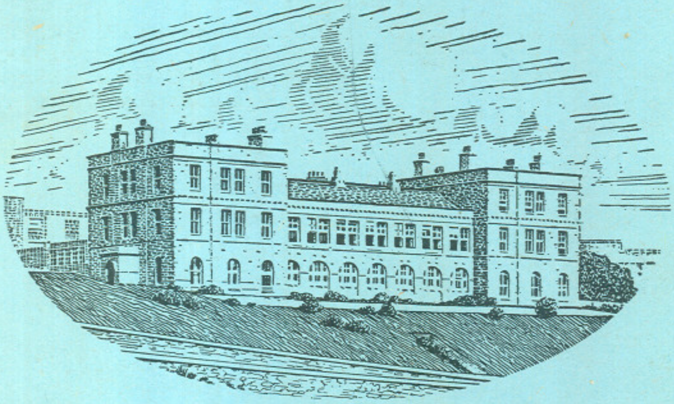
# JOURNAL OF THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM



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# THE DISTRIBUTION OF *GAMMARUS* SPECIES IN ESTUARIES. PART I

By G. M. Spooner, M.A.
Zoologist at the Plymouth Laboratory

(Text-figs. 1–7)

*Editor's note*. This paper and that by Dr S. G. Segerstråle (this *Journal* pp. 219–44), independently bringing forward certain new ideas on the taxonomy of *Gammarus zaddachi* and *G. locusta*, were received for publication simultaneously. As this paper is a report of work largely carried out before the war, of which summarized results have already been referred to in print (e.g. Report of Council in this *Journal*, Vol. XXIV, pp. 444, 691; Huxley, *The Modern Synthesis*, p. 315), it is given precedence. The authors have since consulted each other over matters in which their contributions overlap, in particular over the taxonomic status of the new forms they distinguish and regarding the names to be applied to them. Dr Segerstråle has kindly consented to adopt the two new names introduced by Mr Spooner. In this paper, where appropriate, footnotes giving cross-references to Segerstråle's paper have been inserted.

## CONTENTS

## INTRODUCTION

The work of which an account is here given was largely carried out from the autumn of 1937 to the spring of 1940, when it was interrupted by the war. In taking it up again (in July 1945) while facilities for field work are still limited, the author feels it useful to publish results as they stand and indicate where further work is considered advisable.

In examinations of the free-swimming bottom fauna of the Tamar and other estuaries, attention was inevitably drawn to the populations of *Gammarus* species, which make up the greater bulk of it. Before quantitative observations were planned, some interesting points came to light with regard to the qualitative composition of populations. This aspect lent itself more readily to study and, though by no means a new field for exploration, soon proved worth examining in greater detail than previous workers had attempted.

The broad fact of a replacement of one *Gammarus* species by another in passing up an estuary was well enough known, though exact knowledge for the British Isles only starts from the time when *G. zaddachi* Sexton was recognized as a regular member of the upper estuarine fauna of the Tay (Bassindale, 1933; Alexander, Southgate & Bassindale, 1935) and of the Deben (Serventy, 1935). This species proved to be the main brackish-water species overlapping with the marine *G. locusta* (L.) near the seaward end, and with the fresh-water *G. pulex* (L.) at the river end (or 'head') of the estuary. The status in estuaries of two other brackish-water species, *G. duebeni* Lillj. and *G. chevreuxi* Sexton, remained obscure. It has usually been suspected that salinity conditions are the critical feature of the environment which limits the range of a species in a given area; but Serventy suggested that exclusion through competition limits *G. zaddachi* to the middle reaches of estuaries, while there are known instances, and growing evidence of others, of one species having varying salinity tolerance in different parts of its geographical range. Such problems clearly demanded further study.

Much depends on accurate knowledge of the systematics of the genus. Thanks to the work of Sexton in this country, workers are now in a strong position to identify British material. Yet, as will become clear in the pages which follow, there were (and are) still facts to be added, and confusions to be rectified.

There are several advantages in the choice of *Gammarus* as a subject for ecological study, some of which have only become fully appreciated during the course of the present work. (1) They are among the more abundant of estuarine animals. (2) Being adaptable to varied surroundings and not limited to specialized ecological niches, they do not show gross patchiness of distribution within their habitable range: for example, a continuous population occupying the whole length of an estuary or lagoon can usually be found, even though the proportions of species represented change from one end to the other. (3) Furthermore, it can be said that they are indifferent to the nature of the substratum to a remarkable degree. Provided there is some kind of object which can provide them with cover or shelter, it matters not whether the bottom is muddy or stony, the water turbid or clear. Almost any kind of organic matter provides detritus on which they can feed. This means that, in so far as inanimate environmental factors limit distribution, affect growth rate, or produce any difference between two populations, these are mainly to be sought amongst the more elementary properties of the environment, such as temperature, salinity, and oxygen concentration. (4) The brackish-water species, at least, can be reared in the laboratory and subjected to controlled experimental conditions.

## METHODS

The use of a box sieve makes collecting a simple matter, and overcomes the difficulty of samples getting fouled with mud. The sieve actually used is similar to that designed for handling mud samples, as described by Spooner & Moore (1940). It forms a cube of 1 ft. each way, the bottom made of perforated zinc, the sides of wood, and the top open. A window of perforated zinc in one of the sides facilitates outflow of water. Suitable handles are fitted on each side at the top.

In estuaries, clumps of weed or any other suitable objects, collected from the ground in the intertidal zone or from the bed of the river channel, are placed in the sieve and well shaken in water, the sieve held three-quarters submersed. The larger objects and fragments are shaken out and discarded in turn. The macrofauna which had been contained in them accumulates at the bottom of the sieve with a mass of small fragments and debris. This is well washed by lifting the sieve in and out of the water, and transferred as desired to collecting jars. It is easy to perform these operations without injuring the animals, though care must be taken when gravel or small stones accumulate in the debris. When working in ditches or pools it is often useful to make the collections of weeds, etc., in a strong fine-meshed net, but the net contents should always be sieved, as this is the only effective method of removing mud and of concentrating the catch.

A final washing of the samples may be necessary on return to the laboratory, so that when they are placed in bowls (in appropriate mixtures of sea and fresh water) the contents are free from turbidity. Normally gammarids will comprise the greater bulk of the catch. Animals are killed by addition of strong formalin solution, and preserved in 5% neutral formalin in sea water. Samples were always examined as soon after killing as possible, while the normal colours remained unimpaired.

Examining live, or freshly killed, specimens enormously facilitates rapid diagnosis. Sometimes colour characters, lost after preservation, are valuable taxonomically—the most spectacular example, perhaps, being the orange pigment spots in *G. locusta* immature (see p. 14). In other respects, also, characters seem more easily assessed in fresh specimens, while the tissues still retain their transparency. It is clear that if amphipodists generally were able to concentrate more on fresh material, some of the existing taxonomic difficulties and confusions might never have arisen.

As a preservative, formalin is far superior to alcohol, in which specimens often become very opaque, hard and brittle. The formalin should, however, not be dissolved in water of much lower osmotic concentration than that of the body fluids; otherwise, swelling of soft tissues is apt to occur. A solution of 5% formalin in sea water is perfectly suitable for marine and brackish-water organisms, and, as far as I have tested it, for fresh-water Crustacea as well. Specimens so preserved can always without harm be placed temporarily in tap water for examination.

Microscope mounts of limbs, etc., are conveniently made in a chloral medium, e.g. Faure's Solution, as used by entomologists. No preparation is necessary; the chitin is cleared of soft matter in a short time; the medium hardens sufficiently to make ringing the mount optional; and the preparations normally keep indefinitely. Also if at any time remounting is considered desirable, the mount is simply dissolved in water. Slides intended for more temporary use can be mounted as rapidly as in water, with the advantage that they do not dry up and can be kept permanently if subsequently desired.

Apart from collections made personally, various material collected by other zoologists has been examined, and I am particularly indebted to Mrs E. W. Sexton, Mr G. I. Crawford, the late Dr K. Stephensen (Copenhagen), Prof. A. D. Hobson, Dr L. C. Beadle, Mr R. Bassindale, Mr R. Elmhirst, and Mr H. P. Moon, for the loan or presentation of material. It is a pleasure to record my thanks to Mrs Sexton for her constant interest and for the ready loan of her specimens and literature. Mr G. I. Crawford has sent me material from the British Museum, including samples collected by himself after leaving Plymouth; his earlier collections (see Crawford, 1936, 1937) were available for examination at the Plymouth Laboratory. Mr R. Bassindale's interesting series of samples from the Severn Estuary has already been recorded and commented on in the 'Studies on the Biology of the Bristol Channel' publications (Bassindale, 1941, 1942*a*, 1942*b*, 1943). Prof. Hobson's material included collections from the Inner Hebrides, from streams flowing on to the shore, of which an account is published by Beadle & Cragg (1940).

I wish further to thank Dr Sven Segerstråle for his most helpful cooperation before our respective papers were finally printed.

## TAXONOMIC OBSERVATIONS

It was not possible to proceed far with ecological observations without first going rather thoroughly into the taxonomic aspects of the species under consideration. The chief reasons for this were as follows.

(1) Species of *Gammarus* tend to differ in a number of minor characters in addition to any major differences which may exist. These were repeatedly examined, not only to obtain knowledge of their constancy or variability, but for the more immediate purpose of detecting atypical populations. Sometimes differences, though small, prove remarkably constant and reliable, and are invaluable when specimens are atypical, for some reason or other, in important respects (for example, as a result of stunted growth, inhibited maturity, or regenerating limbs), or with parts missing as a result of damage. It is needless to emphasize that the larger the number of characters available, the stronger is the position of the investigator.

(2) It was very desirable to determine reliably, not merely adult males, for which alone, as a rule, detailed descriptions are available, but individuals of both sexes at all ages. This aspect had to be given special attention, and some original observations are reported below. It was gratifying to find that reasonable characters exist to separate the immature of all species which are liable to occur together in Britain, even down to the smallest growth stages of which account has been taken. The necessity for dealing with specimens of all sizes also demanded closer recognition of the changes which take place during the course of life, particularly during the late immature and early maturity stages. Characters of animals whose development is gradual and whose growth continues throughout life are profitably studied in their four-dimensional aspect.

(3) Even with adult males of British species it was soon apparent that some existing descriptions were still not complete, and that the true value of some diagnostic characters had still to be adequately assessed. It was also possible to separate *G. zaddachi* into two readily identifiable subspecies, which, in addition to their morphological differences, have very different salinity optima.

(4) Most character-differences are comparative. It was intended at least to make a start in expressing some of them more precisely in numerical and statistical terms.

### *Note on the numbering of the peraeopods*

It is necessary to emphasize that one change in descriptive terms has been adopted. Sexton (e.g. 1912, 1942) and Sexton & Spooner (1940) still follow Sars (1895) and Stebbing (1906) in numbering the peraeopods from peraeon segment 3 onwards, so that the limb of segment 3 is peraeopod 1 and of segment 7 is peraeopod 5. Hoping that this confusing habit will soon be abandoned altogether, I propose to follow the more logical and (by now) more general practice of giving the limbs the same number as the segment (as in Chevreux & Fage, 1925). Thus the gnathopods, which are the limbs of peraeon segments 1 and 2, are the modified peraeopods 1 and 2; the first unmodified limb, or 'leg', is peraeopod 3; and the hindmost limb, that of peraeon segment 7, is peraeopod 7. The term 'peraeopod' simply means the limb of a peraeon segment and has no functional implication, whereas the terms 'gnathopod' and 'leg' are functional and denote special forms of peraeopod. It is unfortunate that authorities like Sars and Stebbing have used the terms 'leg' and 'peraeopod' in exactly the reverse sense.

### *Species in estuarine and associated faunas*

The following species have occurred in faunas examined in this work:

*Marinogammarus marinus* (Leach, 1815).
*M. obtusatus* (Dahl, 1938).
*M. finmarchicus* (Dahl, 1938).
*M. stoerensis* (Reid, 1938).
*Gammarus locusta* (L. 1758) G. O. Sars, 1895, *sens.str.*
*G. zaddachi* Sexton, 1912, typical subspecies, as here designated.
*G. zaddachi salinus*, subsp.nov.
*G. chevreuxi* Sexton, 1913.
*G. duebeni* Lilljeborg, 1851.
*G.* (*Rivulogammarus*) *pulex* (L. 1758).

## **Marinogammarus** species

The taxonomy of these essentially marine littoral forms has already been dealt with (Sexton & Spooner, 1940). At the same time a list of the material examined up to the summer of 1940 was included. Stephensen (1940) also gives descriptions and locality records, especially from Norway. Certain additional British material has since been examined; for example, collections made in 1942 and 1943 on the shore near the Millport Laboratory, where five of the species occurred (see Scottish Marine Biological Association, *Annual Report*, 1942–3, pp. 10–11).

In estuaries *M. marinus* alone has been encountered in abundance, extending well into the mid-estuarine reaches. It is, however, much concentrated near high-water levels, and does not enter into the low-water and mid-channel populations to which main attention is subsequently given. More will be said later, from an ecological aspect, about the upward limit of penetration into estuaries, a point which is fairly easily determined by inspection in the field.

*M. olivii* (M.-Edw.), of which a description was included in our 1940 paper, had not at that time been recorded from Britain. Almost simultaneously, however, Reid (1940) reported it from the River Avon in South Hants, where, at Keyhaven, it was living in water which was fresh to slightly brackish (see also Goodhart, 1941). This species, however, is not a widely spread inhabitant of estuaries and is probably extremely local.

## **Gammarus locusta** (L.) G. O. Sars, *sens.str.*

This abundant marine species has been well enough recognized from descriptions in standard works (e.g. Sars, 1895; Della Valle, 1893; Stebbing, 1906; Chevreux & Fage, 1925) so long as purely marine faunas were under examination. In the seas of western Europe there seems to be no species with which it is liable to be confused. But in estuarine and brackish faunas it has been much confused with *G. zaddachi salinus* (pp. 20–1). Existing descriptions are still in need of amplifying to emphasize certain characters which have proved important in distinguishing typical *locusta* from other known species, and to indicate more clearly what variation occurs amongst genuine *locusta* populations.

It is necessary to emphasize that this account applies only to the *locusta* of the temperate eastern Atlantic and the North Sea (and apparently also to the western Mediterranean). I have recently been able to satisfy myself that the form occurring in northern waters (west Norway, Iceland, Greenland, Newfoundland and Arctic coasts) differs in so many respects that it is quite separable.[1] It is possible also that the form of the species which inhabits the western Baltic in much lower salinities than are tolerated, for example, in Britain, may genuinely be less easily separated from *G. zaddachi* in that area.[2] A fuller treatment of the characters of *G. locusta* in its whole range is deferred for a later occasion. The description here, however, is valid for the form which seems to be generally accepted as the type of *locusta*, following the drawings by Sars (though his description by itself is not critical enough).

### *Adult male*

In addition to the descriptions in standard works, Sexton (1942, pp. 600–1, pl. iii, figs. 19–24) gives a list of characters useful for comparison with related species, as well as new drawings of the head, antennae and gnathopods. Only certain comments need be made. In *antenna* 1 the long accessory flagellum is a valuable diagnostic character, especially if consideration is given to the allometric changes which occur during growth. At the onset of maturity it has 7 or 8 segments which increase to 13 or 14 in the largest and oldest individuals. At the start it is about 1½ times the length of peduncle segment 2, but it soon attains twice the length of that segment, and in the end is about 2⅓ times as long. As compared with *G. zaddachi salinus*, young males have about 2 segments more, the oldest about 5. In antenna 1 peduncle the length ratio of 3:2:1 for the first three segments is always closely approached.[3] In

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[1] In essential respects these northern animals seemed much closer to *zaddachi*. Segerstråle (pp. 223 *et seq.*) has independently shown that they are to be included under that species. The description of *zaddachi* has only to be modified in minor respects to include this form, whereas that of *locusta* would need to be drastically revised.

[2] But see comment on p. 18.

[3] Precise micrometer measurements give ratios of 142–153:100:45–49 for the three segments, segment 3 being consistently rather less than half segment 2.

other species segment 1 is always less than the combined length of the other two, and the 3rd is often longer than half the 2nd. *Gnathopod hands.* Once the fully mature adult stage has been reached, the form and arrangement of the palmar spines of both gnathopods are diagnostic and easily recognized. This character should, as always, be given primary weight in critical determinations. The gnathopods are well figured for the first time by Sexton (1942, pl. iii). (N.B. Sars's drawing, 1895, pl. 176, fig. 1 p$^2$♂, is inaccurate, and was probably taken from a specimen of the northern form.) *Gnathopod 2 hand.* The exact shape of this segment is somewhat variable, though it is normally in some sense longer or narrower than in *zaddachi* and *duebeni*. While both the dorsal border and the palm are relatively long, the ventral border is less so; thus the palm tends to approach the length of the ventral border, especially in larger and older animals. The ventral border may diverge somewhat in an apical direction, or at least remain straight and parallel with the dorsal border: only infrequently is it rounded towards the palmar angle in a manner typically found in *zaddachi*. More significant is the arrangement of the palmar spines (Fig. 1). The median palmar spine is succeeded, towards the palmar angle, by a regular series of spines graded in respect to size and distance between successive spines. This arrangement contrasts with a condition more frequently met in *Gammarus* species (including *G. zaddachi*,

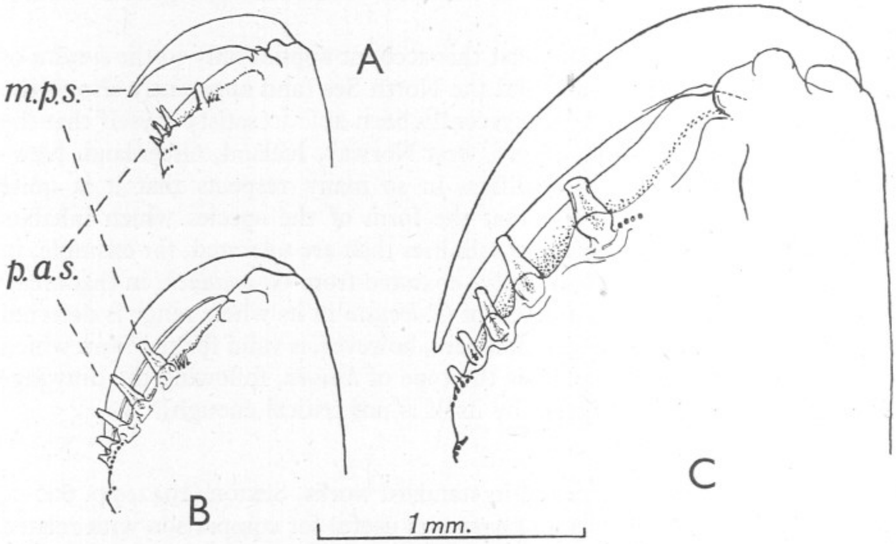

Fig. 1. *Gammarus locusta sens.str.*, male gnathopod 2 hand, distal part, with hairs omitted, to show the arrangement of the palmar spines. A, young mature male, Saltash, River Tamar, 5. iv. 38, showing the median palmar spine (*m.p.s.*) still separated from the palmar angle spines (*p.a.s.*). B, larger and fully mature male from same sample. C, large male, 25 mm., Plymouth Sound, 12. xi. 06. In B and C all the spines tend to form a continuous row with graded intervals.

and the earliest mature stages of *locusta* itself, Fig. 1 A), where an isolated median spine is separated by a marked gap from a cluster of spines arising quite close together at the palmar angle. Only *G. duebeni* (p. 37) shows a graded series at all comparable. It is important to appreciate that the true *locusta* pattern is not finally attained until two or three growth stages after maturity have been reached. Another important characteristic of mature *locusta* hands is seen in the truncate tip and bulbous base of the median palmar spines, and of the larger of the angle spines, which thus become almost 'flask-shaped' (those of *duebeni* retain their original simple shape). *Peraeopods* 6 *and* 7 (examples of *Pp.* 7 in Fig. 2): in these limbs the more apical segments are often provided with some long, stiff, outstanding setae, arising singly or in sparse tufts, particularly noticeable on the middle part of the pre-apical segment (propodite). The posterior border of the basal segment, however, is at most sparsely furnished with short setules. The hair pattern can thus be distinguished from both subspecies of *G. zaddachi* (p. 23 and Fig. 4). All limbs tend to be somewhat elongate and slender compared with other species of the genus, with the exception of *G. wilkitskii* Birula, in which they are more extremely so, and of *G. zaddachi* which differs very little. Peraeopod 7 shows this tendency at least as much as other limbs, and has been selected for standard measurements. The length (*a*) of the carpopodite has been compared with (*b*) its width at the first proximal spine group, and with (*c*) the length of the basal segment. The ratio of $a:b$ is 4·0 to 4·5; of $a:c$ is 0·75 to 0·80. The last ratio is lower in other species considered here; the first lower in all but *zaddachi*. The *telson*, in conformity with the limbs, is also relatively elongate. In adult males the length of one arm is 2·4–2·5 times its greatest width (in immatures and very young males it is still of more normal proportions with the ratio at about 2·0). *Uropod* 3 *inner ramus* is typically subequal in length to the outer ramus: more precisely, it is typically 96–99% the length of the first segment of the outer ramus. No other marine or brackish water *Gammarus* in British waters shows this condition, and only occasional large specimens of *G. zaddachi salinus* even approach it (p. 29). But some populations, especially those subjected to reduced salinity, have an appreciably shorter inner ramus, which may remain as low as 85% in well-developed adults. This variation, whether genetic or environmental, is best thought of as an arrest of the differential growth of the inner ramus; since the latter starts much shorter than the outer ramus and normally steadily catches up on it, or nearly so, during the immature phases. The *urosome segments* dorsally are characteristically strongly raised and laterally compressed in the median line. The elevations are angulate, those on the first two segments forming a right angle in contour, or nearly so (90–110°). In no other form are these elevations so pronounced.

In practice the relatively long accessory flagellum, the proportions of antenna 1 peduncle segments, the form of the hand of gnathopod 2, the dorsal elevations of the urosome, and the long uropod 3 inner ramus, together or

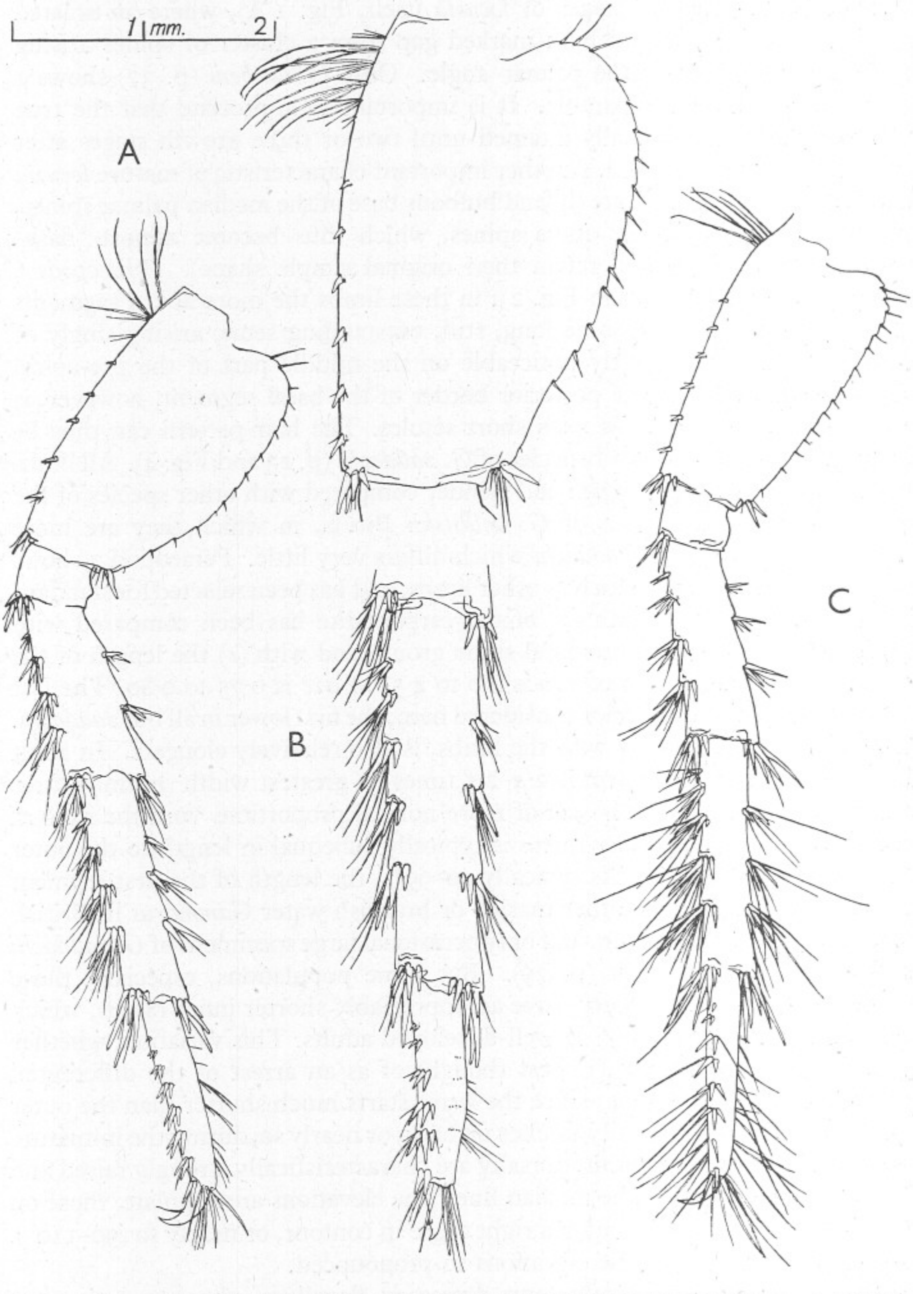

Fig. 2. *Gammarus locusta sens.str.*, peraeopod 7 of male (coxopodite omitted). A, Saltash, River Tamar, 5. iv. 38 (larger specimen than in Fig. 1). B, Plymouth Sound, 12. xi. 06 (same specimen as in Fig. 1), middle segments omitted. C, variety from the Fleet, Dorset, near Langton Herring, 14. xi. 37.

even individually provide quick means of identification. The sparseness of the hairs on antenna 1 peduncle ventrally provides a critical distinction from *G. zaddachi*. Good specific characters also show in the shorter head, the sharply angulate ventral corner of its lateral lobe, the elongate anterior coxal plates, the deep and subrectangular ventral portion of coxal plate 4, and the much produced and pointed inferior angles of epimera 2 and 3. In fresh material the presence of orange pigment spots on the mesosome segments (see below) is also diagnostic, though in larger adults these may be reduced, or absent, or obscured by dense epidermal pigmentation.

### *Adult female*

Most of the characters given for the adult male apply equally to the female. The description has only to be modified in respect to (1) characters which are directly concerned in sexual dimorphism, e.g. the presence of brood-plates, and the structure of the gnathopod hands; and (2) characters which involve appreciable allometric changes during early maturity, and which remain closer to the immature condition in the more conservative female.

The *size* attained is much less than in the male: in south-west England a maximum of 20 mm. length (head to apex of telson) contrasts with 28 mm. maximum in the male. The *accessory flagellum* of antenna 1 in the very largest individuals has 11 segments, when it is 2·2–2·3 times the length of peduncle segment 2. More usually the larger specimens in samples are of the order of 15 mm. body length, and these have an accessory of 8 or 9 segments and of length about twice, or slightly less, that of peduncle segment 2. On *antenna* 2 the flagellum lacks calceoli. The *gnathopod hands*, though much less specialized than in the male, have still some taxonomic value: the hand of gnathopod 2 is unusually elongate, its dorsal and ventral borders very straight and parallel to each other, and its length always more than twice its distal width (in no other form is a ratio of 2·0 exceeded; in *G. zaddachi* it is 1·65 to 1·8). The median palmar spine is lacking. On *peraeopod* 3 the hairs are sparser than in the male. The limbs are less slender than in the male adult: in peraeopod 7 the carpopodite is 3·5–3·9 times as long as broad proximally, and only 0·66–0·70 the length of the basal segment. The *telson* length attains only 2·25 the greatest width of one arm (though this is still longer than in related species except *G. wilkitzkii*). The *urosome* elevations are not quite so pronounced as in the male. The *body pigmentation*, though variable, is usually heavier, a deep blackish blue colour, with pale bands on the antennae, being common. The *eggs* are relatively small (see below), and the numbers in one batch relatively large: as many as 235 have been taken from a specimen of 20 mm. length, and 230 from one of 16 mm.

In mixed samples the female *locusta* is at once distinguished from *zaddachi* by its sparse antennal hairs, its more elevated urosome segments and its elongate gnathopod 2 hand.

## TABLE I. DIMENSIONS OF EGGS IN *GAMMARUS LOCUSTA* AND *ZADDACHI*

*Gammarus locusta*

| Sample | Length of female mm. | Size of brood | $n$=no. of eggs measured | Mean length ($l$) × width ($w$) mm. $\times 10^{-1}$ | Calculated volume cu.mm. $\times 10^{-2}$ |
|---|---|---|---|---|---|
| Newly laid and early development stages | | | | | |
| *b* | 8 | 23 | 22 | 4·429 × 3·691 | 3·16 |
| *b* | 8 | 14 | 13 | 4·848 × 3·632 | 3·35 |
| *b* | 8·5 | 22 | 22 | 4·669 × 3·822 | 3·57 |
| *b* | 8·5 | 25 | 23 | 4·810 × 3·791 | 3·62 |
| *b* | 10 | 44 | 40 | 4·678 × 3·792 | 3·52 |
| *m* | 16 | 230 | 40 | 4·502 × 3·668 | 3·17 |
| *e* | 13·5 | 57 | 40 | 4·632 × 3·786 | 3·48 |
| *e* | 15 | 163 | 25 | 4·614 × 3·981 | 3·83 |
| *d* | — | 68 | 40 | 4·630 × 3.938 | 3·76 |
| *d* | 12 | 84 | 83 | 4·735 × 3·916 | 3·80 |
| *b* | 10 | 29 | 23 | 4·842 × 3·958 | 3·97 |
| *b* | 10 | 12 | 9 | 4·96 × 3·91 | 3·97 |
| *f* | 10 | 24 | 23 | 4·797 × 3·617 | 3·29 |
| *m* | 13·5 | 135 | 50 | 4·746 × 4·018 | 4·01 |
| *b* | 9·5 | 28 | 28 | 4·857 × 3·986 | 4·04 |
| *b* | 10 | 29 | 27 | 4·836 × 4·003 | 4·06 |
| Intermediate development stages | | | | | |
| *e* | 13·5 | 106 | 40 | 5·138 × 3·946 | 4·19 |
| *e* | 16 | 219 | 80 | 4·728 × 4·123 | 4·21 |
| *l* | — | 38 | 30 | 4·995 × 4·160 | 4·53 |
| Embryos advanced | | | | | |
| *d* | 13 | 80 | 25 | 5·302 × 4·416 | 5·41 |
| *e* | — | 46 | 45 | 5·307 × 4·484 | 5·59 |
| *b* | 12·5 | 31 | 15 | 5·355 × 4·437 | 5·52 |
| *b* | 9 | 8 | 8 | 5·420 × 4·500 | 5·75 |
| *b* | 9·5 | 12 | | | |
| Young well-formed or ready to hatch | | | | | |
| *b* | 9 | *c.* 27 | 8 | 5·70 × 4·55 | 6·18 |
| *b* | 9 | 14 | 6 | 5·68 × 4·83 | 6·93 |
| *d* | — | 78 | 25 | 5·661 × 4·618 | 6·32 |
| *d* | 12 | 65 | 25 | 6·045 × 4·781 | 7·23 |
| *f* | 10 | 32 | 25 | 5·907 × 4·656 | 6·71 |

Index to samples from which females were taken:

*a*, River Tamar, Thorn Point, 22. vi. 39.
*b*, River Tamar, Thorn Point, 9. x. 45.
*c*, River Tamar, Ernesettle, 1. iii. 38.
*d*, River Tamar, Henn Point, 5. iv. 38.
*e*, River Tamar, St John's Lake, 5. v. 38.
*f*, River Plym, Laira Bridge, 23. xi. 46.
*g*, River Erme, near mouth, 8. ii. 39.
*h*, River Avon (South Devon), 16. v. 38.
*i*, River Avon (South Devon), 8, i. 39.
*j*, River Avon (South Devon), 20. v. 46.
*k*, Kingsbridge Estuary, Blank's Mill Creek, 22. i. 39.
*l*, Kingsbridge Estuary, Salcombe, viii. 45.
*m*, Brancaster, Norfolk.

TABLE I (*continued*)

*Gammarus zaddachi* *

| Sample | Length of female mm. | Size of brood | $n$=no. of eggs measured | Mean length ($l$) × width ($w$) mm. × $10^{-1}$ | Calculated volume cu.mm. × $10^{-2}$ |
|---|---|---|---|---|---|
| | | Newly laid and early development stages | | | |
| *a* | — | 12 | 8 | 5·42 × 4·44 | 5·59 |
| *a* | — | 19 | 17 | 5·393 × 4·659 | 6·13 |
| *c* | 11 | 44 | 44 | 5·573 × 4·720 | 6·50 |
| *c* | 10·5 | 20 | 20 | 5·720 × 5·080 | 7·73 |
| *c* | 12 | 22 | 21 | 5·989 × 5·067 | 8·05 |
| *c* | 11 | 22 | 20 | 5·856 × 5·120 | 8·04 |
| *i* | 10 | 32 | 32 | 5·680 × 4·725 | 6·64 |
| *h* | 13 | 62 | 25 | 5·594 × 5·005 | 7·34 |
| *k* | 9 | 20 | 19 | 5·726 × 4·855 | 7·07 |
| *k* | 9·5 | 22 | 22 | 5·855 × 4·800 | 7·06 |
| *k* | 9·5 | 31 | 29 | 5·639 × 4·935 | 7·19 |
| | | Intermediate development stages | | | |
| *a* | — | 7 | 3 | 5·84 × 4·96 | (7·52) |
| *h* | 7 | 14 | 11 | 6·044 × 4·909 | 7·63 |
| *i* | 10 | 33 | 32 | 5·898 × 5·065 | 7·92 |
| *i* | *c.* 10 | 29 | 19 | 5·924 × 5·040 | 7·88 |
| *i* | — | 32 | 28 | 5·880 × 5·286 | 8·60 |
| *g* | — | 14 | 10 | 6·347 × 5·184 | 8·93 |
| | | Embryos advanced or young well formed | | | |
| *i* | — | 37 | 7 | 6·24 × 5·51 | 9·92 |
| *h* | 7 | 14 | 8 | 6·52 × 5·30 | 9·59 |
| *h* | 10·5 | 45 | 35 | 6·421 × 5·518 | 10·23 |
| *i* | 11·5 | 42 | 34 | 6·506 × 5·544 | 10·47 |
| *h* | 13·5 | — | 5 | 6·88 × 5·52 | (10·98) |
| *h* | 9·5 | 25 | 20 | 6·872 × 5·740 | 11·86 |
| | | Young about to hatch | | | |
| *c* | 11·5 | 31 | 13 | 7·92 × 5·60 | *c.* 13·0 |
| | 14 | 40 | 10 | 7·120 × 5·944 | 13·17 |

* All specimens belong to subspecies *salinus* (see p. 20).

## *Measurements of eggs*

A number of measurements of batches of eggs from females of *locusta* and *zaddachi salinus* are given in Table I to show the contrast between the two forms. Individual measurements were made in units of 0·008 mm. From the greatest ($l$) and narrowest ($w$) diameters, a value representing the volume has been calculated from the formula $l \times w^2 \times \frac{1}{6}\pi$. It will be observed that the volume is about 0·55–0·6 that of *G. zaddachi* eggs at comparable stages of development. If there is any increase in size of egg with size of parent, this must be very small and negligible compared with other sources of variation. On the other hand, as is well known, the average number of eggs in one batch tends to increase with the size of the parent. The young at extrusion are correspondingly smaller than in *G. zaddachi*.

*Immature*

Almost from the time of hatching a small cluster of reddish orange pigment globules is present on several of the peraeon segments. These are situated on segments 2–7 in the body wall near the base of each limb (Fig. 3). Similar, usually more elongate and more diffuse, patches occur on the metasome, but these are common to several species of *Gammarus* and *Marinogammarus*. The presence of these coloured spots on the peraeon is diagnostic of *Gammarus locusta*. As the young and immature are otherwise colourless and translucent, the spots are very obvious in living and freshly preserved specimens. Though after maturity these pigment spots may be reduced or obscured, they are almost constantly present during immaturity, and provide an excellent means of identifying fresh material, particularly in sorting, for example, mixed populations of *locusta* and *zaddachi*. This is an example of a character which might be thought to be of low taxonomic grade, but which has proved very reliable in practice.

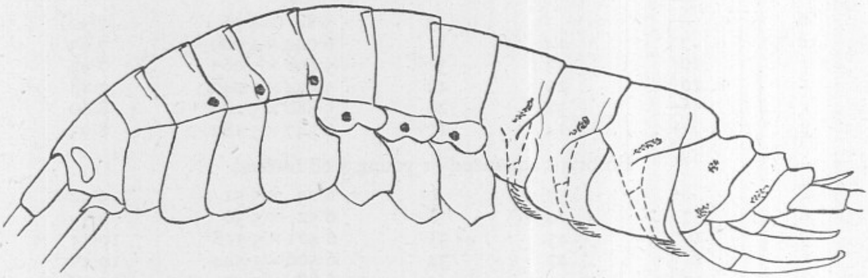

Fig. 3. *Gammarus locusta sens.str.*, body in side view, semi-diagrammatic, to show the position of the orange pigment patches in the body wall. The patches on peraeon segments 2 to 7, which are diagnostic of this species, are shown as rounded black spots.

By the time the immature phase is about half-way through, *locusta* can be distinguished from other species by various structural features. Already there are indications of a relatively long accessory flagellum, raised urosome elevations, and produced epimera. The inner ramus of uropod 3 is long enough to distinguish it readily from that of a *Marinogammarus*. *Gammarus duebeni* is already isolated by the conspicuous produced posterior angles of peraeopod 7 basal segment. The main structural difference from *zaddachi* at this stage is in the hairs on the ventral surface of the antennal peduncles, which in *zaddachi* are by now longer and more numerous.

While male characters are developing in the maturing animal, until the stage at which the fully mature form is reached (two or three stages after functional maturity), the hand of gnathopod 2 is still of a somewhat generalized type (Fig. 1A). The median palmar spine has appeared, but, as in other species at this stage (and in most throughout life), it is still separated by a gap from the spines at the palmar angle, and is not fully truncated distally. Other heterogonic changes are going on at this time, and in very young males comparative measurements may not yield ratios found to be characteristic of the full adult. For example, values nearer those of the female are found for the relative lengths of carpopodite 7 and the telson. In the female the relative length of the gnathopod 2 hand increases from 2·0 to about 2·3 during the first stage of maturity.

### *Notes on variation within the species*

Apart from adult body pigmentation and average size, the character which perhaps varies most noticeably in normal populations concerns the development of hairs on the limbs. This variation, however, is usually only evident after close inspection, and its range is limited. It seems to apply most to those limbs and side-plates where the total number of hairs is at best never large. For example, a sample from the north Norfolk coast near Brancaster is uniformly hairier, on all peraeopods and on the pleon, than Devon populations. But often within a single population quite noticeable differences occur between individuals of comparable stages of development. Though this matter deserves closer study, the general fact is clear enough, and shows that *locusta* is no exception to the rule that the development (i.e. number in a cluster, and length of individual hairs) is always subject to variation in a *Gammarus* species, perhaps sometimes as a more or less direct effect of environmental factors or nutrition, though such an effect has still to be demonstrated experimentally.

Among marine populations an interesting variation has been observed in a sample collected by Mr G. I. Crawford in Whitsand Bay, November 1934, by dredging in shallow water offshore. In one sample (5. xi. 34) the males have very dense setation on antenna 2 and peraeopod 3, and the longer hairs are much curved. Except that the elevations of the urosome segments are somewhat rounded and less compressed than usual, other characters are typical of the species. In a second sample of over 300 (dredged in weed, 16. xi. 34), which contained adults of all sizes, actively breeding, the same features are shown, but the male hairs are not quite so dense and only some of the hairs are curved.

It is, however, among populations living under recognizable atypical conditions that variations are most frequently observed. Some examples from brackish waters can be given.

At the limit of penetration into estuaries, particularly if conditions are deteriorating, as with the onset of winter, animals seem subject to inhibition of growth. Maturing individuals are smaller than usual, and often have a somewhat shortened uropod 3 inner ramus (retention of an immature character). It appears, however, that they soon die off as the salinity drops, and do not survive long enough to produce a persistent modified population. In the continuously habitable parts of estuaries populations resemble those from the sea. Those living in turbid water or on muddy bottoms are usually deficient in epidermal pigment, and tend to retain the immature translucent appearance.

In some localities where the species is established in water of permanently reduced salinity, persistent atypical characters may be shown. Two instances have come to notice: in the Fleet, Dorset, and New England Creek, Essex.

The Fleet is a shallow stretch of water separating the Chesil Beach from the mainland (see Tansley, 1939, chapter XLII, pls. 155, 156), receiving sea water by tidal action through its narrow connexion with Portland Harbour and fresh water by land drainage. Apparently a fairly steady salinity gradient is maintained through its 9-mile length, the incessant fluctuations characteristic of estuaries being largely lacking. At Langton Herring the water is salt enough to support *G. locusta* (in November it measured 26 °/₀₀ at low water). Samples collected here on 14. xi. 37 and 27. iii. 38 show the following characters. (i) Uropod 3 inner ramus short, in adult males only 80–90% of outer ramus segment 1; (ii) hairs unusually dense, especially in the male on antenna 2 peduncle and on hinder peraeopods (Fig. 2 C), the length and number of the stiff outstanding hairs on the latter being particularly noteworthy; (iii) the spines on ventral border of epimera 2 and 3 unusually strong; (iv) side-plates and basal segments of peraeopods (Fig. 2 C) notably narrow; (v) other segments of peraeopods slender, e.g. carpopodite 7 nearly 5 times as long as wide proximally; (vi) average size of adults below normal. All other features are quite characteristic of *locusta*; the male gnathopod 2 is in fact rather an extreme *locusta* type. The orange spots on the peraeon were well developed.

The population from New England Creek, Essex, where the fauna and environment were carefully studied by Howes (1939), is still more aberrant. Mr Howes kindly sent me his *Gammarus* for examination, and my report on their characters is given in his paper (p. 414). It is definitely a dwarfed population of *locusta*, presumably surviving from the time the creek was cut off from the sea by a dam. Ample diagnostic features are shown in the elevated urosome segments, the form of the male gnathopods, the deep ventral portion of coxal plate 4, the produced angular corner of the lateral lobe, the lack of long hairs on basal segments of peraeopods 6 and 7 (though the rest of these limbs is unusually hairy), the sparsity of hairs on antenna 1, etc. Atypical features recorded were as follows: (i) uropod 3 inner ramus relatively short, between 80 and 90% of segment 1 of outer ramus; (ii) hairs unusually dense, even more so than in the Fleet population; (iii) the spines on the ventral border of epimera 2 and 3 in some specimens notably strong; (iv) size much reduced, correlated with which the number of segments in the accessory flagellum did not exceed 8, 7 being a frequent number; (v) in one sample containing the most extreme dwarfed and hairy specimens there was a strong tendency for the hairs on the male antenna 2 to become curled.

It will not escape notice that the variations of these two brackish populations are of a very similar kind. One is tempted to ask whether reduction of salinity alone has not brought about like results in two widely separated localities. It would be very instructive to test the constancy of the characters of populations as these, by rearing in the laboratory under controlled conditions.

Two samples from the shore at Traigh Mor, Barra, Outer Hebrides (coll. K. M. G. Fleming), varied from the normal in the following respects: eye notably broad; hinder peraeopods with long spinose setae; female gnathopods and fore-peraeopods more densely hairy; and body size somewhat reduced.

*Material examined*

(Samples involved in population analyses to be dealt with later are marked with an asterisk. Abbreviations: coll., collected by; Coll., collection.)

**England and Wales.** E. CORNWALL: Whitsand Bay, 5. xi. 34, 16. xi. 34, samples dredged in shallow water by G. I. Crawford. E. CORNWALL and S. DEVON: Plymouth Sound, including Cawsand Bay, various samples on different occasions, including a large sample of well-grown adults from a dense 'swarm' in the open water of the Sound, 12. xi. 06 (Plymouth Laboratory Coll.); Estuary of R. Tamar and branches, numerous samples,* from the Hamoaze and St John's Lake upstream to Weirquay and Bere Ferrers. S. DEVON: various samples* from the seaward end of the estuaries of R. Plym, R. Yealm, including the Cofflete branch, R. Erme and R. Avon; from the shore at Wembury; from the Kingsbridge Estuary; and from the estuaries of R. Exe and R. Axe. DORSET: The Fleet, at Langton Herring, 14. xi. 37, 27. iii. 38, numerous amongst *Zostera hornemanniana* in water of reduced salinity; Lulworth Cove, 26. xiii. 37. S. and N. SOMERSET: Bristol Channel coast at Kilve and Weston (Severn Estuary survey, by R. Bassindale, etc., see references given on p. 39). S. ESSEX: New England Creek, dwarfed population in brackish water (Howes, 1939). N. NORFOLK: sample from Brancaster district, coll. C. F. A. Pantin. NORTHUMBERLAND: Blyth, ditch from salt pans, 4. vii. 34, coll. Prof. A. D. Hobson, adults, breeding (with *G. zaddachi salinus*). DURHAM and N.E. YORKS: River Tees Estuary, Tees Survey material* (Alexander *et al.*, 1935), several from tidal zone and in tow-nettings. ISLE OF MAN: Port Erin, shore and 4–5 fathoms, Port St Mary, in weeds near L.W., ix. 38, coll. G. I. Crawford.

**Scotland.** PERTHSHIRE and FIFESHIRE: R. Tay Estuary, Tees Survey material,* one male from tidal zone of Section XI. CLYDE ISLES: Cumbrae, Kames Bay, R. Elmhirst Coll., 6. iv. 34, a few adults. ARGYLLSHIRE: Clachan Strand, under weed, Prof. A. D. Hobson Coll. INNER HEBRIDES: S. Rona, vii, viii. 37, Prof. A. D. Hobson Coll., 'Dry Harbour', 10 fathoms, 4 ♂♂, 1 imm., 'Big Harbour', shore, small ♂ and ♀, 1 imm.; Raasay, viii. 37, A. D. H. Coll., Churchton Bay, 2–3 fathoms, a number, 'Stephenson's Bay', 1 ♂ (with *G. zaddachi*); Isle of Muck, A. D. H. Coll., in eight samples, from Gallanach, 1. ix. 36, 17. viii. 39, Port Chreadhair, vii. 38, Rudha Caem na Caraich, 30. vii. 38, 16. viii. 39, etc. OUTER HEBRIDES: Barra, coll. K. M. G. Fleming, vii. 36, 37, Traigh Mhor, L.W.S.T., two samples with adults of small average size.

**Belgium**. Ostende, Bassin de Chasse, *c.* 900 ♂♂, 870 ♀♀ and 400 imm., in 71 samples (in collections identified for the Brussels Museum in Jan. 1939).

## **Gammarus zaddachi** Sexton

This is an important species in the economy of estuarine and other brackish waters, being very widespread in spite of the discontinuity of its habitats, and usually plentiful provided there is adequate cover of some sort and, apparently, an adequate oxygen concentration. It is one of the dominant members of the fauna in those parts of estuaries where the salinity fluctuations are greatest, and so most 'rigorous' to life.

The confusion over this species in the past has been considerable. Even after it had been described (Sexton, 1912), British material was still being overlooked and recorded as *duebeni* in fresher habitats, or as *locusta* in more saline waters. Continental authors have not helped matters, either from attempts to sink the species, or, sometimes, in their failure to appreciate its most reliable diagnostic characters.

Sexton (1942) has followed up her careful original description with a further detailed account which emphasizes (1) the differences between *zaddachi* and related species with which it may possibly be confused, and (2) the differences between the two extremes of variation, i.e. between a very hairy 'fresh-water' form inhabiting the lower reaches of the Elbe and Weser, and a sparsely haired, more spiny, 'true brackish water' form living in estuaries and along the coast of East Prussia. The 'fresh-water' form is figured for the first time. The presence of intermediate forms linking the two extremes is stressed. A complete and very valuable summary of the past literature referring to the species is also given. Those who wish to study *G. zaddachi* from any aspect are fortunate in having Sexton's admirable descriptive papers as a background.

There should no longer be any reason for confusions which have invalidated species identifications in the past, at least as concerns Britain. I have to concede that systematists may have a more difficult task in some other parts of Europe. For example, it is now clear that *G. 'locusta'* in west Norway mainly belongs to a northern race which, though larger, is very close to *G. zaddachi* in its body proportions and gnathopod characters (see below); while, judging from published data on *Gammarus* populations from the west Baltic, I can only conclude that populations of *G. locusta* which occur there in low salinities fail to show some of the marked characteristics found in the typical form inhabiting the North Sea, etc.†

The need for giving yet further attention to the taxonomic characters of *G. zaddachi* arises from several causes. (1) Sexton's descriptions and drawings are based primarily on German material: the extent to which they strictly apply to British populations had to be examined. (2) The descriptions are mainly devoted to adult male characters: more complete knowledge of the female and immature had to be acquired, and a clearer picture obtained of heterogonic changes which take place during early maturity. (3) Most important of all, the variation which occurs within the species, at least some aspects of it, demanded attention; and one result has been to show that the species can be split into two well-defined types, as was apparent at an early stage in this investigation.

In erecting two subspecies, I am anxious to be able to refer to type specimens and type localities. Since no type of the species has ever been designated, it is necessary to rectify this omission first. Sexton's original description (1912) covers the species as a whole: selection must therefore be made from the samples she examined and described. For various reasons I choose the samples of the Hamburg 'fresh-water' population to designate the type of the species (Sexton, 1912, p. 660, 'Hamburger Wasserleitung', 5 specimens; Hamburger Wasserleitung, Samuelson, 71 specimens; Hamburg Mus. Coll.). These automatically become the types of the relatively 'hairy' subspecies, namely, *G. z. zaddachi*, which is now recognized as embracing a widespread form which colonizes brackish waters of low salinity, as well as fresh waters to a much more limited extent. Sexton's 'pure brackish water form' becomes subspecies *salinus*, with the type from the estuary of the River Weser: 'Bremerhaven, Herr Klie; Alterhafen, x. 1911' (Sexton, 1912, p. 660, pls. lxxiii, lxxiv). *G. z. salinus* is a characteristic estuarine form in west Europe, intolerant both of full-strength sea water and of water which is fresh or very weakly brackish. It is possible that further investigation will show that the so-called '*locusta*' from northern waters,[1] though essentially a marine form, should be included within *zaddachi* as a third subspecies.[2]

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† Segerstråle (pp. 219–44) has now made it quite clear why there has been so much confusion between *locusta* and *zaddachi* in Scandinavia and in the Baltic. His newly-defined (*z. oceanicus*) is in some ways intermediate between *zaddachi salinus* and *locusta sens.str.*

[1] Excluding *G. setosus* Dement., which is clearly a separate species. See also the footnote on p. 7.

[2] This is precisely the conclusion to which Segerstråle comes (pp. 223 *et seq.*). The northern marine subspecies occurs also in the Baltic as well as *salinus*, and I find that some of Sexton's original 'brackish water' form belong to it, as do also some British specimens from Scotland which I had formerly included under *salinus*.

## THE DIFFERENCES BETWEEN THE TWO SUBSPECIES

| | **G. z. zaddachi** | **G. z. salinus** |
|---|---|---|
| | Figures in Sexton, 1942: fig. 1*a*, pl. i (figs. 1–7), pl. ii (figs. 10–14) | Figures in Sexton, 1912, 1913, and 1942: fig. 1*b*, pl. i (figs. 8–9), pl. ii (figs. 15–18) |
| | Absolute differences | |
| Peraeopods 6 and 7 (setation) | With denser and longer setae: those on the posterior margin of the basal segment of peraeopod 7 are more numerous and much longer (a difference can even be seen in the larger immature). The long projecting hair tufts on the more distal segments are very conspicuous, especially in the adult male (Fig. 4 A, B; see also Sexton, 1942, pl. ii, figs. 10–12 for extreme form) | Much more glabrous, the more distal segments with only a few moderately long hairs at most, and the basal segment posterior margin with short setules. Conspicuous tufts on distal segments lacking. Spine groups more evident owing to sparsity of hairs and to greater average length of spines (Fig. 4 C; see also Sexton, 1942, pl. ii, figs. 15–17) |
| Urosome and telson (setation) | Similarly with longer and more numerous hairs (Sexton, 1942, pl. ii, fig. 13) | With a few shorter hairs only, which are rarely longer than the spines with which they are associated (Sexton, 1942, pl. ii, fig. 18) |
| Epimera 2 and 3 | Posterior distal angles a little less acutely produced (Fig. 6 A). Epimeron 2 posterior margin with a row of several short setules (in adult male at least) | Angles rather more acutely produced (Fig. 6 B). Posterior margins of both epimera with not more than one or two setules |

N.B. The characters given below regarding the length of the accessory flagellum and of uropod 3 inner ramus may provide absolute distinctions if animals from the same region are compared.

| | Average differences | |
|---|---|---|
| General body colour of adult | Body pigment, when normally developed, distinctly dull greenish (with darker bands marking the boundaries of the segments); never infuscated | Body pigment, when developed, less greenish and more brownish (with obscurer banding); sometimes much infuscation may be found in the females (as in *G. locusta*) |
| Antenna 1 accessory flagellum | On average with one segment less (4–7 segments, according to age, in adults); somewhat shorter than peduncle segment 2, or at most about equal to it in older adults (see pp. 26–7) | On average with one segment more (5–9 segments, according to age); at maturity about same length as peduncle segment 2, becoming distinctly longer in older adults (see pp. 26–7) |
| Uropod 3 inner ramus | Relatively shorter; in majority (90 %) of British animals it is 0·67–0·76 length of segment 1 of outer ramus (see pp. 28–30) | Relatively longer; mainly (95 %) 0·78–0·89 length of segment 1 of outer ramus (Fig. 6 D) |

The Differences between the two Subspecies (*continued*)

| | **G. z. zaddachi** | **G. z. salinus** |
|---|---|---|
| Urosome dorsal spines | Lower average number (see pp. 30–2). Average pattern in samples from south-west England:<br>2·2 2·0 2·2<br>2·5 2·0 2·5<br>2·05 2·0 2·05<br>(total: 19·5) | Higher average number. Average pattern in samples from south-west England:<br>3·15 2·4 3·15<br>3·25 2·1 3·25<br>2·5 2·0 2·5<br>(total: 24·3) |
| Telson spines | On average fewer; the subapical spine nearly always missing, and most frequently only two apical spines | On average more; the subapical spine typically present, and apical group nearly always with three |
| Peraeopod distal segments | In mature adults on average a little broader relative to their length, e.g. carpopodite of peraeopod 7 (in male) usually 3·1–4·0 as long as wide near its proximal end | In mature adults somewhat more slender, as in *G. locusta*. Carpopodite of peraeopod 7 ratio (in male) typically, 4·1–4·4 |
| Gnathopod 2 hand of male | Normally a little more rounded and broader | Normally a little more elongate and parallel-sided |
| General setation | Hairs on antennae (Fig. 5), peraeopods 1, 2, 4, etc., on average longer and denser (more tufts and more hairs per tuft) | On average sparser and shorter (but rather variable particularly as between different localities) |
| Habitat | Inhabits the upper end of estuaries (roughly about the top third of the estuarine zone) and brackish waters of low salinities. In some areas can maintain itself under pure fresh-water conditions. Thus its salinity tolerance is lower | Salinity tolerance higher. Inhabits the middle reaches of estuaries where the salinity fluctuation is greatest, mingling with *G. locusta* at the seaward end, and with *G. z. zaddachi* towards the river end. Cannot tolerate fresh water |

### *General setation*

The typical subspecies tends generally to be more 'hairy' than *salinus*, both with regard to number of tufts, number of hairs in each tuft, and to the length of individual hairs. (On any given limb or somatic plate one of these features may be more relevant than the others.) It is now a matter of experience that 'hairiness' within a species of *Gammarus* is subject to local variation (e.g. the examples given for *G. locusta*, pp. 15–17, and similar behaviour in *G. duebeni* could be quoted), some of which may well be phenotypic, though this has still to be demonstrated experimentally. Indeed, there are some interesting variations within both subspecies of *zaddachi*, as here delimitated, more especially as between different areas or habitats. It is therefore necessary, on *a priori* grounds, to be especially cautious in attributing too great a taxonomic significance to differences in setation. On the other hand, the degree to which variation occurs in well-defined species appears to be subject to distinct limitations, and the general pattern and other features of the setation may provide useful diagnostic characters. This statement is necessary in view of Sexton's suggestion (e.g. 1942, p. 576) that characters affecting epidermal outgrowths should be treated in a different category from 'structural' characters (in which is included the shape of different parts and their relative proportions). From a purely morphological standpoint there seems no necessity for this opinion; while from a taxonomic approach it is enough to treat characters on their merits. By this is meant that when setation characters are found to present constant differences, these are of equal value with so-called 'structural' characters which show differences of comparable degree; while, conversely, both 'structural' and setation characters may equally be subject to a degree of variation which renders them unreliable taxonomically.

The variation in general 'hairiness' in *G. zaddachi* is known to be great, decidedly greater than in related species. But the range of habitats is also unusual, especially with regard to salinity. Sexton (1912, 1942) has emphasized the close correlation between the development of hairs and the salinity of the habitat, the hairiest examples having been found in fresh water, and the most glabrous in estuaries or brackish lagoons. Her interesting observations serve at least as a warning that variation in hairiness may be mainly phenotypic.

However, new light has been thrown on this subject by detailed study of *zaddachi* populations from Britain, where the difference between the more extreme hairy and hair-deficient individuals is comparable with that found on the continent. For the first time field study has been supplemented by experimental data. Present conclusions can be summarized as follows. (1) The variation in hairiness is not strictly continuous, but centres round two main types—representing the two subspecies as here defined. (2) The setation of the hinder parts of the animal shows a strong discontinuity between the two types, and provides a safe absolute means of separating them. (3) Estuarine populations of each subspecies, considered separately, fail to show any grading of hairiness correlated with the salinity gradient. (4) Since, also, the two types each retain their essential setation characters when reared at different salinities, the variation must be far from wholly phenotypic. (5) Since the two types are incapable of cross-breeding with each other, there is genetic difference between them; and on this genetic difference part of the variation in hairiness, observed in the species as a whole, must depend.

The use of certain setation characters has thus proved justified. At the same time it is necessary to be more precise than to consider hairiness of the animal as a whole. Variation in the setation of the hinder peraeopods, especially of the 5th, of the urosome, and of the telson, shows the greatest discontinuity, and is of special taxonomic value. This will be described in the next section. By contrast, the setation of the antennae (see Fig. 5), gnathopods, peraeopods 3 and 4, etc., while on the average showing fewer and shorter hairs in *salinus*, is too variable in different populations of each subspecies to be of comparable taxonomic value; though of potential importance in distinguishing some geographical or habitat forms. It is possible, for example, that the pure fresh-water populations may always be recognizable by a maximum development of hairs at the base of antenna 1 flagellum.

### *Setation of peraeopod* 7, *urosome and telson*

Sketches of peraeopod 7 for adult males of both subspecies are given in Fig. 4. The essential features which separate the two forms are as follows:

*G. z. zaddachi.* (1) Basal segment with a row of hairs posteriorly, often of varying lengths, but with at least half of them distinctly long, often several times longer than the intervals between successive hairs. The number increases with the growth of the limb, but at comparable sizes this is somewhat greater than that of the short setules in *salinus*. (2) The hair-tufts on the mero-, carpo- and propodites are very conspicuous in the length and density of the hairs: the longer hairs in each tuft are at least twice the length of the longest spines of the associated group, and each tuft (excluding a few of the smallest) has at least 5 hairs, usually 8 or more. The posterior tufts on the propodite are at least half the length of the propodite itself.

*G. z. salinus.* (1) The posterior margin of the basal segment is provided only with short setules. These may be very short, or about as long as the interval between successive setules, usually distinctly shorter than the intervals. Normally they are more sparsely distributed than the hairs in the typical subspecies. (2) On the more distal segments the spines are more evident, partly because they tend to be somewhat longer, but chiefly because they are not overshadowed by the hair tufts. The latter are much sparser, reduced to 1 or 2 hairs (at most 3 or 4), of which only a single hair here and there may appreciably exceed the length of the associated spines. The posterior tufts on the propodite are similarly reduced, usually to 1 or 2 short hairs, but when less reduced the longest hair does not exceed one-third of the length of the propodite itself.

The spines in *salinus* have been noted as longer, as a rule, but it is doubtful whether the average number per group is greater.

Within each subspecies there is a limited amount of variation, as already indicated. For example, in *G. z. zaddachi*, both the length of the hairs and the density of the tufts appear to be at a maximum in the Hamburg fresh-water population described by Sexton (1912; 1942, pl. ii, fig. 12), but these can be matched by the 'hairiest' specimens found in British brackish waters. In Britain the populations from the Tay and Tees estuaries are on the whole distinctly 'hairier' than those from South Devon estuaries. The hairs of the latter, however, cannot be still further reduced by rearing in water of increased salinity. It seems that in them the limit of variation towards reduction of hairs in *G. z. zaddachi* has been reached.

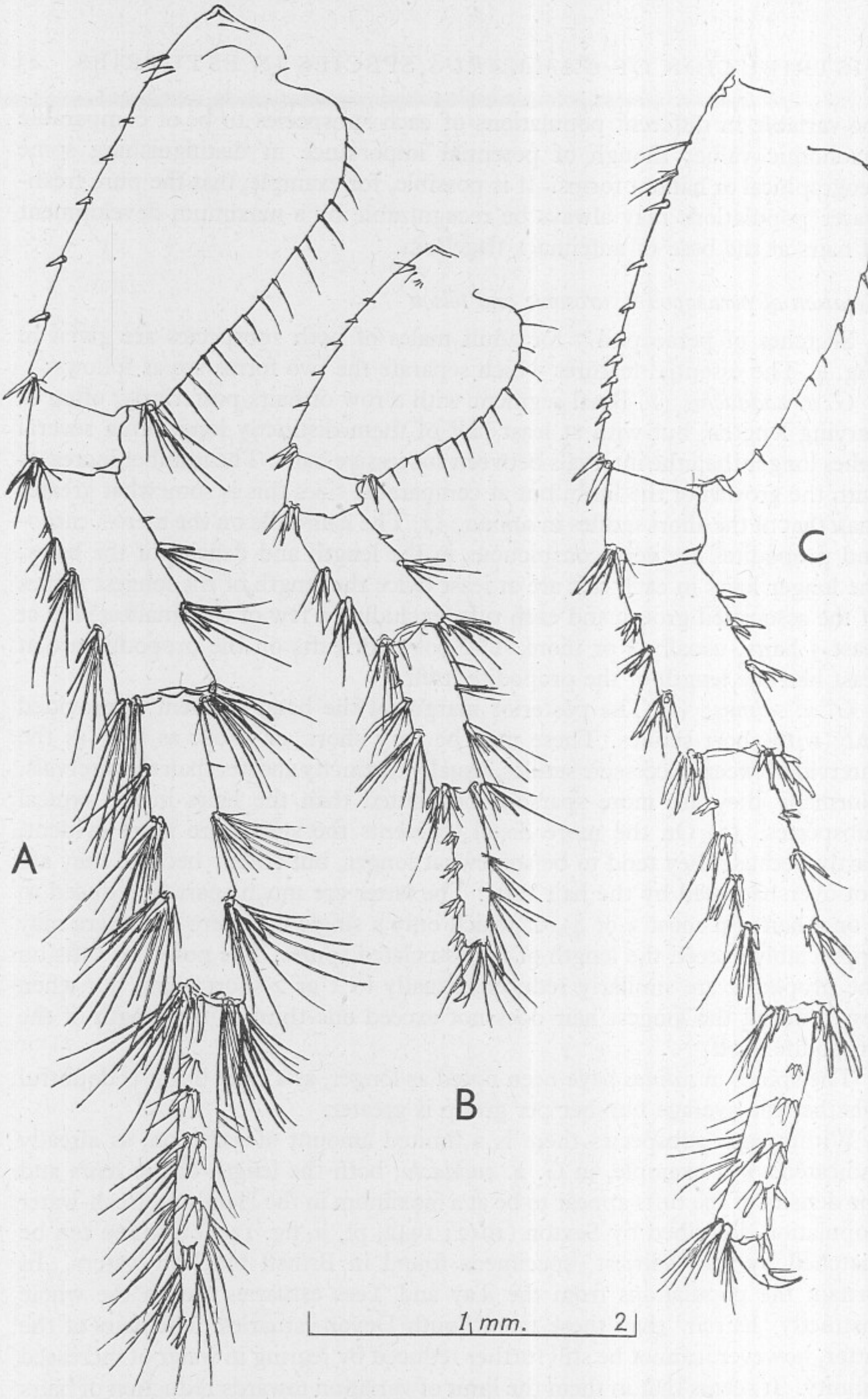

Fig. 4. *Gammarus zaddachi*, peraeopod 7 (coxopodite omitted). A, subspecies *zaddachi*, male (no. 52), Cofflete creek, River Yealm, South Devon, 3. vi. 46 (from moult). B, female of same, from the same sample (from moult). C, subspecies *salinus*, male, 18 mm., River Avon, South Devon, 14. v. 46.

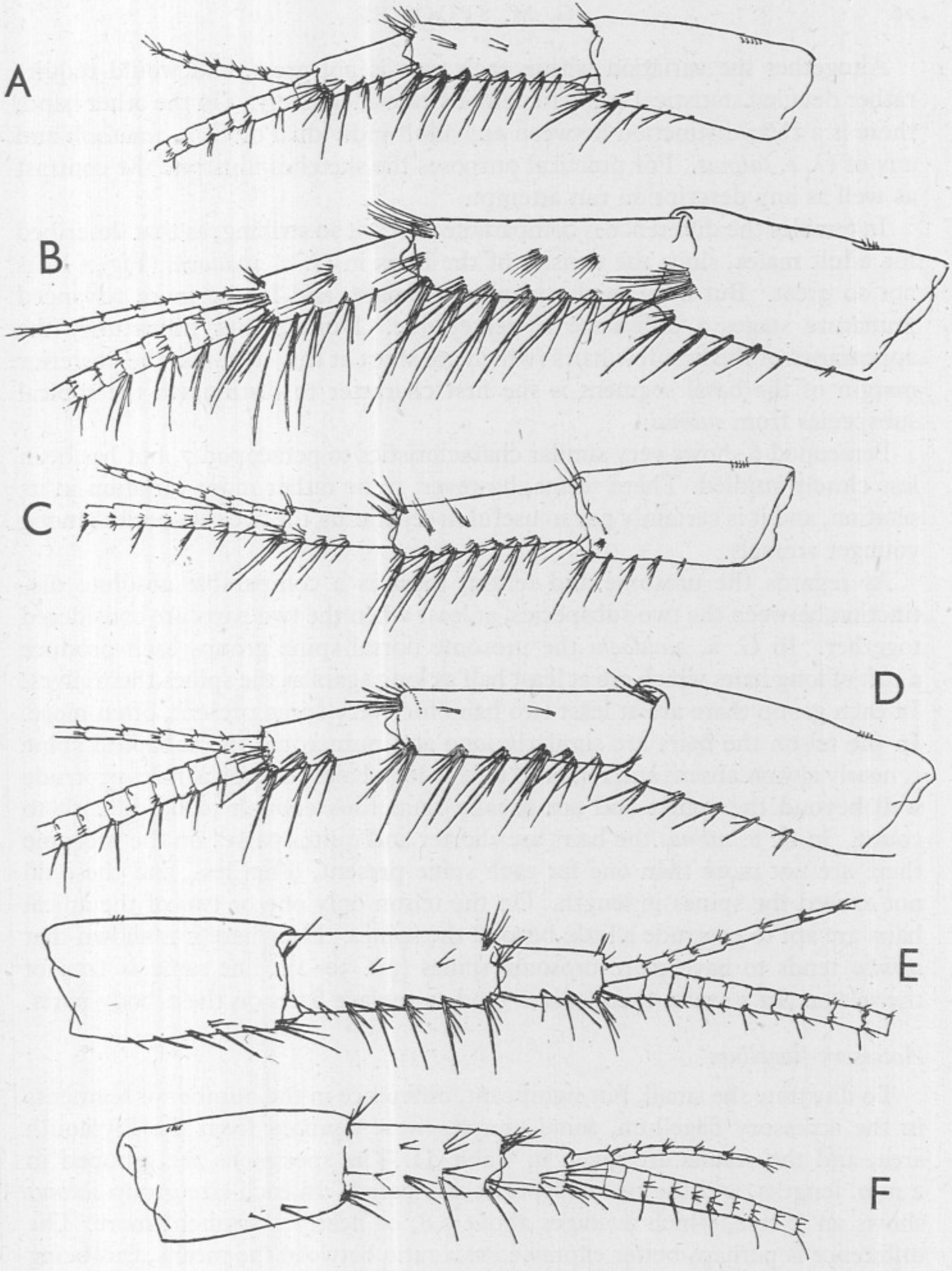

Fig. 5. *Gammarus zaddachi*, peduncle of male antenna 1; A–C, subspecies *zaddachi*, D–E, subspecies *salinus*. A, St John's, River Tamar, 28. iii. 40, 18 mm. B, River Tees, 21 mm. C, Cofflete creek, River Yealm, South Devon (from moult). D, River Severn, 23. vi. 39, 21 mm. E, River Avon, South Devon, 14. v. 46, 18 mm. F, River Tay, section IX. All viewed from inside, except B, in which the bases of the ventral tufts are shown as though seen through the thickness of the segments. (Note, in F, that segments 2 and 3 are relatively short compared with segment 1, and the ventral hair tufts, of which there are only two on segment 1, are relatively sparse.†)

† This compares with the northern subspecies described by Segerstråle on p. 226.

Altogether the variation within each type is not great, and would require rather detailed statistical study to demonstrate adequately. On the other hand, there is a clear distinction between any adult individual of *G. z. zaddachi* and any of *G. z. salinus*. For practical purposes the sketches illustrate the contrast as well as any description can attempt.

In females the difference is comparable, but not so striking, as that described for adult males, since the density of the hairs in *G. z. zaddachi* (Fig. 4 B) is not so great. But even in the youngest females and in the more advanced immature stages a difference is perceptible. During later immaturity the appearance of the first few hairs (which are short at this stage) on the posterior margin of the basal segment is the first character to distinguish the typical subspecies from *salinus*.

Peraeopod 6 shows very similar characteristics to peraeopod 7, but has been less closely studied. There seems, however, to be rather more variation in its setation, and it is certainly not so useful in separating the two subspecies among younger animals.

As regards the urosome and telson, there is a comparable absolute distinction between the two subspecies, at least when the two parts are considered together. In *G. z. zaddachi* the urosome dorsal spine groups each produce a tuft of long hairs which are at least half as long again as the spines themselves. In each group there are at least two hairs for every spine present, often more. In the telson the hairs are similarly long and numerous; the subapical spine is nearly always absent and replaced by 2–5 long hairs; the apical hairs protrude well beyond the spines and are usually numerous enough to be difficult to count. In *G. z. salinus* the hairs are shorter and quite sparse: on the urosome there are not more than one for each spine present, often less, and these do not exceed the spines in length. On the telson only one or two of the apical hairs are apt to protrude a little beyond the spines. Elsewhere it is shown that *salinus* tends to have more urosome spines (pp. 30–2). The same is true of the telson. In a sense, then, spines tend to replace hairs on these body parts.

### *Accessory flagellum*

To illustrate the small, but significant, difference in the number of segments in the accessory flagellum, some samples were counted from the Plymouth area, and the results are given in Table II. The specimens are grouped in 2 mm. lengths, and the two subspecies compared. In each size group *salinus* shows an excess, which averages about 0·8, or nearly 1 segment more. The difference is perhaps better expressed as a ratio between the means, this being about 1·15:1. Thus young mature male *salinus* have an average excess of 0·6, and the largest of at least 1·0.

A similar contrast has been observed in samples from other parts of the British Isles. In *G. z. zaddachi* a total of seven segments is the usual maximum, while a total of nine is not rarely attained in large *salinus*.

TABLE II. NUMBER OF SEGMENTS IN MALE ACCESSORY FLAGELLUM

*G. z. zaddachi*

| Size group (mm.) | Mean length (mm.) | No. of segments | | | | Mean no. | Total specimens |
|---|---|---|---|---|---|---|---|
| | | 4 | 5 | 6 | 7 | | |
| 20 | 19·7 | — | — | 1 | 2 | 6·7 | 3 |
| 18 | 18·1 | — | — | 5 | 5 | 6·5 | 10 |
| 16 | 15·9 | — | 2 | 4 | 4 | 6·2 | 10 |
| 14 | 13·7 | — | 9 | 23 | — | 5·7 | 32 |
| 12 | 12·2 | 7½ | 19 | 5½ | — | 4·9 | 32 |
| 10 | 10·0 | 16½ | 8 | ½ | — | 4·4 | 25 |
| 8 | 8·4 | 3 | — | — | — | 4·0 | 3 |
| | | | | | | | 115 |

*G. z. salinus*

| Size group (mm.) | Mean length (mm.) | No. of segments | | | | | | Mean no. | Total specimens |
|---|---|---|---|---|---|---|---|---|---|
| | | 4 | 5 | 6 | 7 | 8 | 9 | | |
| 20 | 19·5 | — | — | — | — | 2 | 1 | 8·3 | 3 |
| 18 | 18·3 | — | — | — | 2 | 6 | — | 7·8 | 8 |
| 16 | 15·7 | — | — | 1 | 10 | 1 | — | 7·0 | 12 |
| 14 | 13·8 | — | — | 11 | 15 | 1 | — | 6·4 | 27 |
| 12 | 11·8 | — | 12 | 25 | 4 | — | — | 5·8 | 41 |
| 10 | 10·1 | 1 | 31½ | 6½ | — | — | — | 5·1 | 39 |
| 8 | 8·4 | 5½ | 8 | 1½ | — | — | — | 4·7 | 15 |
| | | | | | | | | | 145 |

N.B. Half-values are given when right and left sides are different, or when a segment is nearly but not completely divided.

Difference in the number of segments is reflected in difference in length, which can be made relative to another part of the body, and which is thus a more serviceable character. The accessory flagellum is conveniently compared with peduncle segment 2 (reference may be made to Fig. 5). In *salinus* the two are of about equal length at the onset of maturity, but when the animal is fully mature the flagellum is 25–35% longer (as shown by micrometer measurements). In the typical subspecies the flagellum is distinctly the shorter at onset of maturity, and increases only to 96–105%, or so, with age. At the start, in British brackish-water animals, it is some 75–85%, soon increasing to the region of 100%; but in four well-grown fresh-water males from Hamburg and Bremerhaven (E. W. Sexton Coll.) values fall between 59 and 80% only, while comparably short flagella were observed in a sample from Swinemünde, Prussia (Copenhagen Mus. Coll.). It is possible therefore that a greater contrast in this character difference may be found on the continent.

In females the contrast is very much less, at least in Britain. Those of *G. z. salinus* seldom have an accessory flagellum appreciably longer than peduncle segment 2.

### *Uropod 3 inner ramus*

In British populations there is normally a visible difference in the relative length of the inner ramus of uropod 3, which tends to be longer in *salinus*. It is conveniently compared with the length of segment 1 of the outer ramus. In the data quoted, the uropods were mounted in chloral medium and measured with a micrometer in units of 1/75 mm. The standard end-points of the measurements are shown in Fig. 6 D. The length of the outer ramus of segment 1 gives an absolute length measurement which (unless the limb is regenerating) is a close index of the size of the animal: it averages 1/7·5 the body length (measured from head to apex of telson). The length of the inner ramus is expressed as a proportion of it.

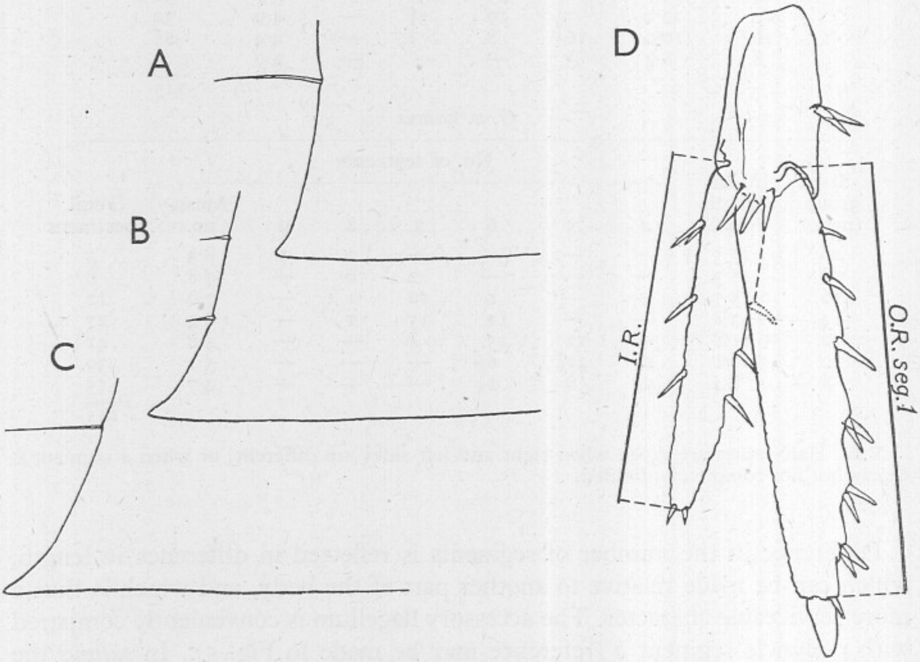

Fig. 6. Examples of the posterior distal angle of epimeron 3, right side, in (A) *Gammarus zaddachi zaddachi*, (B) *G. zaddachi salinus* and (C) *G. locusta sens.str*. (D) *G. zaddachi salinus*, male uropod 3, with setae omitted, showing the end-points of measurements on the inner ramus (*I.R.*) and the first segment of the outer ramus (*O.R.* seg. 1).

In Table III the total results for adult males from south-west Devon are compared. The *G. z. zaddachi* animals were taken from samples from the Rivers Tamar, Tavy, Plym, Erme, and their branches; the *salinus* animals from the Avon, and from the Tamar and its branches. Only animals in which the outer ramus segment 1 was at least 110 units (1·47 mm.) are included.

### TABLE III. RELATIVE LENGTH OF UROPOD 3 INNER RAMUS. *G. ZADDACHI* FROM SOUTH-WEST DEVON

Ratio length of inner ramus to that of outer ramus segment 1

| | 0·66 | 0·67 | 0·68 | 0·69 | 0·70 | 0·71 | 0·72 | 0·73 | 0·74 |
|---|---|---|---|---|---|---|---|---|---|
| *G. z. zaddachi* | 2 | 3 | 9 | 3 | 9 | 13 | 16 | 14 | 15 |
| *G. z. salinus* | — | — | — | — | — | — | — | — | — |

| | 0·75 | 0·76 | 0·77 | 0·78 | 0·79 | 0·80 | 0·81 | 0·82 | 0·83 |
|---|---|---|---|---|---|---|---|---|---|
| *G. z. zaddachi* | 3 | 1 | 2 | 1 | 1 | 1 | — | — | — |
| *G. z. salinus* | — | — | 1 | 5 | 4 | 11 | 17 | 8 | 11 |

| | 0·84 | 0·85 | 0·86 | 0·87 | 0·88 | 0·89 | 0·90 | 0·91 | 0·92 |
|---|---|---|---|---|---|---|---|---|---|
| *G. z. zaddachi* | — | — | — | — | — | — | — | — | — |
| *G. z. salinus* | 10 | 5 | 6 | 4 | 4 | 6 | — | 1 | — |

| | Total | Mean | S.D. |
|---|---|---|---|
| *G. z. zaddachi* | 93 | 0·718 | ±0·0272 |
| *G. z. salinus* | 93 | 0·830 | ±0·0316 |

The mean for the typical form, 71·8%, compares with 83·0% for *salinus*. The overlap is small, and is smaller still when specimens of the same size are compared, as there is a tendency for the ratio to increase slightly with age.

If the data in Table III are split up according to localities, good uniformity in the component samples is shown. There is no significant difference in the localities involved in each set (Table IV).

### TABLE IV. INNER RAMUS RATIOS

| Localities for *G. z. zaddachi* | *n* | Mean | Localities for *G. z. salinus* | *n* | Mean |
|---|---|---|---|---|---|
| R. Tamar, St John's | 25 | 0·723 | R. Tamar, Weirquay | 7 | 0·824 |
| R. Plym | 29 | 0·716 | R. Tamar, Cargreen | 26 | 0·831 |
| R. Erme | 22 | 0·710 | R. Tamar, Tamerton Lake | 21 | 0·829 |
| Misc. (R. Tavy, Tamar, Yealm) | 17 | 0·727 | R. Tamar, Ernesettle | 19 | 0·824 |
| | | | R. Avon | 20 | 0·836 |

Maturing males, represented in size groups 78–109 units, show a comparable difference, though, owing to the heterogony taking place at this stage, the ratio is somewhat lower in each, and the variation is greater (Table V).

### TABLE V. INNER RAMUS RATIO IN MATURING MALES

| | *n* | Mean | S.D. |
|---|---|---|---|
| *G. z. zaddachi* | 28 | 0·700 | ±0·0367 |
| *G. z. salinus* | 56 | 0·808 | ±0·0465 |

The degree to which, after maturity, the ratio may alter with increased size is indicated by the figures in Table VI. There is a definite trend for a small increase which is not altogether negligible.

TABLE VI. INNER RAMUS RATIO AT DIFFERENT SIZES

| Size group (length outer ramus segment 1 in 1/75 mm. units) | *G. z. zaddachi* | | *G. z. salinus* | |
|---|---|---|---|---|
| | *n* | Mean | *n* | Mean |
| Over 200 | 1 | (0·73) | — | — |
| 160–199 | 17 | 0·728 | 14 | 0·842 |
| 135–159 | 29 | 0·729 | 28 | 0·836 |
| 110–134 | 46 | 0·709 | 51 | 0·825 |

Among other measurements on British *G. z. zaddachi* are the following. Ten specimens from the River Char at Charmouth, Dorset, all in the 135–159 group, give a mean of 0·726, conforming with the South Devon samples. A somewhat higher mean of 0·749 is given by a sample of 15 (of various sizes) from Appledore, North Devon. Too great stress is not laid on the exact values of the means, which may well vary a little in different areas: the significant fact is that an appreciable difference is maintained between *G. z. zaddachi* and *G. z. salinus*.

The contrast, however, may be appreciably less on the continent. From ten males of the fresh-water population of *G. z. zaddachi* (nine from Hamburg Wasserleitung and one from Bremerhaven), whose uropods were mounted by Mrs Sexton, the following results were obtained:

| Size group | *n* | Mean ratio |
|---|---|---|
| 160–199 | 4 | 0·794 |
| 135–159 | 2 | 0·802 |
| 110–134 | 1 | 0·76 |
| 96–109 | 3 | 0·758 |

I also observed that some of the specimens of *G. z. zaddachi* from Denmark (Copenhagen Mus. Coll., kindly lent by Dr K. Stephensen) appeared to have a longer inner ramus than is usual in British material. There is no evidence that *salinus* gives a comparably higher value.

### *Urosome dorsal spines*

The pattern of the spine groups on the dorsal surface of the three urosome segments is usually given in descriptive works as a 'spine formula', in the form of the following example:

3 : 2 : 3
3 : 2 : 3
2 : 2 : 2

where the top row represents the number of spines in the left, centre, and right groups of segment 1, the second row those of segment 2, and the third of segment 3. The example given is that recognized as rather characteristic of *G. zaddachi* (e.g. Sexton, 1942, p. 600).

The above numbers are good central values for the species, but there is a marked variation in both directions for most of the groups. Even if full allowance is made for loss of spines through damage, there is frequently a difference between the numbers on the two sides of the body. As will be seen, the formula given above is virtually a minimum for *G. z. salinus*, and a maximum for *G. z. zaddachi*.

For *G. z. zaddachi* counts have been made on 81 males from the following localities: River Tavy, South Devon (8); River Plym, South Devon (47); River Char, Dorset (10); River Severn (16). The average values for the different groups tend to be similar in the four component samples, and there is no appreciable change with the size of the animal, so the total averages can be taken as representative. These are:

2·15 : 2·01 : 2·15
2·50 : 1·99 : 2·44
2·05 : 1·98 : 2·05

The centre groups of all three segments and the lateral groups of segment 3 have nearly a constant number of 2 spines, quite rarely 1 or 3. The lateral groups of segment 1 have usually 2, sometimes 3; and for segment 2 there are 2 or 3 about equally frequently: either may rarely have 1 or 4.

The total number of spines ranges from 13 to 23, 80% of individuals having 18 to 21. The mean value for the sample is 19·4.

By contrast, *G. z. salinus* shows a strong tendency to increased values, but individuals vary much. A sample of 20 from the River Avon, South Devon, gave the following averages:

3·1 : 2·3 : 3·15
3·05 : 2·1 : 3·4
2·4 : 2·0 : 2·5

Total spines: range 21–28, most frequently 22–25; mean value 24·0.

One of 16 from the Severn Estuary gave:

3·23 : 3·08 : 3·23
3·38 : 2·38 : 3·62
2·69 : 2·00 : 2·62

Total spines: range 20–34, most frequently 23–28; mean value 26·3.

The Severn population has the spines noticeably well developed, and the averages are probably higher than usual. The Avon sample appears to be more typical of *salinus* as a whole, judging from notes which have been made on other samples.

In *salinus* the central groups are usually not uniformly 2–2–2, as in the typical form, a constant value of 2 being found only for the third segment. The second segment centre group, though most often 2, is sometimes 3; while the anterior group is more frequently 3 and may be as high as 5. The lateral groups show a still greater average difference: segment 1 has most often 3, sometimes 4, rarely 2 or 5 (as against usually 2, sometimes 3); segment 2 has much the same, except 4 is more frequent (as against 2 or 3 equally frequent); segment 3 values of 2 and 3 about equally frequent (as against a nearly constant value of 2). The total number of spines ranges between 20 and 34 (compared with 13–23), but relatively low values, such as 22 and 24, are common. The mean of 24 compares with 19·4 in *G. z. zaddachi*.

This character difference appears to be shown equally in both sexes, and to hold for both British and continental material.

### *Presence of calceoli in the female*

The peculiar organs known as calceoli, which occur on the more proximal segments of antenna 2 flagellum (see, for example, Sexton, 1942, p. 598, and pl. i, figs. 2, 3), are present in many *Gammarus* males. For example, they occur in the males of *G. locusta*, *G.* sp. (northern '*locusta*'), *G. setosus*, *G. wilkitzkii*, *G. zaddachi*, *G. duebeni* and *G. pulex*; but they are absent in *G. tigrinus* and *G. chevreuxi*. The presence of calceoli seems usually to be a male characteristic; though Sexton has not regarded it as such in *G. zaddachi*, and recently the writer has observed calceoli in females of *G. setosus* and *G. wilkitzkii* (probably a constant feature in these two species).

The position in *G. zaddachi* proves to be unusual, for calceoli may or may not be present in the female. The organs are, indeed, often developed in females of *G. zaddachi salinus*, though they may not begin to appear until after maturity; and they may be completely lacking, even in the largest and oldest individuals. On the other hand, in *G. z. zaddachi*, no females bearing calceoli have so far been observed. While this feature seems to merit further investigation, it is probably safe to say that there is a significant difference between the two subspecies in the tendency for the females to bear calceoli.

### *Habitat*

The rather pronounced difference in the optimum environment and limits of range can be expressed quite satisfactorily in terms of salinity. Detailed discussion is deferred until the full ecological data have been presented. To summarize briefly, *G. z. salinus*, in Britain, inhabits brackish waters of various intermediate salinities with a general mean value of about 17 °/₀₀. The middle reaches of estuaries which do not show too steep a salinity gradient provide habitats where the densest British populations have been found. It is here that the greatest range of salinity fluctuation in the estuary occurs, both diurnal, between high and low water, and periodic, between spring and neap tides; and it is here that the variety of the fauna is at a minimum. But daily fluctuation on its own is not an essential factor, as may be witnessed by the flourishing population towards the mouth of the River Severn. In Britain it is difficult to find brackish lagoons comparable with, for example, Frisches Haff, in Danzig Bay, and no British populations from a habitat of this kind have been observed. The limits of range have therefore to be defined in terms of estuarine conditions.

At the seaward limit of its range it persists so long as there is an appreciable lowering of salinity at high water. It seems not to tolerate a mean high-water salinity of more than 31 ‰, even though the low-water value is much less. At the other end, it disappears when there is too much fresh-water influence at low water, that is when the mean low-water salinity is between 1 and 4 ‰.

*G. z. zaddachi* has an optimum where the low-water salinity is quite fresh or below 1 ‰, but where a marked rise of salinity occurs at high water. Its estuarine limit is roughly defined by a mean low-water salinity of 5 ‰, with a mean high-water salinity of 10 to 15 ‰. At the river end, it may penetrate for several hundred yards, or even miles, into permanent fresh water, but here, in most British rivers and streams, it fails to reproduce. On the other hand, in some areas (e.g. north Irish lakes, River Elbe) it is capable of breeding and flourishing in pure fresh-water environments. The species as a whole shows a marked preference for waters with good currents, and is clearly not so tolerant of stagnant water as is *G. chevreuxi* and *G. duebeni*.

The localities which provide conditions suitable for *G. z. salinus* (in Britain very largely limited to estuaries of rivers) are less numerous than for *G. z. zaddachi*. Nearly every river (and most streams flowing on to the shore) provides, at the head of its estuary (or near high-water mark at its inflow), a region in which *G. z. zaddachi* can exist. On the other hand, in the tidal zone of streams, or in the estuaries of some rivers, the mean salinity gradient may be too steep to provide living space for *salinus*. Under these conditions population samples show *G. locusta* giving place to *G. z. zaddachi* with a narrow zone of overlap in which the *Gammarus* population is sparse.

### *Constancy of character differences*

The separation of the two subspecies, as described above, is justified on morphological grounds alone, since individuals can always be placed in one or other category. It is important, however, to be able to present confirmatory evidence from experimental data. This can be done. Laboratory observations will be described in necessary detail in a later section of this work, but some main results may be summarized at this stage. In one set of experiments, the effect has been tested of rearing *G. z. zaddachi* in salinities higher than those of its normal habitat, e.g. 14, 17·5, 24 ‰, etc. If any of the character differences found between *G. z. salinus* and the typical subspecies are simply the direct effect of differences in the environment, it is in salinity differences that the major effects can only be sought, as indeed Sexton has strongly suggested. Even the mere difference between the equable laboratory environment and the fluctuating conditions of the natural habitat might alter characters. The results so far obtained show complete absence of such effects. The $F_1$ generation retains the same degree of hairiness, etc., possessed by its parents, even when reared at 24 °/oo salinity. Even an $F_2$ animal, reared to late immaturity in pure sea water, as were its parents, was found to retain characters diagnostic of its type. These results are consistent with the field observations that the two forms retain their type characters in the zone where their populations overlap; and that within the range of each of them there is no evident gradation of lesser variations from the fresher to the salter end. It is also noteworthy that *G. z. salinus* from the Baltic coast of Germany, living at more or less constant salinities of 7–8 °/oo, or less, shares the same type characters as those from British estuaries with salinity fluctuating around 17 °/oo, and laboratory-reared animals kept at a constant salinity of 27 °/oo. It is clear that phenotypic variation due to salinity differences can at best be of very limited extent. Results obtained by Höfken (1937) with *G. zaddachi* from the West Baltic had already pointed to this conclusion.

### *Intersterility*

A further, and most significant, piece of experimental evidence comes from breeding experiments which were at first designed to test the genetic relations of the two types by crossing. Results obtained in 1938 have been amply confirmed by a more extensive and detailed experiment carried out in 1946. It is conclusively shown that, under conditions in which both subspecies breed freely and normally (e.g. in 14 °/oo salinity in bowls), they are incapable of producing fertile eggs with one another, whichever way the cross is made. They also mate (i.e. form pairs) less readily with each other than with their own kind. This (*a*) shows that there is important genetic difference between the two types, to which their character differences must be attributed, at least in some measure; (*b*) explains completely how it comes about that the populations remain distinguishable in nature even in the zone where individuals of both mix freely.

The question immediately arises whether sterility may not be prevalent among different populations of the same subspecies, in view particularly of the isolation which occurs between populations of neighbouring watersheds. So far as present information goes, there is no evidence for this, though tests with animals from widely separated areas have yet to be made. For instance, *G. z. salinus* from the River Avon, South Devon, breed normally with those from the River Tamar. *G. z. zaddachi* from Weymouth, Dorset, proved fertile with others from the River Erme and River Yealm, South Devon; while others of this subspecies from several South Devon localities have been bred together.

### *Genotypic versus phenotypic variation*

The results obtained up to now in the study of variation in *Gammarus zaddachi* thus contain an element of surprise. From the evidence brought forward in existing literature, it was at least to be expected that evidence of environmental variation would be quickly forthcoming, and that no taxonomic division of the species would prove possible. Yet positive proof has been found for *genetical differentiation*, in that there are (at least) two main intersterile subdivisions of the species; whereas no positive evidence for *phenotypic differentiation* can yet be given.

It seems that more attention must be given to the possibility of different genetic types within the species, and that where differences are found in the characters of two populations these are not necessarily, or even probably, phenotypic, even if they show correlation with some definable environmental factor. In Britain two main well-differentiated genetic types have been demonstrated. Elsewhere there may be more than two of such 'major types', equally incapable of crossing with the typical subspecies and with *salinus*. If another such form exists, there is little chance that it would be absolutely distinguishable morphologically, and much closer statistical study might be necessary to recognize it. If it happened to bridge the gap between *G. z. zaddachi* and *salinus* an impression of continuous variation might be obtained; or if it closely overlapped one of them, it might escape detection until tested by breeding.

It would be useless to try completely to reconcile the picture presented by Sexton with the present viewpoint, until the former is supported by the necessary experimental observations. However, it is scarcely reasonable to suppose that conditions in the River Elbe, for example, are essentially different from those in British rivers. It has yet to be proved, that, if re-examined in the light of the character differences which hold good for British populations, two major types cannot equally well be separated in Germany, even if the variation within each is somewhat greater. The mystery of the 'intermediates' Sexton records is largely resolved by the discovery that these include *G. z. zaddachi* with somewhat less dense hairs than in the Hamburg 'fresh-water' population, especially on antenna 1 flagellum, but which characterize the bulk of the *G. z. zaddachi* population of south-west England.[1] Until proved to the contrary it can only be assumed that the 'fresh-water' form plus most of the 'intermediates' of Sexton fall within the typical subspecies, while the 'brackish water' form includes *salinus*.

The alternative possibility that the *salinus* types completely intergrade with the typical form towards the more eastern part of the species' range, whereas westwards, in Britain, they have become quite separate and genetically isolated, provides an attractive solution to the problem. Though improbable, this may yet be partially true and would not be without parallel among other animals. But this conclusion would be of too great theoretical interest to be accepted so long as the crucial experimental data for the continental populations is lacking.

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[1] According to Mrs Sexton, who has recently been kind enough to look over some of my material, a large proportion of British *G. z. zaddachi* would be classed, in her original terminology, as 'fresh-water intermediates', a few as the 'fresh-water' form, or very nearly so, and others as grading between the two.

### *Taxonomic status*

The two major genetic types into which *G. żaddachi* has been divided (without prejudice to the fact that others may exist or even that further subdivision may be necessary), behave, for all practical purposes, as two distinct species. Ecologically they can profitably be treated as such. The reasons for not giving them specific rank are briefly as follows:

(1) Though separable on good visible differences in the development of spines and hairs, supported by average differences in various other respects, the two forms are identical, or very closely similar, in structures which normally show diagnostic specific characters, particularly the gnathopods, coxal plates, relative size of antennal segments, etc. Also both have the diagnostic pattern of hair tufts associated with *G. zaddachi*. Taxonomically, therefore, they are closer than other species of the genus are to each other. If they were made separate species, a dangerous precedent might be set for wholesale splitting in other species.

(2) Some uncertainty still remains on the relation between the *salinus* and typical forms in the eastern part of the range of *zaddachi*. Until this matter is clearer, it is advisable to proceed cautiously.†

### *Separation from related species*

*G. z. salinus* has been liable to confusion with *G. locusta* (*sens.str.*), with which it mixes near the mouths of estuaries. They are very easily separated in mixed samples, however, by the longer accessory flagellum of *locusta*, its relatively short segments 2+3 of antenna 1 peduncle, which has very sparse hairs, the more spreading and less graded hair-tufts of antenna 2, the more greatly elevated urosome segments, the deeper and more rectangular ventral half of coxal plate 4, the long uropod 3 inner ramus, etc. In adult males the diagnostic gnathopod 2 hands are alone sufficient. In adult females the hand of gnathopod 2 of *locusta* is notably elongate, easily more than twice as long as broad (except in the youngest individuals), whereas in *zaddachi* it is easily less than twice. Immatures of all sizes can be readily separated, if examined when freshly killed, by the presence of reddish pigment spots on the peraeon segments of *locusta* (absent in *zaddachi*); otherwise the more numerous hairs on antenna 1 peduncle ventrally in *zaddachi* become evident at least by the time the immature are half-grown.

*G. z. zaddachi* is further distinguished from *locusta* by the abundance of hairs on the hinder parts of the body (though the hairs on the distal segments of peraeopod 7 are usually longer and more numerous in *locusta* than in *G. z. salinus*). The habitats, however, are usually well separated.

It is, however, to *G. duebeni* that *G. z. zaddachi* bears the closest superficial resemblance, as older determinations often bear witness. Their habitats are

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† This uncertainty has been largely removed by Segerstråle (pp. 236–40), who, all the same, independently decided that *zaddachi* should not be split into separate species.

liable to overlap, and mixed populations are collected in some localities. Adult males are at once separable on the form of the gnathopods: in *duebeni* the hand of gnathopod 2 is scarcely longer than that of gnathopod 1, while the median palmar spine and the angle spines of gnathopod 2 form a continuous row (Fig. 7). All sizes of *duebeni*, particularly the immature and younger adults, are separable at once by the shape of the basal segment of peraeopods 6 and 7—the posterior distal angle protruding and lacking spines, though this feature tends to be less evident in larger adults. In *duebeni*, moreover, the setation of antenna 1 peduncle is sparser, that of antenna 2 more concentrated in brush-like tufts; coxal plate 4 has a more rounded and U-shaped ventral

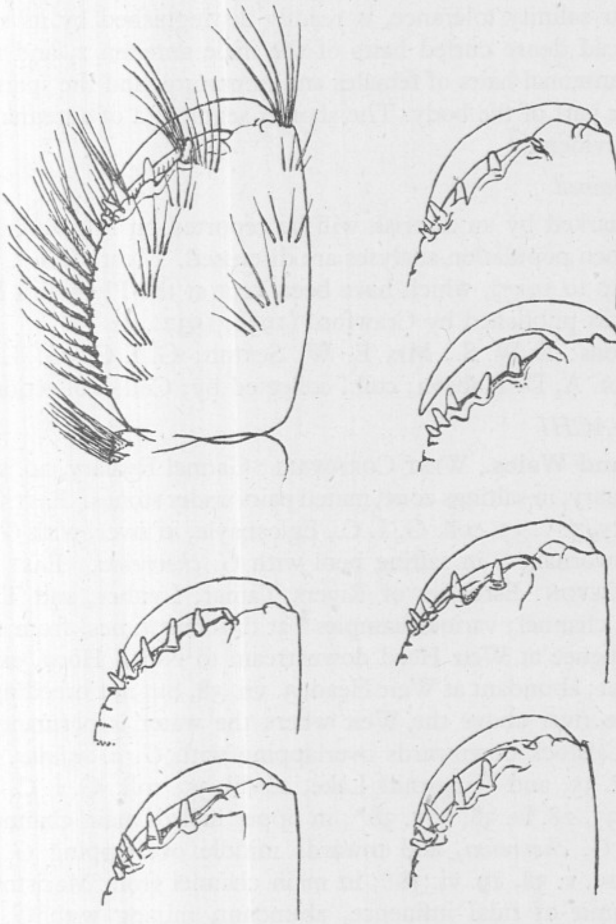

Fig. 7. *Gammarus duebeni*, from Chelson ditches, near Plymouth, male gnathopod 2 hand. One figured complete, and the distal part of six others with setae omitted, to show the arrangement and form of the palmar spines.

expansion; the angles of the epimera are more nearly right angles; and the whole body is distinctly less slender. Immatures can be satisfactorily distinguished, to the smallest sizes, on the strength of the produced distal angle of peraeopod 7 basal segment.

*G. chevreuxi*, which is liable to occur in company with *G. z. zaddachi*, having a very similar salinity tolerance, is readily distinguished by its smaller size, the pronounced dense curled hairs of the male antenna 2, and the sparser, less graded, antennal hairs of females and immature, and the sparsity of hairs on the hinder part of the body. The shorter segment 2 of antenna 1 peduncle is also quite evident.

*Material examined*

Samples marked by an asterisk will be reported on in greater detail subsequently, when population analyses are discussed. Most of G. I. Crawford's collections (up to 1937), which have been kept at the Plymouth Laboratory, refer to records published by Crawford (1936, 1937).

Abbreviations: E. W. S., Mrs E. W. Sexton; G. I. C., G. I. Crawford; A. D. H., Prof. A. D. Hobson; coll., collected by; Coll., collection.

*G. Z. ZADDACHI*

**England and Wales.** WEST CORNWALL: Gannel Estuary, 20. xi. 37, creek at head of estuary, in saltings zone, mated pairs under stones. EAST CORNWALL: Camel Estuary, 5. v. 35, coll. G. I. C., Egloshayle, in river, with *G. chevreuxi*; 28. i. 40, Trewornan, ♀ in salting pool with *G. chevreuxi*. EAST CORNWALL and SOUTH DEVON: Estuaries of Rivers Tamar, Lynher, and Tavy. River Tamar, main channel; various samples* at different times, from the limit of estuarine influence at Weir Head downstream to North Hooe, exceptionally at Thorn Point; abundant at Weir Head, 3. vii. 38, but not breeding, and even present in the river above the Weir where the water is permanently fresh; from about Calstock downwards overlapping with *G. z. salinus*. Whitsame Creek, 12. vii. 35, and Kingsmill Lake, 2. viii. 35, coll. G. I. C. Tamerton Lake, 24. xi. 37, 28. iv. 38, 2. v. 38*; in upper half of main channel of creek, mixing with *G. chevreuxi*, and towards middle overlapping *G. z. salinus*. River Tavy, 19. v. 38, 19. vi. 38*; in main channel from Maristow Ford up to extreme limit of tidal influence, abundant, mixing with *G. chevreuxi*; Maristow and Lopwell areas, main channel and adjacent brackish creeks, 3. vii. 35, coll. G. I. C. River Tavy, Gnatham, 1937, E. W. S. Coll., some large adults in a pool at about extreme H.W. level; Gnatham Creek, 28. vii. 38*, in stream flowing into tidal zone of estuary, mixing with *G. chevreuxi* in tidal zone, and alone in fresh water above tidal influence. St John's Lake, at extreme upper end, in tributary stream by the road bridge, 18. xii. 37, 5. v. 38, 28. iii. 40, 12. xi. 46*, plentiful when adequate cover available, mixing with *G. chevreuxi*; sparingly further down channel in estuarine zone, meeting *G. locusta*. River Lynher: near St Germans, 25. vi. 38, coll. E. Percival, several, with two *G. duebeni*; Sheviock Wood, south end, 18. ii. 38, a number in stomach of a sea-trout, coll. P. H. T. Hartley. SOUTH DEVON: River Plym: in main channel at upper end of estuary, 2. vi. 38, 1. viii. 38*, from extreme upper part of Laira Lake to the river above Marsh Mills, numerous, though water milky with China Clay, mixing with *G. chevreuxi* and overlapping *G. z. salinus*. River Yealm, Cofflete Creek, at head of creek near Spriddlestone, 19. xi. 37, 3. vi. 46*, plentiful, penetrating into fresh water and mixing with *G. pulex*. River Erme, 1. i. 38, 18. ii. 39*, in main channel opposite Holbeton and in three stations down the estuary, overlapping *G. z. salinus*; also in brackish ditch behind an embankment. River Avon, 16. v. 38, 14. vi. 38, 8. i. 39, 14. v. 46*, in main channel from about half a mile below Aveton Gifford up to near limit of estuarine influence, abundant, overlapping *G. z. salinus*. Kingsbridge Estuary, Blank's Mill Creek, 22. i. 39*, in three stations, overlapping *G. z. salinus* in middle of creek, and *G. pulex* in fresh water of stream above tidal influence. Dawlish, 21. vii. 35, coll. G. I. C., in Copenhagen Mus. Coll., a number of dwarfed adults, breeding. River Exe: 'Exeter', R. Elmhirst Coll., 6 ♂♂ and 1 ♀; Countess Weir, 21. vii. 35, coll. G. I. C., several in main stream, 3 ♂♂ in tidal ditch; Powderham, brackish pond, 21. vii. 35, coll. G. I. C., numerous, mixing with *G. duebeni*; Topsham, tidal zone of estuary, 24. x. 38*, several adults, overlapping *G. locusta* (*G. z. salinus* absent). River Axe, 21. xi. 38*, in main channel above Axmouth, overlapping *G. z. salinus*. NORTH DEVON: Torridge Estuary, 14. iii. 38, in brackish ditch near Appledore, large sample. Taw Estuary, Caen River, coll. G. I. C., 3 specs. DORSET: River Char, 21. xi. 38*, in river just above its fall over the beach, large adults. The Fleet, 27. iii. 38, in brackish ditch near Langton Herring. River Wey and Radipole Lake, 2–10. ix. 38*, in several stations, plentiful, though of small average size, in open water and in ditches, crowding amongst tubes of *Mercierella enigmatica* and at roots of *Phragmites*. Lodmoor, Weymouth, ditches near sea sluice, iv. 28, sample of large adults, 26. xii. 37, 14. xi. 37, sparingly. HANTS: River Test, Totton Br., 7. xii. 35, coll. G. I. C., in British Mus. Coll. [1936. 2. 12. 95–99]. SEVERN ESTUARY: In various samples from the upper reaches of the main estuary, coll. R. Bassindale, as reported in the 'Studies on the Biology of the Bristol Channel' series, nos. IV, VII, VIII and XI (Bassindale, 1941, 1942*a*, 1942*b*, 1943), recorded as '*zaddachi*, typical variety, Spooner (*in lit.*)', corrected to 'Form C Sexton';[1] in main channel and tidal zone of estuary from Aust (summer) or Sharpness (winter) to Ashleworth Ferry, also at Kilve where a tributary fresh-water stream flows over the tidal zone; overlapping *G. z. salinus* at Sharpness (summer) and from Aust to Sharpness (winter), while above Epney showing

[1] The correction in Bassindale (1942*b*, p. 314), which was added when the writer was away on war service, is now seen to have been superfluous. 'Typical variety' was the provisional name given to *G. z. zaddachi*; and 'saline variety' to *G. z. salinus*, which in the Severn can be incompletely divided into two forms, A and B (see p. 42). The statement that intermediate forms occur between Forms A and C (i.e. between the two subspecies) was incorrect.

signs of inhibited growth and development, especially in winter. ESSEX: Benfleet, 8. iii. 36, in two places, coll. G. I. C. [British Mus. Coll., 1938. 2. 16. 52–59]. Leigh-on-Sea, 28. vi. 36, coll. G. I. C. [British Mus. Coll., do.]. NORFOLK: Stiffkey, 29. ix. 35, coll. G. I. C. [British Mus. Coll., 1936. 2. 12. 95–99]. DURHAM and NORTH-EAST YORKS: River Tees, Tees Survey collections (Alexander *et al.*, 1935), various samples from sections I, II, III, IV and VIII, in main channel or tidal zone. See pp. 46, 51. CARMARTHENSHIRE: River Towy, 25. viii. 35, coll. G. I. C., 'open stream through salting among Enteromorpha', 9 ♂♂, 2 ♀♀, 8 imm., 'above a sluice among grass', 10 ♂♂, 9 ♀♀, 15 imm. MERIONETHSHIRE: Aberdovey, at head of estuary, coll. E. E. Watkin, several ♂♂. ANGLESEY: Lake Maltreath, brackish water, 27. iii. 40, coll. J. B. Cragg, 6 ♂♂, 1 ♀. ISLE OF MAN: Castletown, Silver Burn, 7. ix. 38, coll. G. I. C., near mouth of fresh-water stream, flowing into the sea, in three stations, dwarfed. WESTMORLAND: River Gilpin, Sampool Br., 16. v. 38, coll. P. H. T. Hartley, 7 ♂♂, 6 ♀♀, 12 imm., average size small.

**Scotland.** FIRTH OF TAY: River Tay, Tees Survey collections (Alexander *et al.*, 1935), identified from sections I, II, III, IV, VI, VIII, IX, X (see pp. 47–8, 52), small-sized from higher sections where salinity very low or mainly fresh water, in the two lowest Sections overlapping *G. z. salinus*. AYRSHIRE: Fairlie Sands, 7. vi. 40, coll. R. Elmhirst, in stream flowing into tidal zone of shore, overlapping *G. duebeni* at the fresh-water end, and *G. z. salinus* at the seaward end of its range (see Scottish Marine Biol. Assoc., *Annual Report*, 1942–3, pp. 11–12). ARGYLLSHIRE: Oban district, coll. H. P. Moon: Gylen Castle, 1. viii. 39, 'stream flowing over beach, just above *Enteromorpha* zone', 9 imm., with *G. duebeni*; Slatroch Bay, 12. viii. 39, 'stream across shore, about middle of bay, amongst *Enteromorpha*, associated with ephemerid *Baetis*', 2 ♂♂, 19 imm. INNER HEBRIDES: Skye, Kyleachin, 31. vii. 33, coll. R. Elmhirst, 'in shallow stagnant inlet of sea', ♂♂, ♀♀, imm., various sizes; 23. viii. 39, coll. H. P. Moon, 'point where stream flows over beach, and into *Enteromorpha* zone', 7 imm., in both samples mixed with *G. duebeni*. Isle of Muck, Port Mor, A. D. H. Coll., in fresh-water stream on shore, 29. vii. 38, 3 ♂♂, 1 imm. South Rona, vii and viii. 37, A. D. H. Coll., in three streams flowing over the shore, in tidal zone but not above mean H.W. (see Beadle & Cragg, 1940, as *zaddachi* 'hairy' variety), mostly small sizes. Raasay, viii. 37, A. D. H. Coll., in stream flowing over shore, above H.W., small ♀ and imm.; Oskaig Salt Marsh, 2 ♂♂, 6 imm., with *G. duebeni*. Mull, Kilbrenan Waterfall, 12. viii. 39, coll. H. P. Moon, 'tidal pool at foot of waterfall, *Pelvetia* zone', 2 young ♂♂, 23 imm.; *Enteromorpha* zone, 1 young ♂, 3 imm. OUTER HEBRIDES: South Uist, 1. viii. 32, R. Elmhirst Coll., Loch Bee, several, mostly males, not fully mature and dwarfed. North Uist, R. Elmhirst Coll., 18. vii. 33, Loch Obisary, brackish, several small-sized adults; 24. vii. 33, Sollas, stream from Loch Sandary, 1 imm.; 28. vii. 33, Loch an Sticar, adults and imm. Harris, near Tarbert, coll. H. P. Moon, 22. viii. 39, Glen Lingadale Burn, *Enteromorpha* zone, 10 ♂♂, 3 ♀♀ (breeding), 3 imm.; 20. viii. 39, Laxadale River, *Enteromorpha* zone, 17 ♂♂, mostly young, 24 young ♀♀ and imm. ORKNEYS: R. Elmhirst Coll., 'W. of Douglas Hill, upstream, amongst green alga and stonefly larvae, fresh water', 8 imm., including 2 developing ♂ characters.

**Ireland.** SOUTH KERRY: Kenmare, 23. vii. 38, coll. G. I. C., small brackish stream, 2 ♂♂, 1 ♀ (with one *G. z. salinus*). Glenbehy, 21. vii. 38, coll. G. I. C., brackish ditch, among *Fucus*, 6 ♂♂, 1 imm., in *Enteromorpha*, a number of smaller sizes (with *G. duebeni*). DUBLIN: River Liffey, at Kingsbridge, 17. vii. 38, coll. G. I. C., just below limit of tidal influence, 5 ♂♂, 16 ♀♀ and imm. (with *G. duebeni*). COUNTY DOWN: The Kinnegar, Holywood, coll. R. Macdonald, 'from a large drain inside the embankment', 6 ♂♂, 4 ♀♀, 10 imm., of very small size (E. W. S. Coll.); ♂ and ♀, 12. i. 36, same locality and captor (Copenhagen Mus. Coll.).

**Belgium.** Schelde Estuary, below Antwerp: Lillo, 'stream along road from Stabroeck', 15. v. 36, 4 ♂♂; Liefkenshoeck, 15. v. 36, 4 ♂♂, 9 ♀♀, 2 imm.; Copenhagen Mus. Coll. (ex Brussels Mus. Coll.).

**Germany.** RIVER ELBE: Hamburg Wasserleitung (conduits connected with former water supply), E. W. S. Coll., series of mounted parts of three males, and mounts of uropod 3 of six others, typical 'fresh-water' form, *teste* E. W. S. RIVER WESER: Bremerhaven, 12. v. 94, E. W. S. Coll., series of mounted parts of large ♂, 'fresh-water' form; 10. xi. 12, R. Elmhirst Coll. (*ex* E. W. S. Coll.), large ♂. (Examples of original material described by Sexton, 1912, 1942.) PRUSSIA: Swinemünde, 5 ♂♂, Copenhagen Mus. Coll. (from Prof. A. Schellenberg, Zool. Mus. Berlin), '*Gammarus locusta* f. *zaddachi*, typische form: A. Schellenberg *det.*' E. PRUSSIA: Danzig, Messina See, brackish water, ♂ and ♀, Copenhagen Mus. Coll. (R. Lucks, Marienburg, *col. et ded.*).

**Denmark.** Samples from Copenhagen Mus. Coll. WEST JUTLAND: Aagab (Holmsland), Ringköbing Fjord, coll. K. O. Leith, 7. vii. 42, one smallish ♂. Vondaa, between Heager and Kloster, coll. K. O. Leith, 27. vii. 42, 8 ♂♂, 7 ♀♀, 2 imm., breeding, abnormally dwarfed. SOUTH-WEST JUTLAND: Maade, 3 km. east of Esbjerg, 24. iv. 43, coll. E. Pedersen and K. O. Leith, ♀ and imm. NORTH-EAST JUTLAND: Randersfjord, Uggelhuse, near Bridden Thor, 19. v. 17, 1 imm. NORTH-WEST ZEALAND: Lammefjordssöen, to 3 m., 3. v. 23, 1 ♂ (Dansk. Biol. Sta. *ded.*).

### *G. Z. SALINUS*

**England and Wales.** EAST CORNWALL and SOUTH DEVON: Estuary of River Tamar, and its tributaries River Lynher and River Tavy. River Tamar, main channel, various samples* from Saltash upwards to Calstock, overlapping *G. locusta* from Saltash to Cargreen (winter) or from Junction of Tavy to above Weirquay (summer), and at the upper end of its range overlapping *G. z. zaddachi* from near Weirquay upwards (winter) or from near North Hooe upwards (summer); absent from St John's Lake. Tamerton Lake,

28. iv. 38, 2. v. 38*, in main channel, overlapping *G. locusta*, *G. z. zaddachi* and *G. chevreuxi*. River Lynher, Sconner Creek, coll. G. I. C., 6. vi. 35, young ♂ and imm. River Tavy, 19. v. 38, 28. vii. 38, from junction with the Tamar to Maristow Ford, in open part of estuary, overlapping *G. locusta* and *G. z. zaddachi*. South Devon: River Plym, 2 and 28. vi. 38, 17. i. 46, in main channel and tidal zone, from near south end of Laira Lake to below Marsh Mills road bridge, plentiful, overlapping *G. locusta*, *G. z. zaddachi* and *G. chevreuxi*; Chelson Sluice, 23. xi. 45, 2 ♀♀. River Yealm, in estuary near Steerpoint station, iv. 40, overlapping *G. locusta* (apparently absent Cofflete Creek). River Erme, 1. i. 38, 18. ii. 39, 5. iii. 39, from near estuary mouth to just below Holbeton, in main channel and tidal zone, plentiful, overlapping *G. locusta* and *G. z. zaddachi*. River Avon, 16. v. 38, 16. vi. 38, 8. i. 39, 14. v. 46, in main channel and tidal zone from near Bantham to a little below Aveton Gifford, abundant, especially in clusters of fucoid algae, as usual overlapping *G. locusta* in one direction and *G. z. zaddachi* in the other, with a long stretch of 'pure' population in the middle of its range. Kingsbridge Estuary, Blank's Mill creek, 22. i. 39, in channel and tidal zone. River Axe, 21. xi. 38, above Axmouth, overlapping *G. z. zaddachi*. Dorset: River Frome, Wareham, coll. G. I. C., 2. ix. 35, 2 imm. Severn Estuary: In various samples from Bristol Channel coast and Severn Estuary, coll. R. Bassindale (see references given on p. 39 and the attached footnote), from at least Blue Anchor (winter) and Kilve (summer) upwards to Sharpness; the population tending to be dimorphic, the recorded 'Variety A' agreeing with *G. z. salinus* from other estuaries, while the more abundant 'Variety B', distinguished by its small eyes, and its unusually long hairs and spines, has been observed only from this estuary; the two varieties not always completely separable, and occurring throughout the range of the subspecies; occurrences correctly reported in Bassindale (1941); as elsewhere, overlapping *G. z. locusta* at the seaward end of its range (Blue Anchor to Weston) and *G. z. zaddachi* at the other end (Aust to Sharpness). Lincs: River Welland, near Holbeach, main dyke running into the river near Holbeach, 20. vii. 39, coll. M. L. Rothschild, 2 ♂♂, 2 imm. Northumberland: Blyth, 'ditch from saltpans', 4. vii. 34, A. D. H. Coll., 3 ♀♀, breeding, with *G. locusta*. Wansbeck, 9. iv. 35, A. D. H. Coll., 'below railway bridge, among *Fucus* in stream', 9 ♂♂, 10 ♀♀, 3 imm.

**Scotland.** Ayrshire: Fairlie Sands, 7. vi. 40, coll. R. Elmhirst, in stream flowing over tidal zone of shore, overlapping *G. z. zaddachi* (see Scottish Marine Biol. Assoc., *Annual Report*, 1942–3, pp. 11–12). Clyde Isles: Cumbrae, east of Keppel Pier, near Lion Rock, shore near L.W., 16. ii. 43, 2 large ♂♂. Argyllshire: Clachan Strand, 2. vi. 35, 'under weed', A. D. H. Coll., young ♂ (with *G. locusta* and *M. marinus*).

**Ireland.** South Kerry: Kenmare, 23. vii. 38, coll. G. I. C., small brackish stream, 1 ♂ (with *G. z. zaddachi*).

**Germany.** RIVER WESER: Bremerhaven, Alter Hafen, Dec. 1911, Herr Klie; E. W. S. Coll., series of mounted parts of young adult, figured by Sexton, 1912, and a few immature specimens (types).

**Denmark.** SOUTH ZEALAND: Stege Nor, opposite Kirkegrund, 25. vii. 29, 1 young ♂, Copenhagen Mus. Coll. (E. Poulsen *ded.*).

The following examples, originally identified with *salinus*, are separable on characters of the antenna 1 peduncle (Fig. 5 F), and by the somewhat more angularly elevated urosome segments. Apart from their relatively small size, they approach very close to the northern *G.* '*locusta*'.† Amongst them is a female specimen, from Raasay, which is unusually large for a British *zaddachi* (21 mm.). Amongst characters shared with *salinus* are all those in which the latter differs from *zaddachi* typical. It is possible that the Cumbrae specimens recorded above should also be included in this category.

**Scotland.** FIRTH OF TAY: Tees Survey collections (Alexander *et al.*, 1935), in sections IX and X of the estuary (see pp. 48, 52). INNER HEBRIDES: South Rona, vii and viii. 37, A. D. H. Coll., in stream flowing over shore, well below H.W., ♂ and imm. (Beadle & Cragg, 1940, as '*zaddachi*, hairless var.'). Raasay, vii and viii. 37, A. D. H. Coll., in stream flowing over shore between tide-marks, 6 ♂♂, 1 ♀, 11 imm.

**Germany.** EAST PRUSSIA: Rauschen, Königsberg, series of mounted parts of adult ♂ and ♀, E. W. S. Coll. (see Sexton, 1912, 1913).

## REVISION OF PUBLISHED IDENTIFICATIONS

### *Fauna of Tamar and Lynher* (Percival, 1929)

The faunistic survey of the Tamar estuary, and its branch the Lynher, carried out by Percival in 1928, has been frequently quoted in comparisons with other estuaries. It is necessary that his statements concerning the *Gammarus* fauna (Percival, 1929, pp. 92–3, 103) should be corrected in the light of present knowledge.

A small reference collection was left by Percival in the Plymouth Laboratory. This, unfortunately, was unknown to Crawford (1936, 1937), and overlooked by Sexton (1942).

Percival did not submit his Gammarids to a specialist for confirmation. This might have seemed unnecessary, as at the time the choice of species apparently lay simply between *G. locusta* and *G. duebeni*. As a result *G. zaddachi* was completely overlooked, and *G. chevreuxi* (at the time known only from Chelson Meadows ditches) missed.

*G. locusta*. Though no specimens were preserved, it is quite clear, as Crawford suspected, that Percival included *G. zaddachi salinus* in this category.

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† Both are now to be included in Segerstråle's third subspecies of *zaddachi* (pp. 223 *et seq* ). This form would appear to replace *salinus* in north Scotland, and so raises a new problem.

The upper limit at Morwell Rocks is in fact rather higher than the point reached by *salinus* in June 1938, but might well represent the extreme upper limit of that form in a dry summer. The true upper limits of *locusta* are found to be at the bend above Weirquay in an average summer, and at Cargreen in the winter. This applies to the region of low water: the species penetrates a little higher in the upper half of the tidal zone.

*G. duebeni*. This species is not a normal inhabitant of the main stream of the estuary, but is virtually confined to backwaters and side channels, e.g. pools near high-water level fed by fresh-water seepage, salting pools, ditches separated from the river by sluices, etc. The form recorded as '*duebeni*' by Percival in the Tamar 'from Cothele Woods to Weir Head' is really *G. z. zaddachi*. Its summer range is thus quite accurately described, and, as Percival noted, it swarms amongst moss at Weir Head. Similarly this is the form which frequents the Lynher 'from Sheviock Wood to Tideford', as is proved by a preserved sample, labelled '*G. duebeni*, R. Lynher, near St Germans, 25. vi. 28'. This sample contained 8 ♂♂, 5 ♀♀ and 1 imm. *G. z. zaddachi*, as well as one large ♂ and one small ♀ *G. duebeni*.

No comment is necessary on the range of *Marinogammarus marinus*, there being good agreement with later observations. It should be emphasized that the population of this species is concentrated in the region of high-water neaps, and usually the species is quite absent from the low-water region, unless the gradient of the intertidal zone is steep.

Amongst other crustaceans in Percival's samples which have been examined are the following:

*Sphaeroma serratum* F. Wyvlescombe Lake, River Lynher, 22. viii. 28, confirmed correct.

*Sphaeroma rugicauda* Leach. River Tiddy and Marsh, 25. vi. 28. 5 ♂♂, 5 ♀♀, confirmed correct.

*Jassa falcata* (Montagu). R. Lynher, 20. vii. 28, 2 ♂♂ of form with large gnathopod hands. Hamoaze, 19. vii. 28, on no. 15 Buoy, 2 ♂♂, 2 ♀♀ (recorded as *Podocerus odontonyx* Sars).

*Cyathura carinata* (Kröyer). As Crawford (1936, p. 37) rightly suspected, Percival's records for *Anthura gracilis* Montagu really refer to this species. Specimens from Rat Island, 30. viii. 28, were preserved.

### *Collections by G. I. Crawford and others*

Subsequent to the discovery of *G. zaddachi* in Britain, estuarine collections of gammarids have been given deserved critical attention. Recent records from the south-west, published by Serventy (1935), Crawford (1936, 1937), Milne (1940), Spooner and Moore (1940), require no further qualifications, except in one respect. In the various records of *G. zaddachi* distinction has to be drawn between the two subspecies.

Serventy (1935) first recorded the occurrence of the species in the Tamar, from collections made at Pentillie Quay, Whitsam, and at a point one mile below Calstock in March 1934. Two tubes of Serventy's specimens have been examined: one labelled Pentillie Quay, and the other without locality label. Both contain *G. z. salinus*, the former 6 ♂♂, 5 ♀♀ and 7 imm., the latter many of various sizes.

Mr G. I. Crawford added much to our knowledge of the distribution of Amphipoda in the west. Most of his preserved collections remain at the Plymouth Laboratory, and it has been possible to re-examine nearly all the *G. zaddachi* he records (Crawford, 1936, p. 102; 1937, pp. 650–60).

From Rivers Tavy, Tamar and Lynher (p. 650), the following records refer to *G. z. salinus*:

Rat Island, low water, 31. v. 35, 2 imm. amongst *G. locusta*.

Neal (or Neille) Point, 2. viii. 35, on buoy, a number, mostly ♀♀ and imm.

Crosspark Wood, 3. ix. 35, among *Obelaria gelatinosa* at low water, small ♀ and imm.

Lynher, Sconner Creek, 6. vi. 35, west bank among Fucus, young ♂ and several imm.

The following refer to *G. z. zaddachi*:

St Budeaux, open creek. Kingsmill Lake, creek above sluice. Whitsam and Haye creeks. All samples from the River Tavy in the region of Blaxton, Mt Jessop and Lopwell, in main channel and creeks.

The *G. zaddachi* recorded from the upper estuarine zone of the River Exe (p .652), River Taw (p. 654), River Camel (p. 654) and River Towy (p. 655), are all *G. z. zaddachi*. The sample from a pond on the Powderham Estate, River Exe region, contained many *G. duebeni* mixed with the *zaddachi*. Two immatures from the River Frome at Wareham, Dorset (p. 102), are *G. z. salinus*.

In his investigation of the fauna of buoys in the seaward part of the Tamar estuary, Milne (1940) again found *G. zaddachi* present on Neal Point Buoy, and his specimens proved to be *G. z. salinus*.

### *Tees Survey Material*

The first comprehensive survey of a British Estuary was carried out on the River Tees, supplemented by observations on the River Tay. The results were published in three parts (Water Pollution Research, *Technical Papers*, no. 2, 1931; no. 5, 1935; no. 6, 1937). In the analysis of fauna of the estuarine zone in Part II (Alexander *et al.*, 1935, p. 44 onwards), five species of *Gammarus sens.lat.* are recognized from the two rivers (p. 55). At the time of the survey, however, the status and distinguishing features of *G. zaddachi* were still not widely appreciated, and the species into which *Marinogammarus marinus* auctt. has recently been separated were still unknown.

Fortunately representative samples of the fauna were deposited at the Plymouth Laboratory, and it has been possible to revise identifications and to make some important corrections. A list of the preserved samples is given in the Appendix.

*River Tees*

*Gammarus pulex* L. Penetration into section I of the estuary, at Yarm, is confirmed, in shore and shrimp-trawl collections. Here it mixes with the more abundant *G. z. zaddachi* (see below). Casual specimens may well occur further down the estuary in the plankton in winter, but the statement 'occasional in plankton down to [section] VII' should be taken with reserve, as two out of five samples labelled '*G. pulex*' from other stations were, in fact, *G. zaddachi*.

*G. zaddachi* Sexton. This was entirely overlooked in the Tees. The typical subspecies, abundant in the upper half of the estuary, was wrongly attributed to *G. duebeni* (sometimes to *G. pulex*). All statements under the heading of '*duebeni*', as affecting the River Tees, should be transferred to *G. z. zaddachi*. Samples have been confirmed from the following sections: I, overlapping *G. pulex*, but more numerous; II and III, where evidently abundant, and the only species; IV, in the tidal zone under *Fucus*, where occurred a mixed population of this and *duebeni*; and in several tow-nettings. Another sample, labelled '*G. duebeni*', proved to be exclusively *G. z. zaddachi*. Unfortunately no samples survive from the main stream or low-water region of sections IV–VII, but it may be assumed that all the '*G. duebeni*' recorded from here are the typical subspecies of *zaddachi*. Had *G. zaddachi salinus* occurred in this region, it would presumably have been recorded as '*G. locusta*', as in the Tay. No evidence can be found for the existence of *salinus* anywhere in the Tees, and it is significant that the centre of its expected range coincides with the polluted zone between Stockton and Middlesbrough, where a wide—and quite abnormal—gap occurred in the *Gammarus* population.

*G. duebeni* Lillj. This species may be expected to occur sporadically in the tidal zone where fresh-water streams or seepage make permanent pools of more or less brackish consistency. It has been confirmed only from the tidal region in section IV, where a number were taken under *Fucus vesiculosus* in company with the preceding species.

*G. locusta* (L.). The range as given, sections XIII and XII intertidally, and in tow-nettings up to IX, is probably entirely correct, as these zones fall well within the anticipated range (up to IX or X in summer and X or XI in winter). One sample tube labelled '*G. locusta*' contains this species only. There are also several in a sample of mixed amphipods from section XIII; and others in tow-nettings labelled 'T21B', 'T23' and 'T25'.

*Marinogammarus marinus* (Leach). There is no opportunity of confirming the species of this genus, except for some true *marinus* from section XIII.

However, the reported distribution of *marinus* from XIII to X intertidally may be taken as correct. The bottom records for XIII to XI and in S XII are more likely to refer to *M. finmarchicus* Dahl (see below).

It will subsequently be shown that the revised picture of distribution of the different species conforms with results obtained from other British estuaries, though the Tees presents one outstanding peculiarity which clearly demands a special explanation. This is the complete break in the continuity of the *Gammarus* population between sections VII and X. In a normal river this gap would be bridged by a slight upward extension of *G. locusta* and by the dominant presence of *G. zaddachi salinus*, which appears to be completely absent. (The last, if present, should overlap *G. z. zaddachi* about up to section VI.) *M. marinus* should occur intertidally at least to section VII. The argument that the poverty of the fauna in this region of the Tees is due to pollution, if otherwise unproved, would have been very strongly reinforced by this further analysis of the *Gammarus* populations.

This point is worth further emphasis. It is now established that *Gammarus* populations remain dense throughout the length of an estuary, and numbers are not affected by the rigorous conditions of the mid-estuary region which reduces the variety of animal forms to a minimum. This is possible because a succession of forms (species or subspecies), each adapted to a special salinity range, and each overlapping its neighbours, occupies the whole stretch from the fresh-water river to the sea. The only natural limiting factor which may effectively reduce numbers is absence of suitable cover. But almost any available cover is made use of, varying from growing weeds to decomposing rubbish, and is never so lacking as to eliminate gammarids altogether. In the middle region of the Tees there is evidently, from accounts, sufficient cover to support a population of *Gammarus*, and absence of the latter indicates some effective polluting agency. Furthermore, since gammarids are not eliminated by contamination of waters with sewage or rubbish, it could be concluded that industrial effluents containing a significant concentration of some toxin was causing pollution. Poisoning was in fact found to be due to cyanides.

### *River Tay*

*G. pulex*. Amongst material which Mrs Sexton has kindly shown me is a pair of *G. pulex* from the River Tay near Elcho, 21. i. 32. This locality is near the limit of tidal influence in the main river, but well away from the influence of brackish water. So far as we know the species is uncommon in the soft waters of Scottish rivers. It is not recorded in the Survey Report from the River Earn, which was chosen for following the conditions at the very upper limit of tidal influence.

*G. zaddachi*. This species was correctly recognized in some samples, but only the typical subspecies in the upper part of its range. *G. z. zaddachi* was correctly recorded from the bottom and tidal zones of sections I–IV. But it occurs equally in samples from various other sections down to X. Here again there was confusion with *G. duebeni*, but the latter species occurred intertidally with greater frequency than is usual (see below). In the upper part of its extensive range in the Tay, i.e. in sections I–IV, or Bridge of Earn to Newburgh, it was colonizing fresh water or water rarely greatly raised in salinity. This tendency is now known to be a usual feature. Characteristically too, the animals from these sections are of a small size and appear to show inhibited development: they were probably not reproducing.

In sections IX and X, in which *G. z. zaddachi* was becoming scarcer, examples of a 'saline' or 'non-hairy' form of *G. zaddachi* occur.† These had presumably been recorded as *G. locusta*, since none of the latter was found in samples higher than section XI, which represents indeed the predictable upper limit. The seaward limit of *G. zaddachi* in the Tay cannot be determined, through paucity of preserved specimens from XI, and their absence from XII and XIII.

*G. duebeni* Lillj. This species, as will be shown elsewhere, does not normally form a member of the estuarine succession, but occurs on the edge of the tidal zone and intertidally where special conditions exist—e.g. marked fresh-water seepage from the land. It appears, however, to have been genuinely more plentiful in the Tay estuary than is usual. Recorded as 'abundant between tidemarks from sections V–X', it has been confirmed in the following samples: V [tidal zone], a number of well-grown adults; VI, tidal zone, large sample in which *G. z. zaddachi* was mixed; VII, tidal zone, large sample in which *G. z. zaddachi* was nearly as plentiful; IX, high-water level, a number of adults (but none low-water level); X, mid-tide level, 39 well-grown adults. The record for the bottom in VI should be referred to *G. z. zaddachi* (four samples are entirely of this species).

*G. locusta* (L.). As pointed out above, the occurrence in sections IX and X should be referred to *G. zaddachi*. It genuinely occurs, however, in section XI, at least at near high-water level. Unfortunately the surviving samples from this zone are scanty, and there are none preserved from sections XII and XIII. The species, however, may be assumed to inhabit the seaward end of the estuary from XI onwards.

*Marinogammarus marinus* (Leach). The correct range was originally given, and the species appears to be normally plentiful in the upper part of the tidal zone, up the estuary to section VIII. It was also well distributed down to low water in sections IX–XI. In section XI, however, the next species was found mixed up with it.

*M. finmarchicus* (Dahl), a species unknown at the time of the survey, can be added to the fauna of the Tay Estuary, as already reported (Sexton & Spooner, 1940). It was, indeed, in revising the Tay material that the writer

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† Not the true *G. z. salinus*, but a form with a more sparsely-haired and shorter antenna 1 peduncle: see p. 43.

first recognized the occurrence of this distinct species in the British Isles, though it has proved easy to collect it below the Plymouth Laboratory. Normally marine intertidal, with the centre of its distribution in the lower half of the tidal zone, it does not appear to extend very far into estuaries, but a stony ground may be essential to it. In the Tay section XI appears to be its upper limit.

The revised picture of distributions again agrees in essential respects with those from estuaries in the south of England. It is incomplete at the lower end, but it would appear that the zone in which a 'saline' form of *Gammarus zaddachi* forms 100% (or nearly so) of the *Gammarus* population is quite narrow. But it is important to remember that the summer and winter distributions are not distinguished. Special features are provided by the unusual abundance of *G. duebeni* in the tidal zone, by the penetration of *Marinogammarus finmarchicus* up to, or even beyond, the limit of *Gammarus locusta*, and by the apparent replacement of *G. z. salinus* by a form more closely akin to the northern *G. 'locusta'* (see p. 43). The dominance of *G. z. zaddachi* for such a long stretch in the upper parts of the estuary is noteworthy, but quite in keeping with its habits elsewhere. It would be interesting to know how far it succeeds in reproducing above the level of Newburgh.

Certain difficulties encountered by Bassindale (1942*a*, p. 138 *et seq.*) in his attempt at comparing the zones occupied by different *Gammarus* spp. in several rivers, are now disposed of.[1] In the Tay *G. locusta* appeared to penetrate further up river than usual, but this was only because the 'saline' form of *G. zaddachi* had been overlooked, and even in section XI of the river *G. locusta* has only been confirmed from the high-water zone. *G. z. zaddachi* had also been overlooked from sections V to X, so that *G. duebeni* finds its proper place as a colonizer of the intertidal zone, and not as an interloper in the main *locusta-zaddachi-pulex* succession.

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[1] Bassindale was mistaken in supposing that all the Tay identifications were correct.

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## APPENDIX

### *Tees Survey Collections: Samples Examined*

**River Tees**

| Section of river | Label on tube | Revised naming | Remarks |
|---|---|---|---|
| I | A. Yarm, 17. ix. 31, shore | *G. pulex*, 3<br>*G. z. zaddachi*, 9: 5 ♂♂, 2 ♀♀, 2 imm. | |
| I | A. Shrimp trawl, 8. x. 31 | *G. pulex*, 1 very large ♂<br>*G. z. zaddachi*, 5 ♂♂, 3 ♀♀, 12 imm. | |
| II | B. White House and Barwick, shore, 17. ix. 31 | *G. z. zaddachi*, large no. adults and imm. | |
| II | B. Shrimp trawl, 8. x. 31 | *G. z. zaddachi*, 13: 5 ♂♂, 4 ♀♀, 4 imm. | |
| III | C. Above Preston Hall, shore, 17. ix. 31 | *G. z. zaddachi*, 34: 26 ♂♂, 7 ♀♀, 1 imm. | |
| III | C. Shrimp trawl, 8. x. 31 | *G. z. zaddachi*, several ♂♂, with 1 ♀ and 2 imm. | |
| IV | Among *Fucus vesiculosus*, '*Gammarus duebeni*' | *G. duebeni*, 19: 12 ♂♂, 7 ♀♀, robust specimens<br>*G. z. zaddachi*, 5: 4 ♂♂, 1 ♀, large | Intertidal |
| IV | D. Shrimp trawl, 8. x. 31 | *G. z. zaddachi*, 8: 2 ♂♂, 3 ♀♀, 3 imm. | |
| ? | '*Gammarus pulex... duebeni*', from 8 | *G. z. zaddachi*, several large ♂♂ | |
| ? | '*Gammarus duebeni*' | *G. z. zaddachi*, 9: 6 ♂♂, 2 ♀♀, 1 imm. | |
| ? | Tow-netting, 9 | *G. z. zaddachi*, ♂ | |
| ? | Tow-netting, 7 | *G. z. zaddachi*, large ♀ with eggs | |
| ? | Tow-netting, 7B | *G. z. zaddachi*, 6: 5 ♂♂, 1 ♀, breeding | |
| ? | Tow-netting, Q11 | *G. z. zaddachi*, very large ♂ | |
| ? | Tow-netting, T21*b* | *G. locusta*, young ♂ | |
| ? | Tow-netting, T23 | *G. locusta*, 2 young ♂♂, 5 ♀♀, several imm. | |
| ? | Tow-netting, T25 | *G. locusta*, 6: 2 ♂♂, 3 ♀♀, 1 imm. | |
| (XI–XIII) | '*Gammarus locusta*' | *G. locusta*, several | |
| XIII | '*Gammarus marinus* Leach' | *Gammarus locusta*, 13<br>*Marinogammarus marinus*, 7<br>*Amphithoë rubricata*, 1<br>*Melita palmata*, 2 | |
| ? | 13. xii, 12. v. 30 '*Gammarus pulex*' | *G. pulex*, several | |
| ? | O.I. 26. vi. 29 '*Gammarus pulex*' | *G. pulex*, two | |
| ? | B9. 10. ii. 30 '*Gammarus pulex*' | *G. pulex*, 8 | |
| ? | A6. 18. xi. 29 '*Gammarus pulex*' | *G. z. zaddachi*, 3 | |
| ? | A56. 23. x. 29 '*Gammarus pulex*' | *G. z. zaddachi*, 3 ♂, 1 ♀ | |

**River Tay**

| Section of river | Label on tube | Revised naming | Remarks. Recorded as: |
|---|---|---|---|
| I | Sect. I | *G. z. zaddachi*: adults and imm., dwarf | ‘*G. zaddachi*’ |
| II | Sect. II | *G. z. zaddachi*, 49: 37 ♂♂, 4 ♀♀, 8 imm., dwarf | „ |
| III | Sect. III | *G. z. zaddachi*: adults and imm., dwarf | „ |
| IV | Sect. IV | *G. z. zaddachi*, several, dwarf | „ |
| V (tidal zone) | Sect. V | *G. duebeni*, a number of well-grown adults | ‘*G. duebeni*’ |
| VI | Sect. VI, tidal zone | *G. duebeni*, large sample, mainly well-grown adults | „ |
| | | *G. z. zaddachi*, 6: 5 ♂♂, 1 imm. (one ♂ dwarf) | „ |
| „ | Sect. VI, 13. Bottom | *G. z. zaddachi*, 7 imm. | „ |
| „ | Sect. VI, 14. Bottom | *G. z. zaddachi*, 11: 2 ♂♂, 2 ♀♀, 7 imm., dwarf | „ |
| „ | Sect. VI, 15. Bottom | *G. z. zaddachi*, several, maturing and imm., dwarf | „ |
| „ | Sect. VI. Bottom | *G. z. zaddachi*, dwarf, ♀ and 4 imm. | „ |
| VIII | Sect. VIII. Tidal zone | *G. duebeni*, 67: 32 ♂♂, 32 ♀♀, 3 imm.; large | „ |
| | | *G. z. zaddachi*, 42: 19 ♂♂, 13 ♀♀, 10 imm., very variable in size, some large, some dwarf | „ |
| | | *Marinogammarus marinus*, 3: 2 ♂♂, 1 ♀ | ‘*G. marinus*’ |
| IX | Sect. IX. High-tide level | *G. duebeni*, a number of adults<br>*M. marinus*, 1 | ‘*G. duebeni*’<br>‘*G. marinus*’ |
| IX | Sect. IX. Low-tide level | *M. marinus*, a number<br>*G. z. zaddachi*, 1 ♂<br>*G. zaddachi*, ‘saline’ form, 5 ♂♂ | ‘*G. marinus*’<br>‘*G. duebeni*’<br>‘*G. locusta*’ |
| X | Sect. X. Mid-tide level | *G. duebeni*, 39: 20 ♂♂, 19 ♀♀, well grown | ‘*G. duebeni*’ |
| X | Sect. X. Low-tide level | *G. z. zaddachi*, 6: 4 ♂♂, 1 ♀, 1 imm.<br>*G. zaddachi*, ‘saline’ form, 5: 4 ♂♂, 1 ♀ | ‘*G. duebeni*’<br>‘*G. locusta*’ |
| | | *Marinogammarus marinus*, a number | ‘*G. marinus*’ |
| XI | Sect. XI. High-tide level | *Gammarus locusta*, 1 ♂<br>*Marinogammarus marinus*, 3<br>*M. finmarchicus*, 1 ♀ | ‘*G. locusta*’<br>‘*G. marinus*’<br>„ |
| XI | Sect. XI. Mid-tide level | *M. marinus*, numerous<br>*M. finmarchicus*, 1 ♂ | ‘*G. marinus*’<br>„ |
| XI | Sect. XI. Low-tide level | *M. marinus*, many<br>*M. finmarchicus*, 2 ♂♂, 2 ♀♀ | ‘*G. marinus*’<br>„ |

# OBSERVATIONS ON FLOUNDERS *PLEURONECTES FLESUS* L. MARKED IN THE ESTUARIES OF THE TAMAR AND LYNHER

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From the Plymouth Laboratory

## INTRODUCTION

In the winter of 1937–8 just over a thousand flounders (*Pleuronectes flesus* L.) were caught, marked and released in the estuaries of the rivers Tamar and Lynher which flow into the west end of Plymouth Sound. The objects of this marking experiment were three. First, to discover the distribution and migrations of the adult flounders which had spent the years of immaturity in the estuaries. Secondly, to obtain observational, as distinct from inductional, data upon the growth of the species. Thirdly, to study changes in the distribution of the stock of immature fish within the estuaries.

The first object of the investigation was not fulfilled. There was but a very small number of returns from the open sea: this may be in part due to the great limitation of fishing along the south coasts of England which resulted from the outbreak of war some 18 months after the marking was completed. The two returns from localities at a distance from Plymouth do no more than hint at possibilities. The information obtained on growth gave proof that the individual variation in growth rates observed by Cunningham (1896) in captive fish was also to be found in the wild, and showed that there is relatively little growth in the winter months. The 152 recoveries of flounders within the estuaries have shown the existence of seasonal movements and redistributions of the fish of the immature stock. It is highly improbable that any more marked fish will be returned, and the results obtained are now summarized.

## THE MARKING EXPERIMENT

The flounders were caught with a 'Saltash Tuck-net' (see Hartley, 1940). On the grounds around Saltash, 659 fish were marked in thirteen netting expeditions between 23 September and 26 November 1937, most of the work being done at night. At Sheviock Wood, on the Lynher, 327 fish were marked in three days' work on 21 and 24 September and 20 October 1937. On the night of 7–8 October 1937, 12 flounders were marked on the West Mud ground. In addition, on 24 February 1938, 41 flounders were marked at Saltash with disks taken from fish already returned. A map of the area will be found in Hartley & Spooner (1938). Two places mentioned in this paper are not shown on the map. They are Cotehele, 2 miles up the Tamar above Halton Quay, and Calstock, which lies a mile upstream from Cotehele. Sandacre, also not marked on the map, is a spit of shoal ground in the Lynher below Forder Creek.

The flounders were kept in shallow baths of salt water until the strength of the tide put an end to fishing. Then each fish in turn was measured from the tip of the closed jaws to the end of the longest caudal ray, marked and at once released. There were no transplantation experiments. All the fish were released on the grounds where they had been caught and within an hour or two of the time of capture. The measurement was accurate to within ± 0·5 cm., this being the margin of error resulting from the measuring of a lively fish by the light of a hurricane lamp in an open boat on a winter's night. The marks were circular vulcanite disks of two sizes, 15 and 7·5 mm. in diameter. Two disks of the same diameter were used to mark each fish, a black disk to lie against the white under surface and a white disk, stamped with the initials PH and a serial number, to lie on the upper side. The white disk was placed with the numbered surface outwards. The disks were linked with a silver wire thrust through the dorsal musculature in the middle of the fish's length and about 1 cm. below the base of the dorsal fin. A little 'play' was allowed between the disks and the fish's flank, and in no case was any suppuration or necrosis of tissue found around the mark of a recovered specimen.

Printed posters were circulated to the waterside villages and to fishing ports, offering rewards for the return of marked fish.

148 flounders were returned between the beginning of marking and 5 May 1940, 116 of those marked at Saltash, 31 of the Sheviock fish and one from West Mud. Several marked flounders caught by Saltash fishermen were brought alive to the slip at that town. These fish were measured by Mr J. Gould and released a second time: seven were recovered again at a later date, and one was caught three times. Details of all recoveries are given in tabular form in the Appendix.

I am happy to be able to express my gratitude to Mr J. Gould for his help with the work of marking and the recording of recovered fish.

## Recoveries at Sea

Of the four flounders recaptured in the sea two male fish, nos. PH 179 and 314 were found in 20–30 fathoms of water on the Looe-Eddystone ground, a known spawning area of the species a few miles south-west of Plymouth. A female fish, no. PH 497, was caught off Sharkham Point, south Devon, some 40 miles by sea to the east of Plymouth, and an unsexed fish, no. PH 815, was recovered 2 miles south of Brighton. This latter fish had made a journey of about 200 miles to the eastward.

Ehrenbaum (1908) found that flounders marked in the Elbe moved westward or south-westward along the coasts of the Low Countries, and had but one recovery from water more than 40 m. in depth. Redecke (1907) recorded the recovery of flounders, marked in the Zuider Zee, on the coasts of Belgium and France as far west as the mouth of the Seine. The two west-country flounders which had moved to a distance from Plymouth (if it be at all permissible to speculate on the import of evidence so small) had travelled in an opposite direction—to the eastward. Yet the emigrations of the flounders from the three areas had this in common, that they were all in the direction of relatively shallow water. Cunningham (1896) has remarked that this species is rarely found in more than 30 fathoms of water, and in the Baltic, Ehrenbaum (1911) observed that spent flounders moved away from the Bornholm Deeps to the shallows of the Pomeranian coast.

## GROWTH

Some 80% of the flounders recovered were caught in the first 6 months after they had been marked, that is in the 'winter' period of October to March. Only a few of these fish had made good any appreciable growth in this period (Table I) within which the fast of the immature members of the stock also occurs (Hartley, 1940).

TABLE I. *PLEURONECTES FLESUS*, THE FLOUNDER. GROWTH OF MARKED FLOUNDERS SHOWING APPRECIABLE INCREMENT IN LENGTH DURING THE SIX WINTER MONTHS (OCTOBER TO MARCH) IMMEDIATELY AFTER MARKING

When a fraction of a month is to be considered, 16 days or more are counted as a complete month, 15 days or less are not counted.

| No. PH | Date of marking | Length at marking (cm.) | Date of recovery | Length at recovery (cm.) | Increment in length (cm.) | Months since marking | Mean increment in length per month (cm.) |
|---|---|---|---|---|---|---|---|
| | | | Females | | | | |
| 9 | 21. ix. 37 | 24·2 | 30. xii. 37 | 25·8 | 1·6 | 3 | 0·53 |
| 328 | 3. xi. 37 | 27·0 | 3. ii. 38 | 28·0 | 1·0 | 3 | 0·33 |
| | | | Males | | | | |
| 115 | 6. x. 37 | 22·5 | 1. ii. 38 | 25·2 | 2·7 | 4 | 0·675 |
| 193 | 13. x. 37 | 19·6 | 7. ii. 38 | 20·6 | 1·0 | 4 | 0·25 |
| 337 | 12. xi. 37 | 20·5 | 12. ii. 38 | 21·5 | 1·0 | 3 | 0·33 |
| 371 | 12. xi. 37 | 21·6 | 19. ii. 38 | 23·3 | 1·7 | 3 | 0·57 |
| 893 | 12. xi. 37 | 19·6 | 9. ii. 38 | 21·2 | 1·6 | 3 | 0·53 |

In Table II are shown the increases in length of all marked flounders which had been at liberty for more than 6 months, with the average increment per month of liberty and also the average increment per month of liberty between the months of April to September inclusive. These are the months of regular feeding and higher 'condition' (Hartley, 1940), and it may be inferred both

TABLE II. *PLEURONECTES FLESUS* THE FLOUNDER. GROWTH OF ALL MARKED FLOUNDERS WHICH HAD BEEN AT LIBERTY FOR MORE THAN SIX MONTHS, WITH INCREMENT IN LENGTH PER MONTH OF LIBERTY, AND ALSO INCREMENT FOR EACH 'SUMMER' MONTH (APRIL TO SEPTEMBER) AFTER MARKING

When a fraction of a month is to be considered, 16 days or more are counted as a complete month, 15 days or less are not counted.

| No. PH | Date of marking | Length at marking (cm.) | Date of recovery | Length at recovery (cm.) | Increment in length (cm.) | Months since marking | Mean increment in length per month since marking (cm.) | 'Summer' months since marking | Mean increment in length per 'summer' month since marking (cm.) |
|---|---|---|---|---|---|---|---|---|---|
| | | | | Females | | | | | |
| 4 | 21. ix. 37 | 35·4 | 11. ix. 38 | 36·2 | 0·8 | 12 | 0·067 | 6 | 0·13 |
| 61 | 24. ix. 37 | 36·4 | 7. viii. 38 | 36·5 | 0·1 | 10 | 0·01 | 4 | 0·025 |
| 65 | 24. ix. 37 | 36·6 | 26. vi. 38 | 36·6 | 0 | 9 | 0 | 3 | 0 |
| 76 | 24. ix. 37 | 27·4 | 12. ix. 38 | 31·2 | 3·8 | 12 | 0·32 | 6 | 0·63 |
| 112 | 24. ix. 37 | 18·6 | 10. vi. 38 | 21·2 | 2·6 | 9 | 0·29 | 3 | 0·87 |
| 236 | 13. x. 37 | 19·1 | 8. viii. 38 | 25·4 | 6·3 | 10 | 0·63 | 4 | 1·57 |
| 272 | 15. x. 37 | 20·3 | 3. vi. 38 | 21·0 | 0·7 | 8 | 0·09 | 2 | 0·35 |
| 276 | 15. x. 37 | 20·1 | 17. v. 38 | 20·6 | 0·5 | 7 | 0·07 | 2 | 0·25 |
| 296 | 20. x. 37 | 36·6 | 15. x. 39 | 39·75 | 3·15 | 24 | 0·13 | 12 | 0·26 |
| 298 | 20. x. 37 | 37·5 | 12. ix. 38 | 38·6 | 1·1 | 11 | 0·1 | 5 | 0·22 |
| 321 | 22. x. 37 | 26·2 | 17. v. 38 | 29·0 | 2·8 | 7 | 0·4 | 2 | 1·4 |
| 363 | 12. xi. 37 | 21·2 | 2. x. 38 | 30·6 | 9·4 | 11 | 0·85 | 6 | 1·57 |
| 380 | 12. xi. 37 | 19·8 | 29. vi. 38 | 23·2 | 3·4 | 8 | 0·425 | 3 | 1·13 |
| 391 | 25. xi. 37 | 20·0 | 5. v. 40 | 37·7 | 17·7 | 29 | 0·61 | 13 | 1·36 |
| | | | | Males | | | | | |
| 57 | 24. ix. 37 | 26·6 | 14. viii. 38 | 29·4 | 2·8 | 11 | 0·25 | 5 | 0·56 |
| 268 | 15. x. 37 | 19·1 | 11. ix. 38 | 22·0 | 2·9 | 11 | 0·26 | 5 | 0·58 |
| 280 | 15. x. 37 | 20·9 | 3. vi. 38 | 22·4 | 1·5 | 8 | 0·19 | 2 | 0·75 |
| 445 | 25. xi. 37 | 23·0 | 2. v. 40 | 30·3 | 7·3 | 29 | 0·25 | 13 | 0·56 |
| 479 | 25. xi. 37 | 20·0 | 29. vi. 38 | 23·2 | 3·2 | 7 | 0·46 | 3 | 1·07 |
| 496 | 26. xi. 37 | 33·0 | 26. viii. 38 | 33·0 | 0 | 9 | 0 | 5 | 0 |
| 525 | 21. ix. 37 | 16·3 | 11. ix. 38 | 24·6 | 8·3 | 12 | 0·69 | 6 | 1·38 |
| 535 | 21. ix. 37 | 16·4 | 25. v. 38 | 16·9 | 0·5 | 8 | 0·06 | 2 | 0·25 |
| 619 | 6. x. 37 | 16·8 | 29. vi. 38 | 19·0 | 2·2 | 9 | 0·24 | 3 | 0·73 |
| 788 | 20. x. 37 | 11·8 | 14. viii. 38 | 18·2 | 6·4 | 10 | 0·64 | 4 | 1·6 |
| 888 | 12. xi. 37 | 17·7 | 11. ix. 38 | 25·0 | 7·3 | 10 | 0·73 | 5 | 1·46 |

from this fact and from the observed lack of growth in fish recaptured in their first winter that these are also the months when most, if not all, of the increase in size is made.

There is obviously great individual variation in both sexes, and it is not possible to make generalizations from these data, though it may be pointed out that the swiftest growth rates are shown by some of the smallest fish. Two flounders marked in Poole Harbour made growths of 8·5 cm. from a length at marking of 21·5 cm., and of 5·5 cm. from a length at marking of 24·5 cm., between 9 October 1925 and the end of May 1927 (Buchanan-Wollaston, 1933). The mean length increments per month of the two fish, 0·425 and 0·275 cm., and the mean increments per 'summer' month of 1·06 and 0·69 cm. are of the same order as those found in flounders from the estuaries of the Tamar and Lynher.

There is individual variation not only in the growth rates but also in the maximum lengths attained. Among the female fish, nos. PH 61 and 65 had reached their full growth of 36·4 and 36·6 cm. at the time of marking. Nos. PH 4 and 298 grew by 0·8 and 1·1 cm. in a year from lengths at marking of 35·4 and 37·5 cm., and no. PH 296 grew by 3·15 cm. in 2 years, although she was already 36·6 cm. in length when she was marked. Only one fully grown male fish was recovered, no. PH 496 which made no growth in 9 months from a length at marking of 33·0 cm.

## MOVEMENTS WITHIN THE ESTUARIES

### *Flounders marked on the Saltash Grounds*

Of the fish marked in the autumn on the Saltash grounds the greater number remained in the immediate vicinity through the winter. Those which did move away went short distances downstream to the shores of the Hamoaze. From the end of March onwards recoveries from the upper reaches of the estuaries, especially around Cotehele, began to come in suggesting a movement of part of the population upstream. It is generally believed by the local fishermen that there is such a spring movement away from the sea of those fish which will summer in the rivers, and the recaptures in the first summer after marking give concrete evidence of its existence. A female flounder, no. PH 240, for example, was marked at Saltash on 15 October 1937, recovered at the same place on 12 December and again released, to be taken a third time at Cotehele Quay on 7 April 1938; another female flounder, no. PH 272, also marked at Saltash on 15 October was recaptured and liberated again at the place of marking on 3 February 1938, and caught once more on 3 June 1938, at Cotehele Quay. It must, however, be pointed out that there is a great increase in the amount of netting in the upper reaches of the estuaries after the opening of the salmon season on 1 March and it is not certain that all the fish taken after that date well above the place of marking had but recently moved away from the seaward grounds. Recoveries such as those of nos. PH 240 and 272 suggest that the redistribution of the stock does not take place until the spring, but do not prove it. The arithmetic mean length at the time of marking of the flounders which had moved downstream from the place of marking was 22·5 cm., and the arithmetic mean length of the fish which had gone upstream was 19·93 cm. The difference between these mean lengths is statistically significant, and confirms the existence of a reassortment of the stock before the breeding season, the larger fish going downstream to the sea, the smaller fish up the river to the more brackish stretches.

Only two flounders were recovered in the Tavy, a male fish no. PH 619 taken at Maristow on 29 June 1938, and a spent female no. PH 391 from Bere Ferrers in May 1940. The latter fish must have been down to the sea at least once to spawn. The two male flounders, nos. PH 268 and 888, marked at Saltash and recovered at Sheviock Wood may have been down to the sea to spawn, for both were large enough to have been mature fish.

### *Flounders marked at Sheviock Wood*

Of the fish marked at Sheviock Wood a number moved downstream to the Hamoaze or to the last reaches of the Tamar at Saltash. Three of the fish which went downstream, a female no. PH 112 and two males, nos. PH 38 and 535, were recovered well up the Tamar in the spring and early summer after marking. All three were under 19 cm. long at the time of marking, and it is probable that they had taken part in the spring-time movement upstream from the Saltash marks. One fish, no. PH 14, was recaptured at St Germans, 1½ miles upstream about 3 weeks after it was marked on 21 September 1937.

There is relatively little netting at Sheviock Wood and it was scarcely to be expected that there would be as many recoveries at the place of marking as were made at Saltash. A male fish, no. PH 59, was marked at Sheviock on 24 September 1937, and recaptured there on 20 October of the same year: by 11 January 1938, it had moved downstream to Petre's, in the Hamoaze. Two other male fish, no. PH 525 marked on 21 September 1937, and no. PH 788, marked on 20 October 1937, were recovered at Sheviock on 11 September 1938, and 14 August 1938 respectively. An unsexed flounder, no. PH 765, was marked at Sheviock on 20 October 1937, and recaptured there on 14 August 1938. The other flounders marked at Sheviock Wood and recovered on the same ground, or farther upstream, had probably been down to the sea and returned again.

## SUMMARY

1039 flounders were marked with numbered vulcanite disks in the estuaries of the Tamar and Lynher.

148 flounders were recaptured and of these seven fish were recovered a second time after one recovery and release, and one fish was recaptured on three occasions after two previous recoveries and releases.

Only two fish were recovered at a distance from Plymouth. Both had moved eastward, up the English Channel.

There was little or no growth in the winter months.

Individual growth rates were found to vary greatly.

The flounders living in the last reach of the Tamar near Saltash tended to remain in one limited area during the winter months, save for a drift downstream of some of the larger fish. In the spring there was an upstream movement of the smaller, immature fish.

Flounders which had gone down to the sea to spawn might return to the river in which they were marked, or to the other river of the two which join to form the Hamoaze, or they might move right away from the area where they were marked.

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## APPENDIX

*Recoveries of flounders marked in the estuaries of the rivers Tamar and Lynher* 1937 *and* 1938

| No. PH | Sex | At marking | | Recoveries | | | | Length at recovery (cm.) |
|---|---|---|---|---|---|---|---|---|
| | | Date (1937) | Length (cm.) | Where marked | Upstream of marking place | Downstream of marking place | Other localities | |
| | | | | Marked at Saltash, river Tamar | | | | |
| 53 | ♀ | 23. ix. | 22·5 | 15. x. 37 | — | — | — | — |
| (Second recovery) | | | | 6. xii. 37 | — | — | — | 22·5 |
| 54 | — | 23. ix. | 21·9 | — | — | Keyham Creek 28. xi. 37 | — | — |
| 115 | ♂ | 6. x. | 22·5 | — | — | Keyham Creek 1. ii. 38 | — | 25·2 |
| 122 | — | 6. x. | 18·7 | 15. x. 37 | — | — | — | — |
| 124 | — | 6. x. | 20·8 | 13. xi. 37 | — | — | — | 20·8 |
| 126 | ♀ | 6. x. | 18·1 | — | — | Eastern Ground 7. x. 37 | — | — |
| (Second recovery after release at Saltash) | | | | *c.* 30. xii. 37 | — | — | — | 18·5 |
| 130 | — | 6. x. | 19·3 | — | — | Rats Island 14. x. 37 | — | — |
| (Second recovery after release at Saltash) | | | | 14. x. 37 | — | — | — | — |
| 133 | ♀ | 6. x. | 21·2 | 24. x. 37 | — | — | — | 21·4 |
| 136 | ♀ | 6. x. | 19·6 | 7. ii. 38 | — | — | — | — |
| (Second recovery) | | | | 9. ii. 38 | — | — | — | — |
| (Third recovery) | | | | 26. ii. 38 | — | — | — | 19·8 |
| 137 | ♂ | 6. x. | 21·8 | — | — | West Mud *c.* 1. ii. 38 | — | 22·7 |
| 153 | — | 6. x. | 19·4 | 15. x. 37 | — | — | — | — |
| 173 | — | 13. x. | 26·6 | 18. xi. 37 | — | — | — | — |
| 179 | ♂ | 13. x. | 24·9 | — | — | — | Looe-Eddystone Ground 1. iii. 38 | 25·6 |
| 183 | — | 13. x. | 22·4 | — | — | Weston Mill Lake 23. xi. 37 | — | — |
| 188 | ♀ | 13. x. | 22·7 | 25. xi. 37 | — | — | — | — |
| (Second recovery) | | | | 24. i. 38 | — | — | — | 22·5 |
| 189 | ♀ | 13. x. | 18·8 | 30. x. 37 | — | — | — | 18·8 |
| 193 | ♂ | 13. x. | 19·6 | 7. ii. 38 | — | — | — | 20·6 |
| 196 | — | 13. x. | 23·1 | 1. ii. 38 | — | — | — | 23·8 |
| 213 | — | 13. x. | 22·2 | 9. i. 38 | — | — | — | 22·8 |
| 216 | ♀ | 13. x. | 20·1 | 12. xi. 37 | — | — | — | 20·1 |
| 221 | ♀ | 13. x. | 20·3 | 13. i. 38 | — | — | — | 19·5 |
| 229 | — | 13. x. | 18·4 | 8. ii. 38 | — | — | — | 18·6 |
| 232 | ♂ | 13. x. | 19·0 | 7. ii. 38 | — | — | — | 18·9 |
| 234 | — | 13. x. | 18·8 | 3. ii. 38 | — | — | — | 18·5 |
| 236 | ♀ | 13. x. | 19·1 | — | R. Tavy 8. viii. 38 | — | — | 25·4 |
| 240 | ♀ | 15. x. | 25·8 | 12. xii. 37 | — | — | — | 25·8 |
| (Second recovery) | | | | — | Cotehele Quay 7. iv. 38 | — | — | 25·5 |

| | | At marking | | Recoveries | | | | Length at recovery (cm.) |
|---|---|---|---|---|---|---|---|---|
| No. PH | Sex | Date (1937) | Length (cm.) | Where marked | Upstream of marking place | Downstream of marking place | Other localities | |
| 250 | — | 15. x. | 26·7 | 9. ii. 38 | — | — | — | 27·7 |
| 264 | ♀ | 15. x. | 21·6 | 2. xi. 37 | — | — | — | 21·5 |
| 267 | — | 15. x. | 23·9 | 10. i. 38 | — | — | — | 24·0 |
| 268 | ♂ | 15. x. | 19·1 | — | — | — | Sheviock Wd. R. Lynher 11. ix. 38 | 22·0 |
| 270 | — | 15. x. | 24·4 | 9. ii. 38 | — | — | — | 25·4 |
| 272 | ♀ | 15. x. | 20·3 | 3. ii. 38 | — | — | — | 20·7 |
| (Second recovery) | | | | — | Cotehele Quay 3. vi. 38 | — | — | 21·0 |
| 276 | ♀ | 15. x. | 20·1 | — | Cotehele Quay 17. v. 38 | — | — | 20·6 |
| 277 | ♀ | 15. x. | 19·5 | 12. xi. 37 | — | — | — | — |
| 280 | ♂ | 15. x. | 20·9 | — | Cotehele Quay 3. vi. 38 | — | — | 22·4 |
| 283 | — | 15. x. | 21·8 | 28. x. 37 | — | — | — | 22·0 |
| 287 | ♂ | 15. x. | 21·7 | — | Cotehele Quay 12. iii. 38 | — | — | 22·1 |
| 319 | — | 21. x. | 26·2 | 21. i. 38 | — | — | — | 26·6 |
| 321 | ♀ | 22. x. | 26·2 | — | Cotehele Quay 17. v. 38 | — | — | 29·0 |
| 328 | ♀ | 3. xi. | 27·0 | — | — | Petre's 3. ii. 38 | — | 28·0 |
| 334 | ♀ | 12. xi. | 19·8 | 10. ii. 38 | — | — | — | 20·0 |
| 337 | ♂ | 12. xi. | 20·5 | — | — | Weston Mill Lake 12. ii. 38 | — | 21·5 |
| 343 | — | 12. xi. | 21·7 | 23. ii. 38 | — | — | — | 23·5 |
| 362 | ♀ | 12. xi. | 24·8 | 5. ii. 38 | — | — | — | 25·4 |
| 363 | ♀ | 12. xi. | 21·2 | — | — | Cove Rock 2. x. 38 | — | 30·6 |
| 370 | ♀ | 12. xi. | 21·4 | — | — | Bull Point 21. xi. 37 | — | 21·4 |
| 371 | ♂ | 12. xi. | 21·6 | 9. ii. 38 | — | — | — | 23·3 |
| 377 | — | 12. xi. | 22·2 | 9. i. 38 | — | — | — | 22·4 |
| 380 | ♀ | 12. xi. | 19·8 | — | Cotehele Quay 29. vi. 38 | — | — | 23·2 |
| 391 | ♀ | 25. xi. | 20·0 | — | Bere Ferrers, R. Tavy 5. v. 40 | — | — | 37·7 |
| 409 | ♂ | 25. xi. | 30·2 | — | — | Henn Point 21. v. 38 | — | 29·7 |
| 434 | ♂ | 25. xi. | 23·2 | — | — | Lower Petre's 4. i. 38 | — | 23·5 |
| 435 | — | 25. xi. | 24·2 | 12. xii. 37 | — | — | — | 24·3 |
| 437 | ♂ | 25. xi. | 27·3 | 25. xii. 37 | — | — | — | 27·9 |
| 440 | ♂ | 25. xi. | 23·1 | — | — | Petre's 13. i. 38 | — | 23·5 |
| 442 | — | 25. xi. | 22·3 | 12. xii. 37 | — | — | — | 22·3 |
| 445 | ♂ | 25. xi. | 23·0 | — | Hole's Hole 2. v. 40 | — | — | 30·3 |
| 448 | ♀ | 25. xi. | 25·5 | 12. xii. 37 | — | — | — | 25·4 |
| 455 | ♀ | 25. xi. | 22·5 | 30. xii. 37 | — | — | — | 22·5 |

| No. PH | Sex | At marking | | Recoveries | | | | Length at recovery (cm.) |
|---|---|---|---|---|---|---|---|---|
| | | Date (1937) | Length (cm.) | Where marked | Upstream of marking place | Downstream of marking place | Other localities | |
| 460 | — | 25. xi. | 21·8 | 23. i. 38 | — | — | — | 22·6 |
| 472 | ♂ | 25. xi. | 23·5 | 30. xii. 37 | — | — | — | 23·4 |
| 475 | — | 25. xi. | 22·6 | 30. i. 38 | — | — | — | 22·8 |
| 479 | ♂ | 25. xi. | 20·0 | — | Neill Quay 29. vi. 38 | — | — | 23·2 |
| 483 | ♂ | 26. xi. | 22·4 | 16. xii. 37 | — | — | — | 22·4 |
| 488 | ♀ | 26. xi. | 23·6 | 30. xii. 37 | — | — | — | 23·3 |
| 496 | ♂ | 26. xi. | 33·0 | — | Neill Point 26. viii. 38 | — | — | 33·0 |
| 497 | ♀ | 26. xi. | 27·8 | — | — | — | Sharkham Pt, S. Devon 24. iii. 38 | 27·8 |
| 568 | ♀ | 23. ix. | 12·9 | 30. i. 38 | — | — | — | 13·0 |
| 616 | — | 6. x. | 18·8 | 3. ii. 38 | — | — | — | 19·1 |
| 619 | ♂ | 6. x. | 16·8 | — | Maristow, R. Tavy 29. vi. 38 | — | — | 19·0 |
| 621 | — | 6. x. | 16·6 | 15. x. 37 | — | — | — | — |
| 626 | ♂ | 13. x. | 19·5 | 28. x. 37 | — | — | — | 19·8 |
| 628 | ♀ | 13. x. | 16·7 | — | 2 miles below Calstock 23. iii. 38 | — | — | 17·3 |
| 630 | — | 13. x. | 19·1 | *c.* 2. x. 38 | — | — | — | 25·3 |
| 636 | ♂ | 13. x. | 18·6 | 26. i. 38 | — | — | — | 18·6 |
| 645 | ♀ | 13. x. | 18·5 | 5. ii. 38 | — | — | — | 18·9 |
| 650 | ♂ | 15. x. | 13·1 | — | Cotehele 29. iii. 38 | — | — | 13·6 |
| 652 | ♂ | 15. x. | 11·3 | 26. ii. 38 | — | — | — | 11·9 |
| 656 | — | 15. x. | — | 13. xi. 37 | — | — | — | — |
| 668 | ♀ | 15. x. | 19·5 | 26. ii. 38 | — | — | — | 19·7 |
| 677 | ♀ | 15. x. | 19·5 | 28. x. 37 | — | — | — | 19·6 |
| 682 | ♂ | 15. x. | 19·1 | 12. xii. 37 | — | — | — | 18·9 |
| 685 | ♀ | 15. x. | 19·3 | — | — | Eastern Gd. 27. i. 38 | — | 19·4 |
| 698 | — | 15. x. | 19·2 | 21. i. 38 | — | — | — | 20·1 |
| 700 | — | 15. x. | 20·0 | 28. xi. 37 | — | — | — | 20·1 |
| 706 | ♀ | 15. x. | 19·2 | 28. x. 37 | — | — | — | — |
| 707 | ♀ | 15. x. | 21·0 | 11. xii. 37 | — | — | — | 20·8 |
| 711 | ♀ | 15. x. | 20·3 | — | — | West Mud 17. i. 38 | — | 20·9 |
| 800 | — | 21. x. | 21·0 | 28. x. 37 | — | — | — | 21·1 |
| 815 | — | 22. x. | 19·4 | — | — | — | 2 miles south of Brighton 10. iii. 39 | 28·0 |
| 821 | — | 22. x. | 19·0 | 1. ii. 38 | — | — | — | 19·2 |
| 830 | — | 22. x. | 17·0 | 2. ii. 38 | — | — | — | 17·4 |
| 845 | ♀ | 22. x. | 12·0 | 25. xii. 37 | — | — | — | 12·5 |
| 869 | ♀ | 3. xi. | 19·2 | 24. xi. 37 | — | — | — | — |
| 888 | ♂ | 12. xi. | 17·7 | — | — | — | Sheviock Wd, R. Lynher 11. ix. 38 | 25·0 |
| 893 | ♂ | 12. xi. | 19·6 | 9. ii. 38 | — | — | — | 21·2 |
| 897 | ♂ | 12. xi. | 17·9 | 4. ii. 38 | — | — | — | 18·5 |
| 911 | — | 12. xi. | 18·5 | 9. i. 38 | — | — | — | 18·6 |
| 912 | ♂ | 12. xi. | 17·2 | 30. i. 38 | — | — | — | 17·5 |
| 919 | ♂ | 12. xi. | 18·6 | 7. ii. 38 | — | — | — | 18·7 |
| 920 | — | 12. xi. | 17·0 | 10. ii. 38 | — | — | — | 17·2 |
| 929 | ♀ | 25. xi. | 19·2 | 26. xi. 37 | — | — | — | 19·2 |
| 931 | ♂ | 25. xi. | 19·3 | 28. i. 38 | — | — | — | 19·2 |

| | | At marking | | Recoveries | | | | Length at recovery (cm.) |
|---|---|---|---|---|---|---|---|---|
| No. PH | Sex | Date (1937) | Length (cm.) | Where marked | Upstream of marking place | Downstream of marking place | Other localities | |
| 947 | ♀ | 25. xi. | 21·0 | 18. xii. 37 | — | — | — | 20·8 |
| 948 | — | 25. xi. | 19·4 | 26. i. 38 | — | — | — | 19·2 |
| 949 | ♀ | 25. xi. | 20·6 | 27. ii. 38 | — | — | — | 20·5 |
| 962 | — | 25. xi. | 17·3 | 9. ii. 38 | — | — | — | 17·1 |
| 963 | ♀ | 25. xi. | 21·0 | 12. xii. 37 | — | — | — | 21·4 |
| 980 | ♂ | 26. xi. | 19·7 | 11. xii. 37 | — | — | — | 19·6 |
| 983 | — | 26. xi. | 18·7 | 8. i. 38 | — | — | — | 19·0 |
| 987 | — | 26. xi. | 18·0 | 7. ii. 38 | — | — | — | 18·2 |
| 216/2 | ♀ | 26. xi. | 22·5 | 25. xii. 37 | — | — | — | 22·3 |
| | | (1938) | | | | | | |
| 59/2 | ♀ | 24. ii. | 21·5 | — | Cotehele Quay 23. v. 38 | — | — | 22·1 |
| 370/2 | — | 24. ii. | 18·5 | — | Cotehele 14. iii. 38 | — | — | — |
| 448/2 | ♀ | 24. ii. | 17·5 | — | 2 miles below Calstock 23. iii. 38 | — | — | 17·2 |
| 592/2 | ♀ | 24. ii. | 13·7 | 27. ii. 38 | — | — | — | 13·6 |

## Marked at West Mud

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| 160 | — | (1937) 7. x. | 17·2 | Recovered at Saltash, 27. x. 37. | | | | |

## Marked at Sheviock Wood, River Lynher

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| 4 | ♀ | 21. ix. | 35·4 | 11. ix. 38 | — | — | — | 36·2 |
| 5 | — | 21. ix. | 22·6 | 24. ix. 37 | — | — | — | 22·6 |
| 9 | ♀ | 21. ix. | 24·2 | — | — | Weston Mill Lake 30. xii. 37 | — | 25·8 |
| 14 | — | 21. ix. | 23·6 | — | St German's Quay 15. x. 37 | — | — | — |
| 20 | — | 21. ix. | 19·4 | 24. ix. 37 | — | — | — | — |
| 38 | ♂ | 21. ix. | 18·9 | — | — | — | Hole's Hole, R. Tamar 20. iv. 38 | 17·8 |
| 57 | ♂ | 24. ix. | 26·6 | 14. viii. 38 | — | — | — | 29·4 |
| 59 | ♂ | 24. ix. | 23·5 | 20. x. 37 | — | — | — | — |
| (Second recovery) | | | | — | — | Petre's 11. ii. 38 | — | 23·9 |
| 61 | ♀ | 24. ix. | 36·4 | 7. viii. 38 | — | — | — | 36·5 |
| 65 | ♀ | 24. ix. | 36·6 | — | — | Henn Point 26. vi. 38 | — | 36·5 |
| 74 | — | 24. ix. | 24·3 | — | — | Saltash 9. i. 38 | — | 25·0 |
| 76 | ♀ | 24. ix. | 27·4 | — | St German's Quay 12. ix. 38 | — | — | 31·2 |
| 86 | ♂ | 24. ix. | 25·1 | — | — | Saltash 8. xi. 37 | — | 25·0 |
| 102 | ♂ | 24. ix. | 23·2 | — | — | Cove Rock 11. i. 38 | — | 23·7 |
| 112 | ♀ | 24. ix. | 18·6 | — | — | — | Halton Quay, R. Tamar 10. vi. 38 | 21·2 |

| | | At marking | | Recoveries | | | | Length at recovery (cm.) |
|---|---|---|---|---|---|---|---|---|
| No. PH | Sex | Date (1937) | Length (cm.) | Where marked | Upstream of marking place | Downstream of marking place | Other localities | |
| 288 | — | 20. x. | 35·1 | — | — | Eastern Ground 30. xii. 37 | — | 35·2 |
| 293 | — | 20. x. | 35·2 | — | — | Saltash 3. vi. 38 | — | — |
| 296 | ♀ | 20. x. | 36·6 | — | — | Saltash 15. x. 39 | — | 39·75 |
| 298 | ♀ | 20. x. | 37·5 | — | St German's Quay 12. ix. 38 | — | — | 38·6 |
| 310 | ♂ | 20. x. | 24·4 | — | — | Henn Point 4. ii. 38 | — | 24·6 |
| 314 | ♂ | 20. x. | 27·3 | — | — | — | Looe-Eddystone Ground 15. ii. 38 | 30·2 |
| 317 | — | 20. x. | 23·6 | — | — | Rat's Island 25. xi. 37 | — | — |
| 513 | — | 21. ix. | 16·6 | 24. ix. 37 | — | — | — | — |
| 525 | ♂ | 21. ix. | 16·3 | 11. ix. 38 | — | — | — | 24·6 |
| 535 | ♂ | 21. ix. | 16·4 | — | — | — | Cotehele Quay, R. Tamar 25. v. 38 | 16·9 |
| 558 | ♀ | 21. ix. | 15·8 | — | — | Sandacre 1. x. 37 | — | — |
| 592 | ♂ | 24. ix. | 15·1 | — | — | Keyham Creek 13. i. 38 | — | 15·1 |
| 758 | — | 20. x. | 17·6 | — | — | Cove Rock 24. i. 38 | — | 17·5 |
| 765 | — | 20. x. | 17·9 | 17. xii. 37 | — | — | — | — |
| 775 | ♀ | 20. x. | 19·1 | — | — | West Mud 4. i. 38 | — | 19·3 |
| 788 | ♂ | 20. x. | 11·8 | 14. viii. 38 | — | — | — | 18·2 |

A number of the flounders marked by Ehrenbaum (1908) showed an apparent *decrease* in length between the times of marking and recovery similar to that shown by several of the fish from the Tamar and Lynher.

# THE SPAWNING OF MACKEREL, *SCOMBER SCOMBRUS* L., AND PILCHARD, *CLUPEA PILCHARDUS* WALBAUM, IN THE CELTIC SEA IN 1937–39

## WITH OBSERVATIONS ON THE ZOOPLANKTON INDICATOR SPECIES, *SAGITTA* AND *MUGGIAEA*

By P. G. Corbin, B.A.

Zoologist at the Plymouth Laboratory

(Text-figs. 1–21)

### CONTENTS

### INTRODUCTION

Large shoals of mackerel collect each spring in the waters to the south of Ireland and off the western entrance to the English Channel. In 1936, at the instance of the Ministry of Agriculture and Fisheries, the Marine Biological Association of the United Kingdom started an investigation of the biology of this mackerel population of the Celtic Sea.

One of the aims of the investigation was to determine the duration and locality of spawning of the mackerel and the distribution of the pelagic young stages. To this end, a survey of the plankton and hydrology of the area was carried out during a series of cruises in the years 1937, 1938 and 1939. Joint co-operation in the programme of cruises by the Fisheries Departments of

Eire and France was agreed at a meeting of the Mackerel Sub-Committee of the International Council for the Exploration of the Sea held at the Plymouth Laboratory in December 1937 (Le Danois, 1939*a*, *b*). The following cruises were made:

**1937**

| | |
|---|---|
| 12–20 April | S.S. *George Bligh* (United Kingdom) |
| 27–30 May | Steam drifter *B.T.B.*, L.T. 1153 (U.K.) |
| 20–22 July | Steam trawler *Elk*, M. 36 (U.K.) |

**1938**

| | |
|---|---|
| 23 March–5 April | S.S. *Quentin Roosevelt* (France) |
| 6–9 April | S.S. *Quentin Roosevelt* (France) |
| 7–12 April | S.S. *Muirchu* (Eire) |
| 7–18 April | S.S. *George Bligh* (U.K.) |
| 31 May–5 June | S.T. *Elk* (U.K.) |
| 19–24 July | S.T. *Elk* (U.K.) |

**1939**

| | |
|---|---|
| 15–18 March | S.T. *Elk* (U.K.) |
| 16–27 April | S.S. *George Bligh* (U.K.) |
| 17–21 April | S.S. *Muirchu* (Eire) |
| 2–7 June | S.T. *Elk* (U.K.) |

Some of the results of this programme of research have already been published. Farran (1939) has described the distribution of mackerel eggs and young stages taken in April 1938 to the south of Ireland by the Irish Fishery Cruiser *Muirchu*. Extensive data resulting from the two cruises made in March and April 1938 by the French Research Ship *Quentin Roosevelt* have been fully reported by Furnestin (1939*a*), and an introductory account of the distribution of mackerel eggs and young stages in the area covered by the Plymouth cruises is included in preliminary reports of the work of the investigation at Plymouth (Steven & Corbin, 1939; Marine Biological Association, 1940*a*, *b*). The distribution of phosphates in the area in April 1938 has been described by Hickling (1938), and the phytoplankton distribution of the 1939 cruises has been examined in detail by Mare (1940).

In addition to the distribution of mackerel eggs and young stages in the Celtic Sea in 1937–9, the present paper gives an account of the spawning of the pilchard[1] and the distribution of certain zooplankton indicators—the *Sagitta* species of the area and *Muggiaea atlantica*. Temperature and salinity conditions are also described briefly; further detailed treatment of the hydrological data will be published at a later date.

The courses of the cruises and station numbers[2] are shown in Figs. 1 and 2. Details of station times and positions, and of numbers of organisms per haul are given in the Appendix (Table VI; pp. 124–32). For data of the French cruises, see Furnestin (1939*a*).

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[1] Furnestin's paper (1945) on the biology of the Atlantic pilchard was received at the Plymouth Laboratory after completion of the present paper.

[2] In the text and figures, the station numbers of the *Muirchu* cruises are shortened by omitting the first two figures of the station number. Thus, Station SR 2872 reads SR 72. Full station numbers are given in Table VI with the last two figures printed in heavy type.

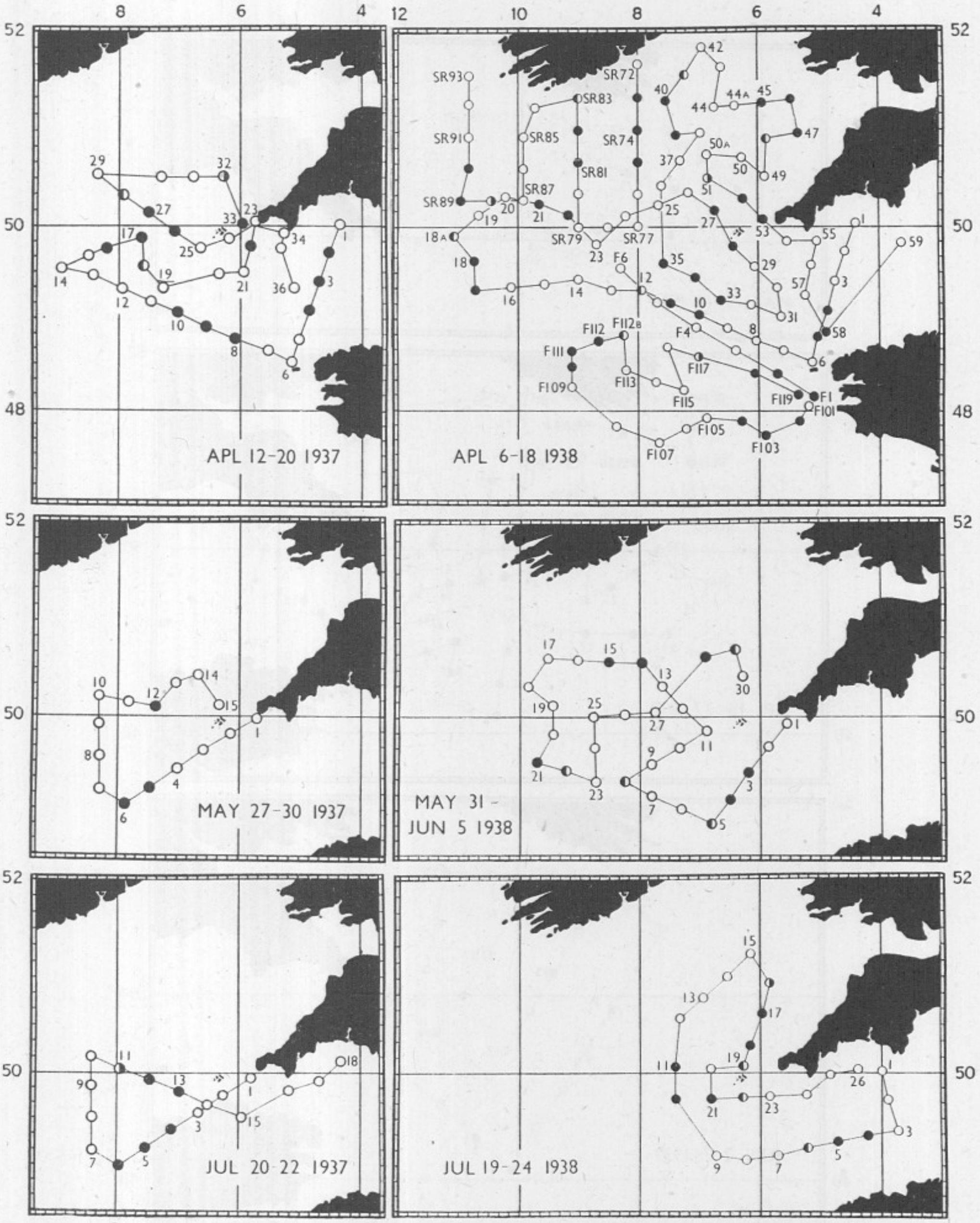

Fig. 1. 1937 and 1938 cruises; station positions. Stations worked by the *Muirchu* have the prefix SR; those worked by the *Quentin Roosevelt* have the prefix F. Only the first six stations (F 1–F 6) of the first cruise of the *Quentin Roosevelt* are shown; all stations (F 101–F 119) of the second cruise are shown. ◐ dawn; ○ day; ◑ dusk; ● night.

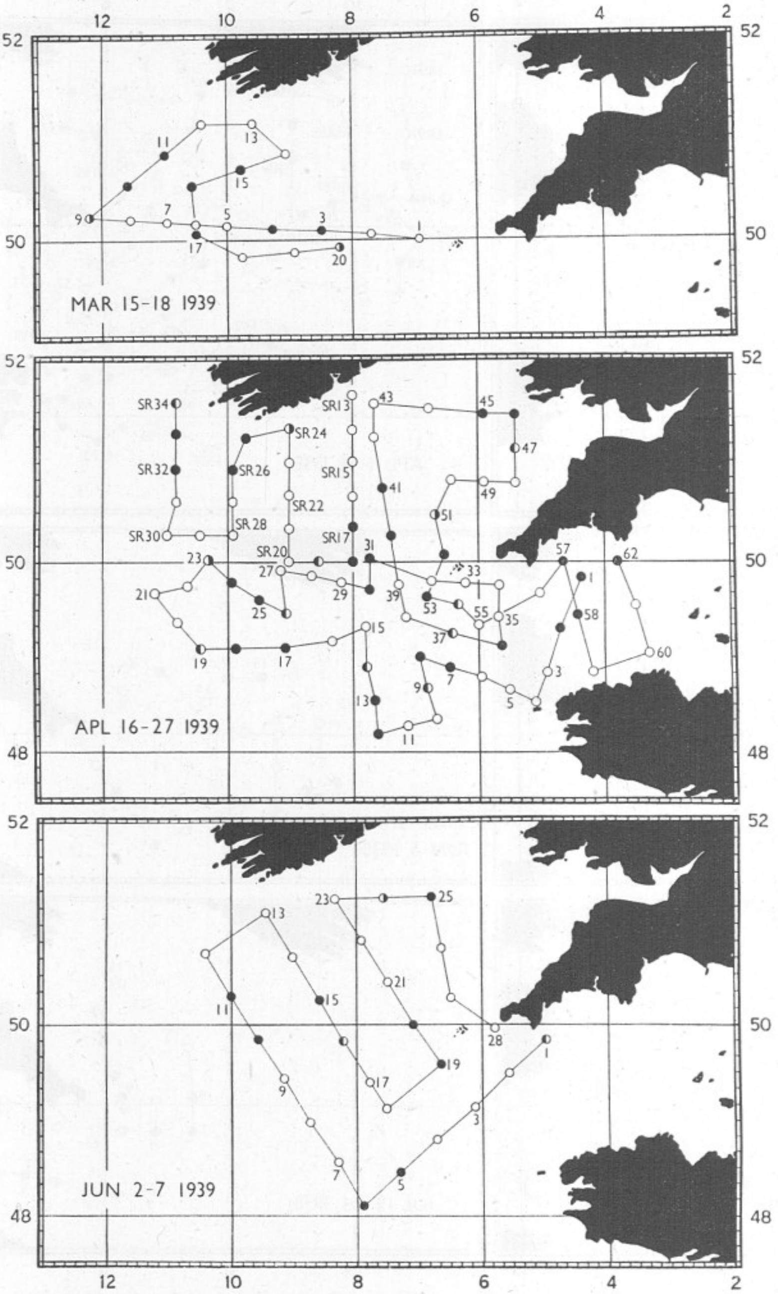

Fig. 2. 1939 cruises; station positions. Stations worked by the *Muirchu* have the prefix SR. ◐ dawn; ○ day; ◑ dusk; ● night.

## COLLECTION AND EXAMINATION OF MATERIAL

Throughout the cruises made from Plymouth and Eire, plankton was collected by half-hour oblique hauls of the 2 m. stramin ring-trawl. The method of fishing was the same as that described by Russell (1930, 1935 *a*), but a slightly greater depth of water was sampled, the marks on the warp being at 10, 20, 35, 50 and 70 fm. (18, 36, 63, 91 and 126 m.) (Le Danois, 1939*a*). The use of a standard method of collection permits some degree of quantitative comparison of the results of different cruises and different years, but no more than broad comparisons can be made since stations were worked both in daylight and darkness during the cruises. On the *Quentin Roosevelt* cruises, hauls were made horizontally (15 min. at surface) or vertically (25–0 m. and 50–0 m.) with a 33 cm. 'petit filet type Boulogne' or a 1 m. 'grand filet Schmidt' (Furnestin, 1939*a*). The data are therefore not quantitatively comparable with those obtained by the oblique hauls of the 2 m. stramin ring-trawl, but are valuable as qualitative records. Water samples and temperature readings were taken with the Nansen-Petterson water-bottle.

All young fish caught in each haul were picked out for counting and identification. The fish-eggs in each haul were also picked out for counting and identification, or, in hauls where they were very numerous, the number was estimated by sampling.[1] The same methods were also used for the indicator species. The eggs were identified largely by inspection; the number dealt with was far too great to permit of identification of individual eggs by measurement of the diameter of the egg and of the oil globule. Inspection alone may perhaps be considered a somewhat uncertain means of identification, but it proves reliable after some experience in the recognition of different species of fish eggs has been acquired, and especially when used in combination with the certain identification characters provided by the chromatophore pattern of the embryo and the oil globule in the later development stages of the mackerel egg (Buchanan-Wollaston, 1911; Holt, 1893).

## GENERAL RESULTS

### *The Spawning of the Mackerel and the Distribution of the Pelagic Young Stages and the Spawning of the Pilchard*

Before discussing the results of the present investigation, it will be of value to recall the existing records concerning the spawning of the mackerel in the seas around the south-west of the British Isles.

Matthias Dunn (1893) is remarkably accurate in his observations on the subject. He writes: '...the period of spawning...as a rule is in May and

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[1] All totals obtained by sampling are indicated in Table VI by * after the number (e.g. 2450*); totals without this notation are exact counts.

June...and the spawning grounds...are in those waters covering the plateau of ground within the two hundred mile limit of our western and south-western shores.' Of the mackerel in the English Channel, he observes: 'They generally spawn late in June, but...I have known their spawning deferred so late as the 10th of August.' Allen (1897), summarizing the records of Cunningham (1890, 1892) for the Plymouth area, and of Holt (1892, 1893) and Green (1894) for the south-west coast of Ireland, gives the following as the chief spawning periods:

| | |
|---|---|
| South-west of England (off Plymouth). | End of May to end of July. |
| South-west of Ireland. | May and June. |

The records of mackerel young stages from Plymouth waters in the years 1906, 1908–9, 1913–14, 1917 and 1919 (Allen, 1917; Lebour, 1918; Clark, 1914, 1920) also led Clarke to observe that spawning in the area takes place from May to July, but he notes that, '...a later spawning period has been observed for some years, *vide* Lebour (1918) for the record of post-larvae in September 1917', and he concludes by giving the spawning period as May–August (Clark, 1920). Ehrenbaum (1923) quotes Allen, Cunningham, Holt and Green. Lissner (1939) gives the spawning period in the Channel and North Sea as (May), June and July, and for Ireland as (April), May, June and July. From records of the occurrence of mackerel young stages in the 2 m. ring-trawl plankton collections made throughout the year at Plymouth, Russell (1930, 1935*a*, 1936*b*, 1937, 1938*b*, 1939*a*, 1940) classifies the mackerel as a summer-spawner in Plymouth off-shore waters, noting however that 'the main spawning region is probably considerably further to the westward' (1926). Farran (1939) records very intense spawning to the south of Ireland in April 1938. Le Gall (1939) states: 'Dès Mars, aux accores du Plateau Continental Atlantique, on constate la présence d'œufs de maquereaux dans le plancton.... La ponte du maquereau débute donc vers mi-Mars à l'entrée occidentale de la Manche. Elle s'intensifie en Avril et en Mai (maximum), se poursuit en Juin, en Manche Occidentale. Nous avons pu l'observer jusqu'à la fin d'Août en Manche Orientale.' In a preliminary report of the present investigation, Steven & Corbin (1939) also state that spawning lasts from March until July or August, with a maximum from mid-April to mid-May, and occurs within the area of the Continental Shelf but mainly off-shore. This observation was based on a detailed examination of the 1937 material of the Plymouth investigation, together with a preliminary inspection of the plankton collections of 1938 and 1939. A full examination of all the material has now been completed and has revealed in considerable detail the locality and period of spawning of the mackerel population of the Celtic Sea in 1937–9. Probably the most outstanding feature of the survey is the similarity in each year of the numbers and locality of mackerel eggs and young stages, and of the sequence of changes with time in these two components of distribution.

Spawning begins in about the second week of March and continues until the end of July and into August. It increases very rapidly in intensity after the start and by mid-April reaches a peak which lasts until May. Thereafter it decreases more gradually, until by the end of July it is only very slight. This changing intensity of spawning is shown in Fig. 3 and Table I.

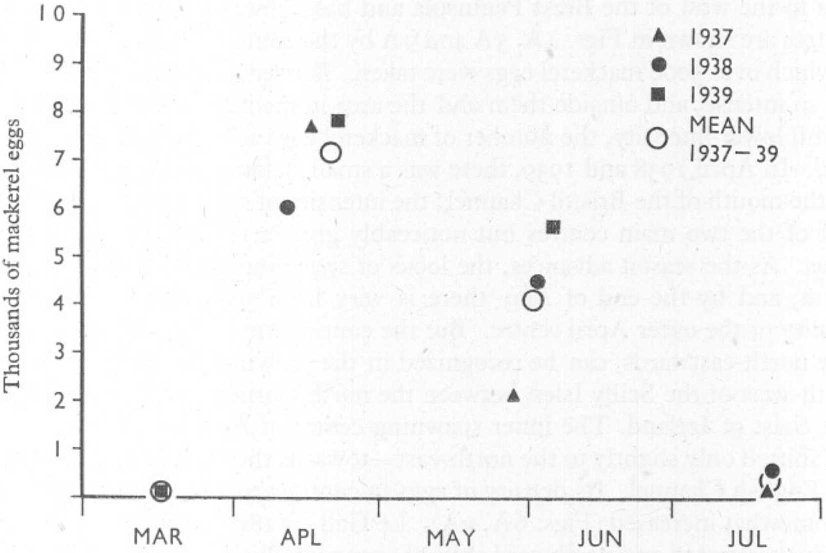

Fig. 3. Variation in intensity of spawning of the mackerel (data in Table I).

TABLE I. AVERAGE FOR EACH CRUISE OF THE TOTAL OF MACKEREL EGGS AT ALL STATIONS WHERE MORE THAN 100 WERE TAKEN

The number of stations from which the averages are obtained is shown in parentheses

| | March | April | May–June | July |
|---|---|---|---|---|
| 1937 | No cruise | 7659 (14) | 2127 (10) | 135 (1) |
| 1938 | No cruise | 6003 (42) | 4485 (23) | 571 (7) |
| 1939 | 118 (1) | 7802 (38) | 5660 (26) | No cruise |
| Mean 1937–9 | 118 | 7154 | 4090 | 353 |

Spawning takes place throughout the Celtic Sea during the period March to July. In the English Channel, and also in the Irish Sea, it is known to continue until August and probably in some years even until September, well after the main activity has finished in the Continental Shelf area. At the beginning of spawning in mid-March, the area is small and is situated well to the south-west of Ireland in the waters overlying the edge of the Continental Shelf (Fig. 8). By the mid-April peak, it has spread eastwards over the whole of the Celtic Sea, as far as the mouth of the English Channel and the entrances of the

St George's and Bristol Channels. There is little evidence that it extends into open oceanic waters beyond the 100 fm. line. The number of eggs, however, varies greatly in different parts of the area, and spawning is concentrated in two centres—to the west and south of the Celtic Sea. Of these, the outer western centre lying to the south of Ireland is the more extensive and contains the higher density of eggs. The inner southern centre covers a smaller area to the west of the Brest Peninsula and has a lower egg density. The two centres are shown in Figs. 4A, 5A and 9A by the contour enclosing all stations at which over 5000 mackerel eggs were taken. Between the centres spawning is not so intense, and outside them and the area immediately between them it is of still lower intensity, the number of mackerel eggs seldom exceeding 500 per haul. In April 1938 and 1939, there was a small isolated concentration of eggs off the mouth of the Bristol Channel; the intensity of spawning was lower than that of the two main centres but noticeably greater than in the surrounding areas. As the season advances, the locus of spawning moves farther east and north, and by the end of May there is very little spawning in the original locality of the outer April centre. But the continuation of it, shifted considerably north-eastwards, can be recognized in the spawning which occurs to the north-west of the Scilly Isles, between the north Cornish coast and the south-east coast of Ireland. The inner spawning centre of April is still present and has shifted only slightly to the north-east—towards the middle of the mouth of the English Channel. Its density of eggs in contrast to that of the outer centre is somewhat increased (Figs. 6A, 9A). Le Gall (1928*a*) draws attention to the gradual eastward and northward shift of spawning during April and May from the region south of Ireland, and he remarks on the presence at the end of May of two spawning areas towards the east—at the entrance to the St George's Channel (51° 18′ N., 7° 03′ W.) and some distance to the west of Ushant (48° 33′ N., 5° 50′ W.). The decrease in intensity of spawning and the eastward shift continue, and by mid-July no eggs are present to the west of Scilly. Their maximum numbers are little more than 1000 per haul in contrast to over 99,000 and 45,000 in April (1938, 1939). The occurrence of the larger hauls in the eastern part of the July spawning area indicates that the movement of spawning eastwards along the Channel and northwards into the Irish Sea still continues (Figs. 4C, 7A). In this connexion, Scott's records from the Irish Sea are especially valuable as they cover a considerable period of years. He found mackerel eggs only once in the northern area (south-west of the Isle of Man) during the years 1907–13. Farther south they were more numerous and he states that 'the eggs are not uncommon in the Cardigan Bay plankton at the beginning of July and it is possible that the majority of fish that arrive in the central area spawn on the way up from the south'. In support of this, he found that mackerel caught off Walney (north Lancashire) early in July (1901–12) were invariably in a spent condition (Scott, 1913, 1914*a*, *b*).

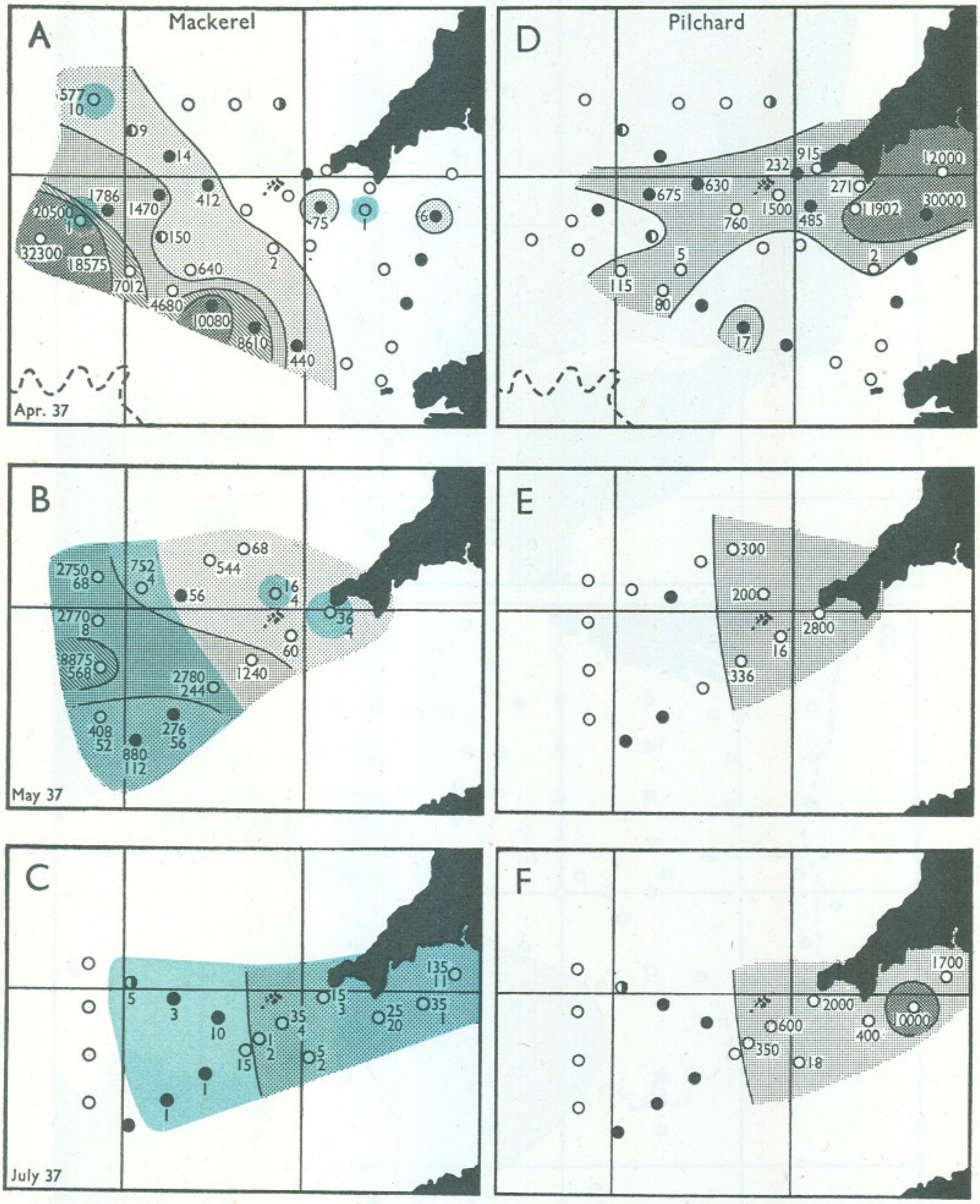

Fig. 4. Distribution of mackerel eggs (1–1000, 1001–5000, 5001–10,000, > 10,000) and young stages (blue areas) (A, B and C), and pilchard eggs (1–5000, > 5000) (D, E and F) in the Celtic Sea in April, May and July 1937. Figures refer to the numbers of eggs and young stages at each station. The broken line in this and succeeding figures indicates the 100 fm. contour.

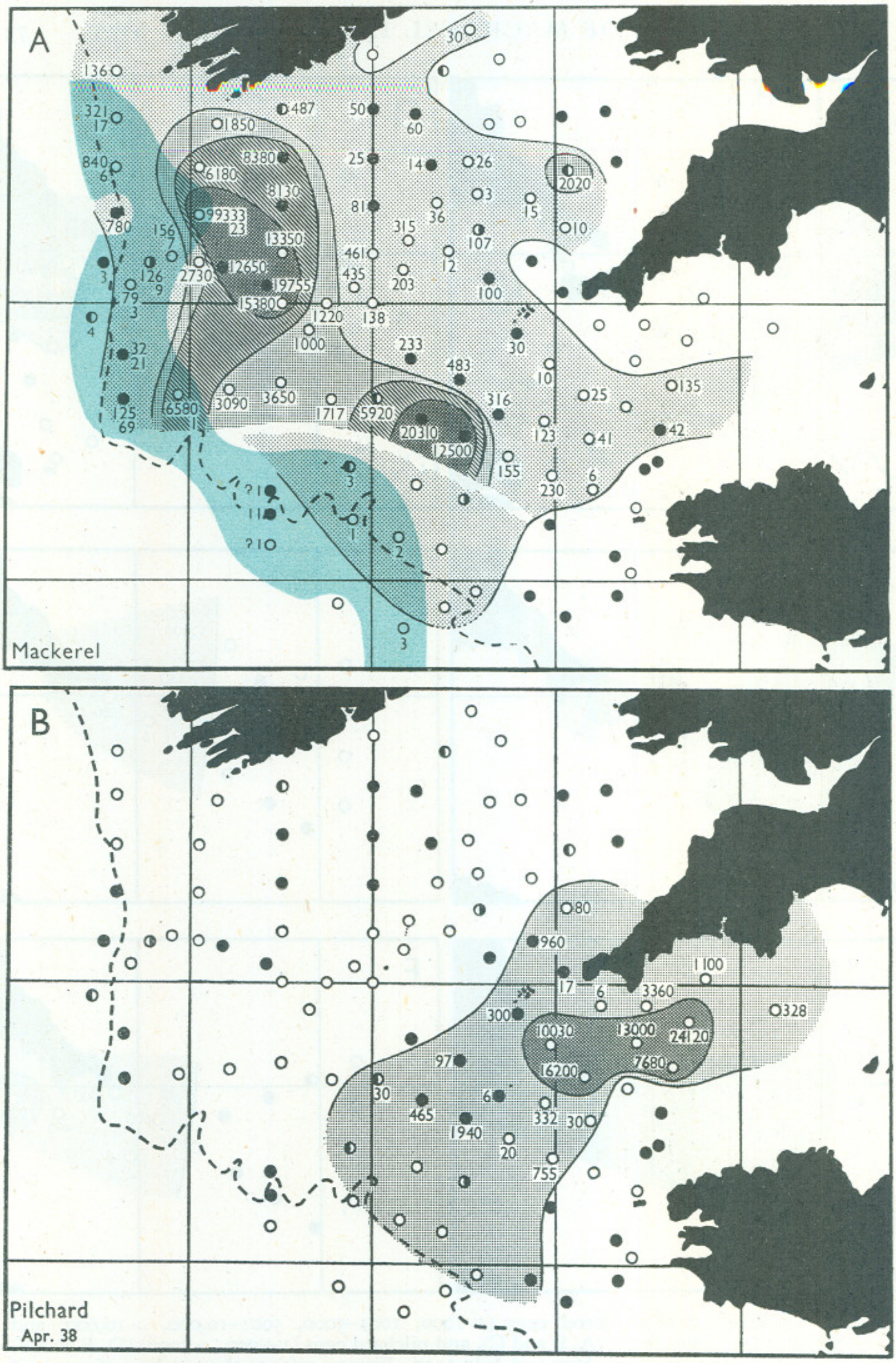

Fig. 5. Distribution of mackerel eggs (1–1000, 1001–5000, 5001–10,000, > 10,000) and young stages (blue area) (A), and pilchard eggs (1–5000, > 5000) (B) in the Celtic Sea in April 1938. Figures refer to the numbers of eggs and young stages at each station. Numbers of mackerel eggs and pilchard eggs at Sts. F 101–F 119 are not given (Furnestin, 1939*a*).

The changes in numbers and distribution of mackerel young stages[1] in the Celtic Sea are very similar to those of the eggs. None occurred in March

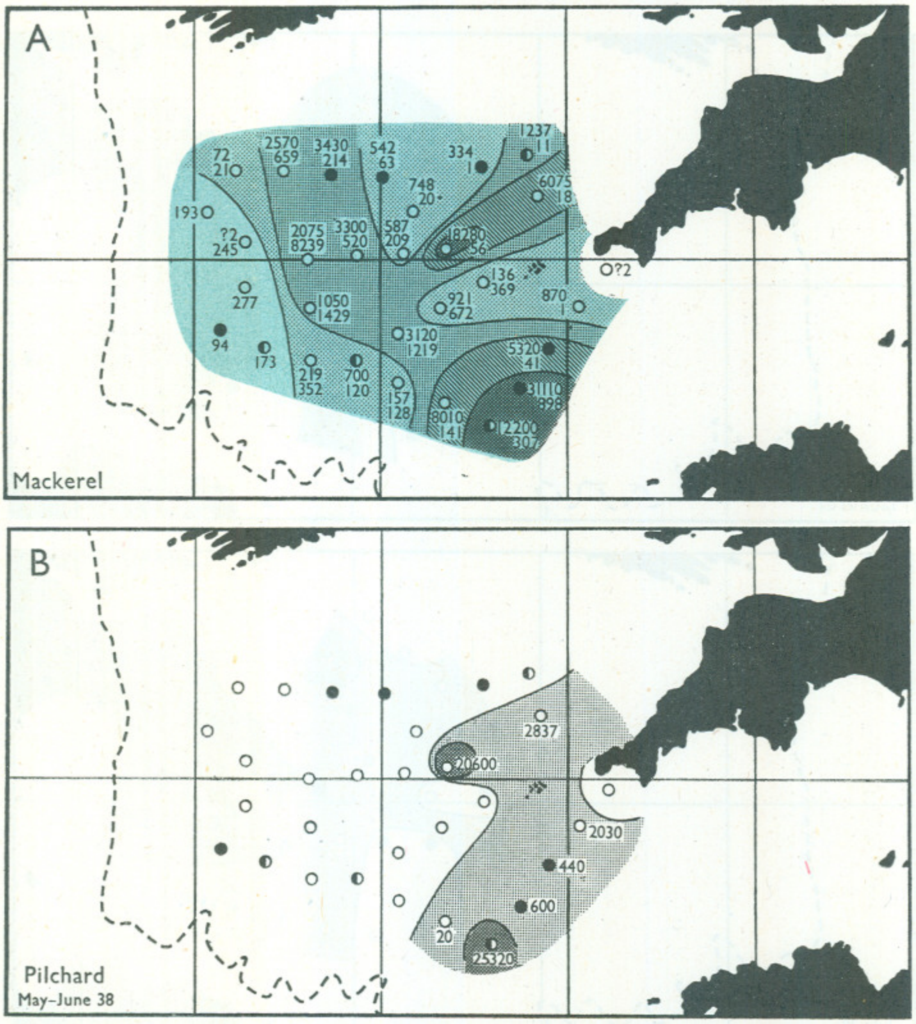

Fig. 6. Distribution of mackerel eggs (1–1000, 1001–5000, 5001–10,000, > 10,000) and young stages (blue area) (A), and pilchard eggs (1–5000, > 5000) (B) in the Celtic Sea in May–June 1938. Figures refer to the numbers of eggs and young stages at each station.

1939, and there appear to be no previous records of any being taken in the area as early as March. In the third week of April, small numbers of larvae and post-

[1] The material consists of 22,203 specimens; the largest measures 21 mm. (including tail) and may be regarded as past the post-larval stage since there is silvery pigment over most of the body and the finlets are developed on the caudal peduncle.

larvae are present in the plankton of the outer margin of the area—beyond the main spawning centres and towards the western and south-western edge of the Continental Shelf (Figs. 5 A, 9 A). The numbers caught in April 1938 and 1939 in this region were almost all under 100 per haul. Le Gall (1928*a*) records young stages in April to the south of Ireland in the region of 50° 50′ N., 10° 00′ W., (18–26 April 1927). They do not occur, or are present in very small numbers only, on the landward side of the spawning centres—in the central,

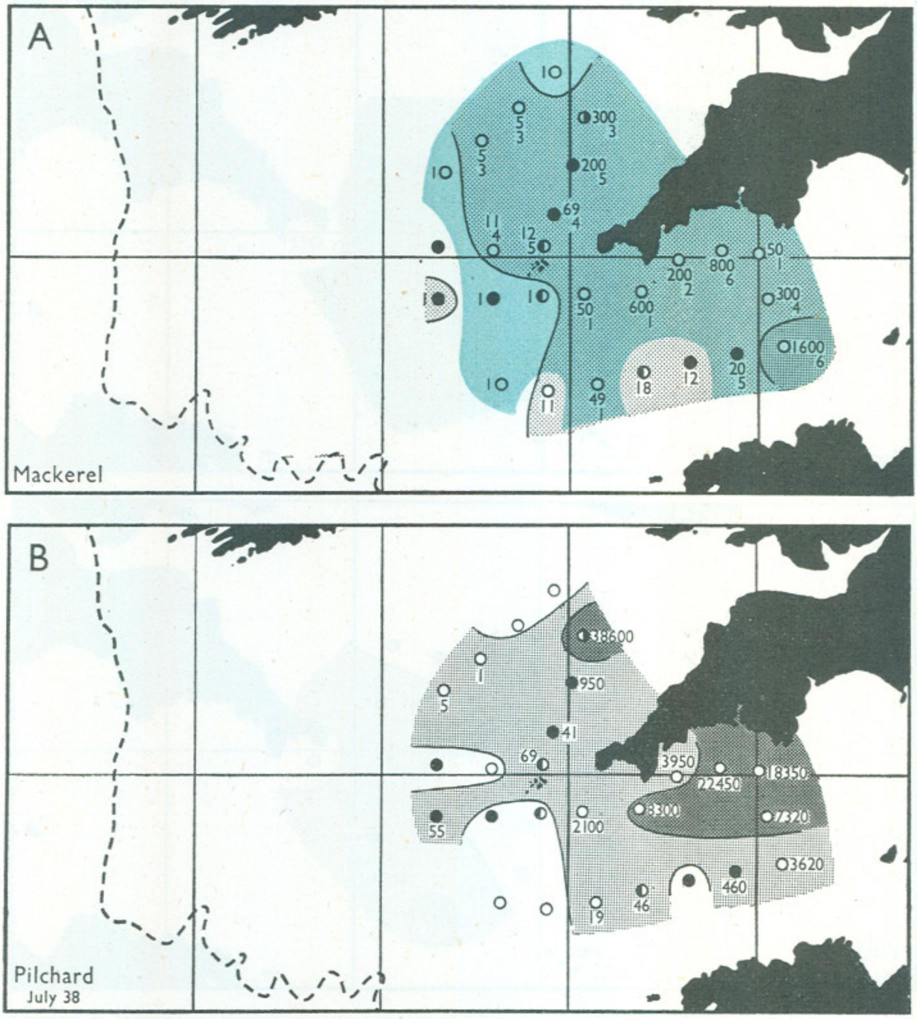

Fig. 7. Distribution of mackerel eggs (1–1000, 1001–5000) and young stages (blue areas) (A), and pilchard eggs (1–5000, > 5000) (B) in the Celtic Sea in July 1938. Figures refer to the numbers of eggs and young stages at each station.

northern and eastern areas of the Celtic Sea. In April 1939, three specimens were taken close to the small concentration of eggs off the mouth of the Bristol Channel. By the end of May and beginning of June, they are present throughout the Celtic Sea and are particularly abundant in the central area stretching from south-west Ireland to the Brest Peninsula (Figs. 4B, 6A, 10A). The largest haul contained 8239 specimens (St. 25, June 1938, day haul). They are less numerous towards the edge of the Continental Shelf, and also eastwards towards the English Channel and northwards towards the entrance to the Irish Sea. They are only occasionally taken at Plymouth in May but occur regularly there in small numbers in June (Allen, 1917; Lebour, 1918; Clark, 1914, 1920; Russell, 1930, 1935*a*, *et seq.*), and Clark (1914) observes that 'it is highly probable that the early stages occur in greater numbers much further out than the area investigated'. The area of abundance of young stages bears the same relationship to the spawning centres at this time of year as did the area of occurrence of young stages in April. It is situated beyond them—towards the edge of the Continental Shelf. By July they are much less abundant, even fewer than in April. Their continued move to the north and east is still evident and they are no longer present in the central area of the Celtic Sea to the west of 8° W. where previously, at the beginning of June, they were so numerous (Figs. 4C, 6A). Table II shows the average total of mackerel young stages taken on each cruise. The maximum at the end of May and beginning of June stands out clearly. At Plymouth, Russell (1930, 1935*a*, *et seq.*) finds a maximal occurrence of young stages in July. They continue to be present in the plankton in August in the majority of years, and even until September (Lebour, 1918 and Russell, 1935*a*; records in September 1917 and 1930, 1931 and 1932). The figures in Table II show that the average for the July cruises (1937, 6; 1938, 2·8) is in close agreement with the July monthly average at Plymouth (period 1930–9; July average, 9).

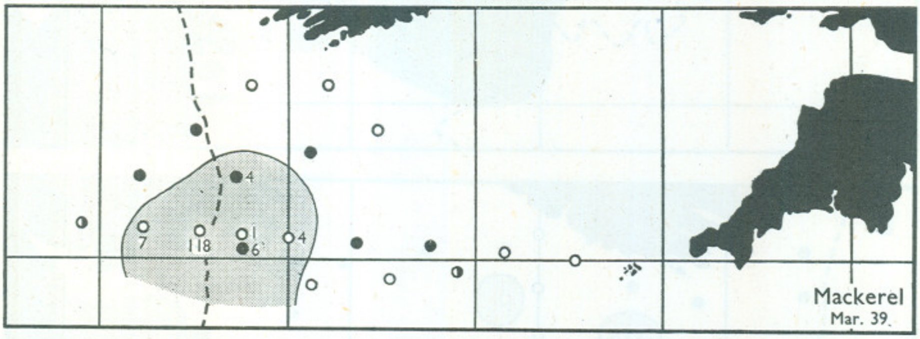

Fig. 8. Distribution of mackerel eggs in the Celtic Sea in March 1939. Figures refer to the number of eggs at each station. No young stages were taken.

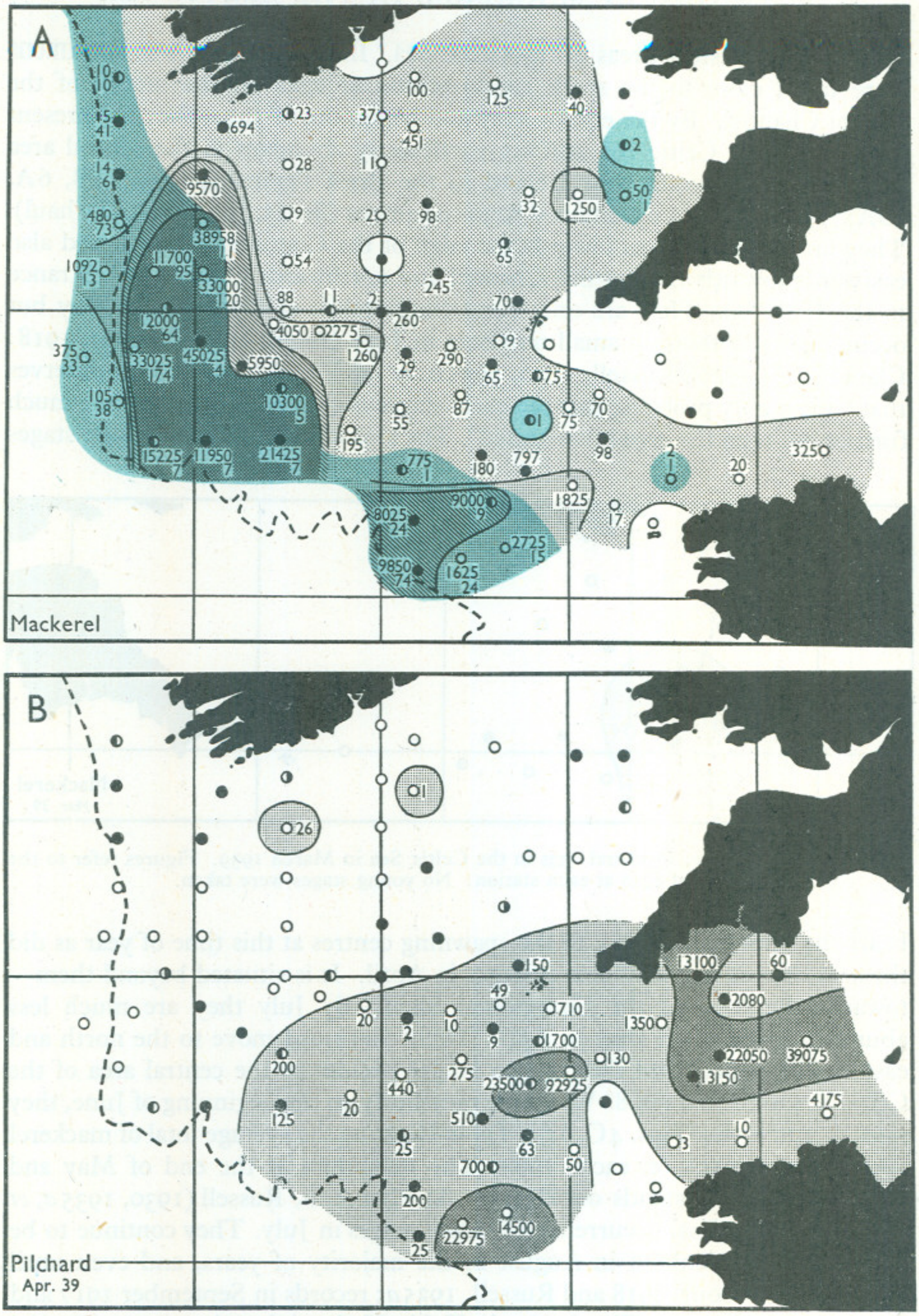

Fig. 9. Distribution of mackerel eggs (1–1000, 1001–5000, 5001–10,000, > 10,000) and young stages (blue areas) (A), and pilchard eggs (1–5000, > 5000) (B) in the Celtic Sea in April 1939. Figures refer to the numbers of eggs and young stages at each station.

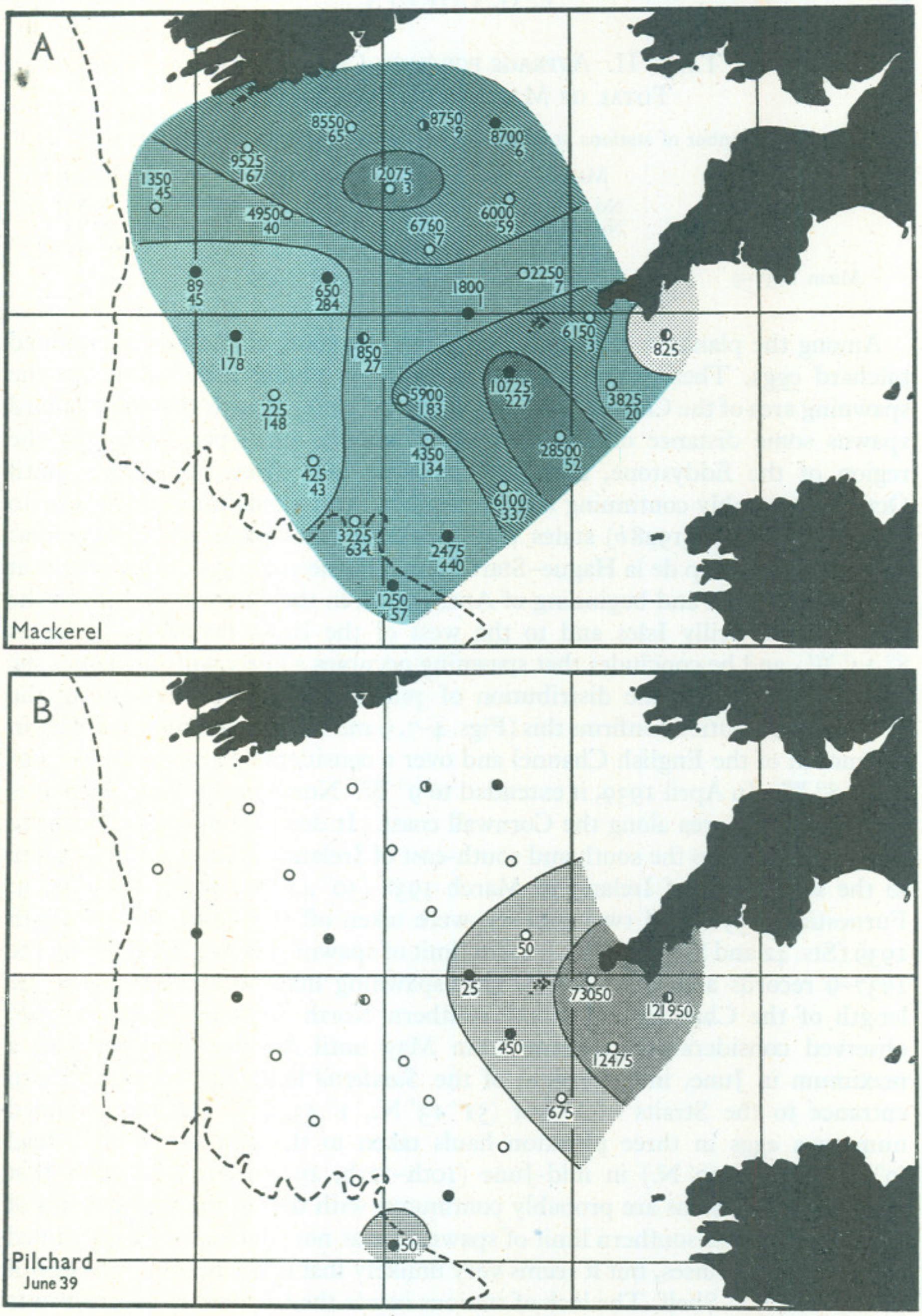

Fig. 10. Distribution of mackerel eggs (1–1000, 1001–5000, 5001–10,000, > 10,000) and young stages (blue area) (A), and pilchard eggs (1–5000, > 5000) (B) in the Celtic Sea in June 1939. Figures refer to the numbers of eggs and young stages at each station.

TABLE II. AVERAGE FOR EACH CRUISE OF THE TOTAL OF MACKEREL YOUNG STAGES

The number of stations at which they occurred is shown in parentheses

| | March | April | May–June | July |
|---|---|---|---|---|
| 1937 | No cruise | 3 (3) | 112 (10) | 6 (13) |
| 1938 | No cruise | 14 (11) | 575 (29) | 2 (21) |
| 1939 | Nil | 33 (26) | 118 (27) | No cruise |
| Mean 1937–9 | Nil | 17 | 268 | 4 |

Among the plankton collected during 1937–9, some of the hauls contained pilchard eggs. These were counted in order to obtain information on the spawning area of the Cornish pilchard. Lebour (1921) records that the pilchard spawns some distance off shore in the Plymouth area—particularly in the region of the Eddystone, and that spawning lasts from mid-March until October, probably continuing into November, with a maximum from June to August. Le Gall (1928*b*) states that spawning takes place within the area: Scilly–Ushant–Cap de la Hague–Start Point. Furnestin (1939*a*) found eggs at the end of March and beginning of April, 1938, in the Channel mouth, to the south of the Scilly Isles and to the west of the Brest Peninsula as far as 8° 14′ W., and he concludes that spawning occupies a fairly wide area over the Continental Shelf. The distribution of pilchard eggs observed during the present investigation confirms this (Figs. 4–7, 9 and 10). Spawning takes place in the mouth of the English Channel and over a considerable area to the west as far as 8° W. In April 1939, it extended to 9° W. North of the Scilly Isles it is confined to the area along the Cornwall coast. It does not appear to occur to any great extent to the south and south-east of Ireland; a single egg was taken to the south-west of Ireland in March 1938 (50° 42′ N., 10° 00′ W.; St. 9; Furnestin, 1939*a*) and twenty-seven were taken off the south coast in April 1939 (Sts. 42 and SR. 23). The eastern limit of spawning is not indicated by the 1937–9 records and it is possible that spawning may occur throughout the length of the Channel and in the southern North Sea. Furnestin (1939*b*) observed considerable spawning from May until August (1931–4), with a maximum in June, in the region of the *Sandettié* lightship in the northern entrance to the Straits of Dover (51° 13′ N., 1° 53′ E.). He also obtained numerous eggs in three plankton hauls taken to the east of Beachy Head (0° 05′ W., 50° 40′ N.) in mid-June (10th–12th, 1938). He concludes that these spawning areas are probably continuous with that at the western end of the Channel. The southern limit of spawning was not conclusively determined on the 1937–9 cruises, but it seems very unlikely that it lies beyond the edge of the Continental Shelf. The lack of stations inside the Channel mouth prevents as comprehensive a survey of the distribution of pilchard eggs throughout each year as was possible with mackerel eggs. It is, however, evident that the main pilchard spawning area lies at the western entrance of the English

Channel, although intense spawning activity also takes place farther to the west, beyond the Channel mouth. In June 1938 and April 1939 two small concentrations, in which eggs were quite as numerous as in the main spawning area, occurred outside the mouth of the Channel (Figs. 6B, 9B). The distribution of pilchard eggs at the end of May and beginning of June, and in July, indicates that the spawning area does not extend in these months quite so far west as in April. Its western limit lies nearer to 7° W. than to 8° W. The average for each cruise of the total of pilchard eggs at all stations where more than 100 were taken is shown in Table III.

TABLE III. AVERAGE FOR EACH CRUISE OF THE TOTAL OF PILCHARD EGGS AT ALL STATIONS WHERE MORE THAN 100 WERE TAKEN

The number of stations from which the averages are obtained is shown in parentheses

| | April | May–June | July |
|---|---|---|---|
| 1937 | 4957 (12) | 934 (4) | 2508 (6) |
| 1938 | 4474 (14) | 8687 (6) | 6895 (10) |
| 1939 | 10,611 (22) | 34,909 (5) | No cruise |
| Mean 1937–9 | 7542 | 21,798 | 6895 |

The 1937 averages show a maximum in April and a minimum at the end of May. In 1938 and 1939, however, the maximum occurred on the May–June cruise each year. It is possible that the irregularity of the 1937 averages may to some extent be due to the use of a smaller net on the May cruise and to the fact that only the fringe of the pilchard spawning area was worked. Pilchard eggs have been a constant and especially marked feature of the Plymouth plankton catches. They occur each year from April to November, with records in March in 1936 and in December in 1931, 1938 and 1939 (Russell, 1935*a*, 1936*b*, *et seq.*). These records have a maximum in June which Hickling (1945) has shown to be coincident with the maximum occurrence of spawning fish and with maxima in gonad weight, feeding activity and growth of the adult fish. Hickling's samples were obtained in the years 1936–8. This evidence strengthens the probability that the 1938 and 1939 averages are the truer reflexion of the changes in intensity of spawning and that the figures for 1937 are not representative.

The relationship of the mackerel and pilchard spawning areas is apparent in Figs. 4–7, 9 and 10. In April the main pilchard spawning in the Channel mouth takes place in an area containing few or no mackerel eggs (Figs. 4, 5, 9). As the season advances, the north-easterly shift of the mackerel spawning centres brings them nearer to those of the pilchard, and by the end of May and early June, there is considerable overlapping. This was particularly evident in May–June of 1938 when the spawning centres of the two species occupied the same areas (Fig. 6). The continued movement of the spawning of the mackerel eventually completes the overlapping of the total spawning areas of the two species—not merely of the centres. This can be seen from the distribution of mackerel and pilchard eggs in July 1937 and 1938 (Figs. 4C, F, 7). The overall spawning areas were identical and it is noteworthy that the largest hauls of mackerel eggs were taken to the eastward in exactly those areas of maximal pilchard spawning activity.

Comparison of the distribution of phytoplankton in 1939 (Mare, 1940) and of mackerel and pilchard eggs gives no indication of any close relationship. In March, there was very little phytoplankton in the region where mackerel spawning was just starting. In April, both mackerel spawning centres were situated in areas of medium phytoplankton density. In May–June, the northern spawning centre was in an area of particularly sparse phytoplankton, while the southern centre lay in the region of greatest phytoplankton density. It must be noted, however, that in May–June phytoplankton production was very low throughout the area of the cruise and at its highest approached only the lower values of April. The main pilchard spawning areas in April were located largely in areas of dense phytoplankton, whereas in May-June, they were in an area of sparse phytoplankton. Far more data are required for further examination of the possibility of any correlation between the spawning of either the mackerel or pilchard and the distribution of phytoplankton.

The salinity and temperature observations of the 1937–9 cruises provide opportunity for examining the possibility of a relation between these factors and the distribution of the spawning centres of the mackerel and pilchard. Le Gall (1939) writes of the mackerel: 'Les déplacements des bancs à l'entrée occidentale de la Manche et à l'entrée sud de la Mer d'Irelande paraissent se faire principalement suivant les axes transgressifs caractérisés par une température et une salinité élevées (salinité supérieure a 35 °/₀₀ et température variant de 10° a 15° suivant l'époque de l'année). La ponte se fait également dans les eaux transgressifes: les œufs et les larves de maquereaux étant nettement plus abondants dans les pêches planctoniques faites dans ces eaux.' Furnestin (1939*a*) also notes: 'la présence d'œufs et de larves de maquereaux semble être strictement limitée aux régions où se manifestent les trois grandes poussées transgressives'; and further, that it was only at stations of salinity near to or above 35·50 °/₀₀ that mackerel eggs and young stages were taken on the *Quentin Roosevelt* cruises in 1938. Farran (1939) on the other hand observes that at the western stations of the *Muirchu* cruise of April 1938 where salinities exceeded 35·60 °/₀₀, the numbers of mackerel eggs were low, in contrast to their particular abundance farther east in water of lower salinity. Of the spawning area of the pilchard Furnestin (1939*a*) remarks that it is 'en rapport étroit avec le mouvement général de la transgression atlantique sur le Plateau Continental. En effet, les différentes stations où nous avons trouvé des œufs de sardine sont situées sensiblement dans l'axe de la transgression. Ailleurs, dans les eaux continentales, nous n'en avons pas trouvé'. According to Fage (1920), the spawning and larval development of the pilchard in the

English Channel require a temperature of above 12° C.[1] and below 15° C. and he records a mean salinity of 35·27 ‰ during the spawning period, May–November. Le Gall (1928*b*) notes, however, that at one of the *Thor* stations[2] in the northern half of the Channel mouth, pilchard eggs were taken in a surface haul in water of 9·90° C., and he concludes that the pilchard in the Channel mouth area certainly spawns in temperatures below 12° C.

Table IV shows the mean temperature and salinity of the upper 25 m. of water in the mackerel and pilchard spawning centres in 1937–9 (means of all stations at which more than 5000 eggs were taken). Since there were indications of marked thermal stratification at 25 m. in May–June 1939 and July 1938, temperatures at surface and 5 m. only have been included; salinity means, however, include the values at 25 m. as vertically homohaline conditions extended to this depth. Mackerel spawning was much reduced (maximum, 1600 eggs) by July in 1938, although pilchard spawning was still very intense (maximum, 38,600 eggs); in order therefore to obtain as valid a comparison as

TABLE IV. MEAN TEMPERATURE AND SALINITY OF THE UPPER 25 M. OF WATER IN THE MACKEREL AND PILCHARD SPAWNING CENTRES

The number of stations from which the means have been calculated is shown in parentheses

| | Salinity ‰ | | Temperature ° C. | |
|---|---|---|---|---|
| | Mackerel | Pilchard | Mackerel | Pilchard |
| April 1937 | 35·36<br>5, 25 m. (4) | 35·18<br>5, 25 m. (2) | 10·50<br>5, 25 m. (4) | 9·51<br>5, 25 m. (2) |
| April 1938 | 35·35<br>0, 5, 25 m. (12) | 35·36<br>0, 5, 25 m. (4) | 10·27<br>0, 5, 25 m. (12) | 10·07<br>0, 5, 25 m. (4) |
| April 1939 | 35·50<br>0, 5, 25 m. (14) | 35·34<br>0, 5, 25 m. (5) | 11·44<br>0, 5, 25 m. (14) | 10·86<br>0, 5, 25 m. (5) |
| May–June 1939 | 35·15<br>5, 25 m. (7) | 35·26<br>5, 25 m. (1) | 14·63<br>5 m. (7) | 11·42<br>5 m. (1) |
| July 1938 | 35·18<br>0, 5, 25 m. (3) | 35·22<br>0, 5, 25 m. (5) | 15·52<br>0, 5 m. (4) | 15·70<br>0, 5 m. (6) |

TABLE V. TEMPERATURE AND SALINITY RANGES IN THE MACKEREL AND PILCHARD SPAWNING CENTRES

Depths and number of stations as in Table IV above

| | Salinity ‰ | | Temperature ° C. | |
|---|---|---|---|---|
| | Mackerel | Pilchard | Mackerel | Pilchard |
| April 1937 | 35·35–35·38 | 35·03–35·43 | 10·30–10·62 | 9·42– 9·71 |
| April 1938 | 35·25–35·49 | 35·30–35·39 | 9·95–11·12 | 9·73–10·29 |
| April 1939 | 35·33–35·58 | 35·10–35·52 | 10·49–12·30 | 10·27–11·80 |
| May–June 1939 | 34·51–35·49 | 35·26–35·27 | 13·22–15·42 | 11·42 |
| July 1938 | 35·06–35·36 | 35·06–35·36 | 14·16–16·30 | 14·16–16·30 |
| Extreme range all cruises: | | | | |
| | 34·51–35·58 | 35·03–35·52 | 9·95–16·30 | 9·42–16·30 |

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[1] Le Gall (1928*b*, p. 23) erroneously quotes this as 14° C.

[2] Fage (1920, p. 36); St. 31, 7 May 1906, 49° 45′ N., 4° 42′ W.; 20 pilchard eggs.

possible of the conditions in the spawning areas of the two species, the means of temperature and salinity for July 1938 have been calculated from the values at all stations where more than 100 mackerel eggs and more than 500 pilchard eggs were taken. Table V shows the ranges of temperature and salinity occurring in the spawning centres of the two species.

Considering first the means, it is apparent that as the season advances, conditions of reduced salinity and increased temperature are encountered in the mackerel spawning centres. In the pilchard spawning centres, salinities remain almost constant from April to July, with an indication of a slight diminution during this period, while temperatures rise from rather lower to slightly higher values than in the mackerel spawning centres. As a corollary to the above, the range of salinity throughout the period April–July, as well as the range in each month, is noticeably greater in the mackerel than in the pilchard spawning centres, while the greater temperature range occurs in the pilchard spawning centres. It has previously been noted that mackerel spawning in July is much diminished. In making any inference from the above figures, it would therefore be more correct to exclude from consideration the conditions pertaining in July in the mackerel spawning area. This was, however, exactly coincident with the pilchard spawning area, so that in fact, the July conditions were common to the spawning areas of both species. Moreover, the above remarks apply if the July conditions in the mackerel spawning area are discounted.

In April 1937, the mackerel spawning centres were entirely confined to water of salinity $>35{\cdot}3\,^0/_{00}$, but it must be noted that this cruise was not as extensive as the April cruises of 1938 and 1939. In April 1938, an intrusion of saline water ($>35{\cdot}5\,^0/_{00}$) lay between the outer and inner spawning centres, where the intensity of spawning was only moderate by comparison with that of the centres. In April 1939, the two mackerel spawning centres were largely situated in water of salinity $>35{\cdot}4\,^0/_{00}$. In May–June 1939, the southern mackerel spawning centre occurred in salinities varying between $35{\cdot}26\,^0/_{00}$ and $35{\cdot}49\,^0/_{00}$, while the values in the northern centre were all lower than $35{\cdot}2\,^0/_{00}$. These figures show the very considerable range of salinity in which intense mackerel spawning activity occurs and point to the somewhat doubtful value of ascribing salinity 'limits' to the spawning areas of the mackerel. It is evident that the shift of spawning during the season brings about the extent of this range to a greater degree than actual changes in salinity itself at one place.

### *The Distribution of the* Sagitta *species and of* Muggiaea atlantica *in Relation to Hydrological Conditions*

Before discussing the distribution of some of the zooplankton indicator species observed during the present investigation, it will be convenient to examine briefly the hydrological data obtained on the cruises of April 1937, 1938 and 1939, June 1939 and July 1938. Further details are given on pp. 109–117. In April 1937, 1938 and 1939 salinities were vertically homohaline generally. The disposition of the isohalines in April and July 1938 and in April and June (upper 25 m.) 1939 is in general agreement with the conception of an anti-clockwise or cyclonic circulation of the waters in the eastern part of the Celtic Sea, as described by Matthews (1914), Harvey (1925, 1929, 1930), Lumby (1925) and others. Medium salinity water (35·3–35·4 ‰), probably derived from the salt water (> 35·5 ‰) lying on the edge of the Continental Shelf to the west of the Brest Peninsula, extended northwards across the mouth of the English Channel and continued through the Land's End–Scilly Channel. Travelling along the north Cornish coast, it was turned west by the course of the circulation in the region of the Bristol Channel, then south-west and finally south, having now become considerably diluted and indistinguishable in salinity from the low salinity tongue (< 35·2 ‰) forming the outer western south-flowing component of the circulation. In April 1937 conditions were rather different from the above. Very low salinity water (< 35·1 ‰) extended from Ushant to the southern tip of the Cornish Peninsula, blocking the Channel mouth and separating medium salinity water (> 35·3 ‰) in the neighbourhood of Plymouth from water of similar salt content to the west of the Channel mouth.

Attention has been drawn to the bearing of this circulation on the biology of the south-western area and its importance as a distributing agent of plankton organisms by the work of Gough (1905), Russell (1935*b*, 1936*a*, *c*, 1939*b*), Mare (1940), Corbin & Panikkar (1942).

The distribution on the 1937–9 cruises of *Sagitta elegans*, *S. setosa*, *S. serratodentata* and *S. lyra*, and of the siphonophore *Muggiaea atlantica* is described on pp. 97–109. Russell (1935*b*, 1936*a*, *c*, 1939*b*) has shown the value of plankton organisms, particularly *Sagitta elegans*, *S. setosa* and *S. serratodentata*, as indicators of water movements in the Celtic Sea. He found that *S. setosa* is associated with Channel water, *S. elegans* with mixed oceanic and coastal water in the area of the cyclonic swirl, and that *S. serratodentata*, a purely oceanic species, occurs in typical *elegans* water in years of strong Atlantic in-flow into the Channel. Water also enters the Channel mouth from the south-west. It may be warm and of purely oceanic origin with a characteristic macroplankton indicator community, which does not, however, carry any *Sagitta* species (Russell, 1935*b*, 1939*b*), or it may be low salinity water entering close round Ushant (Poole & Atkins, 1929). The 1937–9 records clearly show the predominance of *S. elegans* in the central area of the Celtic Sea. Equally evident is the predominance of *S. serratodentata* in the outer area along the edge of the Continental Shelf, and of *S. setosa* in a small area off the mouth of the Bristol Channel and in parts of the English Channel mouth. *S. lyra* was nowhere the dominant species but its occurrence was noticeably limited to the edge of the Continental Shelf (Figs. 11, 12). These distributions are in agreement with Russell's findings. Of the distribution of *S. elegans* in the Celtic Sea, he remarks: 'We do not know how much further this area extends to the south. It may perhaps stretch right across the mouth of the Channel, or it may be reasonably expected that the area changes and lies in fact in the region of the cyclonic circulation known to exist at the mouth of the Channel south of Ireland.' He notes that only *S. serratodentata* occurred in the small area of the Bay of Biscay (centred on 47° 00′ N., 7° 40′ W.) which the *Research* Expedition investigated in 1904 (Russell, 1935*b*). No *S. elegans* were taken beyond the 100 fm. line at the southernmost stations of the *Quentin Roosevelt* cruise of April 1938; *S. serratodentata* only were present (Furnestin, 1939*a*). The distribution of *S. elegans* to the westward in April 1938 and March and April 1939 also indicates that the species does not extend far beyond the western edge of the Continental Shelf. These records show that the distribution of *S. elegans* to the south-west of the British Isles is confined to the Continental Shelf area of mixed oceanic and coastal water (see Russell, 1939*b*, fig. 5, p. 182). It is of interest to compare the above records with the findings of Redfield & Beale (1940) and Clarke, Pierce & Bumpus (1943) in the western Atlantic area of the Gulf of Maine and Georges Bank. In the shallow water (under 100 m.) over Georges Bank there is an anticyclonic eddy carrying a permanent population of *S. elegans* in which no other *Sagitta* species are endemic, although *S. serratodentata*, *S. lyra*, *S. enflata*, *S. maxima* and *Eukrohnia hamata* have been recorded in the area as immigrants from the deeper waters of the Gulf of Maine to the north and the Atlantic to the east. Clarke *et al.* (1943) state: 'The area of relatively homogeneous water overlying the central portion of Georges Bank was found to change in extent from cruise to cruise, but to be sharply delineated from the surrounding stratified water masses, and has been designated as the "Mixed Area".' They also observe that '*S. serratodentata* and *S. enflata*, which were taken chiefly in the September cruise, occurred entirely outside the margin of the Mixed Area.' In the detailed account of the distribution of the *Sagitta* species observed during the present investigation, it is noted that *S. elegans* was most numerous in the southern half of the English Channel mouth and to the west of the Brest Peninsula, particularly in April of each year and to a less marked degree in May–June of 1938 and 1939. In July 1937 and 1938, it was scarce generally. Indications of another area of abundance to the south of Ireland in April 1938 and 1939 rest almost entirely on the evidence from night hauls and cannot therefore be regarded as conclusive, more especially in view of the fact that a small area immediately to the south was devoid of *Sagitta* of any species. The water in the area of the Channel mouth was particularly rich in phosphates in April 1938 (Hickling, 1938) and had a high density of phytoplankton in April 1939 (Mare, 1940). Without further data, it would, however, be premature to correlate the abundance of *S. elegans* with these conditions since the species was not outstandingly numerous at the westernmost stations and in the region off the Bristol Channel mouth where rich phosphate values (April 1938) and dense phytoplankton (April 1939) also occurred.

Gough (1905) gives a comprehensive account of the distribution of *Muggiaea atlantica* over the south-western area in 1904. From the region of Ushant, it spread progressively into the English Channel, the Bristol Channel area, the southern part of the Irish Sea and along the south coast of Ireland. He emphasizes the need for care in drawing conclusions as to water movements from the distribution of an epiplanktonic organism which may be subject to the effects of wind drift in the surface waters and which is capable of rapid asexual reproduction. The hydrological data, however, led Matthews (1909) to agree with his statement that the migrations of *M. atlantica* afforded 'evidence as to the direction of currents during that year'. Russell (1935*b*) also stresses the requirement of caution before including *M. atlantica* in his list of indicators of 'south-western' water. In discussing the occurrence of indicator species at Plymouth in the years 1930–4, he writes: '...it is noticeable that the "south-western" water indicators seem usually to follow the disappearance of "western" water. It appears almost as though we might have here a seasonal phenomenon rather than an indication of water movement, the warm water species increasing when the water is sufficiently warmed.' Evidence from the occurrence of other plankton animals and from hydrological observations is, however, contrary to this interpretation, and he continues: 'There is thus an indication from the plankton observations of a pulse of "western" water entering the Channel, with its maximum about May. This pulse retracts as the pulse of Atlantic water entering the North Sea from the north increases; and this is followed by a pulse of "south-western" water into the Channel.'

In April 1937, *Muggiaea atlantica* was plentiful in the vicinity of Ushant and its distribution extended northwards to the Scilly Isles and westwards from Ushant. It was absent from stations closest to the south coast of Devon and Cornwall (Fig. 13A). Its numbers decreased progessively northwards and westwards from Ushant, pointing to a centre of distribution in that region. It has previously been remarked that a tongue of low salinity water occupied the Channel mouth in April 1937. Comparison of the spread of this fresh water and the distribution of *M. atlantica* leaves little doubt that it carried the *M. atlantica* with it. A single specimen of *M. kochi*[1] was found about 20 miles north of Ushant (St. 5). In this connexion, it should be noted that Russell (1938*b*) records the occurrence in the first half of 1937 of several planktonic species unusual to the Plymouth area. In May and July 1937, no stations were worked in the Ushant area, but *M. atlantica* was present in the northern half of the Channel mouth (including stations nearest the coast), and in the Land's End–Scilly area (Figs. 13B, C). It was considerably more numerous than in April. But this fact and the abundance of the species at Plymouth in the late

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[1] I am indebted to Mr F. S. Russell for confirming the identification of this specimen.

summer and autumn (Russell, 1938*b*) cannot, in view of Russell's and Gough's cautionary remarks, be taken as evidence of continued transport from the Ushant area. The April invasion of the Channel mouth, however, appears to have been definitely associated with the low salinity inflow from Ushant.

In April 1938, *M. atlantica* was absent from the southern half of the Channel mouth and the region of Ushant. It only occurred in the coastal waters around the Cornish Peninsula (Fig. 13D). Low salinity water was present in the Ushant area close to the west coast of the Brest Peninsula and round the north-west coast. It was narrowly confined to the coastal region by a warm salt tongue lying farther off the coast. This penetrated from the south-west towards the southern half of the Channel mouth and, judging from the indications of water mixing in the mouth of the Channel, contributed considerably to the higher salinities there. In May–June 1938, all stations were well to the west of Ushant (about 100 miles) and the Channel mouth. *M. atlantica* was present from north of Scilly to the southermost station—some 110 miles west by north of Ushant (Fig. 13E). In July 1938, the distribution of *M. atlantica* was similar to that of April. It was confined to the coastal waters close to the Cornish Peninsula (Fig. 13F). It is probable that this distribution continued for the greater part of the year since it occurred at Plymouth in every month of the year although in rather low numbers (Russell, 1939*a*).

In April 1939, *M. atlantica* occurred in the southern half of the mouth of the Channel. It extended northwards from Ushant to about half-way across the Channel towards Scilly, and eastwards for some little distance along the north coast of the Brest Peninsula (Fig. 13G). The numbers taken were small, but their disposition with a maximum at the Ushant station, indicated both the origin and direction of spread of the species. Salinity conditions in the area were similar to those of April 1937. Low salinity water which was fairly warm in the deeper layers, flowed northwards close to the French coast past Ushant. It spread about half-way across the mouth of the Channel and also along the north coast of the Brest Peninsula. To the west and closely hemming it in to the Ushant coast, was a tongue of slightly more saline water. This extended northwards across the Channel mouth to Scilly and was evidently derived from the salt water beyond the edge of the Continental Shelf. As in April 1937 there seems to be a close correlation between the distribution of *M. atlantica* and the low salinity inflow round the Brest Peninsula. In May–June 1939, *M. atlantica* occurred well out to the south-west in more saline water than in April. It was not found in the northern half of the mouth of the Channel. No stations were worked near the Brest Peninsula. The invasion foreshadowed in April did not take place and it was 'remarkably scarce' at Plymouth that year (Russell, 1940).

The distribution of *M. atlantica* in 1937–9 throws some light on its value as an indicator species and also on the problem of the origins of the water in the western Channel mouth. In particular, the April records together with the hydrological conditions and the yearly observations at Plymouth on other planktonic species appear to relate to the incursion of 'south-western' water, which itself may be derived from water masses from more than one source (Russell, 1939*b*).

In April 1937, an invasion of *M. atlantica* into the Channel mouth was associated with a strong inflow of low salinity water from Ushant. The oceanic *Sagitta serratodentata* was also more extensively distributed in the area than in April of the other two years, although no strongly saline conditions with which it is usually associated were found in the region of the Channel mouth or to the westward. In the first half of the year at Plymouth, several infrequently recorded planktonic organisms were taken (*Discomedusa lobata*, *Pelagia noctiluca*) and also one species new to the area (*Rhincalanus nasutus*) (Russell, 1938*b*).

In April 1938, *Muggiaea atlantica* occurred in the northern half of the Channel mouth only where apparently it had remained 'resident' since the previous autumn when it was numerous (Russell, 1939*a*). Low salinity water lay to the south of Ushant but did not enter the Channel. It was closely confined to the west coast of the Brest Peninsula by an inflow of saline water from the south-west. This spread eastwards into the Channel mouth restraining any northward flow of the fresh water.

In the region of the saline incursion, there was a break in the distribution of *Sagitta serratodentata*, separating a small community of the species round the north-west coast of the Brest Peninsula from the main population farther to the west along the edge of the Continental Shelf. No unusual planktonic species occurred at Plymouth in the first half of the year (Russell, 1939*a*).

In April 1939, fresh water from the Ushant area spread half-way across the Channel mouth carrying with it small numbers of *Muggiaea atlantica*. To the west of this was a more saline intrusion northwards across the mouth of the Channel, similar to that of April 1938. It did not, however, spread so far eastwards into the Channel and was less saline. In the region of its entry from the south it again appeared to split the distribution of *Sagitta serratodentata*. No unusual planktonic species were recorded at Plymouth and *Muggiaea atlantica* was remarkably scarce throughout the year (Russell, 1940).

These records present something of a paradox. There is little doubt that the low salinity inflow of April 1937 carried with it both the *M. atlantica* and certain plankton species not usually taken at Plymouth. These, including *M. atlantica*, are generally considered to be 'oceanic' (Russell, 1938*a*) and would be expected to occur in saline conditions, and not in the low salinities recorded. But in 1938 and 1939, when the April incursion of saline water into the Channel mouth from the south-west was considerable, there was a lack of 'oceanic' species. Their appearance in early 1937, when the area was filled with water of particularly low salinity, suggests that the fresh water on its way to the Channel mouth, had flowed alongside a body of 'oceanic' water containing the *M. atlantica* and the unusual species, and had gathered them into itself in sufficient quantity to transport them across the Channel.

*M. atlantica* thus transported, was able successfully to maintain a breeding population in an alien locality for a period of at least twelve months (April 1937–8), probably longer, without recruitment or re-seeding from its original stock, and in a considerable salinity range. Without previous records therefore, its presence is unlikely to be of great value in determining the history or origin of the water in which it occurs.

The lack of 'oceanic' species in the saline incursions of April 1938 and 1939, when hydrological conditions would seem to have favoured their occurrence, may be compared with the general lack of plankton in the 'Biscay water' observed off Ushant by Russell in July 1935 (Russell, 1936*a*).

Attempt at more detailed identification of the above records of planktonic species with specific water masses would be little more than groundless speculation. The need, however, for a further extensive series of data in the Channel mouth and to the south—over the edge of the Continental Shelf—is only too apparent. Until this can be achieved, the present records continue to emphasize the acknowledged complexity of the water movements in the Channel mouth and the varied origins of the water masses entering the area.

## RESULTS OF THE CRUISES

### *The Distribution of Mackerel Eggs*

### 1937

12–20 *April* (Fig. 4A).

Spawning was intense in the west and south-west of the area of the cruise. With the exception of Sts. 2 and 22 where less than 100 mackerel eggs per haul were taken, none occurred in the eastern half—in the region of the Channel mouth and to the north of Scilly. The greatest density of eggs was present along the southern line of stations (Sts. 9–15), and their numbers decreased from south-west to north-east of the area. The maximum haul of 32,300 eggs was taken at the westernmost station (St. 14). In the south-west, where spawning was generally intense, there was a concentration (over 18,000 eggs per haul) in the neighbourhood of 49° 30′ N., 8° 40′ W. (Sts. 13–15) and an indication of a second lesser concentration (over 8000 eggs per haul) at 48° 50′ N., 6° 30′ W., some 60 miles east south-east of this and about 60 miles south south-west of Scilly (Sts. 9 and 10).

27–30 *May*[1] (Fig. 4B).

Mackerel eggs were taken at all stations on the cruise, indicating that spawning activity had extended farther to the north-east towards Land's End since April. But a decrease in the intensity of spawning was evident from the fact that the largest haul contained only 8875 eggs (St. 8) compared with 32,300 in April.[2] It was also shown by the smaller numbers of eggs farthest to the south-west (Sts. 5, 6 and 7). The gradation from large numbers of eggs at the westerly stations to few eggs at the easterly stations was again noticeable.

20–26 *July* (Fig. 4C).

The numbers and distribution of mackerel eggs in July revealed that the main spawning to the westward of the Channel mouth had completely finished. No eggs were taken to the west of the Scilly Islands (Sts. 3–13) and only very diminished spawning activity continued inside the Channel mouth. The maximum haul, containing only 135 eggs, was made at the easternmost station off Plymouth (St. 18), and catches at other stations were very considerably less than this.

## 1938

6–18 *April*[3] (Fig. 5A).

Mackerel eggs were present over nearly the whole area of the Celtic Sea. They were absent from the extreme marginal regions of the area: from the two westernmost Stations (Sts. 18A and SR 89), from the north-eastern area off the Bristol Channel and the St George's Channel (Sts. SR 72, 41 and 43–47), from the northern half of the mouth of the English Channel (Sts. 1, 2, 52–56 and 62), from the area of Ushant and the west coast of the Brest Peninsula (Sts. 5, 6, 58, F 101–F 104, F 118 and F 119), and from the southernmost region (Sts. F 107–F 111). Two centres of very intense spawning activity were evident. The larger outer centre was situated to the south of Ireland between 9 and 10° W. and covered a considerable area from 49° 20′ N. to 50° 10′ N. (Sts. 16, 21, 22, SR 82, SR 85 and SR 86). The smaller inner one was centred on 49° 05′ N., 7° 15′ W., some 60 miles south-south-west of the Scilly Isles (Sts. 10–12). In the outer centre, the maximum haul contained the very large number of 99,333 mackerel eggs (St. SR 86) and catches at other stations in the area ranged from over 6000 to over 19,000. In the inner centre hauls contained between 5000 and 20,000 eggs. The two centres of spawning

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[1] On this cruise, plankton was collected by oblique hauls (usual method of working) with a 1 m. stramin net. It has been estimated that the fishing capacity of the 1 m. stramin net is $\frac{1}{4}\times$ that of the 2 m. stramin ring-trawl. Actual numbers of fish eggs, etc. taken on this cruise have therefore been multiplied by four so that comparisons with the results of other cruises may be of the same order.

[2] Station 8 (May 1937) was about 10 miles east of Stations 13 and 15 (April 1937) where 18,570 and 20,500 mackerel eggs were taken.

[3] See also Farran (1939) and Furnestin (1939*a*). A single mackerel egg was taken on 29 March 1938, to the south of Ireland (Furnestin, 1939*a*; St. 12; 50° 22′ N., 9° 55′ W.).

activity were noticeably localized and the density of mackerel eggs outside them was seldom greater than 400 per haul, except at stations immediately between them (Sts. 13–15, 23 and SR 78) where larger hauls of 1000–3090 eggs occurred. At Station 48, off the mouth of the Bristol Channel, 2020 mackerel eggs were taken.

31 *May–5 June* (Fig. 6A).

Mackerel eggs were absent from the westernmost area (Sts. 18–22), but were taken at all other stations on the cruise. Two dense concentrations of eggs were present. The smaller of these lay to the west and north of the Scilly Isles (Sts. 12 and 30; 18,280 and 6075 eggs). The larger was situated to the south of Scilly, outside the mouth of the English Channel (Sts. 3–6; 5320–31,110 eggs). To the west of the two concentrations and between them, mackerel eggs were considerably less numerous. The southern spawning centre of this cruise can be identified with the inner centre of April. The density of eggs was of the same order although slightly larger catches showed an increase of spawning activity since April. Moreover it was situated in the same latitude, having shifted only slightly eastwards from the April position, so that the western station overlapped the position of the eastern station of the April concentration. Mackerel eggs were few or did not occur at all in the area occupied by the large outer spawning centre of April.

19–24 *July* (Fig. 7A).

Spawning was very diminished in intensity compared with that of April and May–June, and no longer occurred in the Celtic Sea to the westward of Scilly. Eggs were present inside the mouth of the Channel as far west as Scilly, and slightly beyond this—to 7° W.—in the area to the north of Scilly. They were absent from the westernmost stations (Sts. 9–12, 21 and 22) and the northernmost station off the Bristol Channel mouth (St. 15). The spawning area had shifted nearly 200 miles eastwards since May–June; the western limit which was then between 9 and 10° W., now lay between 6 and 7° W. The maximum haul of 1600 eggs was taken at the easternmost station (St. 3) and catches were smallest at the westerly stations.

### 1939

15–18 *March* (Fig. 8).

Small numbers of mackerel eggs occurred in a restricted area at the western edge of the Continental Shelf, about 70 miles south-south-west of Ireland (Sts. 5–8, 16 and 17). The maximum haul contained 118 eggs (St. 8). The area of distribution lay between 10 and 12° W. and did not extend farther north than 51° N. The southern limit was not determined.

16–27 *April* (Fig. 9A).

Spawning had greatly increased both in intensity and extent since the third week in March. Mackerel eggs were distributed throughout the area of the cruises, except in the northern half of the mouth of the English Channel (Sts. 1, 2, 33, 37, 56–58, 61 and 62), at the mouth of the Bristol Channel (Sts. 46 and 47), and at single stations close to Ushant (St. 4), off the southern Irish coast (St. SR 13) and in the central area (St. SR 17). As in April 1938, there were two centres of intense spawning activity to the west and south. The outer centre was situated to the south of Ireland between 9 and 11° W. and extended southwards from 51° 00′ N. to the edge of the Continental Shelf (Sts. 17–19, 22–26 and SR 26–SR 29). The largest hauls, containing between 5950 and 45,025 mackerel eggs, were taken in this centre. In the smaller inner centre, lying some 90–100 miles west of the Brest Peninsula and centred at about 48° 30′ N., 8° 00′ W. (Sts. 9, 11 and 12), spawning was less intense and catches did not exceed 10,000 eggs per haul. The southern boundaries of the two centres were not determined, but it seems probable that they were continuous as one area along the southern edge of the Continental Shelf. Outside the centres, hauls usually contained fewer than 500 eggs. At Station 49, off the mouth of the Bristol Channel, 1250 eggs were taken. It has already been mentioned that a similarly isolated large haul of mackerel eggs (2020) occurred in this area in April 1938.[1]

2–7 *June* (Fig. 10A).

Mackerel eggs were taken at all stations on the cruise and were concentrated in two centres. The northern centre in which the lesser intensity of spawning occurred (maximum haul, 12,075 eggs; St. 22) lay between the south-east coast of Ireland and the north coast of Cornwall (Sts. 13 and 21–26). The southern centre in which spawning was more intense (maximum haul, 28,500 eggs; St. 3) was situated immediately outside the Channel mouth (Sts. 3, 4, 17, 19 and 28). To the westward of the centres, in the region of the outer April centre, few eggs were present. Comparison of the positions of the two centres with those of April shows the extent of the north-eastward movement of spawning. In the northern centre which was almost certainly a continuation of the outer centre of April, a considerable diminution in spawning intensity had taken place. While the southern centre, which from its position was clearly identifiable with the inner April centre, showed, as in 1938, an increase in intensity of spawning since April.

### *The Distribution of Mackerel Young Stages*

### 1937

12–30 *April* (Fig. 4A).

It was originally stated that no mackerel young stages were taken in April 1937 (Steven & Corbin, 1939). This record requires correction since the identification of eleven young fish, which in the earlier examination could not be determined with certainty, has now been established. A careful comparison

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[1] St. 48, April 1938, 50° 55′ N., 5° 50′ W.; St. 49, April 1939, 50° 48′ N., 5° 53′ W.

of the specimens with the abundant material of later cruises leaves no doubt that they are young mackerel. Ten specimens were taken to the westward of the area of the cruise (Sts. 15 and 29) and a single specimen was taken to the south of the Lizard (St. 35). Elsewhere on the cruise no mackerel young stages were taken.

27–30 *May*[1] (Fig. 4B).

Considerable numbers of young stages were caught on this cruise and the main area of their distribution lay to the south-west (Sts. 4–11) where mackerel eggs were generally most numerous. Small numbers were also taken between Land's End and Scilly (Sts. 1 and 15). The largest haul, containing 568 specimens, was recorded to the westward (St. 8, day haul) where the greatest number of eggs was taken.

20–22 *July* (Fig. 4C).

Young stages were very much less numerous than in May and were absent from the westernmost area (Sts. 6–10) where previously they had been numerous. They occurred at the easterly stations where spawning still continued, as well as at a number of stations farther west where no mackerel eggs were recorded. The largest catch (20 specimens, St. 16, day haul) was taken to the south of the Lizard, in the eastern part of the area of distribution of the young stages.

### 1938

6–18 *April*[2] (Fig. 5A).

The distribution of mackerel young stages was confined to the extreme western and south-western margins of the area, towards the edge of the Continental Shelf and beyond the two main spawning centres (Sts. 16–20, SR 86, SR 88, SR 89, SR 91, SR 92, F 107 and F 109–F 114). They were absent from the central, northern and eastern areas, on the landward side of the spawning centres. The majority of hauls contained fewer than 20 specimens, although 69 were taken in one night haul (St. 17).

31 May–5 *June* (Fig. 6A).

In comparison with the numbers taken in April, mackerel young stages were exceedingly numerous. They were present throughout the area of the cruise except off Land's End (St. 1). Their distribution had shifted very considerably north-east since April and they now occurred in the central area of the Celtic Sea where previously they were not recorded. They reached maximal abundance (over 500 per haul) in a broad belt extending across the area of the cruise from north-west to south-east (Sts. 4, 9, 10, 16 and 24–26), in the centre of which the very large number of 8239 specimens was recorded in a daylight haul (St. 25). Station 4 was the only night haul in the area of maximal

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[1] See note 1, p. 91.

[2] See also Farran (1939) and Furnestin (1939*a*).

abundance. To the west and south, and more markedly to the north-east of this area, their numbers progressively decreased. It has been noted that in April the young stages occurred beyond the centres of spawning. This was also evident in May–June.

19–24 *July* (Fig. 7A).

Young stages were present in very small numbers (maximum, 6). They occurred at all stations except the two westernmost (Sts. 10 and 11) and three stations in the middle of the Channel mouth (Sts. 5, 6 and 8). As in July 1937, their distribution extended farther west than that of the eggs and it had shifted very considerably eastwards and slightly northwards since May–June. The western boundary on this cruise lay along about 7° 20′ W., while on the May–June cruise it was to the west of 10° W.

### 1939

15–18 *March.*

No mackerel young stages were taken on this cruise.

16–27 *April* (Fig. 9A).

The distribution of mackerel young stages was similar to that of April 1938. They were taken at the westerly and southerly stations, mainly beyond the spawning centres, although this tendency was not so marked as in April 1938. They were also slightly more numerous than in April 1938 (maximum 174, St. 22, day haul). The 1939 cruise was about a week later than in 1938, and in consequence the records probably represent a later stage in the distribution of the young mackerel, when more had hatched into the plankton and their spread north-eastwards from the edge of the Continental Shelf was more extended. Single specimens were taken off Ushant (St. 3) and off the mouth of the English Channel (St. 31), and three occurred near the mouth of the Bristol Channel (Sts. 47 and 48), close to the isolated concentration of eggs (St. 49).

2–7 *June* (Fig. 10A).

Young stages were present throughout the area except near the Lizard (St. 1). They were more numerous than in April and were most abundant (maximum 634, St. 7, day haul) in an area lying to the westward of the spawning centres and extending from the south-west of Ireland towards the Brest Peninsula (cf. May–June 1938). Their numbers progressively decreased to the north and east of the area of maximal abundance, and small catches at some of the westernmost stations (Sts. 6, 8, 11 and 12), showed that beyond it they were also becoming fewer. Off the mouth of the Bristol Channel (St. 26, day haul) 59 specimens were taken, close to the position of the small concentration of eggs which occurred there in April.

### *The Distribution of Pilchard Eggs*

### 1937

12–20 *April* (Fig. 4D).

Spawning occurred in the northern half of the Channel mouth and extended to the west and south-west of Scilly as far as 8° W. The centre of spawning was situated inside the mouth of the Channel, off the south coast of Devon and Cornwall (Sts. 1, 2 and 35; over 10,000 eggs per haul). No eggs were taken in the southern half of the mouth of the Channel (Sts. 3–8, 10, 21 and 22), at the westernmost stations (Sts. 13–16 and 18) and to the north-west of Scilly (Sts. 27–32).

27–30 *May*[1] (Fig. 4E).

Pilchard eggs were taken in the Land's End–Scilly region (Sts. 1–3, 14 and 15); they were absent from the western area (Sts. 4–13). Catches were small (maximum 2800, St. 1) but of the same order of size as those of April from this area. No stations were worked inside the mouth of the Channel where the April concentration was situated.

2–22 *July* (Fig. 4F).

No pilchard eggs were found to the west of Scilly (cf. May 1937) and the spawning area was identical with that of the mackerel (Sts. 1, 2 and 14–18). The largest hauls were taken to the eastward, in the region of the April spawning centre (maximum 10,000 eggs, St. 17).

### 1938

6–18 *April*[2] (Fig. 5B).

Pilchard eggs were present in a broad area extending from the north coast of Cornwall south-westwards across the entrance to the Channel. The centre of spawning was situated, as in April 1937, in the northern half of the Channel mouth (Sts. 2, 3, 29 and 30), where hauls containing from 7680 to 24,120 were taken. No eggs were present in the western and northern parts of the Celtic Sea nor in the southern half of the mouth of the Channel and off the Brest Peninsula.

31 *May*–5 *June* (Fig. 6B).

The distribution of pilchard eggs on this cruise was similar to that of April, extending from north of the Scilly Isles southwards across the mouth of the Channel (Sts. 2–6, 12 and 30). Only the western limit of distribution was determined, since no stations were worked inside the mouth of the English Channel. They were absent off Land's End (St. 1) and from the western area

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[1] See note 1, p. 91.

[2] See also Furnestin (1939*a*). A single pilchard egg was taken on 24 March 1938, to the south of Ireland (Furnestin, 1939*a*; St. 9; 50° 42′ N., 10° 00′ W.).

beyond about 7° 30′ W. The largest hauls were made to the west of Scilly (St. 12; 20,600 eggs) and about 70 miles farther south outside the Channel mouth (St. 5; 25,320 eggs).

19–24 *July* (Fig. 7B).

Pilchard eggs were numerous at the easterly stations. They were absent or scarce to the west of Scilly and towards the southern half of the mouth of the Channel. The main concentrations were situated similarly to those of May–June, off the north coast of Cornwall (Sts. 16 and 17; 950 and 38,600 eggs) and inside the Channel mouth in the northern half (Sts. 1, 2 and 23–26; 2100–22,450 eggs).

### 1939

15–18 *March*.

No pilchard eggs were taken on this cruise.

16–27 *April* (Fig. 9B).

Pilchard eggs occurred at all stations in the Channel mouth and to the westward as far as 9° W. This was considerably farther west than on previous cruises. They were absent from a small area immediately to the north of Ushant, from the westernmost stations and also the area to the north of the Scilly Isles, except for the occurrence of 27 eggs off the south-east coast of Ireland (St. 42, 1 egg; St. SR 23, 26 eggs). Three spawning centres were present. The largest of these occurred inside the middle of the Channel mouth (Sts. 2, 57, 58 and 61; 13,100–39,075 eggs). The two smaller centres lay farther to the west. One was situated immediately outside the middle of the Channel mouth (Sts. 37 and 55; 23,500 and 92,925 eggs); the other occurred farther to the south, about 90–100 miles west of Ushant (Sts. 10 and 11; 14,500 and 22,975 eggs) in an area immediately adjoining the smaller inner concentration of mackerel eggs.

2–7 *June* (Fig. 10B).

Pilchard eggs were found in the easternmost area of the cruise, near Scilly and the tip of the Cornish Peninsula (Sts. 1–3, 19, 20, 27 and 28); elsewhere to the west and north none was taken. No stations were worked inside the mouth of the Channel. They were very numerous to the south of Land's End and the Lizard, and the exceptionally large haul of 121,950 eggs was taken in this area (St. 1).

## *The Distribution of* Sagitta elegans *Verrill*

### 1937

12–20 *April* (Fig. 11A).

No *Sagitta* spp. were taken at Stations 1, 25 and 30. *S. elegans* was taken at all other stations and was the dominant species over the whole area with the exception of the two westernmost stations (Sts. 13 and 14) where *S. serratodentata* was more numerous. The numbers per haul show very considerable variation due to diurnal vertical migration, but a general tendency for the species to be less abundant towards the west is noticeable. The largest haul was taken about 20 miles west of Ushant (4610 specimens, St. 7, day haul).

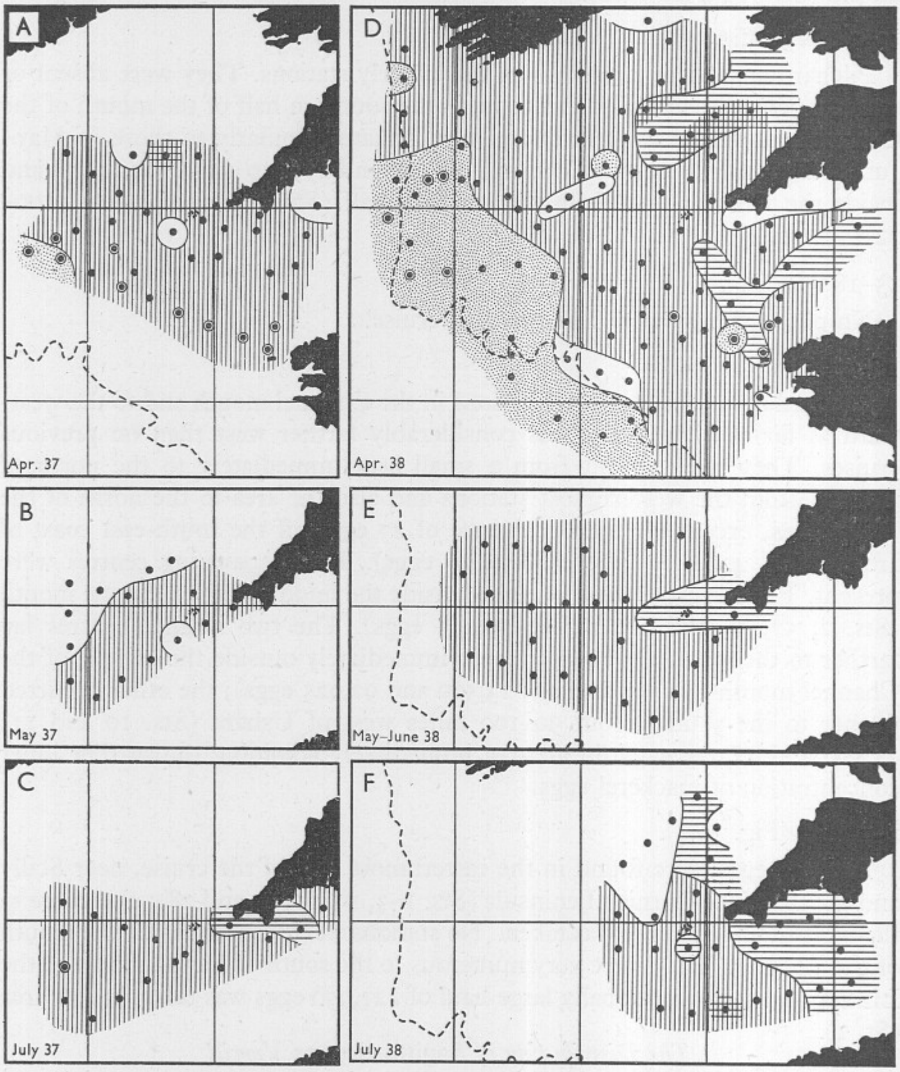

Fig. 11. Areas of dominance of *Sagitta elegans* ||||, *S. setosa* ≡ and *S. serratodentata* ▨ in the Celtic Sea in 1937 (A, B and C) and 1938 (D, E and F). ⊙ *S. lyra* present.

27–30 *May*[1] (Fig. 11B).

No *Sagitta* spp. were taken at Stations 3, 8–11, 13 and 14. *S. elegans* was recorded at all other stations and was the dominant species throughout the

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[1] See note 1, p. 91.

area, although very much less numerous than in April (maximum 300, St. 5, night haul).

20–22 *July* (Fig. 11 C).

The species was taken at all stations on the cruise and was dominant in the whole area with the exception of two separate stations, off Land's End and east of the Lizard, where *S. setosa* predominated (Sts. 1 and 17). Numbers had increased very considerably since May, but were not so great as in April (maxima, 1560 (day) and 2800 (night); Sts. 8 and 13).

### 1938

7–18 *April*[1] (Fig. 11 D).

No *Sagitta* spp. were taken at Stations 1, 24, 25, 42, 54, SR 78, F 101, F 113–F 115. *S. elegans* was distributed over almost the whole area of the Celtic Sea; it was absent from certain marginal areas (St. 42 in the north; Sts. 18 A, 19 and SR 89 in the west; Sts. 16, F 106–F 110 and F 113–F 115 in the south; Sts. 1, 29, 54 and 59 in the northern half of the Channel mouth) and from one station (St. 36) adjoining the central patch in which no *Sagitta* spp. occurred (Sts. 24, 25 and SR 78). The majority of the large catches of *S. elegans* were taken at night stations (see Table VI), and for this reason the greatest reserve is required in pointing out any particular concentration within the distribution of the species. It seems probable, however, that an area of abundance was present in the vicinity of Ushant (Sts. 4 and 5 (night), 2950 and 3270 specimens; Sts. 6 and 7 (day), 287 and 900 specimens) where both day and night hauls were noticeably larger than those of the surrounding stations. Several large catches were made to the south of Ireland (Sts. 21, 22, 39, SR 73–SR 75 and SR 81–SR 83; 600–5200 specimens) but all occurred at night stations and cannot therefore be considered as representing a true concentration of the species. A large daylight haul was also taken about 30 miles south-west of Valencia (St. SR 93; 1405 specimens). *S. elegans* was the dominant species in the central area of the Celtic Sea from southern Ireland to the approach to Ushant. At the western and south-western stations it was outnumbered by *S. serratodentata*, and in the areas off the entrance to the Bristol and English Channels *S. setosa* was the predominant species.

31 *May*–5 *June* (Fig. 11 E).

*S. elegans* was taken at all stations. It was the dominant species throughout the area of the cruise except in the region off Land's End past Scilly in which *S. setosa* predominated (Sts. 1 and 11). In the area west of the Channel mouth, very large catches were taken in day and night hauls (Sts. 2, 7, 8, 10, 11, 24 and 25 (day), 600–5820 specimens; Sts. 3 and 4 (night), 7040 and 29,340 specimens). At the westernmost and northernmost stations numbers were generally lower.

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[1] See also Furnestin (1939*a*).

19–24 *July* (Fig. 11 F).

No *Sagitta* spp. were taken at Stations 12, 14 and 16. The area of distribution of *S. elegans* lay to the west of the Channel mouth and extended slightly to the north of the Scilly Isles. A single specimen was taken at the northernmost station (St. 15) and four occurred off Plymouth (Sts. 1 and 26). The species was very much less numerous than in April and in May–June (maxima: St. 9 (day), 500 specimens; St. 21 (night), 1000 specimens).

## 1939

15–18 *March* (Fig. 12 A).

The species occurred at all stations except the two westernmost (Sts. 8 and 9) and was present in considerable numbers (maxima: St. 1 (day) 700 specimens; St. 20 (dusk) 2850 specimens). It was the dominant species from the area of Scilly westwards to about 10° W. Farther west, *S. serratodentata* was the most numerous species.

16–27 *April* (Fig. 12 B).

No *Sagitta* spp. were taken at Stations 26, 28, 37, 39, 43, 48, 49, SR 13, SR 20, and SR 28. With the exception of the above stations and also Stations 22, SR 21, SR 23 and SR 30, *S. elegans* was distributed over the whole of the Celtic Sea and was taken in particular abundance at the southern half of the mouth of the English Channel in both day and night hauls (Sts. 2–8 and 36; maxima, 6240 (day) and 11,440 (night)). Large catches were also taken in the area to the south of Ireland and west-north-west of Scilly and, although the majority occurred at night stations, two daylight hauls in the area contained considerably greater numbers than at surrounding stations (Sts. 31, 40, 41, 52 and SR 15–SR 19; maxima, 905 (day) and 10,875 (night)). A central patch in which no *Sagitta* spp. occurred (Sts. 26, 28, SR 20 and SR 28) was situated a little to the west of the barren patch of April 1938. *S. elegans* was the dominant species throughout the greater part of the Celtic Sea, including the mouth of the Bristol Channel and the southern half of the mouth of the English Channel. In the northern half of the Channel mouth it was replaced as the dominant species by *S. setosa*, and by *S. serratodentata* in the western area and at some of the southern stations.

2–7 *June* (Fig. 12 C).

No *Sagitta* spp. were taken at Stations 14 and 17. With the exception of these and a single station close to Land's End (St. 28), *S. elegans* occurred throughout the area of the cruise. It was dominant over almost the whole area except at the westernmost station and the southernmost station where *S. serrato-*

*dentata* was more numerous (Sts. 6 and 12), and in the Land's End–Lizard area where *S. setosa* predominated (Sts. 1 and 28). It was most abundant in

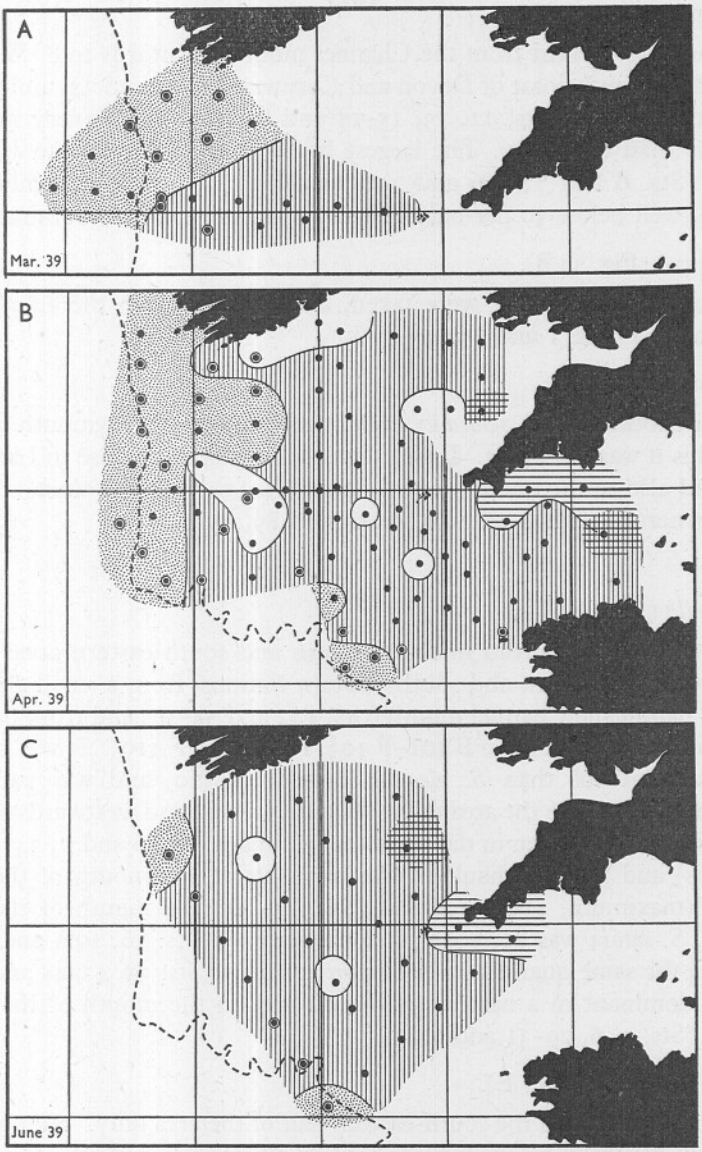

Fig. 12. Areas of dominance of *Sagitta elegans* |||, *S. setosa* ≡ and *S. serratodentata* ▒ in the Celtic Sea in 1939. ⊙ *S. lyra* present.

the area to the west of the Channel mouth (Sts. 3, 4, 5 and 19; 2100, 950 (day), 1125, 2175 (night)).

### *The distribution of* Sagitta setosa *J. Müller*

### 1937

12–20 *April* (Fig. 11 A).

*S. setosa* was present from the Channel mouth westwards to 8° W. It was absent off the south coast of Devon and Cornwall (Sts. 1 and 34) and from the area north of Scilly (Sts. 11, 13, 15–17 and 23–25). It was very much less numerous than *S. elegans*. The largest hauls were taken close to Ushant in daylight (Sts. 6 and 7; 166 and 130 specimens); elsewhere numbers were almost all well below 30 per haul. Nowhere was the species dominant.

27–31 *May*[1] (Fig. 11 B).

Twenty specimens only were taken, at two stations in the Land's End–Scilly Channel (Sts. 1 and 15).

20–22 *July* (Fig. 11 C).

The distribution of *S. setosa* extended westwards from Plymouth to Scilly; west of this it was not taken. It was the dominant species close to Land's End (St. 1) and also to the east of Lizard Head (St. 17). Catches were very much smaller generally than *S. elegans* (maximum 89, St. 1).

### 1938

6–18 *April*[2] (Fig. 11 D).

*S. setosa* was widespread in the northern and south-eastern areas. It was absent from the western and south-western stations, from a small area in the northern half of the Channel mouth (Sts. 1, 2 and 54–57) and from the region to the south of Ushant (Sts. F 101–F 103, F 118 and F 119). It was considerably less numerous than *S. elegans* (maximum 520) and was particularly scarce (maximum 8) in the area to the south of Ireland and westwards to 10° W. Large catches were taken in day hauls near Ushant (Sts. 6 and 7; 345 and 520 specimens) and in night hauls in the area outside the mouth of the Bristol Channel (maximum, 400 specimens, St. 47). Off the mouth of the Bristol Channel, *S. setosa* was dominant at some stations (Sts. 46, 50 A and 51) and present in the same quantity as *S. elegans* at others (Sts. 38, 47, 48 and 50). It was also dominant in a narrow ⊢ shaped area in the mouth of the English Channel (Sts. 3, 6, 29–31 and 62).

31 *May*–5 *June* (Fig. 11 E).

*S. setosa* occurred in the south-eastern half of the area only. Numbers were very small, generally below 100 per haul, at all stations, with the exception of a large haul of 2300 specimens taken to the west of Scilly in daylight (St. 11). It was the dominant species at this station and off Land's End (St. 1).

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[1] See note 1, p. 91.

[2] See also Farran (1939) and Furnestin (1939*a*).

19–24 *July* (Fig. 11 F).

The species was taken in small numbers (maxima: 46 (day), St. 20; 49 (night), St. 18) at the easterly stations, both north of the Cornish Peninsula and in the Channel mouth. It did not occur to the west of Scilly (Sts. 6–14 and 16). It was dominant off the mouth of the Bristol Channel (Sts. 15 and 17) and inside the mouth of the English Channel to the east (Sts. 1–4 and 24–26).

### 1939

15–18 *March* (Fig. 12 A).

One specimen of *S. setosa* was taken about 25 miles south-east of the Fastnet Lighthouse (St. 14).

16–27 *April* (Fig. 12 B).

The area of distribution was restricted to the Bristol Channel mouth and the mouth of the English Channel and did not extend westwards of 6° W., with the exception of three specimens taken immediately west of Scilly (Sts. 32 and 52) and a single specimen off the Channel mouth (St. 8). It was also absent from a small area inside the Channel mouth (Sts. 2, 58 and 59). It did not occur as far west as in April 1938 either outside the Channel mouth or to the south of Ireland. In comparison with the large catches of *S. elegans*, it was scarce (maxima: 38 (day), St. 3; 185 (night), St. 62). It was the dominant species in the northern part of the Channel mouth (Sts. 56, 57 and 62). It was not, however, dominant at the entrance to the Bristol Channel as in April 1938, although at one station in this region it occurred in numbers equal to those of *S. elegans* (St. 48; both species, five specimens). At one station immediately south-west of Scilly (St. 32) it also appeared to be dominant; this is, however, probably not significant as the total of *Sagitta* spp. taken was only three specimens—two *setosa* and one *elegans*.

2–7 *June* (Fig. 12 C).

The species was taken in small numbers (maximum, 300 (day), St. 3) in the eastern half of the cruise—to the west of the Bristol Channel mouth and the English Channel mouth as far as 8° W. Beyond this it did not occur. It was the dominant species close to Land's End and the Lizard although very few specimens occurred here (Sts. 1 and 28; 8 and 2 specimens).

## *The Distribution of* Sagitta serratodentata *Krohn*

### 1937

12–20 *April* (Fig. 11 A).

The area of distribution of the species was continuous from the southern half of the mouth of the English Channel, along the southern line of stations to the western stations both north and south of Scilly. It was absent from the northern half of the Channel mouth (Sts. 1, 2 and 34–36) and from an area extending south-westwards from Land's End to some 50–60 miles south-west of Scilly (Sts. 17, 19, 23–25, 32 and 33). These two areas were nearly cut off from one another in the vicinity of Land's End by a tongue of *S. serratodentata* (Sts. 20–22) which extended northwards between them across the Channel mouth to within 15 miles of Land's End. The species was dominant at the two westernmost stations (Sts. 13 and 14) and was slightly more numerous generally than *S. setosa* (maxima: 262 (day), St. 8; 285 (night), St. 26). Large catches were made at three day stations in the region of Ushant (Sts. 6–8; 233, 225 and 262 specimens).

27–30 *May*[1] (Fig. 11 B).

Very small numbers (maximum 8, St. 6 (night)) were taken in the south-western area only (Sts. 4–7).

20–22 *July* (Fig. 11 C).

Catches were also small on this cruise (maximum 58, St. 8 (day)) and the species occurred only to the west of the Scilly Isles (Sts. 3, 6–9 and 11–13).

### 1938

6–18 *April*[2] (Fig. 11 D).

*S. serratodentata* was widely distributed over the western area of the Celtic Sea from the edge of the Continental Shelf eastwards to about 7° W. It also occurred in the southern half of the mouth of the English Channel and off the Brest Peninsula. It was not taken outside the Bristol Channel (excepting three specimens at St. 47) and the entrance to the St George's Channel, nor in the northern half of the mouth of the English Channel and outside to the south of the Scilly Isles. In the south-eastern area it was absent from several stations (Sts. 8, 9, F 1, F 3, F 101, F 103, F 105 and F 112*b*–F 119) disposed roughly in the shape of a cross (+), the arms of which separated four quarters in which *S. serratodentata* occurred. From a comparison of the distribution in April 1939, it seems probable that the north-south break in distribution was a true discontinuity while the east-west break was not. The numbers per haul of *S. serratodentata* were about equal to those of *S. setosa* except off Ushant (St. 7) where the large catch of 2270 specimens was taken in a day haul. It was the dominant species at this station, over the whole of the south-western marginal area, and at one station in the central area (St. 36), although here only three specimens were taken and no other *Sagitta* spp. were present.

31 *May*–5 *June* (Fig. 11 E).

The species was irregularly distributed over the western half of the cruise and did not occur to the east of 7° W. Very small numbers were taken (maximum 30 (night), St. 7) and it did not predominate in any part of the area.

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[1] See note 1, p. 91.

[2] See also Furnestin (1939*a*).

19–24 *July* (Fig. 11 F).

One specimen only of *S. serratodentata* was taken outside the Channel mouth (St. 8, day haul).

### 1939

15–18 *March* (Fig. 12 A).

*S. serratodentata* was present at all except the two easternmost stations (Sts. 8 and 9). The eastern limit of its distribution lay along 8° W. and it was the dominant species to the west of 10° W. Numbers per haul were about equal to those of *S. elegans* (maxima: 850 (day), St. 8; 2310 (night), St. 11).

16–27 *April* (Fig. 12 B).

*S. serratodentata* was present in the western half of the Celtic Sea and along the southern margin. In the western area, its distribution did not extend eastwards of 9° 30′ W.; it was absent from the area south of the entrance to the St George's Channel and off the Bristol Channel. In the east it was absent from the northern half of the mouth of the English Channel and to the west and south of Scilly. Along the southern margin its distribution was discontinuous. There was a break in the neighbourhood of Ushant (6° W.) which separated a small body of *S. serratodentata* in the southern half of the Channel mouth (Sts. 2–5, 36 and 59) from the western population. This distribution shows a close resemblance to that of April 1938 but, owing to the lack of stations, it was unfortunately not possible to determine the southward extent of the break. The species was most numerous towards the edge of the Continental Shelf. It was dominant in the area west of 10° W., and to the south of Ireland, where an eastward extension of its area of dominance reached as far as 9° 30′ W. It was also dominant at the southernmost stations (Sts. 11, 12 and 14). It occurred in greater numbers than *S. setosa* but was not so numerous as *S. elegans* (maxima: 1510 (day), St. 21; 1305 (night), St. SR 33).

2–7 *June* (Fig. 12 C).

The area of distribution extended over the western part of the cruise (Sts. 4–12, 15 and 18), from south-west of the Fastnet Light to the region well to the west of the Brest Peninsula. It was entirely absent from the area south of Ireland and outside the Channel mouth. Catches were not so large as in April (maxima: 75 (day), St. 8; 600 (night), St. 5) and it was dominant at the westernmost station (St. 12) and the southernmost station (St. 6) only. It was considerably more numerous than *S. setosa*.

### *The Distribution of* Sagitta lyra *Krohn*

*S. lyra* occurred in very much smaller numbers than any of the foregoing three species of *Sagitta*. It was not dominant in any of the areas in which it occurred.

### 1937

12–20 *April* (Fig. 11 A).

The species was taken along the southern line of stations from Ushant westwards (Sts. 5–9, 11, 13–15 and 18; maximum 16, St. 7, day haul).

27–30 *May*.

None was taken on this cruise.

20–22 *July* (Fig. 11 C).

A single specimen occurred at Station 8 (day haul).

### 1938

6–18 *April* (Fig. 11 D).

The species was present in the neighbourhood of Ushant (Sts. 5–7 and 33) and at some of the westernmost stations (Sts. 16, 17, 18 A (maximum 20, dawn haul), 20 and SR 88).

31 *May–5 June, and* 19–24 *July*.

No *S. lyra* were taken on these two cruises.

### 1939

15–18 *March* (Fig. 12 A).

*S. lyra* occurred in the neighbourhood of 10° W. (Sts. 6, 11–13 and 15–18). It was absent from the westernmost stations (Sts. 7–10) and did not occur very far east of 10° W. It was noticeably more numerous in night hauls (maximum 50, St. 15) than in day hauls (maximum 14, St. 12).

16–27 *April* (Fig. 12 B).

The species occurred at a considerable number of stations along the edge of the Continental Shelf from the south-west of Ireland to Ushant. With the exception of a large catch (115 specimens) taken in daylight at the westernmost station (St. 21), no hauls contained more than 18 specimens.

2–7 *June* (Fig. 12 C).

The species was present at the southernmost (Sts. 6–8) and westernmost stations (Sts. 11 and 12). The largest haul contained 28 specimens (St. 6, night haul).

## *The Distribution of* Muggiaea atlantica *Cunningham*

### 1937

12–20 *April* (Fig. 13 A).

*M. atlantica* occurred in the eastern part of the area of the cruise. It was most numerous in the neighbourhood of Ushant where 75, 127 and 107 specimens were taken (Sts. 5–7, day hauls) and its distribution extended thence across the mouth of the Channel in lessening numbers as far as the

Land's End–Scilly Channel and westwards to 7° W. It was absent off the south coast of Cornwall (Sts. 1, 33 and 34) and from the western and north-western region outside the Channel mouth (Sts. 10–18 and 25–32). A single specimen of *M. kochi* was taken about 20 miles to the north of Ushant (St. 5).

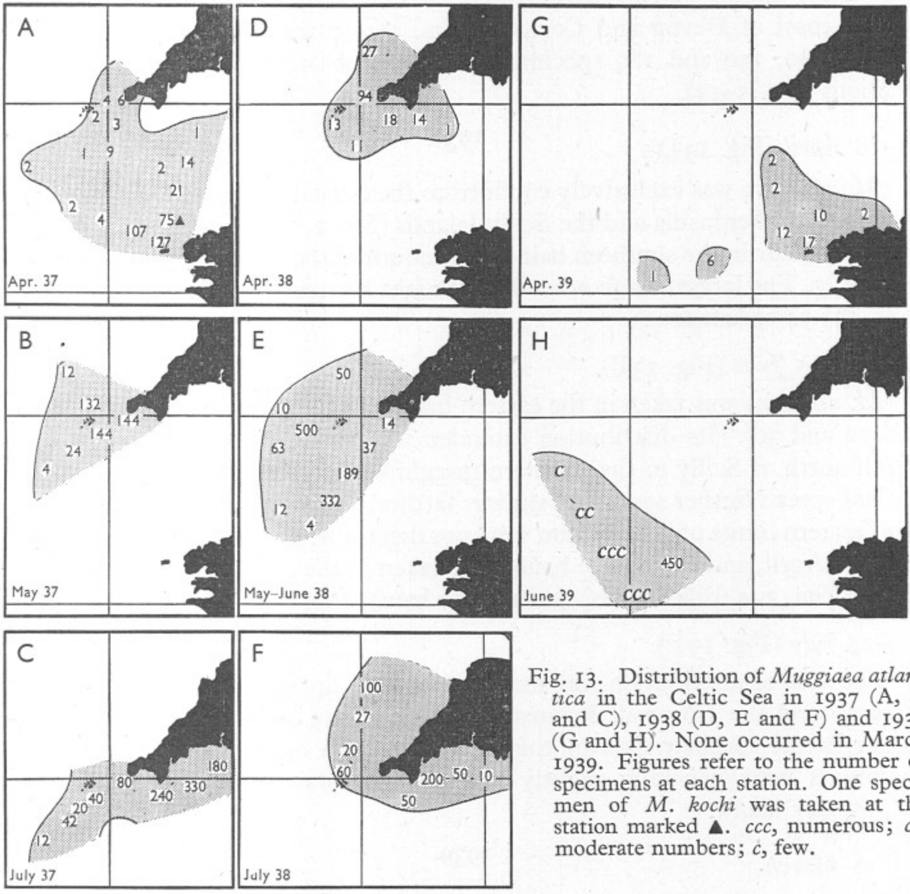

Fig. 13. Distribution of *Muggiaea atlantica* in the Celtic Sea in 1937 (A, B and C), 1938 (D, E and F) and 1939 (G and H). None occurred in March 1939. Figures refer to the number of specimens at each station. One specimen of *M. kochi* was taken at the station marked ▲. *ccc*, numerous; *cc*, moderate numbers; *c*, few.

27–30 *May*[1] (Fig. 13B).

The species was taken in the eastern half of the area of the cruise. The western limit of distribution occurred to the west of Scilly at 7° W. No stations were worked to the east of Land's End, inside the mouth of the Channel. It was most numerous in the region of the Land's End–Scilly Channel (Sts. 1 and 2; 144 and 144 specimens; day hauls) and catches here were rather larger than the maximum of April. It was absent from the western stations (Sts. 5–13).

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[1] See note 1, p. 91.

20–22 *July* (Fig. 13C).

The species was taken in the northern half of the Channel mouth and to the west as far as 7° W. No stations were worked in the southern half of the Channel mouth, and the eastern limit of distribution was not determined as the cruise did not extend eastward of 4° W. The largest hauls occurred off the south coast of Devon and Cornwall (Sts. 16, 17 (day hauls) and 18 (dawn haul); 240, 330 and 180 specimens). It was absent from the westernmost stations (Sts. 5–13).

### 1938

7–18 *April* (Fig. 13D).

*M. atlantica* was exclusively confined to the coastal waters around the tip of the Cornish Peninsula and the Scilly Islands (Sts. 2, 28, 29, 49 and 53–55). It did not occur in the southern half of the mouth of the Channel nor to the west of Scilly. The largest catch was taken at night between Land's End and Scilly (St. 53; 94 specimens).

31 *May*–5 *June* (Fig. 13E).

*M. atlantica* was taken in the eastern half of the area of the cruise (Sts. 1–6, 10–12 and 30). Its distribution extended westwards to about 7° 30′ W. and from north of Scilly to the southern margin of the cruise (48° 50′ N.; St. 5). It had spread farther south and slightly farther west since April. The southern and eastern limits of distribution were not determined. It was more numerous than in April, and three large hauls were taken in the area to the south-west of Scilly (Sts. 3, 4 (night hauls) and 11 (day haul); 189, 332 and 500 specimens).

19–24 *July* (Fig. 13F).

The area of distribution was similar to that of April; it was confined to the area around the Cornwall Peninsula (Sts. 1, 16–19 and 24–26) and did not occur in the southern half of the Channel mouth or to the west of Scilly. Numbers were generally slightly less than in May–June (maximum 200, St. 25, day haul).

### 1939

15–18 *March*.

No *M. atlantica* were taken on this cruise.

16–27 *April* (Fig. 13G).

Very small numbers (maximum 17, St. 4, day haul) were taken in the south-eastern area only—in the southern half of the mouth of the English Channel (Sts. 3–5, 30, 35 and 59) and at two stations some distance to the west of the Brest Peninsula (Sts. 10 and 12).

2–7 *June* (Fig. 13H).

The species was present in the south-western area between 7° W. and 8° 30′ W. (Sts. 5–9). This was considerably farther to the west than on previous cruises. It was absent from the northern and north-western areas and also from the eastern area off the Channel mouth. No stations were worked in the southern half of the Channel mouth, where it occurred in April. Considerably greater numbers were taken than in April (450, St. 5, night haul).

### *Hydrological Conditions, Temperature and Salinity*

No hydrological data were obtained on the cruises of May and July 1937, May–June 1938, and March and June 1939.

12–20 *April.* **1937**

Water samples were taken at 5, 25 and 50 m.[1]

*Salinity* (Fig. 14A). Salinities were vertically homohaline. Water of fairly high salinity (35·31–35·48 ‰) lay to the westward of the Channel mouth. It was separated from water of similar salinity inside the Channel—off Plymouth—by a broad tongue of low salinity (< 35·10 ‰) which extended northwards from Ushant across the Channel mouth as far as the Lizard. North of the Scilly Isles, salinities were also low (35·09–35·21 ‰, total range, all depths; Sts. 32 and 33), but were probably not continuous with the Ushant tongue which appeared to be retained by an eastward extension of slightly more saline water past Scilly to Land's End (35·22–35·30 ‰, total range, all depths; Sts. 23 and 24).

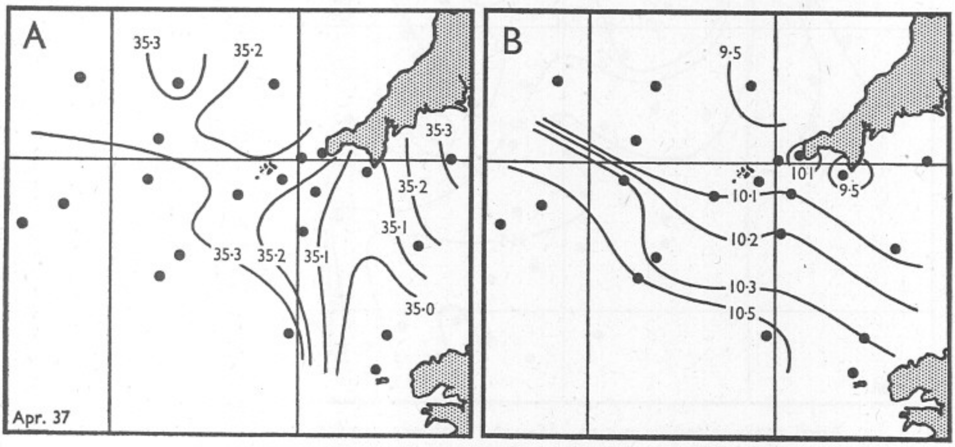

Fig. 14. April 1937; salinities (A) and temperatures (B) at 5 m.

*Temperature* (Fig. 14B). Temperatures were homothermal at all depths. At Station 23, noticeably high values were recorded, which are however, almost certainly attributable to inshore conditions. The station was less than two miles from the coast of Land's End, in a depth of 20½ fms. (37·5 m.).

[1] Salinity and temperature data of the April 1937 cruise have been published in the *Bulletin Hydrographique* for the year 1937 (1939).

## 1938

6–18 *April.*

Water samples were taken at 0, 5, 25, 50 m. and bottom on the *George Bligh* cruise,[1] at 0, 10, 20, 40, 60, 100, 140, 200 m. and bottom on the *Muirchu* cruise,[2] and at 5, 50, 100 m. and bottom on the *Quentin Roosevelt* cruise.[3]

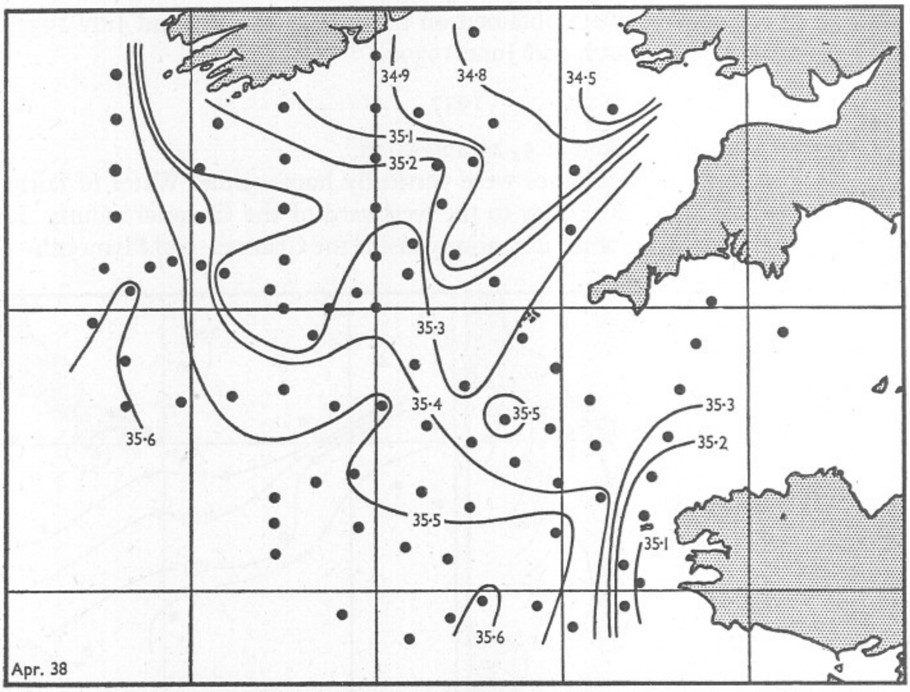

Fig. 15. April 1938; salinities at 5 m. *Muirchu* stations were sampled at 10 m.; there was very little difference between salinities at this depth and at surface.

*Salinity* (Fig. 15). Conditions were homohaline at all depths. Low salinity water (< 35·20 ‰) was present in the south-eastern area—close to the Brest Peninsula, and also in the northern area—from the south coast of Ireland to the mouth of the Bristol Channel. Fairly high salinity water (35·30–35·40 ‰) occupied the northern half of the mouth of the Channel and the region to the

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[1] Salinity and temperature data of the *George Bligh* cruise of April 1938 are to be published in the *Bulletin Hydrographique*.

[2] Salinity and temperature data of the *Muirchu* cruise of April 1938 have been published in the *Bulletin Hydrographique* for the years 1938 and 1939 (1944).

[3] For salinity and temperature data, see Furnestin (1939*a*). Data of the first part of the *Quentin Roosevelt* cruise (23 March–5 April 1938) are not included in the above account owing to their slightly earlier date than the *George Bligh* and *Muirchu* observations; data of the second part of the cruise (6–9 April 1938; Sts. F 101–F 119, this paper; 101–119, Furnestin (1939*a*)) are included.

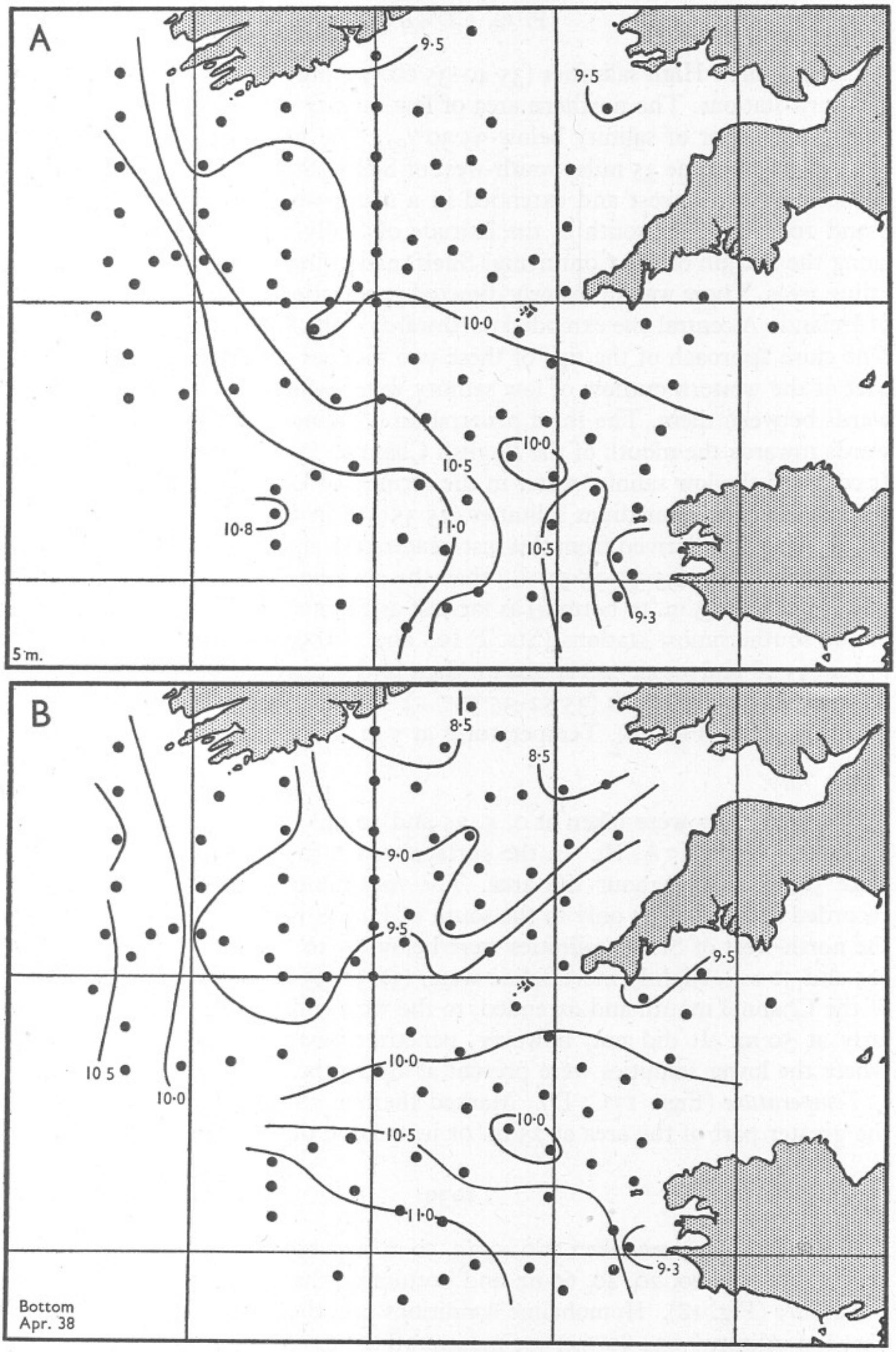

Fig. 16. April 1938; temperatures at 5 m. (A) and bottom (B). *Muirchu* stations were sampled at 10 m.; there was very little difference between values at this depth and at surface.

south of Scilly. High salinities (35·40–35·60‰) prevailed at the western and southern stations. The northern area of low salinity gave rise to two separate tongues of water of salinity below 35·30‰. The first extended southwards along 7° W. to some 35 miles south-west of Scilly (St. 34). The second tongue lay farther to the west and extended in a south-westerly direction between 8 and 10° W., as far south as the latitude of Scilly. The high salinity water along the margin of the Continental Shelf made three incursions into the less saline areas. There was an easterly directed penetration in the area to the south of Ireland. A central one extended northwards along 8° W. to about 50° 30′ N. The close approach of the tips of these two tongues narrowly constricted the root of the western outflow of low salinity water which extended south-westwards between them. The third penetration of saline water, extending northwards towards the mouth of the English Channel, lay off the Brest Peninsula. It confined the low salinity water in the vicinity of Ushant very closely to the French coast. The medium salinities (35·35‰) in the Channel mouth were probably in part derived from this last penetration since small isolated lacunae of higher salinity (35·39–35·51‰) than the surrounding water were found at varying depths (5 m. to bottom) as far east as Station 1 off Plymouth. At two of the southernmost stations (Sts. F 108 and F 109), salinities were slightly lower (35·48 and 35·44‰) at 200 m. than in the upper layers and at stations immediately to the north (35·52–35·59‰).

*Temperature* (Fig. 16). Temperatures at 5 m. and bottom are shown.

19–24 *July*.

Water samples were taken at 0, 5, 25 and 50 m.[1]

*Salinity* (Figs. 17A, B). In the surface waters (0 and 5 m.), low salinities were present throughout the area. The maximum value of 35·34‰ was recorded at one station only to the south of Land's End (St. 23, 5 m.), and to the north-west of Scilly, salinities were below 35·10‰. In the deeper layers (25 and 50 m.), slightly more saline water (35·30–35·46‰) occupied the area of the Channel mouth and extended, to the west and north of Scilly, particularly at 50 m. It did not, however, penetrate eastwards into the Channel, where the lower salinities were present at all depths.

*Temperature* (Figs. 17C, D). Marked thermal stratification occurred over the greater part of the area at 25 m. or just above this depth.

## 1939

6–18 *April*.

Water samples were taken at 0, 5, 25, 50 m. and bottom on the *George Bligh* cruise and at 0, 10, 20, 40, 60 m. and bottom on the *Muirchu* cruise.[1]

*Salinity* (Fig. 18). Homohaline conditions prevailed at all depths. Water of very low salinity (< 34·80‰) was present off the mouth of the Bristol Channel

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[1] Data to be published in the *Bulletin Hydrographique*.

and along the south coast of Ireland. With slightly increased salinity (to 35·10‰), it extended south-westwards from the mouth of the Bristol Channel as far as the latitude of the Scilly Isles and to the west of them (St. 31). With a further slight rise of salinity (to 35·30‰), its influence was traceable as a tongue of considerable breadth lying to the west of Scilly and reaching as far south as 49° N. Low salinities (< 35·20‰) were also present in the vicinity of Ushant and occupied the southern half of the mouth of the English Channel. Between these two regions of low salinity, a slightly more saline tongue (35·30–35·38‰) extended northwards along 6° W.—across the mouth of the Channel as far as Scilly. It was evidently derived from the higher salinity water (> 35·50‰) which was present farther to the south at the edge of the Continental Shelf. This saline water occurred in the western and southern areas, and in addition

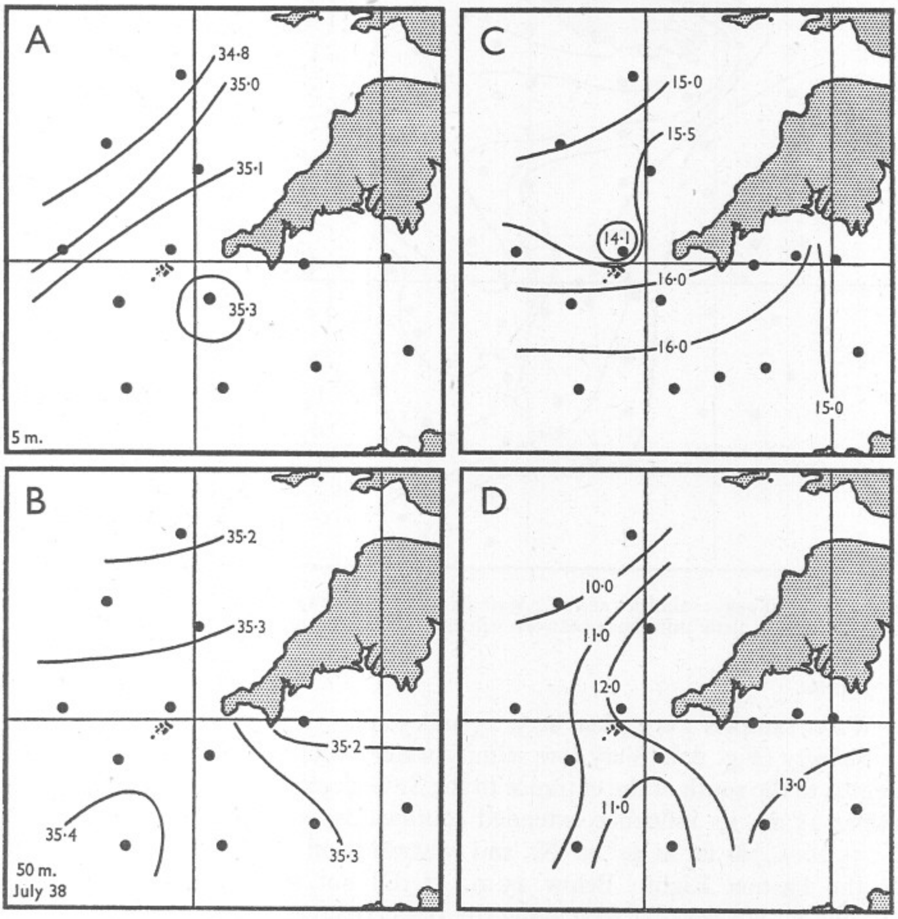

Fig. 17. July 1938; salinities (A and B) and temperatures (C and D) at 5 and 50 m.

to the extension of its influence across the mouth of the English Channel referred to above, there was an easterly directed penetration to the south of Ireland.

*Temperature* (Fig. 19). Temperatures at 5 m. and bottom are shown.

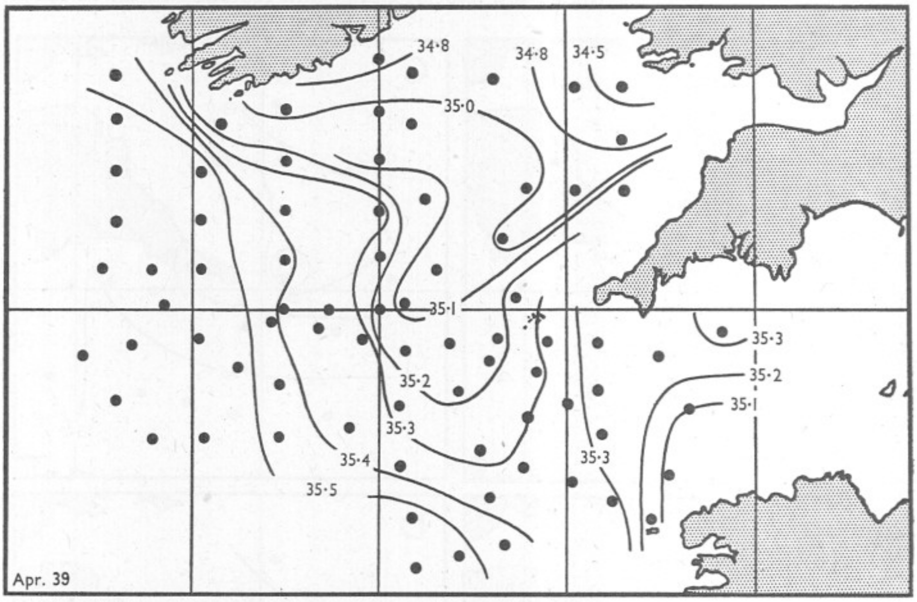

Fig. 18. April 1939; salinities at 5 m. *Muirchu* stations were sampled at 10 m.; there was very little difference between values at this depth and at surface.

2–7 *June.*

Water samples were taken at 5, 25 and 50 m.[1]

*Salinity* (Fig. 20). Very low salinity water (<34·77 °/oo) was present at all depths to the south of the entrance to the St George's Channel (St. 25). In the upper 25 m., its influence extended southwards as a tongue of low salinity (<35·20 °/oo) as far as 49° 20′ N., and westwards off the coast of Ireland as far as the Fastnet Light. Below 25 m., it did not reach farther south than 50° 20′ N., nor very far west along the Irish coast. At the western and south-western stations saline water (>35·40 °/oo) occurred at all depths, and in the upper 25 m. it extended northwards across the Channel mouth to Scilly (35·59 °/oo, 5 m., St. 27, 20 miles north of Scilly) .At 50 m., this northerly flow was checked by slightly fresher water (35·2–35·3 °/oo), which extended westwards from the mouth of the Channel, also blocking at this deeper level the southward flow of low salinity water from the St George's Channel region.

*Temperature* (Fig. 21). Temperatures at 5 and 50 m. are shown.

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[1] Data to be published in the *Bulletin Hydrographique*.

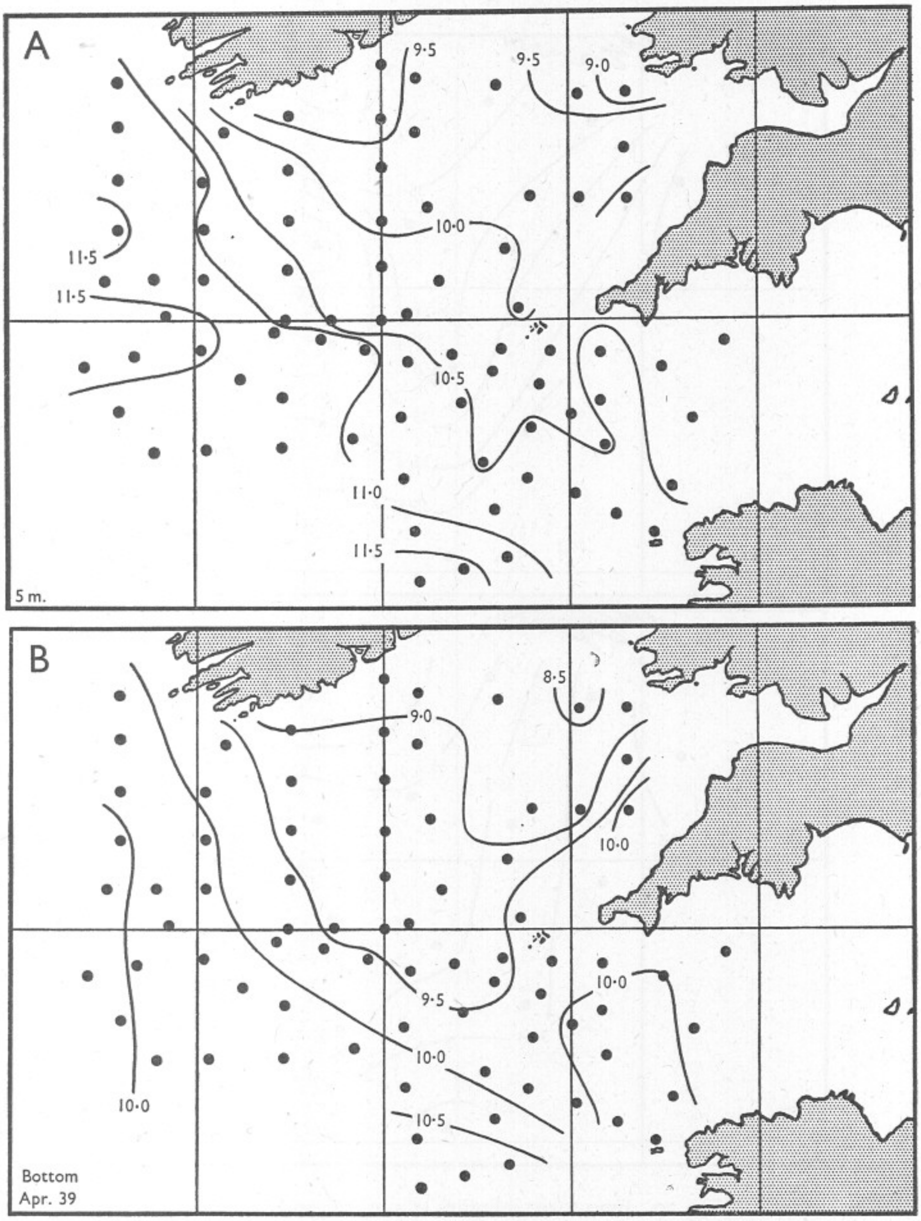

Fig. 19. April 1939; temperatures at 5 m. (A) and bottom (B). *Muirchu* stations were sampled at 10 m.; there was very little difference between values at this depth and at surface.

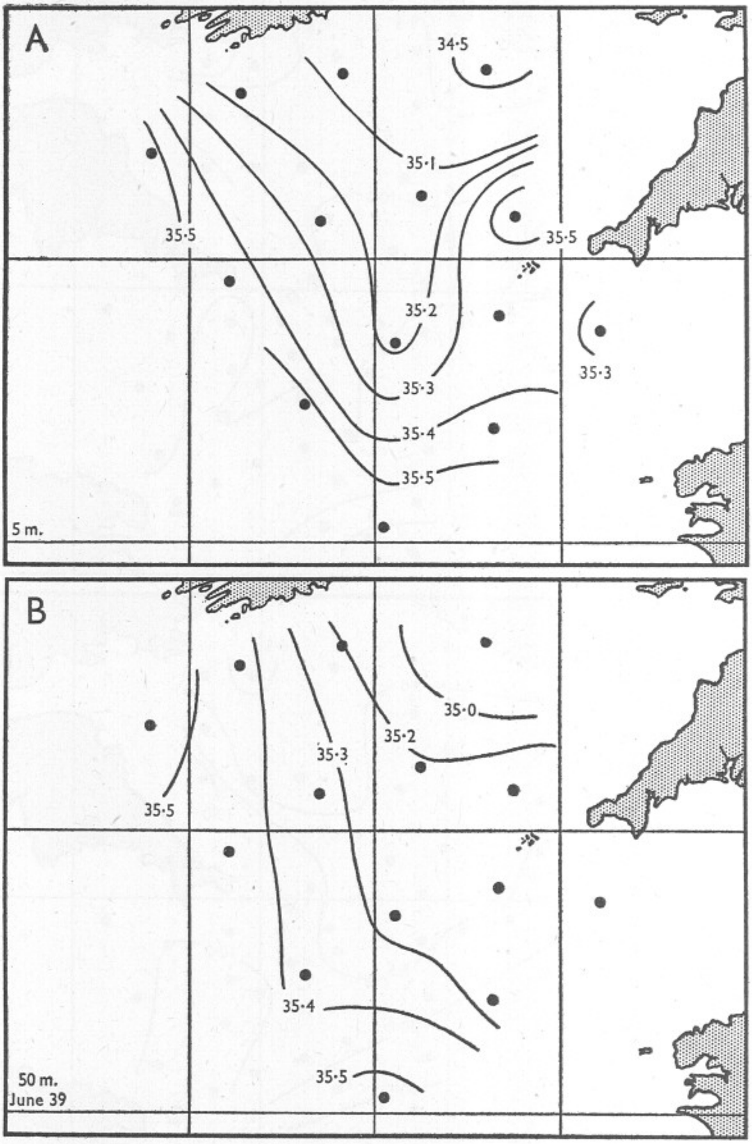

Fig. 20. June 1939; salinities at 5 m. (A) and 50 m. (B).

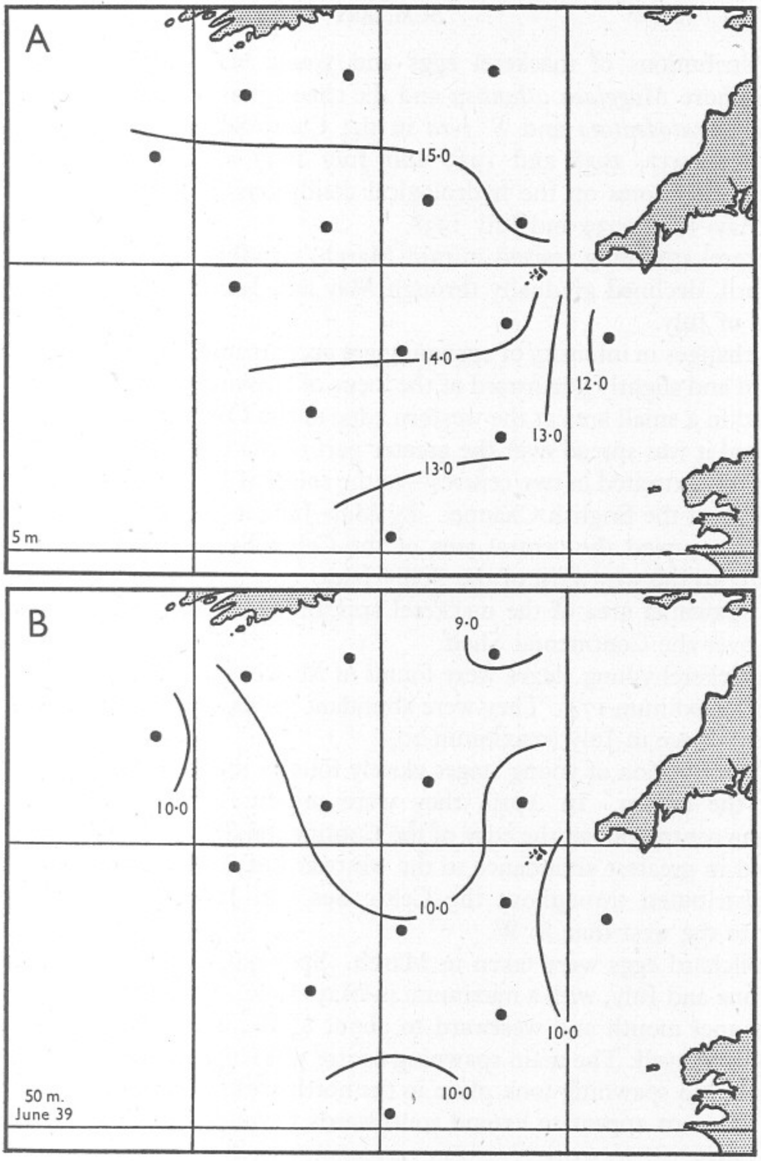

Fig. 21. June 1939; temperatures at 5 m. (A) and 50 m. (B).

## SUMMARY

The distributions of mackerel eggs and young stages, pilchard eggs, the siphonophore *Muggiaea atlantica* and the chaetognaths *Sagitta elegans*, *S. setosa*, *S. serratodentata* and *S. lyra* in the Celtic Sea in March 1939, April, May–June 1937, 1938 and 1939 and July 1937 and 1938 are described, together with notes on the hydrological conditions in April 1937, 1938 and 1939, May–June 1939 and July 1938.

Mackerel spawning started in mid-March, rapidly reached a maximum in mid-April, declined gradually through May and June and was very slight at the end of July.

The changes in intensity of spawning are accompanied by a continuous shift eastward and slightly northward of the locus of spawning. In March spawning occurred in a small area at the western edge of the Continental Shelf only. In mid-April it was spread over the greater part of the Celtic Sea, with the main activity concentrated in two centres—to the south of Ireland and to the west of the mouth of the English Channel. By May–June it had shifted farther to the east and occupied the central area of the Celtic Sea. In July there was no spawning to the westward of the Scilly Isles.

The spawning area of the mackerel appears to be confined to the shallow waters over the Continental Shelf.

No mackerel young stages were found in March. Small numbers occurred in April (maximum 174). They were abundant in May–June (maximum 8239), and very scarce in July (maximum 20).

The distribution of young stages closely follows the movement of spawning during the season. In April, they were present to the westward of the spawning centres, along the edge of the Continental Shelf. In May–June, they occurred in greatest abundance to the westward of the spawning centres, but were distributed throughout the Celtic Sea. In July, they did not occur farther to the west than 8° W.

No pilchard eggs were taken in March. Spawning was observed in April, May–June and July, with a maximum in May–June. It occurred in the area of the Channel mouth and westward to about 8° W., and also along the north coast of Cornwall. The main spawning centre was situated in the mouth of the Channel. No spawning took place in the north-western area of the Celtic Sea and it does not appear to extend southwards beyond the edge of the Continental Shelf.

At the western end of the English Channel, spawning lasts from March until December (Russell). It probably occurs throughout the length of the English Channel (Furnestin).

*Muggiaea atlantica* was not taken in March. It occurred mainly in the mouth of the Channel from April to July. There is evidence that in April 1937

and 1939 it was carried into this area with an inflow of low salinity water from the Ushant area.

*Sagitta elegans* was the dominant *Sagitta* species throughout the central area of the Celtic Sea on all cruises. Its area of distribution did not appear to extend beyond the Continental Shelf. There was evidence of a centre of abundance in April and May–June to the north-west of Ushant immediately outside the Channel mouth.

*Sagitta setosa* occurred mainly in the eastern part of the Celtic Sea. It was dominant in parts of the English Channel mouth and off the entrance to the Bristol Channel.

*Sagitta serratodentata* was distributed over the western and southern areas. It was the dominant species along the edge of the Continental Shelf.

*Sagitta lyra* occurred along the edge of the Continental Shelf. It was more restricted to this area than *S. serratodentata*.

I am greatly indebted to the late Dr E. J. Allen, C.B.E., F.R.S., who was Director of the Plymouth Laboratory when the mackerel investigation began in 1936, for his advice and warm encouragement to a new worker; and to his successor, the late Dr S. W. Kemp, F.R.S., for generous encouragement and help during the work. My sincere thanks are due to the present Director and staff of the Plymouth Laboratory for their interest, encouragement and practical help throughout the work, particularly to Mr G. A. Steven who was in charge of the investigation. I am much indebted to Mr G. P. Farran of the Fisheries Branch of the Department of Agriculture and Fisheries, Eire, for his kindness in allowing me to examine the complete collections made by the Fishery Cruiser *Muirchu* in April 1938 and 1939 and for his generous permission to use these extensive data. I am indebted to Mr P. H. T. Hartley and to the late Mr P. R. Crimp, for valuable help in the work of some of the cruises. My thanks are also due to Captain W. H. Stewart, lately of the Research Ship *George Bligh* (Ministry of Agriculture and Fisheries), to Mr B. Moore, lately Master of the Lowestoft Steam Drifter *B.T.B.*, to Mr W. H. E. Nichols of Plymouth, lately Master of the Steam Trawler *Elk*, and to the members of the crews of these ships for the great care and interest they showed in the work of the cruises. Part of the preparation of this report was done during tenure of a Leverhulme Research Grant, for which I owe acknowledgement to the Trustees of the Leverhulme Research Fellowships.

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# APPENDIX

## Table VI. Numbers of Mackerel Eggs, Mackerel Young Stages, Pilchard Eggs and Indicator Species per ½ hr. Oblique Haul of the 2 m. Stramin Ring-Trawl.

* denotes figure obtained by sampling. Nt, night haul. Dn, dawn haul. Dk, dusk haul.

| Station number (date in parenthesis) | Station position | Time of haul (G.M.T.) | Mackerel eggs | Mackerel young stages | Pilchard eggs | *Muggiaea atlantica* | *Sagitta elegans* | *Sagitta setosa* | *Sagitta serrato-dentata* | *Sagitta lyra* |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | 1937 | | | | | | |
| 12–20 April. S.S. *George Bligh* | | | | | | | | | | |
| 1 (12) | 50° 01′ N., 4° 21′ W. | 17.25–17.55 | .. | .. | 12,000* | .. | .. | .. | .. | .. |
| 2 (12) | 49° 42′ N., 4° 32′ W. | 20.53–21.27 Nt | 6 | .. | 30,000* | 1 | 25 | 1 | .. | .. |
| 3 (13) | 49° 23′ N., 4° 41′ W. | 00.13–00.45 Nt | .. | .. | .. | 14 | 2,680* | 3 | 1 | .. |
| 4 (13) | 49° 05′ N., 4° 51′ W. | 03.41–04.06 Nt | .. | .. | .. | 21 | 975* | 20 | 29 | .. |
| 5 (13) | 48° 46′ N., 5° 01′ W. | 06.54–07.27 | .. | .. | .. | 75<br>(1 *M. kochi*) | 225* | 21 | 48 | 4 |
| 6 (13) | 48° 31′ N., 5° 09′ W. | 10.25–10.55 | .. | .. | .. | 127 | 800* | 166* | 233* | 4 |
| 7 (13) | 48° 38′ N., 5° 32′ W. | 13.08–13.38 | .. | .. | .. | 107 | 4,615* | 130* | 225* | 16 |
| 8 (13) | 48° 46′ N., 6° 05′ W. | 17.03–17.32 | 440* | .. | .. | 4 | 471 | 31 | 262 | 1 |
| 9 (13) | 48° 54′ N., 6° 34′ W. | 21.05–21.36 Nt | 8,610* | .. | 17* | 2 | 645* | 10* | 20* | 1 |
| 10 (14) | 49° 03′ N., 7° 01′ W. | 00.25–00.55 Nt | 10,080* | .. | .. | .. | 1,575* | 2 | 60 | .. |
| 11 (14) | 49° 10′ N., 7° 28′ W. | 04.03–04.35 Nt | 4,680* | .. | 80* | .. | 480* | .. | 2 | 3 |
| 12 (14) | 49° 18′ N., 7° 58′ W. | 07.53–08.22 | 7,012* | .. | 115* | .. | 12 | 1 | 3 | .. |
| 13 (14) | 49° 27′ N., 8° 26′ W. | 11.27–11.56 | 18,575* | .. | .. | .. | 5 | .. | 6 | 1 |
| 14 (14) | 49° 32′ N., 8° 58′ W. | 15.53–16.23 | 32,300* | .. | .. | .. | 12 | 1 | 93 | 13 |
| 15 (14) | 49° 40′ N., 8° 30′ W. | 19.34–20.04 | 20,500* | 1 | .. | .. | 341 | .. | 9 | 2 |
| 16 (14) | 49° 44′ N., 8° 11′ W. | 22.59–23.29 Nt | 1,786* | .. | .. | .. | 350* | .. | 30 | .. |
| 17 (15) | 49° 51′ N., 7° 37′ W. | 02.24–02.54 Nt | 1,470* | .. | 675* | .. | 270* | .. | .. | .. |
| 18 (15) | 49° 33′ N., 7° 35′ W. | 05.43–06.12 Dn | 150* | .. | .. | .. | 350* | 6 | 14 | 3 |
| 19 (15) | 49° 19′ N., 7° 15′ W. | 09.09–09.38 | 640* | .. | 5* | 2 | 25 | 5 | .. | .. |
| 20 (15) | 49° 28′ N., 6° 20′ W. | 15.52–16.20 | 2 | .. | .. | 1 | 2,550* | 14 | 11 | .. |
| 21 (15) | 49° 28′ N., 5° 56′ W. | 18.09–18.38 | .. | .. | .. | 9 | 1,775* | 34 | 127 | .. |
| 22 (15) | 49° 46′ N., 5° 48′ W. | 21.17–21.46 Nt | 75* | .. | 485* | 3 | 22 | 2 | 1 | .. |
| 23 (18) | 50° 02′ N., 5° 44′ W. | 11.54–12.21 | .. | .. | 915* | 6 | 275* | 1 | .. | .. |
| 24 (18) | 49° 51′ N., 6° 10′ W. | 15.14–15.42 | .. | .. | 1,500* | 2 | 32 | 1 | .. | .. |
| 25 (18) | 49° 45′ N., 6° 38′ W. | 18.07–18.36 | .. | .. | 760* | .. | .. | .. | .. | .. |
| 26 (18) | 49° 56′ N., 7° 03′ W. | 21.18–21.48 Nt | 412* | .. | 630* | .. | 1,062* | .. | 285* | .. |
| 27 (19) | 50° 08′ N., 7° 29′ W. | 00.42–01.13 Nt | 14 | .. | .. | .. | 1,127* | .. | 22 | .. |
| 28 (19) | 50° 19′ N., 7° 55′ W. | 03.58–04.27 Dn | 9 | .. | .. | .. | 2,425* | .. | 4 | .. |
| 29 (19) | 50° 31′ N., 8° 20′ W. | 07.04–07.33 | 577* | 10 | .. | .. | 15 | .. | 2 | .. |
| 30 (19) | 50° 30′ N., 7° 16′ W. | 12.57–13.25 | .. | .. | .. | .. | .. | .. | .. | .. |
| 31 (19) | 50° 30′ N., 6° 45′ W. | 15.50–16.20 | .. | .. | .. | .. | 3 | .. | 2 | .. |
| 32 (19) | 50° 30′ N., 6° 15′ W. | 19.05–19.34 Dk | .. | .. | .. | .. | 1,870* | .. | .. | .. |
| 33 (20) | 50° 01′ N., 5° 58′ W. | 01.49–02.19 Nt | .. | .. | 232* | 4 | 138 | .. | .. | .. |
| 34 (20) | 49° 55′ N., 5° 16′ W. | 06.12–06.39 | .. | .. | 271 | .. | 57 | .. | .. | .. |
| 35 (20) | 49° 45′ N., 5° 18′ W. | 08.19–08.49 | .. | 1 | 11,902* | .. | 48 | 2 | .. | .. |
| 36 (20) | 49° 19′ N., 5° 07′ W. | 12.30–13.00 | .. | .. | 2 | 2 | 342 | 3 | .. | .. |

|  |  |  |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|---|---|
| 27–30 May.† Steam drifter *B.T.B.* |  |  |  |  |  |  |  |  |  |
| 1 (27) | 49° 59′ N., 5° 42′ W. | 07.48–08.23 | 36 | 4 | 2,800* | 144 | 76 | 8 | .. | .. |
| 2 (27) | 49° 48′ N., 6° 08′ W. | 11.20–11.51 | 60 | .. | 16 | 144 | 244 | .. | .. | .. |
| 3 (27) | 49° 37′ N., 6° 35′ W. | 14.20–14.52 | 1,240 | .. | 336 | 24 | .. | .. | .. | .. |
| 4 (27) | 49° 25′ N., 7° 00′ W. | 18.13–18.44 | 2,780* | 244 | .. | 4 | 36 | .. | 4 | .. |
| 5 (27) | 49° 13′ N., 7° 27′ W. | 19.24–19.56 Nt | 276 | 56 | .. | .. | 300* | .. | 4 | .. |
| 6 (28) | 49° 02′ N., 7° 52′ W. | 00.47–01.19 Nt | 880 | 112 | .. | .. | 264 | .. | 8 | .. |
| 7 (28) | 49° 12′ N., 8° 17′ W. | 03.53–04.23 | 408 | 52 | .. | .. | 76 | .. | 4 | .. |
| 8 (28) | 49° 33′ N., 8° 17′ W. | 07.20–07.52 | 8,875* | 568 | .. | .. | .. | .. | .. | .. |
| 9 (28) | 49° 54′ N., 8° 18′ W. | 10.33–11.12 | 2,770* | 8 | .. | .. | .. | .. | .. | .. |
| 10 (28) | 50° 12′ N., 8° 18′ W. | 13.45–14.17 | 2,750* | 68 | .. | .. | .. | .. | .. | .. |
| 11 (28) | 50° 08′ N., 7° 48′ W. | 16.43–17.15 | 752 | 4 | .. | .. | .. | .. | .. | .. |
| 12 (28/29) | 50° 05′ N., 7° 21′ W. | 19.30–04.30 Nt‡ | 56 | .. | .. | .. | 88 | .. | .. | .. |
| 13 (29) | 50° 20′ N., 7° 02′ W. | 12.10–12.41 | 544 | .. | .. | .. | .. | .. | .. | .. |
| 14 (30) | 50° 25′ N., 6° 40′ W. | 08.29–09.00 | 68 | .. | 300* | 12 | .. | .. | .. | .. |
| 15 (30) | 50° 06′ N., 6° 19′ W. | 11.31–12.02 | 16 | 4 | 200* | 132 | 28 | 12 | .. | .. |
| 20–22 July. Steam trawler *Elk* |  |  |  |  |  |  |  |  |  |
| 1 (20) | 49° 57′ N., 5° 44′ W. | 12.20–12.45 | 15* | 3 | 2,000* | 80* | 24 | 86 | .. | .. |
| 2 (20) | 49° 45′ N., 6° 12′ W. | 15.15–15.45 | 35* | 4 | 600* | 40* | 17 | 6 | .. | .. |
| 3 (20) | 49° 33′ N., 6° 37′ W. | 18.10–18.40 | .. | 15 | .. | 42 | 280* | 1 | 9 | .. |
| 4 (20) | 49° 22′ N., 7° 03′ W. | 21.20–21.50 Nt | .. | 1 | .. | 12 | 40* | .. | .. | .. |
| 5 (21) | 49° 10′ N., 7° 29′ W. | 00.22–00.52 Nt | .. | 1 | .. | § | § | § | § | § |
| 6 (21) | 48° 59′ N., 7° 56′ W. | 03.45–04.15 Nt | .. | .. | .. | .. | 1,700* | .. | 18 | .. |
| 7 (21) | 49° 09′ N., 8° 22′ W. | 06.45–07.15 | .. | .. | .. | .. | 31 | .. | 3 | .. |
| 8 (21) | 49° 30′ N., 8° 22′ W. | 10.02–10.32 | .. | .. | .. | .. | 1,566* | .. | 58 | 1 |
| 9 (21) | 49° 51′ N., 8° 23′ W. | 13.11–13.41 | .. | .. | .. | .. | 7 | .. | 2 | .. |
| 10 (21) | 50° 10′ N., 8° 23′ W. | 16.34–17.04 | .. | .. | .. | .. | 2 | .. | .. | .. |
| 11 (21) | 50° 02′ N., 7° 54′ W. | 19.30–20.00 Dk | .. | 5 | .. | .. | 92 | .. | 2 | .. |
| 12 (21/22) | 49° 55′ N., 7° 25′ W. | 22.35–23.05 Nt | .. | 3 | .. | .. | 240* | .. | 1 | .. |
| 13 (22) | 49° 47′ N., 6° 56′ W. | 01.35–02.05 Nt | .. | 10 | .. | .. | 2,800* | .. | 1 | .. |
| 14 (22) | 49° 38′ N., 6° 28′ W. | 06.02–06.32 | 1 | 2 | 350* | 20 | 10 | 1 | .. | .. |
| 15 (22) | 49° 30′ N., 5° 54′ W. | 10.00–10.30 | 5 | 2 | 18 | .. | 73 | 27 | .. | .. |
| 16 (22) | 49° 48′ N., 5° 07′ W. | 13.08–13.38 | 25* | 20 | 400* | 240* | 180* | 20* | .. | .. |
| 17 (22) | 49° 54′ N., 4° 37′ W. | 16.02–16.32 | 35* | 1 | 10,000* | 330* | 6 | 38 | .. | .. |
| 18 (22) | 50° 07′ N., 4° 15′ W. | 19.10–19.35 | 135* | 11 | 1,700* | 180* | 18 | 4 | .. | .. |

† See note 1, p. 91.
‡ Metre-net attached to foot rope of mackerel drift-nets which were fishing during the night.
§ Haul lost owing to enemy action before these organisms were counted.

## TABLE VI (*cont.*)

| Station number (date in parenthesis) | Station position | Time of haul (G.M.T.) | Mackerel eggs | Mackerel young stages | Pilchard eggs | *Muggiaea atlantica* | *Sagitta elegans* | *Sagitta setosa* | *Sagitta serrato-dentata* | *Sagitta lyra* |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | 1938 | | | | | | |
| 7–18 April. S.S. *George Bligh* | | | | | | | | | | |
| 1 (7) | 50° 02′ N., 4° 22′ W. | 13.16–13.53 | .. | .. | 1,100* | .. | .. | .. | .. | .. |
| 2 (7) | 49° 43′ N., 4° 32′ W. | 17.18–17.48 | .. | .. | 24,120* | 1 | 1 | 3 | .. | .. |
| 3 (7) | 49° 24′ N., 4° 42′ W. | 20.10–20.40 | 135* | .. | 7,680* | .. | 31 | 36 | .. | .. |
| 4 (7/8) | 49° 05′ N., 4° 50′ W. | 23.52–00.22 Nt | 42 | .. | .. | .. | 2,950* | 350* | 33 | .. |
| 5 (8) | 48° 48′ N., 5° 00′ W. | 04.19–04.50 Nt | .. | .. | .. | .. | 3,275* | 72 | 62 | 3 |
| 6 (8) | 48° 31′ N., 5° 06′ W. | 09.20–09.50 | .. | .. | .. | .. | 287 | 345 | 67 | 2 |
| 7 (8) | 48° 39′ N., 5° 34′ W. | 12.39–13.09 | 6 | .. | .. | .. | 900* | 525* | 2,270* | 3 |
| 8 (8) | 48° 45′ N., 6° 02′ W. | 16.00–16.30 | 230* | .. | 755* | .. | 8 | 6 | .. | .. |
| 9 (8) | 48° 53′ N., 6° 30′ W. | 19.09–19.39 | 155* | .. | 20* | .. | 230* | .. | .. | .. |
| 10 (8) | 49° 02′ N., 6° 58′ W. | 22.27–23.00 Nt | 12,500* | .. | 1,940* | .. | 480* | 5 | 14 | .. |
| 11 (9) | 49° 10′ N., 7° 27′ W. | 01.54–02.24 Nt | 20,310* | .. | 465* | .. | 105* | .. | 7 | .. |
| 12 (9) | 49° 18′ N., 7° 57′ W. | 05.11–05.41 Dn | 5,920* | .. | 30* | .. | 4 | .. | 2 | .. |
| 13 (9) | 49° 18′ N., 8° 27′ W. | 08.38–09.08 | 1,717* | .. | .. | .. | 27 | .. | 46 | .. |
| 14 (9) | 49° 25′ N., 9° 00′ W. | 12.02–12.33 | 3,650* | .. | .. | .. | 2 | 1 | 20 | .. |
| 15 (9) | 49° 22′ N., 9° 34′ W. | 15.22–15.52 | 3,090* | .. | .. | .. | 1 | .. | 21 | .. |
| 16 (9) | 49° 20′ N., 10° 07′ W. | 18.40–19.10 | 6,580* | 1 | .. | .. | .. | .. | 6 | 2 |
| 17 (9) | 49° 18′ N., 10° 42′ W. | 22.06–22.36 Nt | 125 | 69 | .. | .. | 325* | .. | 500* | 1 |
| 18 (10) | 49° 37′ N., 10° 43′ W. | 01.35–02.06 Nt | 32 | 21 | .. | .. | 27 | .. | 51 | .. |
| 18*a* (10) | 49° 53′ N., 11° 03′ W. | 05.21–06.16 Dn | .. | 4 | .. | .. | .. | .. | 63 | 20 |
| 19 (10) | 50° 07′ N., 10° 39′ W. | 13.27–13.57 | 79 | 3 | .. | .. | .. | .. | 9 | .. |
| 20 (10) | 50° 18′ N., 10° 11′ W. | 18.11–18.41 | 156 | 7 | .. | .. | 13 | .. | 74 | 2 |
| 21 (10) | 50° 14′ N., 9° 39′ W. | 22.56–23.26 Nt | 12,650* | .. | .. | .. | 925* | .. | 26 | .. |
| 22 (11) | 50° 07′ N., 9° 10′ W. | 03.30–04.00 Nt | 19,755* | .. | .. | .. | 3,150* | .. | 125* | .. |
| 23 (11) | 49° 48′ N., 8° 41′ W. | 07.33–08.03 | 1,000* | .. | .. | .. | 9 | 2 | 1 | .. |
| 24 (11) | 50° 06′ N., 8° 11′ W. | 11.21–11.51 | 435 | .. | .. | .. | .. | .. | .. | .. |
| 25 (11) | 50° 13′ N., 7° 38′ W. | 14.51–15.21 | 203 | .. | .. | .. | .. | .. | .. | .. |
| 26 (11) | 50° 21′ N., 7° 08′ W. | 18.18–18.52 | 12 | .. | .. | .. | 420* | 100* | 1 | .. |
| 27 (11) | 50° 10′ N., 6° 42′ W. | 22.27–22.58 Nt | 100* | .. | .. | .. | 62 | 1 | .. | .. |
| 28 (12) | 49° 46′ N., 6° 24′ W. | 04.09–04.39 Nt | 30* | .. | 300* | 13 | 24 | 10 | .. | .. |
| 29 (12) | 49° 33′ N., 6° 03′ W. | 07.31–08.02 | 10* | .. | 10,030* | 11 | .. | 2 | .. | .. |
| 30 (12) | 49° 20′ N., 5° 40′ W. | 11.02–11.32 | 25* | .. | 16,200* | .. | 5 | 40 | .. | .. |
| 31 (12) | 49° 01′ N., 5° 36′ W. | 14.23–14.53 | 41 | .. | 30 | .. | 7 | 31 | .. | .. |
| 32 (12) | 49° 09′ N., 6° 06′ W. | 17.42–18.12 | 123 | .. | 332 | .. | 4 | 1 | .. | .. |
| 33 (12) | 49° 11′ N., 6° 37′ W. | 21.01–21.31 Nt | 316 | .. | 6 | .. | 1,675* | 150* | .. | 1 |
| 34 (13) | 49° 26′ N., 7° 01′ W. | 00.26–00.56 Nt | 483 | .. | 97 | .. | 240* | .. | .. | .. |
| 35 (13) | 49° 35′ N., 7° 33′ W. | 03.48–04.18 Nt | 233 | .. | .. | .. | 70* | .. | 2 | .. |
| 36 (13) | 50° 25′ N., 7° 35′ W. | 10.52–11.22 | 315 | .. | .. | .. | .. | .. | 3 | .. |
| 37 (13) | 50° 41′ N., 7° 16′ W. | 14.58–15.36 | 36 | .. | .. | .. | 80 | 52 | 7 | .. |
| 38 (13) | 50° 58′ N., 6° 57′ W. | 18.36–19.06 | 26 | .. | .. | .. | 92 | 93 | 2 | .. |
| 39 (13) | 50° 57′ N., 7° 20′ W. | 21.50–22.20 Nt | 14 | .. | .. | .. | 2,360* | 154 | 8 | .. |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| 40 (14) | 50° 18′ N., 7° 30′ W. | 01.16–01.46 Nt | 60* | .. | .. | .. | 161 | 35 | 9 | .. |
| 41 (14) | 51° 33′ N., 7° 11′ W. | 04.39–05.09 Dn | .. | .. | .. | .. | 62 | 14 | 1 | .. |
| 42 (14) | 51° 50′ N., 6° 55′ W. | 08.07–08.37 | 30* | .. | .. | .. | .. | .. | .. | .. |
| 43 (14) | 51° 38′ N., 6° 36′ W. | 11.22–11.54 | .. | .. | .. | .. | 52 | 10 | .. | .. |
| 44 (14) | 51° 14′ N., 6° 24′ W. | 14.56–15.26 | .. | .. | .. | .. | 71 | 22 | .. | .. |
| 44*a* (14) | 51° 15′ N., 6° 18′ W. | 17.42–17.55 | .. | .. | .. | .. | 88 | 24 | .. | .. |
| 45 (14) | 51° 17′ N., 5° 55′ W. | 20.12–20.42 Nt | .. | .. | .. | .. | 360* | 300* | .. | .. |
| 46 (14) | 51° 19′ N., 5° 25′ W. | 23.29–00.00 Nt | .. | .. | .. | .. | 31 | 36 | .. | .. |
| 47 (15) | 50° 58′ N., 5° 19′ W. | 02.40–03.10 Nt | .. | .. | .. | .. | 400* | 400* | 3 | .. |
| 48 (15) | 50° 55′ N., 5° 50′ W. | 06.04–06.34 Dn | 2,020* | .. | .. | .. | 118 | 112 | .. | .. |
| 49 (15) | 50° 31′ N., 5° 52′ W. | 10.00–10.30 | 10* | .. | 80* | 27 | 76 | 62 | .. | .. |
| 50 (15) | 50° 43′ N., 6° 15′ W. | 13.18–13.48 | 15 | .. | .. | .. | 1 | 1 | .. | .. |
| 50*a* (15) | 50° 45′ N., 6° 50′ W. | 16.33–17.03 | 3 | .. | .. | .. | 72 | 92 | .. | .. |
| 51 (15) | 50° 30′ N., 6° 49′ W. | 19.56–20.26 Dk | 107 | .. | .. | .. | 34 | 55 | .. | .. |
| 52 (16) | 50° 17′ N., 6° 14′ W. | 00.33–01.03 Nt | .. | .. | 960* | .. | 200* | 150* | 1 | .. |
| 53 (16) | 50° 04′ N., 5° 54′ W. | 03.54–04.24 Nt | .. | .. | 17 | 94 | 38 | 7 | .. | .. |
| 54 (16) | 49° 50′ N., 5° 30′ W. | 07.31–08.02 | .. | .. | 6 | 18 | .. | .. | .. | .. |
| 55 (16) | 49° 50′ N., 5° 00′ W. | 11.58–12.28 | .. | .. | 3,360* | 14 | 31 | .. | .. | .. |
| 56 (16) | 49° 34′ N., 5° 06′ W. | 15.43–16.14 | .. | .. | 13,000* | .. | 13 | .. | .. | .. |
| 57 (16)† | 49° 15′ N., 5° 12′ W. | 18.25–18.55 | .. | .. | .. | .. | 68 | .. | .. | .. |
| 58 (17)† | 48° 51′ N., 4° 51′ W. | 01.27–01.57 Nt | .. | .. | .. | .. | 248 | .. | .. | .. |
| 59 (18)† | 49° 49′ N., 3° 37′ W. | 12.22–12.52 | .. | .. | 328* | .. | 12 | .. | .. | .. |
| 7–12 April. Fishery cruiser *Muirchu* | | | | | | | | | | |
| SR 2872 (7) | 51° 40′ N., 8° 00′ W. | 18.07–18.40 | .. | .. | .. | .. | 164 | 6 | 4 | .. |
| SR 2873 (7) | 51° 20′ N., 8° 00′ W. | 21.20–21.55 Nt | 50* | .. | .. | .. | 650* | 9* | 11* | .. |
| SR 2874 (8) | 51° 00′ N., 8° 00′ W. | 00.25–01.00 Nt | 25 | .. | .. | .. | 1,285* | 40 | 24 | .. |
| SR 2875 (8) | 50° 40′ N., 8° 00′ W. | 03.39–04.15 Nt | 81 | .. | .. | .. | 5,200* | 8* | 136* | .. |
| SR 2876 (8) | 50° 20′ N., 8° 00′ W. | 06.40–07.15 | 461 | .. | .. | .. | 22 | 4 | 1 | .. |
| SR 2877 (8) | 50° 00′ N., 8° 00′ W. | 09.30–10.05 | 138 | .. | .. | .. | 8 | 2 | 5 | .. |
| SR 2878 (8) | 50° 00′ N., 8° 30′ W. | 12.22–12.55 | 1,220* | .. | .. | .. | .. | .. | .. | .. |
| SR 2879 (8) | 50° 00′ N., 9° 00′ W. | 15.10–16.00 | 15,380* | .. | .. | .. | 1 | .. | .. | .. |
| SR 2880 (8) | 50° 20′ N., 9° 00′ W. | 18.35–19.09 | 13,350* | .. | .. | .. | 4 | .. | 1 | .. |
| SR 2881 (8) | 50° 40′ N., 9° 00′ W. | 21.54–22.28 Nt | 8,130* | .. | .. | .. | 2,174* | 6* | 69* | .. |
| SR 2882 (9) | 51° 00′ N., 9° 00′ W. | 01.05–01.39 Nt | 8,380* | .. | .. | .. | 1,037* | 4 | 53 | .. |
| SR 2883 (9) | 51° 20′ N., 9° 00′ W. | 04.42–05.16 Dn | 487* | .. | .. | .. | 1,670* | 8 | 12 | .. |
| SR 2884 (9) | 51° 14′ N., 9° 43′ W. | 10.58–11.31 | 1,850* | .. | .. | .. | 24 | 1 | 3 | 2 |
| SR 2885 (11) | 50° 56′ N., 9° 55′ W. | 11.00–11.34 | 6,180* | .. | .. | .. | 285 | 1 | 35 | .. |
| SR 2886 (11) | 50° 36′ N., 9° 55′ W. | 14.07–14.40 | 99,333* | 23 | .. | .. | 21 | 1 | 114 | .. |
| SR 2887 (11) | 50° 16′ N., 9° 55′ W. | 17.18–17.51 | 2,730* | .. | .. | .. | 3 | .. | 4 | .. |
| SR 2888 (11) | 50° 16′ N., 10° 26′ W. | 20.26–20.49 Dk | 126 | 9 | .. | .. | 17 | .. | 40 | 1 |
| SR 2889 (11/12) | 50° 16′ N., 10° 57′ W. | 23.48–00.22 Nt | .. | 3 | .. | .. | .. | .. | 59 | .. |
| SR 2890 (12) | 50° 36′ N., 10° 48′ W. | 03.11–03.45 Nt | 780* | .. | .. | .. | 33 | .. | 23 | .. |
| SR 2891 (12) | 50° 56′ N., 10° 48′ W. | 06.39–07.12 | 840* | 6 | .. | .. | 5 | .. | 1 | .. |
| SR 2892 (12) | 51° 16′ N., 10° 48′ W. | 09.46–10.20 | 321 | 17 | .. | .. | 4* | .. | 28* | .. |
| SR 2893 (12) | 51° 33′ N., 10° 48′ W. | 12.53–13.27 | 136 | .. | .. | .. | 1,405* | .. | 181 | .. |

† Owing to bad weather, a 1 m. stramin net was used; it was fished over the side while the ship drifted. Counts have therefore been multiplied by 4.

## TABLE VI (*cont.*)

| Station number (date in parenthesis) | Station position | Time of haul (G.M.T.) | Mackerel eggs | Mackerel young stages | Pilchard eggs | *Muggiaea atlantica* | *Sagitta elegans* | *Sagitta setosa* | *Sagitta serrato-dentata* | *Sagitta lyra* |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | 1938 | | | | | | |
| 31 May–5 June. Steam trawler *Elk* | | | | | | | | | | |
| 1 (31) | 49° 56′ N., 5° 33′ W. | 15.55–16.25 | 2(?) | .. | .. | 14 | 7 | 85 | .. | .. |
| 2 (31) | 49° 40′ N., 5° 51′ W. | 19.44–20.14 | 870* | 1 | 2,030* | 37 | 1,000* | 90* | .. | .. |
| 3 (31) | 49° 23′ N., 6° 11′ W. | 23.03–23.33 Nt | 5,320* | 41 | 440* | 189 | 7,040* | 170* | .. | .. |
| 4 (1) | 49° 06′ N., 6° 30′ W. | 02.40–03.10 Nt | 31,110* | 898 | 600* | 332 | 29,340* | 30* | .. | .. |
| 5 (1) | 48° 50′ N., 6° 49′ W. | 04.48–05.18 Dn | 12,200* | 307 | 25,320* | 4 | 55 | 5 | .. | .. |
| 6 (1) | 49° 00′ N., 7° 18′ W. | 09.08–09.38 | 8,010* | 141 | 20* | 12 | 4 | .. | .. | .. |
| 7 (1) | 49° 08′ N., 7° 48′ W. | 16.28–16.58 | 157 | 128 | .. | .. | 5,820* | 30* | 30* | .. |
| 8 (2) | 49° 17′ N., 8° 15′ W. | 04.06–04.36 Dn | 700* | 120 | .. | .. | 1,140* | 10* | .. | .. |
| 9 (2) | 49° 28′ N., 7° 48′ W. | 07.37–08.07 | 3,120* | 1,219 | .. | .. | 390* | .. | .. | .. |
| 10 (2) | 49° 39′ N., 7° 20′ W. | 10.46–11.16 | 921 | 672 | .. | 63 | 1,200* | 3 | 1 | .. |
| 11 (2) | 49° 50′ N., 6° 53′ W. | 13.31–14.01 | 136 | 369 | .. | 500* | 600* | 2,300* | .. | .. |
| 12 (2) | 50° 04′ N., 7° 16′ W. | 16.55–17.25 | 18,280* | 56 | 20,600* | 10 | 9 | 4 | 1 | .. |
| 13 (2) | 50° 19′ N., 7° 37′ W. | 19.54–20.24 | 748 | 20 | .. | .. | 70 | .. | 2 | .. |
| 14 (2) | 50° 33′ N., 7° 59′ W. | 23.09–23.39 Nt | 542 | 63 | .. | .. | 120 | .. | 8 | .. |
| 15 (3) | 50° 34′ N., 8° 31′ W. | 02.40–03.20 Nt | 3,430* | 214 | .. | .. | 260* | .. | .. | .. |
| 16 (3) | 50° 35′ N., 9° 03′ W. | 06.00–06.30 | 2,570* | 659 | .. | .. | 10 | .. | .. | .. |
| 17 (3) | 50° 36′ N., 9° 33′ W. | 09.16–09.46 | 72 | 21 | .. | .. | 81 | .. | .. | .. |
| 18 (3) | 50° 19′ N., 9° 52′ W. | 12.17–12.47 | .. | 193 | .. | .. | 196 | .. | 1 | .. |
| 19 (3) | 50° 07′ N., 9° 28′ W. | 15.30–16.00 | 2(?) | 245 | .. | .. | 290* | .. | 2 | .. |
| 20 (3) | 49° 48′ N., 9° 28′ W. | 18.50–19.20 | .. | 277 | .. | .. | 78 | .. | .. | .. |
| 21 (4) | 49° 30′ N., 9° 44′ W. | 00.00–00.30 Nt | .. | 94 | .. | .. | 33 | .. | 10 | .. |
| 22 (4) | 49° 24′ N., 9° 15′ W. | 04.12–04.42 Dn | .. | 173 | .. | .. | 28 | .. | .. | .. |
| 23 (4) | 49° 17′ N., 8° 45′ W. | 07.21–07.51 | 219 | 352 | .. | .. | .. | .. | 4 | .. |
| 24 (4) | 49° 39′ N., 8° 46′ W. | 10.30–11.00 | 1,050* | 1,429 | .. | .. | 1,050* | 1 | 2 | .. |
| 25 (4) | 50° 00′ N., 8° 47′ W. | 13.35–14.05 | 2,075* | 8,239 | .. | .. | 1,525* | .. | 25* | .. |
| 26 (4) | 50° 01′ N., 8° 15′ W. | 16.43–17.13 | 3,300* | 520 | .. | .. | 3 | 1 | .. | .. |
| 27 (4) | 50° 02′ N., 7° 44′ W. | 19.53–20.23 | 587* | 209 | .. | .. | 150* | 1 | 4 | .. |
| 28 (5) | 50° 37′ N., 6° 54′ W. | 01.35–02.05 Nt | 334 | 1 | .. | .. | 270* | .. | .. | .. |
| 29 (5) | 50° 42′ N., 6° 24′ W. | 04.43–05.13 Dn | 1,237* | 11 | .. | .. | 18 | 3 | .. | .. |
| 30 (5) | 50° 25′ N., 6° 17′ W. | 08.35–09.05 | 6,075* | 18 | 2,837* | 50* | 11 | .. | .. | .. |
| 19–24 July. Steam trawler *Elk* | | | | | | | | | | |
| 1 (19) | 50° 01′ N., 4° 00′ W. | 13.34–14.04 | 50* | 1 | 18,350* | 10 | 3 | 10 | .. | .. |
| 2 (19) | 49° 42′ N., 3° 52′ W. | 16.40–17.10 | 300* | 4 | 7,320* | .. | .. | 9 | .. | .. |
| 3 (19) | 49° 22′ N., 3° 42′ W. | 19.34–20.04 | 1,600* | 6 | 3,620* | .. | .. | 26 | .. | .. |
| 4 (19) | 49° 19′ N., 4° 12′ W. | 22.39–23.12 Nt | 20* | 5 | 460* | .. | .. | 5 | .. | .. |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| 5 (20) | 49° 15′ N., 4° 42′ W. | 01.53–02.23 Nt | 12 | .. | .. | .. | 15 | 2 | .. | .. |
| 6 (20) | 49° 11′ N., 5° 12′ W. | 05.25–05.55 Dn | 18 | .. | 46 | .. | 1 | .. | .. | .. |
| 7 (20) | 49° 06′ N., 5° 41′ W. | 08.27–08.57 | 49 | 1 | 19 | .. | 1 | 1 | .. | .. |
| 8 (20) | 49° 03′ N., 6° 13′ W. | 11.29–12.00 | 11 | .. | .. | .. | 1 | .. | .. | .. |
| 9 (20) | 49° 06′ N., 6° 43′ W. | 18.03–18.34 | .. | 1 | .. | .. | 500* | .. | 1 | .. |
| 10 (21) | 49° 42′ N., 7° 23′ W. | 00.42–01·12 Nt | 1 | .. | 55 | .. | 180* | .. | .. | .. |
| 11 (21) | 50° 03′ N., 7° 23′ W. | 03.48–04.20 Nt | .. | .. | .. | .. | 160* | .. | .. | .. |
| 12 (21) | 50° 33′ N., 7° 09′ W. | 07.32–08.02 | .. | 1 | 5 | .. | .. | .. | .. | .. |
| 13 (21) | 50° 47′ N., 6° 56′ W. | 10.44–11.15 | 5 | 3 | 1 | .. | .. | .. | .. | .. |
| 14 (21) | 51° 00′ N., 6° 32′ W. | 13.54–14.24 | 5 | 3 | .. | .. | .. | .. | .. | .. |
| 15 (21) | 51° 13′ N., 6° 08′ W. | 17.06–17.36 | .. | 1 | .. | .. | 1 | 19 | .. | .. |
| 16 (21) | 50° 56′ N., 5° 50′ W. | 20.39–21.11 Dk | 300* | 3 | 38,600* | 100* | .. | .. | .. | .. |
| 17 (21/22) | 50° 37′ N., 5° 58′ W. | 23.44–00.16 Nt | 200* | 5 | 950* | 27 | .. | 32 | .. | .. |
| 18 (22) | 50° 17′ N., 6° 09′ W. | 02.03–02.33 Nt | 69 | 4 | 41 | 20* | 29 | 49 | .. | .. |
| 19 (22) | 50° 03′ N., 6° 16′ W. | 05.10–05.40 Dn | 12 | 5 | 69 | 60* | 1 | 7 | .. | .. |
| 20 (22) | 50° 02′ N., 6° 48′ W. | 08.33–09.04 | 11 | 4 | .. | .. | .. | .. | .. | .. |
| 21 (24) | 49° 42′ N., 6° 48′ W. | 01.06–01.36 Nt | .. | 1 | .. | .. | 1,000* | 46 | .. | .. |
| 22 (24) | 49° 43′ N., 6° 17′ W. | 05.00–05.32 Dn | .. | 1 | .. | .. | .. | 7 | .. | .. |
| 23 (24) | 49° 44′ N., 5° 45′ W. | 08.35–09.05 | 50* | 1 | 2,100* | .. | 2 | 1 | .. | .. |
| 24 (24) | 49° 45′ N., 5° 13′ W. | 11.50–12.20 | 600* | 1 | 8,300* | 50* | .. | 6 | .. | .. |
| 25 (24) | 49° 59′ N., 4° 50′ W. | 15.23–15.55 | 200* | 2 | 3,950* | 200* | .. | 10 | .. | .. |
| 26 (24) | 50° 02′ N., 4° 22′ W. | 17.49–18.19 | 800* | 6 | 22,450* | 50* | 1 | 29 | .. | .. |

**1939**

15–18 March. Steam trawler *Elk*

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| 1 (15) | 50° 00′ N., 6° 55′ W. | 11.44–12.18 | .. | .. | .. | .. | 700* | .. | .. | .. |
| 2 (15) | 50° 03′ N., 7° 40′ W. | 17.09–17.40 | .. | .. | .. | .. | 600* | .. | .. | .. |
| 3 (15) | 50° 05′ N., 8° 29′ W. | 21.45–22.15 Nt | .. | .. | .. | .. | 1,950* | .. | 67 | .. |
| 4 (16) | 50° 07′ N., 9° 17′ W. | 02.16–02.46 Nt | .. | .. | .. | .. | 2,725* | .. | 95 | .. |
| 5 (16) | 50° 09′ N., 10° 00′ W. | 06.42–07.12 | 4 | .. | .. | .. | 175* | .. | 44 | .. |
| 6 (16) | 50° 10′ N., 10° 29′ W. | 09.48–10.18 | 1 | .. | .. | .. | 13 | .. | 225* | 1 |
| 7 (16) | 50° 12′ N., 10° 57′ W. | 12.48–13.18 | 118* | .. | .. | .. | 1 | .. | 350* | .. |
| 8 (16) | 50° 13′ N., 11° 31′ W. | 16.01–16.32 | 7 | .. | .. | .. | 1 | .. | 850* | .. |
| 9 (16) | 50° 14′ N., 12° 12′ W. | 19.20–19.50 Dk | .. | .. | .. | .. | .. | .. | 50* | .. |
| 10 (16) | 50° 34′ N., 11° 34′ W. | 23.18–23.48 Nt | .. | .. | .. | .. | .. | .. | 300* | .. |
| 11 (17) | 50° 52′ N., 9° 03′ W. | 04.14–04.44 Nt | .. | .. | .. | .. | 39 | .. | 2,310* | 42 |
| 12 (17) | 51° 10′ N., 10° 23′ W. | 08.40–09.10 | .. | .. | .. | .. | 4 | .. | 185* | 14 |
| 13 (17) | 51° 10′ N., 9° 35′ W. | 13.05–13.35 | .. | .. | .. | .. | 1 | .. | 150* | 4 |
| 14 (17) | 50° 52′ N., 9° 03′ W. | 16.23–16.53 | .. | .. | .. | .. | 78 | 1 | 435* | .. |
| 15 (17) | 50° 43′ N., 9° 47′ W. | 20.40–21.10 Nt | .. | .. | .. | .. | 700* | .. | 750* | 50 |
| 16 (18) | 50° 33′ N., 10° 33′ W. | 00.34–01.04 Nt | 4 | .. | .. | .. | 109 | .. | 700* | 43 |
| 17 (18) | 50° 03′ N., 10° 29′ W. | 04.45–05.15 Nt | 6 | .. | .. | .. | 354 | .. | 690* | 42 |
| 18 (18) | 49° 49′ N., 9° 46′ W. | 10.05–10.35 | .. | .. | .. | .. | 80 | .. | 52 | 1 |
| 19 (18) | 49° 52′ N., 8° 58′ W. | 14.32–15.02 | .. | .. | .. | .. | 31 | .. | 14 | .. |
| 20 (18) | 49° 55′ N., 8° 12′ W. | 18.45–19.22 Dk | .. | .. | .. | .. | 2,850* | .. | 1 | .. |

## Table VI (*cont.*)

| Station number (date in parenthesis) | Station position | Time of haul (G.M.T.) | Mackerel eggs | Mackerel young stages | Pilchard eggs | *Muggiaea atlantica* | *Sagitta elegans* | *Sagitta setosa* | *Sagitta serrato-dentata* | *Sagitta lyra* |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | 1939 | | | | | | |
| 16–27 April. S.S. *George Bligh* | | | | | | | | | | |
| 1 (16) | 49° 50′ N., 4° 21′ W. | 20.12–20.45 Nt | .. | .. | 2,080* | .. | 420* | 24 | .. | .. |
| 2 (17) | 49° 18′ N., 4° 41′ W. | 01.41–02.11 Nt | .. | .. | 13,150* | .. | 11,440* | .. | 2 | .. |
| 3 (17) | 48° 50′ N., 4° 54′ W. | 06.45–07.14 | 2 | 1 | 3 | 10 | 6,240* | 38 | 111 | .. |
| 4 (17) | 48° 31′ N., 5° 05′ W. | 10.15–10.45 | .. | .. | .. | 17 | 2,480* | 20* | 45 | 1 |
| 5 (17) | 48° 39′ N., 5° 30′ W. | 13.49–14.19 | 17 | .. | .. | 12 | 2,700* | .. | 49 | .. |
| 6 (17) | 48° 47′ N., 5° 58′ W. | 18.07–18.37 | 1,825* | .. | 50* | .. | 925* | .. | .. | .. |
| 7 (17) | 48° 53′ N., 6° 27′ W. | 22.24–22.52 Nt | 797* | .. | 63* | .. | 1,203* | .. | .. | .. |
| 8 (18) | 49° 00′ N., 6° 55′ W. | 02.21–02.51 Nt | 180* | .. | 510* | .. | 6,480* | 1 | 1 | .. |
| 9 (18) | 48° 40′ N., 6° 48′ W. | 06.04–06.35 Dn | 9,000* | 9 | 700* | .. | 32 | .. | 1 | .. |
| 10 (18) | 48° 20′ N., 6° 40′ W. | 09.40–10.10 | 2,725* | 15 | 14,500* | 6 | 63 | .. | 20 | 1 |
| 11 (18) | 48° 16′ N., 7° 07′ W. | 15.16–15.46 | 1,625* | 24 | 22,975* | .. | 15 | .. | 46 | 4 |
| 12 (18) | 48° 10′ N., 7° 35′ W. | 22.14–22.44 Nt | 9,850* | 74 | 25* | 1 | 400* | .. | 575* | 4 |
| 13 (19) | 48° 32′ N., 7° 38′ W. | 02.06–02.37 Nt | 8,025* | 24 | 200* | .. | 525* | .. | 85 | 18 |
| 14 (19) | 48° 53′ N., 7° 45′ W. | 05.49–06.19 Dn | 775* | 1 | 25* | .. | 4 | .. | 14 | .. |
| 15 (19) | 49° 19′ N., 7° 47′ W. | 09.24–10.01 | 55* | .. | 440* | .. | 18 | .. | 1 | .. |
| 16 (19) | 49° 10′ N., 8° 20′ W. | 13.46–14.17 | 195* | .. | 20* | .. | 14 | .. | 4 | 1 |
| 17 (19) | 49° 06′ N., 9° 05′ W. | 20.20–20.50 Nt | 21,425* | 7 | 125* | .. | 850* | .. | 150* | .. |
| 18 (20) | 49° 05′ N., 9° 53′ W. | 00.47–01.17 Nt | 11,950* | 7 | .. | .. | 42 | .. | 20 | 1 |
| 19 (20) | 49° 05′ N., 10° 26′ W. | 04.24–04.55 Dn | 15,225* | 7 | .. | .. | 18 | .. | 21 | 1 |
| 20 (20) | 49° 21′ N., 10° 48′ W. | 07.59–08.29 | 105 | 38 | .. | .. | 3 | .. | 184 | 15 |
| 21 (20) | 49° 40′ N., 11° 10′ W. | 11.05–11.35 | 375* | 33 | .. | .. | 1 | .. | 1,510* | 115 |
| 22 (20) | 49° 44′ N., 10° 39′ W. | 16.27–16.57 | 33,025* | 174 | .. | .. | .. | .. | 30 | 5 |
| 23 (20) | 50° 01′ N., 10° 18′ W. | 19.58–20.28 Dk | 12,000* | 64 | .. | .. | 35 | .. | 46 | .. |
| 24 (20) | 49° 47′ N., 9° 57′ W. | 23.25–23.55 Nt | 45,025* | 4 | .. | .. | 175* | .. | 125* | .. |
| 25 (21) | 49° 36′ N., 9° 30′ W. | 02.45–03.15 Nt | 5,950* | .. | .. | .. | 175* | .. | 11 | 1 |
| 26 (21) | 49° 28′ N., 9° 04′ W. | 06.04–06.34 Dn | 10,300* | 5 | 200* | .. | .. | .. | .. | .. |
| 27 (21) | 49° 55′ N., 9° 10′ W. | 11.25–11.57 | 4,050* | .. | .. | .. | .. | .. | 1 | 1 |
| 28 (21) | 49° 51′ N., 8° 40′ W. | 14.49–15.27 | 2,275* | .. | .. | .. | .. | .. | .. | .. |
| 29 (21) | 49° 47′ N., 8° 10′ W. | 18.29–18.59 | 1,260* | .. | 20* | .. | 2 | .. | .. | .. |
| 30 (21) | 49° 42′ N., 7° 42′ W. | 22.10–22.40 Nt | 29 | .. | 2 | .. | 1,250* | .. | .. | .. |
| 31 (22) | 50° 02′ N., 7° 42′ W. | 02.12–02.42 Nt | 260 | .. | .. | .. | 5,525* | .. | .. | .. |
| 32 (22) | 49° 48′ N., 6° 43′ W. | 07.04–07.34 | 9 | .. | 49 | .. | 1 | 2 | .. | .. |
| 33 (22) | 49° 46′ N., 6° 11′ W. | 10.42–11.12 | .. | .. | 710* | .. | 27 | .. | .. | .. |
| 34 (22) | 49° 45′ N., 5° 40′ W. | No haul | | | | | | | | |
| 35 (22) | 49° 25′ N., 5° 40′ W. | 18.49–19.19 | 70* | .. | 130* | 2 | 3 | .. | .. | .. |
| 36 (22) | 49° 07′ N., 5° 37′ W. | 22.47–23.17 Nt | 98 | .. | .. | 2 | 2,500* | 5 | 43 | .. |
| 37 (23) | 49° 15′ N., 6° 24′ W. | 05.54–06.24 Dn | .. | 1 | 23,500* | .. | .. | .. | .. | .. |
| 38 (23) | 49° 25′ N., 7° 08′ W. | 12.06–12.36 | 87* | .. | 275* | .. | 67 | .. | .. | .. |
| 39 (23) | 49° 45′ N., 7° 14′ W. | 16.17–16.47 | 290* | .. | 10* | .. | .. | .. | .. | .. |
| 40 (23) | 50° 15′ N., 7° 22′ W. | 21.35–22.05 Nt | 245 | .. | .. | .. | 1,850* | .. | .. | .. |

|  |  |  |  |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|---|---|---|
| 41 (24) | 50° 44′ N., 7° 30′ W. | 02.48–03.18 Nt | 98 | .. | .. | .. | 10,875* | .. | .. | .. |
| 42 (24) | 51° 14′ N., 7° 38′ W. | 08.10–08.40 | 451 | .. | 1 | .. | 11 | .. | .. | .. |
| 43 (24) | 51° 34′ N., 7° 37′ W. | 12.08–12.38 | 100* | .. | .. | .. | .. | .. | .. | .. |
| 44 (24) | 51° 31′ N., 6° 46′ W. | 17.05–17.35 | 125* | .. | .. | .. | 9 | .. | .. | .. |
| 45 (24) | 51° 28′ N., 5° 54′ W. | 21.52–22.22 Nt | 40* | .. | .. | .. | 162 | 1 | .. | .. |
| 46 (25) | 51° 28′ N., 5° 22′ W. | 01.33–02.03 Nt | .. | .. | .. | .. | 1,100* | 5 | .. | .. |
| 47 (25) | 51° 08′ N., 5° 22′ W. | 05.05–05.35 Dn | .. | 2 | .. | .. | 20 | 6 | .. | .. |
| 48 (25) | 50° 48′ N., 5° 22′ W. | 08.30–09.00 | 50* | 1 | .. | .. | 5 | 5 | .. | .. |
| 49 (25) | 50° 48′ N., 5° 53′ W. | 12.15–12.45 | 1,250* | .. | .. | .. | .. | .. | .. | .. |
| 50 (25) | 50° 49′ N., 6° 24′ W. | 16.16–16.46 | 32 | .. | .. | .. | .. | .. | .. | .. |
| 51 (25)† | 50° 28′ N., 6° 40′ W. | 19.47–20.17 Dk | 65* | .. | .. | .. | 76 | .. | .. | .. |
| 52 (25)† | 50° 04′ N., 6° 31′ W. | 22.36–23.06 Nt | 70* | .. | 150* | .. | 1,575* | 1 | .. | .. |
| 53 (26)† | 49° 38′ N., 6° 48′ W. | 01.53–02.24 Nt | 65 | .. | 9 | .. | 800* | .. | .. | .. |
| 54 (26) | 49° 33′ N., 6° 19′ W. | 05.48–06.18 Dn | 75* | .. | 1,700* | .. | 3 | .. | .. | .. |
| 55 (26) | 49° 20′ N., 6° 00′ W. | 13.55–14.25 | 75* | .. | 92,925* | .. | 2 | .. | .. | .. |
| 56 (26) | 49° 40′ N., 5° 00′ W. | 17.50–18.20 | .. | .. | 1,350* | .. | 2 | 3 | .. | .. |
| 57 (26) | 50° 00′ N., 4° 38′ W. | 21.35–22.05 Nt | .. | .. | 13,100* | .. | 1 | 3 | .. | .. |
| 58 (27) | 49° 26′ N., 4° 24′ W. | 02.50–03.20 Nt | .. | .. | 22,050* | .. | 168 | .. | .. | .. |
| 59 (27) | 48° 50′ N., 4° 10′ W. | 07.45–08.15 | 20* | .. | 10* | 2 | 350* | .. | 2 | .. |
| 60 (27) | 49° 02′ N., 3° 16′ W. | 13.53–14.23 | 325* | .. | 4,175* | .. | 90 | 50 | .. | .. |
| 61 (27) | 49° 32′ N., 3° 29′ W. | 18.52–19.22 | .. | .. | 39,075* | .. | 8 | 8 | .. | .. |
| 62 (27) | 50° 00′ N., 3° 45′ W. | 22.20–22.50 Nt | .. | .. | 60* | .. | 58* | 183* | .. | .. |
| 17–21 April. Fishery cruiser *Muirchu* |  |  |  |  |  |  |  |  |  |  |
| SR 2913 (17) | 51° 40′ N., 8° 00′ W. | 12.00–12.30 | .. | .. | .. | .. | .. | .. | .. | .. |
| SR 2914 (18) | 51° 20′ N., 8° 00′ W. | 12.30–13.00 | 37* | .. | .. | .. | 37 | .. | 1 | .. |
| SR 2915 (18) | 51° 00′ N., 8° 00′ W. | 15.35–16.05 | 11 | .. | .. | .. | 386 | .. | 2 | .. |
| SR 2916 (18) | 50° 40′ N., 8° 00′ W. | 18.30–19.00 | 2 | .. | .. | .. | 905* | .. | 6 | .. |
| SR 2917 (18) | 50° 20′ N., 8° 00′ W. | 21.45–22.15 Nt | .. | .. | .. | .. | 2,626* | .. | 12 | .. |
| SR 2918 (19) | 50° 00′ N., 8° 00′ W. | 01.10–01.35 Nt | 2 | .. | .. | .. | 6,660* | .. | 2* | .. |
| SR 2919 (19) | 50° 00′ N., 8° 32′ W. | 04.25–04.50 Dn | 11 | .. | .. | .. | 493* | .. | 14 | .. |
| SR 2920 (19) | 50° 00′ N., 9° 00′ W. | 07.35–08.00 | 88 | .. | .. | .. | .. | .. | .. | .. |
| SR 2921 (19) | 50° 20′ N., 9° 00′ W. | 10.40–11.10 | 54 | .. | .. | .. | .. | .. | 2 | .. |
| SR 2922 (19) | 50° 40′ N., 9° 00′ W. | 13.50–14.20 | 9 | .. | .. | .. | 21 | .. | 35 | .. |
| SR 2923 (19) | 51° 00′ N., 9° 00′ W. | 16.50–17.20 | 28 | .. | 26 | .. | .. | .. | 1 | 1 |
| SR 2924 (19) | 51° 20′ N., 9° 00′ W. | 19.42–20.12 Dk | 23 | .. | .. | .. | .. | .. | .. | 1 |
| SR 2925 (19) | 51° 14′ N., 9° 42′ W. | 23.25–23.55 Nt | 694 | .. | .. | .. | 135 | .. | 2 | 1 |
| SR 2926 (20) | 50° 56′ N., 9° 55′ W. | 02.45–03.15 Nt | 9,570* | .. | .. | .. | 700* | .. | 1,024* | 9* |
| SR 2927 (20) | 50° 36′ N., 9° 55′ W. | 06.10–06.40 | 38,958* | 11 | .. | .. | 1 | .. | 7 | .. |
| SR 2928 (20) | 50° 16′ N., 9° 55′ W. | 09.20–09.50 | 33,000* | 120 | .. | .. | .. | .. | .. | .. |
| SR 2929 (20) | 50° 16′ N., 10° 26′ W. | 12.40–13.10 | 11,700* | 95 | .. | .. | 1 | .. | 1 | 5 |
| SR 2930 (20) | 50° 16′ N., 10° 57′ W. | 16.10–16.40 | 1,092* | 13 | .. | .. | .. | .. | 29 | .. |
| SR 2931 (20) | 50° 36′ N., 10° 48′ W. | 19.24–19.54 | 480 | 73 | .. | .. | 6* | .. | 194* | 20* |
| SR 2932 (20) | 50° 56′ N., 10° 48′ W. | 22.24–22.54 Nt | 14 | 6 | .. | .. | 60* | .. | 467* | 12* |
| SR 2933 (21) | 51° 16′ N., 10° 48′ W. | 02.00–02.30 Nt | 5 | 41 | .. | .. | 91 | .. | 1,305* | 1 |
| SR 2934 (21) | 51° 33′ N., 10° 48′ W. | 04.55–05.25 Dn | 10 | 10* | .. | .. | 84* | .. | 384* | .. |

† Owing to bad weather, the net was fished over the side while the ship drifted.

## TABLE VI (*cont.*)

| Station number (date in parenthesis) | Station position | Time of haul (G.M.T.) | Mackerel eggs | Mackerel young stages | Pilchard eggs | *Muggiaea atlantica* | *Sagitta elegans* | *Sagitta setosa* | *Sagitta serrato-dentata* | *Sagitta lyra* |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | **1939** | | | | | | |
| 2–7 June. Steam trawler *Elk* | | | | | | | | | | |
| 1 (2) | 49° 50′ N., 4° 57′ W. | 04.12–04.42 Dn | 825* | .. | 121,950* | .. | 1 | 8 | .. | .. |
| 2 (2) | 49° 29′ N., 5° 33′ W. | 08.34–09.04 | 3,825* | 20 | 12,475* | .. | 75* | Few | .. | .. |
| 3 (2) | 49° 08′ N., 6° 07′ W. | 13.02–13.32 | 28,500* | 52 | 675* | .. | 2,100* | 300* | .. | .. |
| 4 (2) | 48° 47′ N., 6° 43′ W. | 17.22–17.52 | 6,100* | 337 | .. | .. | 950* | .. | 103 | .. |
| 5 (2) | 48° 26′ N., 7° 18′ W. | 22.00–22.30 Nt | 2,475* | 440 | .. | 450* | 1,125* | .. | 600* | .. |
| 6 (3) | 40° 05′ N., 7° 53′ W. | 02.30–03.00 Nt | 1,250* | 57 | 50* | Numerous | .. | .. | 350* | 28 |
| 7 (3) | 48° 32′ N., 8° 18′ W. | 07.23–07.53 | 3,225* | 634 | .. | Numerous | 112* | .. | 50* | 17 |
| 8 (3) | 48° 58′ N., 8° 45′ W. | 12.15–12.45 | 425* | 43 | .. | Moderate | 150* | .. | 75* | 1 |
| 9 (3) | 49° 25′ N., 9° 10′ W. | 17.05–17.35 | 225* | 148 | .. | Few | 325* | .. | 62* | .. |
| 10 (3) | 49° 50′ N., 9° 35′ W. | 21.30–22.00 Nt | 11 | 178 | .. | .. | 150* | .. | Few | .. |
| 11 (4) | 50° 17′ N., 10° 00′ W. | 02.20–02.50 Nt | 89 | 45 | .. | .. | 425* | .. | 287* | 1 |
| 12 (4) | 50° 42′ N., 10° 25′ W. | 07.43–08.13 | 1,350* | 45 | .. | .. | 2 | .. | 31 | 7 |
| 13 (4) | 51° 06′ N., 9° 27′ W. | 13.55–14.25 | 9,525* | 167 | .. | .. | 17 | .. | .. | .. |
| 14 (4) | 50° 40′ N., 9° 02′ W. | 18.50–19.20 | 4,950* | 40 | .. | .. | .. | .. | .. | .. |
| 15 (4) | 50° 14′ N., 8° 36′ W. | 23.20–23.50 Nt | 650* | 284 | .. | .. | 100* | .. | 2 | .. |
| 16 (5) | 49° 49′ N., 8° 12′ W. | 04.15–04.45 Dn | 1,850* | 27 | .. | .. | 325* | .. | .. | .. |
| 17 (5) | 49° 23′ N., 7° 46′ W. | 08.55–09.25 | 5,900* | 183 | .. | .. | .. | .. | .. | .. |
| 18 (5) | 49° 07′ N., 7° 30′ W. | 16.15–16.45 | 4,350* | 134 | .. | .. | 250* | 1 | 4 | .. |
| 19 (5) | 49° 35′ N., 6° 39′ W. | 22.24–22.54 Nt | 10,725* | 227 | 450* | .. | 2,175* | 1 | .. | .. |
| 20 (6) | 50° 00′ N., 7° 04′ W. | 03.15–03.45 Nt | 1,800* | 1 | 25* | .. | 81 | .. | .. | .. |
| 21 (6) | 50° 25′ N., 7° 29′ W. | 07.43–08.13 | 6,760* | 7 | .. | .. | 7 | .. | .. | .. |
| 22 (6) | 50° 50′ N., 7° 55′ W. | 12.15–12.45 | 12,075* | 3 | .. | .. | 116 | .. | .. | .. |
| 23 (6) | 51° 14′ N., 8° 20′ W. | 16.15–16.45 | 8,550* | 65 | .. | .. | 9 | .. | .. | .. |
| 24 (6) | 51° 14′ N., 7° 32′ W. | 21.00–21.30 Dk | 8,750* | 9 | .. | .. | 25 | 1 | .. | .. |
| 25 (7) | 51° 15′ N., 6° 47′ W. | 01.20–01.50 Nt | 8,700* | 6 | .. | .. | 825* | 1 | .. | .. |
| 26 (7) | 50° 45′ N., 6° 38′ W. | 05.50–06.20 | 6,000* | 59 | .. | .. | 2 | 2 | .. | .. |
| 27 (7) | 50° 16′ N., 6° 29′ W. | 11.08–11.38 | 2,250* | 7 | 50* | .. | 10 | .. | .. | .. |
| 28 (7) | 49° 58′ N., 5° 47′ W. | 14.32–15.02 | 6,150* | 3 | 73,050* | .. | .. | 2 | .. | .. |

# SOME NOTES ON PARASITIC COPEPODA

By Robert Gurney, D.Sc.

(Text-figs. 1–2)

## Developmental Stages in the Family Lernaeopodidae

The Lernaeopodidae are a highly specialized group of parasitic Copepoda presumably derived from a Caligoid stem, and some clue to their systematic position should be found in their development. Some stages are known in ten genera, but it is only in *Achtheres*, *Salmincola*, and *Clavella* that the whole, or nearly the whole, series of stages has been described. There is a very strong tendency to suppress the nauplius as a free stage though, when so suppressed, there may be moults corresponding to nauplius and metanauplius (Zandt, 1935). In some species there is certainly a free nauplius, but it probably moults into the copepodid in a very short time.

| With free nauplius | Hatching as copepodid |
|---|---|
| *Achtheres percarum* Nordmann | *Achtheres amblopltis* Kellicott (normally) |
| | *A. pseudobasanistes* Zandt |
| | [Syn. *Basanistes coregoni* Neresh.] |
| *Tracheliastes polycolpus* Nordmann | *Salmincola salmonea* (L.) |
| | *Salmincola mattheyi* Dedie |
| *Clavella uncinata* (Müller) | *Salmincola edwardsi* Olsson |
| *Charopinus dalmanni* (Retz.) | *Basanistes huchonis* (Schrank) |
| *Lernaeopoda galei* Kröyer | *Epibrachiella impudica* (Nordmann) |

I am indebted to Miss Lebour for larvae of *Lernaeopoda galei* hatched in the laboratory at Plymouth (Fig. 1). In this species there is a nauplius, but it probably moults almost at once into the copepodid as all the appendages of the latter can be seen under the skin, and the head filament is quite distinct. One interesting feature of the nauplius is the possession of a mandibular appendage, since in all other species in which a nauplius has been described this appendage is absent altogether. In this species the appendage is, at the time of hatching, empty of tissues, but it is distinctly biramous, with three long setae on the exopod and two on the endopod. Both pairs of antennae have long setae, but they are not feathered, and it may well be that the nauplius does not actually swim.

The copepodid (0·85 mm. long) is slender, but of the usual form. The filament of attachment is fully formed, running backwards to the region of the maxillipede, where it is thrown into a double coil and then runs forwards again to just below the attachment disk. The mouth cone is large, consisting of a bifid lower lip and an upper lip quite distinct from it. The lower lip has a fringe of delicate hairs at the tip, but it is not easy to see, and it may actually be a finely striated membrane. The mandibles lie outside the cone and are simple stylets, but I have seen a minute papilla at the base which may be a vestige of an exopod. The maxillule has two lobes with two and three spines respectively. Maxilla and maxillipede are powerful prehensile organs, the former with a slender claw and the latter with a more massive curved claw, in this respect quite unlike *Clavella* and *Epibrachiella*, and more resembling *Salmincola*. Nothing is known about later stages.

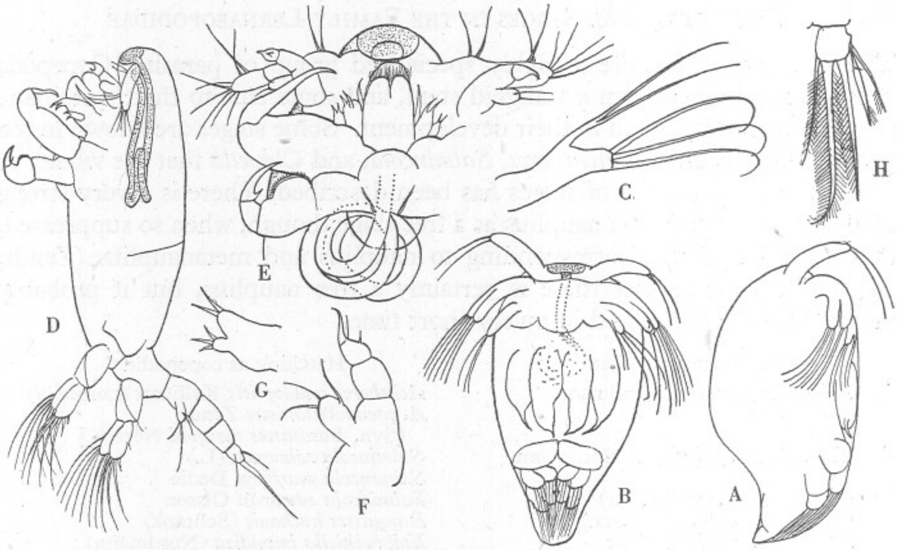

Fig. 1. *Lernaeopoda galei*. A, B, nauplius; C, mandible of nauplius; D, copepodid; E, head region of copepodid, ventral view; F, antenna of copepodid; G, maxillule of copepodid; H, left furcal ramus, ventral view.

There have been three recent papers dealing with the development of Lernaeopods (Zandt, 1935; Dedie, 1940; Friend, 1941) and it is remarkable that there are apparently very great differences in the series of stages. According to Zandt there are no less than six moults, and seven stages in all, which is one more moult and stage than in the development of the free-swimming copepods. Throughout these moults no new appendages are acquired, and the animal remains throughout at the same developmental grade as copepodid I of normal free-swimming Copepoda.

In Table I the series of stages in four species are summarized, and it will be seen that there is a progressive shortening of development. In *S. salmonea*, according to Friend, there are only three moults, and the female has a stage during which she is attached to the host only by the grasping maxillipedes. In *Clavella* there appear to be not more than three moults, and it is possible that the female has a very brief period of freedom after loosing from the head filament and before attachment by the bulla or maxillary disc.

TABLE I. DEVELOPMENTAL STAGES IN FOUR LERNAEOPODS

| | *Achtheres pseudobasanistes* Zandt | *Salmincola mattheyi* Dedie | *Salmincola salmonea* (L.) | *Clavella uncinata* Müller |
|---|---|---|---|---|
| Observer: | Zandt, 1935 | Dedie, 1940 | Friend, 1941 | Gurney, 1934 |
| Stage I | Copepodid 1: free, later attached by head filament | Copepodid 1: the same | Copepodid 1: the same | Copepodid 1: the same |
| II | Copepodid 2: attached by head filament, legs reduced | Metamorphosed; filament detached from head and grasped by maxillae | Filament detached from head and grasped by maxillae | Copepodid 2: legs reduced, attached by head filament |
| III | Filament detached from head and grasped by maxillae | Ditto | Metamorphosed; 1st stage female free, clinging by maxillipedes | Metamorphosed; attached by filament and skin of copepodid |
| IV | Ditto | Ditto | 2nd stage female, attached by bulla | Sexes distinct, female attached by bulla |
| V | Ditto (Legs still traceable) | Sexes distinct; female fertilized, still attached by filament | — | — |
| VI | Approaching adult form; sexes distinct; still fixed by filament | Female attached by bulla | — | — |
| VII | Male free, female fixed by bulla. No further moult | — | — | — |

## THE COPEPODID STAGE OF THE EYE-MAGGOT OF THE SPRAT *LERNAEENICUS SPRATTAE* (SOWERBY)

Leigh-Sharpe (1935) has recorded the occurrence of this species in the spring of 1934 on about 3% of the sprats caught at Hole's Hole in the river Tamar near Plymouth. On 10 April of the same year I found the same percentage of infection on sprats from Hole's Hole, young herrings taken in the same place being entirely free from the parasite. Leigh-Sharpe does not give the actual date of his catch, but it is remarkable that, while his specimens were mature and bearing eggs, not one of mine was full-grown or bore eggs. In no instance was more than one parasite found on one fish. In one specimen a hole was seen in the eye, but no parasite emerging, and on dissection the chitinous remains of an adult specimen were found embedded in a cyst in the eyeball. Sproston & Hartley (1941) found a very much lower percentage of infection of sprats in the Tamar during 1935 and 1936, namely 0·655% among 1376 fish taken throughout the year.

The youngest stage found corresponded to the free-swimming adult stage of *Lernaeocera branchialis* (L.), and was about 3 mm. long, with a part of the abdomen projecting from the hole in the fish's eye, and the head embedded in the tissues at the back of the eye. It is to be presumed that the specimen figured (Fig. 2) is actually the earliest stage in which the fish is attacked. It would seem probable that it does not pierce the eyeball until the abdomen is

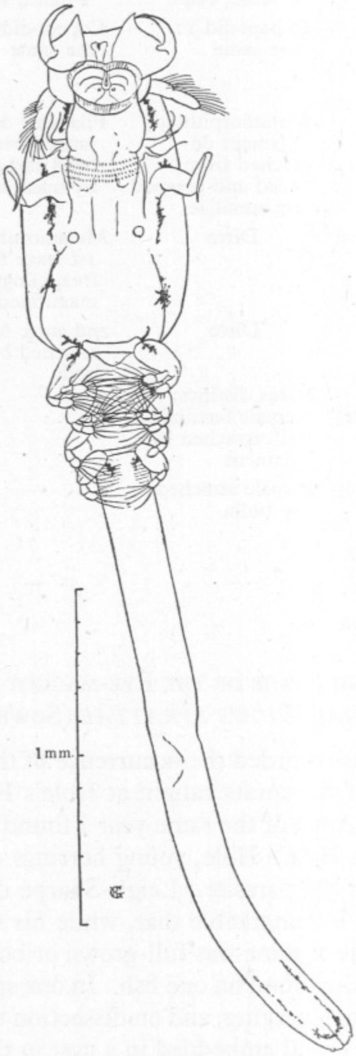

Fig. 2. *Lernaeenicus sprattae* Sowerby. Young specimen from eye of sprat.

long enough to project through the hole made while the head reaches to the back of the eye. The proportion of length of abdomen to cephalothorax is about the same as that in some specimens of *L. branchialis* still attached to the gill of a flounder. While the animal is sufficiently provided with organs of prehension, the circlets of spinules at the base of the mouth cone may also assist in fixation.

I have not found any earlier stages on the body, fins or gills of the sprat, but the number examined is very small and, in view of the rarity of the copepod, the possibility that the early stages are passed on some part of the same host cannot be excluded. I have found none on the gills of a flounder which bore large numbers of larvae of *L. branchialis*.

While it is easy to follow every stage of development on the sprat from the time of attachment to the eye, nothing is at present known about the copepodid stages.

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# THE ANTHEROZOIDS OF *DICTYOPTERIS*

By T. Johnson
Dublin

I should like to place on record the circumstances under which I saw for the first time that the male cells of the *Dictyota* family were not non-motile spermatia but ciliated motile antherozoids.

With the help of a grant from the Royal Society I spent two long vacations (in 1885 and 1886) investigating the marine algae of Plymouth Sound and district, thanks to the facilities provided for such work by the Marine Biological Station at Plymouth. It was usual to spend the morning collecting material by dredging or shore work, sorting it out in the afternoon, and returning for microscopic examination of selected material in the evening. Dredging off the Eddystone yielded male plants of *Dictyopteris* and examination of one piece showed an antheridium in course of breaking up. The contents scattered in all directions as motile bodies starting at the lower right corner, as looked at, and passing gradually to the upper left corner. I never saw anything more clearly under the microscope. I put material in absolute alcohol for further examination but unfortunately did not keep the microscopic specimen or fix the antherozoids with iodine. When I showed my chief (Dr D. H. Scott) my account of the discovery he expressed the opinion, to which I naturally deferred, that it would be incautious to publish anything so startling, based on one observation, and, in consequence, in the published account I spoke of indications that the male cells would prove to be motile. Later on my former pupil Williams (1904) proved the bi-ciliated nature of spermatozoids in the Dictyotales by using material kept in a moist chamber.

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# THE PORTUGUESE MAN-OF-WAR, *PHYSALIA PHYSALIS* L., IN BRITISH AND ADJACENT SEAS

By Douglas P. Wilson, M.Sc., F.R.P.S.

Zoologist at the Plymouth Laboratory

(Plates I–III and Text-figs. 1–5)

CONTENTS

## THE OCCURRENCE OF *PHYSALIA* ON THE ATLANTIC COASTS OF EUROPE

### Past Records

The occurrence of the Siphonophore *Physalia physalis* L. (Portuguese Man-of-war) in large numbers off our south-western shores in the summer and autumn of 1945 was an event almost without parallel in the records for British seas. A search of the literature for the last 100 years or so has produced only the recorded occurrences listed in Table I in which are included strandings on the northern and western coasts of France and of Belgium. The list also includes some hitherto unpublished records preserved at the Plymouth Laboratory; these are discussed in detail below.

Table I. List of Strandings of *Physalia* on the Shores of the British Isles, Northern and Western France and Belgium

| Year | Season or month | Locality | Number | Wind | Reference |
|---|---|---|---|---|---|
| 1834 | March | Ardmore, Co. Waterford | One | — | Thompson (1835) |
| 1852 | — | La Rochelle | Several, at least | S.-S.W. persistent | De Quatrefages (1854) |
| 1862 | Aug. | Isle of Wight | Hundreds | After gale | Rogers (1862) |
| 1862 | Summer | Torbay, S. Devon | Three | — | Gosse (1865) |
| 1884 | Sept. | Dunkerque | One dead | After storm | Théry (1887) |
| 1907 | May | Valentia | One | — | Delap (1924) |
| 1907 | Aug. | At sea, 50° 16′ N., 11° 27′ W. | One | — | Stelfox (1936) |
| 1912 | March | Roscoff | One | — | de Beauchamp (in Caullery, 1912) |
| 1912 | April | Boulogne | Dozen | After westerly gales | Caullery (1912) |
| 1912 | April | Knocke (Belgium) | Three | After westerly gales | Lameere (1912) |
| 1912 | March–April | Seaford, Rye, etc. to Ilfracombe | Thousands | After strong south to south-westerly winds | This paper |
| 1913 | Feb.–April | Bigbury Bay, Plymouth Sound, Looe, and Aberystwyth | Several | After strong south to west winds | This paper |
| 1919 | — | Guéthary | Numerous | — | Pérèz (1929) |
| 1921 | Jan. | Bantry, Co. Cork | Great shoal | — | Delap (1924) |
| 1934 | Oct.–Nov. | Perranporth to Polzeath, N. Cornwall | Several | After strong south to west and north-west winds | This paper |
| 1934 | Autumn | Hook Tower Lighthouse, Co. Wexford | One | — | Stelfox (1936) |
| 1934 | Nov. | Tragumina, Co. Cork | One | — | Stelfox (1936) |
| 1935 | Oct. | Hook Tower Lighthouse, Co. Wexford | One | — | Stelfox (1936) |
| 1935 | Oct. | Mullion Cove, S.W. Cornwall | One | After westerly winds | This paper |
| 1935 | Nov. | Newquay, N. Cornwall | One | After strong westerly winds | This paper |
| 1945 | July–Oct. | Cornwall, Devon, S. and N. Wales, Eire | Large shoals | Fully discussed below | This paper |
| 1945 | July–Oct. | Roscoff | Several | — | Bocquet (private communication) |
| 1945 | Aug.–Sept. | Concarneau | Large numbers | — | Bouxin & Legendre (1946) |
| 1945 | Dec. | Mousehole, Cornwall | Three | After S.W. gale | This paper |
| 1946 | Jan. | Whitsand Bay, Cornwall and Penzance | A few | After S.W. gale | This paper |
| 1946 | July–Sept. | Guéthary to La Rochelle | Enormous swarm | — | Weill (1946) |

Only in 1862 and 1912 does there appear to have been anything comparable with the strandings of 1945. On 7 August 1862 hundreds of *Physalia* were washed ashore on the Isle of Wight (Rogers, 1862) but data for other parts of the coastline do not exist apart from three specimens seen near Torquay that summer (mentioned by Gosse, 1865, p. 256). For 1912 there are very few published data (Caullery, 1912 and Lameere, 1912) but whilst endeavouring to check a reference to strandings under this Laboratory (*Plymouth Marine Fauna*, 1931, p. 84) I found some correspondence relating to the occurrence of *Physalia* in great abundance that year. They were seen at points along the south coast westwards from Rye Bay to the Isles of Scilly and northwards to Aberystwyth during the months of March and April. With the correspondence was the typescript of an unpublished article by Professor J. H. Orton, then a naturalist on the staff of this Laboratory. There were also a few further records for strandings in 1913 and these are listed below together with those for 1912.

TABLE II. RECORDS OF STRANDINGS OF *PHYSALIA* ON THE SHORES OF ENGLAND AND WALES IN 1912 AND 1913

| 1912 | Locality | Number | Observer |
|---|---|---|---|
| | A. SOUTH COAST SERIES | | |
| ? March | Isles of Scilly | — | Mr Ritchie |
| 9 and 10 March | Plymouth Sound | — | Mr (now Professor) J. H. Orton |
| 12 March | Bigbury Bay, Devon | Thousands | Mr F. Chandos-Pole |
| ? March | Looe, Cornwall | — | Mr C. H. Drew |
| 23 March and subsequently | Seaford, Sussex | Very many | Mr S. F. Maurice Dauncey |
| 3 April | Rye Bay, Sussex | One | Mr F. Slade |
| | B. WEST COAST SERIES | | |
| 17 March | Thurlestone Sand, near Aberystwyth, Cardigan | Several | Mr C. L. Walton |
| 20 March | Cardigan Bay | One | Mr H. J. Fleure |
| 2 and 3 April | Ilfracombe, N. Devon | Many | Mr E. S. German |
| 1913 | | | |
| 10 Feb. | Looe, S. Cornwall | Several | Dr A. Adams |
| 17 March | Aberystwyth, Cardigan | One | Mr C. L. Walton |
| 23 March | Bigbury Bay, S. Devon | Several | Mr F. Chandos-Pole |
| 25 March–2 April | Plymouth Sound | Several | Mr (now Professor) J. H. Orton |

Credit for several of the records in 1912 is due to Mr W. R. Adams of Camberwell, London, who wrote to several of his friends on the coast and thereby produced the records for Seaford, Rye and Ilfracombe. On 3 April 1912 he received in London twenty-four living *Physalia* from Ilfracombe; although battered they were placed in the sea-water aquarium of the Horniman Museum where they survived a short while. Mr Adams also got one of his friends to search at Dover but no *Physalia* was found there. He mentions in a letter dated 6 April 1912 that a correspondent writing to *Country Life* stated that the species was washed up at Bognor.

The records for 1934 have not previously been published. They refer to several specimens stranded between Perranporth and Port Isaac on the north coast of Cornwall from 30 October to 12 November. Some of the specimens were sent to the Plymouth Laboratory for identification.

TABLE III. RECORDS OF STRANDINGS OF *PHYSALIA* IN NORTH CORNWALL IN 1934

| 1934 | Locality | Number | Observer |
|---|---|---|---|
| 30 Oct. | Perranporth | One | Mr N. Light |
| 3 Nov. | Polzeath | Several | Mrs B. C. Peirson |
| 5 Nov. | Padstow district | Several | Mr A. G. Blaydes |
| First week Nov. | Newquay | One | Mr F. S. Russell |
| 12 Nov. | Port Isaac | Two | Mr R. A. Todd |

On 18 October 1935 a specimen picked up at Mullion Cove was sent to this Laboratory by Miss E. M. L. Hendriks and on 3 November in the same year another one was seen on Fistral Beach, Newquay, by Mr F. S. Russell. Both these records are here published for the first time; they are included in Table I.

The 1945 records are listed in Table IV and discussed in detail below. Since their occurrence Weill (1946) has recorded an enormous swarm of large *Physalia* on the beaches of south-west France from Guéthary to La Rochelle from the end of July to the end of September 1946. So far as I have been able to ascertain there are no English records for this period.

In addition to the above definite records there are a few other references to be noted. De Quatrefages (1854) obtained specimens at La Rochelle which enabled him to make his extensive studies on the organization of *Physalia*. Gosse stated (1865, p. 255) that 'scarcely a season passes without one or more of these lovely strangers occurring in the vicinity of Torquay'. Perhaps they were more frequent in his day than they are now. In a note to Théry's paper (1887) Giard states that Beltremieux in his *Fauna de la Charente Inférieure* indicates that *Physalia* is found very rarely at La Rochelle and that Lafont has seen it at Arcachon, but no dates are given. Vanhöffen (1906) says that Owen saw it on the coast of Cornwall and McIntosh at Southport and the Hebrides, but gives no references and I have not been able to find them.

It is evident from the above that *Physalia* may be expected to reach French Atlantic and English shores from time to time after absences of several years, but that strandings in great abundance are only likely to take place three or four times in a century. They can arrive in any season of the year. Those who have recorded the presence of *Physalia* have generally referred to stormy weather or to strong or persistent winds from the south to west quadrant preceding the strandings, and this question will be discussed in a later section.

Two points may be made now. If the dates for the main occurrences this century be examined there is a suggestion of an 11-year periodicity, 1912 (no records for 1923), 1934, 1945, close to the sun-spot minima. The remainder of the records, particularly those for the nineteenth century, however, do not seem to bear this out, they do not have a similar periodicity or correspondence with sun-spot activities.

Another feature to be noted is the frequent occurrence of *Physalia*, generally in smaller abundance, the year following a main invasion; thus 1946 after 1945, 1935 after 1934, 1913 after 1912. It suggests that an abundance one year is likely to be followed by further, though fewer, specimens the next.

## THE 1945–46 RECORDS FOR THE BRITISH ISLES

On 31 July 1945 there appeared in *The Times* a letter from Professor J. H. Orton recording the capture of a *Physalia* at Trevone, north Cornwall and requesting the forwarding to him of any further specimens that might be found. On the same day we received at the Plymouth Laboratory a preserved specimen from Major A. A. Dorrien Smith, Tresco, Isles of Scilly taken by him a few days previously; he stated that he first saw the species floating at sea on 2 July. On 3 August we received from him a living specimen in first-class condition; this specimen was kept alive for several days enabling a series of photographs to be taken, three of which are reproduced on the plates accompanying this paper. A set of photographs and an article were despatched on 7 August to *The Illustrated London News* with the aim of calling attention to the presence of *Physalia* in our waters and reinforcing Professor Orton's appeal for specimens and records. The article was not published until 1 September but it had the effect of re-stimulating interest just as the response to *The Times* letter was dying down. Both Professor Orton and I received numerous letters and several specimens and he has very kindly handed all his correspondence over to me and I am therefore able to deal with the observations as a whole.

This is probably the first time that such a complete set of records of the strandings of a subtropical organism on our shores has been got together. Whilst obviously many must have gone unrecorded, for not every one sees the particular newspaper and periodical mentioned, or would take the trouble to write had they done so, it can, I think, be safely assumed that the records do give a fair sampling of the distribution of the *Physalia* and that with the exception of Eire an absence of reports does indicate a real absence of the siphonophore. On that basis the reports will be discussed.

Below is a list of records in order of dates of finding as closely as the correspondents gave them together with their own estimate of the numbers involved. Few gave an estimate of size but from those who did, and from the specimens sent, it is obvious that the pneumatophore length varied from about 2 in. to about 9 in. (5–23 cm.). There is no doubt at all that apart from damage due to stranding the *Physalia* were in excellent condition and those seen at sea

## TABLE IV. LIST OF STRANDINGS OR SIGHTINGS AT SEA OF *PHYSALIA* DURING THE SUMMER AND AUTUMN OF 1945 AND EARLY 1946

| Date (1945) | Locality | Number | Observer |
|---|---|---|---|
| 2 July | Isles of Scilly | One | Major A. A. Dorrien Smith |
| Early July | Sennen Cove, Cornwall | One | Mr G. L. Norris |
| End of first week | Sennen Cove, Cornwall | One | Mr W. Finsbury |
| 6 July | Isles of Scilly | One | Mrs Wakefield |
| 14 July | Polzeath, Cornwall | One | Mrs Robert Fraser |
| Mid-July | Isles of Scilly | Several | Major A. A. Dorrien Smith |
| 20–30 July | Porthgwarra, near Porthcurno, Cornwall | Five | Mr Donald Boyd |
| 22 July | St Ives Bay, Cornwall | One | Mrs Mary Riley |
| 24 July | Trevone, Cornwall | One | Prof. J. H. Orton |
| 25 July | Isles of Scilly | One | Major A. A. Dorrien Smith |
| 28 July | Isles of Scilly | One | Major A. A. Dorrien Smith |
| 28 July | Trevose Head, Cornwall | One | Miss H. J. Wilkins |
| 29 July | Crantock Beach, near Newquay | One | Miss D. M. Wilde |
| 30 July | Port Isaac, Cornwall | Two | Mr P. W. S. Andrews |
| 31 July and previous four days | St Ives, Lelant Beach, Cornwall | One<br>Six | Mrs Denise M. Hinckley |
| 31 July | Penzance, Cornwall | Many | Prof. Hugh Sellon |
| 31 July | Polzeath, Cornwall | One | Mrs Robert Fraser |
| Last week in July | Isles of Scilly | Several hundreds | Mr John Craxton |
| 1 Aug. | St Ives, Cornwall | Three, but numerous in district | Mr A. Naysmith |
| 1–7 Aug. | Isles of Scilly | Seen daily, several | Cadet H. Wakefield |
| 2 Aug. | Near the Bishop Light | Quite eight or ten | Major A. A. Dorrien Smith |
| 3 Aug. | Isles of Scilly | One | Major A. A. Dorrien Smith |
| 3 Aug. | St Ives, Cornwall | Five, but there were a number of others | Master Oliver Hinckley |
| 5 Aug. | Godrevy Beach, St Ives, Cornwall | One | Mrs V. Alport |
| 5 Aug. | Crantock Beach, Newquay, Cornwall | One | Miss D. M. Wilde |
| 6 Aug. | Carbis Bay, St Ives, Cornwall | Two | Miss Phyllis M. Angove |
| Beginning of Aug. | Nevin, N. Wales | Two | Honours Student of Prof. Brambell |
| 6 Aug. | Perranporth, Cornwall | One | Mr Bernard D. Burch |
| 7 Aug. | St Ives, Cornwall | One | Mrs V. Alport |
| 7 Aug. | Lundy Cove, Portquin Bay, Cornwall | Four | Miss Rosalind Fraser |
| 13 Aug. | Isles of Scilly | Two | Major A. A. Dorrien Smith |
| 20 Aug. | Trevone, Cornwall | Two | Mr Edward M. James |
| 23 Aug. | Watergate Beach, Cornwall | One | Miss Mary Stokes |
| 24 Aug. | Sennen Cove, Cornwall | Two | Captain A. Carter |
| 25 Aug. | Croyde Bay, Devon | One | Mr A. A. N. Gardener |
| 25 Aug. | Westward Ho, Devon | Three | Master G. A. Young |
| Last week of Aug. | Nantrum end of Croyde Bay, Devon | Three | Mr G. H. Jenkins |
| 28 Aug. | Seven Stones, Isles of Scilly | Several | Major A. A. Dorrien Smith |
| 29 Aug. | Off Wolf Lighthouse | One | Mrs Wakefield |
| 31 Aug. | Wolf Rock | One (four or five the previous day) | Mr P. H. T. Hartley |
| 1 Sept | Tenby, S. Wales | Two | Lieut. J. N. Atkinson |
| 2 Sept. | Tenby, S. Wales | Several | Mr B. R. Symes |
| 2 Sept | Isles of Scilly and to westward | Quite a number | Major A. A. Dorrien Smith |

TABLE IV (*cont.*)

| Date (1945) | Locality | Number | Observer |
|---|---|---|---|
| Early Sept. | Caldy Island, S. Wales | One | Dr Colin Mathieson |
| Early Sept. | Tenby, S. Wales | Six | Dr Colin Mathieson |
| Second week of Sept. | Bigbury Bay, S. Devon | Two | Lieut.-Com. E. G. Beazley |
| Week prior to 16 Sept. | At sea, near Dartmouth | One | Mr. W. J. Wallis |
| Week before 17 Sept. | St Mawes, S. Cornwall | Several | Mr V. Heather |
| Mid-Sept. | Land's End, Cornwall | Numerous | Prof. Hugh Sellon |
| Second and third week Sept. | Lizard, S. Cornwall | Several | Miss G. M. Puyer |
| 15 Sept. | Porth Nanven, near Land's End, Cornwall | Two | Mr P. H. T. Hartley |
| 17 Sept. | Mill Bay, near Land's End | Scores | Mr Lawrence Leith |
| On or about 17 Sept. | Mousehole, Penzance | A number | Miss Ruth Adams |
| 17 Sept. | Druidston, near Haverfordwest, Pembroke | One | Mr A. N. Grace |
| 18 Sept. | Manorbier, Tenby, S. Wales | One | Miss Gladys Flynn |
| 19 Sept. | St Anthony, S. Cornwall | Three | Mr E. C. Richards |
| 19–23 Sept. | Annestown, near Tramore, Co. Waterford | Considerable numbers | Miss M. A. Walker |
| 23 and 24 Sept. | Woolacombe Bay, Devon | Twenty-seven, and must be others | Mrs Evelyn J. H. Pollard |
| 23 Sept. | Widemouth Bay to Hartland Bay, Bude Bay | Very many | Mr C. D. Barrett |
| 24 Sept. | Croyde Beach, Devon | One | Mrs E. L. Balmer |
| 24 Sept. | Porth Headland, near Newquay, Cornwall | Four | Mr R. S. Funnell |
| Sept. | Bude, Cornwall | Several | Mrs Elsie E. Sampson |
| 25 Sept. | Land's End, Cornwall | Still coming ashore | Prof. Hugh Sellon |
| 25 and 26 Sept. | Combe Martin and Heddon's Mouth, Devon | One at Coombe Martin, two at Heddon's Mouth | Mr J. Hobart |
| 25 and 27 Sept. | Borth, Cardiganshire | Many | Mrs A. M. Nicholson |
| About 25 Sept. | St Bride's Bay, Pembroke | One | Dr Colin Mathieson |
| 26 Sept. | Borth, Cardiganshire | Three | Mrs M. Franks |
| 26 Sept. | Trevone, Cornwall | Five | Dr R. M. Boveri and Mr W. M. Lindley |
| 27 Sept. | Rhosneighr, Anglesey | Ten or so | Mr. P. M. A. Plews |
| 27 Sept. | Cheyne Beach, Ilfracombe | Two | Mr A. S. Cutcliffe |
| 28 Sept. | Westward Ho, Devon | Two | Col. G. H. Young |
| 30 Sept. | Fistral Bay, Newquay | Four | Mr F. S. Russell |
| End of Sept. | Bude, Cornwall | Several | Mr E. G. Ricketts |
| End of Sept. | Perranporth, Cornwall | Hundreds in the sea | Mrs M. Stuart |
| 4 Oct. | Gwenver Beach, near Land's End, Cornwall | One | Mr P. H. T. Hartley |
| 10 Oct. | Isles of Scilly | Several | Major A. A. Dorrien Smith |
| Mid-Oct. to late Oct. | Ballyteige Burrow, S. Wexford | Fairly plentiful, one every ½ mile or so | Mr W. J. Scallan |
| 31 Oct. | Rhosneighr, Anglesey | Two | Mr P. M. A. Plews |
| 20 Dec. | Mousehole, Cornwall, | Three | Mrs E. Pearce |
| 1946 | | | |
| 12 Jan. | Whitsand Bay, S. Cornwall, near Plymouth | One | Mrs Hawkes |
| 13 Jan. | Gwenver Beach, Penzance | A few | Mr T. G. Wm. Fowler |

in full health and vigour and not feeble or dying. Several persons were severely stung, some whilst bathing, and bore testimony to the pain inflicted. Miss M. A. Walker, who in addition to writing to me published her observations, has an amusing note (Walker, 1946) that the 'local people at Annestown were convinced that the balloon-like floats of *Physalia* had poison gas in them and gave them a very wide berth'. Whenever they were stranded in any numbers they aroused much interest among the general public who were attracted by the brilliance and beauty of the colouring.

## METEOROLOGICAL CONSIDERATIONS

*Physalia* is blown along by the wind which seems to have a greater influence on its movements and distribution than the ocean currents. It is to the winds that we should first look in attempting to account for the recurring invasions of our seas by these oceanic organisms of lower latitudes.

### *Past Records*

The references to past strandings have generally been accompanied by mention of strong winds from south to west. Thus de Quatrefages (1854) says that his specimens collected at La Rochelle in 1852 arrived after persistent winds from the south or south-west. In 1862 Rogers refers to a 'terrific gale' and Théry (1887) to 'quelques jours d'un vent assez violent' in September 1884.

For 1912 we have Caullery's statement that preceding the strandings in April 'l'hiver et le début du printemps dernier se sont signalés sur nos côtes de la Manche par des tempêtes d'ouest répétées' and Orton, in the unpublished article already referred to says: 'There can be little doubt that the presence of *Physalia* on the south coast of England in March and April 1912 was due to the almost continuous southerly to south-westerly winds indicated in the eastern part of the Atlantic in the Meteorological Reports for the early part of that year.' This I have checked from the Daily Reports for 1912; they show a great preponderance of strong (Beaufort Scale 4–7) south to west winds throughout the last three weeks of February and most of March in the region of Scilly. From the end of March and in early April the winds were mainly west to north and again strong. From about 12 April for the rest of the month the winds were mainly light with an easterly component between south and north and with north-east and south-east winds frequent. Probably this change of wind was responsible for the disappearance of *Physalia* from the area after the first few days of April. Orton goes on to say: 'It is interesting to note that at the end of March northerly winds set in in the eastern part of the English Channel. This circumstance probably explains why *Physalia* and *Velella* were driven on to the French side of the Straits of Dover.'

The 1913 strandings, which were nothing like as numerous and extensive as were those of 1912, similarly occurred after strong winds mainly from the south and west. The Daily Weather Report shows that in the region about Scilly there was nearly a fortnight of mainly strong west to south winds preceding the stranding at Looe on 10 February. A period of mainly variable south-east to north-east winds followed until the last two days of the month when the wind was light and northerly. On 2 March strong westerly winds set in and were blowing on most days until the strandings at Bigbury on 23 March. Between that date and 2 April (the last date given in Orton's unpublished data for strandings in Plymouth Sound) the wind was often strong but variable in direction, often easterly or from the south or the north-west. Easterly and northerly winds continued for some days.

The 1934 records are for the short period from 30 October to 12 November. The Daily Weather Report shows that at the Scilly Isles strong south to west winds (Beaufort Scale 4–7) were blowing from 20 to 27 October after which the winds went to the west to north quadrant immediately preceding the first stranding at Perranporth on 30 October and remained there until 2 November when they shifted towards the south. On 4 and 5 November the wind was blowing strongly from the north-east and thereafter varied mainly between north and west until the final stranding on 12 November which was followed by a period when strong to light north to north-east winds predominated. *Physalia* at sea may have been blown out of the district by the change of wind, but as no special search was made for them this cannot be established. The few records available for this year arise solely from a few interested persons sending along for identification what were to them strange specimens. There may have been others of which we know nothing.

The 1935 specimens were stranded after winds from a westerly direction. The second half of September in that year was characterised by strong winds at Scilly mainly from between south-west and north-west and except for a few days these winds persisted throughout October and well into November.

### *The* 1945–46 *strandings and the influence of the wind*

For the period in question Monthly Weather Reports have been published by His Majesty's Stationery Office which give summarized data for frequencies of wind force and direction at different stations for the British Isles; those for direction are utilized below. I am greatly indebted to the Meteorological Office of the Air Ministry for this and much other information including daily wind speed and direction for the Scilly Islands and special investigations into the origin and route of various air masses. The Meteorological Service, Dublin, have also been most helpful in supplying wind direction frequencies for Roches Point and Valentia.

The area in which strandings of *Physalia* occurred, or in which it was observed at sea, covers the western approaches to the English Channel and the St George's and Bristol Channels. Leaving aside for the time being the question of the more distant origin of the swarms of *Physalia*, and considering only what happened to them once they had arrived within that area, we can obtain a fairly good picture of the air movements which drove them to and fro therein by combining the wind direction frequencies for the seven stations St Ann's Head, Pembroke; St Athan, Glamorgan; Plymouth, Devon; The Lizard, Cornwall; St Mary's, Scilly Isles; Valentia, Co. Kerry; Roches Point, Co. Cork. For the first four stations I have utilized the data for 09.00 hr. G.M.T. as given in the Monthly Weather Report; for Scilly the wind-rose data from the Summary for the Year 1945, and for Valentia and Roches Point the data for 07.00 hr. G.M.T. sent to me from the Meteorological Service, Dublin. There are no outstanding differences between any of these stations and by combining them in this way an average direction frequency is obtained which can be relied on to represent with sufficient accuracy wind conditions throughout the area. Unfortunately, the data do not permit wind force to be combined with the average directional frequencies, but some idea of the force can be obtained from the wind roses for Scilly published in the Monthly Weather Reports, and from the daily records from the Scilly Islands considered below.

Table V. Average Frequency of Wind Direction from eight points for seven Stations to the nearest whole frequency

| 1945 | N. | N.E. | E. | S.E. | S. | S.W. | W. | N.W. | Calm |
|---|---|---|---|---|---|---|---|---|---|
| June | 2 | 0 | 1 | 1 | 3 | 8 | 8 | 4 | 1 |
| July | 5 | 2 | 1 | 2 | 5 | 5 | 5 | 4 | 2 |
| Aug. | 4 | 3 | 3 | 3 | 2 | 4 | 6 | 3 | 3 |
| Sept. | 2 | 3 | 5 | 2 | 3 | 6 | 4 | 3 | 2 |
| Oct. | 1 | 3 | 7 | 3 | 4 | 4 | 4 | 1 | 4 |
| Nov. | 1 | 3 | 10 | 6 | 2 | 1 | 1 | 1 | 4 |
| Dec. | 2 | 1 | 2 | 4 | 4 | 5 | 6 | 5 | 1 |

Whilst in Table V it is obvious that in June south-west and west winds predominated, winds favourable to the arrival of *Physalia* from the west, and that in November easterly and unfavourable winds prevailed, a clearer picture can be obtained if all favourable winds be grouped together and considered as a whole, and all unfavourable winds grouped in a similar way. Before this can be done, however, it is necessary to consider which winds can be classed as favourable in the sense of blowing the siphonophores once in our area on to our shores, and which unfavourable in that they will blow them back into the open ocean. A map shows that the Scilly Islands are directly exposed to the Atlantic over an arc extending approximately from the south to the north-west. Winds from all points embraced by this arc can therefore be expected to favour the stranding of *Physalia* on our shores once other conditions farther out in the Atlantic have brought them as far east as about 10° W. and north to about 48° N. Thus of the eight-point groupings, south, south-west, west and north-west winds can be considered as being favourable, especially the last three so far as strandings on the north coast of the Devon and Cornwall peninsula are concerned. On the other hand, the north, north-east, east and south-east winds are unfavourable, they blow floating objects away and towards the open sea, though the north wind would favour the stranding on the north coast of Devon and Cornwall of *Physalia* which happened to be in the Bristol Channel, and therefore, rather like the south wind is somewhat neutral in its effect. Table VI shows the eight-point wind frequencies from all seven stations grouped and averaged to the nearest whole frequency in this manner. They have been calculated directly from the original data and not compiled from Table V which is itself an average.

From Table VI it is clear that in June the winds were almost wholly favourable on 20 out of 30 days, blowing from between the south-west and north-west. The Monthly Weather Report for June 1945 states that 'southerly and westerly winds were frequent and the month was windier than usual on the whole in England'. In July 14 days were wholly favourable as against 5 days unfavourable. There were 5 days of winds from the south and 5 days from the north; as will be shown later the north winds were mainly confined to the last week of the month so that the first 3 weeks of July continued the favourable weather of June and the winds from the south to the north-west were often strong during that period.

TABLE VI. AVERAGE WIND DIRECTION FREQUENCIES FROM EIGHT POINTS AT 09.00 HR. G.M.T. GROUPED INTO FAVOURABLE AND UNFAVOURABLE WINDS FOR STRANDING ON THE ASSUMPTION THAT *PHYSALIA* TRAVELS DIRECTLY BEFORE THE WIND

| | Favourable | | | | Unfavourable | | |
|---|---|---|---|---|---|---|---|
| 1945 | S.W., W. and N.W. | S. | Total | Calm | N.E., E. and S.E. | N. | Total |
| June | 20 | 3 | 23 | 1 | 3 | 2 | 5 |
| July | 14 | 5 | 19 | 2 | 5 | 5 | 10 |
| Aug. | 13 | 2 | 15 | 3 | 9 | 4 | 13 |
| Sept. | 13 | 3 | 16 | 2 | 9 | 2 | 11 |
| Oct. | 10 | 4 | 14 | 4 | 13 | 1 | 14 |
| Nov. | 4 | 2 | 6 | 4 | 19 | 1 | 20 |
| Dec. | 16 | 4 | 20 | 1 | 8 | 2 | 10 |

In August the winds continued on the whole to be favourable although there were more occasions on which the wind would tend to move the *Physalia* out to sea. Probably to this is to be attributed the slackening of arrivals during that month. The Monthly Weather Report for August 1945 states that 'the month was less windy than usual. Winds from between north and east were more frequent than the average'.

September showed a somewhat similar balance of favourable and unfavourable winds to that of August, though the daily records reveal that the unfavourable winds were confined mainly to the first 9 days of the month and that thereafter westerly weather with strong winds was frequent and could well account for the abundant strandings during the latter half of the month.

In October there were relatively few strandings and we note that winds from north-east to south-east were more frequent than south-west to north-west winds. In November unfavourable winds greatly predominated; there are no records of strandings for this month. December saw a reversal of these conditions and associated with this some *Physalia* were driven back again and there is one record of strandings for late December and two for the first half of January.

So far we have assumed that *Physalia* sails more or less directly before the wind and that the currents have relatively little effect on its directional movements. It is almost certainly true that ordinary slow currents have less effect on the distribution of *Physalia* than have winds of moderate strength and that for present purposes they can be ignored. We cannot, however, ignore the fact that *Physalia* most probably travels at an angle to the wind. On this point the only definite evidence is that of Woodcock (1944) who states that in the northern hemisphere *Physalia* 'is so orientated physically that it is consistently driven by the wind about forty-five degrees to the left of the direction in which the wind is blowing'. The few specimens which I had and which were well enough preserved to show the typical asymmetry of the crest agreed fairly well with Woodcock's figure for northern hemisphere animals (compare my photograph in Plate II with his fig. 46 left-hand side) and we may therefore accept as a working hypothesis his contention that movement will always be to the left of the wind direction in the northern hemisphere and to the extent of about 45°. Perhaps the extent of the deviation varies with wind strength, a fair breeze giving the full 45° to the left, a storm tending to drive the siphonophore more directly before it. Accepting, however, 45° we can regroup the wind frequencies as in Table VII. West to north winds are now the favourable ones with east to south unfavourable. North-east winds will move the siphonophore in a southward direction and are on the whole unfavourable, whilst south-west winds move it north and favour its appearance in the sea area under consideration.

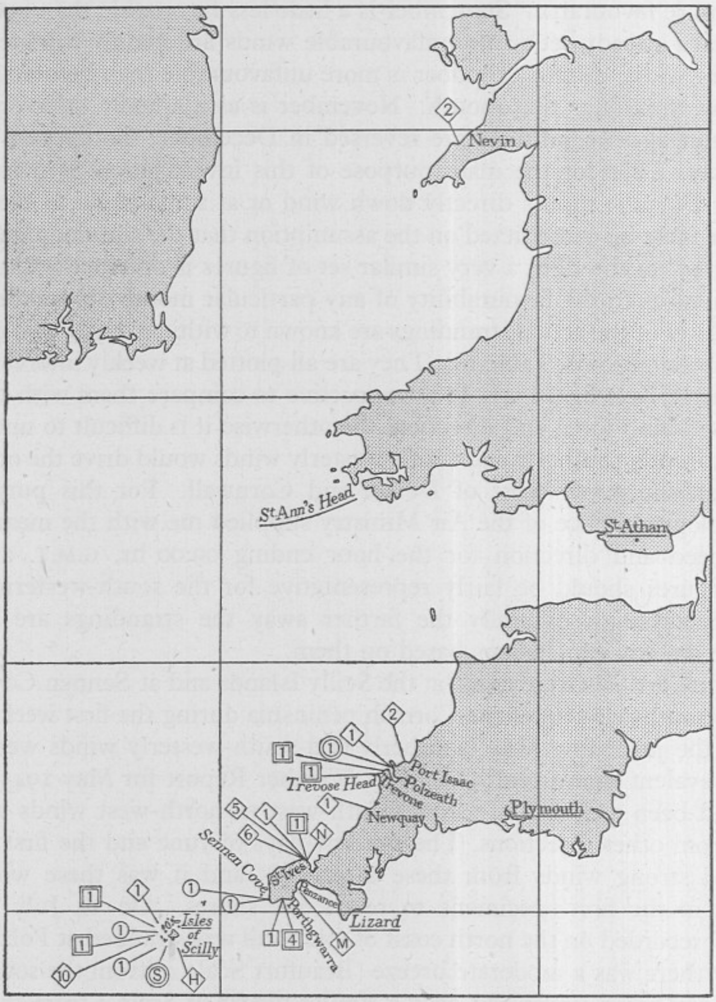
TABLE VII. AVERAGE WIND DIRECTION FREQUENCIES FROM EIGHT POINTS AT 09.00 HR. G.M.T. GROUPED INTO FAVOURABLE AND UNFAVOURABLE WINDS FOR STRANDING ON THE ASSUMPTION THAT *PHYSALIA* MOVES IN A DIRECTION AT 45° TO THE LEFT OF THAT OF THE WIND

| | Favourable | | | | Unfavourable | | |
|---|---|---|---|---|---|---|---|
| 1945 | W., N.W. and N. | S.W. | Total | Calm | E., S.E. and S. | N.E. | Total |
| June | 14 | 8 | 22 | 1 | 6 | 0 | 6 |
| July | 14 | 5 | 19 | 2 | 7 | 2 | 9 |
| Aug. | 14 | 4 | 18 | 3 | 8 | 3 | 11 |
| Sept. | 9 | 6 | 15 | 2 | 10 | 3 | 13 |
| Oct. | 7 | 4 | 11 | 4 | 13 | 3 | 16 |
| Nov. | 4 | 1 | 5 | 4 | 17 | 3 | 20 |
| Dec. | 13 | 5 | 18 | 1 | 10 | 1 | 11 |

It will be seen that grouping in this way makes little difference to the conclusions already reached on the basis that *Physalia* travels directly before the wind. Favouring winds in June are not quite so strongly marked as before but still greatly preponderate. July is hardly affected, whilst August becomes a little more favourable. September is a little less favourable than before but, as we have already seen, the unfavourable winds are mainly confined to the beginning of the month. October is more unfavourable than before and there were few strandings that month. November is as markedly unfavourable as before and again conditions are reversed in December, though not quite so noticeably. Thus for the main purpose of this investigation it matters little whether *Physalia* moves directly down wind or at some angle to the left. If a similar table be constructed on the assumption that the siphonophore would move at 45° to the right a very similar set of figures is obtained and the main conclusions as to the favourability of any particular month are unaffected.

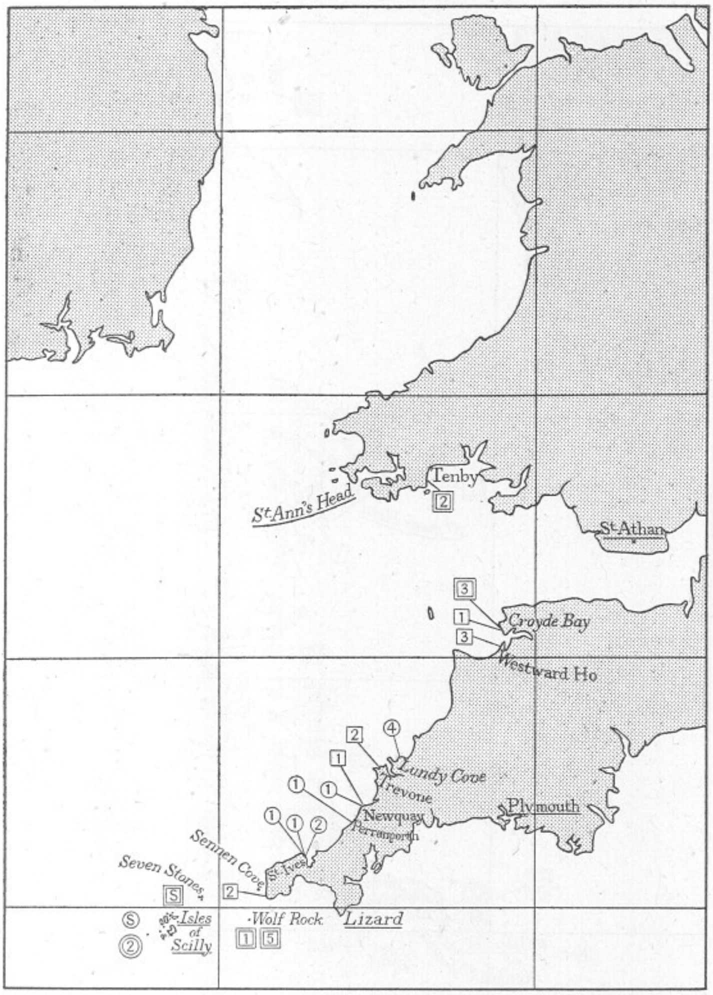
The dates of the actual strandings are known to within a day or two and have already been given in Table IV. They are all plotted at weekly intervals on the four charts (Text-figs. 1–4). It is instructive to compare them with the daily records of wind force and direction, for otherwise it is difficult to understand how apparently southerly and south-westerly winds would drive the organisms ashore on the north coast of Devon and Cornwall. For this purpose the Meteorological Office of the Air Ministry supplied me with the mean hourly wind speed and direction for the hour ending 09.00 hr. G.M.T. at Scilly. These figures should be fairly representative for the south-western area as a whole, although naturally the farther away the strandings are the less accurate are any conclusions based on them.

The first arrivals were noted at the Scilly Islands and at Sennen Cove at the extreme south-west tip of the Cornish peninsula during the first week of July. During the preceding May 'southerly and south-westerly winds were rather more prevalent than usual' (Monthly Weather Report for May 1945), whilst June had been a month of strong south-west to north-west winds with few winds from other directions. The last few days of June and the first week of July had strong winds from these directions, and it was these winds that brought in the first specimens to reach our shores. On 14 July the first *Physalia* recorded on the north coast of Cornwall was stranded at Polzeath; on that day there was a moderate breeze (Beaufort Scale 4) from the south-west, but the day before there had been a similar breeze of Scale 4 from the north-east, and it may have been this wind that brought inshore a specimen which had been travelling up the Bristol Channel. The Trevone specimen of 24 July came ashore on a light north-west wind and the north Cornish ones of 28–31 July were found when the wind was from the north. The other records for this period are for the Scilly Islands and the extreme south-west tip of Cornwall. The strandings at Penzance on 31 July do not fit quite so well into the picture and can only be ascribed to local conditions. The records of large numbers near Scilly for the end of July and the first week of August might just possibly be for specimens which had in mid-July been blown up the St George's Channel and were then travelling back before the northerly winds



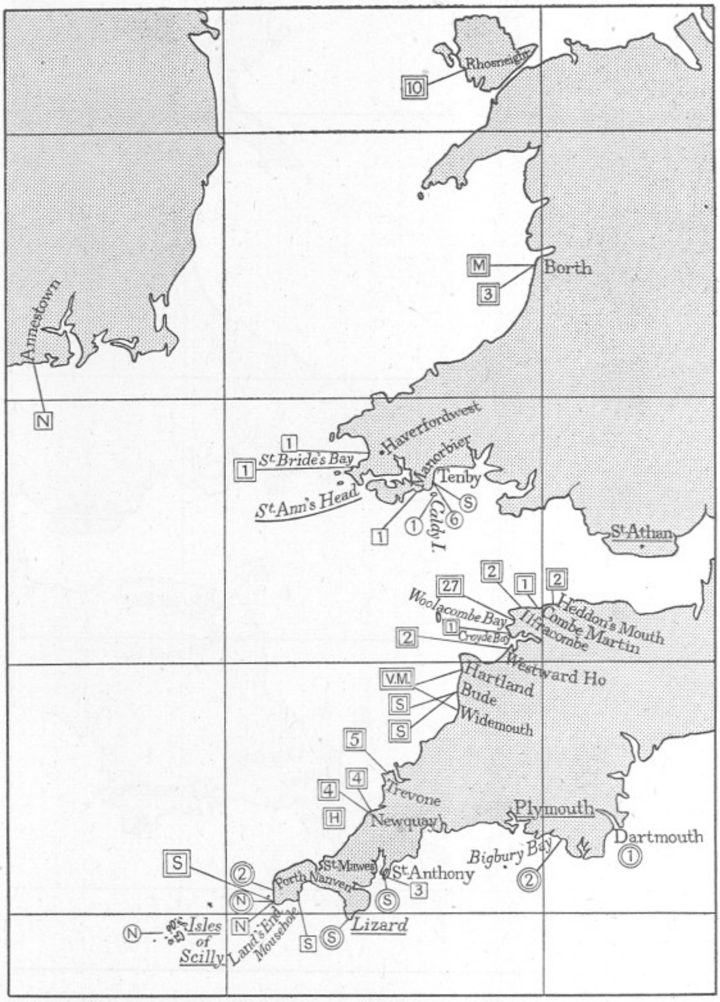
Text-fig. 1. Distribution of *Physalia* in July. ○ 1–7 July; ◎ 8–14 July; □ 15–21 July; ⊡ 22–28 July; ◇ 29 July–4 Aug. Figures and letters indicate number seen. H, hundreds; M, many; N, a number; S, several. Meteorological stations underlined.

which were blowing from about 26 July to 9 August. Colour is lent to this suggestion by a record for Nevin on the Lleyn Peninsula, Carnarvonshire, for the beginning of August. This is an observation by a zoology student at Bangor University College passed on to me by Professor F. W. Rogers Brambell who is convinced, after careful questioning, that the student had indeed seen *Physalia* stranded there at that time. If we accept this observation it does add to the supposition that a shoal of *Physalia* was blown towards the Welsh coasts by the strong south and south-west winds of mid-July. However, we must not lose sight of Woodcock's statement that *Physalia* travels to the left of the wind in which case a north wind would blow the organisms in a south-easterly direction and the large number seen at the Scilly Islands in late July and early August could then have come direct from the Atlantic by skirting the



Text-fig. 2. Distribution of *Physalia* in August. ○ 5–11 Aug.; ◎ 12–18 Aug.; □ 19–25 Aug.; ⊡ 26 Aug.–1 Sept. Figures and letters indicate number seen. S, several. Meteorological stations underlined.

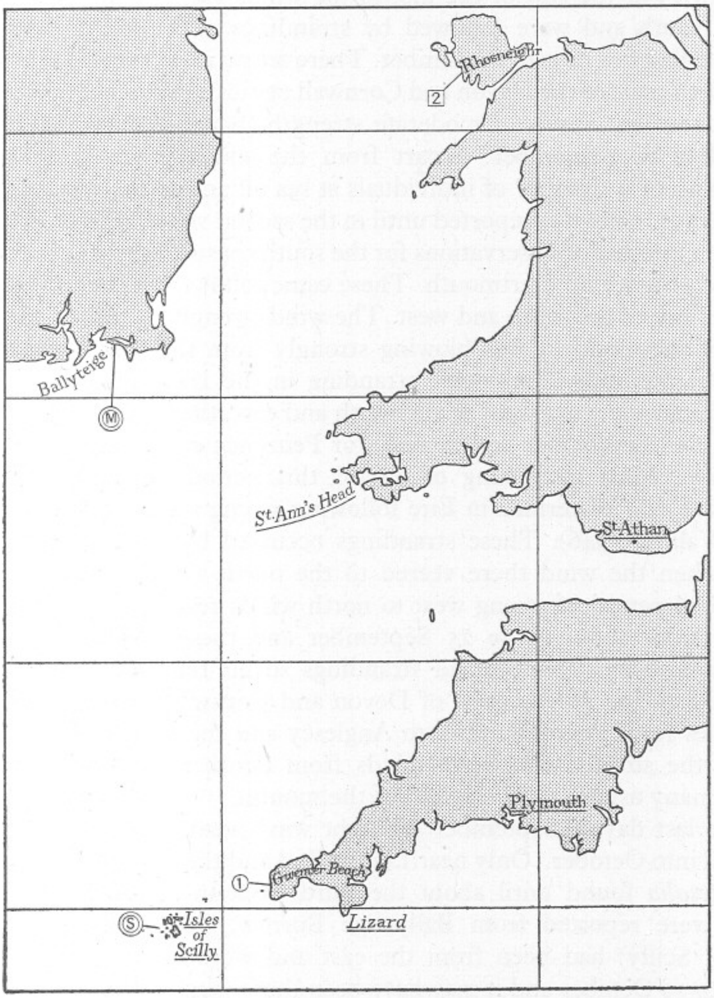
southern shores of Eire. There is always the possibility that the Nevin specimens came through the North Channel though this seems most unlikely in the absence of records farther north. Perhaps a few specimens were carried up the St George's Channel in mid-July, the vanguard of the main shoal which came in from the Atlantic later.



Text-fig. 3. Distribution of *Physalia* in September. ○ 2–8 Sept.; ◎ 9–15 Sept.; □ 16–22 Sept.; ⊡ 23–30 Sept. Figures and letters indicate number seen. H, hundreds; M, many; N, a number; S, several; VM, very many. Meteorological stations underlined.

There are a number of records for 5–7 August, generally of single specimens, on the north coast of Cornwall west of Lundy Cove, Portquin Bay to St Ives.

The wind was mainly from the north and the north-west during this period. Apart from the single observation of two at Scilly on 13 August no more were reported until 20 August. There was a spell of easterly winds (Beaufort Scale 3–5) from 11–14 August which doubtless accounts for the scarcity of records during the middle of the month. Moderate westerly to southerly winds then set in for 3 days after which the wind shifted again to the north and another two specimens were recorded at Trevone on 20 August. On that day a westerly wind was blowing which freshened to a north-west to west gale



Text-fig. 4. Distribution of *Physalia* in October. ○ 4 Oct.; ◎ Mid to late Oct.; □ 31 Oct. Figures and letters indicate number seen. M, many; S, several. Meteorological stations underlined.

on 21 and 22 August and was still blowing strongly from the west and south-west from 23–25 August. Further strandings took place in north Cornwall and for the first time in north Devon at Croyde Bay and Westward Ho on 25 August. For the rest of the month the winds varied mainly between the east and south and were followed by strandings at Tenby in south Wales during the first few days of September. There are no more records of strandings on the north coast of the Devon and Cornwall peninsula until late in September.

North and east winds of moderate strength (Scale 3–4) characterized the first 9 days of September. Apart from the south Wales strandings and the sighting of a number of individuals at sea off and to the westward of the Scilly Islands, none was reported until in the second week when we had for the first time a number of observations for the south coasts of Devon and Cornwall as far east as at sea off Dartmouth. These came following a change of wind on 10 September to the south and west. The wind strength increased until in the middle of the month it was blowing strongly from the south-west. At this time numerous individuals were stranding in the Land's End district. On 17 September the wind went to the south and east, there is another record for Tenby on 18 September and records for Penzance and Falmouth about the same time. Most interesting of all for this period are the strandings at Annestown, Co. Waterford in Eire following strong south-east to south-west winds (Walker, 1946). These strandings occurred between 19 and 23 September when the wind there veered to the north and no more were seen. A disturbed period of strong west to north winds reaching gale force locally occurred from about 21 to 25 September and these resulted in the most numerous and most widespread strandings so far reported. They occurred principally on the north coasts of Devon and Cornwall and on the coasts of west Wales from Pembrokeshire to Anglesey and the quieter weather which followed the storms, with light winds from between west and north, still brought many ashore until the end of the month.

On the last day of September the light wind went to the east and stayed there well into October. Only near Land's End and the Scilly Islands were any more *Physalia* found until about the third week in October when a good number were reported from Ballyteige Burrow, Co. Wexford, Eire. The winds (at Scilly) had been from the east and were strong (up to Scale 7) from 15 to 19 October and it may have been these winds which had blown the *Physalia* remaining in the area away to the westward, stranding some of them on the coasts of Eire. Except for two seen on Anglesey on the last day of the month no more were reported until the end of the year. The easterly winds of November put an end to the visitation except for the few stragglers which came back again on the strong south-westerly winds of December and early January.

Thus by considering the strandings in relation to the wind direction we perceive, in broad outline, the manner in which the shoals of this floating siphonophore as they arrive in our area are driven to and fro by the shifts and changes of the surface air streams, scurried first one way and then another until eventually they either perish by stranding on a lee shore, or are blown back into the ocean whence they came.

### ORIGIN OF THE *PHYSALIA* SWARMS

*Physalia* is a normal inhabitant of the tropical and subtropical Atlantic. Chun (1897) records it as being abundant in the early months of the year at the Canary Islands and states that it is not infrequently blown into the Mediterranean. During the cruise of the *Michael Sars* in 1910 (Murray & Hjort, 1912) *Physalia* with *Velella* was frequently seen while steaming westward from the Canaries to the Azores and on to almost 50° W. in latitudes between 28° N. and 39° N. On the eastward passage higher than 45° N. none was seen. The normal northern limit seems to be about 40° N., but that from time to time the species comes much farther north, sometimes in swarms, is already obvious. Why should this be?

The ready answer to this question is, of course, that it is blown by the wind, that unusual meteorological conditions out in the Atlantic blow it farther towards the north-east than is usual. Unfortunately, an examination of the weather charts for the whole North Atlantic for April, May and June 1945 does not show anything out of the ordinary, except possibly that there were no marked easterly winds between the Azores, Bay of Biscay and south-west England, such as are often, but not invariably, present at that time of year. However, *Physalia* has not appeared in our waters every time easterly periods have been rare. Thus in 1943 there were no easterlies to speak of and only one week (14–21 May) in 1944. (I am much indebted to a friend, Mr B. C. V. Oddie of the Meteorological Office, for the meteorological information recorded in this paragraph.)

In a letter from the Meteorological Office I have received the information that in normal years during the months of May, June and July 'the pressure gradient over the Azores region is normally favourable for winds from between W.N.W. and N.W., except from the 5th to the 29th of June, when the direction is between W. and W.S.W. Over the Canaries or off the coast of Portugal the direction is from between N.W. and N.E. through N.' Assuming that *Physalia* travels at 45° to the left of the direction in which the wind is blowing specimens in the Azores region would travel towards the east or north-east under the influence of these winds and then on nearing Portugal would tend to be diverted southward again. Provided that an abundance of *Physalia* happened to be present in the Azores region during May and June it would not need a very great change in the normal wind direction to carry them towards our shores. Incidentally the surface current charts (M.O. 466, 1945) for these months show that currents north of about lat. 45° N. flow predominantly in our direction whereas off the coast of Portugal and the Canaries, where the winds are also generally unfavourable, they flow in general southward. It seems more probable therefore that the source of an invasion of these waters by *Physalia* is somewhere in the mid-Atlantic Azores region rather than in the region of the Canaries to Gibraltar. The latter cannot, however, be entirely ruled out.

The Meteorological Office has kindly examined the pressure distributions for occasions when the air arriving off the south-west of the British Isles could be traced back more or less directly, (*a*) to the mid-Atlantic Azores region, and (*b*) to the area contained by the Azores, Lisbon and the Canaries. There were three occasions in June and six occasions in July when air originated from north to north-west of the Azores (mainly south of lat. 45° N. and west of long. 20° W.). The time taken by the air to cover this distance varied from about $1\frac{1}{2}$ to 3 days and it is not conceivable that the *Physalia* themselves travelled at that rate though the resultant effect of the air stream would, in the absence of easterlies, have been to push them along in our direction. Air from the Azores, Lisbon, Canaries triangle arrived in June on several occasions during the first 10 days (a period when air also arrived from the Azores district) and during two short periods in July. I feel, however, that these data are too inadequate for conclusions to be based on them.

At the moment it seems impossible to trace these occasional visitations right back to their source. They originate possibly in the first instance through the production of an unusual abundance of individuals brought about by conditions exceptionally favourable for development of the eggs and young. This might take place well to the south and should it coincide with meteorological conditions that drive many farther north than usual, and should they then be caught up in streams of air flowing strongly towards the north-east they will eventually reach the south-westward approaches to these islands, where they will then be driven hither and thither by our local winds as has been shown in the preceding section.

## Associated Organisms

A number of other Atlantic organisms came ashore with the *Physalia*. The records for these are not at all complete and can only be regarded as an indication of what might have been found had the whole of the north Cornish coast in particular been under observation by competent naturalists.

### *Lepas fascicularis* and *L. pectinata*

On 30 September 1945 the Director of this Laboratory, Mr F. S. Russell, found stranded on the Fistral beach at Newquay, along with *Physalia*, several living specimens of the floating barnacle, *Lepas fascicularis* Ellis and Solander, and brought back a number to Plymouth. They varied in size from quite small to specimens with capitula 4 cm. long. They were generally attached to floating strands of *Fucus*, but the larger groups were mainly buoyed up by their gas-bubble floats. With them were a few *Lepas pectinata* Spengler.

*L. fascicularis* has been recorded from time to time before; thus Orton & Rawlinson (1934) report it (with *L. pectinata*) from Trevone, near Padstow, in August 1933 and Professor Orton, in a private letter, tells me that he had it again in September 1944 at the same place. Mr O. D. Hunt (unpublished record) had one specimen, to which were attached three individuals of *L. pectinata* Spengler in the mouth of the River Yealm, S. Devon, in September 1934, the same month and year as Orton & Rawlinson's record. In the museum of the Laboratory there are two small specimens of *L. fascicularis* which were found with *L. anatifera* drifting in Wembury Bay, near Plymouth, in June 1937, and a few *L. pectinata* from a floating buoy in November 1935.

Perhaps both these species would be found in the south-west more frequently than is at present realized were it possible for competent naturalists to keep a constant watch for them along the whole of the coast-line. As it is, Orton & Rawlinson found only seven or eight records of the appearance of *L. fascicularis* 'on the south coasts of England and the same number for the west and north of Ireland'. They also state that '*L. pectinata* has been recorded only about five times since 1803 from the coasts of the British Isles'. Their paper should be consulted for the references. It has been stated (see Murray & Hjort, 1912) that *L. fascicularis* regularly invades the northern North Sea through the Faroe-Shetland channel along with other oceanic forms from the Atlantic and that immense swarms of it are to be found there in May and June.

### *Velella*

Along with the *Lepas fascicularis* and the *Physalia* Mr Russell also found many *Velella* skeletons; there were no living *Velella*. Miss Walker (1946) also found one *Velella* float with the many *Physalia* near Tramore in late September 1945. Professor F. W. Rogers Brambell also informs me that he identified a living specimen of *Velella* which was picked up at Llanbeddr, Merioneth, on 11 June 1945 and that on 21 June numerous floats, denuded of tissue, were found among the flotsam at high-water mark in Malltraeth Bay, Anglesey. These are the only records I have been able to collect for 1945; it seems most unlikely that had many living *Velella* been stranded at the same time as the *Physalia* their bright colours would not have attracted attention and specimens been sent to this Laboratory along with its larger relative. There is not the slightest hint in any of the correspondence that *Velella* was also stranded at the same time and it seems reasonable to conclude that only a relatively few living specimens at most could have been present along with the *Physalia*.

I do not propose to discuss past *Velella* records here. They are much more numerous than are those for *Physalia*. Unfortunately it is not always clear whether the records refer to living specimens or only to the skeletons of the floats which survive for a long time after the death of the living tissues. Future recorders would do well to be clear on this point.

### *Turtles*

Three young Loggerhead Turtles, *Caretta caretta* (L.), were sent alive to the Laboratory in August 1945. They are listed below (Table VIII).

There is no doubt that they were true *Caretta caretta* (L.) and not *Colpochelys kempi* Garman (see Deraniyagala, 1939). No. 1 had some growths of living hydroids on the plastron and neck. They seemed to agree with *Clytia johnstoni* (Alder) and *Obelia geniculata* (L.). No. 2 was clean, probably because although found on 10 August it was 24 August before we actually received it. No. 3 had some hydroids on the paddles: apparently *Obelia geniculata* (L.) and a *Gonothyrea* sp. It was stated to have had a cluster of ship's barnacles (*Lepas*) several inches long attached to the plastron; unfortunately they had been removed and were not seen by us. On the carapace were tufts of an alga identified as the American *Ectocarpus Mitchellae* Harv. (see Appendix, p. 171). A photograph of this turtle appears in illustration of an article by Parker (1946).

TABLE VIII. LOGGERHEAD TURTLES FROM NORTH CORNWALL, AUGUST 1945

| | | | Carapace | | |
|---|---|---|---|---|---|
| Specimen no. | Date | Locality | Max. length (cm.) | Max. width (cm.) | Finder |
| 1 | 7. viii. 45 | In the sea off Hayle | 18·5 | 16·5 | Mr S. J. Thomas |
| 2 | 10. viii. 45 | Ashore on Gwithian Sands, Hayle | 20·0 | 16·5 | Master Richard Buckner |
| 3 | 25. viii. 45 | Ashore on Crooklets Beach, Bude | 20·0 | 18·0 | Mr A. E. Jewell |

Stendall (1945) records a specimen of *Caretta caretta* with a carapace 13 in. long found swimming in the River Bann near Castlerock, Co. Londonderry, on 8 August 1945. Freeman (1946) records two small specimens of the same species washed ashore on Sherkin Island, Co. Cork, during a storm in late December 1945. One seen had a carapace 7½ in. long; the other was of about the same size. Mr H. W. Parker of the British Museum (Natural History) informs me that he received three specimens of *C. caretta* stranded as follows:

(1) Collister Beach, west side of Unst, Shetland, 13 December 1945.
(2) Oxwich Beach, Glamorgan, 7 February 1946.
(3) North Uist (west side), Hebrides, 13 February 1946.

Records of strandings of Loggerhead Turtles are fairly frequent in the literature (e.g. Parker, 1939) but in view of the findings of Deraniyagala (see his 1939 paper for references) some of the earlier identifications may have confused the species and some of the Loggerheads previously recorded may have been Kemp's or Ridley's Loggerhead which breeds only, so far as is known for certain, on the American side. The Loggerhead occurs, of course, on both sides of the tropical and subtropical Atlantic but in a recent popular article Parker (1946) discusses the occurrences of both species of turtle on our coasts and inclines to the opinion that they may possibly originate in the Caribbean whence they are started on their journey across the Atlantic by violent local storms. If this be so—the idea is now strengthened by the occurrence of the American *Ectocarpus* in one of the turtles mentioned above—then the turtles stranded with the *Physalia* in 1945, and possibly also those stranded in early 1946, may have been half-way across perhaps near the Azores region in the spring or summer of 1945. They would there be caught up by the same conditions that favoured the passage to our shores of the shoals of *Physalia*, for like the latter, they are surface organisms and, for much of the time at any rate, expose considerable areas of their bodies above the surface of the water.

### *Lampris luna*

One other possibly associated occurrence should be mentioned. This was the capture in Bigbury Bay, S. Devon, on 2 August 1945 of a Moon-fish or Opah, *Lampris luna* (Gmelin). It was taken by holiday-makers whilst struggling, half-stranded, in shallow water, on a falling tide. It was a male over 3 ft. long and weighed 60 lb. The stomach and intestines were opened by Miss Nora G. Sproston; she found the beaks of forty-one cuttlefishes which appeared to have been eaten quite recently and, in addition, the recognizable remains of four sand-eels, two pilchards and other organisms not possible to identify.

Norman & Fraser (1937) state that *L. luna* is widely distributed in the warmer parts of the Atlantic and that it is 'a not infrequent visitor to the coasts of the British Isles during the warmer months'. They go on to say that 'it probably spends a good deal of its time close to the surface, but there is no doubt that at times it descends into deeper water'. If the Bigbury specimen had been spending much of its time at the surface it is just possible that it too had come under the influence of winds and surface drift that favoured its passage towards our south-west coast. On the other hand, it is equally likely that its appearance at the same time as the *Physalia* and turtles was pure coincidence.

## GENERAL CONSIDERATIONS

The occurrence of a number of other organisms from the warmer parts of the Atlantic along with the swarms of *Physalia* in 1945 might be held to indicate a drift of Atlantic water into the approaches to the Channel. The organisms in question, however, should, on the whole, be regarded as wind-borne types rather than water-borne and it does not seem reasonable to consider them as reliable indicators of water movements in the way that some wholly submerged plankton organisms can be so regarded. Unfortunately, owing to the lack of a suitable vessel it was not possible at the time to make a proper search for any such indications at sea.

Stephen (1938), Russell (1939) and others have referred to the northward spread during the 1930's of warm-water organisms in the North Atlantic corresponding to a rise in temperature of the northern surface waters of that ocean and its branches such as the North Sea. Such a rise, if maintained, might well be a factor in assisting the penetration northward of an organism such as *Physalia*, enabling it perhaps to breed in latitudes higher than is usual, perhaps thus favouring the formation of shoals of the adult in a region whence the winds blow mainly towards our shores. However, Dunbar's recent investigations (1946) into the temperature records for the west Greenland current have shown that whereas a warm period appears to have reached its peak in the middle of the 1930's, more recent years, particularly 1942–4 have shown a cooling due to a weakening of the Atlantic influence. If this return to colder conditions be general for the North Atlantic, *Physalia* and the other organisms penetrated northward in 1945 in spite of rather less favourable temperatures than had perhaps aided their predecessors in 1934. The facts, indeed, once again point to the wind as being the main factor responsible for these occasional visitations of animals from southern regions, water movements playing only a minor role in their distribution.

## THE CAPTURE AND DIGESTION OF PREY

### Historical

The virulence of *Physalia* stings and the strange manner of digestion of its relatively large prey have often been described and yet, as Gudger (1942) truly remarks, 'only a few students of marine life have seen *Physalia* catch and eat fishes, and their accounts are widely scattered in scientific books and journals'. He does a real service by gathering together the few such accounts of any importance which are available, and he gives a number of references not quoted here. According to him the earliest first-hand recorded observation of the fish-eating activities of *Physalia* is by Quoy & Gaimard (1824). Bennett (1837) describes the *tentacula* as 'capable of being coiled up within half an inch of the bladder and then darted out with astonishing rapidity to the distance of 12 or 18 feet'. Food seized by them is rapidly conveyed to the mouths. Years later Bennett (1860) gave a short but graphic description of the seizure and digestion of little fishes. Lesson (1843) often saw small *Physalia* kill fish as strong as a herring and stated that flying-fishes are its principal food. He briefly describes the absorption of the products of digestion by the siphons. De Quatrefages (1854) saw a dead fish, 8–10 cm. long, held by a *Physalia*. It was surrounded by thick mucilaginous matter and in about an hour was almost entirely dissolved. A large siphon had partially engulfed the tail. With a lens he followed the digested matter passing up the siphons. Collingwood (1867) and Wallich (1869) both have interesting observations on *Physalia* seen at sea. The former gives a graphic account of the effect of the stings on a seaman and mentions having seen an albacore swallow a *Physalia* and its accompanying shoal of commensal fishes (*Naucrates*). Wallich wound off the tentacles 'in the same way that one may wind off a skein of silk', stretching them from 3 to 6 in. to 8 or 10 yards. Mortimer (1877) also has observations on the stinging properties of the tentacles and their contractility. Bigelow (1891) gives a fairly detailed account of experiments with living *Physalia* at Woods Hole in July and August 1889 when the organism was abundant in Vineyard Sound and he was able to keep a number of specimens alive in the tanks for a week or more. He well describes the capture of small fishes and their subsequent digestion by the siphons and he gives a rough sketch of the manner in which the latter attach themselves to the prey. This is the only figure I have been able to find which shows this remarkable feature of the alimentary system. Mercier (1924) reported some effects of the stings on human beings. Parker (1928) gives a popular account of the habits of *Physalia* stating that 'it is not unusual to find...the remains of several partly digested fishes still held to the underside of the float. Sooner or later these are cast off.' In 1932 the same author gave a detailed description of the structure of the dactylozooids and showed that their rhythmic contractions are neuromuscular in nature. He stated that they may reach a length of over 9 m. and shorten to one-seventieth of their maximum length. Richet & Portier (1936) describe experiments, performed on frogs and other animals, of the toxicity of the poisons injected by the nematocysts and discuss the phenomenon of anaphylaxis.

Few photographs of living *Physalia* appear to exist. Bouxin (1936) reproduces photographs of two battered pneumatophores from which most of the polypoid persons were missing. Woodcock (1944) gives a figure from a photograph of what seems to have been a recently killed specimen. Buchsbaum (1938) has a fine photograph supplied by the New York Zoological Society, of a specimen eating a small fish. In a private letter to me he has confirmed that the photograph was from life. Unfortunately, only the tail-end of the fish can be seen and the detail of the manner in which it is held is not clear. Photographs of a model appear in Parker (1928), Gudger (1942) and elsewhere.

## OBSERVATIONS AT PLYMOUTH

The living *Physalia* which was received on 3 August 1945 and which had been taken from the sea in the neighbourhood of the Scilly Islands and forwarded to Plymouth by Major A. A. Dorrien Smith enabled me to make a number of observations on feeding and other habits. Most of these confirm earlier writers, whose papers incidentally I did not see until after my notes had been made.

The *Physalia* reached the Laboratory on the evening of 3 August. It was in a large Kilner jar partly filled with sea water and was in fresh condition although its movements were few and slow. It was immediately placed in a clean tank arranged for photography and some records were taken of it at once. The pneumatophore was at this time sausage-shaped with an overall length of about 9 in. (23 cm.) and with the crest a crumpled ridge along the top. The dactylozooids all hung down to the bottom of the tank, for a time almost motionless. The *Physalia* gradually increased its activities, rolling the pneumatophore from side to side, and the dactylozooids began to show rather irregular elongations and contractions. In this condition it was left for the night, a board being placed as a cover over the tank. On raising the board the following morning it was seen that the crest was depressed as on the previous evening, but on splashing sea water over the pneumatophore the crest slowly rose. Whether this was due to the drops of water simulating sea spray, or whether the action produced a 'wind' to which the pneumatophore reacted it is not possible to say. Bigelow (1891) produced erection of the crest by blowing on it with bellows. The crest was depressed and raised two or three times more, but subsequently it remained up for most of the period the *Physalia* was still alive. With the raising of the crest the pneumatophore shortened to about 7 in. (18 cm.).

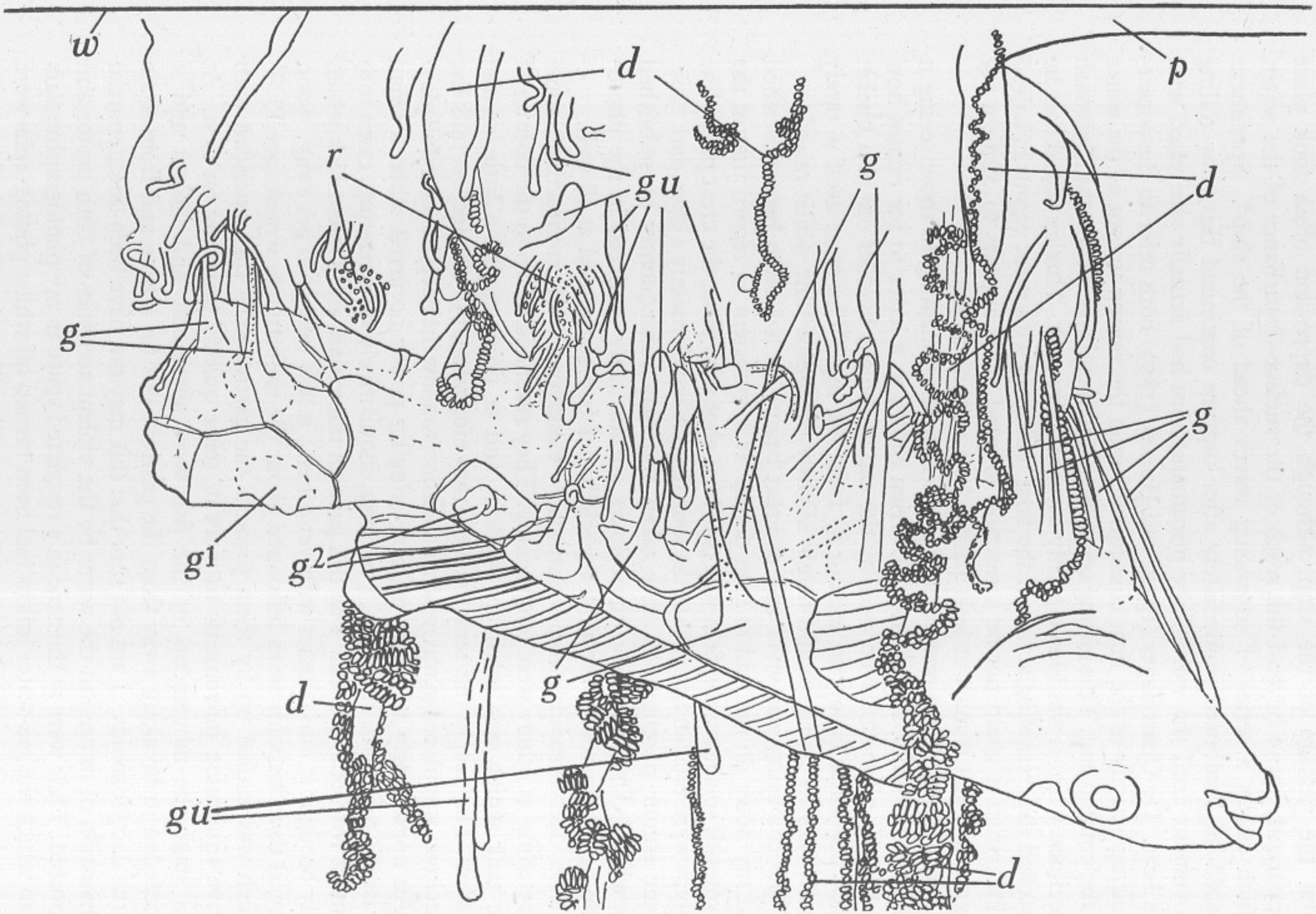
The rolling action of the pneumatophore continued from time to time, the whole thing rolling slowly over first to one side and then to the other, dipping the crest in the water. Plate II shows the pneumatophore over on its right side (regarding the free end of the pneumatophore as anterior) whilst the crest was being slowly raised again after immersion under the surface. It will be noted how the bases of some of the polypoid persons are lifted above the surface; the pneumatophore may have been the more easily able to do this by being in contact on its left side with the background sheet of ground glass. Bigelow (1891) states that his specimens always tended to lie over in this position and never on their left sides. The specimen I had generally went over alternately from side to side, especially when it was floating in a much bigger tank than that in which it was photographed. My impression was that the action was directed towards keeping the surface of the pneumatophore wet, perhaps a necessary precaution in the tropics in calm weather when no spray is flying. Wallich (1869) observed this, or an almost identical action, taking place at sea. He saw *Physalia* turning slowly over on one side as it came 'abreast of the bows of the ship, the state of depression continuing until it is abreast of the stern'. He had 'repeatedly witnessed this wonderful occurrence in moderately calm weather, at distances varying from a few feet to thirty and even fifty yards' and he was inclined to attribute it to some vibratory influence from the passage of the ship, although the depression often took place 'apparently quite beyond the reach of the surface-disturbance of the water, which causes a series of advancing waves ahead of the ship'. Specimens placed on cardboard immediately after capture continued this slow rolling movement until the wall of the pneumatophore had actually shrivelled with the heat. De Quatrefages (1854) and Huxley (1859) both refer to the somersaulting activity of the float consequent upon the raising up out of the water of the pointed end. This raising up of the pointed end was seen in the Plymouth specimen when it was blown gently across a large tank. Huxley stated that he watched the trembling action of the float 'going on with great vigour in a dead calm' when it could not be a reaction to wind. This appears to confirm my suggestion that it may, at least partly, be a wetting action.

The activity of the pneumatophore is indeed astonishing to those seeing it for the first time. Major A. A. Dorrien Smith in a letter to me relates how 'it has the power to lever itself by the cap of the gas bladder out of a bucket when the water is say, an inch or so from the top'. The crest itself is rarely static, varying its shape and height slightly the whole time whilst raised.

The colouring was vivid and of great beauty, it has often been described and my notes do not add to it in detail. It is sufficient to record that in the Plymouth specimen the float was pale blue shot with pink, the crest pink. The polyps were blue and purplish, the long dactylozooids mainly a deep dark blue. Some colour photographs were taken and may subsequently be published elsewhere. Unfortunately, the colours are not truly rendered in the photographic transparency, the pink especially not being recorded at all well.

The dactylozooids were continually elongating and contracting, some shortening as others were lengthening. They extended down to the bottom of the tank which was relatively shallow, and at times trailed a little on the bottom. The deeper the tank the more they elongated, but the deepest tank the specimen was placed in was much too shallow to allow the dactylozooids full play.

An opportunity to judge of their stinging power occurred when a small wrasse (*Ctenolabrus rupestris*), 4 in. long, inquisitively investigating, came into contact with one of them. The fish gave an immediate and violent kick which only brought it into contact with yet others; it was unable to get away. Soon several dactylozooids were festooned about the unfortunate wrasse (see Pl. I) which was hauled up by them towards the gastrozooids that extended with active squirming movements to meet it, some quickly fastening on to it. At this stage the movements of the fish were spasmodic and violent and it succeeded in breaking away from the gastrozooids for a time and from some of the dactylozooids. I am not sure that this may not have been due to partial exhaustion of oxygen in the water by the violent activities of both captor and captured. They were at the time in a restricted space in my photographic tank from which the sea-water inflow had been turned off whilst photographs were being taken. On resuming the water supply the *Physalia*, which had secreted



Text-fig. 5. Key to Pl. III. *d*, dactylozooids; *g*, gastrozooids attached to the fish; $g^1$, a gastrozooid whose main body passes down behind the tail and bends round to spread its lips on this side; $g^2$, gastrozooids broken across during the struggles of the fish; *gu*, unattached gastrozooids; *p*, pneumatophore; *r*, gonozooids; *w*, water surface.

a fair quantity of mucus, recovered from its temporary exhaustion and this time properly secured the fish, which incidentally was turned round in the process. Many gastrozooids got a firm hold and an hour after it had first been caught the wrasse died. The fishes which Bigelow fed to his *Physalia* also took an hour to die. The gastrozooids spread their lips over the wrasse until it was completely or almost completely covered by them. Pl. II shows the dead fish held by the gastrozooids only, the dactylozooids had released themselves from it and were trailing again. This photograph was taken about an hour after that in Pl. I. Pl. III shows in more detail, and with differently arranged lighting, the attachment of the gastrozooids; it was taken about half an hour after Pl. II when digestion had been proceeding for some time. A key-drawing to this photograph is provided so that the main points of interest can be referred to. In all about thirty gastrozooids can be distinguished as being definitely attached to the fish, most of them on the side facing the camera. Others are ttached on the other side and are out of sight, probably in all fifty to sixty rozooids are fixed to it. Of these two had their stems broken across during the early struggles of the fish but still cling tightly to its back (Text-fig. 5, $g^2$). The stems of two or three gastrozooids pass down one side of the fish and curl round to spread their lips on the other side. An example of this is seen at $g^1$. The mouths spread out in trumpet-shaped fashion until the edges of the lips touch one another, or even overlap to some extent. This is most clearly seen on the tail and mid-region of the body. It was found impossible to light the subject so that all details showed with equal clarity at one and the same time, and as the fish was swinging slowly with movement imparted to it by the contractile activities of the various polyps it was not easy to foretell what the effect would be at the instant of exposure. All exposures were by foil-filled flash bulbs so that the light by which the photograph was taken was not that by which it was being observed. Thus the gastrozooids on the head region have not been picked out by the lighting as well as are those on the tail, though to the eye they showed up just as clearly. By the time the plate had been developed and examined the *Physalia* was releasing the remains of its victim so that it was not possible to obtain another picture.

The gastrozooids were very transparent and partly digested particles from the skin of the fish could be seen passing up inside them. These are visible as dark granules in a number of gastrozooids seen in the photograph (dotted in diagram, Text-fig. 5). About an hour after digestion had begun the fish was released and dropped away; much of its surface layer had been digested. Sea-water circulation to the tank was running at the time so that this action does not appear to have been the result of shortage of oxygen. Probably it is normal with a relatively large fish, only a portion being utilized for food.

The gastrozooids covered almost all the surface of the fish except possibly a portion of the dorsal fin, which in the photograph looks to be uncovered on this side. A considerable quantity of mucus is sticking to its posterior lobe.

In the photograph many unattached gastrozooids (*gu*) can be observed and two bunches of gonozooids (*r*) as well as dactylozooids (*d*) of various sizes.

The *Physalia* lived for about 5 days when it was killed with formalin and preserved. By that time it had lost most of its polyps, the gonozooids dropped off about the second day and the dactylozooids broke off, especially when they trailed to the bottom of the tank and caught up against rocks and sea-anemones. Another small *Ctenolabrus* which rushed out to bite at a fragment of tentacle, spat it out immediately and retreated under a rock with very marked discomfiture. Towards the end the pneumatophore had become very sluggish, though it kept the crest at least partly erect most of the time.

## NOTE ON THE SPECIFIC NAME

Recent authorities are of the opinion that there is only one cosmopolitan species of *Physalia*, an opinion with which Mr A. K. Totton of the British Museum (Natural History) tells me that he concurs. In the *Plymouth Marine Fauna* 1931 the name is given as *Physalia* (sp.?) *arethusa* (Browne). It appears that Browne's name is pre-Linnean and that the correct name is *Physalia physalis* Linnaeus.

## ACKNOWLEDGEMENTS

Grateful thanks are due in the first place to all those people who took the trouble to respond to the appeals by Professor Orton and myself for specimens and details of strandings. The names of these ladies and gentlemen are recorded in Tables IV and VIII and on pp. 144–5 and 160; without their aid the first part of this paper could not have been written. A special word of thanks is due to Major A. A. Dorrien Smith for all the trouble he took in observing *Physalia* at sea and in procuring specimens, and especially for the fine living specimen on which the second part of this paper is based.

Some acknowledgements have already been made at appropriate places in the text. A number of other people assisted in various ways, by supplying me with references or copies of references to which I could not otherwise have obtained access. In this connexion Monsieur Ch. Bocquet, Roscoff; Mr P. H. T. Hartley, Oxford; Mr A. W. Stelfox, Dublin; Mr A. K. Totton, London; Prof. R. Weill, Bordeaux, and the Librarian of the London School of Hygiene and Tropical Medicine should be especially mentioned.

The Meteorological Office of the Air Ministry, Harrow, has been most helpful in supplying essential meteorological data and my friend Mr B. C. V. Oddie of the Meteorological Office of the R.A.F., Gloucester, has likewise taken considerable trouble to obtain for me information with regard to the winds over the Atlantic.

I am deeply grateful to Professor J. H. Orton for pooling the whole of his material and records with mine and for allowing me to incorporate the records he collected in 1912 and 1913. Thanks are also due to various members of the staff of this Laboratory and to its Director, Mr F. S. Russell, for their interest and assistance in various ways.

## SUMMARY

The occurrence in the summer of 1945 of a swarm of *Physalia physalis* L. off the south-west coast of the British Isles has initiated a survey into records of its appearance on the Atlantic coasts of Europe during the past 100 years. Unpublished records for 1912, 1913, 1934 and 1935 were discovered and are listed with those already known. The 1945 strandings are considered in detail in conjunction with meteorological data for the period involved. It is concluded that winds, rather than water movements, are the main factor in transporting the swarms towards the British Isles and it is considered likely that the swarms come from the Azores-mid-Atlantic region rather than from the Canaries-Gibraltar district.

Associated with the *Physalia* were *Lepas fascicularis* and *L. pectinata*, some *Velella*, a few turtles (*Caretta caretta*), and possibly an Opah fish (*Lampris luna*), all of them, with some reservation respecting the last-named, surface organisms that would come under the same meteorological influences as the *Physalia*.

A living specimen of *Physalia* gave an opportunity to observe the method of feeding of which few previous first-hand accounts exist. The capture of the prey by the dactylozooids and its subsequent digestion by the gastrozooids is illustrated by photographs from life and is described in some detail. It is suggested that the rolling of the pneumatophore from side to side, dipping the crest in the water, is a calm-weather habit directed to keeping moist the upper surface exposed to the air.

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## EXPLANATION OF PLATES I–III

### Plate I

*Physalia physalis* L. catching a *Ctenolabrus rupestris* (L.). ×¾ approx. The dactylozooids are wrapped about the fish which is still alive. Flashlight photograph from life.

### Plate II

*Physalia physalis* L. eating the *Ctenolabrus rupestris* (L.). ×¾ approx. Gastrozooids are attached to the dead fish whilst the dactylozooids are detached and trail freely. The pneumatophore is heeled over on one side with the crest towards the camera. Flashlight photograph from life about 1 hr. after that shown in Pl. I.

### Plate III

A close view of the gastrozooids of *Physalia* attached to the fish. ×1½ approx. An explanatory key is given in Text-fig. 5. Flashlight photograph from life about half an hour after that shown in Pl. II.

## APPENDIX

Dr M. Parke of this Laboratory and Miss C. T. Dickinson of the Kew Herbarium have kindly identified for me the *Ectocarpus* found growing on Turtle No. 3 (see p. 160), and they have supplied me with the following note:

The *Ectocarpus* species growing on the carapace of Turtle No. 3 was identified as undoubtedly a form of *E. Mitchellae* Harv. Plants bearing both unilocular sporangia and meiosporangia were present but none bearing megasporangia. The material approached most closely the variety *E. Mitchellae* Harv. var. *parvus* Taylor, but was taller and slightly more robust than the type as described by Taylor (1921, p. 254). This variety was recorded by Prof. Taylor from southern Massachusetts, growing affixed to the carapace of a marine turtle and to floating timbers, and fruiting in summer (1937, p. 112).

The material was sent to Prof. Taylor (by C.T.D.) for verification; he replied saying the material was certainly *E. Mitchellae* Harv., and if his var. *parvus* was a true variety it would apply as he thought there was no significant discrepancy in the measurements.

Although *E. Mitchellae* Harv. is now recorded by many workers as occurring in Europe, the European plant was first given the manuscript name of *E. virescens* by Thuret and was published as a *nomen nudum* only by Flahault (Thuret in Flahault, 1888). Owing to the similarity between the Atlantic-American and the European material many phycologists have classed them as one species and have therefore used Harvey's name, *E. Mitchellae* (the older name), for the European records, *E. virescens* Thur. being given as a synonym.

There still seems to be some doubt as to whether the Atlantic-American plant is identical with the European plant. Børgesen (1926, pp. 18–23) and Sauvageau (Børgesen, 1926) keep them separate. Sauvageau, who at first considered they were the same species, later decided that it would be more prudent to maintain the two species separately in spite of their close resemblance.

*Geographical distribution. E. Mitchellae* Harv. is recorded from: West Indies, Bahamas, Texas, Florida, Bermuda, North Carolina, Rhode Island, southern Massachusetts and Nantucket. *E. virescens* Thur. is recorded (sometimes as *E. Mitchellae* Harv.) from Great Britain to the Canary Islands.

C.T.D.
M.W.P.

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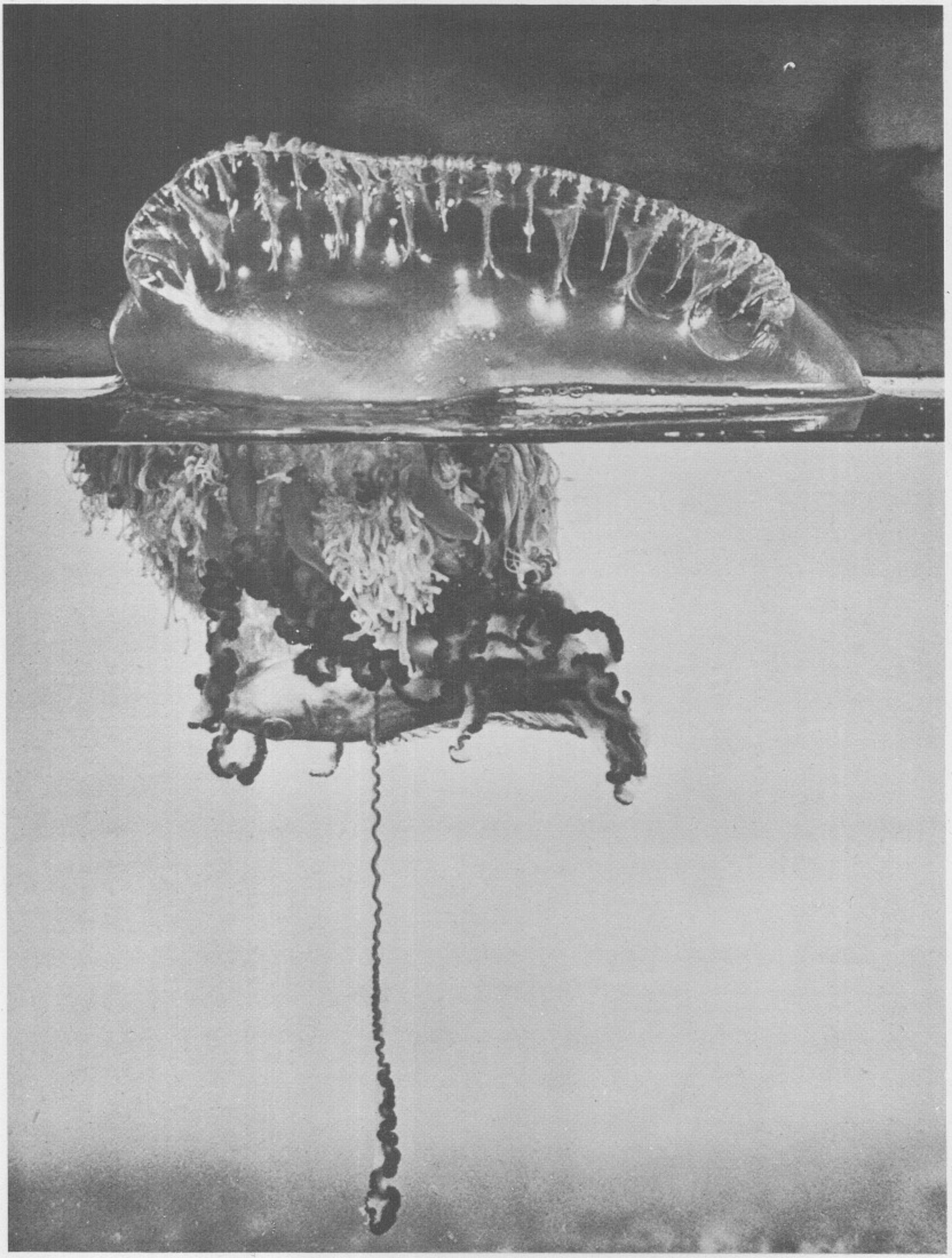
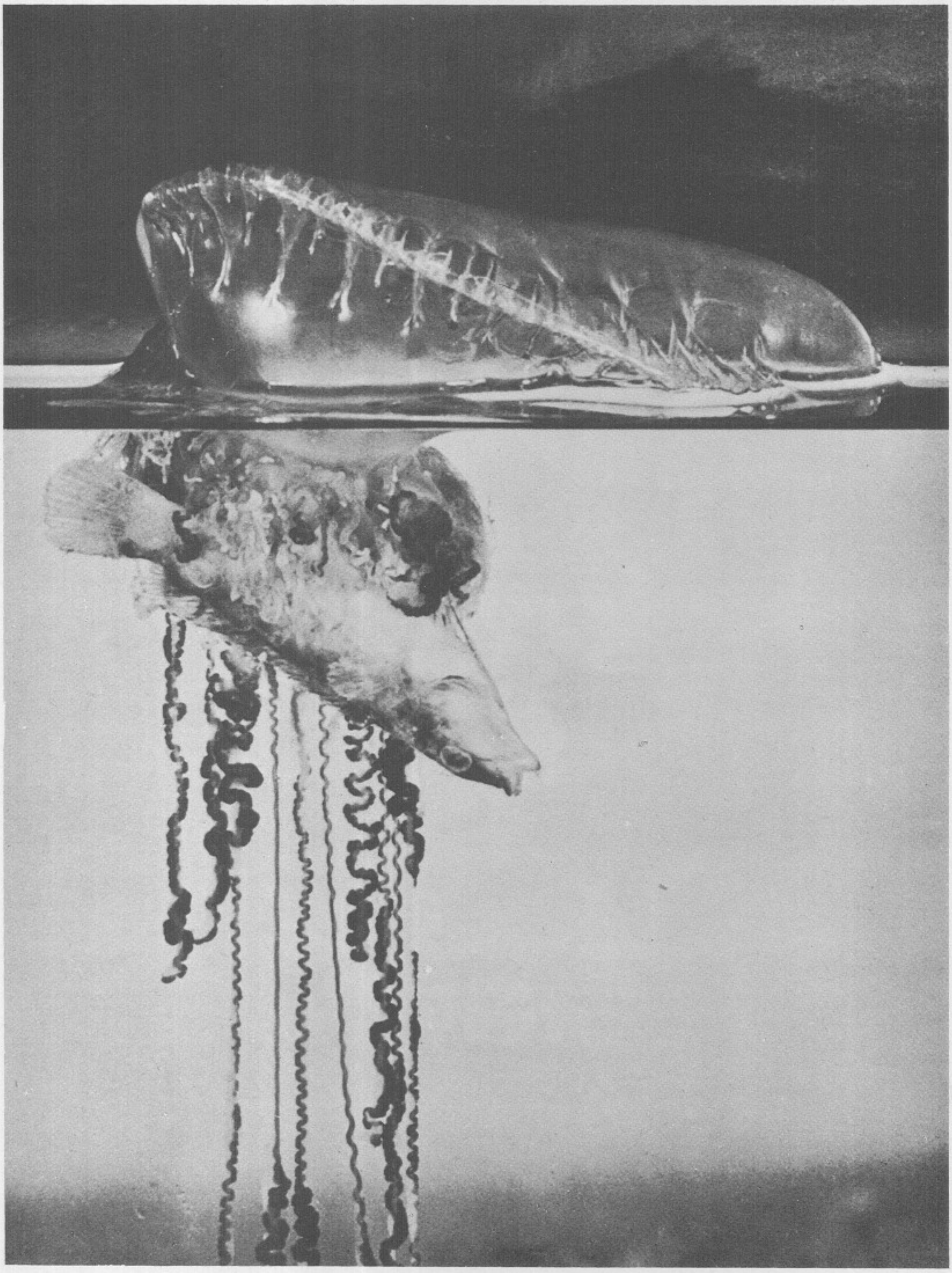
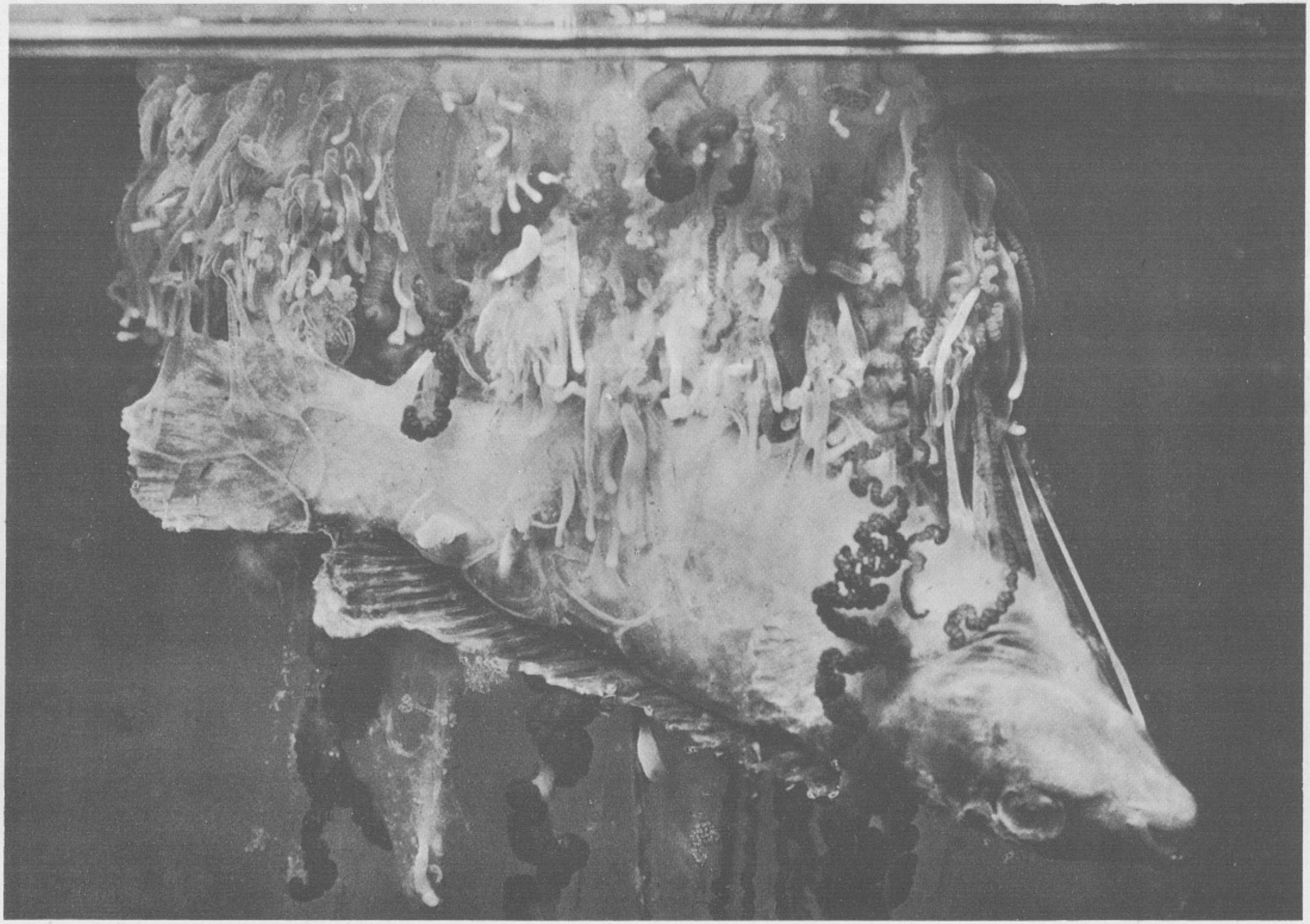


Physalia catching a fish.



Physalia eating a fish.



Gastrozooids of Physalia attached to a fish.

# THE INTERTIDAL ECOLOGY OF SELECTED LOCALITIES IN THE PLYMOUTH NEIGHBOURHOOD

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(Text-figs. 1–14)

CONTENTS

## INTRODUCTION

The importance of surf action, both as a presence or absence factor and as a modifying influence on the nature of littoral distribution, has been demonstrated during a survey of intertidal conditions in Cardigan Bay (Evans, 1947). The coast of mid-Wales, however, is comparatively smooth in outline, and offers little variation in exposure to or shelter from wave-action; consequently it was decided to confirm and amplify certain features of the previous study by the investigation of a much more irregular coastline in the neighbourhood of Plymouth. Here (see Fig. 1) the nature of the coastline is such that localities exposed to maximum wave action and localities almost completely sheltered from surf both occur within a short distance of each other. The extent to which wash, splash, and spray, resulting from heavy surf, may modify the vertical ranges of intertidal plants and animals is known in a general way only; it is here proposed to treat this problem with more attention than it has hitherto received, and to record, if possible, the actual extent to which such modifications may be observed. It is known that splash and spray, by raising the effective (in distinction to the predicted) level of tides, both tend to raise

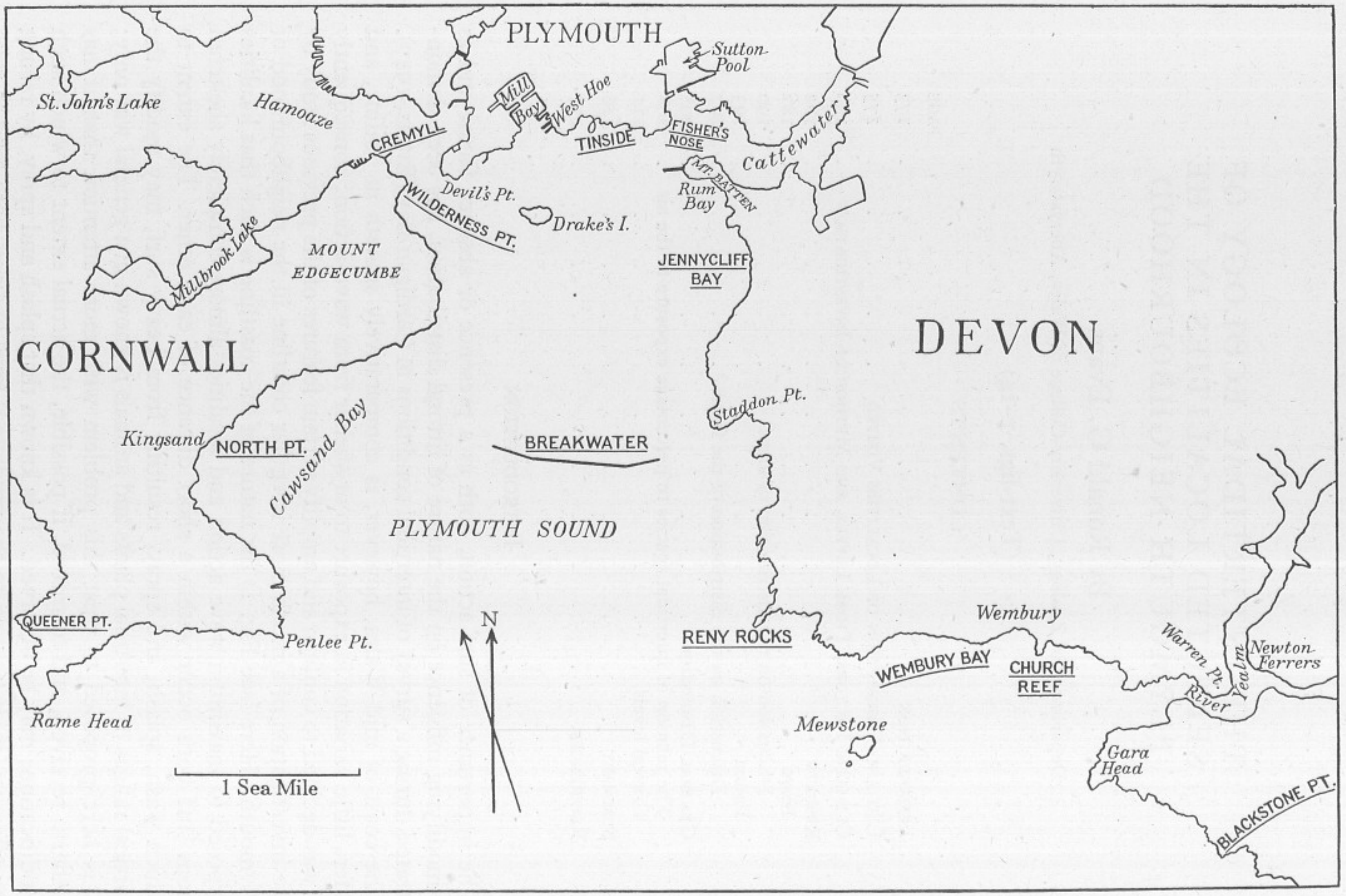

Fig. 1. Map showing localities included in the survey. (After *Plymouth Marine Fauna*, 1931.)

the upper limit of certain species with regard to predicted tidal levels. Moore (1935*a*) has shown that surf also has a lowering effect on the lower limit of *Balanus balanoides*, but whether similar effects may be distinguished in other species remains uninvestigated, and it is proposed to consider this possibility.

Furthermore the existence of 'critical levels' will be examined. It was found (Evans, 1947) that such levels in Cardigan Bay appear to be rather different in position from those described by Colman (1933) as being critical for species on Church Reef, Wembury, and before a true comparison could be made it was decided that this latter area must be restudied more extensively than Colman's traverse-method made possible. Moreover, the position of such critical levels under different local conditions (e.g. of surf action and rock-configuration) is likely to prove interesting.

Finally, by making an extensive study of Church Reef, and comparing the results with those obtained by Colman (1933), it will be possible to obtain some idea of the extent to which the study of a few detailed traverses can give an average picture of distribution in such an area.

The work was carried out in the summer of 1946; twelve localities in the Plymouth region were selected, and the distributions of some of the common plant and animal species were examined and described at each locality.

## LIST AND DESCRIPTION OF LOCALITIES VISITED

These are all shown in the map (Fig. 1), with the exception of Fort Charles and Bolt Head, which lie in the Salcombe estuary, almost 20 miles to the east of Plymouth Sound.

*Bolt Head*. This lies on the west of the entrance to Salcombe estuary and is open to winds and waves from any quarter between east and west. Even when the wind is not strong the swell is appreciable, and the wash, splash, and spray zones are quite extensive. The cliff face is high and the rocks slope steeply down to low water, these slopes generally facing south-south-west and receiving both maximum surf and maximum illumination. Near low-water mark the steep faces tend to flatten out horizontally in some places. Very little loose material occurs, except for a few large boulders or slabs which are occasionally found wedged in narrow crevices.

*Blackstone Point*. Just east of Gara Head (see Fig. 1), this is open to the sea from west to east-south-east, with some little protection on the east from Revelstoke Point and other points on the peninsula. High jagged ridges of Dartmouth Slate slope almost vertically to low water, sometimes from a height of over 50 ft. above chart datum. Deep fissures, running approximately north-south, occur between the slate laminae, which present almost sheer faces to the east and west. Here again considerable surf action is experienced.

*Reny Rocks*. This group of rocks, on the east side of the entrance to Plymouth Sound, is exposed to winds between west and east-south-east. Moreover, Rame Head lies some distance away on the west, and its sheltering effect is small; the same is true of Gara Head and the Mewstone on the east and south-east. The locality is almost as fully exposed, therefore, as Bolt Head or Blackstone Point. Reny Rocks consists of a group of irregular, steep-sided peaks, rising to over 40 ft. above low water, and separated from the mainland by a low-lying stretch of boulders which dries out at mean low water of neaps. (Owing to the inaccessibility of the Rocks except at low water, this area was not investigated as thoroughly as the other localities.)

*Queener Point*. Rame Head itself was inaccessible owing to the presence of anti-invasion defences, consequently Queener Point, on its north side, was chosen for investigation. This is less exposed than Rame Head itself or than Bolt Head, Blackstone Point, or Reny Rocks, being open to the sea only from south to west-north-west. However, the rocks are steep and jagged, rising to 30–40 ft. above chart datum, and running approximately north-east to south-west; and since the swell is usually heavy, a considerable amount of wash, splash, and spray is experienced. Large pebbles and boulders occur in the gullies between the rocky promontories, and on the north and north-west sides of the Point the steep rock levels out to a horizontal stretch just below mean tide level.

*Plymouth Breakwater*. An artificial structure, lying across the entrance to the Sound, at approximately 2 miles from the mainland, this is composed of limestone blocks, with large masses of rough concrete in front. These concrete masses are cubical blocks, 10–12 ft. square, with their bases at low water. They are separated from each other by approximately 6 yards, and from the south slope of the Breakwater by about 15 yards of a fairly level stretch of loose limestone blocks with boulders wedged between them. The whole Breakwater is described in detail by Lysaght (1941). An area in the centre was chosen for investigation, including about 30 yards of the south and north slopes, the top, the sheltering blocks and the level area behind these. The locality is open from south-west to south-east, with some protection outside this quadrant from Penlee and Reny Points. Wave action is strong on the south slope, but the protecting blocks afford some shelter to the lower part of this slope. The north side is, in comparison, fairly sheltered.

*Tinside to West Hoe*. Here the rocks are of limestone, broken and fissured and generally descending rather steeply to low water. The surface is pitted with the holes of boring organisms (e.g. *Saxicava rugosa*), and depressions and rock pools are frequent. Caves and inlets occur along the front, and the natural line of the rocks is interrupted by artificially built concrete walls, steps, quays, etc. Pebbles and boulders are present in coves and channels. The Breakwater, lying about 2 miles offshore, gives comparatively little shelter and a heavy swell is common in the waters of the Sound when the wind is in the south. This, combined with the steep slope of the Tinside rocks, makes for fairly heavy wave shock, but the area is less exposed than those previously described. Towards the east end, in the Fisher's Nose region, the shelter of Mount Batten breakwater (about a quarter of a mile south) begins to be felt, also the shore is less steep here, and the surf is mitigated to some extent.

*Church Reef, Wembury.* Colman (1933) studied only the landward portion of this locality, but the present survey also includes the steep seaward reefs and ridges. The area is very irregular, the angle of dip of the rocks is generally steep and the slopes face seaward, but this is variable. High peaks, which are not completely submerged even at high springs, occur on the south and south-east, but on the north, north-west and north-east corner the general lie of the shore is lower and more regular. The centre of the Reef is occupied by high peaks (e.g. Colman's 'Central Rock'). Pools, inlets, and channels are frequent, often containing shingle and gravel, but large boulders are not common. At the top of the shore the cliff face is low and is footed by shingle on the west, but on the east the shingle disappears and a mass of steep rocks occurs (through which runs Colman's 'Traverse D'). As a whole Church Reef may be described as moderately exposed to surf, receiving some shelter on the west from Reny and Wembury Points, on the south-west from the Mewstone, and on the east from Gara Head. Local variation in wave action is experienced; the south faces of the low-tide reefs are battered by heavy surf, but they create some shelter for the more landward portion of the area.

*North Point.* This lies just east of Kingsand village on the west side of Plymouth Sound, and the area faces almost due south-east. The rocks are felsite, weathering into rounded contours, with few deep fissures, unlike the Mica-schists of Bolt Head, for example. The beach is much more regular than it is at any of the other stations, and the slope is fairly even, while no peaks or high ridges are present, and vertical faces are occasional only. Gravel and shingle are present in pools and gullies. Penlee Point, on the south, provides some shelter, so does Reny Point on the east-south-east, but North Point is open to the sea between these two headlands. It may be described as moderately exposed to surf, and the regularity of the rock formation reduces the range of variation in shelter and surf action.

*Jennycliff Bay.* This is an area on the east side of Plymouth Sound, between Rum Bay on the north and Ram's Cliff on the south. The strata of Staddon Grits weather into small but steep headlands, with intervening areas of lower rock. In these low-lying areas occur boulders and small loose masses from the cliff face, while sand and gravel are present locally. The general dip of the rocks is seaward, but this varies. Though actually enclosed from the open sea on all sides, Jennycliff Bay is not very sheltered; the west side of the Sound and the Breakwater both lie some distance away, and surf action is strong when the wind is in the south, west or south-west. Local variation is again experienced; the level areas are protected by the headlands, and the south and south-west aspects of higher rocks receive the maximum of wave shock. In general, the area may again be considered as moderately exposed.

*Fort Charles, Salcombe*. This lies just south of Salcombe village on the west side of Salcombe estuary, and faces almost due south. Two distinct areas were investigated here; Fort Charles east and Fort Charles west. On the east side (i.e. Fort Charles east) the high cliff face descends steeply to a narrow shingle beach which, a few yards further seaward, rises sharply to a high mass of rocks on which stands a ruined fort. In front of this ruin the rock steps irregularly down to about high-water neaps level, then drops perpendicularly to low water. Offshore, a few small reefs of lower rock occur. On the west side (Fort Charles west) the cliff descends to a jumbled mass of loose rock, passing into a zone of low-lying ledges with scattered boulders, which continues about 50 yards to low water. Here there are no peaks or steep-sided rocky masses of any size. The whole of the Fort Charles locality is open to the sea only between south-south-west and south-south-east; moreover, the shallow estuary and large sandbanks also tend to reduce the violence of surf. However, the high steep rocks of Fort Charles east are more subject to wave shock than the comparatively level shore of Fort Charles west.

*Wilderness Point*. This is an area just east of the Cremyll landing stage, facing slightly east of north. The rock is a continuation of the Plymouth limestone, and similar to it in texture. The shore is backed by a high stone wall, and the upper beach just below this consists of rocky peaks, 4 or 5 ft. high, surrounded by shingle. Proceeding down the beach shingle becomes less abundant and the rocks flatter and more regular. The area is enclosed from the open sea on all sides, and neither surf nor swell is experienced to any appreciable extent. The water is laden with suspended material brought down the Hamoaze, and fucoids tend to trap and filter this, and to lay a deposit of fine silt over the rocks of Wilderness Point.

*Warren Point*. This area lies on the north bank of the river Yealm, about a mile east of Church Reef, and faces south. The cliff face is very low and drops to a stony beach with patches of mud and silt. In places rock ledges protrude through the shingle to as low as extreme high-water neaps level, but usually the rock is covered by shingle from above this level down to low water. The locality is enclosed from the open sea on all sides, and wave action is at a minimum; although the beach is stony, the pebbles are not liable to much movement, and are sufficiently stable to support several plant and animal species.

In addition to the foregoing localities which were studied in detail, notes were also taken at other points on the shore, e.g. in Wembury Bay, at Cremyll, at Newton Ferrers, etc.

It is unfortunate that there exists no adequate means of measuring the degree of exposure to wave action to which various localities may be subjected. Moore (1935*a*) has attempted to do this on a basis of 'the number of days per hundred days in which any wind blows into the exposed aperture of the locality in question'. While this may give some indication of the maximum exposure which can be expected at a given station on the coast, there exists, within each locality, such a degree of variation that the method becomes impracticable in a survey such as the present one. Within an irregular formation of rock such as Church Reef, for instance, some rock faces (e.g. the south faces of the seaward reefs) will be as exposed to surf almost as heavy as that experienced at Bolt Head, while other stretches in the same locality (e.g. flat rocks to the leeward of high ridges) will be as sheltered from the full force of the waves as the shore of Wilderness Point, for example. So many factors combine to produce this variation that it is impossible to derive any satisfactory expression of relative wave-exposure on a given surface. Taking into account the orientation of the rock with regard to the waves and the direction of the prevailing winds, the angle of slope, its proximity to sheltering masses, and its position with regard to tidal levels (see later), it is, however, possible to form some idea of the exposure to which a small area is likely to be subjected. The twelve localities listed above are arranged in order of increasing shelter, the list given in Table I

TABLE I. LIST OF STATIONS NUMBERED IN FIGS. 3–12 ARRANGED IN ORDER OF DECREASING EXPOSURE TO WAVE ACTION

| | | |
|---|---|---|
| *1.* | Bolt Head. Vertical south face | 'Very exposed' |
| *2.* | Reny Rocks. Vertical south face | |
| *3.* | Blackstone Point. Vertical east and south-east faces | |
| *4.* | Queener Point. Vertical south face | |
| *5.* | Blackstone Point. 50° slope facing east | |
| *6.* | Church Reef. South face of seaward reefs | |
| *7.* | Breakwater. South slope | |
| *8.* | Bolt Head. Horizontal rocks | 'Exposed' |
| *9.* | Queener Point. Horizontal rocks | |
| *10.* | Blackstone Point. North-west face | |
| *11.* | Bolt Head. North-east overhang | |
| *12.* | Church Reef. North face of seaward reefs | |
| *13.* | Jennycliff Bay. Vertical south and south-west faces | |
| *14.* | Tinside. Vertical south face | |
| *15.* | Blow-hole in Wembury Bay | |
| *16.* | Church Reef. Landward rocks | 'Semi-exposed' |
| *17.* | Church Reef. Protected south face | |
| *18.* | Church Reef. Flat rocks on north-east | |
| *19.* | North Point. East end | |
| *20.* | Jennycliff Bay. 70° slope, facing east | |
| *21.* | Breakwater. North face | |
| *22.* | Tinside. 40° slope, facing south | |
| *23.* | Fort Charles. East | |
| *24.* | Jennycliff Bay. North face and overhangs | 'Sheltered' |
| *25.* | Bolt Head. Cave | |
| *26.* | Jennycliff Bay. Flat rocks | |
| *27.* | Fort Charles. West | |
| *28.* | Breakwater. Corner on north face | |
| *29.* | Tinside. Horizontal rocks | |
| *30.* | Tinside. Fisher's Nose region | |
| *31.* | North Point. West end | |
| *32.* | Wembury Bay. Sheltered south face | |
| *33.* | Wembury Bay. North face | |
| *34.* | Cremyll | 'Very sheltered' |
| *35.* | Wilderness Point | |
| *36.* | Warren Point | |
| *37.* | Newton Ferrers | |

includes all the areas quoted in the paper and indicated by number (e.g. [*26*]) in Figs. 3–12; these also are arranged in order of decreasing exposure (based on the considerations cited above), and, for convenience, have been classified into five categories, 'very exposed', 'exposed', 'semi-exposed', 'sheltered', and 'very sheltered'.

## CLIMATIC FACTORS, TIDAL LEVELS, AND METHOD OF INVESTIGATION

The climate of Plymouth is mild, and typical of south-west England in general. According to Lysaght (1941), on an average 33% of the winds blow from between south-west and south-east, i.e. from the Channel and from the open Atlantic. Thus, as in Cardigan Bay, the main exposure is from a southerly direction, but from personal observation it is confirmed that such headlands as Bolt Head, Blackstone Point, Reny Point, and Queener Point, are very much more surf-beaten than any locality in the middle of Cardigan Bay. On the other hand, both Wilderness and Warren Points receive far more shelter from waves than any locality on the coast of mid-Wales.

Tidal data are taken from those given for Devonport in the Admiralty Tide Tables, Sect. A, Pt. I, and values for extreme springs and neaps are means for the 10 years 1937–46. The Devonport figures are taken as applicable for all localities except Bolt Head and Fort Charles; for these, the corrections for Salcombe tides are applied. Table II gives the tidal scales for both Plymouth and Salcombe localities, but in the following text-figures the zonations at Bolt Head and Fort Charles are interpolated (with the necessary corrections) on the Plymouth scale, for purposes of comparison. All heights are given as feet above or below Chart Datum which, at Devonport, lies 8·42 ft. below Ordnance Datum.

TABLE II. TIDAL SCALES

(Heights are given as feet above or below Chart datum)

| Tidal level | Plymouth (ft.) | Salcombe (ft.) |
|---|---|---|
| E.H.W.S. | 17 | 17·3 |
| M.H.W.S. | 15·7 | 16 |
| M.H.W.N. | 12·3 | 12·6 |
| E.H.W.N. | 10 | 10·3 |
| M.T.L. | 8·2 | 8·8 |
| E.L.W.N. | 5·7 | 6·6 |
| M.L.W.N. | 4·6 | 5·5 |
| M.L.W.S. | 0·2 | 1·1 |
| E.L.W.S. | −1·6 | −0·7 |

The species selected for attention are those studied in the Cardigan Bay survey (Evans, 1947), but *Himanthalia lorea* (de la Pyl) and *Balanus perforatus* Brugière are additional. *Sabellaria alveolata* (L.), which is not general in the Plymouth neighbourhood, is omitted.

Methods similar to those adopted in the previous survey were followed, i.e. tidal levels were marked by observation of the water-level at different times between high and low water, and zonation was studied by walking along the shore and taking notes, parallel to the water-line, first at one level and then at another as the tide ebbed. In view of the limited period available for the work one innovation was introduced; advantage was taken of an early period of calm weather to mark reference levels at as many stations as possible, the time of marking of the water-level being noted and its height being calculated by using Supplementary Table I of the A.T.T., Sect. A, Pt. I. This procedure has the following advantages. (*a*) Providing that all the localities are marked during one day or during days of similar conditions of wind and tides, then any error in the height of the marked levels will tend to be a constant one, for comparative purposes. The Breakwater, Queener Point, North Point, Wilderness Point, and Jennycliff Bay were all marked during one calm day, and Tinside in the late evening of the same day. Reny Rocks, Church Reef and Warren Point were visited on the following day. A break in the weather delayed the marking of Blackstone Point until a fortnight later, while Fort Charles and Bolt Head were marked on successive days at the same period. (*b*) Having once established such reference points during calm weather, the areas could be studied even when the condition of the sea was not ideal; the actual height of the tide, at the calculated time when it should arrive at the mark, could be checked with reference to this mark, and an approximate estimate of any error due to wind or swell could be made.

The efficiency of this method of assessing vertical heights on the shore and the zonation of species may be judged by comparing results obtained for the zonation of the algae on Church Reef with similar figures obtained from a study of the same area from detailed levelled traverses by Colman (1933). This comparison is made in Fig. 2; it should be noted that the writer has deducted Colman's 'splash allowance' of 2 ft., and has also based the zonation on the tidal scale given in Table I (i.e. using 10-year means for extreme neaps and springs). There is a surprising measure of agreement, though certain points demand comment. While my limits for the 'zones of abundance' of *Pelvetia*, *Fucus spiralis*, and *Ascophyllum nodosum* agree closely with Colman's 'mean limits' of distribution (1933, p. 454, table IV), my absolute limits of distribution are more extended than the latter's 'extreme limits'. Especially is this so for *Pelvetia* and *Fucus spiralis*, both of which, it should be noticed, are zoned by Colman on one traverse only (Traverse D); for *Ascophyllum* and *Fucus serratus*, which he zones on two traverses, the differences are less marked. This appears to be the natural result of a more extensive and broader survey; but, allowing for this, the direct observational study of tide levels and the basing of vertical zonations on this would seem to be at least as accurate as any method based on the detailed examination of surveyed traverses. This is further indicated by the general consistency of the results which the writer has obtained in different areas, both on the coast of mid-Wales and in the Plymouth locality. Thus, if the necessary precautions with regard to calm conditions are observed, the method appears to be fully justifiable, and possesses undoubted advantages for this type of survey.

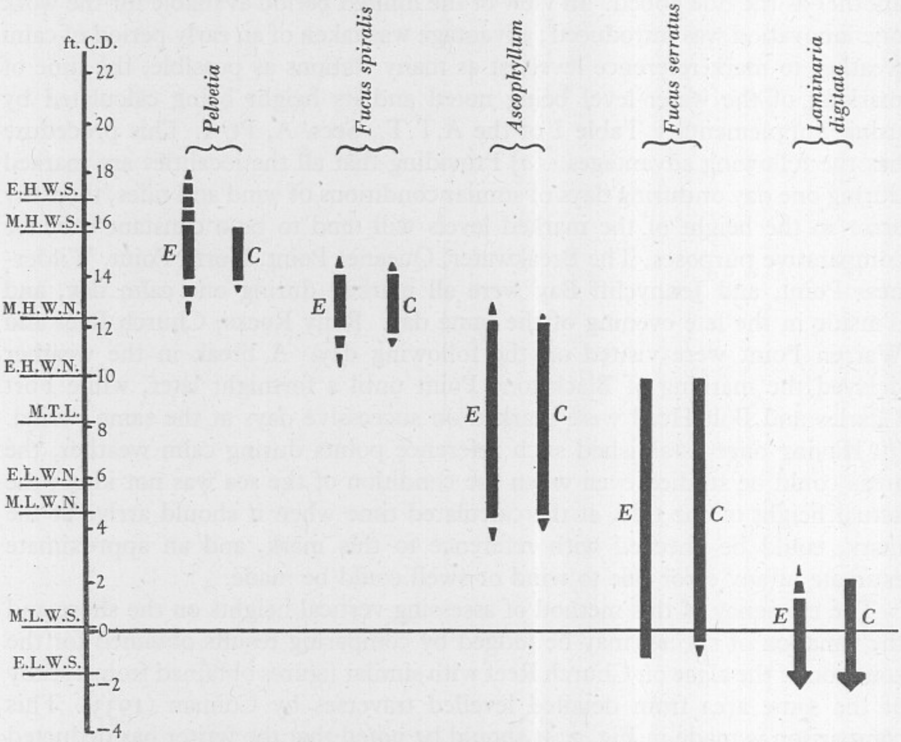

Fig. 2. Comparison of algal zonation on Church Reef, Wembury, with results obtained by Colman (1933). *E*, present results; *C*, Colman's data.

*Note*. In Figs. 2–14 inclusive the same scale is used for vertical heights above or below chart datum.

## RESULTS

The general features of the horizontal distribution of the species studied (with the exception of *Himanthalia lorea* and *Balanus perforatus*) as they occur in Cardigan Bay have been fully discussed in my earlier paper, together with the effects of wave action and other factors on this distribution. The present investigation confirms many of these observations, which it is unnecessary to repeat here, except where any significant differences have been noted.

### *Flora*

*Pelvetia canaliculata* Dcne. & Thur. This is entirely absent from Bolt Head, and represented only as occasional and very stunted plants at Blackstone, Reny, Queener, the Breakwater, and Tinside. A sparse and scattered *Pelvetia* zone

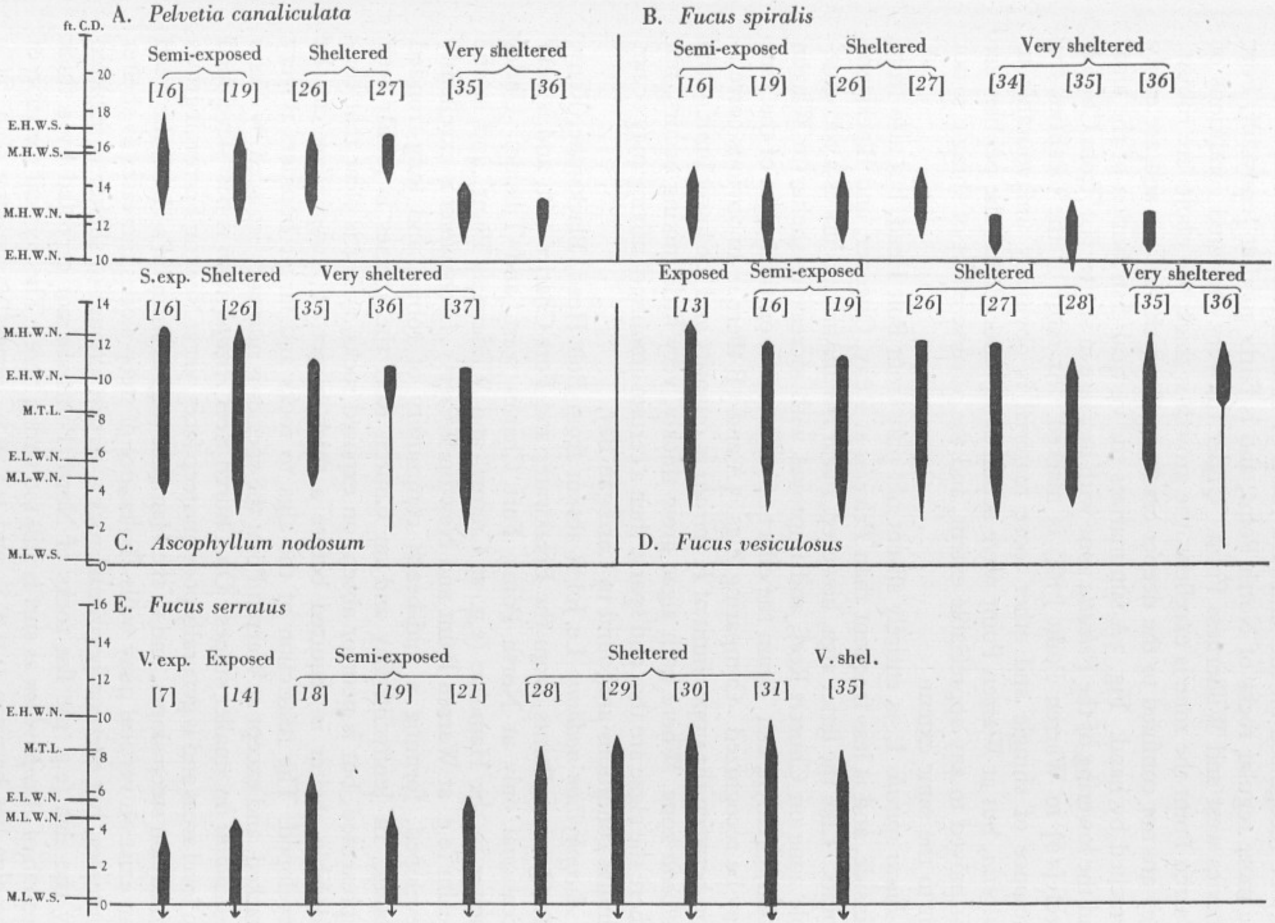

Fig. 3. Zonation of *Pelvetia* (A), *Fucus spiralis* (B), *Ascophyllum* (C), *Fucus vesiculosus* (D) and upper limit of *F. serratus* (E) at different localities.

may be recognized on the landward rocks of Church Reef; this improves on the more regular rocks of North Point, and is fairly good at Jennycliff, Fort Charles west and Wilderness Point. Under the very sheltered conditions of Warren Point the zone is excellent, the growth is thick, the plants are robust, they are not confined to the deeper cracks in the rock surface, and are easily detached by hand. Fig. 3A summarizes the vertical distribution of the alga, and the lowering of the *Pelvetia* zone with increase in shelter (i.e. from Church Reef [*16*] to Warren Point [*36*]) is marked. At most of the localities the presence of shingle and other loose material is obviously unfavourable to *Pelvetia*, but at Warren Point wave action is so reduced that the pebbles are not moved to any appreciable extent, and the adverse effect of shingle is not felt to the same extent.

*Fucus spiralis* L. is entirely absent not only from Bolt Head, but also from Tinside, and is less frequent than *Pelvetia* at Reny, Queener, and Blackstone Points. Like the latter alga, however, *Fucus spiralis* first occurs as a recognizable zone on Church Reef, and improves with increasing shelter to Warren Point, Cremyll, etc. Again the effect of wave action on the height of the zone may be recognized. Comparing Figs. 3A and 3B there is an obvious correlation between the upper limit of *F. spiralis* in quantity and the lower limit of the *Pelvetia* zone. Where both algae grow thickly, very little mixing occurs, but where the algae are thin and sparse then a certain amount of mixing may occur. Similar conditions are found in Cardigan Bay.

*Ascophyllum nodosum* Le Jol is absent from Bolt Head, Blackstone, Reny, and Queener Points, from the Breakwater and Fort Charles east, and is very occasional only at North Point, Fort Charles west, and Tinside. Under shelter in the Hamoaze (e.g. at Cremyll and Wilderness Point) and in the Yealm (e.g. at Warren Point and Newton Ferrers) *Ascophyllum* is excellently developed, forming a mid-beach community of robust and long-fronded plants. In Jennycliff Bay and on Church Reef the species is locally well represented, but is poor or absent on exposed rocks, and it is clear that considerable shelter is required before a thick carpet of *Ascophyllum* can be developed. The restriction of the alga to rocks and larger boulders is very marked, and except at Warren Point the species is normally replaced by *Fucus vesiculosus* on smaller stones. On Church Reef *Ascophyllum* is best developed on level areas and is generally poor on steep faces, yet at Newton Ferrers it grows thickly on steep slopes, and in the Hamoaze (e.g. at Admiral's Hard) the weed can exist on vertical quay walls. Tolerance of steep slopes increases as shelter increases, but even on horizontal rock a certain amount of shelter is required by the alga (e.g. the flat rocks of North Point are not carpeted by a thick growth of *Ascophyllum* as surf is still too strong here). The vertical zonation of the alga lies between M.H.W.N. and M.L.W.N., generally speaking (Fig. 3C), but the upper limit is again higher under conditions of moderate wave action (e.g. Church Reef, Jennycliff Bay) than under conditions of extreme shelter (e.g. Newton Ferrers). There is a correlation between the upper limit of *Ascophyllum* and the lower limit of *Fucus spiralis*, especially where both zones are thick (e.g. Warren Point, Cremyll, etc.), but where the shore rock is irregular this demarcation is not nearly so obvious. The lower limit of *Ascophyllum* varies, but the alga appears to be capable of existing at least as low as M.L.W.S. + 2 ft., though it is generally abundant only above M.L.W.N. Gislén (1930) describes the species as extending lower in sheltered and unclean waters, possibly this explains its low lower limit in the Yealm estuary.

*Fucus vesiculosus* L. Though not entirely absent from any of the stations visited, this alga is extremely poorly represented at Bolt Head, Blackstone, Reny, and Queener Points, and on the south face of the Breakwater. At all these localities *F. vesiculosus* is found only as occasional and tattered plants in cracks on the exposed slopes. On Church Reef the alga is generally less well developed than *Ascophyllum*, but it often tends to replace the latter on the steeper slopes. At Fort Charles west and in parts of Jennycliff Bay *Fucus vesiculosus* may form a fairly pure (i.e. unmixed with *Ascophyllum*) community on the less regular stretches of rock and boulders, but at Wilderness and Warren Points it is definitely dominated by *Ascophyllum*. As in Cardigan Bay, *Fucus vesiculosus* is more tolerant of broken ground, of boulders, of steep faces, and of surf than *Ascophyllum*, and peaks and boulders lying in a thick carpet of the latter alga may be dominated by *Fucus*. The writer has suggested previously (Evans, 1947) that the general infrequency of a thick, pure community of *F. vesiculosus* may be due to the rather sharply set optimum of surf conditions necessary for this; where surf action is too strong the alga occurs merely as isolated plants and clumps, where shelter is pronounced then *Ascophyllum* is developed and competes successfully against *Fucus* for dominance. Generally *F. vesiculosus* is not found much above M.H.W.N. (Fig. 3D), but may occur above this under the influence of splash. It tends to occur to higher levels than *Ascophyllum*, however, which is the reverse of what has been described in Cardigan Bay. The lower limit of abundance lies generally in the region of E.L.W.N. to M.L.W.N., but where the *Fucus serratus* zone is well represented *F. vesiculosus* may be dominated by this alga from E.L.W.N. down. The presence of a stony lower beach at Warren Point prevents both this species and *Ascophyllum* from being anything more than occasional from E.H.W.N. down at this locality, but isolated plants of *Fucus vesiculosus* have been taken here as low as M.L.W.S. + 0·5 ft.

*Fucus serratus* L. As described by most workers, this species requires horizontal or gently sloping rock and a fair amount of shelter from surf, but when shelter is pronounced it may occur on steep slopes, and it may be absent even from a level beach where surf is too violent. The *F. serratus* zone is well represented on Church Reef (except on the seaward slopes of the outer reefs), at Tinside, North Point, Jennycliff, and Fort Charles west; and it achieves its maximum development at Wilderness Point, but the stony lower beach at

Warren Point is again unfavourable. The lower limit of distribution at all localities lies below M.L.W.S., but the lowest level to which the writer has taken the species lies in the region of M.L.W.S. – 1 ft. (at Church Reef, Jennycliff, North Point, and the Breakwater). The absolute upper limit of distribution under optimum conditions (e.g. in the Fisher's Nose region of Tinside [*30*] and at the west end of North Point [*31*]) is E.H.W.N., but the upper limit of abundance is variable. From Fig. 3E it will be seen that the upper limit of the *F. serratus* zone is very markedly affected by the intensity of surf. At Bolt Head and Blackstone Point no distinct zone can be recognized; on the south Breakwater slope [7] the zone extends up to M.L.W.S. + 3 ft. only, but with increasing shelter at different localities this upper limit moves up the shore until, at North Point west end [*31*] (for example) it is as high as M.T.L. Further reduction in wave action, and in the height of wash and splash, results in a subsequent lowering of this upper limit (e.g. at Wilderness Point [*35*]). The ten localities figured in Fig. 3E are chosen from a large selection of data all showing the same general principle, i.e. that with decreasing surf *F. serratus* is enabled to exist higher and higher up the shore, but after a certain optimum is reached, further reduction in wave action results in a slight lowering of the upper limit.

*Himanthalia lorea* Lyngb. This occurs in much more wave-beaten localities than any of the other fucoids, and as Rees (1935), Gibb (1938), and others state, it is characteristic of moderately wave-beaten situations. *Himanthalia* is well represented at Bolt Head, Blackstone, Reny, Plymouth Breakwater, and Church Reef; at North Point it is less frequent; at Fort Charles and Wilderness Point it is occasional only. Fischer-Piette (1936) comments on the paucity of the species in bays such as Lyme Bay, and notes its abundance on projecting headlands with deep off-shore water. He suggests that this may be due to the generally heavy sedimentation of bay water, resulting in a poor penetration of light. This would explain not only the scanty development of *Himanthalia* at Fort Charles and Wilderness Point, but also its absence from Cardigan Bay, for the species can exist much further north than this (Kitching, 1935). *Himanthalia* appears to favour fairly gentle slopes (e.g. on the level stretch behind the protective blocks of the Breakwater there occurs an excellent zone of this alga). On Church Reef, characteristic fringes of *Himanthalia* are found at the bases of exposed 45° slopes which are thickly covered with barnacles and bare of all other fucoids. Kitching (1935) agrees that the species can inhabit slopes up to 80° but that it usually prefers more level ones, and it was only occasionally found on vertical landward faces and on steep gulley banks. Gibb (1938) describes a *Himanthalia* zone between that of *Fucus serratus* and the Laminarians, but in the Plymouth neighbourhood such a zone is best observed where *F. serratus* is poor or absent. Thus, on the south face of the Breakwater [7], *Himanthalia* is definitely the dominant alga up to 1 ft. above the Laminarian zone. On the other hand, where the *Fucus serratus* community is well developed (e.g. at Jennycliff and North Point), *Himanthalia* mixes with this alga, and no separate belt can be distinguished. The species is common to below E.L.W.S. and its upper limit lies in the region of M.L.W.N. (see Fig. 4A), though occasional plants were taken on a north-facing, shaded slope as high as E.L.W.N. at Bolt Head [*1*]. The upper limit of abundance is highest on Church Reef [*6*] and in Jennycliff Bay [*13*], while under the extreme exposure of Bolt Head [*1*] the alga is not common above M.L.W.S. + 1 ft. (though it is occasional to E.L.W.N.), and the height of the *Himanthalia* zone, like that of *Fucus serratus*, appears to be limited by the degree of surf action.

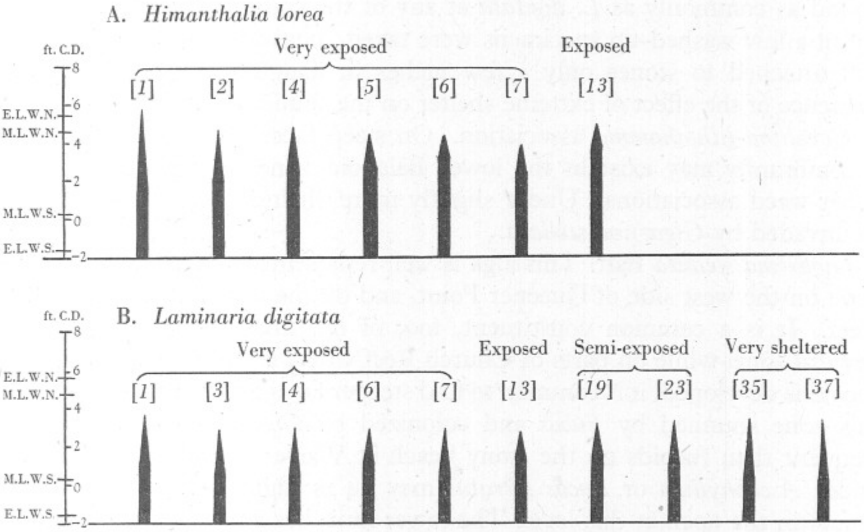

Fig. 4. Upper limits of *Himanthalia lorea* (A) and *Laminaria digitata* (B).

While adult plants are not usual above M.L.W.N., vegetative 'buttons' may be found much higher, e.g. up to M.T.L. or above on the Breakwater blocks, or even to E.H.W.N. under a thick carpet of fucoids.

*Laminaria digitata* Lamour. This occurs in quantity at all the stations visited, except on the stony beach of Warren Point, and is tolerant of a wide range of conditions of surf. The absolute upper limit of distribution lies just below M.L.W.N. (see Fig. 4B), but the alga is not common (i.e. the 'Laminarian zone' does not commence) much above M.L.W.S. This zone may begin as high as M.L.W.S. + 2 ft., e.g. on the flatter rocks on the west side of Queener Point where, although surf action and wave crash are not excessive, there is generally a heavy swell and a broad wash zone. Under conditions of extreme exposure it may not extend much above M.L.W.S. + 1 ft.; on the other hand, where shelter is very pronounced *L. digitata* may not be common above M.L.W.S. Thus the relation between the upper limit of distribution and the intensity of surf, which was demonstrated for *Fucus serratus* and *Himanthalia*, holds good for *Laminaria digitata* also. The effect of slight shelter in allowing the alga to ascend above M.L.W.S. has been noted by Rees (1935), who states with regard to *L. digitata* (p. 93): 'With increasing shelter this alga is no longer confined to channels but spreads out as a belt on the top of the sublittoral, beginning on flat ledges but later, with increasing shelter, occurring as a zone above *Laminaria Cloustoni* on surfaces that do not slope too steeply.'

*Laminaria saccharina* Lamour. As is general in Cardigan Bay and elsewhere, this species is intolerant of excessive exposure to wave action, and it is confined to pools and channels at Bolt Head, Church Reef, Reny, etc. It was never found as commonly as *L. digitata* at any of the stations visited. At Warren Point a few washed-up specimens were taken, measuring up to 2 yards long, but attached to stones only a few inches in diameter, which is a further evidence of the effect of extreme shelter on the stability of such a substratum.

*Corallina-lithothamnia* association. On steep faces at exposed points such a community may exist in the lower Balanoid zone, in the absence of all other weed associations. Under slightly more sheltered conditions this may be invaded by *Gigartina stellata*.

*Gigartina stellata* Batt. This alga is well represented in the lower Balanoid zone on the west side of Queener Point, and on the exposed reefs of Church Reef. It is a common constituent, too, of the undergrowth of the *Fucus serratus* zone, while on parts of Church Reef where a typical belt of the latter fucoid is developed, it is common to find steeper faces and protruding ledges in this zone shunned by *Fucus* and colonized by *Gigartina*. It is also more frequent than fucoids on the stony beach at Warren Point. Its upper limit under *Ascophyllum* or *Fucus serratus* may lie as high as E.L.W.N., but little occurs in the open at this level. The lower limit lies beyond E.L.W.S.

*Laurencia pinnatifida* Lamour. Like *Gigartina* and *Corallina*, this is often common in the undergrowth of a zone of *Fucus serratus*, but also occurs on rocks too exposed for fucoid growth. It is common in patches on rocks thickly encrusted with barnacles, and such *Laurencia-Balanus* communities normally occur above a lower zone of *Gigartina* and barnacles. The upper limit of *Laurencia* at Queener Point lies above M.T.L., but at Bolt Head the alga is restricted to lower levels. It is generally patchily distributed, and does not seem to form a 'continual carpet' such as Rees (1935) describes at Lough Ine.

*Porphyra umbilicalis* (L.) J.G. Ag. is extremely haphazard in its distribution, occurring from conditions of extreme exposure to those of extreme shelter, and is apparently unaffected by either. Steep, barnacle-encrusted reefs, and smooth boulders are equally well colonized by *Porphyra*, and it is also commonly epiphytic on fucoid algae. Cotton (1912) remarks with regard to the *Porphyra* association: 'Doubtless surf and spray are largely responsible...this does not account for all the differences that have been noted.' Though the alga occurs sporadically from the Laminarian zone to above E.H.W.S. on exposed peaks, it often tends to form well-defined bands of growth on such peaks and slopes. Thus on steep faces at Bolt Head a band was noted in the M.H.W.S.-E.H.W.S. region; on the south face of the Breakwater two such bands were observed, one between M.H.W.N. and M.H.W.S., the other at about M.L.W.N., with practically no *Porphyra* in between. The reason for this is not clear.

*Lichina pygmaea* Ag. The distribution of this lichen in the Plymouth area has been described by Naylor (1930), and the present survey confirms the major part of her observations. *L. pygmaea* is best developed on steep exposed slopes, with rough or barnacle-encrusted surfaces (e.g. at Bolt Head, Blackstone, Reny, etc.). Yet, provided water movement is strong enough, the lichen is not restricted to vertical faces, but occurs quite thickly on gentle slopes (e.g. at North Point). It was not taken under the sheltered conditions of Warren and Wilderness Points, nor, as Naylor (1930) describes, is it present in Jennycliff Bay. The lichen is normally thickest and most extensive on slopes facing in a southerly direction, but it is commonly well developed even on rough landward faces where these are covered with barnacles; it also occurs in caves and overhangs when these are exposed to strong water movement, and the restriction of *L. pygmaea* to brightly illuminated surfaces as Naylor (1930) remarks is not at all marked. Similar results have been obtained in Cardigan Bay, and the writer is inclined to believe, despite the absence of the lichen from the shaded shore of Jennycliff Bay, that *L. pygmaea* is primarily dependent on surf action and rough rock, and that no simple light effect can be distinguished.

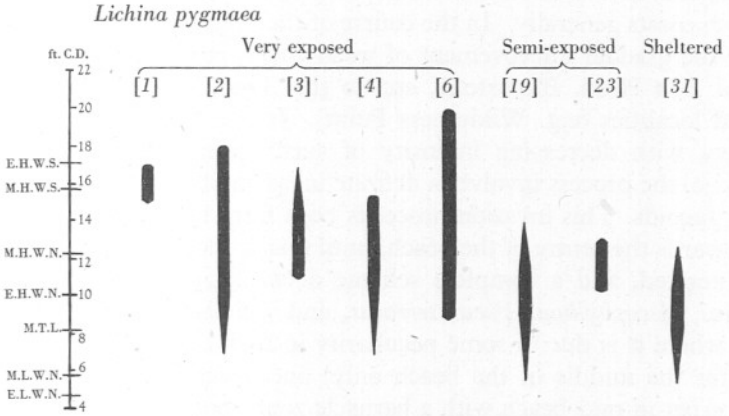

Fig. 5. Zonation of *Lichina pygmaea*.

Naylor (1930) states that the lichen never extends above the *Pelvetia* zone, and generally achieves its lower limit around M.T.L. Only occasionally in the present survey was it taken as low as M.L.W.N., and its lower limit (see Fig. 5) is variable, with no clear relation to surf or any other factor. Where *Lichina* and

*Pelvetia* are both present (e.g. on the landward rocks of Church Reef, at North Point, and at Fort Charles) the lichen always occurs below the alga (compare Figs. 3A, 5), but with increasing exposure to waves the *Pelvetia* zone disappears and the upper limit of *Lichina* rises until (e.g. on the seaward peaks of Church Reef) it extends to above E.H.W.S. At semi-exposed localities the upper limit lies in the M.H.W.N.-M.H.W.S. region. The high upper limit of the lichen on the seaward reefs of Church Reef [*6*] is worth noting: though not quite so exposed to surf as Bolt Head, for example, the low position of these reefs on the shore results in them receiving splash and spray even at low water on rough days.

### *Discussion on the Distribution of Algae*

The correlation between the intensity of wave action and the distribution of littoral algae is as well marked in the Plymouth area as it is in Cardigan Bay and on British coasts generally. In the course of the present survey it was possible to trace the gradual improvement of weed cover, from the typical 'barnacle areas' of Bolt Head, Blackstone, etc. to the 'fucoid areas' characteristic of sheltered localities (e.g. Wilderness Point). It is a significant fact that this transition, with decreasing intensity of surf, appears to follow a definite pattern, i.e. the process involves a definite invasion of the mid-beach Balanoid zone by fucoids. This invasion proceeds both from low water and from high water towards the centre of the beach, until finally the barnacle belt is more or less obliterated, and a complete scheme of weed zonation (*Pelvetia*, *Fucus vesiculosus*, *Ascophyllum*, *Fucus serratus*, and *Laminaria*) is achieved. Thus (except where it is due to some peculiarity in rock configuration resulting in shelter for the middle of the beach only) one never finds a well-developed fucoid carpet in mid-beach with a barnacle zone above and below it. On the other hand, a mid-beach Balanoid zone passing into fucoids above and below is quite general in semi-exposed situations. Thus at Bolt Head and Blackstone Point, the entire beach from M.L.W.S. upward is occupied by *Balanus* and *Chthamalus*, merging into a zone of *Littorina rudis* and *L. neritoides* at high-water mark, and in such areas there are no intertidal fucoid communities whatsoever. Under slightly more sheltered conditions (e.g. on the west side of Queener Point), not only does the *Laminaria digitata* belt creep up from M.L.W.S. but also *Corallina*, *Gigartina* and *Laurencia* tend to invade the lower part of the Balanoid zone. The next stage is the appearance of a belt of *Himanthalia* above the Laminarian zone, when surf action decreases to the extent it does on the Breakwater and on the seaward parts of Church Reef. Still more sheltered conditions lead to the appearance of *Fucus serratus* as a zone at low water, and the upward extension of this zone, as the intensity of surf decreases, has already been demonstrated (Fig. 3E). Under slightly less sheltered conditions than those required by *F. serratus*, first *Pelvetia* and then *Fucus spiralis* make their appearance at the top of the shore, and the downward extension of the zones of these algae has also been noted (Figs. 3A, B). This is the typical state found in semi-exposed localities, and may be summarized thus: *Littorina* zone, *Pelvetia*, *Fucus spiralis*, barnacles (with scattered plants of *F. vesiculosus*), *F. serratus*, Laminarians. *F. vesiculosus* has been present from an early stage in the transition, but as occasional and tattered plants only; now, as shelter improves, the alga becomes more frequent and the individuals more robust. Still further reduction in the intensity of surf allows *Ascophyllum* to appear; this soon becomes dominant, and where surf is reduced to a minimum (e.g. at Wilderness Point, Newton Ferrers, etc.) the *Ascophyllum* community occupies the mid-beach to the complete exclusion of the Balanoid zone.

Such a process cannot, however, be ascribed to the decreasing energy of surf action alone; were this so, one would expect to find the *Fucus vesiculosus* zone the first to appear, since individual plants of this alga are apparently extremely tolerant of surf. The writer would suggest that not only is the actual force of wave shock important with respect to the algae, but that the relative frequencies with which different shore levels are subjected to wave shock must also be taken into consideration. Stephenson (1941) mentions a suggestion made by D. P. Wilson that the frequency and duration of wave action may determine the upper limits of distribution of low-tide algae, and this certainly appears to be true for *Fucus serratus*, *Laminaria digitata*, etc. (see Figs. 3E, 4B). At the level of M.L.W.S. the shore is comparatively seldom exposed to breaking waves, for during most tides such levels remain submerged; similarly M.H.W.S. and levels above this are only relatively occasionally reached by surf. At M.T.L., however, direct wave shock is experienced twice during every complete tide, and the same is true at all levels between E.L.W.N. and E.H.W.N. From both these levels, proceeding towards low water and high water respectively, there is a progessive decrease in this frequency factor. Both (*a*) the actual force of wave shock, and (*b*) the frequency of this effect will act adversely on the fucoids, and it is reasonable to suggest that the reduction in one of these will mitigate, to some extent, the combined adverse effect of both. Thus, reduction in the factor of intensity of wave force enables *Fucus serratus* (for example) to withstand the frequency factor to a greater degree, and so to exist higher up the shore. (The frequency remains comparatively unaltered, though the intensity of surf will also tend to determine the width of the zone affected by the breaking waves to some extent.) For *Pelvetia* and *Fucus spiralis* at the top of the shore the same argument applies, though since such algae are more limited in their potential depth of zonation than *F. serratus*, the downward extension of these algae with increasing shelter is not so marked as the upward extension of *F. serratus*. Still further reduction in the intensity factor results in still greater tolerance of the frequency factor, and in still further extension of such algae towards mid-beach. Finally the actual force of wave shock becomes so much reduced (e.g. at Wilderness Point) that the frequency with which different shore levels are subjected to breaking waves has little effect, and the entire beach is favourable to fucoid growth.

The presence of weed-free zones in mid-beach has been noted by various workers, and attributed to different causes. Grubb (1936) describes a 'bare zone' between the *F. spiralis* and the *Laurencia-Corallina* associations at Peveril Point, Dorset, and suggests two possible causes. She points out that in this region of the beach (M.H.W.N. to M.L.W.N.) there occurs the maximum fluctuation in periods of submergence and emergence, and that any alga colonizing such levels would need a very adaptable physiology. Secondly, Grubb (1936) remarks that the 'bare zone' is covered or uncovered during the third and fourth hours of tidal flow or ebb, when the rate of water movement is greatest, and that (p. 409), 'this comparatively rapid movement may have something to do with the absence of vegetation here'. Yet the same worker also states (p. 409) that: 'In the sheltered places at Peveril Point...*Fucus serratus* may grow in this region, but for the most part the rocks are too exposed for this species, or for *Ascophyllum*, and since no other species has taken their place, they remain bare.' The presence of *Fucus serratus* in the 'bare zone' at Peveril Point when shelter is experienced is significant, and it appears that this is only another example of what has already been described. Indications of the same phenomenon were noted in Cardigan Bay, but in this locality the range in conditions of exposure and shelter is not wide enough to enable one to describe the process of algal invasion of the mid-beach with the clarity with which it can be seen on the more irregular coastline studied in the present survey. To summarize then, both the actual intensity of wave shock and the frequency of this factor must be taken into account when considering surf effects.

Various opinions have been expressed with regard to the relative tolerance to surf exhibited by the fucoids, especially by *Ascophyllum* and *Fucus vesiculosus*. Both Børgesen (1908) and Zaneveld (1937) appear to hold that the former alga can withstand greater intensity of water movement, but most workers (e.g. Cotton, 1912; Kitching, 1935, and others) take the opposite view. Both David (1941) and the present writer have found *F. vesiculosus* to be the least affected by surf in Cardigan Bay. Cotton (1912) arranges the algae in the following order of decreasing tolerance: *F. spiralis*, *F. vesiculosus*, *Pelvetia*, *Ascophyllum*. Gislén (1930) gives the series as: *Fucus vesiculosus*, *F. serratus*, *F. spiralis*, *Ascophyllum*; while Kitching (1935) gives: *Fucus vesiculosus*, *Pelvetia*, *Fucus spiralis*, *Ascophyllum*. From observations in the Plymouth locality the writer would arrange the algae studied in the following order: 'lithothamnia', *Porphyra umbilicalis*, *Corallina*, *Fucus vesiculosus*, *Himanthalia*, *Laminaria digitata*, *Laurencia pinnatifida*, *Gigartina stellata*, *Pelvetia*, *Fucus spiralis*, *F. serratus*, *Ascophyllum*. This series demands some comment, in view of what has just been said with regard to wave shock and wave frequency. (1) *Fucus vesiculosus* not only exists under conditions of extreme surf intensity, but also at levels where the frequency of waves is at a maximum, and this species must be considered as exceptionally tolerant of the adverse effects of surf. It exists, even, on slopes too exposed for the appearance of *Himanthalia*, *Laminaria*, *Laurencia* or *Gigartina* above M.L.W.S. (2) The apparent intolerance of *Ascophyllum* may be largely due to its position in mid-beach. This would explain a phenomenon previously commented on in the Cardigan Bay investigation, i.e. the presence of solitary and very battered plants of this alga on low-level reefs. Yet it is obviously less tolerant than any of the other fucoids to the factor of wave shock alone, even allowing for the frequency factor. (3) *Pelvetia* exists in a few localities where *Fucus spiralis* is absent, and though its zone is slightly further from the zone of maximum wave frequency (i.e. E.H.W.N. to E.L.W.N.) than that of the latter alga the difference in frequency cannot be very great, therefore *Pelvetia* appears to be the more tolerant of the two species. (4) Both *Fucus spiralis* and *Pelvetia* are more frequent in local shelter at exposed points than is *Fucus serratus*, which therefore appears to be the least tolerant of these three. Here, however, a further complication is introduced. While *Pelvetia* and *Fucus spiralis* spend most of their time above water level, *F. serratus* (and low-level algae in general) is, for the greater part of the time, submerged, and though actual wave crash may not be experienced during the whole of the time of submergence, the effects of back-wash, currents, tidal drag, and swell are likely to be important. (5) *Laminaria digitata* occupies levels which are not often exposed to breaking waves, and it may be argued that its apparent high degree of tolerance of wave shock is due to its low zonation, and that actually it is no less susceptible to this factor than is *Fucus serratus*. But the sharp demarcation between a profuse Laminarian zone and a zone bare of *F. serratus*, which may be observed at many exposed points, does not favour this suggestion, for the factor of wave frequency is not likely to change so sharply within such a narrow vertical range to account for this. Furthermore, the strong holdfast, the leathery and much-divided fronds, and the supple stipe of *Laminaria digitata* would seem to indicate that this species has a very high degree of tolerance of surf. (6) The same is true of *Himanthalia* but, judging from its rather more frequent appearance than *Laminaria* above M.L.W.S., it would appear to be slightly more tolerant than the latter. (7) The ability with which species like lithothamnia, *Corallina*, *Porphyra*, *Gigartina* and *Laurencia* appear above M.L.W.S. under conditions of extreme exposure indicates that these are extremely tolerant both of the actual force of wave shock and of the frequency of this factor.

### *Fauna*

*Barnacles*. Three species of Cirripedes are considered, *Balanus perforatus* Brug., *Balanus balanoides* (L.), and *Chthamalus stellatus* (Poli). The last two thrive best at exposed points, and constitute the 'Balanoid zone' characteristic of such localities; *Balanus perforatus* is commonly found under rather more sheltered conditions and will be considered later.

Fischer-Piette (1933) and Moore & Kitching (1939) describe the distributions of *Balanus balanoides* and *Chthamalus stellatus* along British coasts; and it appears that Plymouth lies in an intermediate position on the south coast. Further west, towards Cornwall, *Balanus* dies out until *Chthamalus* only is left; further east, towards the Isle of Wight, it is *Balanus* which becomes increasingly dominant, and *Chthamalus* eventually disappears. In the Plymouth neighbourhood, however, both species occur freely, *Chthamalus* being dominant on the upper beach and *Balanus* on the lower beach. The effect of surf on the state of development of the Balanoid zone, and the negative correlation with fucoids have already been considered in this paper; various other general features are discussed in the work on Cardigan Bay, and here it is necessary only to consider the features of vertical distribution of the two species.

The upper limit of barnacles in quantity, or the '*Chthamalus*-line', usually best marked on steep exposed surfaces, varies in height in relation to the intensity of surf experienced (see Fig. 6A), and so does the absolute upper limit of *Chthamalus*. The outer reefs of Church Reef are thickly encrusted with this barnacle to above E.H.W.S., which is a reflexion not only of the exposure to strong surf but also of the low position of these reefs on the shore: they receive splash on a rough day even from low tides. Elsewhere the upper limit of barnacles in quantity varies from just above M.H.W.S. (at Bolt Head [*1*], etc.) to just above M.H.W.N. (e.g. on sheltered north faces at Jennycliff [*24*]). When shelter increases still further no distinct line can be recognized, and barnacles are reduced over the whole beach.

The lower limit of the barnacle belt, too, is frequently marked as a line on exposed vertical faces, i.e. the '*Balanus*-line'. In general this is less well marked than the *Chthamalus*-line, and is distinct only on steep faces at low-tide levels, but in places (e.g. at North Point), even when the rocks are horizontal, it is possible to recognize a fairly definite limit, below which barnacles in quantity die out. It is difficult to choose definite localities at which both the *Chthamalus*- and *Balanus*-lines are clearly recognizable, and at which the intensity of exposure is approximately equivalent at the top and the bottom of the shore, but an attempt is made to do this in Fig. 6A. It will be seen that, with increasing shelter, the lower limit of the Balanoid zone rises from M.L.W.S. to the region of M.L.W.N.; Fig. 6B gives a more comprehensive picture of this process. The same feature has been described in the Isle of Man by Moore (1935*a*). At many localities (e.g. North Point) it would appear that this raising of the lower level of the Balanoid zone is caused by the upward extension of the lower-shore fucoid belt, and this may be partially true. However, surf in itself also seems to have a more direct effect on the lower limit of barnacles in quantity. It is common to find protruding rocks near low-water level with a well-marked *Balanus*-line on their seaward face just above M.L.W.S., and with nothing below this line but a thin sheet of calcareous algae; obviously here

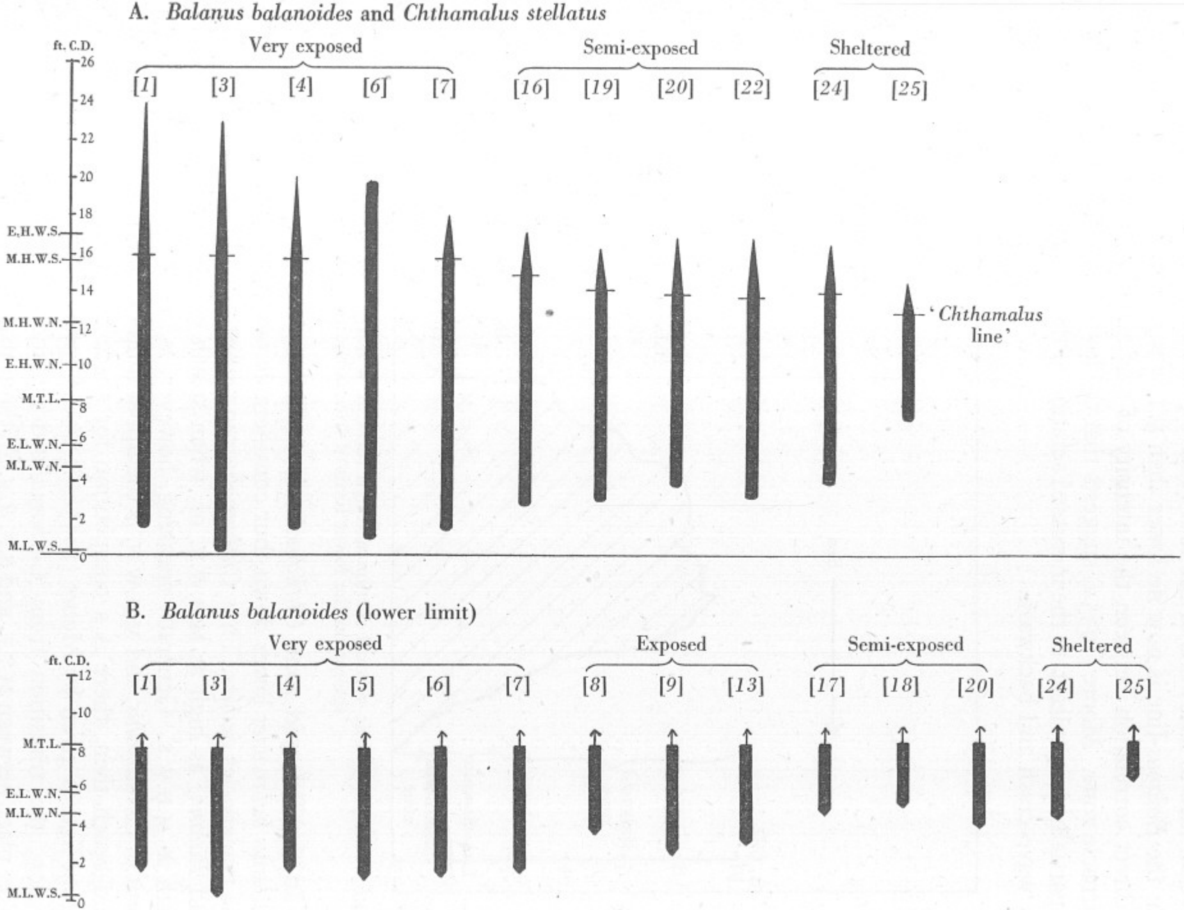

Fig. 6. Zonation of barnacles. (A) The vertical width of the Balanoid zone at different localities; (B) The lower limit of the Balanoid zone under different degrees of exposure to wave action.

fucoids are not limiting for the lower limit of *Balanus*. Moreover, on a similar vertical face to landward of the first (Fig. 7), there may be no fucoids again, but the *Balanus*-line is now no lower than M.L.W.N.; thus there appears to be a direct correlation between the intensity of surf and the lower limit of the barnacle zone. Moore (1935 *a*) suggests that the lowering of this limit by surf is partially due, at least, to the increased aeration of the water to greater depths, by wave-crash and backwash.

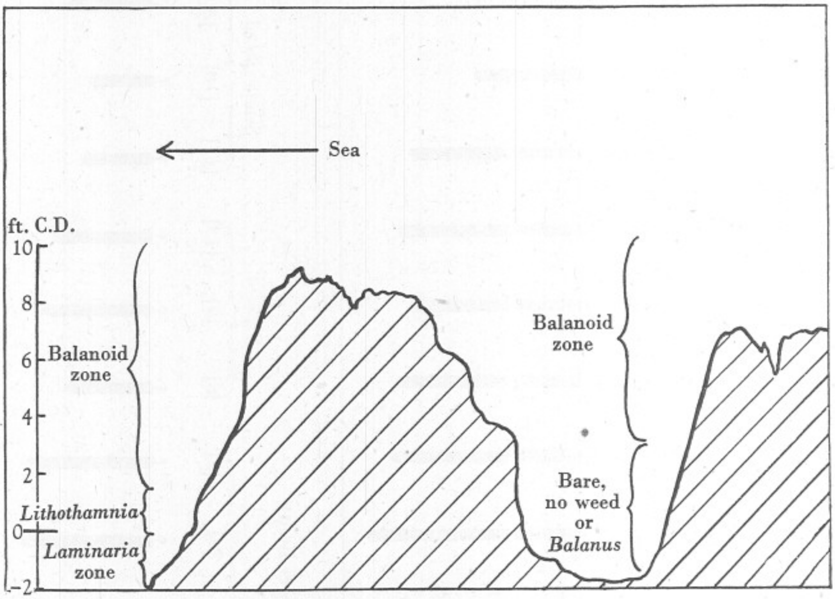

Fig. 7. Diagrammatic vertical section through reefs in Wembury Bay to show the effect of shelter on the lower limit of the Balanoid zone.

In the Balanoid zone *Chthamalus* is dominant on the upper shore, and *Balanus balanoides* lower down, but considerable overlapping of the zones of the two species occurs. Thus *Chthamalus* can persist as low as M.L.W.S. + 2 ft., and *Balanus* as high as M.H.W.N. or, when splash effects are introduced, as high as M.H.W.S. Generally speaking, however, M.L.W.N. is about the lower limit of *Chthamalus*, and M.H.W.N. is the upper limit of *Balanus balanoides*. In mid-beach then, there is a competition for space between the two species. From figures given by Moore (1935 *b*) it would appear that, in the Plymouth region, the transition from *Chthamalus*-dominance to *Balanus*-dominance takes place between M.T.L. and E.H.W.N. Without making a detailed analysis of the barnacle population at different points it is impossible to be certain, but the writer has gained the impression during this survey that the intensity of wave action may be a modifying factor in this respect. In Jennycliff Bay and on the north face of the Breakwater the transition occurs in the region of M.T.L., but on steep, exposed slopes at Bolt Head and Blackstone Point *Chthamalus* may be dominant as low as E.L.W.N.

Summarizing, then, intense wave action tends (*a*) to raise the upper limit of the Balanoid zone; (*b*) to lower the lower limit of the Balanoid zone; (*c*) possibly to lower the level at which the transition from *Chthamalus*-dominance to *Balanus*-dominance occurs.

*Balanus perforatus* Bruguière. Unlike the other two barnacles studied, this species is not overfond of strong surf, yet it favours a certain amount of water movement. Fischer-Piette (1936) has noted its scanty development on projecting headlands such as Start Point, and its improvement at wave-beaten positions in bays. It is obvious from the present survey, too, that *B. perforatus* is characteristic of semi-exposed situations; thus it was not found at Bolt Head or Blackstone, and is only occasional under extreme conditions of shelter (e.g. at Wilderness Point). In moderately exposed localities (e.g. Jennycliff Bay, Church Reef, North Point) the species is common in cracks, fissures, overhangs, etc., where surf is not too strong, and in such positions it may be the dominant barnacle over a small area of rock surface. On the flatter rocks on the west side of Queener Point, and on parts of the West Hoe rocks *B. perforatus* is very well represented and commonly associated with patches of *Mytilus edulis*. Mussels do not always occur where the barnacle is profuse, however, and the association, though frequent, is probably purely coincidental, as Fischer-Piette (1936) suggests.

*Balanus perforatus* extends to below M.L.W.S. in quantity, and its upper limit lies in the region of E.H.W.N.; though on north-facing overhangs on the outer reefs of Church Reef this may be raised by splash as high as M.H.W.N.

*Littorina neritoides* (L.). In the Plymouth locality, as in Cardigan Bay, this species is best represented on steep, rough, and very exposed surfaces, and is especially abundant at Bolt Head, Blackstone, and Queener Points. In semi-exposed localities (e.g. Jennycliff, Church Reef landward rocks, etc.), it is reduced in numbers; at North Point it is comparatively infrequent on the horizontal rocks; at Wilderness Point only very occasional specimens were found; while at Warren Point it was not taken at all. This agrees with the results of Lysaght (1941), who finds that *L. neritoides* is favoured by a barnacle-covered substratum but disfavoured by excessive development of weed. Both Lysaght (1941) and Colman (1933) discuss the tropic reactions of this snail, and Colman concludes that its restriction to cracks and crevices above high water is prompted by its need for shelter from wave shock. Yet, at Queener Point for example, it is common to find literally hundreds of individuals congregated on steep exposed surfaces in mid-beach, where the intensity and frequency of surf action are both high. It is probable that the adhesive powers of the snail are considerably stronger when it is wet than when it dries out, for *L. neritoides* above M.H.W.S. level can be easily blown off the rock.

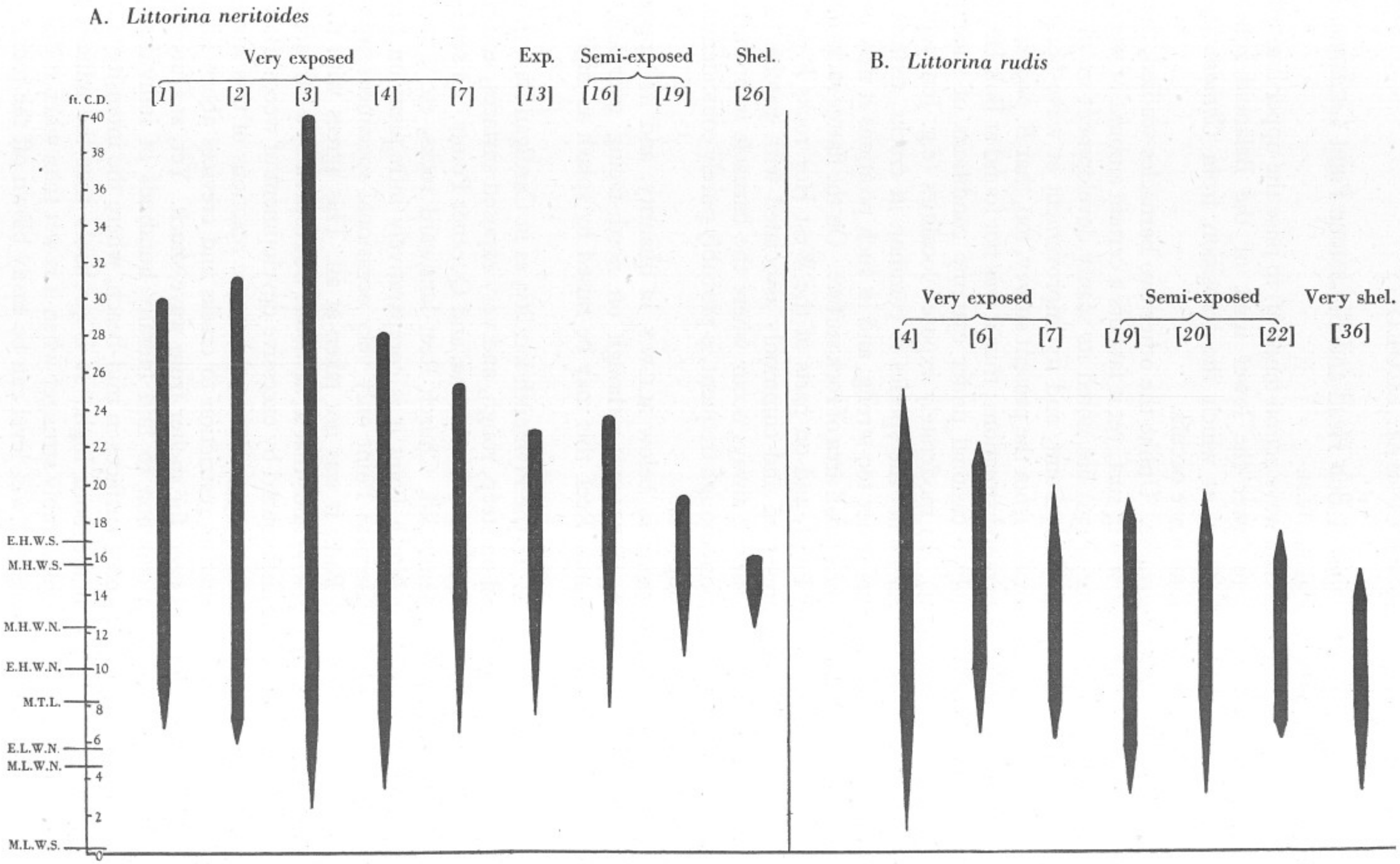

Fig. 8. Zonation of *Littorina neritoides* (A) and *L. rudis* (B).

The species is usually described as inhabiting levels above high-water mark, and, while it is admittedly most characteristic of such levels, occasional specimens were taken in Cardigan Bay as low as M.L.W.N. Lysaght (1941) records it to below M.T.L. on the Plymouth Breakwater, and reports the finding of mature snails on piles permanently submerged for at least a year. This being so, it is likely that Colman's (1933) lower limit, which he confesses is 'somewhat uncertain', is considerably too high. During the course of the present survey the species was definitely taken to below M.T.L. even on the landward portion of Church Reef, while at Blackstone Point it was found occasionally down to M.L.W.S. + 2 ft. (Fig. 8A). Although it was found to M.L.W.N. in Cardigan Bay, *L. neritoides* is never common much below M.H.W.S. in the region; in the Plymouth region, however, the writer has found dense congregations of the species in the M.T.L.-E.L.W.N. region (e.g. at Bolt Head, Reny, Blackstone, and Queener Points). Such groups are inevitably restricted to steep, rough faces, with a thick barnacle cover; on neighbouring flatter surfaces at the same shore level *L. neritoides* may be very occasional only. From Fig. 8A it can be seen that the intensity of surf raises the upper limit of distribution, and lowers the lower limit.

*Littorina rudis* (Maton). This species favours less exposed situations than *L. neritoides*, and is generally inferior to it in numbers at places such as Bolt Head, Blackstone, and Reny Rocks. On barnacle-covered slopes, *L. rudis* is largely confined to the shelter of empty barnacle shells. At North Point, Jennycliff Bay, Wilderness Point, and other semi-exposed or sheltered localities the species is more frequent than *L. neritoides*, occurring in large numbers among the sparse zones of *Pelvetia* and *Fucus spiralis* and at heights above these; but at Warren Point it is most abundant on shingle and boulders, and does not appear to favour the thick weed cover met with here. *Littorina rudis* is fond of somewhat irregular and broken rock, with plenty of pools, cracks, crevices, etc., while boulder areas (e.g. at Sandhill Point in the Salcombe Estuary) are usually well colonized by the snail. Vertical surfaces, unless deeply fissured and not exposed to excessive wave action, are not generally as popular as more level rock.

The upper limit (Fig. 8B) is lower than that of *L. neritoides* but may be raised by splash. The species is usually not very common much below M.T.L., and the intensity of surf does not appear to have any marked modifying effect on the lower limit of distribution. On the Breakwater, *L. rudis* was not taken below E.L.W.N., but on Queener Point specimens were found as low as M.L.W.S. + 1 ft.; Moore (1940) also describes the lower limit of this species as variable.

*Littorina littorea* (L.). This is even less tolerant of surf than *L. rudis*, and no specimens were recorded at Bolt Head, Reny, Blackstone, or the Breakwater, while at Queener Point it is occasional only in sheltered gulleys. At North Point, and in Jennycliff and Wembury Bays it occurs very commonly on level broken ground where weed is not too profuse. In the Yealm estuary *L. littorea* is abundant on the stony beach in the neighbourhood of Warren Point, and may be the dominant animal species on such a substratum. Its habit of congregating on boulders, on isolated weed clumps, in shallow pools, etc., is well marked, and leads to a somewhat local distribution. Curiously, *L. littorea* was not found, even in local shelter or on suitable ground, in the Tinside-West Hoe region, and was only occasionally recorded at Wilderness Point, both of which are limestone areas.

The upper limit of distribution (Fig. 9A) is variable, and appears to be raised by splash. The lower limit is not well defined either; the snail generally occurs lower on stones (e.g. at Warren Point) and in gulleys than it does when the lower shore is densely covered by fucoids. It is most abundant above M.L.W.S. + 2 ft., but at Warren Point [*36*] it is common as low as M.L.W.S. − 0·5 ft.

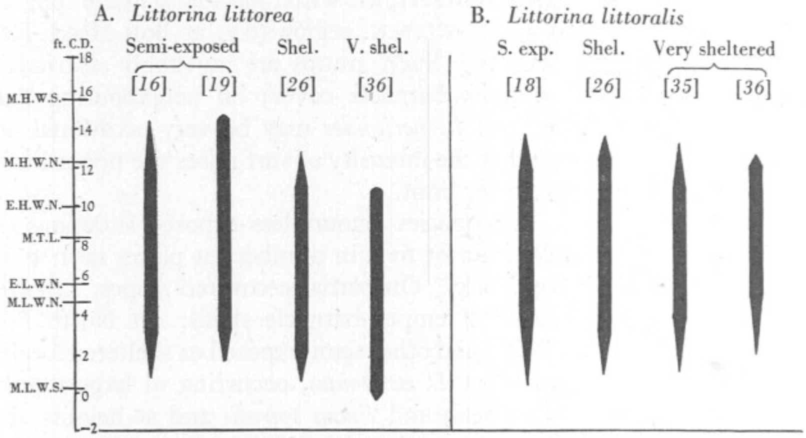

Fig. 9. Zonation of *Littorina littorea* (A) and *L. littoralis* (B).

*Littorina littoralis* (L.). As usual, *L. littoralis* is confined to fucoid areas, and was found to be most abundant in weed zones at Church Reef, Wilderness Point, Warren Point, and Jennycliff. Yet at Fort Charles west, where the *Fucus vesiculosus* belt is good, *Littorina littoralis* is surprisingly poorly represented. In its vertical distribution, too, *L. littoralis* is influenced by the distribution of fucoids. Thus the scarcity of weed on the stony lower beach at Warren Point (Fig. 9B [*36*]) results in the occasional presence of the snail. Generally speaking the zone of abundance of *L. littorea* lies between M.H.W.N. and M.L.W.N. (Fig. 9B), but occasional specimens have been taken as high as M.H.W.N. + 1 ft. and as low as M.L.W.S. In moderately exposed and sheltered localities (e.g. Jennycliff Bay and Warren Point) *L. littoralis* occupies a somewhat higher zone on the beach than *L. littorea*.

*Osilinus lineatus* (da Costa). *Osilinus* is intolerant of excessive exposure to surf, and was not found at Bolt Head, Blackstone, on the south face of the Breakwater, or on the outer reefs of Church Reef. At Queener Point the species is entirely confined to the shelter of gulleys and channels. It was not taken at Tinside, and only a single specimen was discovered, after prolonged search, at Wilderness Point; Moore (1940) also records its absence from Rum Bay, which is another limestone area, yet on the Staddon Grits of Jennycliff Bay, a short distance away, *Osilinus* is quite common. The favourite habitat of the species is the same as it is in Cardigan Bay, i.e. fairly sheltered level rock, or areas of boulders and shingle, especially when these occur in gulleys. On such ground the snail is common in Jennycliff Bay, and very frequent along the shore of Wembury Bay to Church Reef. On Church Reef, it is local in distribution on the landward portion, but is not as restricted in its horizontal distribution as Colman (1933) describes. At Warren Point, though *Osilinus* does occur under weed, it is much more abundant on shingle areas, and an '*Osilinus* zone' may be recognized at the top of the stony beach here, as in many places in Cardigan Bay. On steep faces, when these are very sheltered, the snail is occasional, but it was never found on overhanging surfaces.

Colman (1933) describes a very narrow vertical range for *Osilinus*, between M.H.W.N. and E.H.W.N. In Cardigan Bay the species has been found to occupy a much wider range, from above M.H.W.N. to M.L.W.N., while Moore (1940) has described a similar range at Wembury. Fig. 10B shows that its general zonation lies between high and low water neaps at the four localities at which it occurs in numbers. It would appear that here, again, splash is effective in extending the upper limit. The low lower limit at Warren Point [*36*] may be due to the stony lower beach, which is an ideal habitat for *Osilinus*. Above E.H.W.N. the snail is frequent on open rock surfaces, below this level it is confined to gulleys, though not necessarily to gulleys with a fresh-water influence as Walton (1915) suggests. Possibly this restriction of the species to gulleys at levels below E.H.W.N. may be due to the frequency of wave shock at such levels.

*Gibbula umbilicalis* (da Costa). At Bolt Head, Blackstone and Reny, *G. umbilicalis* is confined to pools and crevices; and while it is intolerant of excessive surf action, it is rather more tolerant of this factor than *Osilinus* or *Littorina littorea*. However, it favours similar ground to the last two species, i.e. flat, fairly sheltered rocks, boulders and stones, etc., though it is more commonly associated with fucoids than is *Osilinus*. Lithothamnia-encrusted pools often contain a few *Gibbula umbilicalis*, and on exposed points the species may be entirely restricted to such pools. This species, again, is poor on the limestone of Wilderness Point, and very occasional from Tinside to West Hoe. Yet it is fairly common on the limestone blocks of the Breakwater and in the holes and cracks between these blocks.

*G. umbilicalis* is slightly lower in its vertical distribution than *Osilinus* (see Fig. 10C); its upper limit lies generally between E.H.W.N. and M.H.W.N., but may be raised by splash. In the M.L.W.N.-M.L.W.S. region the species tends to die out in numbers, but it may often be found as low as M.L.W.S., or slightly lower than this.

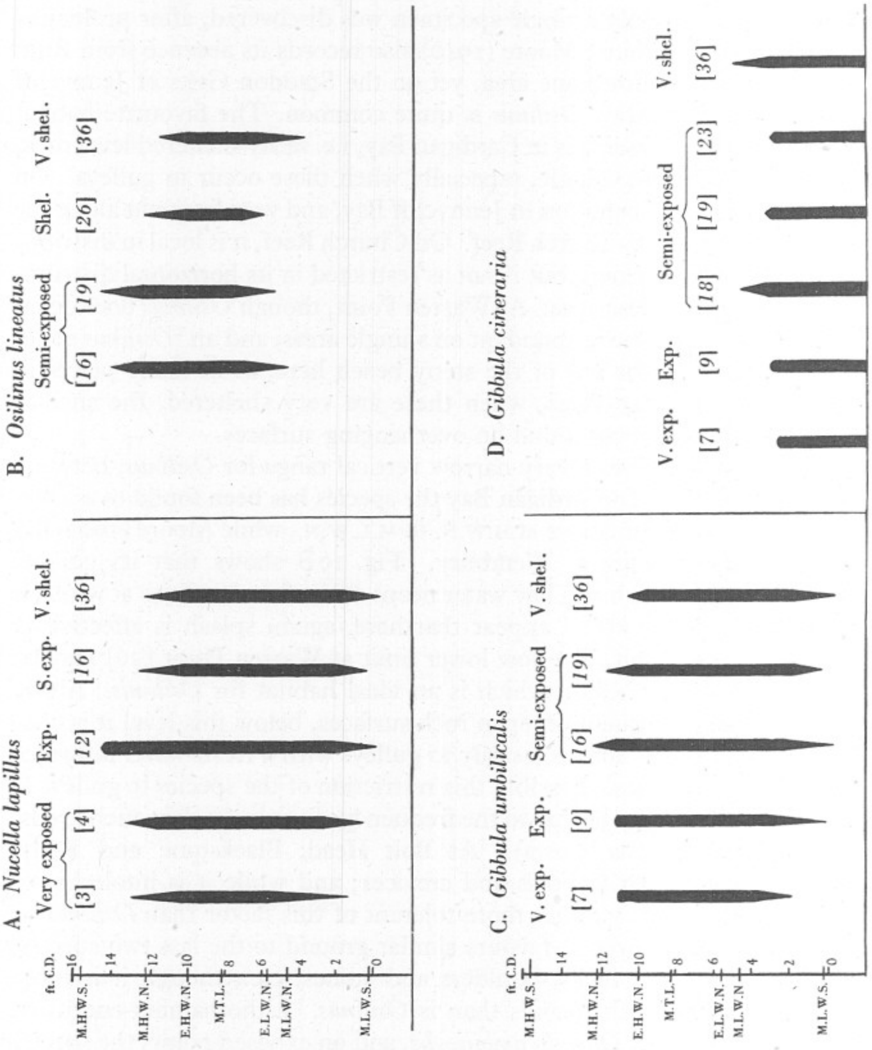

Fig. 10. Zonations of *Nucella lapillus* (A), *Osilinus lineatus* (B), *Gibbula umbilicalis* (C) and upper limit of *G. cineraria* (D).

*Gibbula cineraria* (L.). This is absent or extremely rare at exposed points such as Bolt Head, Blackstone, Reny, and Queener Point, but may be fairly common in more sheltered localities, with the exception of Tinside and Wilderness Point. Its favourite habitat is stony gulleys near low-water mark, where it commonly occurs under the stones. Specimens have also been taken on rock under weed, e.g. in the Laminarian zone at Fort Charles, and in the *Himanthalia* zone on the Breakwater.

From the sublittoral *Gibbula cineraria* extends up to about 3 ft. above C.D., while occasionally it was found to M.L.W.N. Except for a single specimen found in a crack as high as 6 ft. above C.D., on the south face of the Breakwater, the species was not recorded above M.L.W.N. anywhere (Fig. 10D).

*Nucella lapillus* (L.). *Nucella*, though it is not tolerant of heavy surf, may be quite common even on exposed headlands provided local shelter is available; thus at Blackstone Point the snail is present in appreciable numbers in the deep crevices between the steep ridges of slate. Yet, at North Point, where surf action is considerably less intense than it is at Blackstone, the species is not at all common; presumably this is due to the smoother contours of the rock and the absence of deep cracks and fissures in the felsite strata. Normally *Nucella* is not over-fond of a thick cover of weed (e.g. at Warren Point), possibly because of the paucity of barnacles (one of its main articles of diet) in such areas, yet at North Point it is curious to find a larger number of the snails under clumps of weed than on neighbouring bare rock. It appears that the shelter afforded by weed, on such a level beach as North Point, may be important. Except in sheltered conditions *Nucella* is not favoured by steep or vertical faces, but is frequently found in groups on such faces when they face away from the sea; and as the writer has already suggested in Cardigan Bay, there is some indication that, at the top of its distribution, *Nucella* may seek such surfaces partly at least because of their shade. This species, again, is poor on the Tinside-West Hoe limestone rocks and on Wilderness Point, though in the latter case the paucity of barnacles may be partially responsible. It is not particularly well represented in Jennycliff Bay either, though barnacles and local shelter are both available here.

The vertical zonation of *Nucella* is depicted in Fig. 10A. The upper limit of the species in quantity lies between E.H.W.N. and M.H.W.N. at most places, but in cracks and fissures on the landward faces of the low-tide reefs at Wembury [*12*] it occurs up to between M.H.W.N. and M.H.W.S. in numbers. At Warren Point [*36*], with decreased splash, *Nucella* is common as high as E.H.W.N. only, but even here it is occasional to M.H.W.N. The lower level of abundance lies in the M.L.W.N.-M.L.W.S. region, except at Blackstone Point [*3*]; here the rock configuration changes in the neighbourhood of E.L.W.N., and below this level local shelter (crevices, etc.) is infrequent, so that *Nucella* too is infrequent. Moore (1938) states that *Nucella* extends to below low water, and it has been definitely recorded to below M.L.W.S. at Church Reef and Warren Point. Comparing Figs. 10A and 6A it will be noted that the zone of abundance of the gastropod lies, in all instances, within the Balanoid zone.

*Patella vulgata* L. One of the most ubiquitous animals on the shore, this species ranges from conditions of extreme exposure to those of extreme shelter from surf. Yet it does not particularly favour the thick weed zones of sheltered localities, and where weed is profuse limpets are generally most numerous on bare protruding peaks and ledges. Hatton (1938) describes a denser settling of *Patella* on exposed faces than on sheltered ones, and it is possible that the filtering effect of the algal fronds is important in this respect during the time of settling. Moreover, where weed is thick (e.g. at Wilderness Point), the underlying rock is frequently coated with a layer of silt, smaller algae, sponges, and hydroids, forming a dense mat. Such a substratum is shunned by *Patella*, which is restricted to areas of barer rock. On very wave-beaten slopes (e.g. the seaward peaks of Church Reef), the competition between *Patella* and barnacles for space is often very noticeable. Where barnacles extend over practically the whole of the available space (even over the limpet shells themselves) *Patella* is almost invariably represented by small individuals only; larger shells are found only where barnacles are less dense. This, too, is commented upon by Hatton (1938) who, in addition, has observed a denser settling of limpet larvae on bare or artificially-denuded surfaces, than on those thickly covered with barnacles. The same worker describes experiments which demonstrate that the size of *Patella* is limited by the density of the surrounding barnacle population. With regard to rock slope and texture, *P. vulgata* is very tolerant; it occurs on the roughest rocks and on smooth pebbles; it is frequent on all angles of slope, including overhangs, and may even exist on very small stones where these are not subject to much movement (e.g. at Warren Point).

*P. vulgata* definitely persists to below M.L.W.S., but does not appear to reach E.L.W.S.; however, it occurs lower than the lower limit of 2 ft. above C.D. described for it by Colman (1933). Just above M.L.W.S. there is some evidence of its dying out in numbers, and *Patella athletica* becomes the dominant limpet on exposed rocks at such levels. With regard to the upper limit of *P. vulgata*, Orton (1929) considers that the orientation of the rock surface, the height of splash, the latitude of the locality, and the epoch of the day at which low springs occurs, are all important. Within the geographical limits of the present survey the last two factors are constant, and variations in the upper limit of the species can be ascribed to variations in the first two influences. It is often difficult to disentangle these two effects, for usually south-facing surfaces receive both maximum splash and maximum illumination, one factor tending to raise, the other to lower, the upper limit of distribution. In Fig. 11 is presented a selection of data arranged to illustrate the effects both of splash and shade. On south faces at Warren Point [*36*], on sheltered south faces at Jennycliff, and on similar rocks in Wembury Bay [*32*], *P. vulgata* occurs only to just below M.H.W.N. in the open, and is common only from E.H.W.N. down. These localities are represented in the centre of the text-figure. Proceeding to the left of this figure, all the localities are south-facing, and the illumination factor is therefore constant. Exposure to wave action, and the amount and height of splash are increasing, however, and it is obvious that the upper limit of *P. vulgata* is rising, until, on the seaward reefs of Church Reef [*6*], the

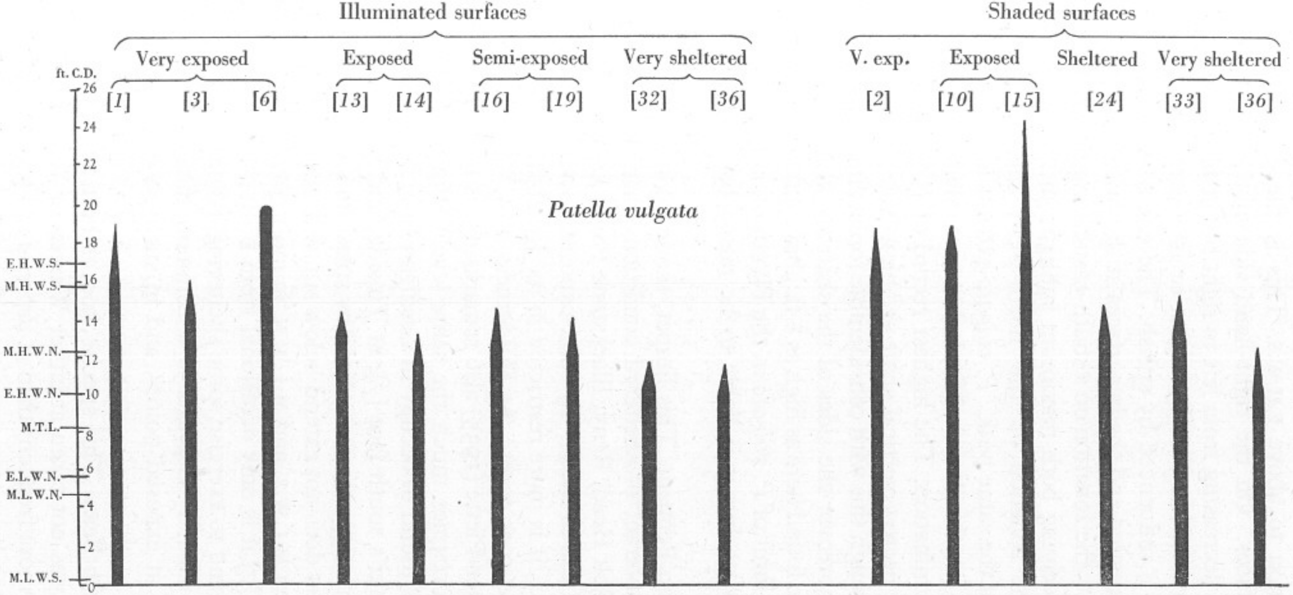

Fig. 11. Variations in the upper limit of distribution of *Patella vulgata* under different conditions of exposure to wave action and illumination.

species is common to above E.H.W.S. This is the effect of splash on fully illuminated surfaces. On the right-hand side of the figure surf action and splash are again decreasing from left to right but at all these localities *P. vulgata* is either situated on a shady aspect or is covered by weed. Here again the upper limit is influenced by splash. The effect of shade may be seen by comparing illuminated and shady surfaces at the same locality. Column [*3*] in Fig. 11 represents the zonation on a south-east-facing rock at Blackstone Point, i.e. a surface receiving both maximum sunlight and maximum wave action; column [*10*] the zonation on the north-west, and therefore shaded and sheltered, face of the same peak. *P. vulgata* extends almost 4 ft. higher on this north-west face, i.e. the absence of splash is more than compensated for by the reduction in illumination. The highest record of *P. vulgata* made during the survey was in a narrow vertical shaft or 'blow-hole' in Wembury Bay [*15*]; water rushes through this with considerable force, and splash is experienced to great heights, moreover the sides of the shaft are almost perpetually shaded, and limpets were found here as high as 8 ft. above E.H.W.S. Generally speaking, then, the upper limit of *P. vulgata* in the Plymouth neighbourhood, lies in the region of M.H.W.N., but it is liable to be raised by shade, weed-cover, and splash.

*Patella depressa* Pennant. This limpet, though commonly taken during the survey, is less tolerant of sheltered conditions than *P. vulgata*, and is best represented at Bolt Head, Reny, Blackstone Point, Queener Point, and on the outer reefs of Church Reef. In semi-exposed localities such as Jennycliff, North Point, etc., it is more restricted in its distribution, occurring locally on vertical, exposed rock faces. At Wilderness and Warren Points it was not recorded. Fischer-Piette (1935) also remarks on its need for exposure to surf.

The species occupies much the same levels (Fig. 12A) in the Plymouth locality as it was found to occupy in Cardigan Bay; it extends up to M.H.W.N. on the Breakwater's south face [7], at Tinside, and in Jennycliff Bay, but at Bolt Head [*1*] this upper limit is raised by splash to E.H.W.S. The lower limit is vague, *P. depressa* does not extend below M.L.W.S. anywhere, and it dies out in numbers between M.L.W.S. and M.L.W.N. in most places. On the south face of the Breakwater [7] it is only occasional from E.L.W.N. down, as the protective blocks in front tend to exercise some sheltering influence on the lower part of this slope. As usual *P. depressa* is a common inhabitant of lithothamnia-encrusted pools at exposed points, and in such pools it may be common to above E.H.W.S.

*Patella athletica* Bean. This species, too, is best on wave-beaten reefs and headlands, and was not taken at either Warren or Wilderness Points. However, it is rather more frequent than *P. depressa* at Fort Charles; moreover, it is generally found on less steep rocks than the other, giving the impression that here, as in Cardigan Bay, it is somewhat less demanding of surf than *P. depressa*. Fischer-Piette (1935) is inclined to adopt the opposite view.

*P. athletica* is characteristic of exposed reefs on the lower shore, where fucoids are poor or absent and *Corallina* is the chief alga, but it has also been found in shaded overhangs. In lithothamnia-encrusted pools it is common to above high water, and in such pools it is usually more frequent than either *Patella vulgata* or *P. depressa*.

Whenever it occurs, *P. athletica* is common down to the lowest level examined. The upper limit (Fig. 12B) is again affected both by splash and shade; on very exposed surfaces it may reach almost to M.T.L., on more sheltered reefs it extends as high as M.L.W.N. only, while under overhangs it was occasionally taken above M.T.L. as in Cardigan Bay.

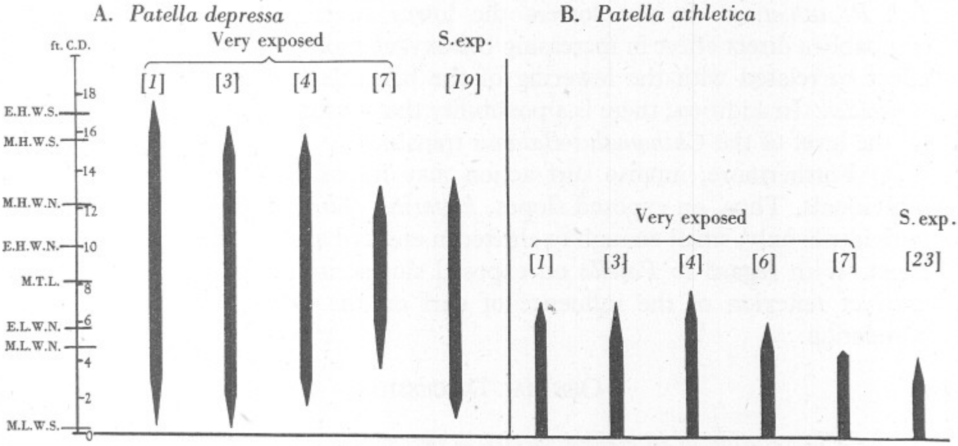

Fig. 12. Zonation of *Patella depressa* (A) and upper limit of *P. athletica* (B).

### *Discussion on the Distribution of the Fauna*

It has been shown that, for algae, surf acts chiefly, (*a*) as a presence or absence factor, and (*b*) as a modifying influence on the extent and position of algal zones. Much the same is true with regard to the fauna:

(1) As a presence or absence factor, wave action determines the density of the population of *Chthamalus*, *Balanus balanoides*, *Littorina neritoides*, *Nucella lapillus*, *Patella vulgata*, *P. athletica*, all of which species favour somewhat exposed conditions. The effect of surf on such animals may be directly concerned with transport of food, larvae, oxygen, etc. (as is probably true for barnacles); or it may be concerned in that it determines the height and frequency of splash and spray (e.g. for *Littorina neritoides*). With *Patella vulgata*, Hatton's (1938) experiments have shown that heavy surf favours a denser settling of larvae; the same is probably true for *P. depressa* and *P. athletica*, though for these two limpets there appears to be an additional effect restricting them to exposed localities. The nature of this influence is unknown.

For *Nucella* the effect of surf is indirect, in that it provides an abundant barnacle population which the gastropod can utilize for food; for barnacles themselves, too, surf has an indirect as well as a direct effect, in that it tends to remove algal competition. For *Littorina littoralis* this effect is reversed, i.e. surf, by discouraging fucoids, also discourages the snail. The adverse influence of excessive wave action on free-living gastropods such as *Osilinus*, *Littorina littorea* and *Gibbula* is, in all probability, a purely mechanical one, tending to knock such animals off the rock and damage their shells.

(2) As a modifying factor on vertical zonation, exposure to surf raises the upper limits of *Balanus balanoides*, *B. perforatus*, *Chthamalus stellatus*, *Littorina neritoides*, *L. rudis*, *L. littorea*, *Osilinus*, *Gibbula*, *Patella vulgata*, *P. depressa* and *P. athletica*. It also lowers the lower limit of *Balanus balanoides* (probably a direct effect in increasing the oxygenation), of *Nucella* (an indirect effect correlated with the lowering of the barnacle limits) and of *Littorina neritoides*. In addition, there is a possibility that surf may have some influence on the level of the *Chthamalus-Balanus* transition.

(3) Furthermore, intense surf action may impose a limit on the size of individuals. Thus, on exposed slopes, *Littorina rudis* is represented by small individuals only, small enough to shelter in empty barnacle shells, i.e. a direct effect. With regard to *Patella* on exposed slopes, its reduction in size is an indirect reflexion of the influence of surf on the density of the barnacle population.

## General Discussion

### *The relation of intertidal species to percentage exposure to the air*

The figures of Colman (1933, table VI, p. 456) for percentage exposure to the air at different shore levels are here taken as applicable; these are based on the 1930 tides, but are not likely to vary greatly from year to year. For comparison with Cardigan Bay I have chosen the landward portion of Church Reef. This locality represents intermediate conditions between the extreme exposure of Bolt Head and Blackstone Point, for instance, and the extreme shelter of Warren and Wilderness Points; as nearly as can be judged, the exposure to surf here is roughly equivalent to that experienced on the Cardiganshire coast; moreover, the results can be compared with those of Colman (1933). Fig. 13 summarizes the zonation of the various species studied on Church Reef, with the percentage-exposure curve superimposed. Table III compares the percentage-exposure limits of the species: (1) on Church Reef (present survey); (2) on Church Reef (according to Colman, 1933)—again the 'splash allowance' has been deducted, and the figures are based on Colman's 'extreme values' (1933, p. 454, tables IV and V); (3) in Cardigan Bay. In addition, (4) the extreme limits to which the species were found anywhere during the South Devon survey are also figured.

Comparing columns (1) and (2), the advantage of a wide-scale survey over a detailed but local traverse survey is obvious; for practically all the species, excepting *Fucus serratus*, *Littorina littorea*, *L. littoralis*, and *Gibbula cineraria*, were found to have a wider distribution on Church Reef than appeared from Colman's traverses. *Fucus serratus* and the two species of *Littorina* are similarly zoned by both surveys, but *Gibbula cineraria* was recorded much higher by Colman than by the present worker; and the same is true of the upper limit of *Lichina pygmaea*.

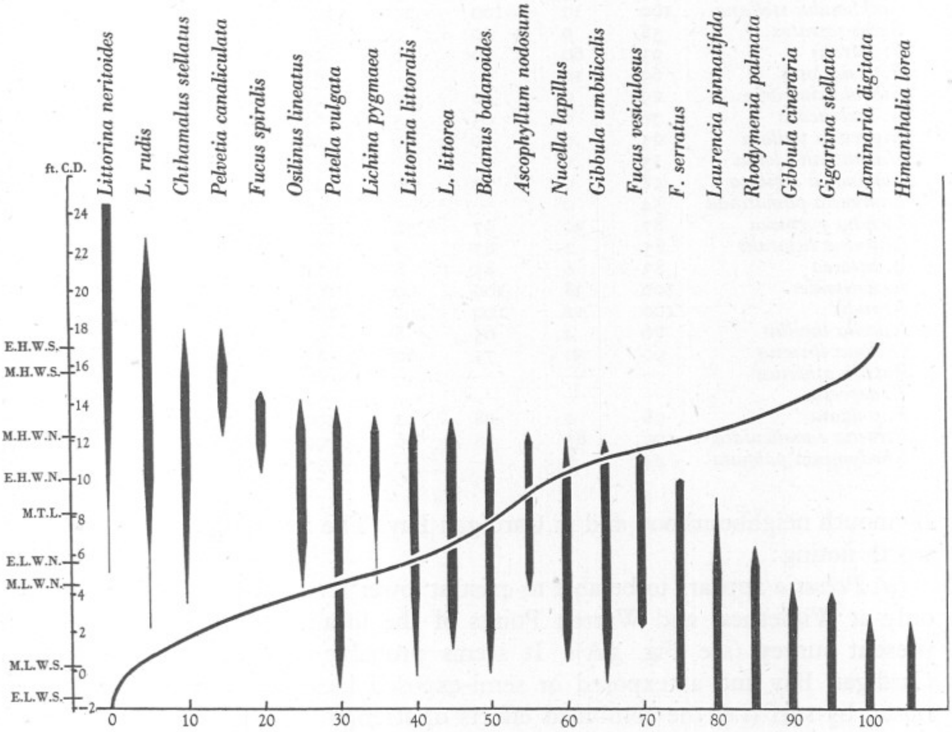

Fig. 13. Zonation of species on the landward portion of Church Reef, Wembury. The curve representing the percentage exposure to the air at different tidal levels is superimposed.

It appears, from a comparison of columns (1) and (4) that, with few exceptions, the plants and animals on Church Reef do not occupy the whole ranges possible to them. Here, however, the factor of exposure to wave action and splash is introduced, and it is obvious that at places like Bolt Head the vertical ranges are widened by this factor.

Comparing columns (3) and (4) it will be seen that, generally speaking, there is a fair degree of similarity between the zonation of littoral species in the

TABLE III. PERCENTAGE EXPOSURE TO THE AIR OF SPECIES IN CARDIGAN BAY, ON CHURCH REEF, AND IN THE PLYMOUTH NEIGHBOURHOOD

| | (1) Church Reef (1946) | | (2) Church Reef (Colman) | | (3) Cardigan Bay | | (4) Plymouth neighbourhood | |
|---|---|---|---|---|---|---|---|---|
| Species | Upper limit (%) | Lower limit (%) | Upper limit (%) | Lower limit (%) | Upper limit (%) | Lower limit (%) | Upper limit (%) | Lower limit (%) |
| *Ascophyllum nodosum* | 77 | 25 | 75 | 30 | 71 | 15 | 83 | 10 |
| *Balanus balanoides* | 83 | 3 | 80 | 5 | 83 | 0 | 96 | 0 |
| *Chthamalus stellatus* | 100 | 17 | 100 | 20 | 100 | 28 | 100 | 10 |
| *Fucus serratus* | 58 | 0 | 60 | 0 | 56 | 0 | 58 | 0 |
| *F. spiralis* | 93 | 60 | 90 | 70 | 96 | 55 | 94 | 56 |
| *F. vesiculosus* | 69 | 16 | — | — | 63 | 8 | 83 | 5 |
| *Gibbula cineraria* | 29 | 0 | 40 | 0 | 21 | 0 | 33 | 0 |
| *G. umbilicalis* | 76 | 0 | 65 | 5 | 63 | 2 | 76 | 0 |
| *Gigartina stellata* | 25 | 0 | 20 | 0 | 26 | 0 | 39 | 0 |
| *Himanthalia lorea* | 15 | 0 | — | — | — | — | 41 | 0 |
| *Laminaria digitata* | 18 | 0 | 12 | 0 | 20 | 0 | 25 | 0 |
| *Laurencia pinnatifida* | 54 | 0 | — | — | 60 | 0 | 56 | 0 |
| *Lichina pygmaea* | 87 | 30 | 97 | 52 | 100 | 22 | 100 | 33 |
| *Littorina littoralis* | 85 | 2 | 87 | 7 | 81 | 4 | 85 | 2 |
| *L. littorea* | 83 | 6 | 85 | 8 | 71 | 7 | 93 | 1 |
| *L. neritoides* | 100 | 38 | 100 | 90 | 100 | 20 | 100 | 13 |
| *L. rudis* | 100 | 12 | 100 | 60 | 100 | 8 | 100 | 7 |
| *Nucella lapillus* | 76 | 4 | 65 | 8 | 62 | 0 | 93 | 0 |
| *Osilinus lineatus* | 90 | 30 | 75 | 60 | 82 | 22 | 93 | 24 |
| *Patella athletica* | — | — | — | — | 42 | 0 | 45 | 0 |
| *P. depressa* | — | — | — | — | 92 | 0 | 100 | 0 |
| *P. vulgata* | 98 | 0 | 98 | 12 | 100 | 0 | 100 | 0 |
| *Pelvetia canaliculata* | 100 | 85 | 98 | 86 | 100 | 87 | 100 | 65 |
| *Rhodymenia palmata* | 44 | 0 | — | — | 35 | 0 | 47 | 0 |

Plymouth neighbourhood and in Cardigan Bay. The following exceptions are worth noting:

(*a*) *Pelvetia* appears to be able to exist at lower levels in South Devon, but only at Wilderness and Warren Points of the localities investigated in the present survey (see Fig. 3A). It seems probable that its lower limit in Cardigan Bay and at exposed or semi-exposed localities near Plymouth is raised by surf (i.e. the combined effects of strength of wave shock and frequency of wave shock) as already described. Conditions as sheltered as those at Wilderness and Warren Points are not met with anywhere on the part of the Cardiganshire coast investigated. Moreover, the effect of splash in raising the effective height of tides is important; thus the level of M.H.W.N. at Bolt Head may be almost as damp as E.H.W.N. at Warren Point, and if the lower limit of *Pelvetia* is determined by some ill-effect of immersion then the effective (as opposed to the predicted) height of tides will be important. At Church Reef, it should be noted, the lower limit of the alga is very similar to that in Cardigan Bay, and here surf effects are more or less equivalent.

(*b*) The algae *Rhodymenia*, *Gigartina* and, to a lesser extent, *Laminaria digitata*; the barnacle *Balanus balanoides*, and the limpets *Patella depressa* and

*P. athletica*, all have higher upper limits in the Plymouth neighbourhood than they do in Cardigan Bay. *Littorina neritoides* and *Ascophyllum* have lower lower limits. Yet, comparing the semi-exposed locality of Church Reef with the coast of West Wales, the discrepancies are less marked. It has already been shown that surf exerts an elevating effect on such upper limits (and a depressing effect on the lower limit of *Littorina neritoides*), and the differences are probably due to the extreme exposure to surf encountered at Bolt Head, Blackstone, etc., which is unparalleled anywhere in Cardigan Bay. The same is possibly true with regard to the upper limits of *Fucus vesiculosus* and *Ascophyllum*. While these are only able to tolerate a certain maximum of surf, which is often exceeded in Cardigan Bay, it is possible to discover their existence in local shelter (fissures, etc.) at exposed points near Plymouth, where they receive more splash, and their environment is considerably damper, than it is anywhere on the Cardiganshire coast, at an equivalent level.

(*c*) The lower limit of *Chthamalus* is interesting. Moore & Kitching (1939) describe how, proceeding eastward along the south coast, and northwards along the west coast of Britain, this barnacle not only tends to die out in numbers, but becomes less tolerant of conditions on the lower beach. This, these workers suggest, is due to the fact that, as certain factors (lack of Atlantic water?) become critical for the barnacle, it becomes less tolerant of the ill-effects of immersion. This explains the difference in lower level of *Chthamalus* in Cardigan Bay from that in the Plymouth neighbourhood.

Apart from these exceptions, the zonations of *Fucus spiralis*, *F. serratus*, *Laurencia pinnatifida*, *Littorina rudis*, *L. littoralis* and *Patella vulgata*, are very similar in both localities. Thus, out of twenty-two species common to the two surveys, no fewer than sixteen are either similar in their zonation at both places or the differences can be explained by the known facts of surf effects, while the differences for *Chthamalus* are also explicable. The exceptions are: *Osilinus*, *Nucella*, *Gibbula umbilicalis*, *G. cineraria* and *Littorina littorea*. All these appear to be somewhat more tolerant of exposure to the air in the Plymouth neighbourhood than they are in West Wales, and since the differences in the upper limits of these species are also manifested under the semi-exposed (to surf) conditions of Church Reef, splash effects can hardly be held to account for this. No satisfactory explanation or suggestion can, as yet, be put forward.

### *Critical Levels*

Certain levels have been shown (Evans, 1947) to be more critical than others in connexion with the distribution of intertidal plants and animals in Cardigan Bay. These are:

(1) Between M.L.W.S. and E.L.W.S., where the majority of intertidal species achieve their lower limits.

(2) Between M.L.W.S. and M.L.W.N., which marks the lower limits of certain other intertidal species.

(3) Just above M.L.W.N., where several sublittoral species reach their upper limits of penetration into the intertidal zone.

(4) Just below M.H.W.N., marking the upper limit of one set of intertidal species.

(5) Between M.H.W.S. and E.H.W.S., where a further set of intertidal plants and animals achieve their upper limits.

These were compared with levels described by Colman (1933) as critical for a similar set of species on Church Reef, and the points of difference were discussed. During the present work the writer has attempted to recognize such levels, not only on Church Reef, but also at the other localities studied. However, at many stations (e.g. Bolt Head, Blackstone, Reny, etc.) so many species are unrepresented or occur very infrequently that such localities are best omitted from the discussion. Sufficient data are available for North Point, Queener Point, Jennycliff Bay, and Wilderness Point, and since these display a fair range in conditions of shelter and exposure to surf, the discussion will be based on these. The method used by Colman (1933, p. 463) to elucidate critical levels has been followed, i.e. the number of upper and lower limits occurring between −2 ft. and +1 ft. C.D., between −1 ft. and +2 ft. C.D., between 0 and +3 ft. C.D., etc., was calculated for each station. Graphs were drawn in the way that Colman describes, and the peaks of such graphs were taken to mark critical levels. The results are summarized in Fig. 14; the brackets embrace the levels (e.g. +2 ft. and +6 ft. C.D.) between which the various maxima occur. The Cardigan Bay results are included in the same figure, also results achieved by interpreting Colman's (1933) data for Church Reef (without a splash allowance). The numbers (1) to (5) are equivalent at all localities.

It will be observed that levels (1) and (2), which are separate entities in Cardigan Bay, at Church Reef, North Point and Wilderness Point, are not distinguishable from each other at either Queener Point or Jennycliff; neither do they appear as separate levels from Colman's survey of Church Reef. At the first two localities in Fig. 14 (i.e. Cardigan Bay and Church Reef), these levels mark the lower limits of the following intertidal species.

LEVEL (1): *Patella vulgata*, *Balanus balanoides*, *Littorina littoralis*, *L. littorea*, *Gibbula umbilicalis*, *Nucella lapillus* and *Fucus serratus*.

LEVEL (2): *Littorina rudis*, *Chthamalus stellatus*, *Lichina pygmaea*, *Ascophyllum nodosum*, *Fucus vesiculosus*, and *Osilinus lineatus*. (In Cardigan Bay, *Littorina neritoides* also ends within this region, at Church Reef it ends slightly above it.)

At Queener Point there is a single maximum, marked on Fig. 14 as (1 and 2). Within the levels enclosed by this bracket all the species represented in levels (1) and (2) of Cardigan Bay achieve their lower limits, with the exception of *Littorina littorea*, *L. littoralis*, *Ascophyllum*, *Fucus serratus* and *Osilinus*, all of which are either totally absent from Queener Point or occur too infrequently to zone. Thus the merging of (1) and (2) into a single critical level at this locality is due to the lowering, by intense surf action, of the lower limits of *Chthamalus*, *Littorina rudis* and *L. neritoides*; so that the two separate critical levels cannot be distinguished, and there occurs a single maximum between −1 ft. and +3 ft. C.D.

At North Point we appear to have what is an intermediate stage between Cardigan Bay and Queener Point. Here, (1) and (2) overlap; again due to the depression of the lower limits of *Chthamalus* and *Littorina rudis*, and also of *Osilinus*; but *Littorina neritoides* achieves its lower limit higher up.

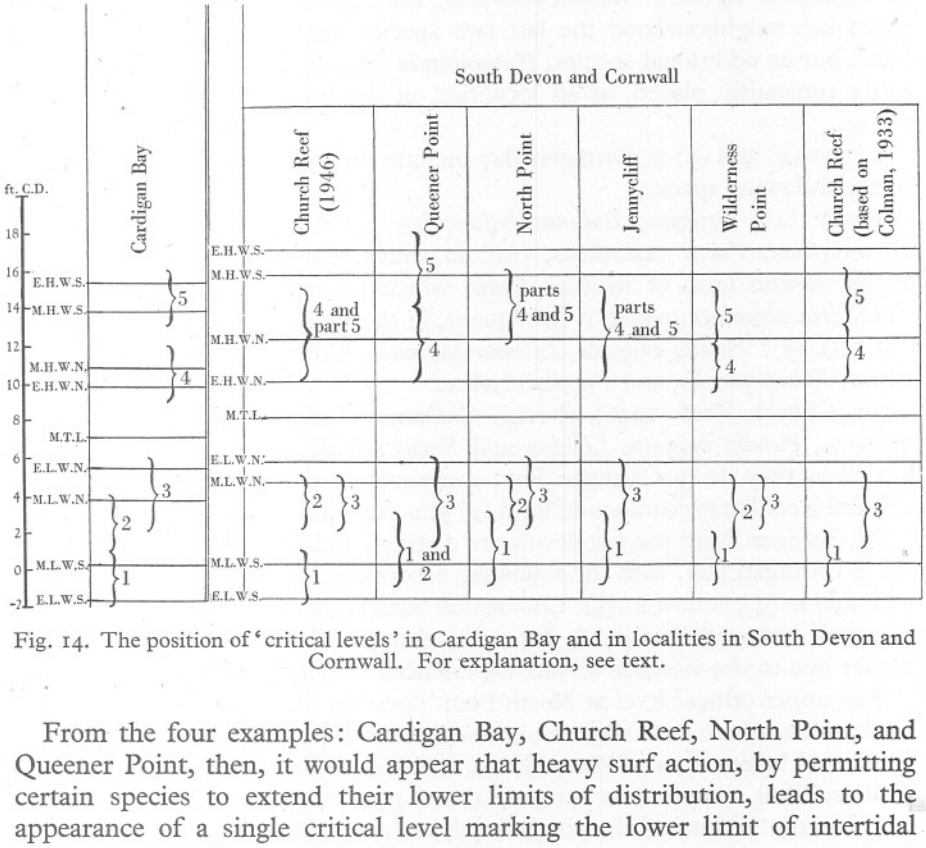

Fig. 14. The position of 'critical levels' in Cardigan Bay and in localities in South Devon and Cornwall. For explanation, see text.

From the four examples: Cardigan Bay, Church Reef, North Point, and Queener Point, then, it would appear that heavy surf action, by permitting certain species to extend their lower limits of distribution, leads to the appearance of a single critical level marking the lower limit of intertidal species instead of two such levels.

In Jennycliff Bay, however, level (1) does not represent a combination of (1) and (2); here the lower limits of *Littorina rudis*, *L. neritoides*, and *Osilinus* are raised by shelter, *Lichina* is unrepresented. Moreover, though *Ascophyllum* and *Fucus vesiculosus* end in the M.L.W.N. region, the number of limits becomes spread out, and no clear maximum can be recognized except the one just above M.L.W.S., i.e. level (1). Thus, in Jennycliff Bay, critical level (2) is unrepresented.

At Wilderness Point an overlap occurs, due to the raising (by shelter) of the lower limits of *Littorina rudis*, *Chthamalus*, *Ascophyllum*, and *Fucus vesiculosus*, and to the absence of *Osilinus* and *Lichina*.

With regard to the lower limit of intertidal species, then, either two maxima or one may be recognized; but the M.L.W.N.-M.L.W.S. region is definitely critical for such species, unless a few are permitted to penetrate beyond M.L.W.S. under the influence of strong surf action.

Level (3) in Cardigan Bay marks the upper limit of sublittoral species such as *Laminaria digitata*, *Gibbula cineraria*, *Rhodymenia* and *Gigartina*. In the Plymouth neighbourhood the last two species may extend up beyond this level, but an additional species, *Himanthalia lorea* is introduced. This level is fairly constantly placed, at all localities, in the M.L.W.N. to M.L.W.N. − 1 ft. region.

Levels (4) and (5) in Cardigan Bay include the upper limits of distribution of the following species:

LEVEL (4): *Osilinus*, *Balanus balanoides*, *Littorina littorea*, *L. littoralis*, *Ascophyllum*, *Fucus vesiculosus*, *Gibbula umbilicalis*, *Nucella*, *Laurencia* and *Fucus serratus* (also of *Mytilus edulis*, which has not been studied, and of *Sabellaria alveolata*, which is infrequent, in the Plymouth neighbourhood).

LEVEL (5): *Patella vulgata*, *Lichina pygmaea*, *Pelvetia canaliculata*, *Chthamalus*, *Fucus spiralis*, and *Patella depressa*.

On Church Reef (1946), though *Chthamalus* and *Pelvetia* extend above E.H.W.S., *Patella vulgata*, *Lichina* and *Fucus spiralis* do not exist to as high a level as they do in Cardigan Bay; consequently this single critical level at Church Reef (1946) consists of level (4) plus part of level (5) of Cardigan Bay.

At Queener Point the two levels are distinct, and are equivalent to (4) and (5) of Cardigan Bay, with the following exceptions: *Osilinus*, instead of being included in (4), is now in (5); *Chthamalus* achieves its upper limit higher than (5); and *Littorina littorea*, *L. littoralis*, *Ascophyllum* and *Fucus serratus* are absent due to the violence of surf experienced at Queener Point.

The upper critical level at North Point does not include the upper limit of *Chthamalus*, which ends above it; of *Fucus vesiculosus*, *F. serratus* or *Laurencia*, which end below it; or of *Ascophyllum*, which is too infrequent to zone at this locality. Thus it represents parts of (4) and parts of (5).

The same is true of the single level in Jennycliff Bay. *Chthamalus* and *Pelvetia* end above it; *Laurencia* ends below it; while *Lichina* is unrepresented.

At Wilderness Point the two levels are equivalent to those of Cardigan Bay, with the following exceptions: *Osilinus* is absent; *Littorina littorea* is infrequent and was not included in the results, neither was *Laurencia*; *L. littoralis* (under the cover of *Pelvetia*) extends upshore to end in (5) and not in (4); the upper limit of *Littorina rudis* is lowered by the sheltered conditions, and comes to lie in (5) instead of well above it as it does in more exposed localities. However, the levels are more or less equivalent, and have been numbered accordingly.

Summarizing these results, it would appear that, while generalizations can be made with regard to certain levels on the shore being more critical than others for intertidal plants and animals, any arbitrary method of graphing specific limits and deriving critical levels from these graphs (as Colman, 1933, and the present worker have done) will inevitably yield somewhat inconsistent results at different localities. Both the number and type of species studied will be important; and any local modifications or variations in environmental factors are likely to have varying effects on the upper and lower limits of different species, and so to cause variation in the position of critical levels at different localities. The factor of exposure to wave action is obviously of great importance in this respect; there is often a considerable difference between the 'predicted' height of tides and their 'actual' or 'effective' height, which is determined by the amount of wave action and splash. Zoning species on a basis of predicted tidal levels will inevitably yield different results at different localities; and the difficulty is to evolve some method of assessing the actual, effective height of tides at localities exposed to varying degrees of surf action. Other modifying factors which may upset the scheme of vertical zonation and displace the critical levels are: rock slope, the presence of shading influences, the presence of thick algal cover, etc. Nevertheless, despite the discrepancies in the positions of critical levels at different places along the coast, certain generalizations can be made:

(*a*) The region between M.L.W.S. and M.L.W.N. is critical in the sense that the majority of intertidal plants and animals reach their lower limits here. Often two sets of such species may be distinguished: (1) those for which the neighbourhood of M.L.W.S. is critical, and (2) those which reach their lower limits in the M.L.W.N. region.

(*b*) While certain sublittoral species may succeed in penetrating into the littoral region, these generally extend only as high as a level just below M.L.W.N.

(*c*) Levels between E.H.W.N. and M.H.W.S. are critical for intertidal species in the sense that many of them reach their upper limits here; though some, normally limited in the M.H.W.N.-M.H.W.S. region, may be elevated by splash to above this.

(*d*) It is very clear, at all the localities without exception, that the region of the shore between E.L.W.N. and E.H.W.N. is the least critical for intertidal plants and animals. Here, not only are the relative times of submergence and emergence (together with the change in environmental conditions correlated with these states) regular, but the factor of 'non-tidal' exposure to the air is not introduced.

Colman (1933) and Chapman (1941) both discuss the significance of critical levels on the shore and the possible factors which may account for them. It would appear that far too little is known of the requirements of individual species (e.g. the relative periods of submergence and emergence which they require, or are able to withstand), and a study of these, correlated with the analysis of tidal data, is likely to prove the most promising approach to the problem.

## SUMMARY

The work includes an investigation of the intertidal distribution of several species previously studied in Cardigan Bay. Twelve localities in the neighbourhood of Plymouth were selected for study, showing a range from conditions of extreme exposure to surf action to conditions of maximum shelter. The main features of rock configuration and surf action at the different localities are briefly described.

The method of investigation is described, and results obtained for the zonation of the fucoids on Church Reef are compared with the results of Colman (1933). It is concluded that the method of survey adopted in the present work yields results of a high degree of accuracy.

The horizontal and vertical distributions of the flora are described and related to the intensity of surf action. This is followed by a discussion of the effects of wave intensity and wave frequency on the distribution of algae in general. The importance of the frequency of wave shock in the mid-tidal region of the shore, and its influence on algal colonization, is stressed. An attempt is made to arrange the algae studied in order of decreasing tolerance of surf.

The distribution of the selected species of animals at the different localities is described; and a discussion follows on the effect of wave action as a presence or absence factor in horizontal distribution, and as a modifying factor on vertical zonation. The effect of surf on the size of individuals of certain species is also commented upon.

The relation of the plant and animal species to different percentage exposures to the air at different shore levels is discussed. Results obtained from an extensive survey of Church Reef, Wembury, are compared with those obtained from Colman's (1933) traverse survey of the same area, and with the Cardigan Bay results. The percentage air-exposure limits of species in the Plymouth neighbourhood are also compared with similar limits in Cardigan Bay. It is concluded that there is a great degree of similarity in intertidal zonation at the two localities, though certain species appear to be more tolerant of exposure to the air in South Devon than they are on the Cardiganshire coast.

The existence of 'critical levels' for intertidal species in Cardigan Bay and at five localities near Plymouth is investigated. It is shown that the position of such levels changes in relation to local variations in surf action, rock configuration, illumination, etc.; nevertheless the existence of critical levels is an actuality. Generally speaking, the following regions of the shore may be

described as more critical than others for littoral plants and animals: (*a*) from M.L.W.S. (or just below this) to M.L.W.N.; (*b*) just below M.L.W.N.; (*c*) from E.H.W.N. to M.H.W.S. The least critical levels on the shore are between E.L.W.N. and E.H.W.N.

The writer wishes to thank Prof. T. A. Stephenson for his help and criticism of the manuscript, and to acknowledge a grant from the Royal Society which made the work possible.

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# NEW OBSERVATIONS ON THE DISTRIBUTION AND MORPHOLOGY OF THE AMPHIPOD, *GAMMARUS ZADDACHI* SEXTON, WITH NOTES ON RELATED SPECIES

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(Text-figs. 1–7)

*Editor's Note*. This paper and that by Mr G. M. Spooner (this *Journal*, pp. 1–52), independently bringing forward certain new ideas on the taxonomy of *Gammarus zaddachi* and *G. locusta*, were received for publication simultaneously. As Mr Spooner's paper is a report of work largely carried out before the war, of which summarized results have already been referred to in print (e.g. Report of Council in this *Journal*, Vol. XXIV, pp. 444, 691; Huxley, *The Modern Synthesis*, p. 315), it is given precedence. The authors have since consulted each other over matters in which their contributions overlap, in particular over the taxonomic status of the new forms they distinguish and regarding the names to be applied to them. Dr Segerstråle has kindly consented to adopt the two new names introduced above by Mr Spooner, and to make considerable alterations to his original manuscript.

## CONTENTS

## INTRODUCTION

As is well known, the species *Gammarus zaddachi*, established by E. W. Sexton in 1912 on material from European brackish and fresh-water localities, has caused great confusion among zoologists, as the characteristics distinguishing it from various related species, particularly *Gammarus locusta*, *G. duebeni* and *G. pulex*, have been very frequently disregarded. This confusion still persists to-day—that is amply shown by the material received for the present investigations from various museums.

In view of the drawbacks brought about by this confusion, not the least on account of the fact that *G. zaddachi* has been accepted as a typical salinity indicator in ecological work while, on the other hand, *G. locusta* is a favourite object for physiological investigations on osmotic regulation in water animals, zoologists are deeply indebted to Mrs Sexton for a paper, published in this *Journal* in 1942, the aim of which was to clear up the problems that have arisen around *G. zaddachi*. In this paper the author discussed the whole literature on the subject, and was in many cases able to correct previous errors by re-examining the original material. In addition, the author gave a new detailed description of the two forms of the species, the 'saline' and the strikingly hairy 'fresh-water' one, accompanied by numerous excellent figures. Finally, the paper contained a comparison between *G. zaddachi* and the species with which it has most often been confused.

The main differences between *zaddachi* and *locusta* mentioned, and as a rule depicted in Sexton's paper, refer to the setose armature of the peduncle of antenna 1 (in *zaddachi*, numerous clusters of well-developed hairs present; in *locusta*, the peduncle almost glabrous); to the shape of gnathopod 2 (in *locusta*, narrower proportionately, etc.); to the shape of side-plate 4 (in *zaddachi*, inferior margin almost semicircular; in *locusta*, lower portion deep and almost rectangular); to the epimeral plates 2 and 3 (in *zaddachi*, hind-corners subacute; in *locusta*, acutely produced); to the pleon segments 4–6 (in *zaddachi*, dorsal humps only slightly raised; in *locusta*, elevated and prominent); etc.

A characteristic referring to the head sinus should be added to these principal points of difference. In *zaddachi* the sinus is much deeper than in *locusta*. Sexton says that both the species have a slight sinus, but in her figures (1 and 19) the divergence is clearly seen. The deep head sinus in *zaddachi* has been correctly depicted already by Stephensen (1940, fig. 40, I, II, p. 317), in connexion with the description of an atypical form of *locusta*, occurring in his material from northern Norway and adjacent waters; as seen below, it is in reality identical with *G. zaddachi*. To show the difference in shape of the epimeral plates of both species Fig. 1 may be given (cf. also Sexton's text-fig. 1). Fig. 2 illustrates the differences between *zaddachi* and *duebeni*, mentioned in Sexton's paper.

A historical remark may be added here. Oddly enough, it seems probable that the species nowadays regarded as the true *locusta* is not identical with the form found by Linnaeus in 1741 on the seashore at Gothland and named by him (in 1745) *Cancer macrourus coeruleus*, and later on (1761, etc.) *C. locusta*, but rather that he had had to do with *Gammarus zaddachi*. The famous naturalist points out in his description that the last pair of legs had the inner ramus shorter than the outer. As the difference in length is very small in the 'modern' *G. locusta*, but in *G. zaddachi* constitutes one of the most striking characteristics, and, furthermore, as *zaddachi* occurs very commonly together with *locusta* on the shores of Gothland (see below, pp. 236–9), it appears definitely more probable that the amphipod observed by Linnaeus belonged to *zaddachi*. A similar view has already been expressed by the Swedish zoologist Liljeborg. In his account of the Scandinavian species of the genus *Gammarus* (1855) he emphasized that the species meant by Linnaeus was obviously not *G. locusta* M. Edwards (in which the rami of the last uropods are, as in the *locusta* of the present day [depicted by Sars etc.], 'presque égaux entre eux' [M. Edwards, 1840, p. 45]). He therefore gives this species the name *mutatus* and regards the '*locusta*' found in the Baltic by Zaddach (1844, 1878), i.e. the same which in 1912 was called *G. zaddachi* by Sexton, as Linnaeus's species. In the diagnosis of the two species Liljeborg especially points out the differences in the relative length of the inner ramus of the last uropods, giving for *mutatus* 'rami pedum spuriorum ultimorum circiter aequales' and for *locusta* 'rami pedum spuriorum ultimorum insigniter inaequales, interior exteriore saltem tertia parte minor'.

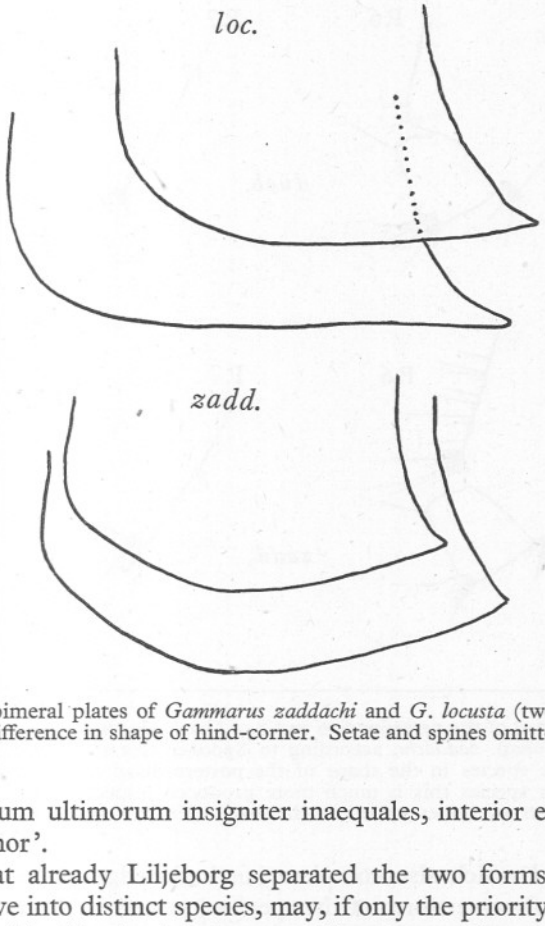

Fig. 1. Second epimeral plates of *Gammarus zaddachi* and *G. locusta* (two of each; males), to show the difference in shape of hind-corner. Setae and spines omitted. Material from the Baltic.

The fact that already Liljeborg separated the two forms of *Gammarus* mentioned above into distinct species, may, if only the priority of the nomenclature suggested by him is taken into consideration, motivate changing of the names *locusta* and *zaddachi*, used nowadays, into *mutatus* and *locusta* respectively. But in view of the great new confusion which no doubt would be the consequence of this change, the present author has the decided opinion that the modern names should be retained as '*nomina conservanda*'. This idea is supported by the fact that Liljeborg erroneously listed the independent species *G. duebeni* as synonymous to *G. locusta*, thus making the value of the diagnosis of this species somewhat doubtful.

In connexion with studies on the *Gammarus* fauna carried out in the Finnish coastal waters since 1941, the present author has obtained results which cast a new light on the distribution and ecological character of the saline form of *G. zaddachi* and which also complete our knowledge of the morphology of this and the fresh-water form of the species in essential points. These results which, I hope, may considerably facilitate the recognition of *G. zaddachi*, are dealt with in the present paper. In connexion with this subject the relationship between *G. zaddachi* and the closely allied species *G. setosus* and *G. wilkitzkii* will be discussed.

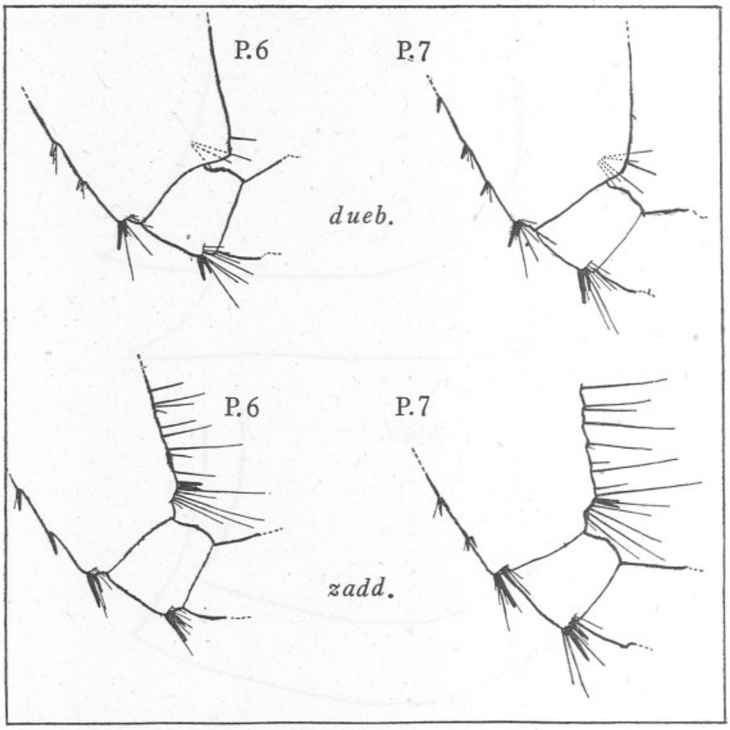

Fig. 2. Segments 2–4 of the peraeopods 6 and 7 of *Gammarus duebeni* and *G. zaddachi* fresh-water form (=ssp. *zaddachi*, according to Spooner; see p. 5), to show the difference between these species in the shape of the postero-distal angle of the basal segment. In the former species this is much more produced (especially in the 6th peraeopod) and lacks the strong spines present in the latter. (From Segerstråle, 1946.)

The author feels deeply indebted to Mrs E. W. Sexton (Marine Biological Laboratory, Plymouth) for her most valuable and kind help in sending material and discussing in letters questions concerning the subject. He is also indebted to the late Museumsinspektör K. Stephensen, of the Museum of Copenhagen, for his kindness in repeatedly supplying collections of *Gammarus* from Danish and Arctic waters. The other museums from which material was received for the present investigation, with the names of those to whom the author's thanks are similarly due, are as follows: Bergen Museum, Conservator H. Tambs-Lyche; British Museum, Dr Isabella Gordon; State Museum of Natural History, Stockholm, the late Prof. Dr Sixten Bock; Zoological Museum, Berlin, Prof. Dr Adolf Schellenberg. In addition, Mr D. M. Reid (Harrow) and Cand. phil. Erik Dahl (Lund) have kindly sent samples of various forms of *Gammarus*.

In total the material available embraces collections from the northern Atlantic and the Arctic (Massachusetts, Labrador, Greenland, Iceland, Norway, Spitsbergen, Murman Coast, Novaya Zemlya), the North Sea (Heligoland, coast of Denmark), the Cattegat, the waters around the Danish Isles, and the Baltic.

As mentioned already by Spooner, in his paper in this *Journal*, pp. 1–52 (see Editorial note, p. 219), the results obtained by him and by the present author partly overlap. Thus we have both distinguished Sexton's 'fresh-water form' from two other types of *zaddachi* and have described it. Thanks to the good offices of the Editor we have had the opportunity of going through our papers reciprocally before publication. The name *G. zaddachi* subspecies *zaddachi* given by Spooner to the above-mentioned form will be used also in the present paper. Another form found by both of us and designated subspecies *salinus* by Spooner will also be quoted here under his name. The third form which has been studied mainly by the present author will be described below as subspecies *oceanicus*.

The author wishes to present his thanks to Mr Spooner for most valuable comments and suggestions in letters.

## SURVEY OF THE RESULTS CONCERNING THE DISTRIBUTION AND MORPHOLOGY OF *GAMMARUS ZADDACHI*

*The distribution of the saline form.*[1] The saline form of *G. zaddachi* (also formerly called the brackish-water form by Sexton) has hitherto been recorded

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[1] As shown by Spooner, Sexton's 'saline form' of *zaddachi* embraces the subspecies *salinus*, erected by him, as well as the subspecies *oceanicus*, described for the first time in this paper. The 'saline form', spoken of here, refers to the latter subspecies.

only from waters with reduced salinity (the southern coast of the Baltic and the estuary of the Elbe, etc.), and has consequently been regarded as a typical brackish-water animal. In reality, this form is, however, mainly marine as, besides being distributed in brackish water, it is also widely found in the northern Atlantic and the Arctic (Fig. 4). In the samples from these waters, labelled *locusta*, the saline form is extremely common, whereas the true *locusta* is almost entirely lacking (besides *zaddachi* the Arctic samples of '*locusta*' frequently contain the species *G. setosus* and *G. wilkitzkii*). Structurally the form in question agrees strictly with the saline one living in the Baltic in all essential characteristics, the only difference being its size, which is much larger (body length up to 38 mm.).[1]

The northernmost localities from which records of the true *locusta* originate are situated on the north-east coast of Iceland (Bakkafjordur; Cop. Mus.) and northern Norway (Loppa, *c.* 70½° N.; Stephensen, 1940, p. 318). Thus, the species does not penetrate as far north as does the saline form of *zaddachi*. *Locusta* also does not nearly attain the same size as this form (maximum observed length of *locusta* 29 mm.; Stephensen, 1940, p. 318; a clear difference seen also in the Baltic). The previous literature records of Arctic specimens of *G. locusta* greater than *c.* 30 mm. might consequently refer to the saline form of *G. zaddachi* (or to the likewise very large allied species *G. setosus* and *G. wilkitzkii* which also hitherto have frequently been determined as *G. locusta*). The saline form of *G. zaddachi* is very euryhaline; in this respect it distinctly surpasses *G. locusta* (for details, see pp. 236–8).

The existence in the northern marine areas of a very *zaddachi*-like form of *G. locusta* has already been realized by Stephensen. In the above-mentioned important paper on the Amphipoda of northern Norway and Spitsbergen with adjacent waters (1940), he points out that the material of *G. locusta* (by him named *G. locusta locusta*) included, besides the typical form, also a deviating one which was much more common in the collections, and which in certain respects agreed with *G. zaddachi*, particularly in the shape of the 4th side-plate. As the collections used for the present investigation contain a number of samples from Stephensen's material, the author has had the opportunity of examining them. The form discussed by Stephensen is a typical *G. zaddachi*, saline form. Stephensen's including it in the species of *locusta* is partly accounted for by the incorrect records of the head sinus in *G. zaddachi* given in previous literature.

*The morphology of the saline and the fresh-water form.* As is well known, the setose armature of the two forms differs greatly, as it is much more developed in the fresh-water form, especially on the hinder peraeopods, the pleon segments 4–6, the telson, and the uropod 3. It is, however, striking that the difference in hairiness between the 1st antennae of both forms,

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[1] The author's determination of the Baltic saline form has kindly been confirmed by Mrs Sexton.

although generally quite distinct, has not been observed so far.[1] This may probably be explained by the aim of the descriptions of *zaddachi* mainly having been to point out the characteristics which separate the species from *locusta*; with respect to the 1st antenna, namely, both forms of *zaddachi* clearly differ from this species. But, on the other hand, the comparatively poor hairiness of the antennae in typical saline specimens of *zaddachi* obviously gives it a resemblance to *locusta* great enough to cause confusion with this species. The difficulty of identification has been augmented by the shortness of the peduncle of the 1st antenna in the saline form, a characteristic which has also been overlooked.

The above-mentioned inequality in length of the peduncle of the 1st antenna shows that the view prevailing nowadays of the differences between the saline and the fresh-water form being confined to the strong hairiness of the latter is not correct as the structure of the two forms also differs. In addition, the present investigation has revealed a second structural disparity, viz. in the relative length of the 2nd antenna in the fresh-water form being, in spite of the longer peduncle of the 1st antenna, distinctly greater than in the saline one.

Furthermore, the study of freshly captured animals from Finnish waters has shown that the body colour differs in the two forms of *zaddachi*. The difference is mainly caused by the existence in the fresh-water form of a pattern of transverse and longitudinal bands on the dorsal part of the body; in the saline form there is no pattern. Mrs Sexton's not having observed the divergence is due to the fact that her material consisted only of preserved animals; in alcohol and formol the pattern is completely deleted.[2]

Finally, the fresh-water form is smaller in size, even in comparison with the Baltic saline form which lives together with the former; if the large Arctic saline form is subjected to the comparison the difference is of course much more marked.

It may be added that the investigation of the comparatively extensive material available to the present author, containing among others the large Arctic specimens, has considerably widened the variation range for certain characteristics (number of spines on pleon segment 4–6, number of spines and setae on the telson, number of joints on the flagella of the antennae).

*The 'combined' form.* Transitional forms between the saline and the fresh-water forms of *G. zaddachi* have previously been found by several authors,

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[1] Sexton (1942, p. 597) states: 'In all the animals, saline as well as freshwater, both peduncles and the flagella carry on the under margin dense tufts or clusters of long stiff outstanding setae, some of each cluster extending far beyond the rest.' Strictly, however, the records given (on pp. 597 and 600) of the number of hair clusters on the peduncle of antenna 1, as well as of the length of the peduncle, hold good only for the fresh-water form.

I can now add that Spooner, too, has noted differences in setation of the antennae between the fresh-water and those 'saline' animals which are here called *oceanicus*.

[2] As Sexton mentions (1942, p. 593) that 'the chitinous cuticle varies in the two forms, being thick, strong and opaque in the freshwater, thin and transparent in the brackish water specimens', this difference, according to records kindly given by Mrs Sexton to the present author in a letter, is obviously not real, but due to different preserving methods.

mainly in the Baltic (Sexton, 1912, 1913; Schellenberg, 1934; Höfken, 1937; Dahl, 1944).[1] Specimens of this type are common also in the material from brackish areas available to the present author. Höfken emphasizes that these forms are not properly transitional, but combine characteristics of the saline and the fresh-water form (called by him *G. locusta* and *G. zaddachi*). This agrees with Dahl's statement that the specimens in his material from the Baltic, more or less intermediate between both forms (by him determined *G. locusta* f. *locusta* and f. *zaddachi*), have rather setose antennae (= fresh-water characteristic) but otherwise are very sparsely provided with hairs (= saline characteristic). In the collections from the Baltic examined by the present author this peculiar combined type is abundant. It has proved to be identical with Spooner's subspecies *salinus*.

In the following account details will be given of the morphology and distribution of the different forms of *zaddachi*, as observed in the material studied (distribution records from other areas included).

As will be shown, the combination of the following characteristics is diagnostic of the new subspecies *G. zaddachi oceanicus*: (1) the shortness and sparse setation of the peduncle of antenna 1; (2) the sparse setation of the hinder peraeopods, the pleon segments 4–6, and the telson. (In the description a characteristic from the last peraeopod and the telson has been chosen as indicator of the hairiness of the hinder parts of the body. With respect to this character, *oceanicus* shows almost complete agreement with *salinus*.)

Unless otherwise stated, the descriptions refer to the *male* (the female has been less thoroughly studied; most characteristics are somewhat less marked in this sex). The records given refer to specimens of at least *c.* 8 mm. in length (in smaller animals the characteristics are mostly not fully developed). All measurements are taken from the tip of the rostrum to the insertion of the telson.

In the list of synonyms an asterisk designates that the author has had the opportunity of examining specimens used for the paper concerned.

### **Gammarus zaddachi** Sexton subsp. **oceanicus** subsp.nov.

SYNONYMS

Sexton, 1912, 1913, 1942; *G. zaddachi*; brackish-water or saline form *in part.*, cf. footnote, p. 223.

*Stephensen, 1917: *G. locusta* var. *Zaddachi*, *in part.*; intermediate form between *G. locusta* and *G. locusta* var. *Zaddachi* (*in part.*). 1940: *G. locusta locusta*, *in part.*

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[1] Also the form, found by Poulsen in Danish waters and determined *G. zaddachi* (Poulsen, 1932, p. 6 and fig. 3), seems to belong to the intermediate type. According to Spooner (p. 35), in reality the animals regarded as intermediates by Sexton generally belong to the fresh-water form (= subsp. *zaddachi* Spooner).

*Hellén, 1919: *G. locusta, in part.*
*Blegvad, 1922: *G. locusta, in part.*
*Segerstråle, 1933: *G. locusta* (*in part.*). 1944: *G. locusta* f. *typica.*
*Schellenberg, material sent to the author: *G. locusta.*
*Valovirta, 1935: *G. locusta* f. *typica.*
Höfken, 1937: *G. locusta.*
*Suomalainen, 1939: *G. locusta* (*in part.*).
*Dahl, 1944: *G. locusta* f. *locusta.*

## MORPHOLOGY

*Maximum size.* Male: Arctic 38 mm. (Stephensen, 1940, pp. 318, 320; north Norway), Baltic 26 mm. (Schellenberg, 1934, p. 11, records a '*G. locusta*', captured near Kiel and measuring 32 mm.; probably a male of *G. zaddachi oceanicus*). Female: Arctic 28 mm. (Stephensen, 1940, p. 319; north Norway), Baltic 22 mm.

*Body colour* (studied in freshly captured specimens from Finnish waters). Greyish, yellowish, or greenish brown, semi-transparent; usually darker in the female. No dorsal pattern nor, usually, red spots of oil globules on the sides of pleon segments 1–3.

*Setose armature of peraeopods, pleon segments* 4–6, *telson, and uropods.* Weak development of the setae, as seen in Sexton's figures (1942, saline form). Peraeopod 7, longest seta in subapical cluster on hind margin of segments 4 and 5 not surpassing tip of spines in the same cluster (Fig. 3 *g* in the present paper).[1] Telson, longest apical seta shorter than distance from its insertion to tip of subbasal spines (Fig. 3 *e*, *f*).[2] In marine specimens the telson setae may be comparatively long and partly feathery (Fig. 3 *f*).

*Length of antenna* 2 *in percentages of antenna* 1, from 18 males, length 13–20 mm., from the Baltic, Iceland and Labrador; specimens with broken or regenerating flagella excluded: 68–77, average 73 %.

*Maximum number of segments in the flagella* (body length in brackets):

| | | Male | Female |
|---|---|---|---|
| Antenna 1: | primary flagellum | 57 (31 mm.) | 38 (25 mm.) |
| | accessory flagellum | 10 (31 mm.) | 11 (25 mm.) |
| Antenna 2 | | 21 (33 mm.) | 22 (25 mm.) |

*Length of peduncle segments of antenna* 1 (Fig. 3 *a–d*; segment 1 measured from tip of the rostrum to distal end of the segment). Ratio of length of segments 2 and 3 combined to that of segment 1, from 1·0:1 to 1·3:1, generally *c.* 1·1:1. Length of segment 3, 0·4–0·5 of that of segment 2. The end of the

---

[1] The difference in hair development between *z. zaddachi*, on the one hand, and *z. oceanicus* and *z. salinus*, on the other, is more marked on the posterior than on the anterior margin of the hinder peraeopods.

[2] This method for measuring the seta concerned has been chosen instead of comparison with the corresponding spines in order to reduce the inaccuracy of results arising from the variability of the spine length.

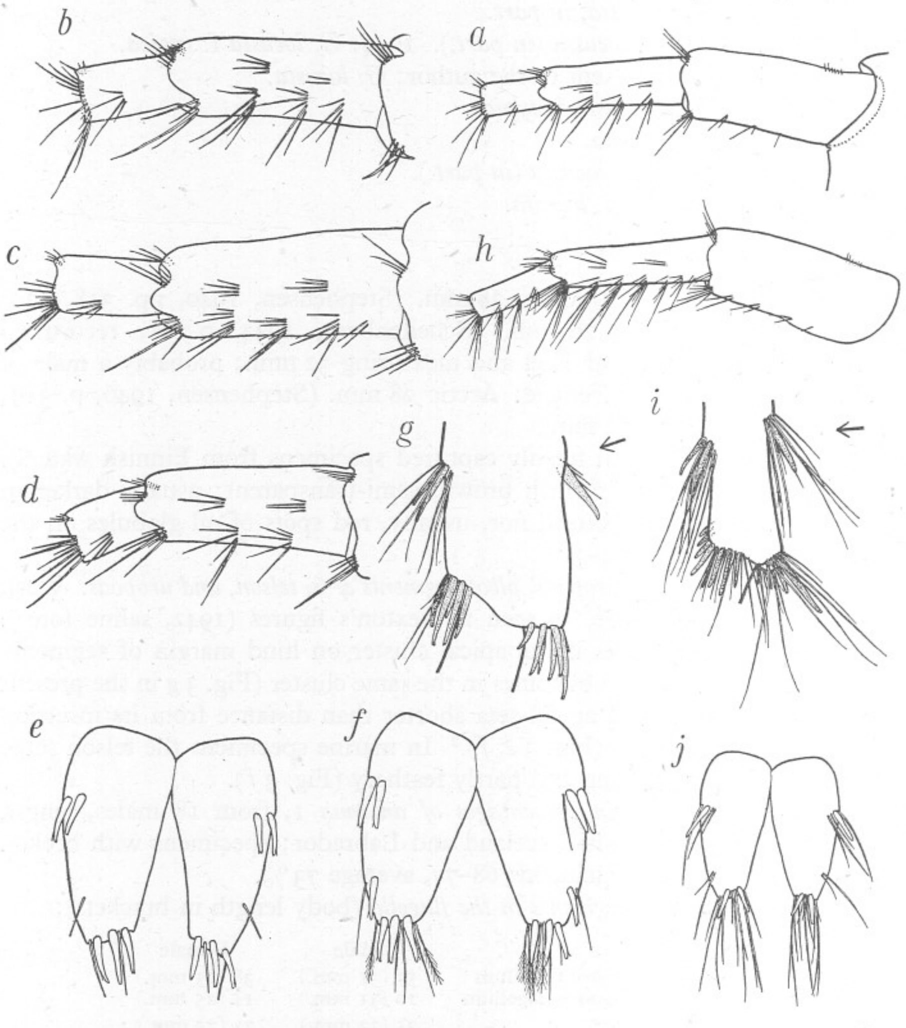

Fig. 3. *Gammarus zaddachi* (male). *a–g*, *z. oceanicus*; *h–j*, *z. zaddachi*. *a–d*, peduncle of 1st antenna (right, from the inner side; in *b–d* only segments 2 and 3 depicted): *a*, south-west Finland (body length 16 mm.); *b*, north Norway (27 mm.); *c*, north Greenland (31 mm.); *d*, north Norway (27 mm.). *e–f*, telson: *e*, north Norway (26 mm.); *f*, Massachusetts (26 mm.). *g*, peraeopod 7, distal part of segment 5 and proximal part of segment 6, west Greenland (27 mm.; the arrow shows the cluster used as a characteristic in the diagnosis; the specimen depicted has comparatively long setae on the anterior margin of segment). *h*, peduncle of 1st antenna, south Finland (16 mm.). *i*, peraeopod 7 (for part depicted and arrow, see above), south Finland (19 mm.; the specimen has unusually short setae; for maximum length, see Sexton 1942, fig. 12). *j*, telson, south Finland (18 mm.).

peduncle (when stretched forward, to continue the dorsal line) reaches at least as far as to the end of segment 4 of antenna 2 and at most to somewhat less than half the length of segment 5, generally to about a quarter of this joint.

*Number of hair clusters on the under-margin of peduncle segments* 2 *and* 3 *of antenna* 1 (*including apical cluster*) (Fig. 3). Segment 2, 3–5, generally 4, clusters; segment 3, 1–2.

*Pleon segments* 4–6, *spine formula:*

| | |
|---|---|
| 4th segment | 3–6 : 2 : 3–6 |
| 5th segment | 3–5 : 2 : 3–5 |
| 6th segment | 2–3 : 2 : 2–3 |

*Telson, number of spines and setae:*

| | Spines | Setae |
|---|---|---|
| Apical | 3–4 | 1–5 |
| Subapical | 0–1 | 0–2 |
| Subbasal | 1–3 | 0–2 |

*Uropod* 3 *inner ramus*, length about three-quarters that of the outer, excepting in large marine specimens in which it may be up to seven-eighths.[1]

### ADDITIONAL NOTE

The following differences between *z. zaddachi* and *salinus* observed by Spooner, have proved to exist also between the former subspecies and *oceanicus* (material from Finnish waters).

As does *salinus*, *oceanicus* differs from *z. zaddachi* in the following respects: (1) accessory flagellum, number of segments and length somewhat greater; (2) gnathopod 2, a little narrower and hinder margin clearly bulging (in *z. zaddachi* almost straight); (3) epimeral plate 3, posterior distal angle distinctly more acutely produced (epimeral plate 2, difference less pronounced); (4) distal segments of last peraeopod, somewhat more slender; (5) last uropod, inner ramus a little longer. The measurements—certainly few in number—of characteristics 1, 4 and 5 fall within or very near the variation limits given by Spooner for *z. zaddachi* and *salinus*.[2]

### DISTRIBUTION

The form in question is widely spread in the northern Atlantic (material from waters south of the North Sea not available) and in the Arctic, but occurs abundantly also in the brackish water of the Baltic (observed minimum salinity in places of capture *c.* $2{\cdot}5\,^{\circ}/_{\circ\circ}$) (see map of the Baltic in Fig. 6; for details see p. 236).[3] Depth records: 0–25 m.

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[1] It is a common feature in the amphipods that the inner ramus of the last uropods increases with age, as is well known.

[2] The author has not found calceoli in the (mature) female of *z. zaddachi*. These organs were lacking also in the examined females of *oceanicus* (Spooner mentions that he often found calceoli in the female of *z. salinus* but not of *z. zaddachi*).

[3] Spooner has now shown (p. 43) that the subspecies in question occurs also in northern Scotland.

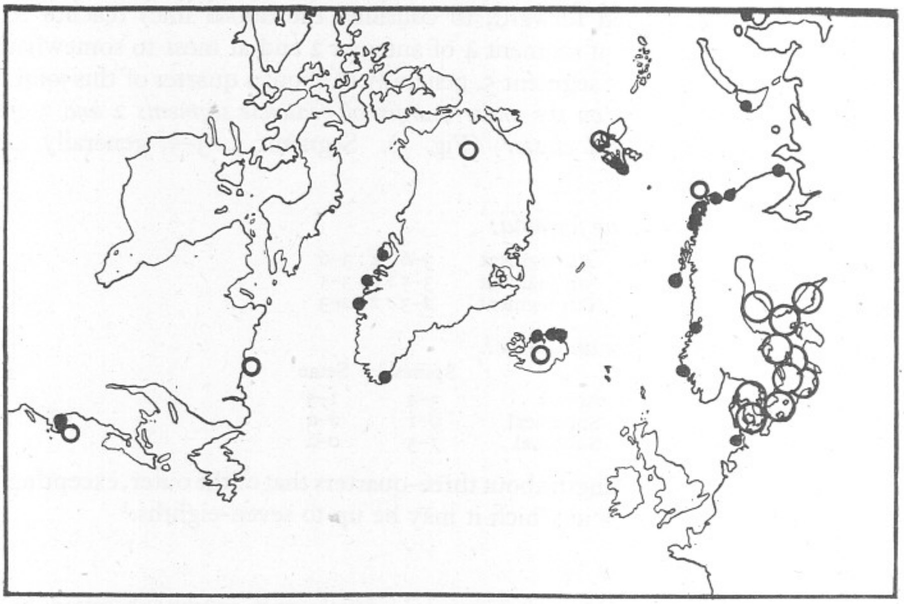

Fig. 4. The distribution of *Gammarus zaddachi oceanicus* according to the material investigated (samples not available from waters south of the southernmost localities seen in the map). Large open rings: more thoroughly studied areas (for details, see p. 236). Small open rings: record of locality not exact or insufficient ('Massachusetts', 'Labrador', 'North Greenland, Norsovak', 'Iceland', 'Spitsbergen, Kobbe Bay', 'Finmarken').

### **Gammarus zaddachi** Sexton subsp. **zaddachi** Spooner 1947.

SYNONYMS

Hoek, 1889: *G. locusta*, var. A.[1]

Sexton, 1912, 1913, 1942: *G. zaddachi*, fresh-water form.

Tesch, 1915: *G. locusta*, var.[1]

*Stephensen, 1917: *G. locusta* var. *Zaddachi* (*in part.*); intermediate form between this form and *G. locusta* (*in part.*). 1927: *G. duebeni* (at least *in part.*).

*Hellén, 1919: *G. locusta* (*in part.*); *G. duebeni* (*in part.*).

Tesch, 1922: *G. locusta*, Hoek's var. A.

---

[1] This form, which already Sexton (1942, p. 582) has regarded as belonging obviously to *zaddachi*, seems to be identical with *z. zaddachi*, owing to the presence of long setae on pleon segments 4–6 and telson (Hoek's figs. 11′ and 11″, pl. X) and of red spots on the pleon; the extremely low salinity in some of the recorded localities is also a favourable indication.

The two specimens, described by Tesch (1915) from the southern part of the North Sea and regarded by him as closely related to Hoek's var. A, might also belong to *z. zaddachi*. Their occurrence in the open sea was due presumably to transport from adjacent coastal waters with reduced salinity.

Gurjanova, 1930: *G. zaddachi.*[1]
Dementieva, 1931: *G. setosus* f. *baltica.*[2]
Schijfsma, 1931: *G. locusta,* Hoek's var. A.
*Poulsen, 1932: *G. duebeni.* 1933–36: *G. duebeni (in part.).*
Oldevig, 1933: *G. locusta (in part.).*
*Segerstråle, 1933: *G. locusta (in part.).* 1944: *G. zaddachi.*
*Schellenberg: *G. locusta* f. *zaddachi* (determination of samples, Helsinki Mus.).
Serventy, 1935: *G. zaddachi.*[1]
*Valovirta, 1935: *G. locusta* f. *zaddachi.*
Lucks, 1937: *G. locusta-zaddachi.*
Höfken, 1937: *G. zaddachi.*
*Reid, 1939: *G. sarsi.* 1945: *G. ochlos* nom.nov. (=*G. sarsi*).[3]
*Suomalainen, 1939: *G. locusta (in part.).*
*Dahl, 1944: *G. locusta* f. *zaddachi, G. locusta* f. *setosus.*

## MORPHOLOGY

*Maximum size.* Male 22 mm., female 15 mm.

*Body colour* (studied in freshly captured Finnish specimens). Ground colour distinctly lighter than in *oceanicus*: pale greyish green, sometimes greyish yellow. On the dorsal parts of the body a darker pattern, pale or darker brownish green in colour (Fig. 5). This pattern, the colour intensity and extension of which varies considerably, is composed of a system of transverse and longitudinal bands.[4] *Transverse bands.* Present on the posterior margin of head and of all body segments, excepting pleon segments 4–6 (the colour effect of these bands is augmented by the partial intervention of each segment into the preceding one; on that account these portions seem especially dark). On account of the bands the body of the animal is distinctly transversely striped. On the anterior margin of head, the first peraeon segment, and all pleon segments, transverse bands also occur. Finally, there are median bands on the peraeon segments (excepting the 1st) and on pleon segments 1–3 (the pleon bands are comparatively strongly developed). The median bands

---

[1] In view of the very low salinity in the locality, where Gurjanova captured '*zaddachi*' ('almost fresh' water, in the estuary of the Sewernaja Dvina), she very likely had to do with *z. zaddachi*. The same conclusion holds good for the specimens caught by Serventy at the more inland stations in the estuary investigated (River Deben, England).

[2] The comparatively slight head sinus depicted by Dementieva (fig. 10) is conceivably due to somewhat inaccurate drawing or may refer to a specimen of the true *locusta*; the telson figured is of typical *z. zaddachi* shape.

[3] The author has found no essential differences between this very small form (length *c.* 6 mm.), described on material from the brackish Loch of Stennes, Orkney, and mature specimens of *G. z. zaddachi* of the same size from the Baltic (material kindly sent by Mr Reid).

[4] Palmer (1933, p. 65) observed brown transverse bands on the body segments and on the appendages of a form of *G. zaddachi*, captured in brackish water on the English coast; it was probably *z. zaddachi* or *z. salinus*.

are frequently more or less reduced, sometimes missing, even on the pleon. *Longitudinal bands.* A median band, more strongly developed on the pleon but sometimes even here strongly reduced (see Fig. 5), runs along the whole length of the body. As a rule it is accompanied on both sides by a band, more developed on the peraeon. The colour pattern is observed also on the antennae (peduncle, flagella), on the peraeopods (especially on segments 1,

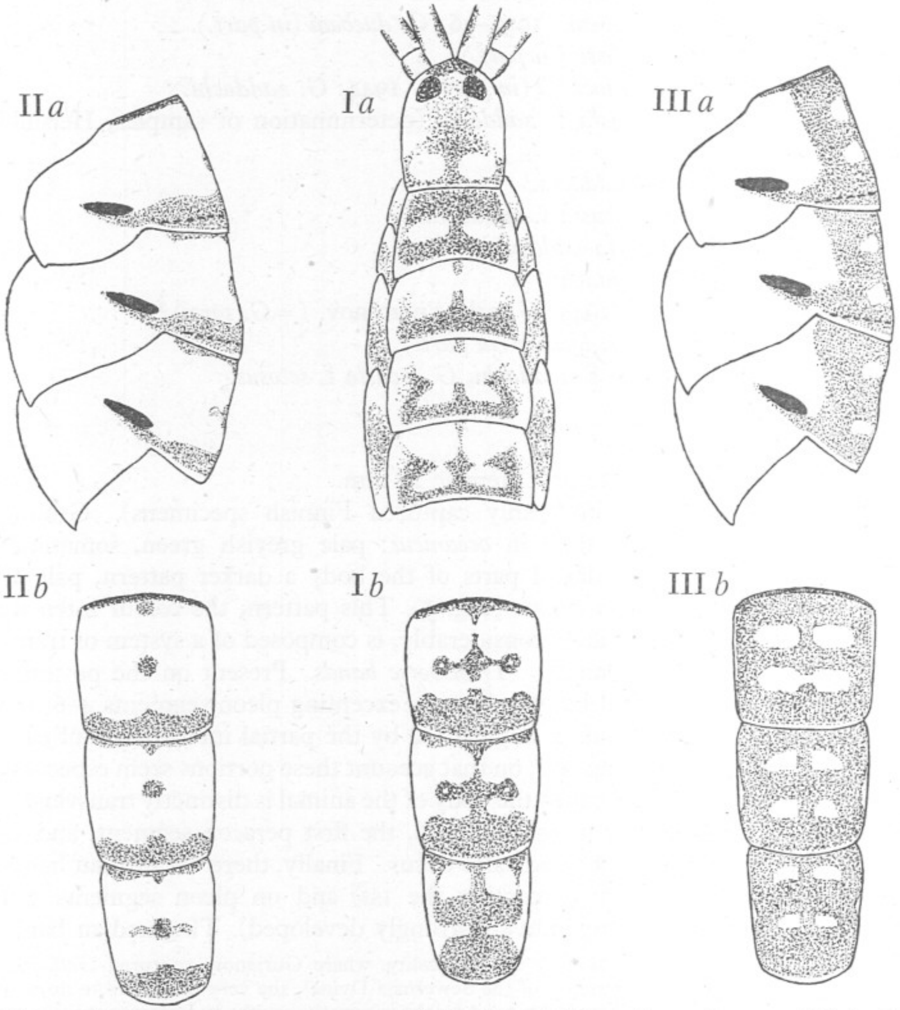

Fig. 5. The pattern in *Gammarus z. zaddachi*. (Material from the south coast of Finland; males.) Three specimens (partly) depicted, to show variation. I *a*, anterior part of body; I *b*, pleon segments 1–3 of the same animal. II *a* and III *a*, pleon segments 1–3 of two other animals, from the side; II *b* and III *b*, the same segments from above. The black oblong patches show the position of the red spots of oil globules.

3, 5–6), uropods and telson, and, weakly, on the side-plates. A pattern resembling the one just mentioned has been described by Sexton (1939) in *G. tigrinus*.

On the sides of pleon segments 1–3 there are almost invariably red spots of 'red oil globules', known from various other species of the genus *Gammarus* and mentioned in *G. zaddachi* by Sexton (cf. also Palmer, 1933). These are shown in Fig. 5. The pattern and the red spots disappear in preserved animals.

*Setose armature of peraeopods, pleon segments 4–6, telson and uropods.* Strong development of the setae, as seen in Sexton's figures (1942, fresh-water form). Last peraeopod, longest seta in subapical cluster on hind margin of segment 5 surpassing end of the segment (Fig. 3 *i* in the present paper). Telson, longest apical seta longer than distance from its insertion to insertion of subbasal spines (Fig. 3 *j*). Number of telson setae, see below.

*Length of antenna 2 in percentages of antenna 1*, from 17 males from the Baltic and the Danish lake Lammefjordssöen, length 13–20 mm.: 78–89, average 84%.

*Maximum number of segments in the flagella* (body length in brackets):

| | | Male | Female |
|---|---|---|---|
| Antenna 1: | primary flagellum | 39 (21 mm.) | 31 (15 mm.) |
| | accessory flagellum | 8 (20 mm.) | 6 (15 mm.) |
| Antenna 2 | | 19 (20 mm.) | 14 (15 mm.) |

*Length of peduncle segments of antenna* 1 (Fig. 3 *h*; for measuring method see p. 227). Ratio of length of segments 2 and 3 combined to that of segment 1, from 1·3:1 to 1·7:1, generally *c.* 1·5:1. Length of segment 3, 0·5–0·7 of that of segment 2. End of peduncle reaching at least to about one-fifth, as a rule to somewhat less than half the length of segment 5 of antenna 2.

*Number of hair clusters (including apical cluster) on the under-margin of peduncle segments* 2 *and* 3 *in antenna* 1 (Fig. 3). Segment 2, 5–9 clusters, generally 6–7; segment 3, 3–5, generally 4.

*Pleon segments* 4–6, *spine formula:*

| | |
|---|---|
| 4th segment | 2–3 : 2 : 2–3 |
| 5th segment | 2–3 : 2 : 2–3 |
| 6th segment | 2–3 : 2 : 2–3 |

*Telson, number of spines and setae:*

| | Spines | Setae |
|---|---|---|
| Apical | 1–3 | 4–17 |
| Subapical | 0–1 | 1–2 |
| Subbasal | 1 | 2–4 |

*Uropod* 3 *inner ramus*, length about three-quarters that of the outer.

### DISTRIBUTION[1]

Brackish and, locally, fresh water in north and west Europe (highest salinity recorded *c.* 14–18 °/₀₀).[2] In the Baltic district found practically only in brackish water (the only exception being the record from the Danish Lake Lammefjordssöen, see below).[3]

Great Britain: see the numerous records given by Spooner. To them may be added Loch of Stennes, Orkney (brackish water, locality for *Gammarus ochlos (sarsi)* = *G. z. zaddachi*; see p. 231).

Ireland: Lakes Lough Nadarragh, Lough Keenaghan, Lough Awaddy, Lough Tullynabour, Lough Erne (Sexton, 1912).

France: Nantes and Belle-Île-en-Loire (Sexton, 1942, p. 583).

Belgium: see Spooner.

Netherlands: mouth of the Rhine and the Waal, Zuiderzee (Hoek, 1889; Tesch, 1922; and Schijfsma, 1931: *G. locusta* var. A).

Germany: see Spooner.

Denmark: Lake Lammefjordssöen (north-west Sealand; Copenh. Mus.); for marine localities see below. Spooner also gives several records from Danish waters.

Norway: Bolstadfjorden (near to Bergen; Bergen Mus.).

Baltic: all over the area, throughout the Gulf of Bothnia and the Gulf of Finland, to the Danish waters (for details see pp. 236–8).

? White Sea, mouth of the Sewernaja Dvina (see p. 231, footnote 1).

### **Gammarus zaddachi** Sexton subsp. **salinus** Spooner 1947

As mentioned previously, in the *Gammarus* material studied by the author from the Baltic, a form of *zaddachi* was often found to which a peculiar combination of characteristics of the forms now named *z. zaddachi* and *z. oceanicus* is typical. The peduncle of antenna 1 is about as setose and elongate as in the former subspecies, whereas the hinder peraeopods, the pleon segments 4–6, and the telson are almost glabrous, as in the latter.

The opportunity given to the author of reading Spooner's manuscript and our reciprocal examination of British and Finnish material respectively has made it clear that the 'combined' Baltic form is identical with Spooner's subspecies *salinus*.

As this 'combined' type was captured only in waters where also *z. zaddachi* and *oceanicus* occurred, it seemed possible to the author at the first sight that it represented a curious result of crossbreeding between these two forms. Now,

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[1] In order to make the list more useful it has been completed by references to Spooner.

[2] Tesch, 1922, Zuiderzee (Hoek's var. A).

[3] Compare *Gammarus duebeni*, which, in this area, is confined to brackish water, though in western Europe, etc. it is found also in fresh-water localities (cf. Segerstråle, 1946).

however, Spooner's interesting statement of *salinus* and *z. zaddachi* being incapable of producing fertile eggs with one another has given evidence of the genetical independence of the former type, and thus has motivated the establishing of it as an independent subspecies.

As already indicated the separation of *salinus* from *zaddachi* is easy, whereas the limit between the former subspecies and *oceanicus* may sometimes appear to be vague, owing to the partial overlapping of the main distinguishing characteristics, viz. the length and setation of the peduncle of antenna 1. As to the latter characteristic which is more useful in practice, it is typical that *salinus* has at least six tufts on the under-margin of peduncle segment 2, against four tufts in typical *oceanicus*. But the range of variation of both subspecies also includes the tuft number of five, and this number seems to be comparatively common in *salinus*. As pointed out previously, the number of tufts on the last peduncle segment might, in such instances, be a reliable distinctive characteristic. In *oceanicus*, from purely marine localities, where the brackish *salinus* is not to be expected, more than two tufts have practically never been found by the author, whereas *salinus* ♂ typically has at least three.[1] Specimens with five tufts on the second peduncle segment and three on the third might consequently belong to *salinus*, not to *oceanicus*. In freshly captured animals also the colour will, presumably, prove to be a good distinctive characteristic. The examination of a number of such specimens of typical *salinus* from Finnish waters showed that they all had the pattern which is found in *z. zaddachi* (p. 231), though it was generally much less distinct than in that form (the red spots were also present in many specimens). Further observations on more extensive material are necessary, but the foregoing statements seem at any rate to make it very likely that the colour will prove an additional characteristic which reliably distinguishes *salinus* from *oceanicus*.

In the material from the Baltic specimens have also been observed in which the setation of the last peraeopods, or of the telson (the two characteristics chosen as indicator of the hairiness of the hinder parts of the animal), or of both, is somewhat more strongly developed than in typical *oceanicus*. The setose armature of antenna 1 in these specimens is never as sparse as in typical *oceanicus*. The author is inclined to suppose that these varieties belong to *salinus*.

Details of the distribution of *salinus* in the Baltic, as well as in Danish waters, are given in the following section. Regarding the occurrence of the subspecies outside this district, see Spooner (pp. 41–3).

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[1] The only exception refers to a couple of specimens observed in the material from Heligoland. They bear three hair clusters on the segment in question, and the length of the last peduncle segment compared with the length of the second segment is 0·6, against at most two and 0·5 respectively in the typical marine form. It does not seem quite impossible that these specimens have been transported to Heligoland from adjacent brackish waters on the continental coast (cf. the assumed transport in another case, p. 230, note 1).

## THE DISTRIBUTION OF *GAMMARUS ZADDACHI* AND *G. LOCUSTA* IN CERTAIN WATERS

### *The Baltic and Denmark (excluding Randers Fjord and Ringköbing Fjord)*

*Material.* Number of samples investigated (abbreviations of Museum names: Cop. = Copenhagen, Hels. = Helsinki-Helsingfors, St. = Stockholm): Finnish waters, *c.* 230 (Hels., and the author's collections); the archipelago from Stockholm to Kalmar, 12 (St.); coast of Blekinge, 4 (St.); Gothland, 20 (St.); Bornholm, 5 (St., Cop.); Danzig, 1 (St.); east of Rügen, 2 (Cop.); Rügen-Danish Isles, 12 (Cop.); The Sound, 3 (Cop., St.); Falster-Sealand, 6 (Cop.); Great Belt, 6 (Cop.); Little Belt and adjacent southern waters, 3 (Cop.); Ise Fjord, 2 (Cop.); Cattegat, 10 (Cop.); west coast of Denmark, 5 (Cop.).

Regarding the literature records, the surveys by Stephensen (1928, 1929), Oldevig (1933) and Schellenberg (1942) could not be used, as the differences between *G. locusta* and *zaddachi* are here not recognized. But the data published by Poulsen (1932) and Dahl (1944), though not correct in the species determinations, can be reinterpreted in the light of the samples of these authors' material available to the writer. From the south coast of the Baltic *G. zaddachi oceanicus* has been recorded (as saline form) by Sexton (1912, 1913) who also records, and figures, *locusta* from these waters.

*Gammarus zaddachi oceanicus.* This form is the main *Gammarus* in the Baltic and around the Danish Isles. It is lacking only in the 'innermost' parts of the Gulf of Bothnia and of the Gulf of Finland (Fig. 6; in the Gulf of Bothnia, which has been studied less thoroughly, the northernmost record of *oceanicus* is *c.* 63° 30′ N.) and other strongly diluted localities. In the Gulf of Finland the 'innermost' records (Virolahti: Kiuskeri and Pien Kalastaja) lie at the isohaline of *c.* 2·5 °/₀₀ salinity (surface, year average). On the south coast of Finland, from which area a great quantity of material has been investigated, the form in question greatly outnumbers *z. zaddachi* in the outer parts of the archipelago, at least as far eastward as in Pellinge, and even in a sample from the island Peninsaari (near Lavansaari, at 28° 2′ E.) *oceanicus* is clearly predominating (115 *oceanicus* against 4 *z. zaddachi*). On the Finnish coast *oceanicus* is especially common in the *Fucus* vegetation (cf. Segerstråle, 1944; *oceanicus* here called *G. locusta* f. *typica*). The bulk of the material of *oceanicus* originates from a depth of a few metres, but there are also a number of samples from the open sea between Rügen and the Danish Isles with depths of *c.* 20 m.

In the samples from the Cattegat *oceanicus* is sparsely represented and entirely lacking in the material from the Danish west coast.

*Gammarus zaddachi zaddachi* is represented in the material from the very end of the Gulf of Bothnia and the Gulf of Finland to the Sound (Isle Hven). In the 'innermost' parts of the Gulfs (Fig. 6) and other strongly diluted areas it is the only abundant *Gammarus* (in addition *G. duebeni* occurs here locally; cf. Segerstråle, 1946). The author found the amphipod in great numbers inhabiting the vegetation of *Phragmites* in estuarine localities. The animal is

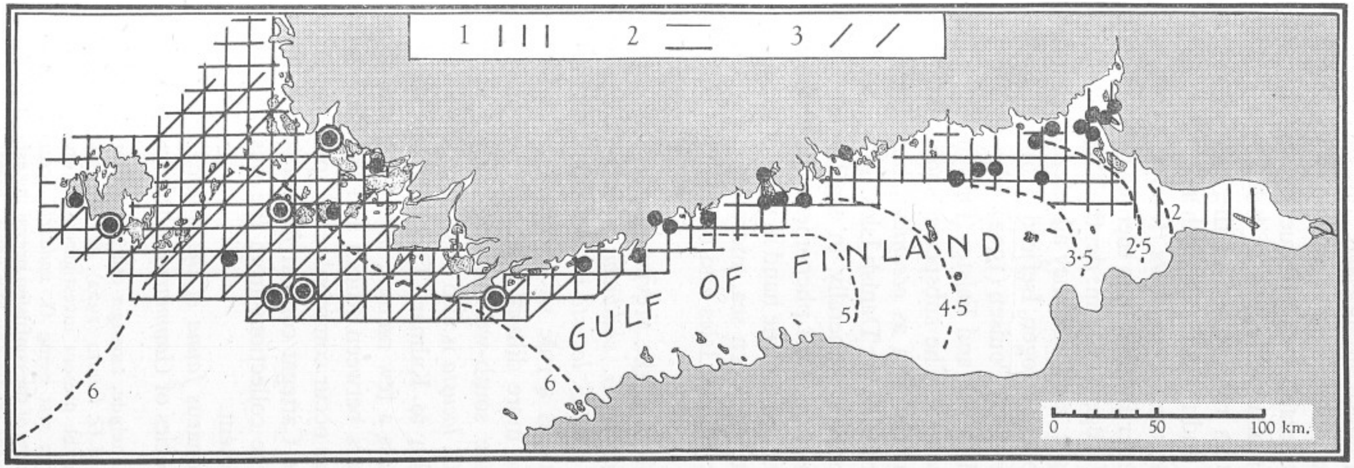

Fig. 6. The occurrence of *Gammarus zaddachi zaddachi* (1), *G. zaddachi oceanicus* (2), and *G. locusta* (3) along the north coast of the Gulf of Finland and in the south-west Finnish waters. The black dots show the origin of the material investigated. Localities for *G. locusta* indicated by rings. As seen, there are three *Gammarus* zones: (*a*) in the innermost part of the Gulf only *G. z. zaddachi* occurs, (*b*) westward from here to near the mouth of the Gulf *oceanicus* also is found, (*c*) the south-west waters are inhabited, in addition, by *G. locusta*. In addition, *G. z. salinus* occurs in the area, having about the same distribution as does *oceanicus*. Broken lines represent isohalines ($^{\circ}/_{\circ\circ}$).

common also in the Finnish archipelago, but, as mentioned above, less numerous than *oceanicus* in the *Fucus* vegetation of the outer zone. However, it generally occurs considerably more frequently than does *oceanicus* in very shallow water (with a maximum depth of half a metre or so) in this zone. From the Swedish waters represented in the material, i.e. the coast from Stockholm to Blekinge, and the coast of Gothland, there are numerous finds; also Dahl frequently captured *z. zaddachi* (for synonymy, see p. 231) in the latter waters. From deeper Baltic waters there is only one sample containing *z. zaddachi* taken east of Rügen, in 21 m. depth. The Danish material includes some samples containing *z. zaddachi*; they all refer to a depth of at most a few metres (Ore Strand: Sliphavnskrogen, Isefjord: Hovvig). But from this district there are also records given by Poulsen (1932), who captured the form in the waters between Sealand, Möen and Falster (for synonymy, see p. 231).

*Gammarus zaddachi salinus.* The subspecies shows, on the whole, the same limits of distribution in the area as *oceanicus*, but it is not present in the material from localities outside the Danish Isles. The type in question is found in most *Gammarus* samples, generally in small numbers, but locally it occurs in striking abundance. This phenomenon is observed in localities of quite different natures, viz. on the one hand in parts of the Finnish archipelago, which are not exposed to the open sea, and on the other in the open waters between Rügen and the Danish Isles and on the coast of the Great Belt (at Nyborg).

*Gammarus locusta.* Most of the previous records of this species from the Baltic area actually refer to *G. zaddachi*, mainly to subsp. *oceanicus* (for synonymy, see p. 227).[1] But *G. locusta* is also widely distributed in the Baltic district, though it is not as a rule so abundant as *zaddachi* and does not penetrate as far into the more diluted waters. Thus *locusta* on the Finnish coasts is confined to the south-west waters with a minimum salinity of *c.* 5–6 °/₀₀ (see Fig. 6). *G. locusta* is also missing in the Swedish samples from the waters off Stockholm to Kalmar. The depth in the places of capture generally does not surpass a few metres; in the material from the open and comparatively deep waters between Rügen and the Danish Isles, where *zaddachi oceanicus* and *salinus* occur commonly, the species is practically missing.

The samples from the Cattegat contain *locusta* in much greater numbers than *zaddachi*, and in the collections from the west coast of Denmark only the former species is present.

*Summary of the* Gammarus *fauna of the Baltic.* The forms treated above are the only common species of *Gammarus* of this area. Besides them the area

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[1] The Danish collections include, amongst other, the material used by Blegvad for his investigation on the biology of *G. locusta* (1922). Of *c.* 210 specimens from this collection, examined in connexion with the present investigation, *c.* one-third (70 specimens) proved to belong to this species, the rest being *G. zaddachi oceanicus*, and *salinus*. This result is by no means surprising in view of the confusion prevailing especially in earlier years. Blegvad also observed that the specimens studied by him varied greatly.

seems to harbour only *G. duebeni*, which is confined to very shallow water and to special localities (it occurs mainly in brackish rockpools and similar small basins on the shore of islands, exposed to the sea; see Segerstråle, 1946). There is no evidence for the occurrence of *G. setosus* Dement. Dementieva's *G. setosus* f. *baltica* and Dahl's *G. locusta* f. *setosus* from Baltic localities are attributed to *G. z. zaddachi* (see synonyms, p. 231).

### *Randers Fjord*

A comparatively large collection of *Gammarus*, made by Johansen and Ussing during their investigations of the invertebrate fauna of this water, situated on the north-east coast of Jutland in Denmark and interesting because of the decreasing salinity from the mouth to the more inland parts, is discussed in Stephensen's paper of 1917. He records the following species and forms from the area: *G. locusta*, *G. locusta* var. *Zaddachi*, an intermediate form between *G. locusta* and this form, as well as *G. duebeni* and *G. pulex*. Later on, in 1927, Stephensen identifies some of the intermediates between *G. locusta* and *G. locusta* var. *Zaddachi* as *G. duebeni*. The material concerned was deposited in the Museum of Copenhagen, and all of it, excepting that of *G. pulex* and *G. duebeni*, was kindly sent by Mr Stephensen to the author, who has thus had the opportunity of going through it.

The results are as follows. Most specimens labelled *G. locusta* are correctly determined (one being an intermediate between the subspp. *oceanicus* and *zaddachi* of *G. zaddachi*). The form called *G. locusta* var. *Zaddachi* is mainly *G. z. zaddachi*, whereas the 'intermediate form between *G. locusta* and *G. locusta* var. *Zaddachi*' includes all three subspecies of *G. zaddachi*; in addition, there are some *G. locusta* and one *G. duebeni* (this species captured at St. 9, depth 0 m.). In a number of samples of *G. zaddachi*, the subspecies could not be determined, on account of the very small size of the animals. The study of the material has given the following ranges of distribution:

| | |
|---|---|
| *G. zaddachi zaddachi:* | St. 2 (salinity from 1–2 to 12 °/₀₀) |
| *oceanicus:* | St. 8–10 (salinity from 5 to at least 24 °/₀₀) |
| *G. locusta:* | St. 10 (salinity from *c.* 17 to at least 24 °/₀₀). |

As seen from the above records the subspecies of *zaddachi*, as well as *locusta*, follow one another in the same order as in the Baltic area. The salinities at the most inland localities for *z. oceanicus* and for *locusta*, are higher in Randers Fjord than in the Baltic, but this phenomenon is obviously due to the comparatively scanty material from the Fjord.

### *Ringköbing Fjord*

This water, located on the west coast of Jutland, is connected with the North Sea through only a narrow opening. The water is consequently brackish, the (surface) salinity averaging in the main part of the area *c.* 4–8 °/₀₀. The

*Gammarus* fauna has been treated by Poulsen (1933–6). He records the following species: *G. locusta*, occurring only in the very opening of the Fjord; *G. duebeni*, common everywhere, excepting in the saltest part, and observed also in the lowermost course of the river Vondaa; *G. zaddachi*, found only in a small basin, which is separated both from the Fjord and from the North Sea.

Fortunately, the collection received for the present investigation from the Copenhagen Museum includes about forty samples of the Ringköbing Fjord material (the determination, however, is not given on the labels), thus enabling the author to check the records which were given by Poulsen and of which some appeared doubtful.

The results are as follows. (1) The main *Gammarus* of the Fjord is not *duebeni*, but *zaddachi*. All the specimens of this species, which are large enough to be identified, belong to *z. zaddachi*. *G. duebeni* is certainly present in the material, but occurs only in a few samples, all taken in very shallow water (0–0·5 m.). The localities are: the mouth of the River Vondaa; near the bridge in this river; off Gammelsogns Mölle; on the shore *c.* 200 m. east of the mouth of the River Falen; Gjödel Canal, near the bridge at Lönne Klit.

(2) *G. z. zaddachi* occurred in different parts of the Fjord, from the shore to open areas with depths of *c.* 3 m. (maximum depth of the area *c.* 6 m.). In addition, one sample has been collected in the mouth of the River Vondaa, near the bridge (3 July 1921).

(3) The true *locusta* was found only in one sample (Söndre Dyb, 3·5 m.). Poulsen records the species from the saltest parts of the Fjord. These samples are lacking in the material available to the present author, but as the characteristics given for this species by Poulsen are quite correct there is no reason to doubt these determinations.

(4) The '*G. zaddachi*' mentioned in Poulsen's paper seems not to be included in the preserved material, but the illustrations given suggest that the form of the species in question is *oceanicus*.

## THE RELATIONSHIP BETWEEN *GAMMARUS ZADDACHI* AND THE SPECIES *G. SETOSUS* AND *G. WILKITZKII*

In the material from the Arctic there are numerous samples containing the large species *G. setosus* and *G. wilkitzkii* (many of the samples are labelled *G. locusta*), thus enabling the author to compare them with *G. zaddachi*.

*G. setosus* (material: about thirty-five samples from Arctic Canada, Greenland, Iceland, Spitsbergen, east coast of Murman, Novaya Zemlya, Kara Sea, the Arctic Sea off Siberia). This species was separated from *G. locusta* and established as an independent species by Dementieva (1931), mainly on material from Arctic waters (the amphipod regarded by this author as a Baltic form of *setosus* is obviously identical with *G. z. zaddachi*). Stephensen

(1940) records it as *G. locusta* subsp. *setosus*, and gives the first accurate description of the form.

The examination of the specimens in the present material showed that the species is as little allied to the true *locusta* as is *zaddachi*, but there is a close relation between *setosus* and the last-mentioned species, especially subsp. *oceanicus*. As in *zaddachi* the head sinus is deep, the 4th side-plate has the same semicircular lower margin, the pleon epimera show no difference in shape, the last uropods have the inner ramus of the same relative length, and as to the relative length of the peduncle of antenna 1 there is a strict agreement with *zaddachi oceanicus*.

The main differences are as follows. (1) The common occurrence of plumose setae in *setosus*, particularly on peraeopods 5–7 (segments 4–6), pleon segments 4–6, and the telson; here practically all the setae are feathery (cf. Stephensen, 1940, fig. 41). In addition the apical hairs on the telson are markedly longer than in *z. oceanicus* (in the male about three times as long as the corresponding spines (or longer), against at most about twice the length in *z. oceanicus*). (2) The 2nd and 3rd peduncle segments of antenna 1 bear hair clusters, on the under side, from 5 to about 7, and 2–3 respectively, whereas *z. oceanicus* has 3–5 and 1–2 respectively. (3) The eyes are generally distinctly smaller in *setosus*. (4) The 2nd gnathopod in this species is as a rule considerably stouter and its hind margin much more bulging; besides, the gap between the mid-palm spine, present in the male, and the palmar-angle spine-row is usually far less pronounced (Fig. 7) (in addition, in the female the latter spine group occupies a greater part of the palma in *setosus* than in *z. oceanicus*).

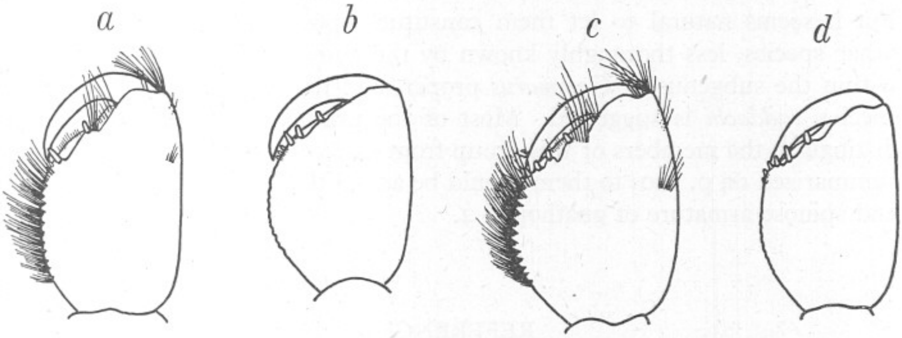

Fig. 7. Second gnathopods of *Gammarus zaddachi oceanicus* (*a*, *b*) and *Gammarus setosus* (*c*, *d*) (males) to show variation in shape. *a*, *oceanicus*, typical (Murman Coast, body length 30 mm.). *b*, *oceanicus*, approaching typical *setosus* (Spitsbergen, 25 mm.). *c*, *setosus*, typical (east Greenland, 32 mm.). *d*, *setosus*, approaching typical *oceanicus* (the Arctic Sea off Siberia, 26 mm.). In *b* and *d* the setae are omitted.

According to the author's observations only the characteristics mentioned above under (1) always separate *setosus* from *zaddachi oceanicus*, whereas, when comparing the former species with large specimens of *oceanicus*, the other characteristics may overlap more or less (Fig. 7). Even in the occurrence of feathery setae there may be some transition, *oceanicus* occasionally having single plumose hairs on the last uropods, pleon segments, and telson (Fig. 3 *f*), but the difference is nevertheless very marked.

Besides *G. setosus*, the very large Arctic species *G. wilkitzkii* (length up to 48 mm.; Gurjanova, 1930) is closely allied to *zaddachi*. It has even been reported by some writers, amongst others Stephensen, as possibly being identical with this species. In fact, the differences between *z. zaddachi* and *wilkitzkii* are small.[1] They seem, however, to be great enough to justify retaining the latter as an independent species, as suggested by Sexton (1942). The same conclusion appears to hold good regarding *setosus*. If these two forms were considered subspecies of *zaddachi*, the still closer relation between the subspecies *zaddachi*, *oceanicus*, and *salinus* would not be so clearly seen. But it seems natural to let them constitute—possibly together with some other species, less thoroughly known by the author—an independent group within the subgenus of *Gammarus* proper, and naming this group after the species *zaddachi* is suggested. Most of the principal characteristics which distinguish the members of this group from *G. locusta* are the same as those summarized on p. 220; to them should be added the differences in the shape and spinose armature of gnathopod 2.

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[1] The following divergence observed in material investigated by the author may be added to those listed by Sexton (1942). The peduncle of antenna 1 is still longer than in *z. zaddachi*, viz. as long as the distance from tip of rostrum to hind margin of peraeon segment 2; in *z. zaddachi* the peduncle reaches at the most to the middle of the said segment.

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# THE STRUCTURE, TADPOLE AND BUDDING OF THE ASCIDIAN *PYCNOCLAVELLA AURILUCENS* GARSTANG

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(Text-figs. 1–3)

*Pycnoclavella aurilucens* was recorded and briefly described by Garstang in 1891 from a limited locality in the Plymouth area, and has not been found with certainty of identification from any other region. There has been a tendency to subordinate it as a species of *Clavelina*, but the dissimilarities are greater even than the original description implies and this procedure is not justified. The genus is accordingly retained, and a more detailed account of the colony, with the first description of the tadpole larva and process of budding, is presented.

Colonies are usually found growing on gorgonians, large hydroids and calcareous algae at depths of 25–30 m. associated with coarse shell gravel and polyzoa such as *Lepralia*. It is known to occur only in the Plymouth region, unless the form known as *Clavelina nana* reported from Roscoff and Banyuls (Giard, 1873, Lahille, 1890) turns out to be identical with it. The external appearance of the colonies and of the constituent zooids has been well described by Garstang in the second volume of this *Journal*. In brief, the colonies are encrusting, the thoracic parts of the small delicate zooids extending freely from a greenish matrix in which the abdomens are embedded. The endostyle and peripharyngeal bands are picked out in yellow or white pigment and are very striking; the zooids are very contractile.

## STRUCTURE OF THE ZOOID

The zooids (Fig. 1) in general structure are much like those of *Clavelina*. They are much smaller and consequently have a less elaborate branchial sac, there being seven rows of gill-slits, rarely eight or nine. The endostyle is comparatively massive, as noted by Garstang, and the siphons independent and without lobes as is in other members of the Clavelinidae. Dorsal languets, corresponding in number to the rows of stigmata, occur along the dorsal line of the branchial sac. The oesophagus is long, the stomach squarish in cross-section as in *Clavelina* and leading into a typical post-stomach, the latter in turn connected with the intestine proper by a vertically aligned mid-intestine. The rectum opens into the atrial cavity level with the most posterior row of

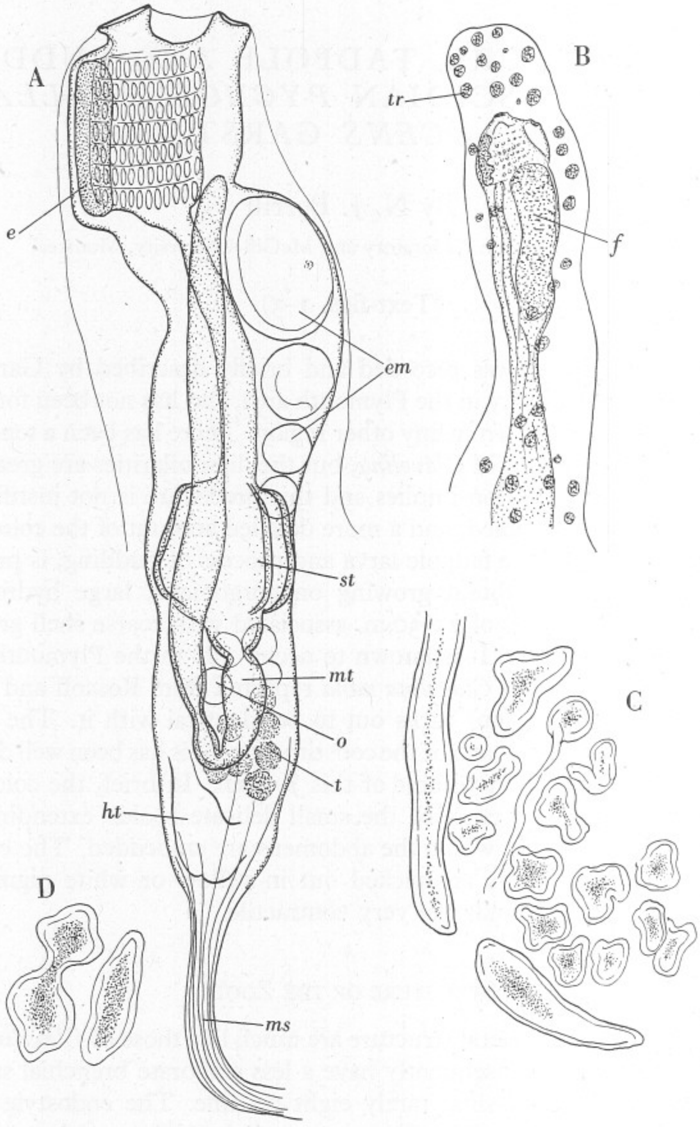

Fig. 1. A, mature zooid of *Pycnoclavella*, with ventral stolon incomplete and embr veloping within oviduct. B, zooid undergoing resorption after end of sexual b phase, with large 'trophocytes' accumulating in test. C, distal end of ventra showing separation of ampullary bud chambers and fragmentation of stolo D, isolated buds from another part of colony. *e*, endostyle; *em*, embryos; *f* trapped in resorbing intestine; *ht*, heart; *ms*, muscle fibres in ventral stolon; *m* intestine; *o*, ovary; *st*, stomach; *t*, testis; *tr*, trophocyte.

gill-slits. The heart lies posterior to the loop of the digestive canal, and is virtually straight. The epicardium extends throughout the length of the abdomen in a fused condition, its double nature indicated only by a shallow bilobed condition at its posterior extremity level with the bend of the gut-loop, and anteriorly as a pair of horns ending blindly just beneath the branchial sac from which it arises during development.

As in *Clavelina* there is a prolonged post-abdominal extension of the body wall in which the longitudinal retractor muscles are included. Other structures or organs do not extend into this stalk or stolon, so that it is not a post-abdomen of the kind encountered in the Synoicidae. Posteriorly the stolon tends to branch and processes may be reflected along the sides of the abdomen.

The gonads lie posterior to the stomach alongside the posterior part of the gut-loop. Both the sperm duct and oviduct open at the base of the atrial cavity. The oviduct is wide and eggs are fertilized while within it, early cleavage stages occurring near the level of the stomach and later stages up to the mature tadpole larva being found more anteriorly.

## Budding

The process of budding is apparently essentially similar to that of species of *Clavelina*. The posterior end of the post-abdominal stolonic extension branches and breaks up into ampullary chambers, somewhat larger fragments arising from fragmentation of the main stalk. These pieces consist of a layer of epidermis of irregular form, and contain mesenchymatous tissue that served originally as part of the mesenchymatous septum separating the afferent and efferent blood flow in the stolon. Actual separation of a united ampullary cluster into isolated fragments appears to be mainly a phenomenon of early or mid-winter, and development into new zooids never takes place while tissue continuity is retained with the parent zooid.

Nutrition of a bud appears to be somewhat different from that of *Clavelina* proper, though it is none too well known and neither is the development of the bud itself. There is clearly some concentration of reserve food cells within the bud fragments, but not to a comparable degree, and it is possible that the medium of the common matrix external to the buds may become nutritional as in *Distaplia*. In any event, as the zooids of a colony begin to resorb after the close of the sexual breeding phase, cells lying within or migrating into the thoracic and abdominal tunic become greatly enlarged and closely resemble the trophocytes of other forms, and such cells together with other dissolution products undoubtedly comprise the entire source of nutrition for the buds in *Distaplia* colonies. The process of resorption follows an orderly course and the reduction of structures and tissues is in general like that described for *Clavelina* by Huxley (1926).

## DEVELOPMENT AND STRUCTURE OF TADPOLE

The egg is comparatively yolky and as such is relatively small, of about 0·28 mm. diameter (Fig. 2A). Fertilization occurs at the base of the oviduct by sperm entering from the atrial chamber. The pattern of early cleavage is not known, though in the equally yolky eggs of *Amaroucium* (Scott, 1945) the basic pattern established by Conklin (1905) for the smaller eggs of *Styela*, *Ciona* and *Phallusia* is not significantly affected. During embryonic development there is considerable growth, the trunk of the tadpole exclusive of the tail having a length several times the diameter of the egg.

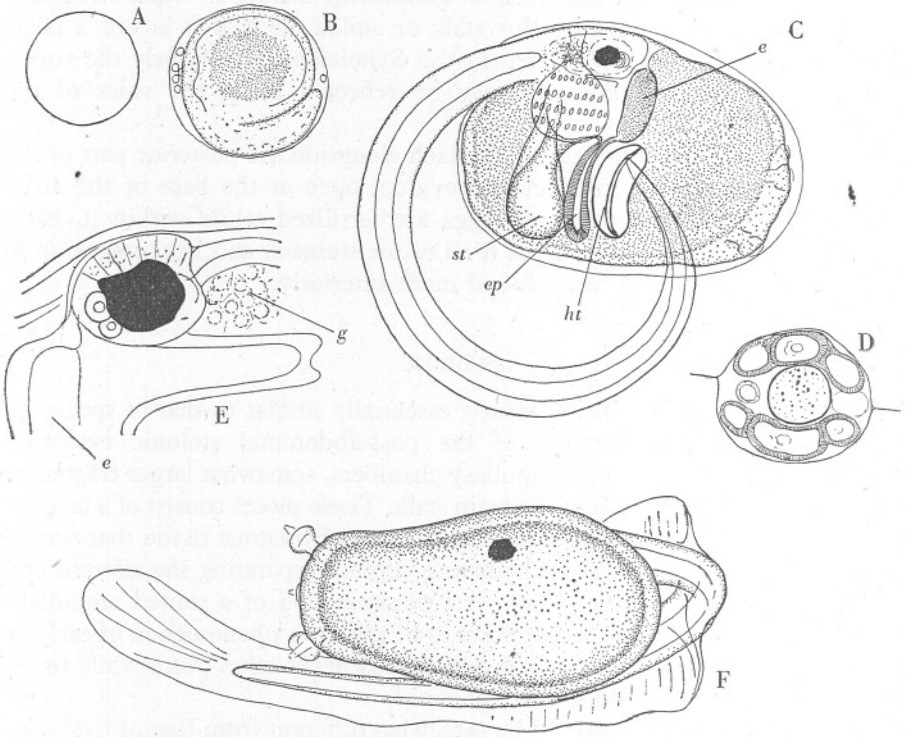

Fig. 2. *Pycnoclavella*, development of tadpole. A, egg. B, embryo within membrane. C, tadpole near time of liberation, all drawn to same scale. D, cross-section through horizontally twisted tail showing central notochord cell and lateral bands of muscle cells. E, sensory vesicle of tadpole at higher magnification, showing absence of otolith and presence of large mass of ocellus pigment together with two spherical lens cells. F, fully developed tadpole drawn from living specimen. *e*, endostyle; *ep*, epicardium; *g*, ganglion; *ht*, heart; *st*, stomach.

At the time of liberation of the tadpole the trunk is greatly distended and the permanent ascidian structure contained within is considerably advanced

(Fig. 2C). The tail is large and well developed, having a broad cuticular fin throughout its length and extending as a blade beyond, the whole being twisted through 90°, as in all ascidian tadpoles developing from large or yolky eggs excepting those of the *Pleurogona* (Ptyochobranchia). Muscle tissue lies on each side of the central notochord as a band three cells wide (Fig. 2D). The notochord itself consists of about 40 cells. The free-swimming period of the few living tadpoles studied lasted approximately 1 hr., a period consistent with the very local and selective habitat of the species. At 18° C. the stroke of the tail was 25–30 per sec. and the speed about 3 mm. per sec.

The trunk of the living tadpole (Fig. 2F) is a dense green and the internal organs hard to distinguish. The green colour is due to enormous numbers of peculiar bladder cells congesting all internal space not otherwise occupied. There are three typical adhesive organs at the anterior end, each with a stalk deeply invaginated. Of the larval organs *per se* the sensory vesicle is unique. While a number of ascidian tadpoles are known with only an otolith but no ocellus, *Pycnoclavella* alone of those so far examined has an ocellus but no otolith (the Thaliacean condition is not relevant to this discussion). The vesicle (Fig. 2E) is not noticeably abnormally small, yet it contains no trace of an otolith while the ocellus itself is a little unusual. The mass of pigment is relatively large although the associated retinal cells do not appear to be correspondingly numerous. The lens cells, however, which are three in the great majority of ascidian tadpoles, are here represented only by two.

As in most yolky ascidian eggs, the development of the larval (tadpole) structure is relatively retarded, probably as in other forms due to the slow differentiation of yolk-laden notochord cells (cf. Berrill, 1935*a*, *b*). Accordingly the permanent ascidian structure is relatively well developed within the active tadpole, and lies mainly in the posterior half of the trunk with the axis vertical to the long axis of the tadpole. The mouth is formed though not functionally open, and the pair of peribranchial sacs that appear independently on each side at an earlier stage are fused dorsally to form the atrial aperture. The endostyle is short and thick. Adjacent to it on each side the peribranchial sac is perforated by four rows of definitive stigmata, with nearly the same number per row as in the mature zooid. In the ventral part of the trunk, the pharynx opens into the oesophagus and stomach, the digestive canal as a whole forming a vertical U-shaped tube. Immediately in front of the oesophageal opening and behind the base of the endostyle, a second outgrowth extends ventrally from a pair of initial evaginations from the floor of the pharynx to form the epicardium. It later loses its connexion with the pharynx. Anteriorly to the epicardium and ventrally to the endostyle, but not connected with either, lies the large pericardium and heart.

## POSTLARVAL DEVELOPMENT

After settling the tail is rapidly absorbed, complete absorption taking not more than an hour. After about 12 hr. (at 18° C.) the tail consists of a compact, more or less spherical, mass of cells attached to the posterior end of the trunk; the adhesive organs no longer are recognizable, and at the anterior region three large epidermal outgrowths appear (Fig. 3 A). The rate of further development is somewhat variable, the permanent organs still being in a non-functioning state 3 days later, but after 5 days varying from an inactive condition to one in which the heart, siphons and gill-slits are all fully functional (Fig. 3 B, C). At this time the thorax has become transparent and virtually colourless, except for a pair of prominent pigment patches, one on each side of the pharynx in front of the most anterior row of stigmata. The abdomen is greatly elongated, and dense with the green cells noted in the tadpole. The heart now lies at the base of the abdomen. Of the three epidermal outgrowths, one usually continues to grow and the others shrink. At the end of two weeks (Fig. 3 D) little further change has occurred, at least under laboratory conditions, the only obvious growth being that of a sheet of tunicin, richly impregnated with small brown cells, over the substratum.

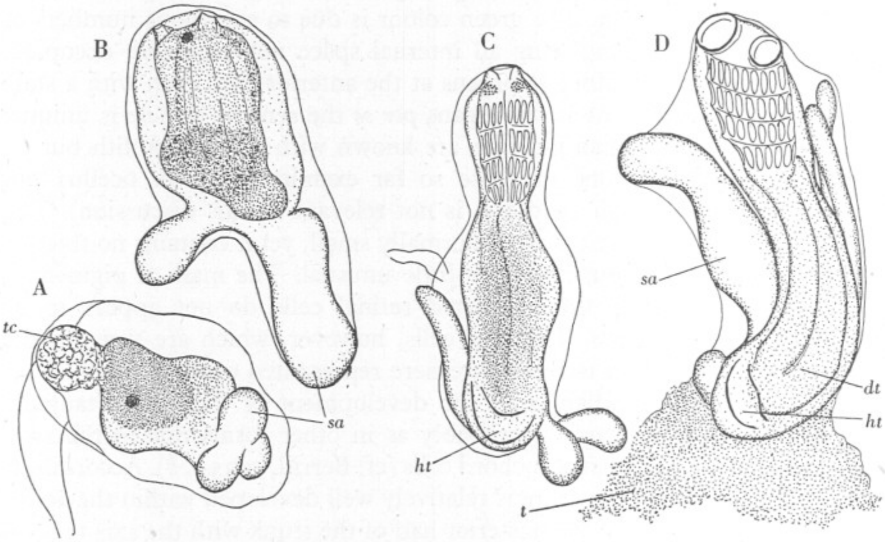

Fig. 3. *Pycnoclavella*, metamorphosis and post-larval development (at 18° C.). A, 12 hr. after attachment with tail absorbed and anterior ampullae growing. B, C, 3–5 days later, showing abdominal extension, further growth of ampullae, and formation of active gill slits. D, individual two weeks after attachment with sheet of test substance growing over substratum. *dt*, digestive tube; *ht*, heart; *sa*, stolonic ampulla; *t*, test substance; *tc*, mass of tail cells.

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# ABSTRACTS OF MEMOIRS

## RECORDING WORK DONE AT THE PLYMOUTH LABORATORY

### UNTERSUCHUNGEN ÜBER DIE EIWEISSVERDAUUNG *IN VIVO* UND *IN VITRO* BEI EINIGEN GASTROPODEN

By **Greta Hörstadius**, geb. **Kjellström**, und **Sven Hörstadius**

*Pubb. Staz. Zool. Napoli*, Vol. 18, 1940, pp. 151–249

The digestion of proteins was studied in some marine Gastropoda, and the results that refer to work performed at The Marine Biological Laboratory, Plymouth, are as follows:

In *Hermaea dendritica* phagocytosis was with certainty shown to occur in the 'liver' by feeding the animals with algae containing chloroplasts of different size (*Bryopsis* and *Codium*). In the ingested chloroplasts the characteristic starch reaction could be demonstrated.

In *Pleurobranchaea meckeli* phagocytosis was proved with gold fibrin as well as with carmin, in *Archidoris britannica* with gold fibrin (visible colloidal gold particles embedded in fibrin).

In the carnivore *Pleurobranchaea meckeli* the juice in the crop hydrolyzed casein at *p*H 5·5, fibrin at 7, gelatin and pepton-Witte at 7. Glycyl-glycin was not hydrolyzed at *p*H 7·5. Extract of the digestive diverticula (liver) hydrolyzes the same substrates as the juice of the crop, and also glycyl-glycin. The strength of the enzymes in the crop shows during the first 10 hr. after feeding a maximum after 3 hr. The dipeptidases do not vary in strength. The juice is very active on Spritblaufibrin, but the extract is inefficient, although both of them hydrolyze casein and gelatine equally. S.H.

### RESTING AND ACTION POTENTIALS IN SINGLE NERVE FIBRES

By **A. L. Hodgkin** and **A. F. Huxley**

*Journ. Physiol.*, Vol. 104, 1945, pp. 176–95

A technique for introducing micro-electrodes into the interior of a giant axon from *Loligo* is described. The axon was stimulated electrically and direct measurements of the action potential and resting potential were made with an amplifier and oscillograph. Experiments with external electrodes showed that the action potential was conducted for at least a centimetre beyond the tip of the micro-electrode and that the introduction of a micro-electrode had no effect upon the ability of the nerve to conduct impulses. The absolute magnitude of the action potential and resting potential are given as about 90 and 45 mV.

Measurements with external electrodes show that the action potentials of *Homarus* and *Carcinus* nerve fibres are also much larger than the resting potential.

These results have an important bearing on theories of nervous conduction. They show that classical physiologists were right in thinking that electrical changes originate at the surface membrane of a nerve fibre, but were wrong in believing that the action potential arose solely from a breakdown of the pre-existing resting potential.

The experiments described in this paper were completed in 1939 but the outbreak of war delayed publication of a full account of the results until 1945.
A.L.H.

## The Neurological Basis of the Locomotory Rhythm in the Spinal Dogfish (*Scyllium canicula, Acanthias vulgaris*).

### I. Reflex Behaviour

By H. W. Lissmann

*Journ. Exp. Biol.*, Vol. 23, 1946, pp. 143–61

The idea that rhythmically co-ordinated movements of animals are driven and governed by an automatic mechanism within the central nervous system has been steadily gaining ground. Previous research on the dogfish led to the conclusion that the persistent locomotory rhythm, characteristic of spinal preparations, arises from bursts of motor impulses emanating spontaneously from the central nervous system, and is not essentially dependent on afferent stimulation.

The present investigation of body and fin reflexes makes it difficult to accept this picture for the following reasons. (i) If swimming is induced in inactive preparations through a localized exteroceptive stimulus, the position of the initial swimming posture depends solely on the site of stimulation. (ii) Diffuse touch to the ventral surface of a spinal preparation inhibits the swimming movements. Some dogfish remain immobile after the inhibitory stimulation has been discontinued, but they resume their persistent swimming on application of a single excitatory stimulus. (iii) Through feeble transitory stimuli any individual swimming stroke can be retarded, temporarily arrested, reversed, accelerated and augmented. The reaction depends on the site of stimulation and on the momentary phase of the swimming movement at which it is applied. The rhythm emerging after the application of a transitory stimulus is, as a rule, out of phase with the rhythm as recorded prior to the application of the stimulus.
H.W.L.

## THE NEUROLOGICAL BASIS OF THE LOCOMOTORY RHYTHM IN THE SPINAL DOGFISH (*SCYLLIUM CANICULA*, *ACANTHIAS VULGARIS*).

## II. THE EFFECT OF DE-AFFERENTATION

By **H. W. Lissmann**

*Journ. Exp. Biol.*, Vol. 23, 1946, pp. 162–76

The persistent swimming rhythm, typical of a spinal dogfish, is completely abolished as soon as all afferent excitation is cut off by severance of all the dorsal roots. The rhythm still emerges clearly when about half the number of the dorsal roots is transected, irrespective whether the anterior or the posterior half of the animal be de-afferentated, or whether complete unilateral de-afferentation is performed. Extensively de-afferentated preparations may exhibit swimming movements only after exteroceptive stimulation or after electrical stimulation applied directly to the spinal cord; these swimming movements do not persist. If only a small patch of the body surface remains sensitive, then, on stimulation of this region, the preparation exhibits a static reflex posture.

No evidence has been found to support the view that the locomotory waves of the spinal dogfish result from a spontaneous and automatic activity in the central nervous system; the experimental findings suggest that the locomotory waves can be essentially considered as moving sites of nervous integration, and that peripheral stimulation plays a fundamental role in this process.

H.W.L.

## RELATIVE GROWTH OF THE EUROPEAN EDIBLE CRAB, *CANCER PAGURUS*.

## III. GROWTH OF THE STERNUM AND APPENDAGES

By **Donald C. G. MacKay**

*Growth*, Vol. 7, 1943, pp. 401–12

The results of a study of form changes in the European edible crab, *Cancer pagurus*, have been analysed by Huxley's method and have been presented in three papers of which this is the third and final one. The study was carried out at the Marine Biological Laboratory at Plymouth during the year 1934–5.

The results of the study indicate that males and females differ only slightly in the growth of the sternum. In male crabs, both immature and mature, the appendages studied display positive heterogony. In females the chelae are positively heterogonic, the walking legs negatively so. The growth coefficient is higher for the chelae of mature males than for immature ones. Growth changes are such as to produce larger chelae and longer legs in males than in females of corresponding carapace length.

Altogether twenty-six body measurements were studied. The highest growth coefficients in males were found for the chelae of immature crabs (for length, $k = 1{\cdot}48$; for width, $k = 1{\cdot}40$). For females the highest growth coefficient was found for the 4th abdominal segment of adults ($k = 1{\cdot}50$).

In general, *C. pagurus*, like *C. magister* which had been studied previously, shows a low degree of heterogony and consequently is able to grow to a considerable size (10–12 lb.) without marked changes in the form of the body.

D.C.G.M.

## THE DETERMINATION OF THE DEPTHS AND EXTINCTION COEFFICIENTS OF SHALLOW WATER BY AIR PHOTOGRAPHY USING COLOUR FILTERS

By J. Grange Moore

*Phil. Trans. Roy. Soc. Lond.* A, Vol. 240, pp. 163–217

Submerged beaches viewed vertically from the air vary in apparent brightness with the depth and effective extinction coefficient of the water. If one be known, the other may be calculated from sensitometric measurements on a single air photograph taken through a suitable filter.

If neither be known, a pair of photographs is taken simultaneously through contrasting filters; in average coastal water and with suitable photographs, depths exceeding 20 ft. may then be determined with an error of less than ± 10%, by making use of a general relationship between extinction coefficients at any two given wavelengths; from these depths extinction coefficients may then be calculated.

The theoretical and practical details, the limitations and uses of the method, and the results obtained during a year's work over Cornish and Mediterranean beaches and elsewhere, are described and illustrated. Records for interpretation by oceanographers, marine surveyors and engineers can rapidly be obtained over large areas of coastline.

J.G.M.

# LABORATORY REGULATIONS

At a Council Meeting, held on 12 April 1947, the regulations with regard to the admission of visiting workers to the Plymouth Laboratory were amended as follows:

1. Any Governor or Founder of the Association is entitled to occupy personally a table at the Plymouth Laboratory without payment. A Governor or Founder shall have the privilege, upon signifying to the Director his intention to forgo in any year the right of personally occupying a table in the Laboratory, of nominating an eligible person to make use of a table for one month in that year free of charge.

2. The charge for a table shall be 50 guineas a year, 5 guineas a month, and £1. 10*s*. a week, to be paid in advance.

3. Members of the Association have the first claim to become renters of tables, and shall have the privilege of occupying a table for one week in each year free of charge.

4. The Council of the Association may remit, in whole or in part, the payment of rent for a table in special cases.

5. Applications from Members and others desiring to occupy tables must be made in writing to the Director, and a notice of at least seven days will be expected before any table is ready for use.

6. The Association undertakes, so far as possible, to supply the material required for any investigation, and such facilities for obtaining and working with it as may be at the command of the Association. No visiting worker can be permitted to make biological collections in the Laboratory. The Association undertakes to supply collections of marine animals and plants at a fixed price to those who wish to buy them. This rule must be understood to apply only to general biological collections. Visiting workers are at liberty to collect and take away with them any material that is necessary for the prosecution of their research on payment of the cost of microscope slides, cover-slips, glass tubes, expensive reagents, bottles and packing cases necessary for its removal.

7. Visiting workers are expected to furnish the Director with a summary statement of the published results of investigations carried on by them in a form suitable for publication in the *Journal* of the Association.

8. Visitors working in the Laboratory will have free access to the tank-room, but they are not permitted to have access to the interior of the tanks without the permission of the Director. Facilities for conducting experiments on a large scale will be granted as far as space permits.

9. The Director has control over the Laboratory, boats, equipment and apparatus of the Association. Visiting workers are admitted on condition that they accept this control, and agree to abide by the regulations drawn up by the Council of the Association.

# MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM

## Report of the Council for 1946–47

### The Council and Officers

The Council have to report with regret the death of two Vice-Presidents of the Association during the year: Lord Mildmay of Flete, P.C., a Vice-President since 1939, and Sir Joseph Barcroft, F.R.S., who served for many years as an active member of the Council and was also an Associate Member.

The following changes have been made in the Annual Governors during the year. Mr P. D. H. Dunn, C.M.G., O.B.E., has been appointed as representative of the Ministry of Agriculture and Fisheries on the resignation of Mr A. T. A. Dobson, C.B., C.V.O., C.B.E. The new Prime Warden of the Fishmongers' Company is Mr Benjamin Travers, A.F.C. Admiral Sir Aubrey C. H. Smith, K.B.E., C.B., M.V.O., has resigned as an Annual Governor representing the Fishmongers' Company. The Council wish to record their appreciation and thanks for the great services rendered to the Association by Mr A. T. A. Dobson and Admiral Sir Aubrey Smith.

Four ordinary meetings of Council were held during the year, two in the rooms of the Royal Society, one in the rooms of the Linnean Society and one at Plymouth. At these the average attendance was 14. The Association is indebted to the Councils of the Royal Society and the Linnean Society for the use of their rooms.

### The Plymouth Laboratory

During the year all remaining minor repairs necessary to complete the restoration of the Laboratory have been finished, except in the centre block of the main building for which certain materials are still awaited. The outside tank destroyed by the bombing has been rebuilt and a new outside circulation bench constructed. Much needed painting to the exterior of all buildings has been done.

A grant has been sanctioned by H.M. Treasury towards the rebuilding of the Director's House as laboratory accommodation, and the work has now been started.

A small building on the pier at Newlyn, in Cornwall, has been rented by the Association for use as a temporary laboratory in which samples of fish or material collected in the research ship while cruising in the vicinity can be dealt with. It is essential, for instance, that there should be the least possible delay in certain chemical analyses of water samples after their collection.

### Aquarium

During the year the repairs to the aquarium were completed and the tank room was reopened to the public on 5 November 1946, by the Lord Mayor of Plymouth, the Rt. Hon. Isaac Foot, P.C. The opportunity has been taken to rebuild the rockwork using local wave-worn boulders from the beach. The work has been done by laboratory staff under Mr D. P. Wilson's supervision. The finished product is generally considered to be a great improvement, both artistically and as representative of the natural surroundings; this it owes especially to the skill of Mr F. G. C. Ryder. Screens have also been erected to improve the lighting and viewing of the main tanks.

Over 4000 members of the public visited the aquarium during the first fortnight after it was reopened, and a good attendance is being maintained. Parties of school-children are again making use of the educational facilities afforded.

### The Ship and Motor Boat

The 90-ft. motor fishing vessel (M.F.V. 1564) chartered from the Admiralty, and now registered as Research Vessel *Sabella*, was handed over to the Association on 29 May 1946. The vessel was built by the Wivenhoe Shipyard Ltd. at Wivenhoe, Essex, and Mr G. A. Steven gave much time and attention to supervising the alterations necessary to fit her for scientific research purposes. Mr Steven was present at the trials off Brightlingsea on 28 May, and he accompanied her on the trip to Plymouth where she arrived on 1 June. After a spell in harbour necessary for fitting out with research and fishing equipment she went into service on 13 June. Since then she has been in continuous commission and has proved in most respects highly satisfactory for the work. Her captain is Skipper W. J. Creese, who before the war was mate on the *Salpa*.

The motor boat *Gammarus* has worked throughout the year. In September 1946 she was given a major overhaul by the original builders. The hull and woodwork are in excellent condition, and the boat should be fit for many more years' service.

The *Salpa* has not yet been released by the Ministry of Transport, but the off-survey is in progress.

### Government Surplus Equipment

Through the help of the Development Commissioners the Association has obtained a 10 h.p. Hillman army utility van. This is proving most serviceable for carrying material from the ship and for collecting purposes.

Full opportunity is being taken of the facilities offered by the Ministry of Supply and other departments for obtaining equipment and apparatus from government surplus disposal stores. Dr W. R. G. Atkins and Mr F. J. Warren have spent much time on the selection of material and as a result the laboratory is becoming very well stocked with electrical fittings and other equipment useful for research purposes. The workshop is also now well equipped with machine and other tools.

## The Staff

Mr P. G. Corbin was appointed to the staff of the Plymouth laboratory as Scientific Officer as from 1 January 1947. Prior to that date he had been working at Plymouth since 7 May 1946, with a grant from the Ministry of Agriculture and Fisheries for the completion of the mackerel investigations made before the war.

Mr H. G. Vevers, M.B.E., has been appointed Administrative Bursar on the scientific staff of the Plymouth laboratory. He joined the staff on 1 June 1946, and has given very great assistance in the administrative work necessary to put the laboratory on a peace-time footing.

Dr J. F. Danielli resigned from the post of Physiologist in the autumn of 1946 on his appointment to a Readership in Cell Physiology in the University of London tenable at the Royal Cancer Hospital.

Mr G. A. Steven was promoted to Principal Scientific Officer as from 1 October 1945; and Dr L. H. N. Cooper and Mr G. M. Spooner were promoted to Senior Scientific Officers as from 1 October 1945, and 1 April 1946, respectively.

Mr A. D. Mattacola resumed his duties on the technical staff on 27 May 1946, after war service with the Royal Tank Corps.

Mr A. G. Butler, the Assistant Caretaker, retired in October 1946, after nearly 27 years of faithful service to the Association.

Mr F. S. Russell and Dr H. W. Harvey attended the thirty-fourth meeting of the International Council for the Exploration of the Sea at Stockholm in August 1946.

Members of the staff have attended a number of meetings of scientific societies during the year, including the Joint Meetings of the Challenger Society and Representatives of Marine Laboratories which have now been resumed.

Dr W. R. G. Atkins and Dr H. W. Harvey have continued their work on the Marine Corrosion Committee of the Iron and Steel Institute.

On 6 March 1947 Mr F. S. Russell delivered a lecture to the Royal Society on the Plymouth Laboratory; this was the first of a series of lectures to be given at the Royal Society on British laboratories.

During the Michaelmas term 1946, Mr T. R. Tozer of the technical staff spent six weeks in the Zoological Department at Cambridge gaining experience in laboratory technique.

## Occupation of Tables

The following seventy-two workers have occupied tables at the Plymouth Laboratory during the year:

B. C. Abbott, London (General biology and histochemistry).
C. W. M. Adams, London (Study of Ascidians and Tunicates).
Dr C. Amirthalingam, Ceylon (Library).
Miss E. Batham, Cambridge (Nerve-net of Actinozoa).
Dr Anna Bidder, Cambridge (Digestive mechanism of *Loligo*).
Miss C. H. Brown, Cambridge (Skeletal proteins of Invertebrates).
D. A. Brown, New Zealand (Polyzoans).
Miss E. M. Brown, London (Parasitic dinoflagellates in plankton).
Dr H. H. Brown, Colonial Fisheries (Library).
A. Bulliard, Paris (General zoology).
Dr M. Burton, British Museum (Sponges).
A. T. Campbell, Penzance (General zoology).
W. T. Catton, Sheffield (Fish-blood development).
P. G. Corbin (Mackerel investigations).
E. J. Denton, London (General biology and histochemistry).
P. S. B. Digby (Planktonic Copepods).
Miss N. Duncan, Leicester (General zoology).
R. G. Evans, Aberystwyth (Intertidal ecology).
J. E. Forrest, London (Nudibranch Molluscs).
Dr V. Fretter, London (*Rissoa*).
Dr A. Graham, London (Prosobranchs).
Miss U. M. Grigg, Cambridge (Molluscs).
N. Guppy, London (Library).
R. Hamond (General zoology).
Dr J. D. F. Hardenberg, Batavia (Library).
Dr R. Harkness (Measurement of hydrogen-ion concentration).
Dr T. J. Hart, Discovery Committee (Falkland Islands' fisheries and ice diatoms).
P. H. T. Hartley, Wray Castle (Blennies).
Dr R. S. Hawes, Exeter (Gregarines of Polychaetes).
M. R. Haywood, Leicester (Mechanics of the blood vascular system in *Ascidiella*).
M. N. Hill, Cambridge (Seismic prospecting of sea-bed).
E. Hollowday (Rotifers).
N. A. Holme, Cambridge (Reproduction in Annelids and Molluscs).
G. M. Hughes, Cambridge (Neuromuscular movements in *Carcinus*).
A. Ibbotson (Library).
Dr M. W. Jepps, Glasgow (Structure of sponges).
F. G. W. Knowles, Marlborough (Colour changes in Crustaceans).
Fl.-Lieut. F. L. Litchfield (General zoology).
Miss J. Lorch, London (Bone formation in larval fish).
Dr A. G. Lowndes (Density of aquatic organisms).
Dr C. E. Lucas, Hull (Oceanography).
Miss J. Marchant, Birmingham (General zoology).
H. P. Moon, Leicester (Mechanics of the blood vascular system in *Ascidiella*).
Miss V. Moyle, Cambridge (Excretion in Amphipods).
J. A. C. Nicol, Oxford (Nervous system of Polychaetes).
Dr A. P. Orr, Millport (General).
Dr C. F. A. Pantin, Cambridge (Nerve physiology of Actinozoa).
Dr M. W. Parke (Algae).

A. Rifaat, Fouad I University, Cairo (Plankton).
J. Riley, London (Seashore Diptera).
M. J. Ritchie, London (General biology).
Dr D. M. Ross, London (General zoology).
Miss H. G. Q. Rowett, Plymouth (Library).
A. A. E. Sagay, Exeter (General zoology).
Dr P. N. Sarangdhar, Department of Fisheries, Bombay (Elasmobranchs and aquarium management).
Miss M. Sharman, Birmingham (Systematics of Lamellibranchs).
Dr J. E. Smith, Cambridge (Staining of nervous tissue of Echinoderms).
B. Sparrow (Diatoms).
Miss N. G. Sproston (Parasites of marine animals).
Miss F. A. Stanbury, Plymouth (Antifouling research).
Miss M. Sutton, London (General biology).
F. J. Taylor, Leicester (Phytoplankton and Algae).
Miss M. Taylor, Exeter (Parasites of *Phascolosoma*).
J. Theodorides, Paris (Shore entomology).
G. Thomas, Birmingham (General zoology).
A. K. Totton, British Museum (Siphonophores).
Y. R. Tripathi, Allahabad University (Parasites of fishes).
D. W. Tucker, Exeter (General zoology).
Miss Vidya Vati, Lucknow University (Fish embryology).
D. R. Wilkie, London (Measurements of hydrogen-ion concentrations).
P. T. Willmore, Cambridge (Seismic prospecting of sea-bed).
R. L. Woolley, St Andrews (Study of *Sepia* spermatophore by X-ray).

During this year of reconstruction a very large number of visitors have taken the opportunity of spending a day or two in Plymouth to see the work of the laboratory. Among these, the following have come from overseas:

Dr G. P. Baerends, Holland; Prof. K. N. Bahl, Lucknow University; Dr R. Dohrn, Naples; Dr Hermann Einarsson, Iceland; Prof. E. Fauré Frémiet, Paris; Prof. Z. Grodzinski, Cracow; Dr S. L. Hora, Bengal; Prof. J. J. Izquierdo, Mexico; Dr L. Linderstrøm-Lang and Dr H. Holter, Carlsberg Laboratory, Copenhagen; Dr A. W. H. Needler, Canada; Dr M. H. van Raalte, Leiden; Prof. S. Skowron, Cracow; Prof. R. Spärck, Copenhagen and Prof. H. C. Trumble, Australia.

Many workers from the Admiralty and other departments have also come specially for discussions with members of the Laboratory staff.

The usual Easter Vacation Courses in Marine Zoology were conducted by Mr D. P. Wilson and Mr G. A. Steven, and were attended by forty-one students from the following Universities, University Colleges and other institutions: Oxford, Cambridge, London, Aberdeen, Bristol, Leeds, Reading, Sheffield, Southampton, Cardiff, Exeter, Hull, Newcastle, Nottingham, Wray Castle and Plymouth Technical College.

Also during the Easter vacation Mr A. H. Lewis brought eight boys from Wellington College.

On 29 May 1946, the Danish research vessel *Atlantide* paid a second visit to Plymouth on her return voyage from the West African coast.

## Scientific Work of the Plymouth Laboratory Staff

### *Physics and Chemistry of Sea-water*

Dr W. R. G. Atkins, in collaboration with Dr H. H. Poole, is continuing the work with cube and other photometers, for the measurement of submarine illumination and Dr Cooper has made further determinations of the extinction coefficient using the Pulfrich photometer.

With the assistance of Dr M. A. Ellison, Dr Atkins has completed a survey of the records obtained by the photo-electric daylight recorded from 1930 to March 1941, when they ceased on account of war damage. The recorder, which was in use in the Meteorological Section of a large R.A.F. Station from 1943 to 1945, is once more installed and working at Plymouth.

The resumption of photo-electric work necessitated the restandardization of the cells and the examination of newer types as to their general suitability. With the assistance of Mr F. J. Warren a counter was incorporated in the J. H. J. Poole neon tube photometer, but its use at sea has so far been limited on account of electrical leaks. Photo-electric apparatus required for a visitor's researches upon the physiological effects of light was also provided.

During the war Dr Atkins served on the Sandbag Committee of the Ministry of Home Security. It is interesting now to record that the Danish copper naphthenate preservative, introduced to England (and subsequently manufactured here) by net-tests at Plymouth, was used on at least 22 million sandbags, and that the Olie ammoniacal copper sulphate method, also introduced by the Plymouth net-tests, was used on over 187 million bags. The bags thus treated had an average life of 2 years, at a cost for treatment of one farthing each. The grease compounded by Dr Atkins for the Admiralty before the war was adopted as the standard supply for certain largely used weapons of under-water warfare.

Investigations are much needed on the distribution of total dissolved phosphorus in the sea, because the phosphate present in the water at the beginning of each year has shown a close relation to the number of young fish caught and the general level of plankton population during the ensuing summer, throughout a period embracing 16 years' observations. With this aim Dr H. W. Harvey has been seeking a simple technique for measuring the total phosphorus present as phosphate, as dissolved organic compounds in solution, and in the microplankton, in samples of water. Hydrolysis at 140° C. has proved effective in setting free phosphate from organic compounds. Its subsequent estimation has necessitated research on the formation of molybdenum blue in order to attain sufficient precision to track down possible sources of error. This in turn has necessitated the development of a photo-electric absorption-meter. A suitable method of storing samples of sea-water for subsequent analysis has also needed investigation, in order to overcome the rapid growth of bacteria attached to, and the physical adsorption of organic phosphorus compounds on the walls of the storage vessel. Satisfactory results were obtained by 'baiting' the storage bottles with freshly precipitated aluminium hydroxide which was dissolved with acid immediately before transferring the waters to the reaction vessels.

During the early part of the year Dr Harvey completed a research on requirements for growth by species of flagellates and a *Chlorella*. At that time the inshore waters lacked sufficient manganese in solution for their continued growth. For vigorous growth the addition of about 1 mg. of this element to a ton of sea-water was necessary. The results are being published in Vol. XXVI, No. 4, of the *Journal*.

It has not been possible, owing to the lack of a research vessel during the spring, to continue the regular observations on phosphate, but Dr L. H. N. Cooper is restarting this work.

In marked contrast to the correlation between the distribution of young fish off Plymouth and the winter maximum of phosphate it has never proved possible to find any relation whatever between biological events and the hydrological environment as measured by salinity. This negative result has become so definite that it can have only one meaning—the presence of waters of similar salinity but very different hydrological and biological histories. With these two facts in mind Dr Cooper has been surveying all the physical and chemical data available in the area and trying to relate them to quantitative biological records. Correlations of inorganic phosphates have been found with the landings of herrings, spurdogs and rays and skates.

For an understanding of the distribution of salinity on the continental shelf it is essential to study the ocean waters to the west and south-west. It would appear that there are three types of high salinity water: (*a*) North Atlantic central water, with a well-defined temperature-salinity diagram, occupying the upper 600 m. well to the west and south-west, (*b*) the Mediterranean Tongue between 800 and 1200 m. with a salinity in excess of 35·5 ‰ and 67–70 % saturated with oxygen which may possibly under certain conditions be projected on to the continental shelf, and (*c*) the 'shelf blanket' formed by winter cooling of high salinity waters on the banks to the west and south-west of Ireland with a salinity usually over 35·5 ‰ and an oxygen-content over 90 % saturated. The problems are complex, so that a number of distinct but interlocking investigations have proved necessary, each of which ought to be completed before a coherent account can be published. Dr Cooper hopes to publish the results separately under the following headings:

1. The kinetic energy of the tides of the English Channel and Celtic Sea and its effect on turbulence, vertical mixing and stability of thermoclines.
2. A review of earlier work on the adjacent waters of the eastern North Atlantic.
3. A review of the hydrology of the Celtic Sea including the data collected by the mackerel investigations in 1937–39.

4. An analytic study of the dependence of water movements in the area on wind, density differences, tides and bottom configuration.

5. The contrasted hydrological distribution in the seas of the siphonophores *Muggiaea atlantica* and *M. kochi* which show much promise as biological indicators.

6. The correlation of the seasonal, annual and geographical distribution of nutrient salts with biological events, such as landings of marketable fish and distribution of plankton and bottom-dwelling invertebrates, incorporating the results of the above five papers.

### *Plankton*

Mr F. S. Russell has resumed the observations on the abundance of young fish in relation to other plankton animals which had been made for many years before the war. Collections started in June when the research ship became available and they show that during summer, autumn and winter the conditions were very similar to those existing immediately before the war. *Sagitta setosa* was still dominant though present only in small numbers. *Muggiaea atlantica* also still predominates although for the first time a few specimens of *M. kochi* have occurred with it. Taking all things into consideration it appears fairly certain that there has been no marked recurrence of the rich *Sagitta elegans* water off Plymouth during the war.

In connexion with the researches on the biology of the mackerel population off the western entrance to the English Channel, Mr P. G. Corbin has now completed a report on the spawning of the mackerel and the distribution of the pelagic young stages. As indicated in previous reports of the Council (1938 and 1939–40), mackerel-spawning was observed in 1937–39 in the continental-shelf area from mid-March until the end of July. It starts in the west and south-west over the edge of the continental shelf, and as the season advances it shifts eastwards and slightly northwards across the area. Maximum spawning intensity occurs from mid-April until mid-May and by the end of July there is scarcely any spawning in the area, although it still continues inside the mouth of the English Channel eastwards of the line Land's End—Ushant, and also in the Irish Sea.

The 1937–39 cruises provided material for a study of the spawning of the pilchard and the distributions of the two *Sagitta* species which occur at Plymouth—*S. elegans* and *S. setosa*, and of the more oceanic *S. serratodentata* and *S. lyra*, and also of the siphonophore *Muggiaea atlantica*.

Large catches of pilchard eggs were taken from April to July at the western end of the Channel, in the area Land's End—Start Point—Cap de la Hague—Ushant. This region appeared to be the main spawning centre of the species although eggs were found well to the westward of the Scillies.

From the above remarks, it is clear that in April the spawning areas of the mackerel and pilchard are separate. By July, however, there is almost complete overlapping, brought about by the eastward shift of the mackerel-spawning area.

In the continental-shelf area, *Sagitta elegans* appeared to be the dominant *Sagitta* species, while *S. setosa* dominated the restricted regions of the Bristol Channel mouth and the English Channel mouth. *S. serratodentata*, although occurring within the continental-shelf area, was dominant only along the edge, above the 100 fathom line. *S. lyra* was entirely restricted to the edge of the continental shelf and was never dominant.

*Muggiaea atlantica* occurred mainly in the mouth of the English Channel and was seldom taken far to the west of the Scillies except in June 1939. Its distribution in April 1937 and 1939 appeared to show a correlation both in extent and numbers with an inflow into the Channel mouth of low salinity water ($<35{\cdot}10$ ‰) from the Ushant area. In April 1938 when there was scarcely any inflow of fresh water into the southern half of the Channel mouth, it was entirely absent from this region.

A paper on the distribution of the pelagic young stages of teleosteans other than the mackerel is in course of preparation, and it is hoped that the plankton collections will yield sufficient material to enable the life-cycle of *Sagitta serratodentata* to be worked out.

### *Fauna of the Sea-floor*

Mr D. P. Wilson has made further observations on polychaetes and has been successful in rearing for the first time a member of the family Opheliidae, *Ophelia bicornis* Sav. which has a pelagic development lasting normally about two weeks. The early larva is a small trochosphere with a large apical tuft, a broad prototroch and a small telotroch. At metamorphosis it has three bristle segments and is provided with a number of papillae which enable it to cling firmly to solid objects such as sand grains. This seems to be an adaptation to settlement on sand banks swept by swift tidal currents, as are those of Exmouth where the species is plentiful. The adult lives in very clean moderately coarse sand and striking results were obtained when larvae ready to metamorphose were tested with a variety of bottom deposits, natural and artificial. Briefly it can be stated that when given sand from the normal adult habitat larvae metamorphose readily, but much less readily, or not at all, when kept in vessels containing deposits of a different character. They retain the ability to metamorphose for several weeks. Further experiments to determine as far as possible the nature of the stimulus initiating metamorphosis will be undertaken during the next breeding season.

Mr Wilson published, in the *Journal*, Vol. XXVI, No. 3, an account of the capture of prey by *Sepia officinalis* L. This was illustrated by photographs revealing a number of points not previously recorded. The paper gives a fuller account of the hunting methods of this cuttlefish than has previously been available in the literature. Mr Wilson's observations on the triradiate and other forms of *Nitzschia closterium* (Ehr.) W. Sm. forma *minutissima* Allen and Nelson also appeared in the same number of the *Journal*.

During the year the National Oil Refineries Ltd., Neath, asked the Association for advice on methods of combating the ravages of *Teredo*, which had appeared in abundance towards the end of the war in the piles of the jetties and breasting blocks in their Queen's Dock at Swansea. Mr Wilson and Mr Steven, in January 1946, went to Neath to make an inspection on the spot. A full report was made to the Company who were advised to try the effect of detonating small explosive charges under water close to the piles. This was done and samples of blasted and unblasted timber sent to Plymouth showed clearly a very high death-rate among *Teredo* near the explosions, with no damage to the wood. Blasting was, therefore, carried out on an extensive scale and further samples have shown that the majority of the *Teredo* have been killed throughout the dock. It is evident, however, from examination of test-blocks that a source of infection still exists and further blasting to kill the young *Teredo* has been advised. Results obtained give reason to hope that *Teredo* attack can be kept at negligible intensity by regular and adequate blasting.

Mr G. M. Spooner has written up part of his studies on the distribution of *Gammarus* species in British estuaries, which will appear in Vol. XXVII, No. 1, of the *Journal*. This contribution deals mainly with the taxonomy of the species. Apart from attempting to fill existing gaps in detailed description of adult males, it was necessary to establish reliable means of identifying the females and immatures from mixed samples. This has been successfully accomplished. The useful, and unexpected, discovery (reported before the war) that the variable *G. zaddachi* can be separated into two distinct morphological forms, with different salinity optima, has necessitated some detailed additions to existing descriptions of this species. The two forms are separated as subspecies: *G. z. zaddachi* the more hairy form (embracing the 'freshwater' and 'intermediate' forms of Sexton) is retained as the typical subspecies, from which *G. z. salinus* ('brackish water' form of Sexton) is separated. The variation due to environmental influences must at least be more limited than has previously been supposed. However, within *G. z. zaddachi* itself there is appreciable variation in the density and length of hairs, and it is still possible that populations breeding in pure fresh water (e.g. River Elbe and North Ireland) may prove to belong to a distinct race: though they cannot be absolutely separated from the hairiest of animals living at the heads of estuaries.

The next contribution will deal with the population samples from different estuaries. The changes in the *Gammarus* population follow closely the salinity gradient, oscillating with it between winter and summer conditions, and (where the tidal zone is broad) showing comparable differences between the upper part of the tidal zone and low water. The *Gammarus* population can therefore serve as a 'biological indicator' for salinity conditions.

Another aspect of the work involves experimental observations on living *Gammarus zaddachi* in the laboratory. As reported before the war, preliminary observations had indicated that the 'brackish water form' of *G. zaddachi*, now named subspecies *salinus*, was incapable of breeding with the typical 'hairy' form of the species. A detailed experiment to verify this important conclusion was carried out this year, and the summer months were devoted to this experiment almost exclusively. The results confirm completely that the two forms are sterile to one another, whichever way the cross is made. The eggs may pass through the early stages of segmentation, but they never produce embryos. An equal number of control matings were made concurrently, and the animals were given turns in crosses and controls. At the same time further evidence has been obtained that the similar forms from different estuaries are normally fertile with one another.

Further experiments in hand are designated to test other preliminary observations which have shown that the two subspecies retain their diagnostic characters whatever the salinity of the water in which they are reared.

To supplement the morphological work on British species, a useful collection of samples from northern Europe, kindly lent by the late Dr K. Stephensen of Copenhagen, has been examined.

Mrs E. W. Sexton has continued her work on the Amphipod species *Jassa falcata* (Mont.). She has traced its history from its establishment in 1808, through its many changes of name, generic as well as specific, which have caused so much confusion. The diverse developmental forms, described by different observers as new species, have been shown to be only the growth stages of the one species. It is a littoral or sub-littoral species, with a wider distribution than any other amphipod yet known to science. Its records, ranging from the coasts of Norway to the Antarctic, have been investigated, and are given with the names of the authors responsible for them.

Mr H. G. Vevers has started investigations on some aspects of the breeding biology of the Plymouth echinoderms. It is already well known that after the breeding season echinoderm gonads in general undergo a marked atrophy accompanied by phagocytosis, and a detailed study is now being made of the histological changes occurring in the gonads of a number of echinoderms at different times of the year. The present investigation and later experiments are designed to throw some light on the factors controlling the various phases of the breeding cycle in this group. The relationship between temperature and the breeding cycle is still by no means clear. More attention should be paid to other factors, e.g. chemical or nutritional, which may enter into the problem. Concurrently with this work data are also being collected on the sex ratio of populations of echinoderms, and here again the observations collected at different times of the year are being recorded separately, as there is evidence from the work of a French author that, in at least one species (an Echinoid), the sex ratio varies according to season.

A review is being prepared of existing knowledge on sexual dimorphism in echinoderms (apart from that associated with brood protection), and observations are being made on a number of species to determine whether sexually dimorphic characters exist. Such characters are already known and easily demonstrable in *Psammechinus miliaris* and *Echinocyamus pusillus*, and in view of the many uses to which the genital products of echinoderms are put in experimental work it is desirable that satisfactory methods should be found of sexing the individuals of as many echinoderm species as possible, without killing the animals. A fairly satisfactory method has already been found of sexing ripe *Ophiothrix fragilis* without permanent injury to the animals themselves.

Preliminary work is also being done on a method of administering natural and synthetic sex hormones to Crustaceans, with a view to tracing the effect of these substances on the morphogenesis of sexually dimorphic characters in this group.

### *Physiology of Marine Animals*

Dr J. F. Danielli, who left the staff in October 1946, has been developing new methods for cytochemistry, particularly for the cytological localization of tryptophane, phenols, histidine and nucleic acid. These methods have been used in the study of chromosome structure. They show that the greater part of the nucleic acid, histidine, tryptophane and tyrosine of chromosomes is concentrated in the chromomeres. Under his direction Miss J. Lorch has been studying mechanisms of bone formation in fishes.

### *Fishes and Fisheries*

Supplementary to his work on vertebral variation in teleostean fishes, Mr E. Ford has been studying the variation in the form of the neurocranium in gadoid species. The gadoid fishes were chosen because a good representative collection of skulls, prepared before the war, had escaped damage when the laboratory was wrecked by bombing. Mere cursory comparison between the skulls of the different species showed that they had much in common, and it was thought that it would be instructive to determine whether, by following the method of transformations suggested by D'Arcy Thompson in *Growth and Form*, one could arrive at some one basic gadoid form of neurocranium. There arose, however, the practical difficulty of finding a method of orientating in space such a complex figure as the outline of a fish's skull. The one eventually adopted was to mark dots in indian ink at what appeared to be the natural centres of symmetry for each of the individual bones of the neurocranium, as indicated by the radial striations and concentric growth rings. Having done so, the dots were seen to be disposed in an orderly, geometric network. Investigation of the geometry of this network in the cod most strongly indicated that it conformed very well to an hexagonal system of symmetry. This indication has been followed up, with interesting results, on the hypothesis that the skulls of other gadoid species conform to the same system of symmetry as seen in the cod.

Mr G. A. Steven has been writing up the results of Mackerel Researches carried out from this laboratory before the outbreak of the war. Extremely interesting and important information on the migrations of this fish are emerging from the work. It has been found that mackerel of the English Channel, Irish Sea and Celtic Sea areas have only one main spawning ground in the open sea about 100 miles west of the Scilly Islands. After spawning they disperse all along the shores until late autumn when they concentrate in restricted and localized positions on the sea-floor. These concentrations take place in the close vicinity of well-defined irregularities in the level of the sea-bottom—e.g. acclivities caused by raised banks such as the Vergoyer at the entrance to the Dover Straits, and declivities provided by sharp depressions such as the Hurd Deep, in the English Channel—and are independent of depth. Some fish therefore remain at suitable places in the English Channel, others near the Smalls and Saltees on either side of St George's Channel. Still more seek bottom around the many banks and deeps in the Celtic Sea, and many—perhaps the great majority—concentrate along the edge of the continental slope itself. In spring they all rise and become pelagic again and migrate to the spawning ground. Thus fish converge on this ground from all directions in the spring; and there is not a simple anadromous migration from deep to shallow water to spawn as has previously been thought.

Data on age, growth-rate, and spawning habits are also being worked up.

In the course of the year two Reports, originally submitted to the Sierra Leone Government during the war, have been partly rewritten for publication by the Crown agents for the Colonies.

### *Research on Parasites*

During the year Miss N. G. Sproston has continued her researches on marine parasites. *Ichthyosporidium hoferi*, the fungoid organism causing disease in mackerel and pilchard, has received further study regarding its effects on the fish. A decline in the mackerel fishery has restricted samples from all sources this year; but some mackerel have been obtained from time to time from the Torry Research Station, Aberdeen, and a visit was made to Newlyn where a large sample of fresh pilchard was examined. The results from the Scottish mackerel agreed with those from locally caught fish in showing a remission in both the intensity and the incidence of this pathogenic infection as the season advanced; this is the first time a sustained and generalized remission in the endemic has been found since the disease was first noted in mackerel at Plymouth in 1940. The similar disease in pilchard showed a comparable remission, though the percentage of infection was not reduced so markedly as in the mackerel.

During the examination of these fishes the usual metrical data have been collected, partly for analysis of the factors correlated with the disease, and partly for the use of Mr G. A. Steven in his long-term investigations on the mackerel stock. The data thus accumulated since 1940 have been treated statistically by Mr G. M. Spooner who has confirmed the results of the preliminary graphical analyses, that there is no significant change in the condition factor of the mackerel associated with the severity of the disease: a fact difficult to explain in view of the extensive necrosis of the vital organs when the infection is active. In addition, there have emerged from Mr Spooner's statistical analysis certain other facts associated with the condition factor of this fish, which it is thought will have significance in the study of other species.

Investigations on the parasitic fauna of fishes have been continued, and include the examination of some rare visitors to these coasts. Some sea-birds have also been examined, with a view to tracing the adults of larval parasites occurring in fishes. During the year some sixty species of Helminth and Crustacean parasites have been found which require reinvestigation, and some of these will undoubtedly prove to be new to science. A study is now in progress on the phyllobothriid cestodes of selachians—up till now rather poorly represented in our fauna, but recent dissections have provided a wealth of material.

The long work on the monogenetic trematodes has now been published in the *Transactions of the Zoological Society of London.*

Miss Sproston left Plymouth at the beginning of March 1947, to take up an appointment as Research Fellow in the Academia Sinica, Shanghai.

### *Research on Algae*

Although the mass of data collected by Dr M. W. Parke has not yet been fully worked up, many interesting facts have already emerged. The study of *Laminaria saccharina* has been completed. This is the shortest lived of perennial British Laminariaceae, reaching its peak of growth during the second year and not surviving much beyond three years.

There is evidence that the gametophyte generation can be fertile throughout the year and may itself under certain conditions be perennial. The sporophyte generations can be initiated at any time of year, but under certain circumstances—e.g. in the exposed littoral zone—they may not persist to maturity, nor do winter-developed sporophytes occur in the sublittoral zone. The bulk of the population found on the shore at any time of year consists of spring-developed plants.

Although the sporophyte shows continuous growth throughout life there are alternating periods of rapid and slow growth. Growth is most rapid from January to July gradually increasing until March, remaining at a maximum until May or June and gradually slowing down to a minimum during the period September to December. Rate of growth also shows variations according to age and habitat.

These changes in rate of growth are shown as light and dark rings in sections of the perennial stipe and holdfast, the darker rings representing the slow growth. These rings form a valuable index of the age and growth of a plant.

The development of the new series of haptera in the holdfasts takes place during the period of rapid growth, although the beginning of new meristematic tissue above the old haptera can sometimes be detected as early as November. The detachment of plants during their third year is probably because new haptera are rarely formed in that year of growth.

The fruiting of the sporophyte appears to depend on the age of the tissue surviving on the distal part of the frond, which must be at least 6 months old. The age of the distal frond tissue appears to be controlled by the time of initiation of the plant and the nature of its habitat.

In British waters *L. saccharina* plants can become mature when eight to nine months old, and fruiting plants can be found at all times of year with a maximum from October to February.

### The Library

The thanks of the Association are again due to numerous foreign Government Departments, and to Universities and other Institutions at home and abroad for copies of books and current numbers of periodicals presented to the Library, or received in exchange for the *Journal*. Thanks are also due to those who have sent books or reprints of their papers, which are much appreciated.

### Published Memoirs

Vol. XXVI, No. 3, of the *Journal* of the Association was published in July 1946, and Vol. XXVI, No. 4, is nearing completion.

The following papers, the outcome of work done at the laboratory, have been published elsewhere than in the *Journal* of the Association:

ATKINS, W. R. G., 1945. Daylight and its penetration into the sea. *Trans. Illuminating Eng. Soc.* (London), Vol. X, No. 7, pp. 1–12.

FOX, D. L. & PANTIN, C. F. A., 1941. The colours of the plumose anemone *Metridium senile* (L.). *Phil. Trans. Roy. Soc.* Ser. B, Vol. CCXXX, pp. 415–50.

FOX, D. L. & PANTIN, C. F. A., 1944. Pigments in the Coelenterata. *Biol. Rev.* Vol. XIX, pp. 121–34.

FRETTER, VERA, 1946. The pedal sucker and anal gland of some British Stenoglossa. *Proc. Malacol. Soc.*, Vol. XXVII, pp. 126–30.

HALL, D. M. & PANTIN, C. F. A., 1937. The nerve-net in the Actinozoa. V. Temperature and facilitation in *Metridium senile*. *Journ. Exp. Biol.*, Vol. XIV, pp. 71–8.

HARVEY, H. W., 1946. *Fertility of the Ocean.* Discussion on Oceanography, Linnean Society of London, 1946, pp. 5–8.

HODGKIN, A. L. & HUXLEY, A. F., 1946. Potassium leakage from an active nerve-fibre. *Nature*, Vol. CLVIII, pp. 376–7.

LEBOUR, M. V., 1946. The Oyster, I. *School Science Review*, Vol. XXVIII, pp. 81–6.

LISSMANN, H. W., 1946. The neurological basis of the locomotory rhythm in the spinal dogfish (*Scyllium canicula, Acanthias vulgaris*). I. Reflex behaviour. *Journ. Exp. Biol.*, Vol. XXIII, pp. 143–61.

LISSMANN, H. W., 1946. The neurological basis of the locomotory rhythm in the spinal dogfish (*Scyllium canicula, Acanthias vulgaris*). II. The effect of de-afferentation. *Journ. Exp. Biol.*, Vol. XXIII, pp. 162–76.

LOWNDES, A. G., 1947. Recent work on flagellar movement. *Science Progress*, Vol. XXXV, pp. 62–8.

MOORE, J. GRANGE, 1947. The determination of the depths and extinction coefficients of shallow water by air photography using colour filters. *Phil. Trans. Roy. Soc.*, Ser. A, Vol. CCXL, pp. 163–217.

ROSS, D. M. & PANTIN, C. F. A., 1940. Factors influencing facilitation in Actinozoa. The action of certain ions. *Journ. Exp. Biol.*, Vol. XVII, pp. 61–73.

RUSSELL, F. S., 1946. What is Biology? *School Science Review*, Vol. XXVIII, pp. 69–79.

RUSSELL, F. S., 1946. *Marine Zoology*. Discussion on Oceanography, Linnean Society of London, 1946, pp. 8–10.

SANDERS, F. K. & YOUNG, J. Z., 1940. Learning and other functions of the higher nervous centres of *Sepia*. *Journ. Neurophys.*, Vol. III, pp. 501–26.

SMITH, J. E., 1946. The mechanics and innervation of the starfish tube foot-ampulla system. *Phil. Trans. Roy. Soc.*, Ser. B, Vol. CCXXXII, pp. 279–310.

SPROSTON, NORA G., 1946. A synopsis of the monogenetic Trematodes. *Trans. Zool. Soc.*, London, Vol. XXV, pp. 185–600.

THOMAS, H. J., 1944. Tegumental glands in the Cirripedia Thoracica. *Quart. Journ. Micro. Sci.*, Vol. LXXXIV, pp. 257–82.

WILSON, D. P., 1946. The seashore life of the British Isles. *Geographical Magazine*, Vol. XIX, pp. 264–71.

## Membership of the Association

The total number of annual members on 31 March 1947 was 351, being 27 more than on 31 March 1946. The number of life members was 61. The number of associate members is now four, Sir Joseph Barcroft, F.R.S., having died during the year.

## Finance

*General Fund.* The thanks of the Council are again due to the Development Commissioners for their continued support of the general work of the laboratory.

*Private Income.* The Council gratefully acknowledge the following generous grants and donations for the year:

From the Fishmongers' Company (£500), the Royal Society (£50), British Association (£50), Physiological Society (£30), Magdalen College, Oxford (£25), and the Cornwall Sea Fisheries Committee (£10). The following sums have also been received as rentals of tables in the laboratory: the Universities of Cambridge (£105), London (£105), Oxford (£52. 10*s*.), Bristol (£25), Birmingham (£15. 15*s*.), Manchester (£10. 10*s*.), Leeds (£20), Nottingham (£10. 10*s*.), Leicester (£10. 10*s*.), Exeter (£10. 10*s*.), Sheffield (£5), the Ray Lankester Fund (£20) and the Imperial College of Science and Technology (£10).

## President, Vice-Presidents, Officers and Council

The following is the list of those proposed by the Council for election for the year 1947–48:

*President*

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

*Vice-Presidents*

The Earl of Stradbroke, K.C.M.G., C.B., C.V.O.
The Earl of Iveagh, C.B., C.M.G.
Viscount Astor
Sir Nicholas Waterhouse, K.B.E.
Sir Sidney Harmer, K.B.E., Sc.D., F.R.S.
Col. Sir Edward T. Peel, K.B.E., D.S.O., M.C.
The Rt. Hon. Sir Reginald Dorman-Smith
Prof. Walter Garstang, D.Sc.
The Rt. Hon. Tom Williams, M.P.

COUNCIL

*To retire in* 1948
Prof. C. M. Yonge, D.Sc., F.R.S.
Admiral Sir John Edgell, K.B.E., C.B., F.R.S.
Prof. J. H. Orton, D.Sc.
E. Baldwin, Ph.D.
G. P. Wells

*To retire in* 1949
G. E. R. Deacon, D.Sc., F.R.S.
Prof. J. E. Harris, Ph.D.
N. A. Mackintosh, D.Sc.
Edward Hindle, Sc.D., F.R.S.
R. S. Wimpenny

*To retire in* 1950
H. Cary Gilson
C. F. Hickling
Morley H. Neale
Prof. Lily Newton, Ph.D.
Prof. J. Z. Young, F.R.S.

*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., The Laboratory, Citadel Hill, Plymouth

The following Governors are also members of the Council:

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
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)

# THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM

## BALANCE SHEET 31st MARCH 1947

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|---|---|---|---|---|---|---|---|---|---|
| Sundry Creditors: | | | | | | | | | |
| Accrued Expenses | | | | 409 | 17 | 11 | | | |
| Subscriptions received in advance | | | | 31 | 9 | 0 | | | |
| Grant received in advance | | | | 125 | 0 | 0 | | | |
| Admiralty—Hire of R.V. 'Sabella' | | | | 1150 | 0 | 0 | 1716 | 6 | 11 |
| Bank Overdraft | | | | | | | — | — | — |
| Aquarium Guide Printing Fund: | | | | | | | | | |
| As at 31st March 1946 | | | | 22 | 8 | 6 | | | |
| | £ | s. | d. | | | | | | |
| *Add:* Sale of Aquarium Guides | 14 | 12 | 4 | | | | | | |
| Sale of Postcards | 7 | 6 | 0 | | | | | | |
| | | | | 21 | 18 | 4 | | | |
| Transfer to Aquarium Sinking Fund | | | | 10 | 17 | 1 | | | |
| | | | | 55 | 3 | 11 | | | |
| *Less:* Purchases | | | | | | | | | |
| Guides | 22 | 8 | 7 | | | | | | |
| Postcards | 32 | 15 | 4 | | | | | | |
| | | | | 55 | 3 | 11 | — | — | — |
| Aquarium Sinking Fund: | | | | | | | | | |
| Transfer from Income and Expenditure Account | | | | 343 | 1 | 0 | | | |
| *Less:* Transfer from Aquarium Guide Printing Fund | | | | 10 | 17 | 1 | 332 | 3 | 11 |
| Special Apparatus Fund: | | | | | | | | | |
| As at 31st March 1946 | | | | 10 | 4 | 11 | | | |
| *Less:* Expenditure | | | | 10 | 4 | 11 | — | — | — |
| E. T. Browne—Bequests Funds: | | | | | | | | | |
| Building Fund, as at 31st March 1946 | 1227 | 16 | 5 | | | | | | |
| Interest on Investment | 37 | 5 | 4 | 1265 | 1 | 9 | | | |
| Library Fund, as at 31st March 1946 | 1085 | 0 | 8 | | | | | | |
| Interest on Investment | 33 | 1 | 5 | 1118 | 2 | 1 | | | |
| Special Apparatus Fund, as at 31st March 1946 | 2466 | 1 | 5 | | | | | | |
| Interest on Investment | 74 | 15 | 11 | 2540 | 17 | 4 | | | |
| Scientific Publications Fund, as at 31st March 1946 | 1849 | 10 | 10 | | | | | | |
| Interest on Investment | 56 | 1 | 10 | 1905 | 12 | 8 | 6829 | 13 | 10 |
| 'Salpa' Depreciation Fund: | | | | | | | | | |
| As at 31st March 1946 | | | | 5899 | 15 | 8 | | | |
| *Add:* Amount receivable from Ministry of Transport on account of Hire | | | | 402 | 0 | 0 | | | |
| Interest on Investments | | | | 175 | 8 | 0 | 6477 | 3 | 8 |

| | | | | £ | s. | d. | £ | s. | d. |
|---|---|---|---|---|---|---|---|---|---|
| Boats and Equipment, at valuation as estimated by the Director at 31st March 1941 plus Additions at Cost: | | | | | | | | | |
| S/S 'Salpa' | | | | 2000 | 0 | 0 | | | |
| Motor Boat 'Gammarus': | £ | s. | d. | | | | | | |
| As at 31st March 1946 | 150 | 0 | 0 | | | | | | |
| Additions during the year | 50 | 0 | 0 | | | | | | |
| | | | | 200 | 0 | 0 | | | |
| Nets, Gear and General Equipment: | | | | | | | | | |
| As at 31st March 1946 | | | | 50 | 0 | 0 | 2250 | 0 | 0 |
| Laboratory Apparatus, Engines and Pumps, at valuation as estimated by the Director at 31st March 1941, plus additions a cost: | | | | | | | | | |
| As at 31st March 1946 | | | | 4300 | 0 | 0 | | | |
| Additions during the year | | | | 500 | 0 | 0 | 4800 | 0 | 0 |
| Library, at valuation by Mr [illegible] Trout in January 1941 plus additions [illegible]: | | | | | | | | | |
| As at 31st March 1946 | | | | 16070 | 0 | 0 | | | |
| Additions during the year | | | | 30 | 0 | 0 | 16100 | 0 | 0 |
| Stocks on Hand, as valued by th[illegible]irector: | | | | | | | | | |
| Specimens | | | | 600 | 0 | 0 | | | |
| Chemicals | | | | 250 | 0 | 0 | | | |
| Journals | | | | 400 | 0 | 0 | 1250 | 0 | 0 |
| Sundry Debtors. | | | | | | | | | |
| Sales of Specimen[illegible] | | | | 333 | 3 | 0 | | | |
| Ministry of Transpo[illegible]ire of S/S 'Salpa' | | | | 33 | 10 | 0 | | | |
| Ministry of Agricu[illegible]nd Fisheries—Fourth instalment of Gr[illegible]n Development Fund for 1945–6 | | | | — | — | — | | | |
| | | | | | | | 366 | 13 | 0 |
| Prepayments | | | | | | | 174 | 13 | 0 |
| Recoverable Expen[illegible] | | | | | | | | | |
| Research Fund—M[illegible]. Sproston: | | | | | | | | | |
| Expenditure | | | | 436 | 13 | 9 | | | |
| *Less:* Grant receive[illegible] | 262 | 10 | 0 | | | | | | |
| Balance at 31st [illegible]1946 | 8 | 5 | 11 | | | | | | |
| | | | | 270 | 15 | 11 | | | |
| | | | | | | | 165 | 17 | 10 |
| General Fund Investment, at market value as at 31st March 1931 of £352. 2*s.* 3*d.* 3% Local Loans, converted during the year to £352. 2*s.* 3*d.* 2½% Treasury Stock | | | | | | | 232 | 7 | 10 |
| (Market value at date £338. 0*s.* 7*d.*) | | | | | | | | | |
| E. T. Browne—Bequests Funds Investment, at cost: | | | | | | | | | |
| £6905. 3*s.* 6*d.* Conversion Loan 3% | | | | | | | 6829 | 13 | 10 |
| (Market value at date £7008. 15*s.* 0*d.*) | | | | | | | | | |
| 'Salpa' Depreciation Fund Investments, at cost: | | | | | | | | | |
| £590. 6*s.* 0*d.* 2½% Treasury Stock | | | | 506 | 10 | 9 | | | |
| £5823. 16*s.* 2*d.* Conversion Loan 3% | | | | 5937 | 2 | 11 | | | |
| (Market value at date £6477. 16*s.* 9*d.*) | | | | | | | 6443 | 13 | 8 |

|  |  |  |  |
|---|---|---|---|
| **REPAIRS AND RENOVATIONS FUND:** |  |  |  |
| As at 31st March 1946 |  | 501 17 6 |  |
| *Add:* Transfer from Income and Expenditure Account |  | 50 0 0 |  |
| Interest on Investment |  | 12 17 10 |  |
|  |  | 564 15 4 |  |
| *Less:* Transferred to 'Gammarus' Replacement Fund |  | 564 15 4 |  |
|  |  |  | — — — |
| **'GAMMARUS' REPLACEMENT FUND:** |  |  |  |
| Transfer from Repairs and Renovations Fund |  |  | 564 15 4 |
| **COMPOSITION FEES FUND:** |  |  |  |
| As at 31st March 1946 |  | 362 5 0 |  |
| *Add:* Fees Received |  | 110 5 0 |  |
|  |  |  | 472 10 0 |
| **RESEARCH FUND—P. S. B. DIGBY:** |  |  |  |
| Grant received |  | 229 0 0 |  |
| *Less:* Expenditure |  | 221 6 2 |  |
|  |  |  | 7 13 10 |
| **BIOLOGICAL INVESTIGATIONS ON ALGAE FUND:** |  |  |  |
| Grant received |  | 713 13 11 |  |
| *Less:* Balance at 31st March 1946 | 71 18 11 |  |  |
| Expenditure | 633 13 9 |  |  |
|  |  | 705 12 8 |  |
|  |  |  | 8 1 3 |
| **MACKEREL RESEARCH FUND:** |  |  |  |
| Grant received |  | 425 0 0 |  |
| *Less:* Expenditure |  | 415 4 1 |  |
|  |  |  | 9 15 11 |
| **BUILDINGS RECONSTRUCTION FUND:** |  |  |  |
| Received during the year |  | 1042 19 8 |  |
| *Add:* Transfer from Surplus Account |  | 1879 3 9 |  |
|  |  | 2922 3 5 |  |
| *Less:* Balance due at 31st March 1946 | 1400 0 0 |  |  |
| Expenditure | 150 0 0 |  |  |
|  |  | 1550 0 0 |  |
|  |  |  | 1372 3 5 |
| **CAPITAL RESERVE ACCOUNT:** |  |  |  |
| As at 31st March 1946 |  |  | 21688 8 2 |
| **SURPLUS ACCOUNT:** |  |  |  |
| As at 31st March 1946 |  | 4497 19 1 |  |
| *Add:* Excess of Income over Expenditure for the year |  | 801 3 7 |  |
|  |  | 5299 2 8 |  |
| *Less:* Transfer to Buildings Reconstruction Fund |  | 1879 3 9 |  |
|  |  |  | 3419 18 11 |
|  |  |  | £42,898 15 2 |

JOHN E. HARRIS
O. D. HUNT } *Members of the Council.*

|  |  |  |
|---|---|---|
| **'GAMMARUS' REPLACEMENT FUND INVESTMENT, at cost:** |  |  |
| £553. 8*s*. 6*d*. Conversion Loan 3% |  | 564 15 4 |
| (Market value at date £561. 14*s*. 6*d*.) |  |  |
| **COMPOSITION FEES FUND INVESTMENTS, at cost:** |  |  |
| £18. 8*s*. 6*d*. 2½% Treasury Stock |  15 15 0 |  |
| £447. 8*s*. 2*d*. Conversion Loan 3% | 456 15 0 |  |
| (Market value at date £471. 16*s*. 2*d*. |  | 472 10 0 |
| **CASH AT BANK AND IN HAND:** |  |  |
| Coutts and Company | 2650 3 6 |  |
| Lloyds Bank Limited | 547 11 5 |  |
| Cash in Hand | 50 15 9 |  |
|  |  | 3248 10 8 |
|  |  | £42,898 15 2 |

TO THE MEMBERS OF THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM:

We report that we have examined the above Balance Sheet with the Books of the Association and have obtained all the information and explanations we have required. Capital Expenditure on erection of Buildings on Land held on Lease from the War Department is excluded. Subject to this remark we are of opinion that the Balance Sheet is properly drawn up so as to exhibit a true and correct view of the state of the Association's affairs as at 31st March 1947 according to the best of our information and the explanations given to us and as shown by the books of the Association.

PRICE, WATERHOUSE & CO.
*Prudential Buildings, George Street, Plymouth.*
*15th May*, 1947.

## INCOME AND EXPENDITURE ACCOUNT FOR THE YEAR ENDED 31st MARCH 1947

| | £ | s. | d. | £ | s. | d. |
|---|---|---|---|---|---|---|
| To Salaries, including Association's Contributions to Superannuation and War Bonuses | | | | 10308 | 17 | 5 |
| ,, Laboratory and Boats' Crews' Wages, including National Insurance, Contributions to Superannuation Scheme, War Bonuses and Employers' Liability Insurance | | | | 8243 | 1 | 2 |
| ,, Upkeep of Library | | | | 366 | 14 | 3 |
| ,, Scientific Publications, less Sales | | | | 612 | 11 | 0 |
| ,, Upkeep of Laboratories and Aquarium, etc.: | | | | | | |
| Buildings and Machinery | 859 | 5 | 0 | | | |
| Electricity, Oil, Gas, Coal and Water | 499 | 4 | 1 | | | |
| Chemicals and Apparatus | 940 | 18 | 7 | | | |
| Fire Insurance, Tithe, Ground Rent and Rent of Store | 86 | 3 | 11 | | | |
| Travelling Expenses | 313 | 14 | 3 | | | |
| Stationery, Postages, Telephone, Carriage and Sundries | 624 | 11 | 3 | | | |
| Specimens | 187 | 15 | 1 | | | |
| Architect's Fee for Plans for Reconstruction of Buildings | — | — | — | | | |
| | | | | 3511 | 12 | 2 |
| ,, Expenditure in Connection with R.V. 'Sabella' | | | | 674 | 9 | 8 |
| ,, Maintenance and Hire of Boats: | | | | | | |
| Petrol, Oil, Paraffin, etc. | 173 | 19 | 7 | | | |
| Maintenance and Repairs with Nets, Gear and Apparatus | 373 | 3 | 6 | | | |
| Purchase of Materials for Nets, etc. for Sale | 349 | 7 | 5 | | | |
| Boat Hire and Collecting Expenses | 53 | 14 | 5 | | | |
| Insurances | 331 | 11 | 0 | | | |
| Hire of R.V. 'Sabella' | 1150 | 0 | 0 | | | |
| | | | | 2431 | 15 | 11 |
| ,, Bank Charges | | | | 34 | 12 | 2 |
| ,, Transfer to Repairs and Renovations Fund | | | | 50 | 0 | 0 |
| ,, Transfer to Buildings Reconstruction Fund | | | | — | — | — |
| ,, Transfer to Aquarium Sinking Fund | | | | 343 | 1 | 0 |
| ,, Balance, being Excess of Income over Expenditure for the year | | | | 801 | 3 | 7 |
| | | | | £27,377 | 18 | 4 |

| | £ | s. | d. | £ | s. | d. |
|---|---|---|---|---|---|---|
| By Grants: | | | | | | |
| Ministry of Agriculture and Fisheries Grant from Development Fund | 23111 | 12 | 0 | | | |
| Fishmongers' Company | 500 | 0 | 0 | | | |
| British Association | 50 | 0 | 0 | | | |
| Royal Society | 50 | 0 | 0 | | | |
| Physiological Society | 30 | 0 | 0 | | | |
| Cornwall Sea Fisheries Committee | 10 | 0 | 0 | | | |
| | | | | 23751 | 12 | 0 |
| ,, Subscriptions (excluding Subscriptions received in advance) | | | | 353 | 16 | 7 |
| ,, Donations | | | | 26 | 16 | 0 |
| ,, Fees for Tests of Materials (*less* £60 for Raft) | | | | 137 | 8 | 0 |
| ,, Sales: | | | | | | |
| Specimens | 1432 | 9 | 7 | | | |
| Photographs (*less* purchases) | 95 | 5 | 5 | | | |
| Fish | 125 | 11 | 5 | | | |
| Nets, Gear and Hydrographical Apparatus | 276 | 19 | 11 | | | |
| | | | | 1930 | 6 | 4 |
| ,, Table Rents (including University of Cambridge £105; London £105; Oxford £52. 10*s.* 0*d.*; Bristol £25; Leeds £20; Birmingham £15. 15*s.* 0*d.*; Manchester £10. 10*s.* 0*d.*; Leicester £10. 10*s.* 0*d.*; Nottingham £10. 10*s.* 0*d.*; Exeter £10. 10*s.* 0*d.*; Sheffield £5; Imperial College £10; Trustees of Ray Lankester Fund £20 and Ministry of Works £104) | | | | 800 | 17 | 7 |
| ,, Aquarium Receipts: | | | | | | |
| Admission Fees | 342 | 0 | 0 | | | |
| Donation | 1 | 1 | 0 | | | |
| | | | | 343 | 1 | 0 |
| ,, Interest on Investments | | | | 21 | 5 | 10 |
| ,, Sale of Dr M. V. Lebour's Book | | | | 4 | 17 | 6 |
| ,, Sale of 'Plymouth Marine Fauna' | | | | 7 | 17 | 6 |
| ,, Balance of Expenditure on War Damage Repairs written off in earlier years recovered from War Damage Commission | | | | — | — | — |
| | | | | £27,377 | 18 | 4 |

# THE GERMAN HYDROGRAPHIC JOURNAL

The Inter-allied Board of Directors of the German Hydrographic Institute, now functioning in Hamburg, propose soon to start the publication of a new journal, to be known as the *German Hydrographic Journal*. It will appear under the supervision of Dr G. Boehnecke, who is the German Director of the Institute, and will be edited by Dr Arnold Schumacher.

The *German Hydrographic Journal* will be the medium for the publication of articles on those branches of science which are the concern of the German Hydrographic Institute. These are: coastal and open sea surveying, nautical science, navigation, chronometry, terrestrial magnetism, ship's magnetism, nautical technics, tides, and physical and chemical oceanography—the latter inclusive of reports on sea-bottom geology and lithology. The journal will, in effect, so far as the subjects named are concerned, take the place of the former *Annalen der Hydrographie und Maritimen Meteorologie* which were published by the German Admiralty from 1873 to 1891, and thereafter by the Deutsche Seewarte up to 1944.

Maritime meteorology and climatology, being now the concern of the Meteorological Office for North-Western Germany, will receive attention in the new journal only in oceanographical connexions.

As far as possible, each issue will contain articles on a variety of the subjects named above, and will include also notices on hydrographic institutions and other related matters.

In addition, notices and/or reviews of publications of interest to the Institute will appear in the pages of the journal, together with a current bibliography relating to the special fields of research enumerated.

An ultimate aim is gradually to list all German and other publications of relevance which have appeared since autumn 1939, though such a bibliography cannot be compiled in proper time sequence.

# 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) 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 a research vessel 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.

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The Council of the Marine Biological Association wish it to be understood that they do not accept responsibility for statements published in this *Journal* excepting when those statements are contained in an official report of the Council.

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