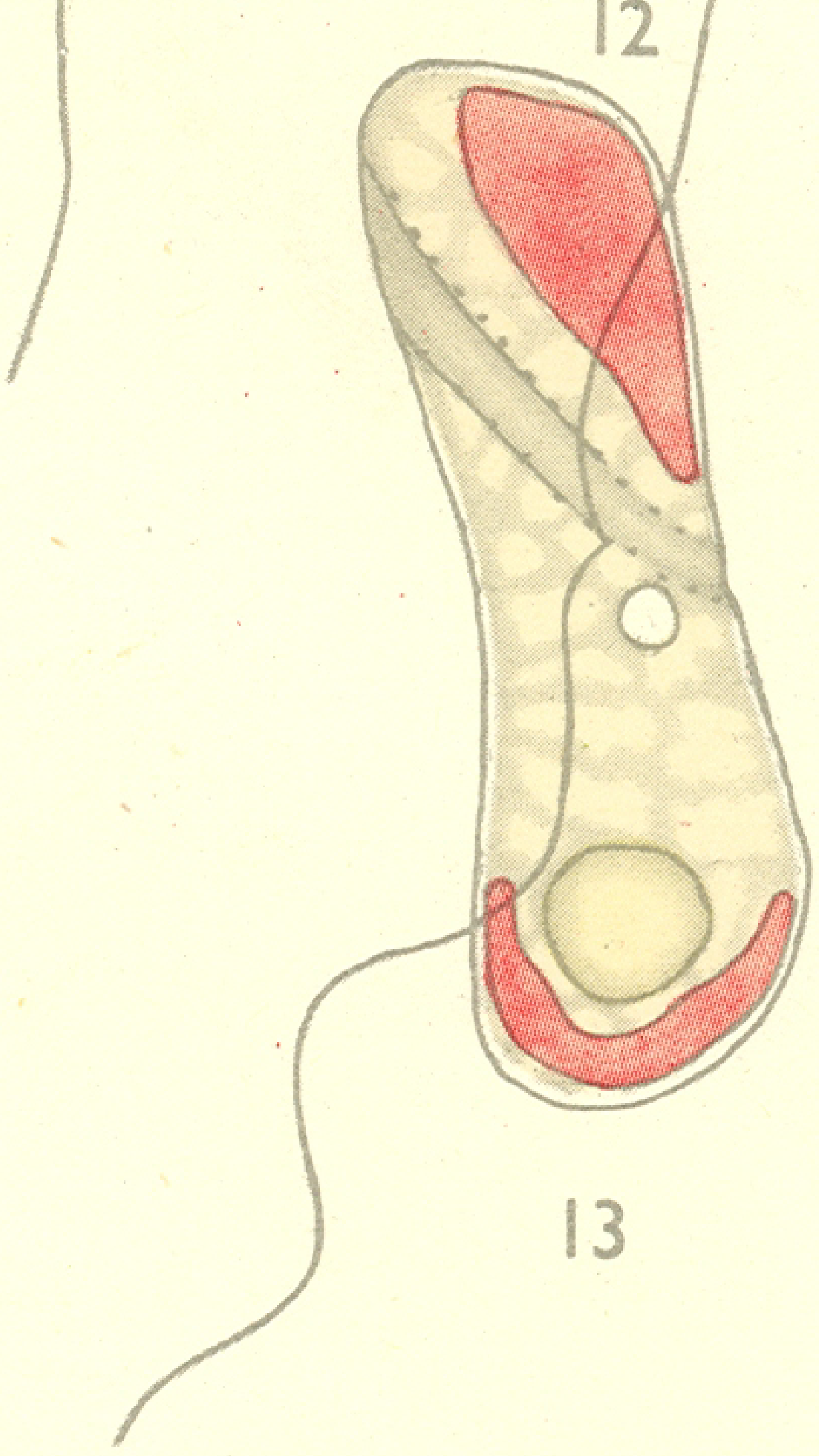

14

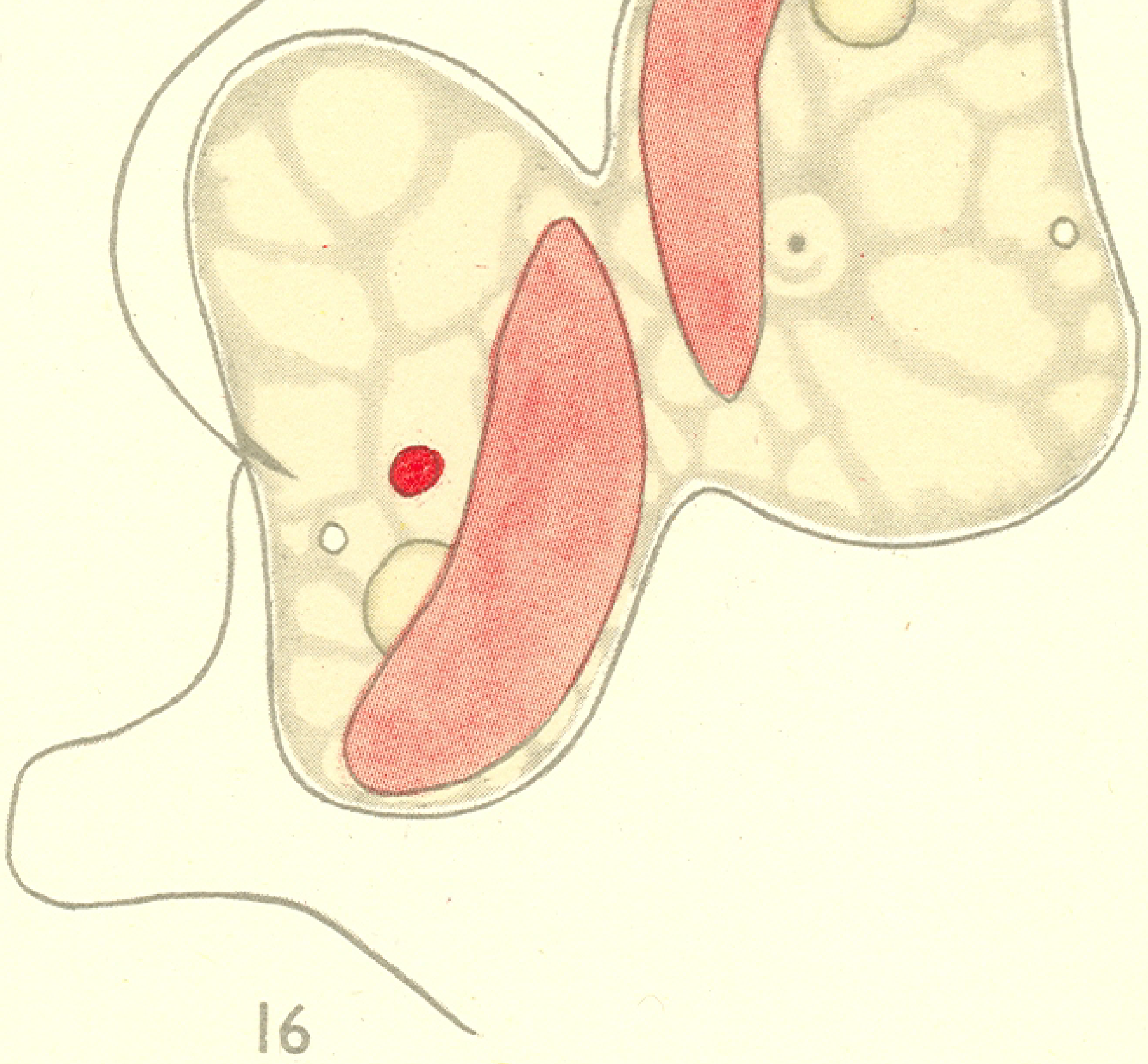

17


18


12


15


13


16

THE POST-LARVAL SAND EELS (AMMODYTIDAE) OF THE CELTIC SEA AND PLYMOUTH AREA

By P. G. Corbin, B.A.
Zoologist at the Plymouth Laboratory
and Vidya Vati, M.Sc.
Indian State Scholar, Lucknow University

(Plates I & II and Text-figs. 1–6)

CONTENTS

INTRODUCTION

The young stages of certain species of sand-eels (Ammodytidae) can be distinguished by differences in their pigmentation. Ford (1920) has described the post-larvae of *Ammodytes lanceolatus* Lesauvage and *A. tobianus* L. The post-larva of *A. marinus** Raitt has been identified by Kändler (1941), and Fage (1918) has given an account of the post-larva of *Gymnammodytes cicerellus* (Rafinesque). In addition to post-larvae of *lanceolatus*, *tobianus* and *marinus*, a fourth *Ammodytes* post-larva, with a pigmentation pattern distinct from those of the above four species, has been found in collections from the Celtic Sea and Plymouth area.

The occurence of four *Ammodytes* post-larvae in this area is of particular interest in relation to the observations of Kändler (1941), who also found four *Ammodytes* post-larvae in the southern North Sea and Baltic. He records post-larvae of *lanceolatus*, *marinus* and two forms of *tobianus*, a spring brood form and an autumn brood form, both differently pigmented. These Kändler refers to two races of *tobianus* which he is able to distinguish in the

---

* Duncker & Mohr (1939) do not accept *A. marinus* as a separate species. The identification of the post-larva by Kändler (1941) and the specific scale distribution pattern in the adult (paper in manuscript, P.G.C.) leave no doubt, however, that it is a valid species, distinct from *A. tobianus*.

adults—the spring spawners and the autumn spawners. The pigmentation of the fourth *Ammodytes* post-larva from Plymouth and the Celtic Sea agrees very closely with the description of the pigmentation of the autumn-brood *tobianus* post-larva from the North Sea and Baltic (Kändler, 1941, p. 66).

The fourth post-larva from the Celtic Sea and Plymouth area is also of interest in relation to the four species of adult Ammodytidae (*A. lanceolatus*, *A. tobianus*, *A. marinus* and *G. semisquamatus* (Jourdain)) recorded by Raitt (1934, 1935) in Scottish waters. In this connexion, it is to be noted that Duncker & Mohr (1935, 1939), in their revision of the Ammodytidae, placed the smooth sand eels in a new genus, *Gymnammodytes*, and divided the former single European species, *A. cicerellus*, into two species, *G. cicerellus* and *G. semisquamatus*. It may be anticipated from this division that specific differences will be evident in the young stages of these two species, including differences of pigmentation which would distinguish the post-larvae of *G. cicerellus* from those of *G. semisquamatus*. The young stages of *G. cicerellus* described by Fage (1918) were all taken in the Mediterranean, with the exception of four specimens caught off the mouth of the River Tagus, Portugal. No other occurrence of a similar post-larvae is recorded throughout the widespread and detailed investigations on the young fish of European Atlantic waters. Duncker & Mohr (1939) assign all former records of *A. cicerellus* from the Mediterranean, including the post-larvae described by Fage, to *G. cicerellus*, and those from the Atlantic coastline of Europe to *G. semisquamatus**. On the basis of this distribution, the young stages of *G. semisquamatus*, if separable by differences of pigmentation according to the above inference, have not hitherto been captured or identified.

There seemed then at the outset to be two possible interpretations of the fourth *Ammodytes* post-larva from the Celtic Sea and Plymouth area. It might belong to the Atlantic *G. semisquamatus* which is known from Raitt's records of the adult to be abundant in the north-east Atlantic. Or, to judge from its close resemblance to Kändler's autumn brood *tobianus* post-larva, it might belong to *Ammodytes tobianus*. In this latter event there would then be two forms in the south-western area as well as in the North Sea and Baltic.

The present study leads, however, to the conclusion that neither of these two possible interpretations applies, and that the fourth post-larva from the Celtic Sea and Plymouth area, although undoubtedly belonging to the family Ammodytidae, is not attributable to a known species.

Before discussing the evidence which leads to this conclusion, it will be relevant briefly to review some of the previous literature.

---

* A strict interpretation of this would ascribe the four post-larvae caught off the mouth of the Tagus to *G. semisquamatus*. Fage, however, considered them to belong to the series of young stages of *G. cicerellus* taken in the Mediterranean. But it must be recalled that this was before Duncker & Mohr's separation of the two species.

PREVIOUS EUROPEAN RECORDS OF AMMODYTIDAE

In addition to the two commonly known British species, *Ammodytes lanceolatus* and *A. tobianus*, Raitt (1934, 1935) recorded *Gymnammodytes semisquamatus* and a new species, *A. marinus*. He found *marinus* to the north and west of Scotland and in the North Sea in greater abundance than any of the other three species. It is now also known to occur in the Irish Sea off the Isle of Man*, in addition to the present records of the young stages from the Celtic Sea and off Plymouth. Adult *marinus* have not, however, been taken in the south-western area. Raitt also found *G. semisquamatus* in very considerable numbers to the north and west of Scotland, but less commonly on the east coast and in the open North Sea. Before this discovery of the abundance of this species in Scottish waters, it was considered to be restricted, with the exception of a very few isolated records from northern waters (Shetlands, one specimen as *A. siculus*, Günther, 1867: Southern Norway, five specimens as *A. cicerellus*, Collett, 1904; Grieg, 1912: Sweden, Lönnberg, 1915), to the St Malo region in the southern half of the mouth of the English Channel (Jourdain, 1879; Moreau, 1891), the Atlantic coastline of France (Acloque, 1900), Portugal and Spain (de Buen, 1935). It has recently been found in the Irish Sea* and in the English Channel off Plymouth*. It did not occur in the extensive collections made by Kändler (1941) in the Baltic and southern North Sea although it is recorded by Poll (1947) from the latter area. The distribution of the adults of the European Ammodytidae may be summarized from the above records and those of other authors:

A. lanceolatus. Iceland[1,2],† Norway[3], Faroes[1,2], Baltic[4], North Sea[4,5,6], west coast of Ireland[6], Irish Sea[7], English Channel[6], France (Biscay)[8], Spain (Biscay)[9], Portugal (south to mouth of River Tagus)[10]; very rarely found in Mediterranean[6], not recorded from Spanish Mediterranean coast[9].

A. marinus. Greenland[1,2], Iceland[1,2], Norway[11], Faroes[1,2], Baltic[4], North Sea[4,5], Irish Sea[12]; not recorded from west coast of France, Spain, Portugal, or from Mediterranean.

The present distribution records of *marinus* post-larvae have a southern limit in the mouth of the English Channel (pp. 307–9), and consequently the possibility of the species occurring even farther to the south cannot be excluded.

A. tobianus. Greenland (one specimen)[1], Iceland[1,2], Norway[11], Faroes[1,2], Baltic[4], North Sea[2,4,5], Irish Sea[6] (*marinus* not then distinguished), English Channel[6] (*marinus* not then distinguished), France (Biscay)[8], Spain[9], Portugal[9], Mediterranean (Balearic Islands and Spanish coast from Franco-Spanish border to Cape Nao)[9].

The records of *tobianus* to the south of the English Channel are included here since *marinus* has not yet been identified to the south of the Channel.

---

* Records to be published in a further communication.

† For explanation of figures see page 291.

Day (1880–84) records *tobianus* as common round the Irish coast. The preponderance of *marinus* to *tobianus* on the west coast of Scotland (Raitt, 1934) strongly suggests that *marinus* may occur on the Atlantic coast of Ireland.

G. semisquamatus. Norway[13, 14], Sweden[15], North Sea[5, 16], Irish Sea[12], western English Channel[12, 17, 18], France (Brittany)[19], Spain (not coast of Galicia)[9], Portugal[9].

G. cicerellus. Mediterranean[20], Black Sea[20].

The distribution of the young stages of the European Ammodytidae cannot be so fully outlined as that of the adults owing to the fact that *tobianus* and *marinus* were not distinguished in the earlier accounts* before Kändler's (1941) identification of the post-larva of *marinus*. Only those records, therefore, in which the possibility of confusion of these two species does not occur, are included in the following summary:

A. lanceolatus. Baltic[4], north and west coasts of Scotland[12], North Sea[4, 12], Irish Sea[21], Celtic Sea[22], Plymouth[22, 23].

A. marinus. Faroes[12], Baltic[4], north and west coasts of Scotland[12], North Sea[12, 20], Celtic Sea[22], Plymouth[22, 23].

A. tobianus. Baltic[4], north coast of Scotland[12], North Sea[12, 20], Celtic Sea[22], Plymouth[22, 23].

G. semisquamatus. Norway, Bergen (3 specimens, 47·5, 60·0 and 78·0 mm.)[13]; Channel Islands (2 specimens, 50·0 and 55·0 mm.)†; ? this species, Portugal, off River Tagus (4 specimens, 35·0–45·0 mm.)[24]. Fage (1918) refers these specimens to the series of post-larvae of *G. cicerellus* from the Mediterranean although, as previously pointed out (p. 288, footnote), the locality of capture suggests, according to the distribution of the two species given by Duncker & Mohr (1939), that they may be attributable to *G. semisquamatus*. This possibility is given support by the fact that a detailed comparison of the distribution of the individual melanophores which make up the gross pigmentation and of the gross pigmentation itself showed no differences between the specimens of *semisquamatus* found in the Channel Islands and examples of *cicerellus* of similar size from Sebastopol in the Black Sea (12 specimens, 47·0–63·0 mm.) and also from the Naples area (21 specimens, 52·0–68·0 mm.)‡. There was, however, no difficulty in identifying the two species by their respective long (*cicerellus*) and short (*semisquamatus*) ventro-lateral skin fold (Duncker & Mohr, 1939), and all

---

* See Appendix on pages 311–12.

† The writers are much indebted to Miss Ursula M. Grigg for the two specimens from the Channel Islands, which, as far as is known, are the only records of any young stages of *G. semisquamatus* from British waters. They were both found dead on the sand near low water (50 mm., Petit Port, Guernsey, 7 September 1948; 55 mm., Beau Port, Jersey, 31 August 1948).

‡ The writers' thanks are due to Dr E. Trevawas, British Museum (Natural History), for permission to examine the Black Sea specimens, and to Dr R. Dohrn, Director of the Stazione Zoologica, for kindly providing the specimens from the Naples area.

these juvenile specimens were referable to the genus *Gymnammodytes* by the characteristic structure of the lateral line (Jourdain, 1879; Duncker & Mohr, 1939). Concerning the four specimens taken off the mouth of the River Tagus, Fage wrote "Il est donc impossible de distinguer ces individus de ceaux à peine plus âgés (3 specimens, 10–12 cm.) pris le 21 Février 1911 à Messine...". And of the Mediterranean post-larvae of *G. cicerellus*, he observed that the striking melanophore pattern of the earlier stages (Figs. 5 & 6; 7·5 and 11·0 mm.; Fage, 1918) becomes less pronounced with increased size (Fig. 7; 25·0 mm.; Fage, 1918). There is thus, in the late post-larvae and juveniles of these two species of *Gymnammodytes*, a similar difficulty of specific identification (by pigmentation alone) to that found in the same stages of the three species of *Ammodytes* (p. 294), although no such difficulty occurs in the earlier stages of the *Ammodytes* spp.

G. cicerellus. Western Mediterranean, Alboran Sea, Balearic Islands, Tyrrhenian Sea, Straits of Messina[24]; eastern Mediterranean, off Alexandria[22]; ? this species, Portugal, off River Tagus[24] (see above).

[1] Bruun (1941).
[2] Jensen (1941).
[3] Wollebæck (1924).
[4] Kändler (1941).
[5] Raitt (1934).
[6] Day (1880–84).
[7] Moore (1937).
[8] Joubin & LeDanois (1924).
[9] de Buen (1935).
[10] Gonçalves (1942).
[11] Soleim (1945).
[12] Records to be published in a further communication.
[13] Collett (1904).
[14] Grieg (1912).
[15] Lönnberg (1915).
[16] Poll (1947).
[17] Jourdain (1879).
[18] Moreau (1891).
[19] Acloque (1900).
[20] Duncker & Mohr (1939).
[21] Bal (1944).
[22] Present records.
[23] Ford (1920).
[24] Fage (1918).

PROBLEMS IN IDENTIFYING THE POST-LARVAE

The pigmentation of the *A. lanceolatus* and *A. tobianus* post-larvae in the present collections is in full agreement with the figures and descriptions given by Ford (1920), and the pigmentation of the *A. marinus* post-larvae agrees with Kändler's (1941) figure and description. The pigmentation of the post-larva of *G. cicerellus* (Fage, 1918, Figs. 5–7) is strikingly different from that of the above three species and from that of the species IV post-larva occurring in the Celtic Sea and Plymouth area. It has already been mentioned that the two post-larval forms of *tobianus* from the southern North Sea and Baltic are each distinguishable by a different pigmentation pattern (Kändler, 1941). The post-larvae of the spring brood (*id.*, fig. 3*c*, p. 64) are more heavily pigmented in general than those of the autumn brood (*id.*, p. 66), and Kändler (*id.*, p. 65) identifies the darker spring form with the Plymouth *tobianus* post-larva described by Ford (1920). Ford's specimens were caught in late summer, July, August and September (Clark, 1920), and the *tobianus* post-larvae of the present collections also show a maximal occurrence in August and September (Table III, p. 304).

As earlier remarked, the melanophore pattern of Kändler's more lightly pigmented autumn brood *tobianus* post-larva, of which he gives a full description, but unfortunately no figure, very closely resembles the pigmentation of the species IV post-larva which occurs in this area in the spring (Table III, p. 304).

It is important to emphasize the agreement of pigmentation in the lightly pigmented pair of post-larvae (species IV, this area; *tobianus*, North Sea and Baltic, Kändler) and in the dark pair (*tobianus*, this area, Ford; *tobianus*, North Sea and Baltic, Kändler), since the times of occurrence of each member of the two pairs are exactly opposite in the two areas:

	Celtic Sea and Plymouth		Southern North Sea and Baltic	
	Light form	Dark form	Light form	Dark form
Spring	Species IV	..	..	*tobianus* (Kändler)
Autumn	..	*tobianus* (Ford)	*tobianus* (Kändler)	..

Notwithstanding this inversion in the times of occurrence, the two forms from each of the two areas might well be considered on the criterion of pigmentation to be identical. If this were so, a spring brood and an autumn brood of *tobianus* post-larvae, similar to the double brood found by Kändler in the North Sea and Baltic, could be recorded from Plymouth and the Celtic Sea. This appears, however, to be excluded by the following evidence obtained from a study of the number of vertebrae in the post-larvae (Table II and pp. 301–4).

There is a separation of 5·67 ± 0·400 between the means of the number of vertebrae of the *tobianus* (66·33 ± 0·360) and species IV (72·0 ± 0·175) post-larvae from Plymouth and the Celtic Sea, and there is no overlap in their ranges (*tobianus*, 64–69: species IV, 70–74). A difference of this magnitude between the mean vertebral numbers of the two different *Ammodytes* post-larvae occurring in the same area, although at different seasons, is considered to preclude the possibility of their belonging to the same species.

Although Kändler has not examined the number of vertebrae in the post-larval *tobianus* of the spring and autumn broods from the southern North Sea and Baltic, his counts of adult spring and autumn spawners show only a very small difference of less than 1·0 between their means (Kändler, 1941, Table 25, p. 122):

	North Sea	Baltic
Spring	63·09	63·17
Autumn	64·08	63·49
Difference	0·99	0·32
Error of difference	± 0·071	± 0·061

It is noteworthy that the means of the North Sea and Baltic autumn-spawning adult *tobianus* (64·08 North Sea; 63·49 Baltic), which give rise to the autumn brood of post-larvae with the light pigmentation corresponding to species IV, are considerably lower than the mean of the *tobianus* post-larvae

(66·33) from this area. The differences (7·92, 8·51) between the means of these North Sea and Baltic autumn-spawning adult *tobianus* and that of species IV are thus even greater than the difference (5·67) between the means of species IV and the *tobianus* post-larva of this area. It is considered as before that these wide differences preclude the possibility of identifying the species IV post-larva with the *tobianus* post-larvae, in particular the light form, from the North Sea and Baltic.[*]

It has already been mentioned that the pigmentation of the post-larvae of *G. cicerellus* described by Fage (1918) is very distinct from that of the species IV post-larvae, and also that no post-larvae have hitherto been found which can be attributed to the adult *G. semisquamatus*, which occurs commonly in Scottish waters (Raitt, 1934). A sample of these Scottish *G. semisquamatus*[†] was found to have a mean vertebral number of 68·16 ± 0·127 (Table II, p. 302). This figure is 3·84 ± 0·022 less than the mean of species IV (72·0), and although it is the nearest approach to the species IV mean, it seems highly unlikely that an adult with a mean vertebral count of 68·16 could be related to a post-larva with a mean of 72·0, even allowing for geographical variation.[‡]

It is therefore concluded from the above evidence that the post-larval *Ammodytes* species IV is not related to the Atlantic *Gymnammodytes semisquamatus* or to *A. tobianus* from either the Celtic Sea and Plymouth area or the southern North Sea and Baltic.

It appears then that the species IV post-larva cannot be attributed to a known adult, and it can only be concluded that it belongs to another species of *Ammodytes*. If this interpretation proves to be correct, the number of species of Ammodytidae in the Celtic Sea and Plymouth area is thus increased to five:

Adult:	*A. lanceolatus*	*A. tobianus*	*G. semisquamatus*	Not recorded	Not known
Post-larva:	*A. lanceolatus*	*A. tobianus*	Not recorded	*A. marinus*	Species IV

The description (pp. 299–500) and figures (Pl. II, fig, 2) of the species IV post-larva show that the type of development, the general body form and the scheme of pigmentation all very closely resemble the same characters in the post-larvae of *lanceolatus*, *tobianus* and *marinus*, and such conformity is held to substantiate the inclusion of species IV in the family Ammodytidae, although no certain distinction between the genera *Ammodytes* and *Gymnammodytes* can be made.

No great numbers of adult Ammodytidae have been collected and examined from this south-western area. With sufficient search it appears likely that adult

---

[*] Kändler's vertebral counts of adult *tobianus* from the North Sea and Baltic are here taken as representative of the vertebral counts of the post-larvae from the area.

[†] These specimens, part of Dr D. S. Raitt's original material, were kindly provided by Dr R. S. Clark, lately Director of the Marine Laboratory of the Scottish Home Department, Aberdeen.

[‡] There are no vertebral count data of Mediterranean *G. cicerellus* from which a mean can be calculated. Fage (1918) gives the range as 66–69 and Duncker & Mohr (1939) give the figure 67 (39 + 28). It is not stated whether these figures are inclusive or exclusive of the urostyle.

marinus will be found. It remains to be seen whether further search will also bring to light the adult of species IV.

Despite the almost exclusive relation to post-larval stages of the present data, it is felt that they are worth publication in order that the numerous questions which call for further study may be brought to the notice of other workers. Some of the questions awaiting solution are at once apparent.

Vertebral count data of adult *lanceolatus*, *marinus* and species IV from this area are needed for comparison with the present post-larval data.

Further data are required to resolve the anomalous difference between the number of vertebrae in adult and post-larval *tobianus* from this area (p. 303).

A search for the adult of species IV must be made and, if successful, its identification will need to be established.

These problems arise directly from the present study. Others of wider relevance are also evident. Thus vertebral count data of both adult and post-larval *G. cicerellus* from the Mediterranean are required; while intimately connected with this is the need for continued search for the post-larva of the Atlantic *G. semisquamatus*, and for an investigation of the breeding habits of this species.

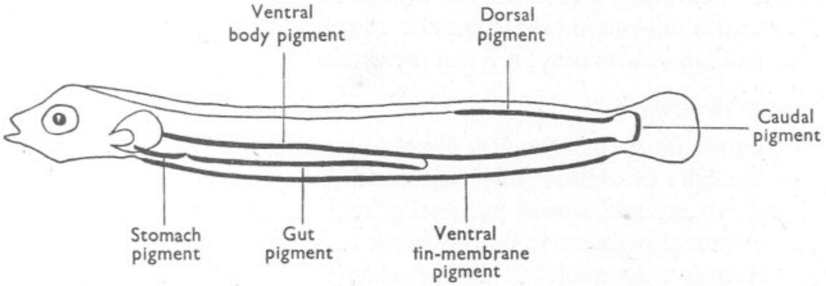
Of rather different character, but none the less important, is the need for full confirmation of the identification of the known Ammodytidae post-larvae with the known adults. *A. lanceolatus* appears to be the only species in which the post-larvae can with certainty be linked with the adult (pp. 301–3). The available facts give every indication that the post-larvae of *A. tobianus*, *A. marinus* and the Mediterranean *G. cicerellus* are correctly assigned to their respective adults. It must, however, be admitted that the chain of evidence is not entirely complete. In none of these three species has it yet been possible fully to apply Schmidt's classic method of seriation from early larva to adult or recognizable adolescent. The frequently encountered difficulty of obtaining a full series of adolescent stages, intermediate between the late post-larva and the juvenile with adult characters, may be in part responsible for the gap. Moreover, in *lanceolatus*, *tobianus* and *marinus*, the specificity of the post-larval pigmentation lessens with increasing age until it is extremely difficult to separate the late post-larvae and early adolescents. Rearing from artificial fertilizations of known parentage should, however, provide material for comparison with the existing descriptions of the post-larvae of *A. tobianus*, *A. marinus* and *G. cicerellus*. But the difficulty of rearing a large enough number of young stages to a size suitable for alizarin staining presents considerable obstacles to the solution of the vertebral count problems. And were it achieved, it is certain that the laboratory conditions would greatly differ from the spawning ground conditions which are generally thought to have considerable influence on the definitive number of vertebrae.

MATERIAL

The material for the present paper was collected by standard ½ hr. oblique hauls of the 2 m. stramin ring-trawl on the 1937–39 mackerel investigation cruises in the Celtic Sea (Corbin, 1947), and in the weekly plankton collections of 1930, 1931 and 1935–37 taken near the Eddystone light-house for the purpose of observing the yearly fluctuations in the abundance of young fish in the Plymouth area (Russell, 1930–47). More than 6000 *Ammodytes* post-larvae from the 1937–39 cruises have been examined together with some 850 specimens from the Plymouth collections. They range in length from about 5 mm. to about 30 mm. The writers are much indebted to Mr F. S. Russell for the loan of the Plymouth young fish collections of 1930–37 and of specimens of *G. cicerellus* post-larvae from the Eastern Mediterranean off Alexandria, and to Mr G. M. Spooner for his help with the calculations. Further acknowledgements occur in the text.

THE PIGMENTATION OF THE POST-LARVAE

The nomenclature used to describe the pigmentation of the post-larvae is shown in Fig. 1. An identification key is given on p. 300.



Text-fig. 1. Diagram showing the nomenclature of the pigment rows.

Ammodytes lanceolatus (Plate I, fig. 1)

Post-larva 4·5 mm. (a)

The fin-membrane is entire from the head, round the body and tail to the throat. Ventral body pigment extends from behind the head to the tail; it is a double line of melanophores in the pre-anal region, a single line post-anally. The stomach pigment and gut pigment form a single row of melanophores, but are distinguishable by the closer spacing of the melanophores on the stomach. Ventral fin-membrane pigment is present as a row of melanophores extending from the stomach nearly to the tail. There is seldom any indication of a dorsal pigment row at this early stage.

Post-larva 7·5 mm. (b)

The fin-membrane is still complete. Ventral body pigment, stomach, gut and ventral fin-membrane pigment rows are as in the preceding stage. The first rudiments of caudal fin-rays show ventrally to the tip of the notochord, and caudal pigment is present as one or two melanophores at the base of the developing rays. The specimen illustrated has rather heavier caudal pigmentation than is usual at this stage. Dorsal pigment is represented by two or three melanophores in the immediate pre-caudal region. The specimen figured is in this respect also slightly more heavily pigmented than typically.

Post-larva 12·5 mm. (c)

The dorsal and ventral fin-membranes are still complete, and dorsal and anal fin-rays are developing post-anally. Caudal fin-rays are well developed. Dorsal, caudal, ventral, stomach, gut and ventral fin-membrane pigmentation is similar to the preceding stage. Post-anally the ventral body pigment is a double row of melanophores almost to the tail. Teeth-like structures (Ford, 1920) are present on the upper jaw. It is of interest to compare this figure with the specimen illustrated by Ford (1920, Fig. 1, p. 243) which, although very slightly smaller (12·0 mm.), shows considerably more development of the dorsal, caudal and anal fin-rays, and almost complete disappearance of the ventral fin-membrane and loss of its pigment line.

The ventral fin-membrane pigment row is characteristic of the earlier post-larva of *lanceolatus* only; it is not present in *marinus*, *tobianus* or species IV.

Post-larva 18·5 mm. (d)

The ventral fin-membrane has almost completely disappeared. The anal fin-rays are fully or almost fully developed. The dorsal fin-rays are further developed but are still absent pre-anally in the reduced fin-membrane. The dorsal and caudal pigment is slightly more developed. Pre-anally the ventral body pigment is very much less distinct than post-anally and is only visible by transparency through the abdominal walls. It becomes obscured by the thickening and downward growth of the walls of the abdomen. The stomach and gut pigment is much reduced at this stage or even absent. Teeth-like structures are present on the upper jaw.

Post-larva 26·5 mm. (e)

Fin-rays are developed throughout the length of the dorsal fin. The dorsal pigment extends from the tail to just in front of the anus and is considerably more developed than in the preceding stage. The caudal pigment has increased. The pre-anal ventral body pigment is further obscured. The gut pigment is lost and the stomach pigment may be absent (as in the specimen figured) or represented by one to four small melanophores, seldom more.

Ammodytes marinus (Plate I, fig. 2)

Larva 6·25 *mm.* (*a*)

The fin-membrane is entire and an oil globule of considerable size is present. The earliest stages of *lanceolatus*, *tobianus* and species IV taken in the present collections are smaller than this larval *marinus*, but none has an oil globule. Dorsal pigment is absent. Ventral body pigment is present as a row of melanophores extending from behind the head to the end of the notochord. Pre-anally the row is double, post-anally it is single. The four or five terminal melanophores are not always as prominent as in the specimen illustrated. Stomach pigment is present. Gut pigment is lacking.

Post-larva 7·5 *mm.* (*b*)

Pigmentation is similar to the preceding stage. The oil globule has been resorbed. The first indications of the developing caudal fin-rays are present.

Post-larva 11·0 *mm.* (*c*)

The dorsal pigment row is present as two or three melanophores. Considerable development of the caudal fin-rays is evident, and what will later be the caudal pigment row is clearly seen at the base of the caudal rays. Other pigmentation resembles the preceding stage.

Post-larva 14·0 *mm.* (*d*)

Dorsal and ventral fin-rays are starting to develop in the post-anal region. The caudal pigment forms a prominent line of melanophores at the base of the caudal fin-rays which are now well developed. A slight increase in the number of melanophores in the dorsal pigment row is usual at this stage, although not apparent in the specimen figured. The gut pigment develops at this stage or a little earlier; it shows considerable variation. It may consist of a well-marked regular line of melanophores from stomach to anus, it may be completely lacking, or it may be an incomplete and interrupted row (see below, post-larvae of 18·5 and 19·0 mm.).

Post-larva 18·5 *mm.* (*e*)

The dorsal and anal fin-rays are almost fully developed in the post-anal region. Fin-ray development is not yet complete in the pre-anal region where the dorsal fin-membrane is reduced. The dorsal pigment is slightly increased and some gut pigment is present.

Post-larva 19·0 *mm.* (*f*)

This specimen which is at the same developmental stage as the above specimen of 18·5 mm., has generally heavier pigmentation, particularly in the dorsal row and on the gut.

Post-larvae 23·0 *and* 27·5 *mm.* (*g* and *h*)

A forward extension of the dorsal pigment is seen in these specimens. Other pigmentation remains essentially the same. Fin-ray development in the dorsal fin is complete.

From about 10 mm. onwards, the pre-anal ventral body pigment of *marinus* is very prominent. Although situated on the inner side of the walls of the abdomen, it remains markedly conspicuous and is not obscured by the increasing thickening of the developing abdomen wall until a much later stage than in *lanceolatus*, *tobianus* and species IV.

Ammodytes tobianus (Plate II, fig. 1)

Post-larva 5·25 *mm.* (*a*)

The fin-membrane is entire. The dorsal pigment consists of two melanophores situated a short distance forward of the tip of the notochord. The ventral body pigment extends from behind the head to a point just short of the tip of the notochord. Stomach pigment consists of a closely spaced row of melanophores which under certain conditions of expansion give the appearance of an almost continuous line. The gut pigment line continues on from the stomach pigment to the anus, but the melanophores are more openly spaced than in the stomach pigment line.

Post-larva 8·0 *mm.* (*b*)

The dorsal pigment row has developed considerably since the preceding stage. There is a small pre-anal group of melanophores and a fairly well-developed row post-anally. This interrupted appearance of the dorsal row, before the development of an unbroken line, is very characteristic of the earlier post-larvae of *tobianus*. Kändler (1941) makes this observation. Caudal fin-rays have begun to develop, but no dorsal or anal rays yet.

Post-larva 8·75 *mm.* (*c*)

Dorsal and anal fin-rays have begun to develop in the post-anal region. The caudal fin rays are well developed. The dorsal pigment line has increased since the preceding stage; it extends the full length of the body from the nape of the neck to the tail. It is more pronounced in the post-anal half; the melanophores are regularly spaced and larger than those in the pre-anal region where the spacing is somewhat uneven. The pre-anal ventral body pigment is less prominent than the post-anal section owing to the opacity of the abdomen walls. The contrast between the close spacing of the stomach pigment and the open spacing of the gut pigment is more evident here than in the earlier stage. No caudal pigment is present.

Post-larva 11·0 *mm.* (*d*)

Pigmentation is very similar to the preceding stage. Fin-ray development is further advanced.

Post-larva 15·5 *mm.* (*e*)

Fin-ray development in the dorsal fin is complete. For comparison it may be recalled that no pre-anal dorsal fin-rays are present in *lanceolatus* and *marinus* post-larvae of 18 or 19 mm. Ford (1920) observed this earlier development in *tobianus*. The dorsal pigment is complete from the neck to the tail, but is still more prominent in the posterior half. Two caudal melanophores are present. The gut pigment line is slightly broken.

Post-larva 23·0 *mm.* (*f*)

Caudal pigmentation is considerably increased. A medio-lateral line has begun to develop posteriorly. The pre-anal ventral body pigment is entirely obscured by thickening of the abdominal wall. The gut pigment line is further broken and reduced, but the stomach pigment is still prominent and characteristically closely spaced.

Ammodytes species IV (Plate II, fig. 2)

Post-larva 5·5 *mm.* (*a*)

The fin-membrane is entire. Dorsal pigment is represented by three melanophores in the pre-caudal region. Ventral body pigment extends from the region of the stomach to the tail, but not to the extremity of the notochord. Stomach pigment is present, but no gut pigment.

Post-larva 9·0 *mm.* (*b*)

Considerable caudal fin-ray development is evident. The dorsal pigment line now extends from the position of the anus to the root of the tail. No caudal pigment is present.

Post-larva 13·0 *mm.* (*c*)

Dorsal and anal fin-rays are beginning to develop in the post-anal region of the fin-membranes, and caudal fin-ray development is further advanced. Pigmentation is similar to that of the preceding stage. The dorsal and post-anal ventral body pigmentation is more pronounced.

Post-larva 17·5 *mm.* (*d*)

Caudal and anal fin-ray development is complete. Dorsal fin-rays are starting to develop pre-anally. A slight forward increment of the dorsal pigment is evident. A single melanophore is present at the base of the caudal fin-rays. The pre-anal ventral body pigment is becoming obscured by the thickening of the abdominal walls.

Post-larva 26·0 *mm.* (*e*)

Dorsal fin-ray development is complete. The dorsal pigment row has extended forward to the neck region, but post-anally it is more prominent.

Caudal pigmentation is now fairly pronounced. A medio-lateral pigment line is present in the pre-caudal region.

The foregoing descriptions of the pigmentation of *lanceolatus*, *tobianus*, *marinus* and species IV post-larvae have been confined to the longitudinal pigment rows shown in the diagram in Text-fig. 1. Another pigmentation feature common to *marinus*, *tobianus* and species IV, but not found in *lanceolatus*, is the presence of a melanophore at the base of each pectoral fin. This pair of pectoral melanophores is present in the post-larvae of *marinus* and species IV from a length of about 10–12 mm. onwards. In *tobianus* it is generally present earlier, from a length of about 7–8 mm.

Certain additional differences both of pigmentation and form are also to be noted. Ehrenbaum (1904) observed that the length of the upper jaw in relation to the diameter of the eye is greater in *lanceolatus* than in *tobianus*. Ford's (1920, Table II, p. 245) detailed measurements of these features show that this difference is apparent at all observed lengths but becomes particularly marked above a length of 8–10 mm. It was immediately noticeable in the mixed hauls of the present collections that the snout of the *lanceolatus* post-larvae is relatively longer than that of *marinus* and species IV as well as that of *tobianus*. Ford (1920) also noted that *tobianus* post-larvae are more advanced in structural development than *lanceolatus* post-larvae of the same length, and, it may now be added, than *marinus* and species IV post-larvae. The earlier development of the pectoral melanophores referred to above and the earlier replacement of cartilage by bone (p. 301) in *tobianus* post-larvae is in agreement with this observation. It should be further noted that the differences in the caudal pigmentation of the early and middle post-larvae of the four species described are lost in the late post-larval stage when the development of fin-rays is complete in the dorsal fin. The caudal pigment is then present in each of the four species as a row of melanophores at the base of the caudal fin-rays (Pl. I, fig. 1*e*, fig. 2*h*; Pl. II, fig. 1*f*, fig. 2*e*).

Identification key to the Ammodytes *post-larvae of the Celtic Sea and Plymouth area*

1 (2) Ventral fin-membrane pigment row present. Pectoral melanophores absent. Teeth-like structures on upper jaw present. Vomerine teeth present. **A. lanceolatus**

2 (1) Ventral fin-membrane pigment row absent. Pectoral melanophores present. Teeth-like structures on upper jaw absent. Vomerine teeth absent. **3**

3 (4) Caudal pigment strongly marked from earliest post-larval stage; not always present in earliest larvae with large oil-globule. **A. marinus**

4 (3) Caudal pigment absent or very reduced until late post-larval stages. **5**

5 (6) Ventral gut pigment present. **A. tobianus**

6 (5) Ventral gut pigment absent. **A. *species IV***

THE NUMBER OF VERTEBRAE IN THE POST-LARVAE AND ADULTS

The number of vertebrae was counted in alizarin-stained post-larvae of *lanceolatus*, *marinus*, *tobianus* and species IV. These data are given in Table I, together with a count of the number of vertebrae in a sample of adult *tobianus* from Exmouth (September 1947)*. Counts were made only from those specimens in which staining revealed that bone had fully replaced cartilage. This takes place in *tobianus* post-larvae at a length of about 13 mm., whereas *lanceolatus*, *marinus* and species IV post-larvae will not successfully stain below a length of 18–19 mm. This difference is in agreement with the previously noted earlier development of *tobianus* post-larvae.

TABLE I. THE NUMBER OF VERTEBRAE IN THE POST-LARVAL *AMMODYTES* SPP. OF THE CELTIC SEA AND PLYMOUTH AREA

No. of vertebrae (including urostyle)	Number of specimens				
	A. tobianus		*A. lanceolatus* (post-larvae)	*A. marinus* (post-larvae)	*Ammodytes* species IV (post-larvae)
	Post-larvae	Adults (Exmouth)			
62	..	1	..	..	..
63	..	12	..	..	..
64	1	23	1	..	..
65	1	10	..	..	..
66	6	6	1	..	..
67	2	..	9	5	..
68	1	..	24	16	..
69	1	..	15	18	..
70	..	..	2	6	2
71	..	..	..	..	4
72	..	..	..	..	16
73	..	..	..	..	4
74	..	..	..	..	2
Total no. of specimens	12	52	52	45	28
Mean vertebral no.	66·33	64·15	68·08	68·56	72·00
Standard error of mean	±0·360	±0·134	±0·082	±0·128	±0·175
σ	1·247	0·969	0·997	0·857	0·926

Alizarin staining of post-larval *lanceolatus* clearly showed the denticles on the upper jaw, a specific recognition character of the post-larva (Ford, 1920), and also made visible the pair of teeth on the vomer. It is of some importance to draw attention to the vomerine teeth in the post-larva of *lanceolatus*. They are a primary specific character of the adult. But as far as is known, there is no reference in the literature to their presence in the post-larva, which thus establishes a complete chain of specific characters in the development of *lanceolatus* from the late larva to the adult. The ventral fin-membrane pigment

---

* The writers are indebted to Mr N. A. Holme for kindly obtaining these specimens.

TABLE II. THE NUMBER OF VERTEBRAE IN THE NORTH ATLANTIC SPECIES OF AMMODYTIDAE

The standard deviation (σ) and the standard error of the mean have been calculated from the data of the authors quoted, with the exception of Kändler (1941), who gives values for the latter.

		Author	No. of specimens	Mean no. of vertebrae	Standard error of mean	Range of no. of vertebrae	σ
		A. tobianus					
Iceland		Bruun (1941)	52	62·56	±0·125	60–65	0·902
Faroes		Bruun (1941)	22	64·45	±0·200	63–66	0·940
Baltic, spring spawners		Kändler (1941, table 25, p. 122)	961	63·17	±0·033	60–67	1·035
autumn spawners			566	63·49	±0·051	60–67	1·216
North Sea, spring spawners			274	63·09	±0·057	61–65	0·944
autumn spawners			566	64·08	±0·043	61–68	1·031
Northern North Sea		Raitt (1934)	199	63·37	±0·063	60–66	0·984
Denmark		Jensen (1941)	82	63·37	±0·108	61–65	0·982
Exmouth		Present records	52	64·15	±0·134	62–66	0·969
Plymouth, post-larvae		Present records	12	66·33	±0·360	64–69	1·247
		A. lanceolatus					
Baltic		Kändler (1941, table 23, p. 120)	126	66·73	±0·076	65–69	0·853
North Sea			293	66·85	±0·047	65–69	0·805
Celtic Sea, post-larvae		Present records	52	68·08	±0·082	64–70	0·997
		A. marinus					
Greenland		Jensen (1941)	38	69·39	±0·195	67–72	1·204
Iceland		Bruun (1941)	97	71·53	±0·112	68–73	1·104
Iceland		Kändler (1941, table 24, p. 120)	31	71·13	±0·217	69–73	1·208
North Norway	Grense Jakobslev 17 July 1939	Soleim (1945)	200	71·74	±0·088	69–75	1·243
	Grense Jakobslev 30 Oct. 1939		168 (170)	72·06	±0·088	69–74	1·145
	Tana 16 Sept. 1939		89	71·88	±0·119	69–74	1·120
South Norway	Bergen 2 Sept. 1941		200	69·53	±0·076	67–72	1·074
Faroes		Bruun (1941)	129	69·67	±0·084	68–72	0·950
Northern North Sea		Raitt (1934)	205	69·21	±0·079	67–72	1·131
North Sea, German Bight		Kändler (1941, table 24, p. 120)	67	69·75	±0·124	67–72	1·015
Central Baltic, Pomerania			114	68·90	±0·107	66–72	1·142
East Baltic, East Prussia			291*	68·50	±0·066	65–72	1·135
Celtic Sea, post-larvae		Present records	45	68·56	±0·128	67–70	0·858
		Ammodytes *species IV*					
Celtic Sea, post-larvae		Present records	28	72·00	±0·175	70–74	0·926
		G. semisquamatus					
West Scotland and northern North Sea		Present records	51	68·16	±0·127	65–70	0·901
		A. dubius					
West Greenland		Jensen (1941)	179	75·10	±0·082	73–78	1·099
West Greenland		Jensen (1944, p. 15, note 5)	53	75·07		?–80	

* This figure is given, evidently in error, as 191 in Kändler's paper.

row (p. 296) still persists when the denticles on the upper jaw appear (Pl. I, fig. 1 *c*), and these in turn are still present when the adult character of the vomerine teeth appears in the later post-larvae.

For comparison with the vetebral counts of the post-larvae of this area (Table I), data obtained by other investigators from other north Atlantic areas are given in Table II.

Ammodytes tobianus

The number of *tobianus* post-larvae of stainable size was unfortunately small. There is, nevertheless, a significant difference between the mean number of vertebrae of the Plymouth post-larvae and of the adults from Exmouth and elsewhere. The excess, 2·18, of the Plymouth post-larvae over the Exmouth adults is more than five times its error: in fact the two populations appear to differ by at least 1·40. Until further data from this area are obtainable on the number of vertebrae in both the adults and post-larvae, this difference will remain something of an anomaly. The mean of the Exmouth sample is in keeping with the findings of other authors. But the mean of the post-larvae suggests, despite the smallness of the sample, that what are here taken to be *tobianus* do not in fact belong to the species. On the other hand, the pigmentation and time of occurrence of the post-larvae are characteristic of *tobianus*. The pigmentation of each individual was very carefully noted before staining and without exception was in full agreement with the figures and descriptions of Ford (1920) and Kändler (1941) (dark form, spring brood).

Ammodytes lanceolatus

Kändler's figures (1941, Table 23, p. 120) are the only published data from large samples on the number of vertebrae in adult *lanceolatus*. Their means are noticeably lower than the mean of the Celtic Sea post-larvae. As mentioned above, the identification of the post-larvae was confirmed by the denticles on the upper jaw and the pair of vomerine teeth.

Ammodytes marinus

The data for this species show the very considerable range of the mean number of vertebrae.

Mr P. A. Soleim informed us that his original data were not available; they were unfortunately lost during the course of post-war changes. The data in Table II relating to his samples of *marinus* were therefore calculated from careful measurements (in hundredths of an inch) of his published graphs (Soleim, 1945: fig. 7, p. 13 and fig. 10, p. 16). From the given total of specimens in each sample, the number at each different vertebral count was calculated, and hence the mean, standard deviation (σ) and standard error of the mean for each sample. In the Grense Jakobslev sample of 30 October 1939, the total number of specimens calculated from measurement is 168 instead of 170 as given by Soleim. This small discrepancy is unlikely to make any great difference in the ensuing calculations. In the other three samples, the totals calculated from measurement agree with those given by Soleim.

Ammodytes species IV

The nearest approach to the mean number of vertebrae of this post-larva occurs in adult *marinus* from northern Norway (Soleim's samples from Grense Jakobslev and Tana).

Data for *G. semisquamatus* and *A. dubius* are included for comparison with the foregoing species.

TABLE III. THE SEASONAL OCCURRENCE OF POST-LARVAL *AMMODYTES* SPP. IN PLYMOUTH WATERS IN 1930–31 AND 1935–37

Owing to loss and damage of some specimens, the monthly totals do not always agree with Mr F. S. Russell's original figures. The discrepancies are, however, not sufficient to distort the general results.

Monthly averages for the five years are shown in parentheses. The number of hauls per month are given under *A. lanceolatus* against the total of specimens taken in the month.

* denotes months in which a species occurred on the 1937–39 cruises.

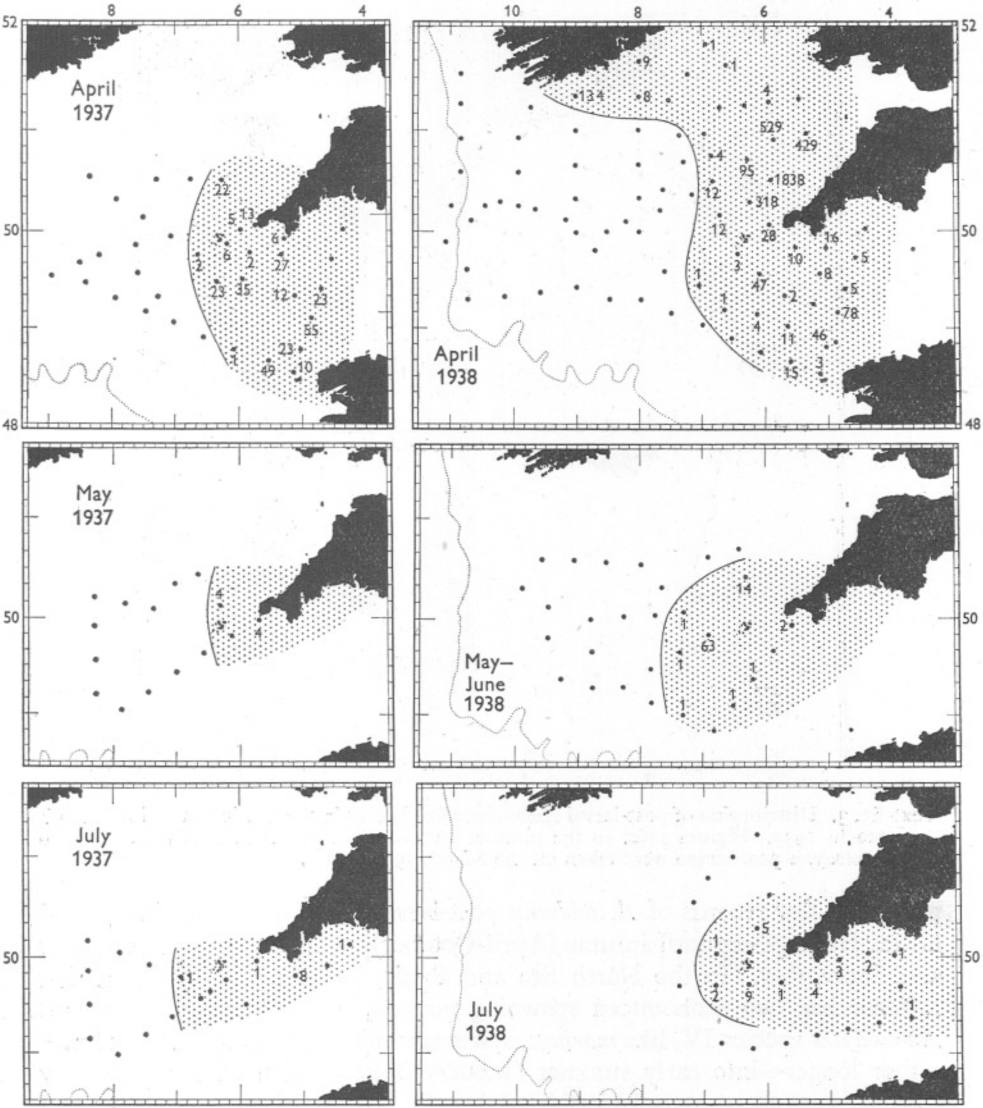
	A. lanceolatus						*A. marinus*					
	1930	31	35	36	37		1930	31	35	36	37	
Jan.		..^{6}	..^{6}	..^{5}	..^{4}			..	..	4	..	(0·2)
Feb.	..^{4}	..^{4}	1^{3}	..^{3}	4^{4}	(0·3)	..	..	..	18	..	(1·2)
Mar.	..^{4}	2^{2}	5^{3}	4^{4}	30^{5}	(1·9)	2	31	21	6	4	(5·1)
Apr.	..^{5}	1^{5}	8^{6}	19^{4}	12^{4}	(1·86)*	..	..	..	..	..	*
May	4^{3}	2^{4}	16^{7}	4^{4}	21^{5}	(1·86)*	..	..	..	..	..	
June	4^{3}	11^{3}	4^{2}	10^{4}	5^{3}	(2·2)	..	..	..	..	..	
July	17^{5}	15^{4}	6^{6}	14^{4}	4^{4}	(2·5)	..	..	..	..	..	
Aug.	53^{4}	5^{4}	5^{4}	4^{4}	3^{4}	(3·5)	..	..	..	..	..	
Sept.	1^{4}	3^{4}	1^{5}	..^{5}	..^{5}	(0·2)	..	..	..	..	..	
Oct.	..^{4}	..^{5}	..^{5}	1^{2}	..^{4}	(0·1)	..	..	..	..	..	
Nov.	..^{4}	..^{1}	..^{2}		..^{4}		..	..	..		..	
Dec.	..^{4}	..^{5}	..^{3}	..^{3}	..^{4}		..	..	..	..	..	

	A. tobianus						*Ammodytes* species IV					
	1930	31	35	36	37		1930	31	35	36	37	
Jan.		..	..	..	..			..	3	28	85	(5·0)
Feb.	..	..	..	..	..		..	5	17	26	86	(5·4)
Mar.	..	..	..	..	..		9	35	53	13	37	(7·4)
Apr.	..	..	..	..	..	*	1	3	9	5	6	(1·0)*
May	..	1	..	..	..	(0·05)	1	..	..	..	..	(0·07)
June	..	1	..	..	..	(0·07)	..	..	..	..	..	
July	..	1	..	..	2	(0·2)	..	..	..	..	..	
Aug.	1	..	..	10	..	(0·6)	..	..	..	..	..	
Sept.	..	1	8	3	..	(0·5)	..	..	..	..	..	
Oct.	..	1	5	..	..	(0·2)	..	..	..	..	..	
Nov.	..	..	..		..		..	..	..		2	(0·10)
Dec.	..	..	..	..	..		..	..	..	..	..	

The March and August averages of *A. lanceolatus* are high owing to single large catches of twenty-seven and forty-seven specimens on 1 March 1937 and 7 August 1930 respectively. The January average of *Ammodytes* species IV is similarly weighted by a catch of eighty-two specimens on 27 January 1937.

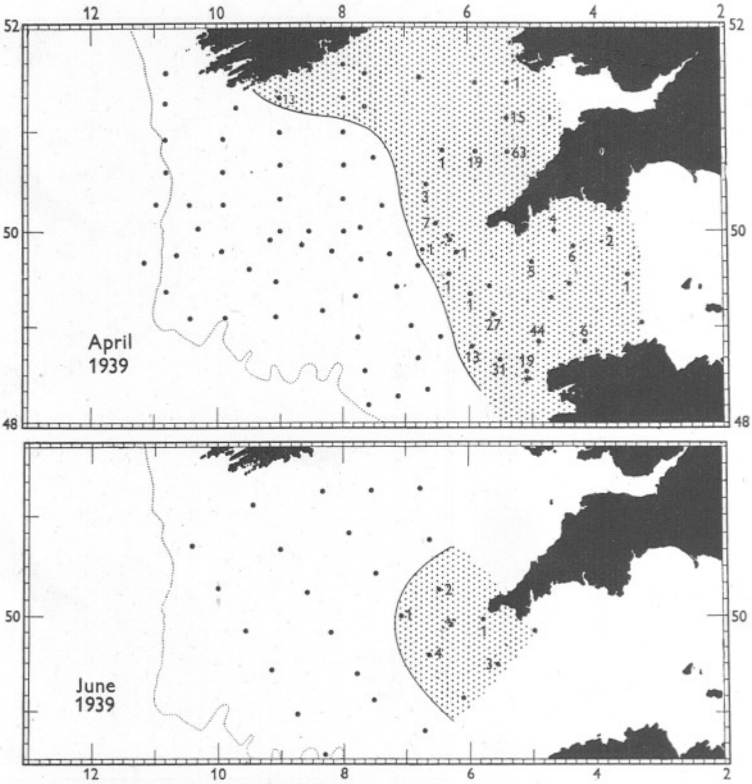
THE SEASONAL OCCURRENCE AND DISTRIBUTION OF THE POST-LARVAE

The seasonal occurrence of the four species of *Ammodytes* post-larvae in the Plymouth area in the years 1930, 1931 and 1935–37, together with the occurrences on the 1937–39 cruises in the Celtic Sea, is shown in Table III. It is evident that *A. lanceolatus* has a long spawning period lasting from early spring



Text-fig. 2. Distribution of post-larval *Ammodytes lanceolatus* in the Celtic Sea and Plymouth area in 1937 and 1938. Figures refer to the number of post-larvae caught at each station. The dotted line in this and succeeding figures indicates the 100-fathom contour.

until autumn (February–October) with a maximum in mid-summer. *A. marinus* spawns in winter and early spring (January–April). The spawning times of these two species are in agreement with Raitt's observations for Scottish waters (1934) and Kändler's for the North Sea and Baltic (1941). The com-

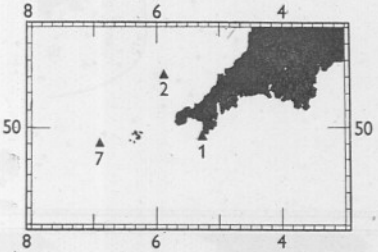


Text-fig. 3. Distribution of post-larval *Ammodytes lanceolatus* in the Celtic Sea and Plymouth area in 1939. Figures refer to the number of post-larvae caught at each station. No *Ammodytes* post-larvae were taken on the March 1939 cruise.

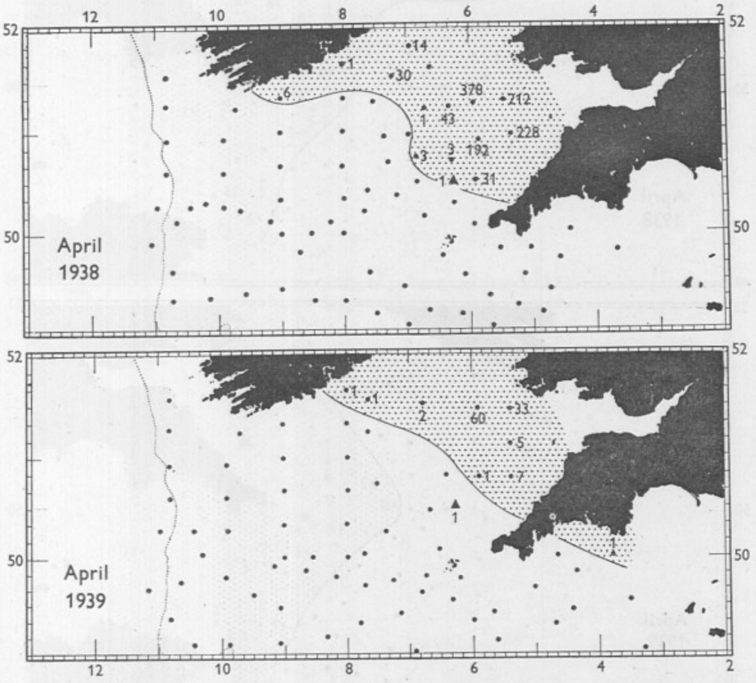
paratively few records of *A. tobianus* post-larvae point to a spawning period lasting from spring until autumn (April–October), with a maximum in August and September. In the North Sea and Baltic, Kändler (1941) found that *tobianus* has two pronounced spawning periods, in spring and in autumn. *Ammodytes* species IV, like *marinus*, starts spawning in winter, but continues rather longer—into early summer (January–May), and it may occasionally start in late autumn as is indicated by the record of two post-larvae in November 1937.

The numbers and distribution of the post-larvae taken on the 1937–39 cruises are shown in Text-figs. 2–6. For details of station numbers, positions, etc. see Corbin (1947), Figs. 1 and 2, pp. 67–8 and pp. 124–32.

No post-larvae were caught more than about 60 miles from land. They occurred in the eastern part of the Celtic Sea—at the western end of the English Channel and off the St George's and Bristol Channels—and not in the western area towards the edge of the Continental Shelf. The post-larvae of *lanceolatus* (Text-figs. 2 and 3) and *Ammodytes* species IV (Text-fig. 6) were present throughout this region extending from south-west Ireland to the Brest Peninsula. The small number of *tobianus* post-larvae (ten specimens)

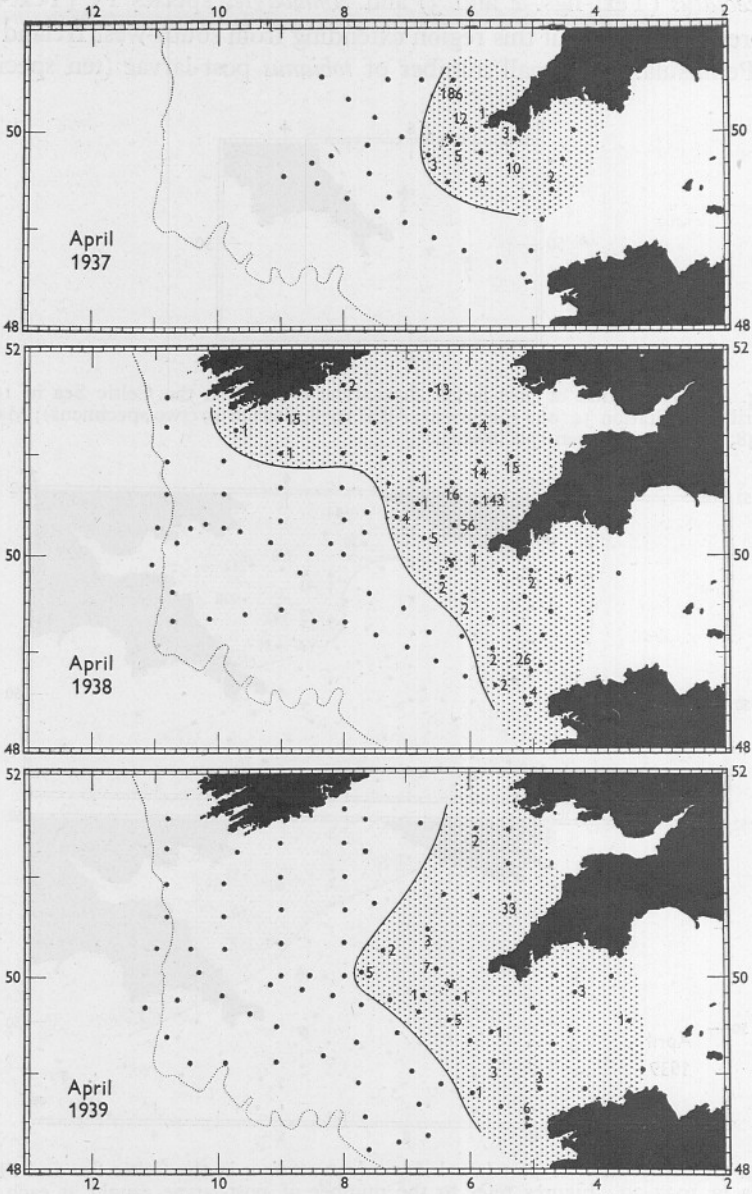


Text-fig. 4. Distribution of post-larval *Ammodytes tobianus* in the Celtic Sea in 1937–39. April 1937, Station 34 (one specimen); April 1938, Station 49 (two specimens); May–June 1938, Station 11 (seven specimens).



Text-fig. 5. Distribution of post-larval *Ammodytes marinus* in the Celtic Sea and Plymouth area in 1937–39. Figures refer to the number of post-larvae caught at each station. Station 32 of the April 1937 cruise, at which a single specimen was taken, is marked ▲ on both charts of this text-fig.

were all taken fairly close to land (Text-fig. 4). The distribution of *marinus* post-larvae was peculiarly restricted (Text-fig. 5). All specimens, with the exception of one taken off Plymouth (St. 62, April 1939), were caught in the



Text-fig. 6. Distribution of post-larval *Ammodytes* species IV in the Celtic Sea and Plymouth area in 1937–39. Figures refer to the number of post-larvae caught at each station.

north-eastern area—off the St George's and Bristol Channels. On the April 1938 and 1939 cruises, the species thus appeared to have a southerly limit of distribution along a line joining south-west Ireland and Land's End. The occurrence of only a single *marinus* post-larva on the April 1937 cruise is in agreement with this. It was taken about 35 miles north-west of Land's End (shown ▲ in both charts of Text-fig. 5), just on the southern limit of the *marinus* post-larva area of the April 1938 and 1939 cruises. All other stations of the April 1937 cruise were outside—to the south and west of—the 1938–39 *marinus* boundary. The presence each year of *marinus* post-larvae in the 1930–37 collections from the Plymouth area reveals, however, that they regularly occur there and confirms the single specimen taken off Plymouth (St. 62) on the April 1939 cruise. Kändler (1941) states that it may be concluded that the dispersal area of *marinus* ranges as far as the western end of the English Channel. It will be of interest to know from further observations whether the southern limit indicated by the April 1937–39 cruises should be continued across the western end of the English Channel from Land's End to, say, the Channel Islands. This would include the Plymouth area, but not the Land's End–Ushant region of the Channel mouth where none was taken at the numerous stations worked during the April 1937–39 cruises.

SUMMARY

The post-larval sand-eels (Ammodytidae) occurring in the Celtic Sea and Plymouth area are identifiable as *Ammodytes lanceolatus*, *A. tobianus*, *A. marinus* (not previously recorded from the area), and a fourth species of *Ammodytes*, the adult of which, it is concluded, is not yet known.

Adult *Gymnammodytes semisquamatus* (not previously recorded from the Plymouth area), the young of which are not yet known, increases the number of species in the area to five.

REFERENCES

Acloque, A., 1900. *Faune de France*. Tome I. Mammifères, Oiseaux, Poissons, Reptiles, Babaciens, Protochordes. Paris 1900, pp. 1–540.

Bal, D. V., 1944. A study of fish eggs and larvae from Manx waters. II. Observations on the fish larvae. *J. Univ. Bombay*, Vol. xii, Pt. v, pp. 14–41.

Bruun, A. F., 1941. Observations on north Atlantic fishes. 2. The *Ammodytes lancea* group. *Vidensk. Medd. naturh. Foren.*, Bd. 104, pp. 329–40.

Buen, F. de, 1935. Fauna Ictiológica. Catálogo de los peces Ibéricos: aguas dulces, pelágicos y de los abismos próximos. Primera parte. *Notas Inst. esp. Oceanog.*, No. 88, pp. 1–149.

Clark, R. S., 1920. The pelagic young and early bottom stages of teleosteans. *Journ. Mar. Biol. Assoc.*, Vol. xii, pp. 159–240.

Collett, R., 1904. Meddelelser om Norges Fiske i Aarene 1884–1901. (3die Hoved-supplement til 'Norges Fiske') II. *Forh. VidenskSelsk. Krist.* 1903, No. 9, pp. 1–175.

CORBIN, P. G., 1947. The spawning of mackerel, *Scomber scombrus* L., and pilchard, *Clupea pilchardus* Walbaum, in the Celtic Sea in 1937–39. *Journ. Mar. Biol. Assoc.*, Vol. XXVII, pp. 65–132.

DAY, F., 1880–84. *The Fishes of Great Britain and Ireland*, London 1880–84, Vol. I, pp. 1–336.

DUNCKER, G. & MOHR, E., 1935. Die nordeuropäischen *Ammodytes*-Arten des Hamburger Zoologischen Museums. *Zool. Anz.*, Bd. 110, pp. 216–20.

—— 1939. Revision der Ammodytidae. *Mitt. zool. Mus. Berl.*, Bd. 24, Heft 1, pp. 8–31.

EHRENBAUM, E., 1904. Eier und Larven von Fischen der deutschen Bucht. III. Fische mit festsitzenden Eiern. *Wiss. Meeresuntersuch.*, Bd. VI, Abt. Helgoland, Heft 2, pp. 127–200.

—— 1909. Eier und Larven von Fischen. *Nord. Plankt.*, Bd. I, Teil II, pp. 217–414.

EHRENBAUM, E. & STRODTMANN, S., 1904. Eier und Jugendformen der Ostseefische. I. Bericht. *Wiss. Meeresuntersuch.*, Bd. VI, Abt. Helgoland, Heft 1, pp. 57–126.

FAGE, L., 1918. Shore fishes. *Rep. Danish oceanogr. Exped. Medit.*, No. 4, Vol. II (Biology), A. 3, pp. 1–154.

FORD, E., 1920. The post-larval stages of *Ammodytes* species captured during the cruises of S.S. *Oithona* in Plymouth waters in the year 1919. *Journ. Mar. Biol. Assoc.*, Vol. XII, pp. 241–48.

GONÇALVES, B. C., 1942. Colecção oceanográfica de D. Carlos I. Catálogo dos peixes. *Trav. Sta. Biol. marit. Lisbonne*, No. 46, pp. 1–108.

GRIEG, J. A., 1912. Icthyologiske notiser III. *Bergens Mus. Aarb.*, 1911, Nr. 6, pp. 1–38.

GÜNTHER, A., 1867. Additions to the British Fauna. *Ann. Mag. nat. Hist.*, Vol. XX (Third Series), Part 2, pp. 288–91.

JENSEN, A. S., 1941. On subspecies and races of the Lesser Sand Eel (*Ammodytes lancea* s. lat.). *K. danske vidensk. Selsk. Skr.*, Biologiske Meddelelser, Bind XVI, Nr. 9, pp. 1–33.

—— 1944. On specific constancy and segregation into races in sea-fishes. *K. danske vidensk. Selsk. Skr.*, Biologiske Meddelelser, Bind XIX, Nr. 8, pp. 1–19.

JOUBIN, L. & LE DANOIS, E., 1924. Catalogue illustré des animaux marins comestibles des côtes de France et des mers limitrophes avec leurs noms communs français et étrangers. I. Poissons osseux. *Mém. Off. sci. tech. Pêch. marit.*, No. 1, pp. 1–220.

JOURDAIN, S., 1879. Sur les *Ammodytes* des côtes de la Manche. *Revue de Sciences Naturelles*, Tome I, pp. 203–10.

KÄNDLER, R., 1941. Untersuchungen über Fortpflanzung, Wachstum und Variabilität der Arten des Sandaals in Ost- und Nordsee, mit besonderer Berücksichtigung der Saisonrassen von *Ammodytes tobianus* L. *Kieler Meeresforschungen*, Band V, Heft 1, pp. 45–145.

*LÖNNBERG, E., 1915. *Sveriges Ryggradsdjur*. 3. Kraldjur, Groddjur, Fiskar., Stockholm 1915, pp. 1–331.

MOORE, H. B., 1937. Marine fauna of the Isle of Man. *Proc. Lpool. biol. Soc.*, Vol. L, pp. 1–293.

MOREAU, E., 1891. *Histoire naturelle des poissons de la France. Supplément*, Paris 1891, pp. 1–144.

POLL, M., 1947. *Faune de Belgique*. Poissons Marins, Bruxelles 1947, pp. 1–452.

RAITT, D. S., 1934. A preliminary account of the Sand Eels of Scottish Waters. *J. Cons. int. Expl. Mer*, Vol. IX, pp. 365–72.

RAITT, D. S., 1935. The occurrence of four species of Sand Eels, of economic importance, in Scottish waters, one of which is new to science. *Scot. Nat.*, No. 211, pp. 61–62.

* This reference has not been consulted personally.

RUSSELL, F. S., 1930–47. On the seasonal abundance of young fish. Parts I–VIII. *Journ. Mar. Biol. Assoc.*, Vols. XVI, pp. 707–22; XX, pp. 147–79 and pp. 595–604; XXI, pp. 679–86; XXII, pp. 493–500; XXIII, pp. 381–6; XXIV, pp. 265–70; XXVI, pp. 605–8.

SOLEIM, P. A., 1945. A contribution to the knowledge of the Lesser Sandeel (*Ammodytes lancea*) in north-European waters. *Rep. Norweg. Fish. Invest.*, Vol. VIII, No. 1, pp. 1–28.

WOLLEBÆK, A., 1924. *Norges Fisker.*, Kristiania 1924, pp. 1–239.

APPENDIX

The earlier work of Ehrenbaum & Strodtmann (1904) and Ehrenbaum (1904, 1909) on the larvae and post-larvae of *Ammodytes* contains several errors of identification, due in part to the fact that *A. marinus* and its young stages were unknown at the time. The following notes attempt to correct the misidentifications. Corrections already made by Ford (1920) and Kändler (1941) are also included.

Ehrenbaum & Strodtmann (1904)

Fig. 8, p. 104 (also Ehrenbaum (1909), Fig. 106*c*, p. 298), post-larva 20·5 mm.; ascribed to *A. tobianus*.

Kändler (1941) points out that the pigmentation and date of capture (February) of this specimen identify it as *A. marinus*.

Ehrenbaum (1904), Taf. VII

Fig. 70 (also Ehrenbaum (1909), Fig. 107*a*, p. 300), larva 4·2 mm. and Fig. 71, larva 5·1 mm.; both ascribed to *A. lanceolatus*.

The specimens were reared from artificially fertilized eggs. In these circumstances it seems very unlikely that an error would have occurred in the identification of the parents of the fertilization had they been specimens of *lanceolatus*. Neither of the larvae, however, shows the ventral fin-membrane pigment row which is specifically characteristic of the earliest stages of *lanceolatus* (p. 296), and the ventral gut pigment is also very much heavier than in early *lanceolatus*. The pigmentation is in all respects characteristic of *A. tobianus*. Both pigmentation and date of fertilization (June) rule out *A. marinus* and *Ammodytes* species IV.

Fig. 72 (also Ehrenbaum (1909), Fig. 107*b*, p. 300), post-larva 12·5 mm.; ascribed to *A. lanceolatus*.

Ford (1920) points out, and Kändler 1941 agrees with him, that the pigmentation of this specimen identifies it as *A. tobianus*.

Fig. 80, larva 2·2 mm. and Fig. 81, larva 4·0 mm.; both ascribed to *A. tobianus*.

These specimens hatched prematurely from artificially fertilized eggs. The date of fertilization (September) is therefore likely to be the only reliable criterion for identification, and indeed supports Ehrenbaum's identification.

Fig. 82, larva 4·5 mm.; ascribed to *A. tobianus*.

This specimen evidently resulted from the same artificial fertilization as those in figs. 80 and 81. Ehrenbaum's identification is thus supported by the date of fertilization. This and the lack of ventral gut pigment are in agreement with Kändler's (1941) lightly pigmented autumn-brood *tobianus* post-larva of the North Sea and Baltic.

Fig. 83, larva 4·7 mm.; ascribed to *A. tobianus*.

The specimen is figured from the dorsal side and cannot therefore be identified by its pigmentation. The date of capture (September) supports Ehrenbaum's identification.

Fig. 84 (also Ehrenbaum (1909), Fig. 106*a*, p. 298), larva 6·6 mm. and Fig. 85, larva, anterior end; both ascribed to *A. tobianus*.

The date of capture (January) of these specimens, their pigmentation, the noticeably slender form, and particularly the length while still carrying a large oil globule (fig. 84, 6·6 mm.) are evidence that they belong to *A. marinus*.

Fig. 86 (also Ehrenbaum (1909), Fig. 106*b*, p. 298), post-larva 16·2 mm.; ascribed to *A. tobianus*.

Kändler (1941) points out that the pigmentation is clearly that of *A. marinus*.

It is of interest that Ehrenbaum and Strodtmann evidently did not procure any post-larvae of *A. lanceolatus*.

EXPLANATION OF PLATES I & II

The drawings were made from specimens preserved in formalin. All specimens are drawn to the same scale (see inset on Plates), with the exception of the specimen in Pl. I, fig. 2*a*. All specimens were taken in half-hour oblique hauls of the 2 m. stramin ring-trawl in the Celtic Sea or Plymouth area, with the exception of the specimen in Pl. I, fig. 2*a*.

PLATE I.

Fig. 1. *Ammodytes lanceolatus* Lesauvage

a. Post-larva 4·5 mm. Station L3–L4, Plymouth, 19. iii. 1937.
b. Post-larva 7·5 mm. Eddystone, 26. iv. 1937.
c. Post-larva 12·5 mm. Station 48, Celtic Sea, 25. iv. 1939.
d. Post-larva 18·5 mm. 4 miles SSE. of Mewstone, Plymouth, 22. vii. 1936.
e. Post-larva 26·5 mm. Eddystone, 13. vii. 1937.

Fig. 2. *Ammodytes marinus* Raitt

The scale for *a* is above the drawing. The scale for *b–h* is below *h*.

a. Larva 6·25 mm. Station 15(1), North Sea, 24. i. 1947, Cruise 3, R.V. *Platessa*, Hensen net, vertical.
b. Post-larva 7·5 mm. Station 46, Celtic Sea, 14. iv. 1938.
c. Post-larva 11·0 mm. Station 45, Celtic Sea, 14. iv. 1938.
d. Post-larva 14·0 mm. Station 45, Celtic Sea, 14. iv. 1938.
e. Post-larva 18·5 mm. Station 48, Celtic Sea, 25. iv. 1938.
f. Post-larva 19·0 mm. Station 45, Celtic Sea, 24. iv. 1939.
g. Post-larva 23·0 mm. Station 46, Celtic Sea, 25. iv. 1939.
h. Post-larva 27·5 mm. Station 45, Celtic Sea, 24. iv. 1939.

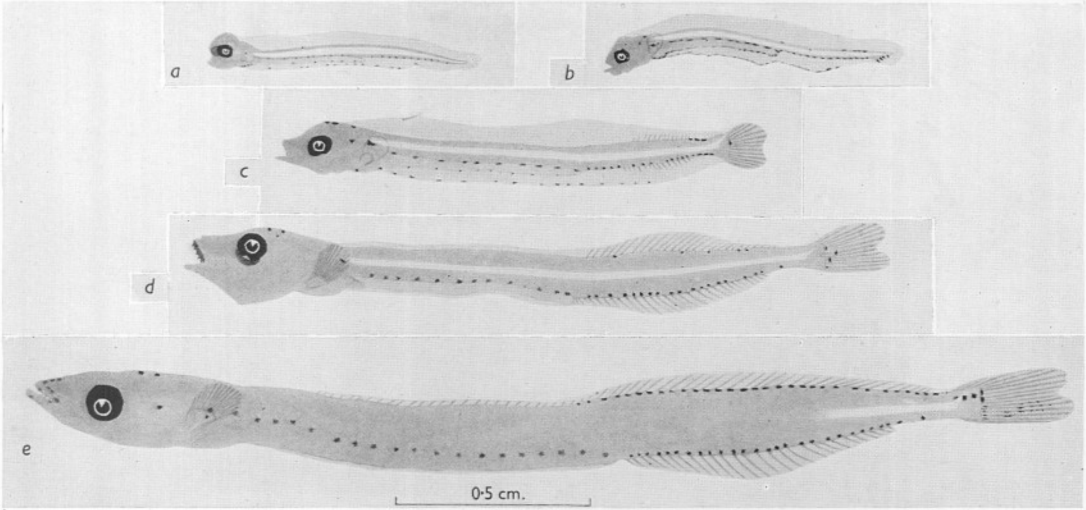


Fig. 1. *Ammodytes lanceolatus*

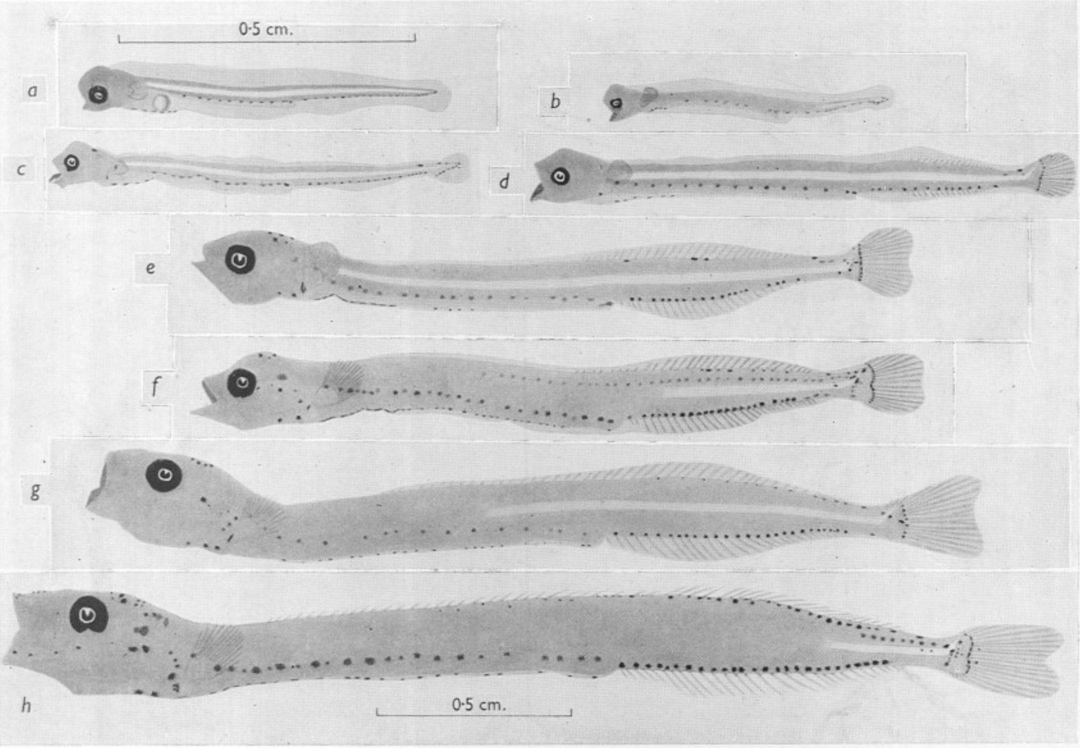


Fig. 2 *Ammodytes marinus*

del. V.V.

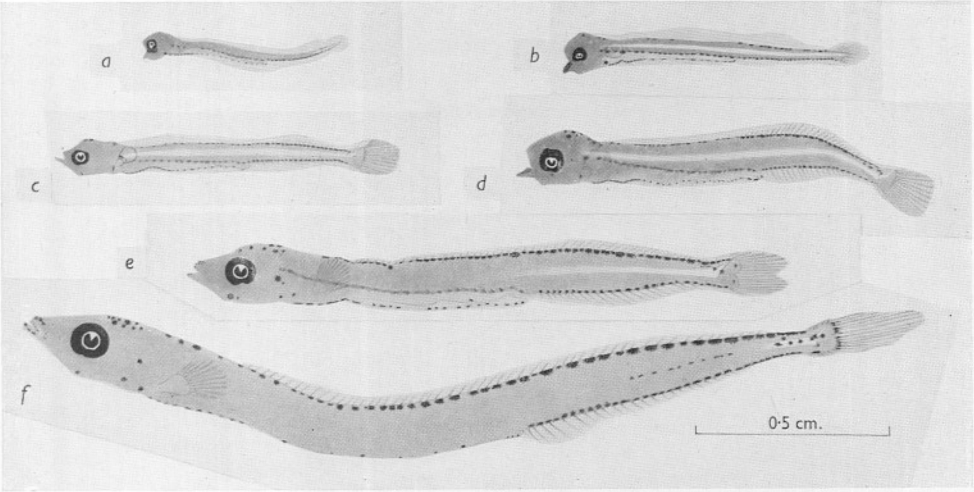
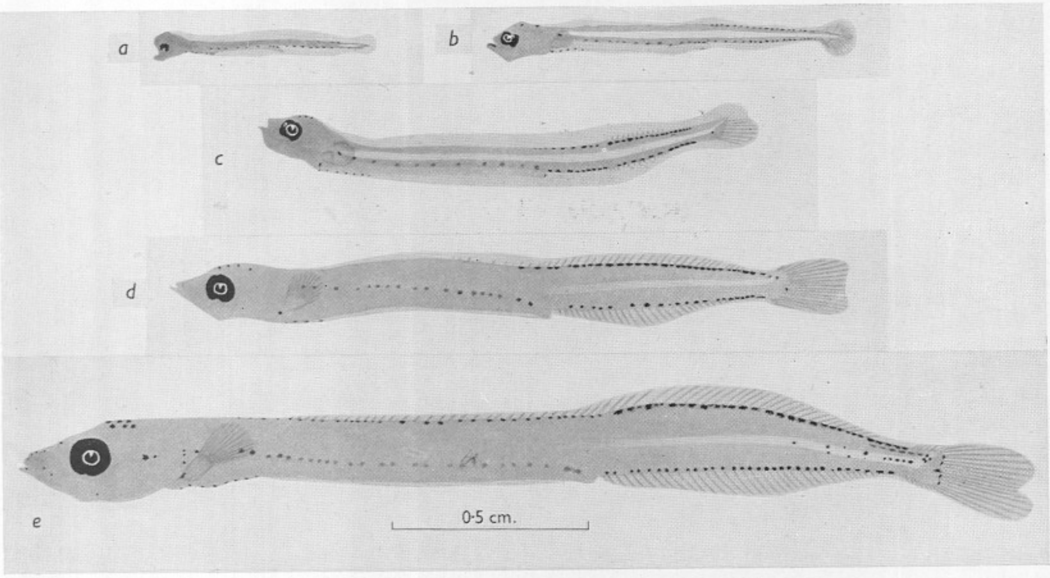


Fig. 1. *Ammodytes tobianus*



del. V.V.

Fig. 2. *Ammodytes* species IV

Plate II.

Fig. 1. *Ammodytes tobianus* L.

a. Post-larva 5·25 mm. Station 11, Celtic Sea, 2. vi. 1938.
b. Post-larva 8·0 mm. Station 11, Celtic Sea, 2. vi. 1938.
c. Post-larva 8·75 mm. Eddystone, 11. viii. 1936.
d. Post-larva 11·0 mm. Eddystone, 24. vi. 1947.
e. Post-larva 15·5 mm. Eddystone, 9. x. 1935.
f. Post-larva 23·0 mm. Eddystone, 7. viii. 1930.

Fig. 2. *Ammodytes* species IV

a. Post-larva 5·5 mm. Bolt Head E. × S.: Stoke Point N., Plymouth, 27. i. 1937.
b. Post-larva 9·0 mm. Station 33, Celtic Sea, 20. iv. 1937.
c. Post-larva 13·0 mm. Station 33, Celtic Sea, 20. iv. 1937.
d. Post-larva 17·5 mm. Station 40, Celtic Sea, 23. iv. 1939.
e. Post-larva 26·0 mm. Station 51, Celtic Sea, 25. iv. 1939.

ABSTRACTS OF MEMOIRS

RECORDING WORK DONE AT THE PLYMOUTH LABORATORY

Photoelectric Measurements of the Seasonal Variations in Daylight at Plymouth, from 1938 to March 1941, Compared with the Years 1930 to 1937

By **W. R. G. Atkins** and **M. A. Ellison**

Proc. Roy. Soc., A, Vol. 191, 1947, pp. 467–84

Measurements were made throughout with a vacuum sodium photoelectric cell and a Cambridge 'thread recorder'. The illumination during the last three years was below the average, but the three were closely similar. Of the eleven, 1930 was much the brightest, followed by 1934. The remainder were rather uniform. Of the eleven years May was brightest in six, June in four, July in one—1930. The mean value of the December illumination, found from the area of the intensity-time curve, is 1·37%, with May 15·61% and June 15·59%, calculated on the light of the year. The range of the monthly means lies between 20% for June and 59% for November.

There is no simple relation between the illumination integral and the number of hours of sunshine, rainfall, number of days with rain or wind direction. Calm days are never exceptionally bright; such days usually have wind force 3.

The illumination on days showing complete cloud cover throughout was during 1930 and 1936, 0·326 and 0·304 respectively of that on the brightest days, calculating on a month-to-month basis. Illumination on sunless days of 1930 was above that on similar days in 1936, a year of average illumination. On comparing Plymouth records with those got near Stockholm by Aurén it is seen that similar wide ranges in light intensity, within the same month, were found in both. W.R.G.A.

Note on the Spectroscopic and Biological Detection of Potassium in Sea Water and 'Potassium-Free' Artificial Sea Water

By **W. R. G. Atkins**

Journ. Conseil, Vol. XV, 1948, pp. 169–72

Using sea water evaporated in silica dishes Moore and Philpot of Scientific Instrument Research Association showed lines 4044 and 4047 A were less effective for detecting potassium than were 7699·0 and 7664·9 sought on F. Twyman's advice. After reducing glare by careful cleaning the latter pair were detected in sea water supposedly potassium free. Glare was best eliminated by a selenium red glass. In the 'potassium free' water the ratio of potassium to sodium by weight was about 7 to 100 million, as found by a biological method of analysis. When the water was exhausted by maximal diatom growth potassium was still detectable spectroscopically in the filtrate, but this is not diatom free and accidental breakage of a centrifuge tube may have liberated some potassium. War prevented further work. W.R.G.A.

DAYLIGHT AND ITS PENETRATION INTO THE SEA

By W. R. G. Atkins

Trans. Illuminating Eng. Soc. (*London*), Vol. X, No. 7, 1945, 12 pp.

A lecture delivered at the Annual General Meeting of the Society, summarizing work on the variation of daylight throughout the year and with latitude; the measurement of submarine illumination; and the consequent changes in the phosphate and oxygen of the sea which give a measure of the production of phytoplankton. W.R.G.A.

A SUGGESTED REPELLENT FOR SCHISTOSOME CERCARIAE

By W. R. G. Atkins

Journ. Hygiene, Vol. 45, No. 4, 1947, p. 468

Attack by cercariae of *Schistosoma haematobium*, *S. mansoni* and *S. japonicum* causes in man debilitating diseases which in certain countries are widespread. Infection is mainly through the skin. In U.S.A. and Canada a dermatitis only is caused by cercariae liberated from *Stagnicola emarginata* and other freshwater snails. Possibly copper oleate, stearate or palmitate might be effective repellents when applied in 1–5% dilution in mineral jelly or crude lanoline for cercariae and could be tried first against the relatively harmless species. Such copper compounds have been useful as anti-fouling agents and preservatives for ropes, etc. W.R.G.A.

THE NUTRIENT BALANCE IN THE SEA

By L. H. N. Cooper

Research, Vol. I, pp. 242–7

The interdependence of changes in the chemical composition of sea water and of variations in plant and animal production is reviewed. The account, not intended to be 'popular', is largely based on papers published from the Plymouth Laboratory during the past twenty-five years. L.H.N.C.

THE DISTRIBUTION AND BIOLOGY OF HAKE

By T. John Hart

Biol. Rev. Vol. 23, 1948, pp. 62–80

Recent advances in our knowledge of the general biology, taxonomy and economic importance of the genus *Merluccius* are described by way of introduction to a detailed discussion of its distribution.

It is shown that all the species conform to the same distributional pattern in relation to major hydrological features, within the limits of their normal range. Where relatively cold currents flow towards the equator in the warmer half of the normal habitat of any one of these species, its range is extended in that direction; but if a relatively warm current is flowing pole-wards, the range in the direction of the equator is restricted. In the colder half of the normal habitat of each species the converse relationship holds good.

Surface isotherms have been used as the most reliable general criterion symptomatic of the environmental complex that leads to this type of distribution because in many parts of the world more detailed hydrological data are not yet available; but it is emphasized that other factors, more or less intimately interrelated with the direct effect of temperature, are also involved.

The distribution of the genus offers a good example of the wider aspects of the phenomenon of 'organic polarity' discussed by Wimpenny (1941), while the bionomics of the better known individual species show some more detailed aspects of it with great clarity. T.J.H.

THE GIANT NERVE-FIBRES IN THE CENTRAL NERVOUS SYSTEM OF *MYXICOLA* (POLYCHAETA, SABELLIDAE)

By J. A. C. Nicol

Quart. Journ. Micr. Sci., Vol. 89, 1948, pp. 1–46

A study of the giant axon in the central nervous system of *Myxicola infundibulum* has shown that this structure possesses many peculiar features. It occupies a large volume of the nerve cord and extends throughout the length of the animal. Its diameter is greatest anteriorly, about 1 mm., and tapers off posteriorly. In each segment it gives off branches to the longitudinal muscle fibres in the body wall. The giant fibre is connected with nerve cells in the supra-oesophageal ganglia, and with nerve cells in each segment. It is concluded that the giant fibre of this animal is a large syncytial structure extending throughout the nervous system and body wall.

Added evidence for its syncytial nature has been adduced by cutting it and examining the axon after 16 days. The giant axon failed to degenerate in front of or behind the cut owing to the existence of nerve cells at all levels. The giant axon is similar in the related species, *M. aesthetica*.

The large diameter, rapid conduction velocity, and through nature of the axonic pathway have been correlated with the sedentary mode of existence and quick withdrawal reflex of these animals, and are regarded as having survival value. J.A.C.N.

PURE AND ALLIED SCIENCE OF THE SEA

(being the Ludwig Mond Lecture, delivered at the University of Manchester on 11 March 1948)

By F. S. Russell

Science Progress, Vol. XXXVI, 1948, pp. 423–35

Some aspects of marine research are reviewed historically to show how advances in our knowledge of the sea have been much influenced by the interdependence of pure and applied science. F.S.R.

FURTHER EXTENSION OF THE RANGE OF *CREPIDULA FORNICATA* (L.)

By G. M. Spooner

Journ. Conchology, Vol. 22, 1947, p. 243

During the war years the Slipper Limpet, *Crepidula fornicata* (L.) spread into Weymouth Bay and by 1946 had become a dominant member of the fauna. In spreading westwards down the English Channel coast, the species had taken about twenty years to cross the gap between Studland Bay and Weymouth Bay. G.M.S.

THE BRITISH SPECIES OF PSENINE WASPS (HYMENOPTERA: SPHECIDAE)

By G. M. Spooner

Trans. R. Ent. Soc. London, Vol. 99, 1948, pp. 129–72

Existing knowledge of the British species of the genera *Psenulus*, *Psen*, and *Mimesa* (slender fossorial wasps which prey on aphides and jassid plant-bugs) is summarized, covering both taxonomy and general biology. Much hitherto unpublished matter is incorporated, including records of prey kindly supplied by Dr O. W. Richards. New identification keys for the two sections of *Mimesa* are given. *M. bruxellensis* Bondr. is recorded as British for the first time, and *M. celtica*, a form inhabiting sand dunes in the west, is split off from *M. unicolor* (Lind.) as a new species. G.M.S.

REPORT ON THE SEA FISHERIES OF SIERRA LEONE

By G. A. Steven

London: Crown Agents for the Colonies, Millbank. 1947. 66 pp.

This Report is based on work carried out by the author on behalf of the Government of Sierra Leone for their guidance in developing the fisheries resources of the colony. It includes a survey of the methods of fishing already fully established, together with recommendations for their improvement. The results of experiments with methods new to that region, e.g. trawling and trammel-netting, are also described. Trials with a motor trawler based on Freetown gave very encouraging returns in regard to both the quantity and quality of fish available.

Most of the work was done during the recent war when fishing gear was hard to obtain. Ropes and twines made by hand by the natives themselves from local fibres had largely to be used but proved unsatisfactory. A hand-operated ropemaking machine was therefore introduced and local fishermen taught to use it. This proved a great boon and saved the beach-seining industry from collapse in particularly difficult times.

Fish preservation and transportation are two problems of special difficulty and importance in tropical regions. Native methods are crude and effective for only short periods. Recommendations are therefore made for exhaustive and prolonged experimentation so that new and improved techniques, appropriate to the commodity and the climate, may be devised and perfected. Particular attention is directed to the potentialities of dehydrated fish products for native use.

The report concludes with proposals and recommendations for the formation of a Fisheries Department, and the building of a local Fisheries Laboratory on a site already available on the outskirts of Freetown. The difficulty of recruiting well-qualified and adequately trained staff is fully realized, but it is pointed out that even a single energetic and competent fisheries biologist, assisted by educated and intelligent native helpers, backed by an enlightened public and supported by courageous Government policy, could do much to plan, prepare and initiate further development. G.A.S.

THE BRITISH RAIIDAE

By G. A. Steven

Science Progress, Vol. XXXV, 1947, pp. 220–36

Fishes of the genus *Raia* (Rays and Skates) collectively make an important contribution to the total landings of British food fishes. Just over a dozen species occur in British waters, and of these no less than eleven are present on the fishing grounds around Devon and Cornwall where they are caught with little variation in numbers over the whole year. This indicates a minimum of migratory movement which is strikingly confirmed by marking experiments. In over 60% of the recaptures of marked *Raia clavata* (on which most work has been done) the fish were caught in precisely the same place as they were liberated, after periods varying from 12 days to over 3½ years. Because of this, the same fish can often be recaptured several times after marking. The record so far is held by a fish living in a depth of 25 fathoms that was captured five times within a year.

It is found that on the various grounds where different kinds occur there is a fairly rigid segregation of the species and at certain times, a segregation also of the sexes.

Growth rates have been obtained for *Raia clavata*. In fishes over a size-range of 20–50 cm. disc width an increment of from 4 to 8 cm. in width takes place in one year, chiefly in the summer and autumn. Male fish reach maturity when about 7 years of age but females are several years older before becoming sexually mature. G.A.S.

BOOK NOTICE

THIS GREAT AND WIDE SEA

By **R. E. Coker**

The University of North Carolina Press: Oxford University Press, 1947. Price 27*s*. 6*d*. net

The theme of this American book is the salt water of the whole wide world. Between the covers of one normal-sized volume the author moves in a broad steady sweep from the chemistry and physics of sea water on through the pasturage of the sea, and the many ramifications of the animal life it sustains, to that final crowning manifestation of metabolic efficiency, the growth rate of whales. The book is divided into three parts: the first of these summarizes the history of oceanography and the major expeditions, with some account of the great oceanographers and marine biologists of the past, not forgetting mention of the marine stations scattered thinly and irregularly round the borders of the great ocean basins whose topography is briefly considered. The second part comprises seven chapters devoted to the chemistry and physics of sea water, the bottom deposits, oceanic circulation and the tides, and the heating effect of the sun on the sea. The third and longest part surveys the plant and animal life, the plankton, benthos and nekton, the variations in structure and habit, adaptations and interrelations. With an ease of style and wealth of illustrative detail this overall review of the oceans and the life they contain gives to the student a well-proportioned, up-to-date, and sound framework of knowledge on which to build, while the experienced worker in some corner of the field will find himself refreshed and stimulated by it.

It is a pity that a text so informative and well balanced should not be more worthily illustrated. The ninety-one half-tone plates are a very mixed bag, some good, some bad and many indifferent. A few have relatively little bearing on the text, some are new and interesting, but far too many are of poor quality photographically and unworthy of inclusion. It is to be hoped that in a future edition these half-tone insets will be drastically revised and better printed. A few more carefully chosen line drawings would enliven the text and increase its attractiveness to the general reader. Some indication of scale should be given to the drawings of various microscopic and other organisms at present included.

D.P.W.

THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM

THE ASSOCIATION was founded in 1884 to promote accurate researches leading to the advancement of zoological and botanical science and to an increase in our knowledge of the food, life, conditions and habits of British fishes. The work of the Association is controlled by a Council elected annually by its subscribing members.

Professor T. H. Huxley took the chair at the initial meeting held in the rooms of the Royal Society and was elected the first President. Among those present were Sir John Lubbock (afterwards Lord Avebury), Sir Joseph Hooker, Professor H. N. Moseley, Mr G. J. Romanes, and Sir E. Ray Lankester who, after Professor Huxley, was for many years president of the Association. It was decided that a laboratory should be established at Plymouth where a rich and varied fauna is to be found.

The Plymouth Laboratory was opened in June 1888. The cost of the building and its equipment was £12,000 and, since that date, a new library and further laboratory accommodation have been added at an expenditure of over £23,000.

The Association is maintained by subscriptions and donations from private members, scientific societies and public bodies, and from universities and other educational institutions; a generous annual grant has been made by the Fishmongers' Company since the Association began. Practical investigations upon matters connected with sea-fishing are carried on under the direction of the Council, and from the beginning a Government Grant in aid of the maintenance of the Laboratory has been made; in recent years this grant has been greatly increased in view of the assistance which the Association has been able to render in fishery problems and in fundamental work on the environment of marine organisms. An account of the Laboratory and the scope of the work undertaken there will be found in Vol. XV (p. 735) and Vol. XXVII (p. 761) of this *Journal*.

The Laboratory is open throughout the year and its work is carried out under the supervision of a Director and with a fully qualified research staff. The names of the members of the staff will be found at the beginning of this number. Accommodation is available for British and foreign scientific workers who wish to carry out independent research in marine biology and physiology. Arrangements are made for courses for advanced students to be held at Easter, and marine animals and plants are supplied to educational institutions.

Work at sea is undertaken by two research vessels and by a motor boat and these also collect the specimens required in the Laboratory.

TERMS OF MEMBERSHIP

		£	*s.*	*d.*
Annual Members	per annum	1	1	0
Life Members	Composition fee	15	15	0
Founders		100	0	0
Governors		500	0	0

Members of the Association have the following rights and privileges: they elect annually the Officers and Council; they receive the Journal of the Association free by post; they are admitted to view the Laboratory at Plymouth, and may introduce friends with them; they have the first claim to rent a place in the Laboratory for research, with use of tanks, boats, etc.; they have the privilege of occupying a table for one week in each year free of charge; and they have access to the books in the Library at Plymouth.

All correspondence should be addressed to the Director, The Laboratory, Citadel Hill, Plymouth.

CONTENTS

CAMBRIDGE UNIVERSITY PRESS
CAMBRIDGE, AND BENTLEY HOUSE, LONDON
CANADA AND INDIA: MACMILLAN

Printed in Great Britain at the University Press, Cambridge
(Brooke Crutchley, University Printer)