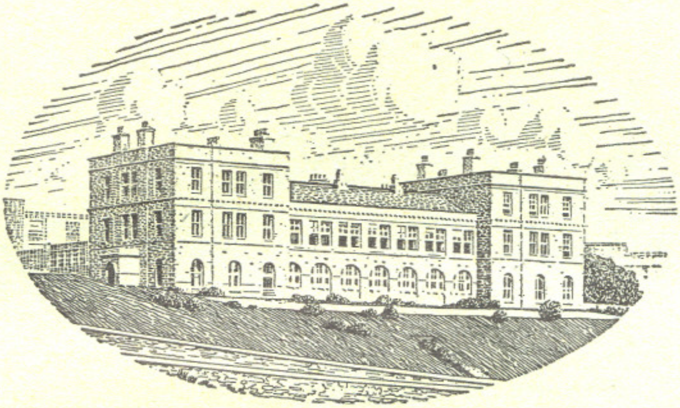
JOURNAL OF THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM



THE PLYMOUTH LABORATORY

VOLUME XXIII, No. 1

(*issued November 1938*)

CAMBRIDGE
AT THE UNIVERSITY PRESS
1938

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OBSERVATIONS ON BRITISH AND NORWEGIAN HYDROIDS AND THEIR MEDUSAE

By W. J. Rees, M.Sc.

Research Assistant at the Plymouth Laboratory

(Text-figs. 1–12)

CONTENTS

INTRODUCTION

This paper contains observations on British and Norwegian Hydromedusae made at Plymouth and Bergen respectively. Observations on *Campanulina paracuminata* n.sp., *Rhizorhagium album* n.sp., *Staurocoryne filiformis* Rees 1936 and on the hydroid of *Leuckartiara octona* (Fleming) were made at Plymouth during 1936 and 1937. The observations on the Norwegian forms are some of the results of a six weeks' stay at the Bergens Museum Biological Station at Herdla near Bergen.

The main object of my visit to Herdla was to work out the life history of *Perigonimus muscoides* M. Sars 1846. In addition to this life history, observations were made on several other interesting hydroids and medusae, of which the following species are described in this paper: *Leuckartiara abyssi* (G. O. Sars 1873), *Rhizorhagium roseum* M. Sars 1877, *Thamnostoma russelli* n.sp., *Corymorpha annulicornis* M. Sars 1859. Notes are included on *Stauridium productum* Wright 1858, and *Boreohydra simplex* Westblad 1937.

I am indebted to the Challenger Society for a grant to cover my expenses at Bergen. I also wish to express my thanks to the following: to Professor August Brinkmann, Director of the Biological Station at Herdla, who gave me every facility to pursue my work; to Amanuensis D. Rustad for much help in collecting material and in setting up special apparatus; to Dr Jöran Hult (Uppsala) for the use of his "sledge dredge" at Herdla and for material from Northern Norway. My thanks are also due to Mr F. S. Russell for helpful criticism at all times.

Bougainvillia muscoides (M. Sars 1846)

Synonym: *Perigonimus muscoides* M. Sars 1846.

This species was first described by Michael Sars (1846) as *Perigonimus muscoides*. He found it growing on the test of *Ascidia mentula* Linn. and on the tubes of *Tubularia indivisa* from depths between 20 and 30 fathoms in the Mangerfjord. It has since been found by a number of investigators from Scandinavian seas and the hydroid is accurately figured by Jäderholm (1909). Stechow (1923) has described a closely related species from the Mediterranean under this name. A careful comparison of the descriptions of this hydroid and those of better known so-called "*Perigonimus*" hydroids convinced Stechow that the latter were not cogeneric with the genotype, *P. muscoides*. Rees & Russell (1937) accepted Stechow's revision in part and accordingly removed certain species from *Perigonimus*. Further revision of the British species was impossible without knowing for certain what the medusa of *P. muscoides* was, and it was this which prompted me to go to Bergen to search for it.

During my stay at Bergen numerous colonies of this hydroid were found and its medusa proved to be a *Bougainvillia*. *Perigonimus* therefore becomes a synonym of *Bougainvillia*, and the species must henceforth be called *B. muscoides* (M. Sars 1846).

B. muscoides was found on the first day of my stay at Herdla. It was taken at Bognøstrømmen in the Mangerfjord living on the test of *Ascidia mentula* Linn. dredged from depths between 10 and 80 m. It was in this fjord that Sars originally found the species growing on *Ascidia mentula* and on the tubes of *Tubularia indivisa*.

Below are given my records of this hydroid:

2. viii. 37. Bognøstrømmen, Mangerfjord. Four colonies, on four out of five specimens of *Ascidia mentula* dredged between 10 and 80 m. One colony had medusa buds and a few medusae were liberated in the laboratory on the same day.

6. viii. 37. South of North Bratholmen, Hjeltefjord, *ca.* 100 m. One small poorly developed colony, with a few medusa buds, growing on *Sertularella gayi*.

19. viii. 37. Bognøstrømmen, Mangerfjord, 40–50 m. A large well-developed colony, with numerous medusa buds, growing over the stems of *Tubularia indivisa*. A colony of *Rhizorhagium roseum* M. Sars was growing over both hydroids.

THE HYDROID. The colonies consist of upright rhizocaulome formations arising at intervals from a network of stolons running over the test of the ascidian or over the tubes of the *Tubularia*. The appearance of the colonies is quite distinct from other Norwegian hydroids. The upright branches are thicker and less branched, and the secondary branches are shorter and fewer than in young stages of other *Bougainvillia* hydroids. Sars gives an excellent coloured figure of the living hydroid and Jäderholm (1909) gives a good figure of the rhizocaulome formation.

The stems reach a height of 2 cm. and are covered by a chitinous perisarc. When the colony is young only the central tube is present. This thickens in diameter with age, and stolons from the base creep up along it on all sides so that there may be four to seven auxiliary tubes in addition to the main stem. A thick polysiphonous rhizocaulome is thus formed (Fig. 1 *a*). A similar condition has been described by Browne (1907) in *Bimeria biscayana*.

The central tube is 0·25–0·3 mm. in diameter and the auxiliary tubes are 0·1 mm. Both can give rise to hydranths. The polyps are somewhat irregularly distributed; they may occur terminally, at the ends of branches or laterally on short stems; sessile polyps also occur on the rhizocaulome itself. The hydranths are typical of *Bougainvillia*, with a prominent conical hypostome and a whorl of filiform tentacles. The terminal hydranths are usually the largest, 0·5–1·0 mm. in length and 0·2–0·3 mm. in diameter. The lateral hydranths (Fig. 1 *a*) are smaller and have eight to eleven tentacles, a feature also noted by Sars (1846). Unless the colony was very old the terminal hydranth originated from the central tube. In some of the oldest colonies seen, however, the coenosarc of the central tube had disappeared and a new terminal hydranth had developed from an auxiliary tube.

The perisarc of a stem supporting a hydranth may be slightly wrinkled and enlarges a little distally to form a slight cup into which the posterior third of the hydranth can contract. The coenosarc narrows gradually below this point to form a thin tube. The smallest hydranths, which are almost sessile on the rhizocaulome, arise from the sides of the central and auxiliary tubes. Their stalks are usually thin and have about the same diameter as the auxiliary tubes. These hydranths appear to be young ones in which the stalk later becomes much thicker and longer.

The most remarkable feature of this hydroid is the great number of medusa buds. These arise directly from the rhizocaulome and its branches (Fig. 1 *a*). They are frequently situated in rows on the auxiliary tubes and are almost sessile, having only very short stalks. A fruiting colony with its reddish polyps and the red and white medusa buds is a beautiful object when seen under a low-power lens. The largest buds are 0·4 mm. long by 0·3 mm. in diameter. When the medusa bud is almost fully developed the reddish manubrium and the brownish bulbs of the four tentacles show clearly through the thin hyaline perisarc which protects the bud. The last structures to develop in the bud are the four single oral tentacles on the manubrium. Sars' original colony had medusa buds, but these were not quite fully developed, and the bud which he pressed out of its envelope (Sars, 1846, tab. 1, fig. 21) showed the manubrium and the four marginal tentacles, but not the four oral tentacles.

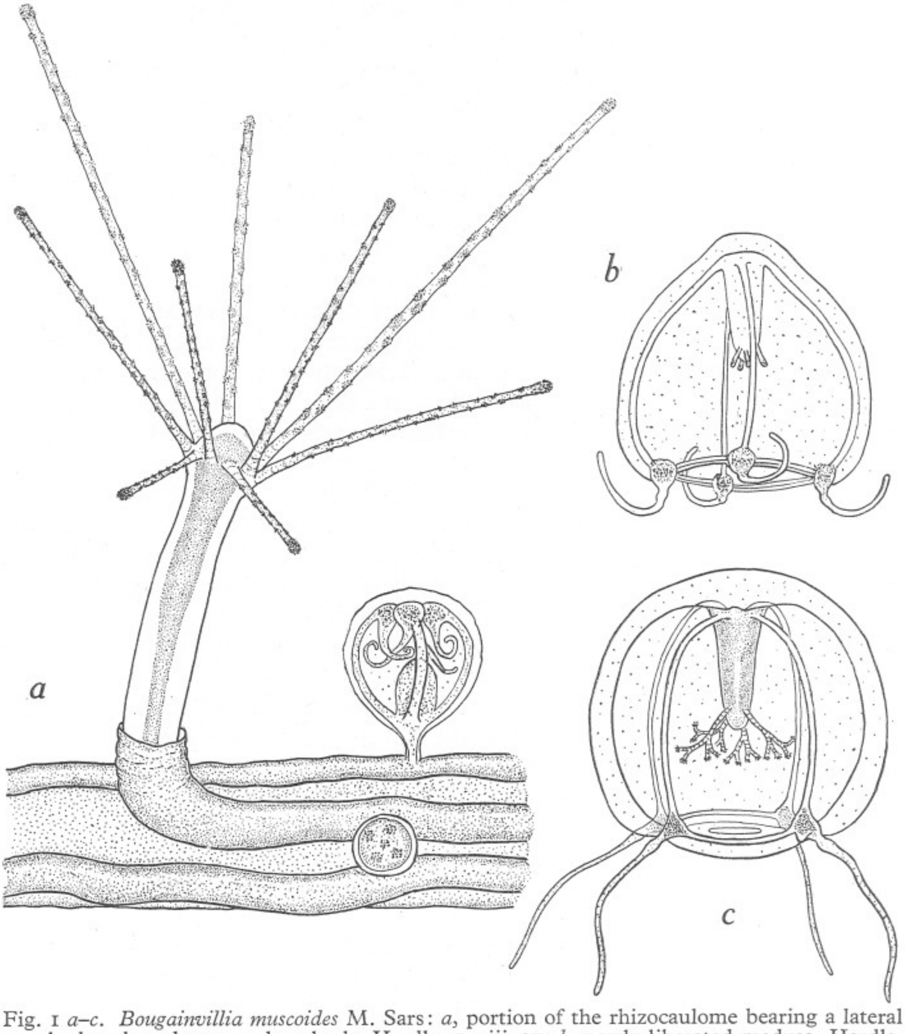

Fig. 1 *a–c*. *Bougainvillia muscoides* M. Sars: *a*, portion of the rhizocaulome bearing a lateral hydranth and two medusa buds, Herdla, 7. viii. 37; *b*, newly liberated medusa, Herdla, 3. viii. 37; *c*, young medusa obtained from the plankton in the Hjeltefjord, 30. viii. 37.

Allman (1863) was thus led to believe that the medusae were of a similar type to those of *Atractylis repens* (Wright, 1857) and accordingly placed this and other similar species in *Perigonimus*. Later authors, with the exception of Stechow (1923) and Rees & Russell (1937), have followed Allman and have referred this species to the Pandeidae (Tiaridae).

The newly liberated medusa (Fig. 1 *b*) is bell-shaped, as high as wide, with a diameter of 0·55–0·65 mm. The jelly is thin, but thicker nearer the apex than elsewhere, and there are numerous scattered nematocysts on the exumbrella. The velum is well developed. The stomach is short and conical, barely reaching to half the height of the subumbrellar cavity. Four unbranched oral tentacles, 0·07 mm. in length, with a few terminal nematocysts, arise above the mouth margin. The four radial canals and ring canal are narrow. There are four well-developed perradial bulbs, each with a single tentacle. There is a slight swelling at the base of each tentacle just before it joins the bulb, and this appears to be characteristic of this medusa. There are no ocelli. The reddish colour of the manubrium, so conspicuous in the bud, is less brilliant in the newly liberated medusa, but the reddish brown pigment in the tentacle bulbs is quite distinct. The oral tentacles of one medusa kept for a few days in the laboratory were beginning to branch. This medusa measured 0·85 × 0·8 mm.

I obtained a young medusa (Fig. 1 *c*) from plankton from the Hjeltefjord on August 30 1937. This was in a later stage of development than those I had been able to rear. The medusa was immature and measured 1·55 mm. high and 1·65 mm. in diameter. The oral tentacles on the manubrium were twice dichotomously branched. On each marginal bulb there was a rudiment of a second tentacle developing on the right side of the existing one. Each marginal tentacle possessed the characteristic swelling at its base near the bulb. There were no ocelli. The colour of the manubrium varied from reddish orange to red, and the tentacle bulbs were yellowish brown.

The medusa was identified as *Bougainvillia nordgaardi* (Browne). Kramp & Damas (1925) have described various stages in the development of this medusa. My medusa from the plankton corresponds to their Stage 2. The stage which Kramp & Damas call Stage 1 is a medusa several days old in which the oral tentacles have become branched. Their medusa appears to have lost its four tentacles.

The similarity between the medusa taken from the plankton and those reared from the hydroid points to the extreme probability that the medusa of *B. muscoides* is *B. nordgaardi* (Browne).

SYSTEMATIC DISCUSSION ON *PERIGONIMUS*

The discovery that the medusa of *Perigonimus muscoides* is a *Bougainvillia* is of considerable importance in the classification of those species which have up to now been referred to the genus *Perigonimus*. It necessitates the revision of all so-called "*Perigonimus*" hydroids because *Bougainvillia muscoides* was the genotype of *Perigonimus*.

Since *Bougainvillia* is the older generic name, *Perigonimus* becomes its synonym and the latter name can no longer be used for those species of "*Perigonimus*" whose medusae are not Bougainvillids. Stechow (1923) expressed the opinion that *P. muscoides* was not cogeneric with the other species of "*Perigonimus*" then referred to the genus, and accordingly restricted the name *Perigonimus* to this species and included provisionally also *Bimeria biscayana* Browne 1907. He proposed the use of the medusa name *Leuckartiara* Hartlaub 1914 for the hydroids producing medusae with two opposite tentacles. Two of these species have since been removed to the genus *Amphinema* Péron & Lesueur 1809 by Rees & Russell (1937). The advisability of using the generic name *Leuckartiara* will be discussed under the account of this genus.

Any revision of the genus *Perigonimus* in its widest sense must also include the genera *Atractylis* Wright 1858, *Wrightia* Allman 1872, *Dinema* van Beneden 1866, *Rhizorhagium* M. Sars 1877, *Gravelya* Totton 1930, and to a certain extent *Bougainvillia* Lesson 1836. It is necessary to clarify the position of these forms with fixed gonophores at present referred to some of these genera.

The differences between the trophosomes of *Bougainvillia* and *Leuckartiara* are very slight. Usually the *Bougainvillia* hydroid is more branched, but there are exceptions, and the presence of a dilatation of the perisarc around the base of the hydranth in many species of *Bougainvillia* makes them very difficult, if not at present impossible, to distinguish from *Leuckartiara*. However, their medusae belong to the Bougainvilliidae and the Pandeidae. To which of these families are we to refer the non-medusa-bearing forms? Our knowledge of many of these is very incomplete at the present, and it would be inadvisable to put them into either *Leuckartiara* or *Bougainvillia*. The only alternative is to put them into a genus of their own until their exact systematic position can be ascertained.

There are several generic names which come under consideration. Allman (1872) restricted the genus *Atractylis* Wright 1857 to *A. arenosa* Alder (1862), which has fixed gonophores. Later he discarded *Atractylis* because it was preoccupied by a plant of that name. In its place he erected his genus *Wrightia*, although he knew it was preoccupied by *Wrightia* Agassiz (1862), a genus synonymous with *Campanulina* van Beneden which had priority over it. Totton (1930) has selected *Atractylis ramosum* (= *Bougainvillia ramosum*) as the genotype of *Atractylis*, so that this genus is now sunk under *Bougainvillia* Lesson.

The oldest valid* generic name is *Rhizorhagium* M. Sars 1877, and this genus is discussed further below.

THE GENUS *RHIZORHAGIUM* M. SARS 1877

Synonyms: *Wrightia* E. S. Russell 1907.
Gravelya Totton 1930.

The genus *Rhizorhagium* was erected by Sars (1877) for a Norwegian species which he called *R. roseum*. He laid particular stress on the fixed nature of the gonophores as the chief character of his genus. Bonnevie (1898) described a new species, *Perigonimus sarsii*, which together with *Rhizorhagium roseum* she

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* *Dinema* van Beneden 1866 is preoccupied by *Dinema* Fairmaire 1849, an insect genus.

referred to the genus *Perigonimus*. Stechow (1923) referred the above, together with *Perigonimus antarcticus* Hickson & Gravely 1907 and *Atractylis coccineus* Wright (see Russell, 1907), to *Rhizorhagium*.

The last of these, as will be shown later, is in all probability identical with *R. roseum* Sars. For reasons already given (see p. 6) these species hitherto referred by some authors to "*Perigonimus*" must be kept separate from *Bougainvillia* and *Leuckartiara* until later work with living material reveals their exact systematic position.

Levinsen (1892) described *Rhizorhagium roseum* from Greenland as *Garveia groenlandica* (Broch, 1916). This raises the question whether all the above species should not be included in the genus *Garveia* Wright 1859. The chief characters of *Garveia* as defined by Allman (1872) were the well-developed branching hydrocaulus, the fusiform hydranth with a whorl of filiform tentacles around a conical proboscis, and reproduction by means of fixed gonophores borne on short stalks. Torrey (1902) united *Garveia* with *Bimeria* Wright 1859, a step which I cannot but regard as retrogressive (see p. 25). He referred *Perigonimus formosus* Fewkes, an unbranched form closely resembling *Rhizorhagium roseum*, to his genus "*Bimeria*".

The creeping hydrorhiza with the simple unbranched stems each bearing a single hydranth is characteristic of all these species with fixed gonophores previously referred to *Perigonimus*, and I feel hesitant in referring them to a genus such as *Garveia* where the hydrocaulus is typically a well-developed branched tree-like growth. For the present therefore it appears best to retain *Rhizorhagium* for the following species: *R. roseum*, *Perigonimus sarsii*, *P. antarcticus*, *P. formosus* Fewkes and a new species *Rhizorhagium album* to be described later.

The genus *Gravelya* was founded by Totton (1930) for *Perigonimus antarcticus* and was defined as follows: "Monoecious *Bougainvillidae* with numerous dimorphic cryptomedusoid gonophores scattered over the hydrorhiza." His genus clearly falls into the synonymy of *Rhizorhagium*. No stress can be laid on the word "Bougainvillidae" in his definition because the trophosome is distinctly like that of the hydroid of *Amphinema dinema*. Neither can the degree of development of the gonophore be stressed as a generic character; it is more suitable as a specific one.

The genus may be defined as follows:

Polyp stems, simple, unbranched and arising either from a creeping anastomosing hydrorhiza or from a weakly developed rhizocaulome formation; polyps clavate or fusiform with a single whorl of filiform tentacles around the base of a conical proboscis and partially retractile into a slight dilatation of the perisarc. Gonophores fixed, borne on short stalks on the hydrorhiza or on the rhizocaulome formation.

The above diagnosis does not differ in essentials from that of Sars. The specific characters of *Rhizorhagium roseum* which were included by Sars have been omitted and the definition of the genus emended so as to include *Peri-*

gonimus sarsii Bonnevie 1898 and *Rhizorhagium album* n.sp.; *Perigonimus antarcticus* falls naturally into the genus.

Rhizorhagium roseum M. Sars 1877

Synonyms: ? *Atractylis coccineus* Wright 1861.
Perigonimus roseus Bonnevie 1898.
Atractylis coccineus Russell 1907.
Wrightia coccineus Russell 1907.
Garveia groenlandica Levinsen 1892.
Perigonimus (*Rhizorhagium*) *roseus* Broch 1928.

This species I found at Herdla on several occasions. Colonies were found growing on *Tubularia indivisa* at Rong Sund and Bognøstrømmen. One colony from Bognøstrømmen was creeping over the stems of *Bougainvillia muscoides*.

The measurements of a fruiting colony are given below:

Measurements in mm.

Length of hydranth	0·4 –0·45
Diameter of hydranth...	0·3 –0·35
Length of hydrocaulus	3·0 –3·5
Diameter of hydrocaulus	0·12–0·2
Length of gonophore	0·9 –1·2
Diameter of gonophore	0·5 –0·75
Length of gonophore stalk	0·35–0·7

According to Broch (1916) the stalks may reach a length of 12 mm. in larger colonies. The tentacles vary from six to twelve in number. The whole colony when alive had a rosy colour. Sars (1877) and Jäderholm (1909) give excellent figures of this hydroid.

I can find no fundamental difference between the descriptions of the *Atractylis coccineus* described by Russell (1907) and *Rhizorhagium roseum*. Sars (1877) states that the gonophore is naked, while that of Russell's species is covered by a thin perisarc. A close examination of living material at Herdla revealed the presence of this thin perisarc. Broch (1916) also found a perisarc covering the gonophore, and states that it flays off when the gonophore is fully grown. The hydranth in *Atractylis coccineus* Russell is nearly always bent at an obtuse angle with the stalk, and the same characteristic has been figured for *Rhizorhagium roseum* by Sars & Jäderholm. It was also characteristic of all my colonies from Herdla. The habitat, the colour, the wrinkling of the perisarc, and the short-stalked gonophore are alike in both, and there seems little doubt that they are identical.

Whether this species is the same as the original *Atractylis coccineus* described by Wright (1861) is impossible to tell because the original description lacked a figure and no gonophores were found. It is therefore noted as a doubtful synonym of *Rhizorhagium roseum*.

The species is very common around the Norwegian coast and has been found in the White Sea and Novaya Zembla (Schydlowsky, 1901). It was first recorded from Greenland by Levinsen (1893) as *Garveia groenlandica*. A re-examination of the original specimen by Broch (1916) showed that the specimen in question should have been referred to *Rhizorhagium roseum*. Jäderholm (1909) has given an excellent figure and a list of Swedish records. There are numerous records from east and west Greenland (see Kramp, 1914, 1932 *a*, *b*). According to Fraser (1937) it is found on the Pacific coast of North America. To these we must add Russell's record from Millport on the west Scottish coast.

Rhizorhagium sarsii (Bonnevie 1898)

Synonym: *Perigonimus sarsii* Bonnevie.

This hydroid has only been recorded from Norway. Bonnevie found it at Christiansund, but states that it had been previously found in the Oslofjord by G. O. Sars and later by Greig at Bognøstrømmen in the Mangerfjord. It has since been found by Broch (1905), one colony on *Portunus depurator* and another on *Corystes cassivelaunus*. A redescription of this species from living material is much to be desired. Several points in Miss Bonnevie's description need amplifying and verifying. During my stay at Herdla I spent much time searching for this hydroid at Bognøstrømmen, but did not succeed in finding it. I did, however, find a colony of *Rhizorhagium roseum* growing over the stems of *Bougainvillia muscoides*. When alive the stolons of the two hydroids could easily be distinguished by their colour, but when preserved the stolons were indistinguishable. It appears possible to me that a well-developed colony of *Rhizorhagium roseum* growing over a dead colony of *Bougainvillia muscoides* could easily be mistaken for *Rhizorhagium sarsii*.

Rhizorhagium album n.sp.

A very small hydroid found by Mr F. S. Russell growing on small weeds in a rock pool at Newquay, Cornwall, has proved to be a new species. Mr Russell kindly gave me the hydroid to rear and describe. When found the hydroid appeared to be a creeping or a juvenile form of a *Bougainvillia* or a species of "*Perigonimus*". Styloid gonophores, however, were developed. The species could not be referred to any known species with certainty and has therefore been described as new. It approaches nearest to and may be identical with *Eudendrium pudicum* Van Beneden 1866. Van Beneden regarded his species as identical with *Trichydra pudica* Wright, which, however, is quite a different kind of hydroid from the one he figures. Gonophores were not observed by Van Beneden, and there is no certainty that his species is identical with mine. *Eudendrium pudicum* Van Beneden is therefore noted as a doubtful synonym. The systematic position of this species is discussed later in this paper.

Three small colonies were found on a filamentous alga. The polyps could be distinguished with the naked eye as minute white specks. The colonies were not reproducing and did not do so until they had been four months in captivity.

The stolons creep over the alga or over each other and sometimes branch (Fig. 2 *a*). They are covered by a thin transparent perisarc which is irregularly wrinkled. They are 0·1 mm. in diameter. The stems are very short, and sometimes the polyps are subsessile. The stems, like the stolons, are irregularly wrinkled and rarely exceed 0·3 mm. in length. The perisarc of the stems expands to form a close-fitting pseudohydrotheca around the base of the hydranth. How far it extends on the hydranth itself was very difficult to determine. The hydranths are tubular with a single whorl of six to ten filiform tentacles around a small but distinct hypostome (Fig. 2 *b*). The polyps vary from 0·35 to 0·55 mm. in length with a transverse diameter of 0·1–0·14 mm.

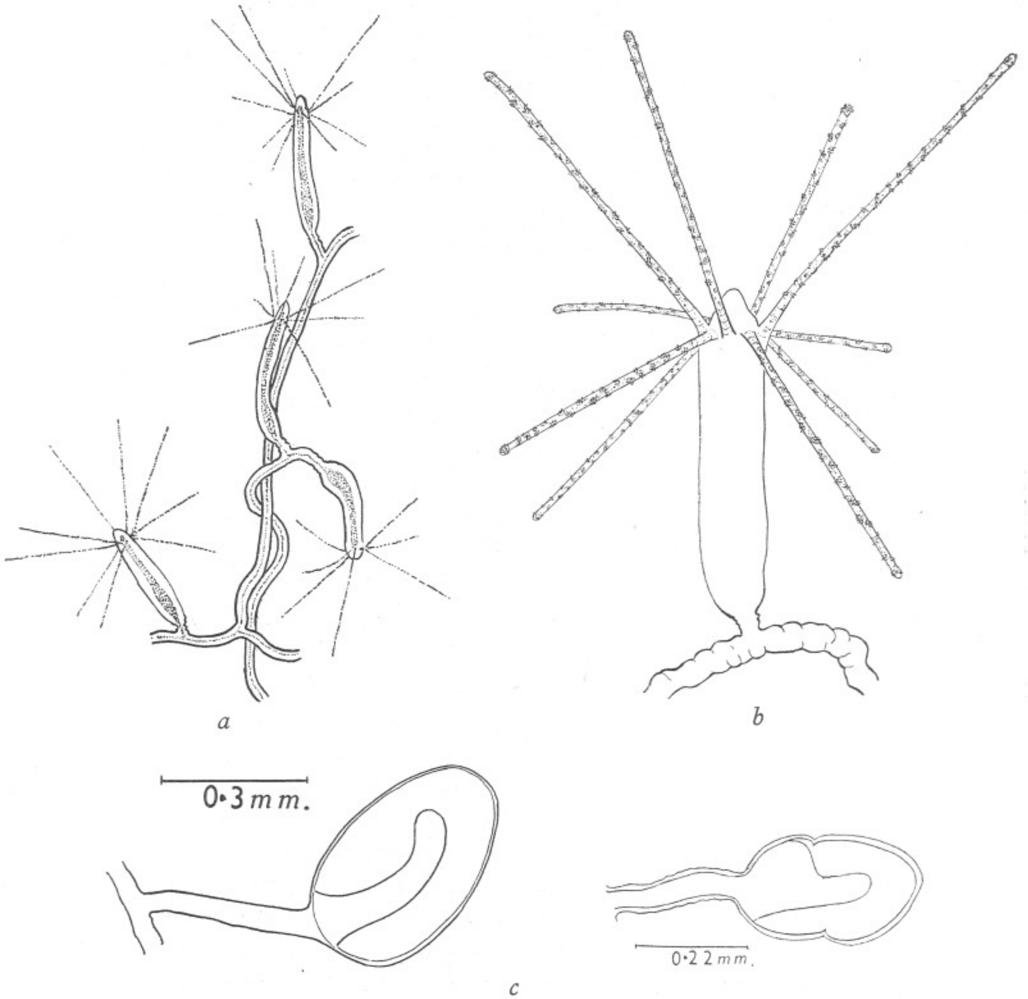

Fig. 2 *a–c*. *Rhizorhagium album* n.sp.: *a*, general appearance of a colony kept in the Plymouth Laboratory, 5. iv. 37; *b*, single hydranth, 6. iv. 37; *c*, male gonophores.

The polyps themselves are white in colour with a light brown endoderm. Gonophores were observed developing on April 3 1937. These were fully developed seven days later. Others were developed later in the year. On all three colonies only male gonophores were developed (Fig. 2 *c*). These were typical styloid gonophores borne on fairly long stalks 0·3–1·0 mm. long. The largest gonophore seen had a diameter of 0·4 mm.

This species differs in many characters from other species now placed in *Rhizorhagium*. The hydranths are almost sessile, and the gonophores stalked, as compared with the long-stalked hydranths and almost sessile gonophores in typical species of *Rhizorhagium*. Owing to the unsatisfactory state of our knowledge of the *Bougainvillia-Leuckartiara* type of hydroids I feel hesitant in erecting a new genus to take this species and provisionally therefore include it in *Rhizorhagium*.

The following is a concise definition of the new species:

Rhizorhagium album n.sp. (Fig. 2)

Synonym: ? *Eudendrium pudicum* van Beneden 1866.

Stems and stolons covered by a distinct, irregular, and sometimes faintly wrinkled perisarc. Hydranths tubular with a whorl of six to ten filiform tentacles around a bluntly conical proboscis and borne on very short hydrocauli.

Gonophores: male gonophores are styloid, borne on distinct stalks. Female gonophores unknown.

Distribution: Newquay, coast of north Cornwall.

THE GENUS *LEUCKARTIARA* HARTLAUB 1914

Hydroid Synonyms: *Atractylis* Wright 1858 (in part).
Perigonimus Allman 1863 (in part).
Dinema van Beneden 1866.

The genus *Leuckartiara* was erected by Hartlaub (1914) for three species of pandeid medusae. The hydroids of this and allied genera had been referred by Allman (1863, 1864 *b*) and later workers to the genus *Perigonimus* Sars. It has been shown earlier in this paper that *Perigonimus* can no longer be used for hydroids of this type which produce pandeid medusae. Stechow (1923) has used the name *Leuckartiara* for hydroids of this type, which produce medusae with two tentacles. Great care, however, must be taken to use this name correctly, because a great many of the so-called "*Perigonimus*" hydroids produce medusae which do not belong to the medusa genus *Leuckartiara*; for example, *Perigonimus serpens* Allman 1863 is the hydroid of *Amphinema dinema* Péron & Lesueur. Apart from the hydroids at present referred to the genus *Amphinema*, the only two hydroids, producing pandeid medusae, whose life histories are known with certainty are *Perigonimus repens* (which is the hydroid of the medusa *Leuckartiara octona*) and *Perigonimus cirratus* Hartlaub 1914, of which the medusa is *Halitholus cirratus*. Both hydroid and medusa should be called *H. cirratus*.

Those species whose newly liberated medusae with two opposite tentacles are obviously pandeid medusae should, I think, be referred provisionally to *Leuckartiara* as "*Leuckartiara*" spp. *Perigonimus nudus* Stechow 1919 obviously has no affinities with *Bougainvillia* or *Leuckartiara*. Indeed, as Stechow himself observes it is probably related either to *Campanopsis*, *Hydranthea* or to *Halecium*; it needs a new generic name.

I have provisionally included *Perigonimus abyssi* G. O. Sars 1873 in *Leuckartiara* as *L. abyssi*.

The Hydroid of Leuckartiara octona (Fleming 1823).

The hydroid of *Leuckartiara octona* (Fleming) is best known by the name *Perigonimus repens* (Wright 1857). It is one of the commonest species occurring in British waters. The species is very variable in form, and this led earlier workers to regard certain types of growth as distinct species. The various descriptions of this hydroid are very scattered in the literature, and there is no single adequate description. It is therefore considered desirable to re-describe this species and to record the variations to which it is subject under different conditions of habitat. The medusa is well described by Hartlaub (1914).

HISTORICAL. The species was originally described by Wright (1857) as *Eudendrium pusillum*. He found it growing on the back and walking legs of spider crabs and on sertularians. At the same time he described another species, *E. sessile*, which he found growing on shells from deep water in the Firth of Forth and declared that the medusae on liberation seemed to be identical. It will be shown later in this paper that *E. sessile* is the creeping form of *E. pusillum*. A year later, in 1858, Wright refers to his *E. pusillum* as *E. repens*, though he gives no reason for the change of the name. A search through the literature reveals that a species of *Halecium* was described by Sars (1857) as *Eudendrium pusillum*. Perhaps this is the reason for the change of name.

In the same paper (1858) Wright dismembers the old genus *Eudendrium* Erhenberg into *Eudendrium* proper with a trumpet proboscis and *Atractylis*. He referred his two "*Eudendrium*" species to this latter genus with *E. ramosum* (van Beneden, Dalyell) (=*Bougainvillia ramosa*) as the genotype. Allman (1863, 1864) removed Wright's two species to the genus *Perigonimus* Sars 1846, and to this genus he also referred a new species, *P. minutus*, which he found living on the operculum of *Turritella communis* Lamarck from the Shetland Islands. Opinion is divided as to whether this species is synonymous with *Perigonimus repens*. Hincks (1868) lists it as a synonym of *P. repens*, but Allman (1872) separates them again.

The species described by van Beneden (1866) as *Dinema slabberi* is undoubtedly this species.

The next important contribution to the life history is that of Hartlaub (1895) who succeeded in rearing the medusa to a stage when it could be recognized as a young pandeid (*Tiara*). He also found medusa buds developing from both the stolon and the hydrocaulus, which made him doubtful of the identity of his species. Later (1914) he refers it to *Perigonimus repens* and gives the synonymy of the species and an excellent description of the medusa for which he erected the genus *Leuckartiara*.

Broch (1916) discussed the distribution of the species and the nature of the pseudohydrotheca. Stechow (see p. 11) was the first to separate this species from *Perigonimus*. In later papers he refers to the hydroid as *Leuckartiara pusilla* (Stechow, 1929).

Records of this hydroid are very numerous, but only the more important references are given in the bibliography.

THE HYDROID. The hydroid is nearly always found living in association with other animals. It occurs chiefly on the shells of molluscs and on the legs and carapace of various crabs, but has been found growing on a number of other animals. Colonies vary greatly in their mode of growth, depending on the nature of the host and on the substratum. I propose to describe below typical colonies from the shell and operculum of *Turritella communis* Lamarck, *Scaphander lignarius* (Linn.), *Corystes cassivelaunus* (Pennant), and *Agonus cataphractus*.

Shells of living *Turritella communis* dredged from Rame mud frequently carried small colonies with almost sessile hydranths arising from a creeping reticulate stolon 0·05 mm. in diameter. The hydranths were small (Figs. 3 *a*, *b*), rarely with a height (to top of hypostome) of more than 0·5 mm. They possessed a distinct conical hypostome and a single whorl of 4–8 filiform tentacles. The close-fitting perisarc of the hydranth was thin and reached as far as the base of the tentacles. Medusa buds were borne at intervals on the creeping stolon. Like the hydranths they were also almost sessile with a very short stalk. The newly liberated medusae were typical specimens of young *Leuckartiara*; some were reared in the Laboratory until the gonads began to appear when the species could be recognized for certain as *Leuckartiara octona*.

Colonies from the opercula of living *Turritella* shells and those on the "upper sides" of shells of the same species inhabited by small hermit crabs were very similar in appearance (Figs. 3 *a*, *c*). A portion of a typical colony growing on a shell inhabited by a hermit crab is shown in Fig. 4 *a*. The stems were fairly long, smooth, sometimes ringed at the base, generally unbranched, but occasionally a single stem bore two hydranths. The total height of the stems was 1·5–2·5 mm. In this colony young and old polyps were found. The hydranths were fusiform with a loose-fitting, irregularly wrinkled perisarc, reaching as far as the base of the tentacles. The largest hydranths had a length (to top of hypostome) of 0·5 mm. and had 8–10 tentacles. The smallest hydranths had 4–8 tentacles. Medusa buds were borne on both hydrocaulus and hydrorhiza. The medusa buds had distinct stalks with a smooth or wrinkled perisarc. The stalks were never longer than the medusa buds. The "sides" and "lower side" of the shell showed transitional polyps between the sessile form and the

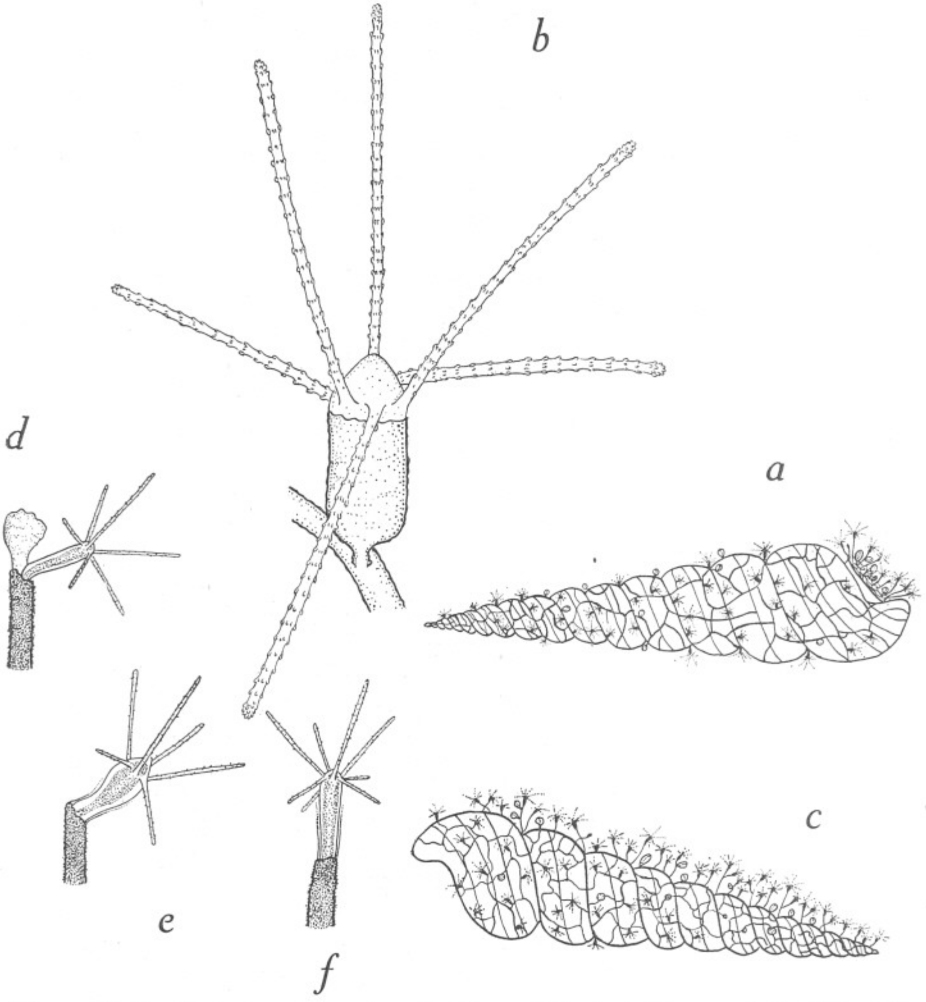

Fig. 3 *a–f*. *Leuckartiara octona*: *a*, creeping form of the hydroid on a shell of *Turritella communis* with the branched form on the operculum, 2. vii. 37; *b*, single hydranth of the creeping form on a living *Turritella* shell, 12. iii. 36; *c*, the branched form of the hydroid on the "upper side" of a shell of *Turritella* inhabited by a hermit crab, with the creeping form on the "lower side", 16. iii. 36; *d–f*, regeneration of a new hydranth from an old stem growing on *Scaphander lignarius*, 17. ii. 37; all from Plymouth.

branched form on the upper part of the shell (Fig. 4 *b*). Medusae were also reared from these colonies and they developed into typical *Leuckartiara octona* medusae.

Colonies living on the shells of *Scaphander lignarius* usually grow on the posterior part of the shell. The stolons form an open network. The stems are long, of uniform thickness and covered with a layer of fine mud particles. The stems bear one or two hydranths. The hydranths are usually small, rarely having a diameter much greater than that of the stem. The hydranths frequently die down and new ones are formed from the side of the hydrocaulus just below the position of the old hydranth (Fig. 3 *d*, *e*, *f*). Medusa buds are borne on the hydrocauli and only rarely on the stolons. A single hydrocaulus may have one to three medusa buds.

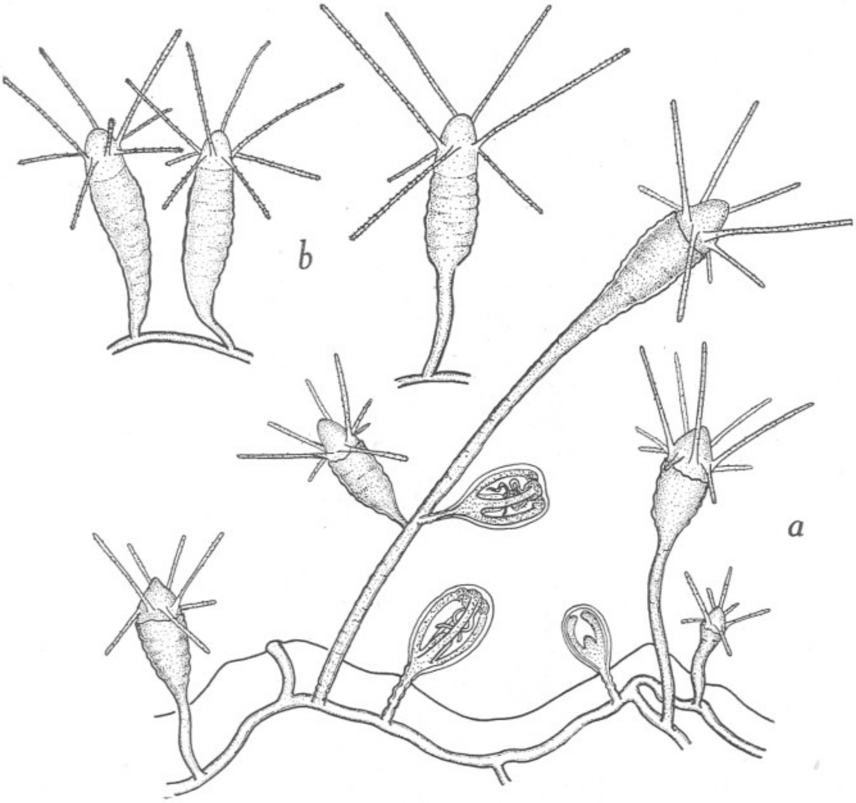

Fig. 4 *a*, *b*. *Leuckartiara octona*: *a*, hydroid colony growing on a *Turritella* shell inhabited by a hermit crab; *b*, transitional polyps on the same *Turritella* shell; Plymouth, 16. iii. 36.

Specimens of *Corystes cassivelaunus* found at Plymouth frequently carry well-developed colonies which cover the sides of the carapace, the underside and the walking legs. The following description is based on a colony caught in Cawsand Bay on June 29 1937. The hydroid had a tufted appearance, the hydranths appeared white and the stems brownish or horn coloured (Fig. 5). The stolons were 0·05–0·07 mm. in diameter and formed an open network with well-developed branched stems arising at frequent intervals from it. The stems were branched three or four times, rising to a height of 2·5–3·0 mm. At their point of origin the stems were annulated having 2–6 annulations, and at this point having a diameter of 0·06–0·08 mm. Above, the stems were slightly and irregularly wrinkled but never annulated. The perisarc widens below the hydranth to form a cup-shaped or funnel-shaped pseudohydrotheca which was much wrinkled. The pseudohydrothecae were 0·4–0·45 mm. in length and 0·21–0·3 mm. in diameter; they reached as far as the base of the tentacles. The hydranth itself was spindle-shaped with a distinct hypostome and a whorl of 8–10 tentacles held rather stiffly. Sometimes the tentacles were alternately elevated and depressed. The total length of the hydranth from the base of the pseudohydrotheca to the hypostome was 0·5–0·6 mm. The hydranths and the upper part of the stems were covered by adhering particles of mud. The pseudohydrothecae were slightly gelatinous and mud particles stuck to them very easily.

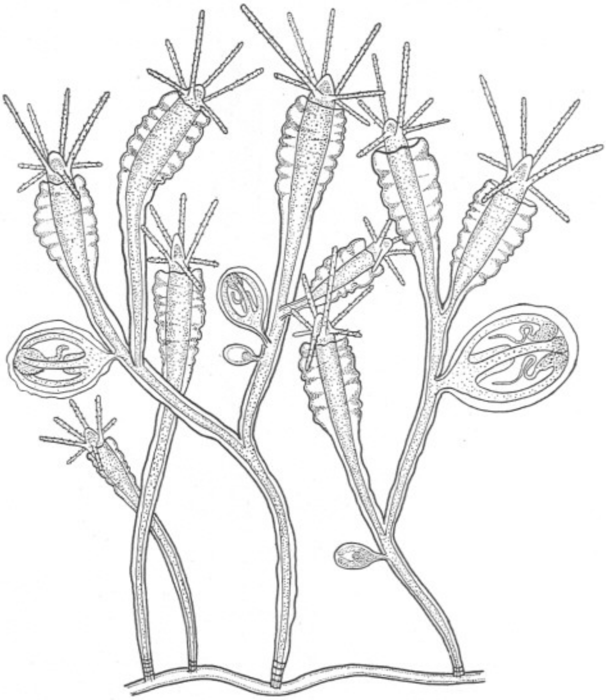

Fig. 5. *Leuckartiara octona*; well-developed colony on *Corystes cassivelaunus*; Plymouth, 29. vi. 37.

Medusa buds were borne at all levels on the hydrocauli, but very few were seen developing from the hydrorhiza. There were never more than four medusa buds on the same hydrocaulus. The stalks of the medusa buds were short, and the largest buds seen had a diameter of 0·3–0·35 mm. and a length of 0·35–0·45 mm.

Mr A. J. Smith found a colony of this hydroid growing on a fish, *Agonus cataphractus*, captured in the Cattewater, Plymouth, in February 1910. The hydroid covered portions of the back, fins and the under side of the fish with a luxuriant growth. The stems arose from a creeping network of anastomosing stolons 0·05 mm. in diameter. The stems were usually unbranched, but occasionally stems bearing two hydranths were found. The perisarc was thin, rarely ringed at the base and formed a loose sheath covering the lower part of the hydranth as far as the base of the tentacles. The hydranths were spindle-shaped with six to ten tentacles. Medusa buds were very numerous and were borne on both stems and stolons on distinct stalks with an irregularly wrinkled perisarc. The stems bore from one to four medusa buds. The table below gives measurements of fully developed hydranths and fully developed medusa buds.

Measurements in mm.

Total height (to hypostome)	3·8
Length of hydranths	0·65–0·7
Diameter of hydranths	0·25–0·3
Diameter of hydrocaulus	0·08–0·12
Length of medusa buds	0·6
Diameter of medusa buds	0·45–0·5
Length of stalk of medusa buds ...	0·1 –0·3
Diameter of stalk of medusa buds ...	0·05

In appearance this colony compares favourably with the figure of *Perigonimus pugetensis* Heath 1910, also found on a fish. Hartlaub (1914) doubted whether this species was distinct from *P. repens*.

Discussion. The great variability shown by this hydroid in its mode of growth probably depends largely on the nature of the host and on the substratum on which the host lives.

The creeping form on the shells of living *Turritella communis* may be a juvenile form, but, as the colonies have medusa buds at the right season, it is more likely that this creeping form is an adaptation to life on a shell which is nearly always buried in mud. The shell is dragged along by the snail and probably frequently rolls over so that no one surface is free from friction. The hydranths remain almost sessile because the depressions on the shell afford them some measure of protection. It was this form which Wright (1857) described as *Eudendrium sessile*.

Colonies living on the opercula of *Turritella* shells have much more protection, and they have an erect hydrocaulus which may be branched. Colonies on the "upper side" of shells of this species inhabited by hermit crabs also develop an upright branched hydrocaulus (Fig. 3 *c*). The shells inhabited by hermit crabs are much more stable, and the polyps on the "upper side" have the opportunity to grow up into branched colonies while the lower side still has the creeping form (Fig. 3 *c*). Intermediate polyps between the branched form and the creeping form are frequently found on shells of *Nassarius* *reticulatus*. The strong branched growth found on *Corystes* and other crabs will be discussed below.

The perisarc, especially the pseudohydrotheca, is subject to great variation which may possibly be influenced by the kind of food that the colony is able to obtain. Polyps of the creeping form on *Turritella* shells probably feed on micro-organisms in the mud, so that the coelenteron of each polyp is never dilated by big food masses and so remains as a close-fitting sheath on the hydranth. However, the colonies on the opercula and on the shells inhabited by hermit crabs are moved about more quickly and therefore have a better chance of gorging themselves. The polyps on the shell of the hermit crab may also catch some of the pieces of an animal caught by the hermit crab. This would cause the hydranth and its pseudohydrotheca to become considerably distended. After the digestion of the food the hydranth would shrink to its normal size leaving the perisarc as a loose-fitting sheath. A slight shrinking of the latter would result in the irregular wrinkling so typical of the pseudohydrothecae of well-developed colonies. The colonies on crabs are subject to more movement than those on shells and may receive larger particles of food from the host so that the pseudohydrothecae are largest in these colonies. The perisarc was thickest and more strongly developed in colonies from *Corystes* and other crabs. It was sometimes ringed at the base, but this character was very variable. When newly formed the perisarc was thin and transparent. The colony figured by Allman (1872) as *Perigonimus minutus* appears to me to be a young colony of this species.

In all my living specimens the pseudohydrothecae never extended beyond the base of the tentacles, but in some preserved specimens the contraction of the hydranth made it appear that the hydranth was largely retractile. *P. vestitus* Allman 1864 *b* has been regarded by Hartlaub (1914) and Kramp (1927) as synonymous with this species. Moreover, *P. vestitus* has, according to Allman's text and figure, a continuation of the perisarc beyond the base of the tentacles as a thin transparent membrane which is continued almost as far as the mouth. It must, therefore, be retained as a separate species. Stechow (1923) has placed this species in the medusa genus *Cytaeis* as *C. vestita*, although Allman's figure clearly shows that this medusa is a typical pandeid.

The position of the gonophores on the hydrocaulus and on the stolon, together with the branched and sessile hydranths in his two forms, led Wright to regard his *Eudendrium pusillum* and his *E. sessile* as two distinct species. Medusae have been reared in the Plymouth Laboratory which leaves no doubt that *E. sessile* is identical with the branched form.

The hydroid, as has already been stated, grows on a wide range of animals. Stechow (1929) found this species growing on the under side and between the parapodia of *Aphrodite aculeata*. It has not yet been recorded from this species at Plymouth.

The hydroid and medusa seem to have a cosmopolitan distribution. The hydroid has been recorded from Arctic seas by Kramp (1938), from the Pacific coast of North America by Calkins (1899), Torrey (1902) and Fraser (1937), from South America by Stechow (1919) and from the Indian Ocean by Leloup (1932), to mention only a few of the records.

The synonyms of the hydroid are given below:

Leuckartiara octona (Flemming, 1823)

Hydroid synonyms: *Eudendrium pusillum* Wright 1857; *E. sessile* Wright 1857; *E. repens* Wright 1858; *Atractylis repens* Wright 1858; *A. sessilis* Wright 1858; *Perigonimus minutus* Allman 1863; *P. sessilis* Allman 1864; *P. pusillus* Allman 1864; *Dinema slabberi* van Beneden 1866; ? *Perigonimus pugetensis* Heath 1910; *Leuckartiara pusilla* Stechow 1929.

Leuckartiara abyssi (G. O. Sars, 1873)

Synonym: *Perigonimus abyssi* G. O. Sars.

This small species was found living on the shells of *Nucula timidula* at Herdla. It was originally described by G. O. Sars (1873) from Hitvingsø, growing on shells of living *Dentalium* at depths varying from 80 to 200 fathoms, and also on shells of *Nucula timidula* from the Hardangerfjord down to 400 fathoms. Since then there have been numerous records from Scandinavian seas (for details see Jäderholm, 1909; Ritchie, 1913; and Broch, 1916). It has also been reported from Greenland by Kramp (1911), as *Perigonimus* sp. by Broch (1916), and from Spitzbergen by Broch (1909) from very shallow water. The only British record is that of Ritchie (1913), who records it from the Atlantic off south-west Ireland at a depth of 900 fathoms on *Nuculana pustulosa*.

Bonnevie (1899), in her report on the Hydroida of the Norwegian North Atlantic Expedition, states that the gonophores "probably develop into free medusae", but in her table of species she states that the gonosome is a free-swimming medusa with four radial canals and four tentacles. I can find no reference to this in literature previous to 1899, but all later authors have apparently quoted Bonnevie with respect to the medusa (Broch, 1916; Kramp, 1935).

Sars (1873) and Jäderholm (1909)* are the only authors who have figured this species with medusa buds, but their figures and descriptions are from preserved material. There is no published figure of the liberated medusa. I have therefore thought it desirable to redescribe the species in detail from living material.

Colonies of this hydroid were obtained from two localities at Herdla. Three colonies on *Nucula timidula* were obtained from a depth of 100–200 m. in the Herdlafjord on July 31 1937 by Dr Hult in his "sledge dredge". Dr Hult kindly gave me these colonies for examination, of which two had each a single gonophore. On August 6 1937, about a hundred *Nucula timidula* were obtained by the same apparatus in the Hjeltefjord, south of Toska at a depth

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* The hydroid figured by Jäderholm may be a different species.

of 300–400 m. Twelve of these molluscs had colonies growing on them, but only three colonies carried gonophores.

The stolons form an open network on the surface of the valves of the shell (Fig. 6 *a*). They are of a light brown colour and 0·05–0·07 mm. in diameter. The stems are unbranched rising to a maximum height (to top of hypostome) of 1·1 mm. and are covered by a dark brown or horn-coloured perisarc with adhering mud particles. The perisarc of both hydranth and hydrocaulus is often irregularly wrinkled throughout, but never ringed at the base. It becomes dilated around the base of the hydranth to form a pseudohydrotheca, reaching almost to the base of the tentacles where it thins out and disappears. Too much stress has been laid by some authors on the wrinkling of the perisarc, distinguishing the species by this means from the hydroid of *Leuckartiara octona* (Fleming).

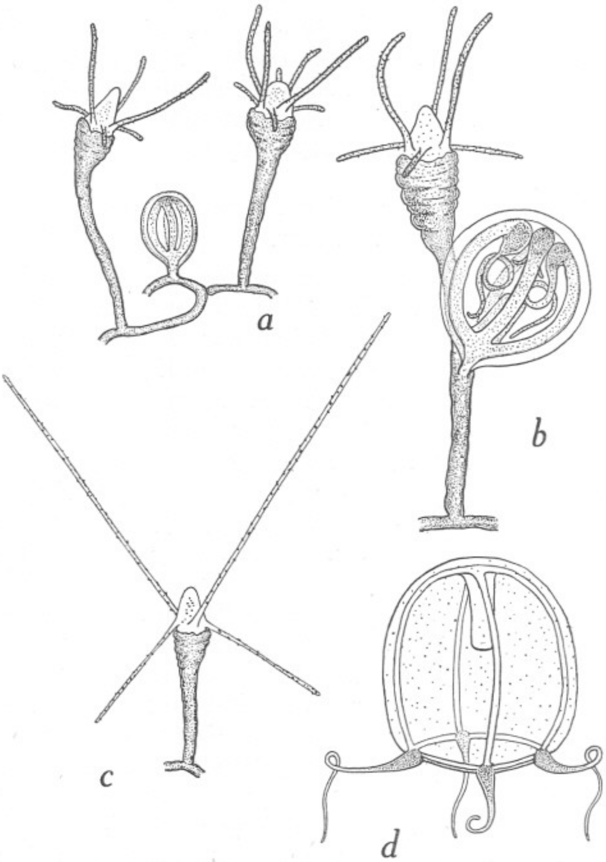

Fig. 6 *a–d*. *Leuckartiara abyssi* (G. O. Sars): *a*, portion of colony with a gonophore developing from the stolon, Herdla, 6. viii. 37; *b*, polyp with a fully developed gonophore on the hydrocaulus, Herdla, 9. viii. 37; *c*, young polyp with its tentacles fully expanded, Herdla, 6. ix. 37; *d*, newly liberated medusa.

Either the very pronounced wrinkling shown in Jäderholm's figure is due to bad fixation or the species figured is distinct from Sars' species. A comparison of Fig. 6 *a–c* with those of the hydroid *Leuckartiara octona* (Figs. 3–5) reveals that the wrinkling of the perisarc cannot be used as a specific character to distinguish the two species.

The hydranth is fusiform or flask-shaped, with a well-developed conical hypostome and a whorl of six to eight filiform tentacles held fairly stiffly, alternately elevated and depressed, the longer tentacles held almost vertical and the shorter ones almost at right angles to the hydrocaulus. Frequently the whole hydranth is so covered with mud particles that only the white tip of the hypostome and the ends of the tentacles can be seen.

The limits of hydranth and hydrocaulus are not clearly marked, the transition being gradual. When extended the tentacles are very thin and the nematocysts appear to be scattered irregularly on them. The fully extended tentacles may reach a length of 1·2 mm. (Fig. 6 *c*).

Only three living colonies with gonophores were found, and in each there was only one developing gonophore.* Sars (1873) also noted that few colonies had gonophores and that in these the gonophores were particularly few.

In two of the colonies the bud was developing from the stolon (Fig. 6 *a*) and in the third from the hydrocaulus. The gonophore developing from the hydrocaulus was in an advanced stage of development (Fig. 6 *b*) when found on August 6 1937. The young medusa bud was covered by a thin hyaline perisarc and was 0·45 mm. long by 0·45 mm. in diameter. It had a very short stalk 0·05 mm. in length. Three days later it had grown to 0·5 mm. long by 0·45 mm. in diameter. The bud was liberated as a free medusa on the same day by rupture of the perisarc.

The newly liberated medusa (Fig. 6 *d*) was of a deep bell shape, 1·15 mm. in height and 1·05 mm. in diameter. It had a fairly thin jelly of uniform thickness with no apical projection. Numerous nematocysts were scattered in the surface of the exumbrella. The velum was present. The stomach was short, quadrangular in section, reaching to about one-third the height of the umbrella cavity. The mouth was simple without distinct lips. The four radial canals and ring canal were fairly broad. There were four perradial tentacles with elongated hollow conical bulbs; of these, two opposite tentacles were better developed than the other two. There were no ocelli, and the colour of the tentacle bulbs and manubrium was a pale yellowish green.

The structure of the newly liberated medusa clearly shows that it belongs to the family Pandeidae. The hydroid appears to be very closely related to the hydroid of *Leuckartiara octona* (Fleming) (=*Perigonimus repens* (Wright, 1857)). The structure of the newly liberated medusa, however, shows it to be quite distinct from this species. The medusa differs from that of *Leuckartiara octona* in having partly developed tentacles on the two smaller perradial bulbs; it is much larger and more globular, there is no apical projection, and the

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* Dr Hult's specimens were already fixed when handed over to me.

colour is distinct. The species may be the hydroid generation of another species of *Leuckartiara* or possibly *Neoturris pileata* (Forskål). Provisionally at least it appears best to place this species in the medusa genus *Leuckartiara*, as the generic name *Perigonimus* can no longer be used for the hydroids of pandeid medusae. The name of this species therefore becomes provisionally *Leuckartiara abyssi* (G. O. Sars, 1873).

Thamnostoma russelli n.sp.

A small hydroid closely resembling *Thamnitis cidaritis** (Weismann 1883) was caught in the Mielck net in the Herdlafjord at a depth of 270 m. on August 31 1937. The species carried medusa buds and in nearly all respects appeared to be almost identical with Weismann's species from the Mediterranean. The structure of the newly liberated medusa, which differed in several respects from that of *T. cidaritis*, indicated that the species can probably be regarded as distinct.

The species described below is a form of some importance in that the structure of its medusa indicates that two medusa genera, at present kept separate, should be united under one genus.

THE HYDROID. The species was a mud-living form anchored in the mud by a twisted network of branching stolons (Fig. 7 *a*). When found the colony was covered with mud with only the tips of the tentacles and the hypostomes of the hydranths visible. The stolons were thin, being 0·05 mm. in diameter. The perisarc of the stolons, the hydrocauli and the hydranths, was of a brownish colour and non-annulated. The polyp stems were unbranched and 2–5 mm. in length with a diameter of 0·10–0·12 mm. They were usually irregularly bent and only occasionally straight.

The hydranths (Fig. 7 *b*) were fusiform, 0·3–0·5 mm. in length and 0·25–0·4 mm. in diameter. They had a single whorl of ten to fifteen filiform tentacles around a conical hypostome. The hydranths were covered by a loose irregularly wrinkled perisarc, which was continued over the body of the hydranth to within a short distance of the mouth and formed a sheath on the proximal portion of each tentacle. This tubular sheath was 0·03 mm. in diameter. The distal end of the tentacle was club-shaped with numerous nematocysts at the tip forming a battery. Each tentacle had an endodermal core consisting of a single row of cells.

The stems carried one, two or three medusa buds on very thin stalks 0·3–0·35 mm. long. Fully grown medusa buds were 0·5–0·55 mm. in length with a diameter of 0·5 mm. The gonophore was covered by a very thin perisarc which was ruptured when the young medusa was liberated.

THE MEDUSA. The newly liberated medusa had a height of 1·2–1·6 mm.

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* This species was described by Weismann as *Perigonimus cidaritis*. Brückner (1914) redescribed both hydroid and medusa and gave the medusa the name *Thamnitis dichotoma*. Stechow (1919) referred the hydroid to *Thamnitis cidaritis* as the species is clearly not a *Perigonimus*.

and a diameter of 1·2–1·35 mm. (Fig. 7 *c*). The umbrella was deep bell-shaped, a little higher than wide, with a thin jelly of fairly uniform thickness. There was a slight apical projection, and here the jelly was a little thicker than elsewhere. There were a large number of nematocysts scattered over the surface of the exumbrella. The stomach was short, cylindrical and reached to almost one-third of the height of the subumbrella. The mouth was simple with four

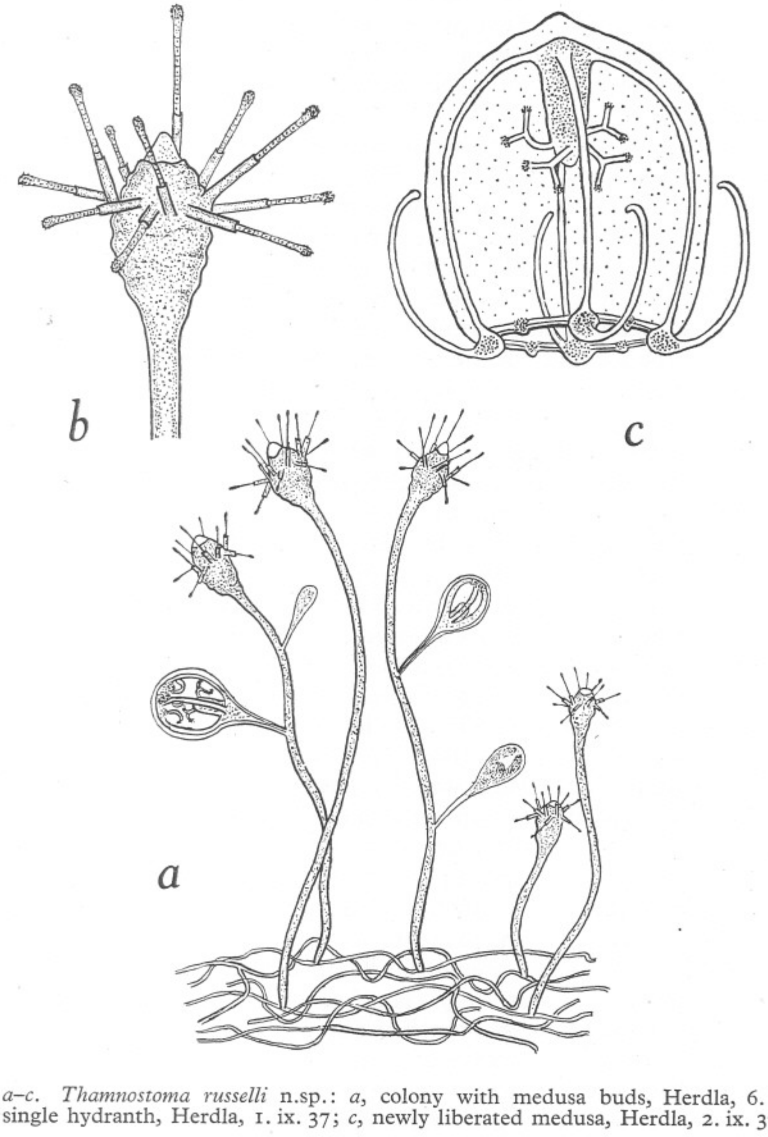

Fig. 7 *a–c*. *Thamnostoma russelli* n.sp.: *a*, colony with medusa buds, Herdla, 6. ix. 37; *b*, single hydranth, Herdla, 1. ix. 37; *c*, newly liberated medusa, Herdla, 2. ix. 37.

branched oral tentacles arising from the manubrium a little above the mouth. Each oral tentacle divided once, each arm having a small battery of nematocysts at its distal end. The radial canals and the ring canal were narrow. There were four well-developed perradial bulbs each with a tentacle and four interradial smaller bulbs without tentacles. There were no ocelli. The tentacle bulbs were yellowish brown in colour, and the base of the stomach was green and its tip reddish brown.

After three days' growth in the laboratory a medusa developed four short interradial tentacles, and the oral tentacles on the manubrium were beginning to branch a second time. The development was not studied further.

This species from Norway is evidently closely related to the Mediterranean species *Thamnitis cidaritis*. The hydroids appear to be almost indistinguishable, but the medusae differ in several respects. Brückner (1914) referred the medusa of the Mediterranean species to the genus *Thamnitis* as *T. dichotoma* on account of the presence of the branched oral tentacles and the four single perradial tentacles. His species differs from my species principally in the absence of interradial bulbs, in its smaller size, and also in the better development of the capitate knobs on the oral tentacles.

Browne (1905) found two small medusae in the Firth of Clyde, Scotland, which he referred to *Thamnitis* as *Thamnitis* sp. Except for the absence of interradial bulbs they appear to be almost identical with my species. The medusa of my hydroid is also related to the medusa *Thamnostoma dibolia* (Busch 1851) from the Gulf of Trieste. This species is only known in the adult stage and nothing is known of its hydroid. It possesses a peculiar spur on the tentacles, and the tentacles also possess ocelli.

It is possible that *Thamnostoma dibolia* and *Thamnitis cidaritis* are stages in the life history of the same species. If this proves to be so then the question whether my species is distinct from *T. cidaritis* will have to be considered. It appears possible that in warm waters the medusae are liberated at an earlier stage of development at which the interradial bulbs have not been developed. For the present it is necessary to keep my species distinct. The close similarity between the hydroid of my species and that of *T. cidaritis*, and the fact that the medusa has more than four tentacles, indicate that the retention of both the generic names *Thamnitis* and *Thamnostoma* is no longer justified. Mayer (1910) placed all the species previously assigned to *Thamnostoma* in the genus *Lymnorea* Péron & Lesueur 1809. Hartlaub (1911) has shown that Mayer draws no distinction between branched oral *lips* and branched oral *tentacles*, and he therefore restricts *Lymnorea* to medusae of the *Podocoryne* type with branched oral lips and numerous marginal tentacles.

Haeckel (1879) placed his genera *Thamnitis* and *Thamnostoma* in his family Thamnostomidae with *T. dibolia* as the genotype of his genus *Thamnostoma*.

Thamnostoma is redefined as follows to include *Thamnitis*:

MEDUSA. Thamnostomid medusae with four or more marginal tentacles and four branched oral tentacles above the mouth.

HYDROID (where known). Stems rarely branched arising from a creeping stolon both covered by a brownish perisarc. Hydranths fusiform, with a single whorl of filiform tentacles around a conical hypostome, covered almost as far as the mouth by an investing perisarc which also forms a sheath around the base of each tentacle. Medusa buds, stalked, borne on the hydrocauli.*

The following species, *Thamnostoma dibolia* (Busch 1851), *T. macrostoma* Haeckel 1879, *Thamnitis tetrella* Haeckel 1879, *T. cidaritis* (Weismann 1883) and *Thamnitis* sp. Browne 1905 can be referred to this genus. To these we must add the new species described above, which I propose to call *Thamnostoma russelli* after Mr F. S. Russell.

The following is a concise definition of this new species:

Thamnostoma russelli n.sp. (Fig. 7)

Stem slender, unbranched, rooted by a tufted mass of thread-like stolons, the whole of the coenosarc enclosed in a brownish non-annulated perisarc; hydranths fusiform, with a single whorl of ten to fifteen filiform tentacles around a conical hypostome, the body and the lower half of each tentacle clothed in a thin perisarc which is irregularly wrinkled on the body of the hydranth. Gonophores medusoid, borne on very slender pedicels on the hydrocauli. Medusa (at liberation) bell shaped, jelly thin, with numerous scattered exumbrellar nematocysts. Umbrella with a slight apical projection. Velum present. Stomach short, cylindrical, with a simple mouth with four dichotomously branched oral tentacles arising above mouth margin. Four radial canals and ring canal narrow. Four perradial marginal tentacles with enlarged basal bulbs and four interradial bulbs with developing tentacles. Tentacular bulbs brownish, stomach green at base, reddish brown distally.

Distribution: Bergen coast (Herdlafjord).

THE HYDROID OF *EUPHYSA AURATA* FORBES 1848

Many specimens of the mud-living hydroid *Corymorpha annulicornis* M. Sars 1859 were obtained at Herdla, and from them young specimens of the medusa *Euphysa aurata* Forbes were liberated. Until recently the hydroid *Corymorpha nana* Alder 1859 has been almost universally accepted as the hydroid of this medusa (e.g. Kramp, 1927; Mayer, 1910). Browne (1896), alone of modern authors, was convinced that it was not the right hydroid of this medusa. The description given by Alder for *C. nana* differs in so many respects from that of *C. annulicornis* that they cannot possibly be the same species. The newly liberated medusae, however, are rather similar, and the medusa of *C. nana* may prove to be another species of *Euphysa*.

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* There is a close similarity between these two hydroids and *Bimeria vestita* Wright 1859 which has fixed gonophores. It is premature at present to place these species in *Bimeria*. This genus has been united with *Garveia* Wright, which has no tubular perisarc sheaths covering the tentacles of the hydranth, by some authors, e.g. Torrey (1902), Browne (1907), and Stechow (1919), while others, e.g. Fraser (1937), have kept them separate. A revision of the *Bimeria*-*Garveia* hydroids is greatly to be desired.

Although the figures of both hydroid and medusa are by no means typical, the hydroid, described by E. S. Russell (1906) as *Trichoriza brunnea* (*Rhizotrichia* of Stechow, 1919), is undoubtedly identical with *Corymorpha annulicornis*.

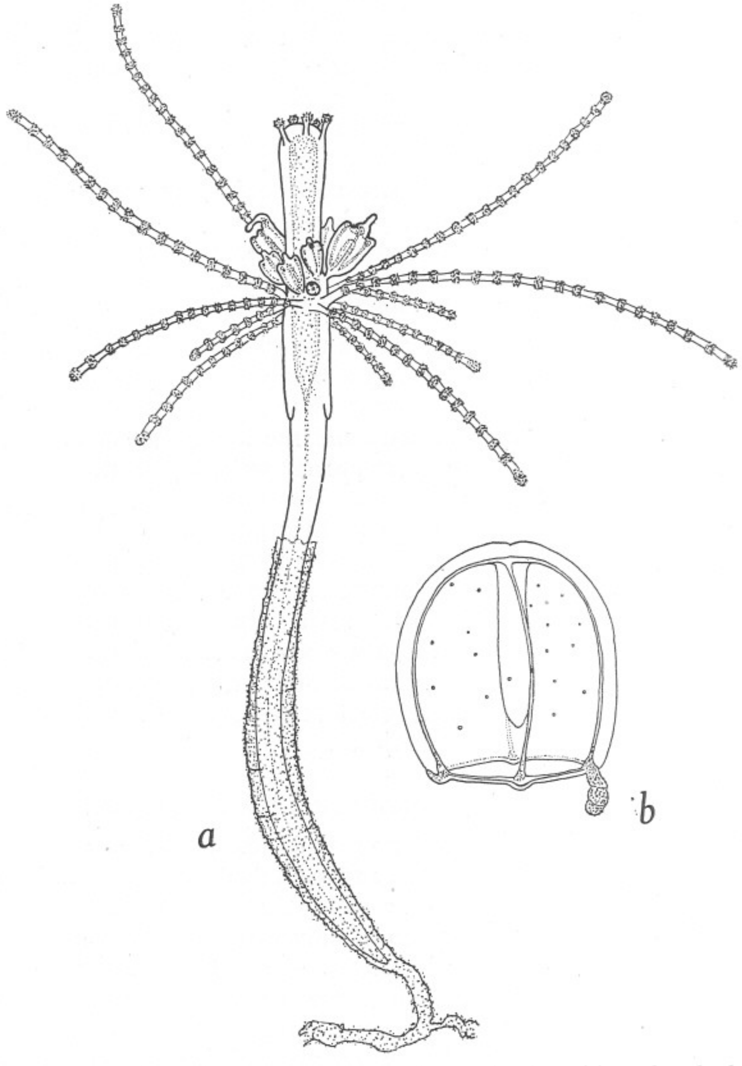

Fig. 8 *a*, *b*. *Corymorpha annulicornis* M. Sars: *a*, expanded polyp with medusa buds, Herdla, 12. viii. 37; *b*, young medusa newly liberated from the hydroid, Herdla, 11. viii. 37.

Having seen young specimens of *C. annulicornis* alive at Herdla I have now no hesitation in referring the specimens I described from Plymouth (Rees, 1937) as *Heterostephanus* sp. to this species.

Dahlgrenella farcta Miles 1937 is very closely related if not identical with *Corymorpha annulicornis*. The validity of the genus *Dahlgrenella* will be discussed later in this paper.

The hydroids were obtained at Herdla with a similar "mud-tangle" apparatus to that described by Miles (1937). The list of localities where the hydroid was found is given below:

9. viii. 37. Ypsøsund, 70 m., 11 specimens.
9. viii. 37. Iø, 20 m., 3 specimens.
9. viii. 37. Rosslandspollen, 30–40 m., 4 specimens.
9. viii. 37. Herdlafjord, 100 m., 2 specimens.
14. viii. 37. Mangerfjord, 200–300 m., 1 specimen.
18. viii. 37. Ypsøsund, 70 m., 33 specimens.
4. ix. 37. Ypsøsund, 70 m., 12 specimens.

The two specimens from the Herdlafjord were obtained by Dr Hult in his "sledge dredge", and the single specimen from the Mangerfjord by washing and sieving the mud from the upper part of the trawl netting. All the other specimens were obtained by dragging the "mud-tangle" along the bottom for 20 min. Each record represents a single haul.

Of all the specimens obtained about 50 per cent carried medusa buds, about 10 per cent were fully grown without buds, and the remainder were young polyps.

Five young hydroids of this species were obtained from Jennycliff Bay, Plymouth Sound, on September 27 1937.

THE HYDROID. The stems are unbranched consisting of a claviform or club-shaped head and a tubular hydrocaulus (Figs. 8, 9). The limits of the hydranth and the stalk are not always clearly marked; in some specimens the head merges imperceptibly into the stalk. The head varies greatly in shape and carries two whorls of tentacles. Some idea of the variation in number of the tentacles and in the size of the medusa-bearing polyps can be obtained from the following table. The measurements are from specimens fixed in Bouin's fluid. When alive the polyps can expand to four or five times the length of the contracted state:

Measurements in mm.

Total length	1·15–4·55
Length of head...	0·6 –1·8
Diameter of head	0·35–0·9
Length of hydrocaulus	0·15–1·8
Diameter of hydrocaulus	0·2 –0·5
Number of oral tentacles	3–8
Number of aboral tentacles	6–14
Number of medusa buds	1–27

The oral tentacles are capitate and generally four in number. The aboral tentacles are moniliform, situated near the posterior end of the hydranth; their usual number is eight to ten.

The aboral tentacles consist of longer and shorter tentacles which alternate and appear to be in two closely approximated whorls, the longer tentacles always arising a little in front of the shorter tentacles. This can only be seen in fully developed individuals. In full-grown polyps bearing medusa buds the number of annulations on each aboral tentacle varies from six to twenty-five. At the posterior end of the hydranth there is a whorl of three to six backwardly directed papillae, and there are also occasionally some on the upper part of the hydrocaulus. One individual had three of these processes, and three other polyps had one each. Similar processes are found scattered on the upper part of the

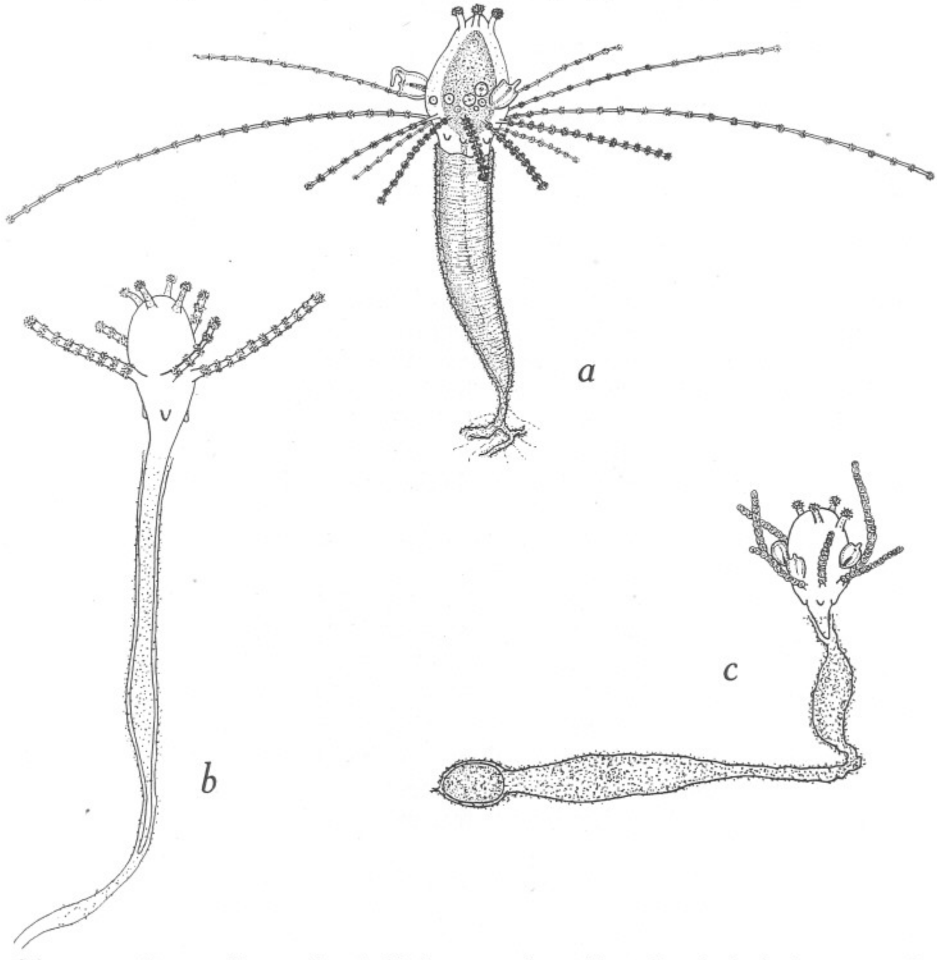

Fig. 9 *a–c*. *Corymorpha annulicornis* M. Sars: *a*, polyp with medusa buds, body contracted, tentacles expanded, Herdla, 10. viii. 37; *b*, young polyp developed by asexual budding from the stolon, Herdla, 9. viii. 37; *c*, polyp with an asexual body in the stolon, Herdla, 4. ix. 37.

hydrocaulus of *Dahlgrenella farcta*; according to Miles (1937) they develop into anchoring filaments, but I saw no indication of this in my specimens. The original specimens taken by Sars near Bergen seem to have been much larger than mine from the same district. His polyps possessed eight to ten oral tentacles, about twenty aboral tentacles and six to eight backwardly directed papillae.

The simple hydrocaulus is covered by a distinct slightly gelatinous membrane which covers the greater part of the hydrocaulus. When the hydrocaulus is expanded the membrane forms a smooth loose-fitting sheath reaching two-thirds of the way up the hydrocaulus; when the hydrocaulus is contracted the membrane contracts with it and appears to be transversely wrinkled. It is almost always covered with fine particles of mud which adhere to it. Below the base of the hydrocaulus the tube may narrow abruptly to form an irregularly branched or unbranched stolon which serves as an anchoring filament. In specimens which have been kept alive in small glass dishes, very thin hair-like anchoring filaments or frustules frequently appear from the posterior fourth of the hydrocaulus and fix the animal securely to the substratum. In the specimens I kept there were never more than ten of these filaments.

Among the eleven specimens obtained from Ypsøsund on August 9 1937 there was one polyp with an asexual bud developing from the body of the hydranth. It was a reversed bud similar to the one described (Rees, 1937) for this species from Plymouth. In this instance no tentacle of the parent polyp was carried away by the bud, which had four oral and four aboral rudiments of tentacles. As in the Plymouth specimen the parent polyp was immature and without gonophores.

The development of young polyps from the stolon is common in this hydroid, and for this Ypsøsund proved to be the most interesting station. Such buds have been described by Broch (1937) for *Corymorpha annulicornis* and by Miles (1937) for *Dahlgrenella farcta*.* Broch notes the presence of a rounded body in the stolon below the hydrocaulus and suggests that it may be a schizospore. In the material from Ypsøsund (September 4 1937) there are several such bodies in the periderm of different polyps. In one the lower part of the hydrocaulus was becoming constricted off (cf. *D. farcta*); in another the proximal end of the periderm contained a rounded body (Fig. 9 *c*). It has already been mentioned that a large percentage of the polyps found were very young ones.

Few, however, of these young polyps were attached by their stolons to the parent polyps, and it is very probable that, in the process of washing and straining the mud, the thin periderm, connecting most of them to their parent polyps, becomes severed.

The youngest polyp still attached to its parent polyp by the periderm possessed four oral tentacles, four aboral tentacles and four backwardly directed processes (Fig. 9 *b*).

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* Murbach (1899) has also described such buds in *Hipolytus peregrinus*, a form which approaches nearest to *Corymorpha obvoluta* Kramp and with which it is almost certainly cogeneric.

Measurements of this bud (when alive) are given below:

Measurements in mm.

Total length	1·75
Length of head	0·65
Diameter of head	0·32
Length of hydrocaulus	1·1
Diameter of hydrocaulus	0·12–0·2

The oldest bud still attached to its parent by the periderm had seven medusa buds and a proximal whorl of ten tentacles.[*]

Broch (1937) suggests that the British species of *Vorticlava*, *V. humilis* Alder 1856 and *V. proteus* Wright (1863), may possibly be young *Corymorpha annulicornis*, but I cannot agree with this suggestion. Alder and Wright examined their specimens alive, and it is hardly likely that such careful workers would have missed such a striking feature as the annulation of the tentacles had the tentacles been annulated. It appears more likely that these young forms are larval tubularians as suggested by Brink (1925).

Sexual Reproduction. The medusa buds are borne singly or in groups of two to six just above the aboral whorl of tentacles. It is questionable whether the small protuberances on which these buds are borne can be called blastostyles. Each bud is naked. It arises as a globular swelling which gradually enlarges, becoming bell-shaped. The manubrium and the four radial canals develop, and at the margin of the bell opposite one of these radial canals a small finger-like tentacle is formed (Fig. 8 *a*). The tentacle as it grows bends inwards like a hook and develops two or three nematocyst batteries. At first its colour is green, but when the medusa is about to be liberated it becomes golden yellow.

When liberated the medusa (Fig. 8 *b*) is of a deep bell shape; the jelly is uniformly thin and there are a few large scattered nematocysts on the exumbrella. The velum is well developed. The stomach is tubular and well developed; the mouth is simple. The stomach is about two-thirds of the length of the subumbrellar cavity. The four radial canals and the ring canal are narrow. There is only one tentacle; this is short and club-shaped when contracted, when expanded it is moniliform, having two or three nematocyst batteries. The tentacle bulbs on the other perradii are small and rudimentary. Each bulb clasps the margin of the bell.

Newly liberated medusae are when alive 0·55–1·0 mm. in height by 0·55–1·0 mm. in diameter. Individual medusae range from brightly coloured specimens to almost colourless ones. The subumbrella and radial canals are faintly pink in some, in others colourless. In brightly coloured medusae the ring canal

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[*] Since this paper was written I have received from Dr Hult a species of *Corymorpha* obtained in the Trondheimsfjord from a depth of about 480 m. It approaches very near to and may be identical with *C. annulicornis*. It is much larger than my Herdla specimens, having a total length of 9·5 mm. There are well-developed *branched* blastostyles bearing gonophores which are distinctly medusoid in form. Without more knowledge of the gonophore, however, I prefer not to refer this specimen to *C. annulicornis*.

appears as a crimson circle. There is always a crimson pigment spot at the tip of the manubrium, the remainder is yellow, sometimes with brownish pigment at the base. The upper part of the tentacle bulbs including the junction of the radial and ring canals is vivid scarlet or crimson with a few black pigment granules at the ends of the radial canals. The single tentacle is golden yellow in colour and the lower part of the tentacle bulbs which clasp the margin are also yellow.

The newly liberated medusae and the various stages seen in the townets at Herdla confirm Broch's opinion that this species is identical with *Euphysa aurata* Forbes. The newly liberated medusae (of which one was captured in the townets) correspond to those described by Browne (1896). Browne states that: "The shape of the umbrella, of the tentacle bulbs, and of the large tentacle is similar in all stages: thus there is no difficulty in identifying the earliest forms."

The youngest stage captured in the Herdlafjord on September 2 1937 was obviously a newly liberated specimen and differed in no way from those already described. It was 0·75 mm. in height by 0·7 mm. in diameter.

A slightly older specimen caught in the Hjeltefjord on September 23 1937 possessed a slightly thicker jelly and a slightly longer tentacle. It was immature and was 1·1 mm. high and 1·05 mm. in diameter.

A ripe male medusa was obtained in a haul in the Hjeltefjord south of Toska on September 21 1937. It only differed from specimens previously described here in its greater size, greater thickness of jelly, length of tentacle and the presence of the gonad on the manubrium. It was 2·5 mm. high by 2·0 mm. in diameter.

Euphysa aurata is the only species of its genus with the same distribution as the hydroid *Corymorpha annulicornis*. According to Kramp (1927) the medusa occurs from the English Channel to the Murman coast. It has also been reported from Greenland (Kramp, 1926) and from the Mediterranean. It is very common along the Scottish coasts and along the Norwegian coast.

The records of the hydroid are few, probably because the species is a mud-living form and necessitates a special apparatus to catch it. Sars (1859) found two species at Flören (Sondfjord) in the Bergen district. Russell (1906) has recorded it from the Firth of Clyde as *Trichorhiza brunnea*, and the present writer has found it abundant at Herdla (Bergen), and also less commonly at Plymouth.

The only other north European species of *Euphysa* is *E. tentaculata* (Linko 1904) which is only known from the Barents Sea and a few localities in the southern Kattegat and the Belt Sea (Kramp, 1927).

It is therefore almost certain that the medusa *E. aurata* can be linked with the hydroid *Corymorpha annulicornis*.

The species was originally described by Michael Sars (1859) as *C.* ? *annulicornis*: Sars himself was doubtful which generic name this species should bear. Allman (1864 *a*) erected the genus *Heteractis* (later he changed it to *Heterostephanus*) for this species because of the peculiar ringed nature of the proximal tentacles. Recently the species has been redescribed by Broch as *Corymorpha* (*Euphysa*) *annulicornis*. This raises the question of what name the species should bear.

The capitate oral tentacles, the moniliform aboral tentacles, the backwardly directed papillae, the few frustules, the almost sessile gonophores and the characters of the medusa all apparently justify the separation of this species from *Corymorpha*. Indeed, the medusae have been kept under different genera, viz. *Corymorpha* (*Steenstrupia*) and *Euphysa*.

The separation seems justified when we compare the hydroid of *C. nutans* with the hydroid of the present species, but if all other species of *Corymorpha* are taken into consideration it appears evident that the so-called generic characters of *Heterostephanus* are possessed by other species of *Corymorpha*.

C. obvoluta Kramp 1933 possesses, like *C. annulicornis*, moniliform proximal tentacles, sessile gonophores and backwardly directed papillae. It differs in having (among other characters) fixed gonophores, a well-developed periderm and moniliform oral tentacles. The relations of *C. obvoluta* to other Corymorphinae has been fully discussed by Kramp (1933), and so they need not be discussed here.

The chief difference distinguishing medusae of the genus *Steenstrupia* from *Euphysa* is the presence of an apical projection to the umbrella which is perhaps more suitable as a specific character than as a generic one.

It may be that all species of *Euphysa* are liberated from *Corymorpha* hydroids with moniliform aboral tentacles, but at present it is premature to lay too much stress on the significance of these annulations because the hydroids of all *Euphysa* medusae (except *Corymorpha annulicornis* and *Dahlgrenella farcta*) are unknown. For the present there is no justification for separating *Euphysa* from *Corymorpha*, and the species described here has been referred to as *C. annulicornis*. Now that the hydroid has been linked with the medusa *Euphysa aurata* Forbes the name of both hydroid and medusa must become *Corymorpha aurata* (Forbes 1848)* if the dual classification is eventually superseded.

Miles (1937) founded his genus *Dahlgrenella* chiefly on the peculiar asexual reproduction of his hydroid. It has been shown by Broch (1937) and in the present paper that budding from the stolon takes place normally in *Corymorpha annulicornis*, and there is now no reason why the species should not be included in the genus *Corymorpha* as *C. farcta*. Even if it should become necessary to remove these species from *Corymorpha*, then the claims of *Euphysa* Forbes 1848 and *Heterostephanus* Allman 1864 would have priority over *Dahlgrenella* Miles 1937, and also over *Hipolytus* Murbach 1899. The medusa liberated from *Corymorpha farcta* is a typical *Euphysa* and may possibly be the immature stage of *E. virgulata* A. Agassiz 1865 which is common along the American North Atlantic coast. Opinion is divided as to whether

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* *Corymorpha* Sars 1835 has priority over *Euphysa* Forbes 1848, and the species name "*aurata*" Forbes 1848 has priority over "*annulicornis*" Sars 1859.

this species is distinct from *E. aurata* (see Mayer, 1910, p. 35). The hydroids *Corymorpha annulicornis* and *C. farcta* are very closely related and may prove to be identical.

Campanulina paracuminata n.sp.

A small colony of a *Campanulina* was found on a clinker trawled in the Cattewater, Plymouth, on February 4 1936. As the colony was not reproducing it was kept in a finger bowl and fed at intervals. On October 3 the colony was transferred to the apparatus described by Rees & Russell (1937). Here the polyps were able to feed more satisfactorily and more rapidly, and by March 7 1937, more than a year after its capture, the colony was in a thriving condition with about fifty hydranths. Gonophores were observed for the first time on April 15 1937, and two days later medusae were liberated.

The trophosome of the hydroid appeared to be almost identical with *Campanulina acuminata* (Alder), but my colony was less branched than the latter and very rarely possessed more than two polyps on the same hydrocaulus. The structure of the newly liberated medusa showed that the hydroid was distinct from *C. acuminata*.

THE HYDROID. The stems were slender rising to a height of 1·5–2·5 mm. from a branched creeping stolon. The stems were imperfectly annulated throughout their length, being 0·05 mm. in diameter. The hydrocaulus carried one or two hydranths, the second hydranth usually arising just below the hydrotheca of the terminal hydranth. The hydrothecae were cylindrical, square below and tapering to a fine point above (Fig. 10 *a*). Their perisarc was thin and finely striated along their length; they were 0·38–0·42 mm. long by 0·09–0·1 mm. wide. The hydranth was very extensile and might extend to a height of 1·1 mm. from the base of the hydrotheca. There were about twenty tentacles around the base of a bluntly conical hypostome. These were united at the base by a well-developed membranous web. This web usually contained a number of large bean-shaped nematocysts approximately 0·015 mm. in length (Fig. 10 *b*). With chlorazol black E these bodies stain a dense blue-black and can then be seen in numbers scattered in the coenosarc of the stolon and hydrocaulus and also in the body. Their number and arrangement was never constant; very few were present in the earliest polyps seen. The tentacles extended to a maximum length of 0·6 mm. They had an endodermal core of a single row of cells, and the nematocysts were irregularly distributed. The hydranths could not be distinguished from those of *Campanulina acuminata* with which they were compared in the living condition. Both colonies were grown in the laboratory, and their mode of branching may not be typical of colonies obtained from nature.

Gonophores were observed on April 15. These were borne on the hydrocauli just below the hydranths (Fig. 10 *a*). The fully developed gonophores were large and cylindrical and attached to the hydrocaulus by an imperfectly ringed stalk of varying length (but always shorter in length than the gonotheca itself).

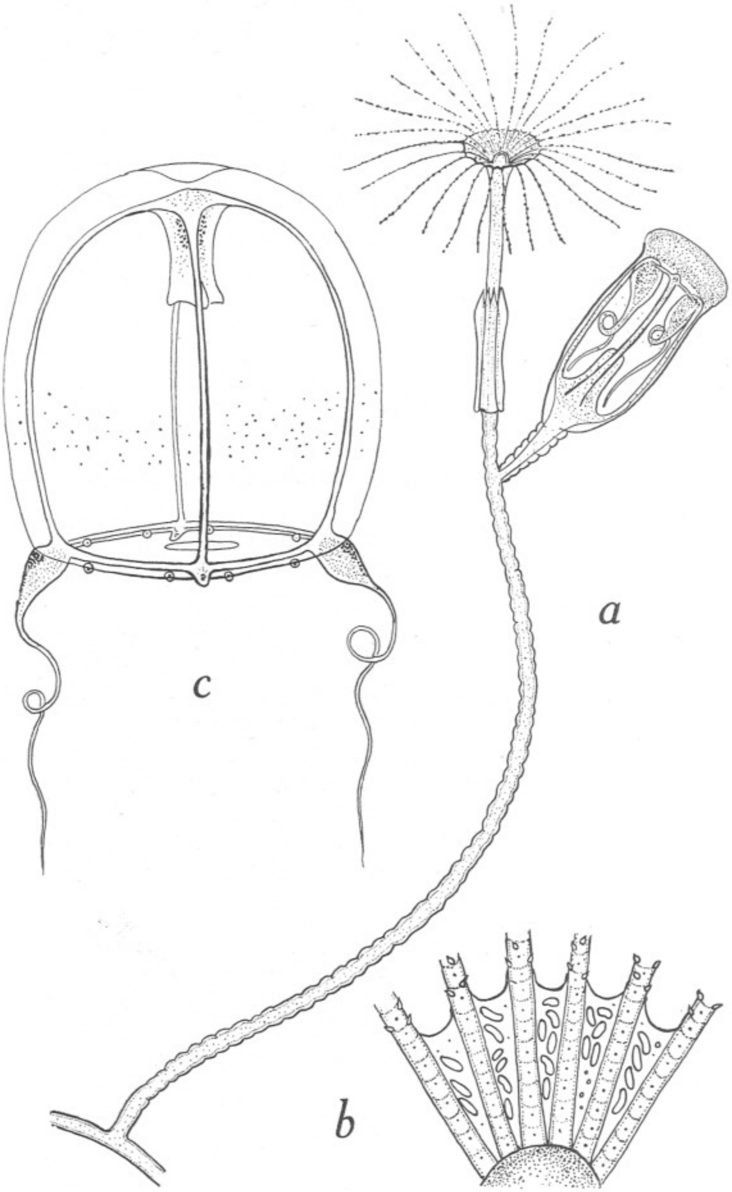

Fig. 10 *a–c*. *Campanulina paracuminata* n.sp.: *a*, single polyp with a fully developed gonophore, Plymouth, 4. ii. 37; *b*, a small portion of the web of a hydranth showing the bean-shaped nematocysts, Plymouth, 20. iii. 37: *c*, newly liberated medusa with a diameter of 1·1 mm., Plymouth, 22. ii. 37.

The gonotheca and stalk were 0·75–1·1 mm. in length, while the diameter was 0·3–0·4 mm. The gonophore contained one medusa (rarely two), borne on a thin blastostyle which enlarged distally to form a distinct cap to the gonotheca. When fully developed the medusa escaped from the gonotheca partially by its own efforts and by partial collapse of the thin membranous gonotheca which regained its shape once the medusa came out.

THE MEDUSA. The newly liberated medusa was of a deep bell shape a little higher than wide (Fig. 10 *c*). It was 1·4 mm. high and 1·1 mm. in diameter. The jelly was moderately thick and had a slight depression at the apex. There was a conspicuous band of nematocysts on the exumbrella just below the middle or widest part. The velum was broad. The stomach had a slight apical projection; it was short and quadrangular in section; the mouth had four simple lips. The four radial canals and ring canal were narrow. There were two opposite perradial tentacles with elongated bulbs and two smaller perradial opposite bulbs without tentacles. There were eight closed globular marginal vesicles, adradial in position, each with a single concretion. There were no excretory pores.

This species is more closely related to *Campanulina acuminata* (Alder 1857) than to any other known species of *Campanulina*. *C. tenuis* van Beneden 1847 was regarded by Alder as identical with his *C. acuminata*, but even if (judging from van Beneden's figures) it may possibly prove to be distinct from *C. acuminata*, it is certainly quite distinct from my species. A comparison of the trophosome of my species with that of living *C. acuminata*, kindly sent to Plymouth from Cullercoats by Dr H. O. Bull, revealed no visible difference between the trophosome of the two species. The *C. acuminata* sent by Dr Bull was kept for six months under the same conditions as my species. Both colonies produced gonophores at the same time and so it was possible to compare the newly liberated medusae. The essential differences between the two species are indicated below.

	Campanulina acuminata (Alder) Medusa	*Campanulina paracuminata* n.sp. Medusa
Umbrella.	Deep bell-shaped with a fairly thick jelly. No apical depression.	Deep bell-shaped a little higher than wide; jelly less thick. Apical depression present.
Nematocysts.	Scattered over the whole exumbrella.	Confined to a band around the lower middle part of the exumbrella.
Colour of subumbrella.	Vivid yellowish green.	Vivid bluish green.
Colour of stomach.	Colourless.	Reddish yellow.
Colour of tentacles.	Yellow with two lateral strips of blue-black.	Yellow with a single central strip of blue-black pigment.
Height.	1·6 mm.	1·4 mm.
Diameter.	1·6 mm.	1·1 mm.

Wright (1861) reared the first polyps of a webbed *Campanulina* hydroid from the planulae of *Aequorea vitrina* Gosse. He declared that, as far as he could recall, the young form which he reared from *A. vitrina* was identical with the hydroid of *Campanulina acuminata*. Strong (1925) has reared the first polyps of an *Aequorea*, *A. victoria* (Murbach & Shearer 1903), giving the hydroid the name *Campanulina membranosa*.

I am much indebted to Mr F. S. Russell for permission to make use of his unpublished observations on the life history of *C. acuminata*. Several young medusae found in the plankton at Plymouth, corresponding to the newly liberated medusae of *C. acuminata* but in later stages of development, leave no doubt that the medusa develops into a species of *Aequorea*. One specimen found on May 23 1934 was 1·8 mm. high by 2·5 mm. wide and had a bell-shaped umbrella a little wider than high and a fairly thick jelly of uniform thickness. It possessed four radial canals, four fully developed tentacles, four small interradial tentacles and eight adradial rudiments. The stomach was short, quadrangular in section, with four simple well-developed oral lips. In colour it agreed exactly with the newly liberated medusa of *C. acuminata*.

Another specimen found on November 7 1935 was 4·1 mm. in diameter. It was in a much more advanced stage than the previous specimen. The umbrella was dome-shaped with a thick apical jelly becoming thin towards the margin. The stomach reached to about half the height of the subumbrellar cavity and its oral lips were further developed. It possessed eight complete radial canals and eight developing canals. There were four radial tentacles, four interradial tentacles, eight adradial tentacles and sixteen rudiments of tentacles between every two tentacle bulbs. The marginal vesicles were twenty-six in number with concretions varying from one to four in number. The subumbrella was a bright yellowish green in colour, and the tentacle bulbs were yellow with two lateral strips of blue-black pigment. The specimen had the appearance and characters of young *Aequorea* and was identified as such. *Campanulina acuminata* and the hydroid of *Aequorea vitrina* are sufficiently related to *Campanulina paracuminata* n.sp. to permit the supposition that the medusa liberated from *C. paracuminata* develops into a species of *Aequorea*. Our knowledge of the various species of *Aequorea* is still very unsatisfactory, and I have therefore placed this species provisionally in the genus *Campanulina* van Beneden 1847 as defined by Hincks (1868).*

The species may be defined as follows:

Campanulina paracuminata n.sp.

Stem slender, more or less branched, imperfectly annulated throughout, branches developed on the hydrocaulus a little below the hydranth. Hydrothecae thin, membranous, finely striated longitudinally, elongate pod-shaped, square below and tapering to a fine point above. Polyps extensile with about

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* It is not proposed here to discuss the various so-called species of *Campanulina* which have been referred to this genus.

twenty tentacles, united for about one-fifth of their length by a membranous web with bean-shaped nematocysts embedded in it.

Gonothecae large, cylindrical, with an imperfectly ringed stalk, borne laterally on the primary stems.

Medusa, pale bluish green, umbrella deep bell-shaped, a little higher than wide with a band of nematocysts confined to the lower middle part of the subumbrella and with an apical depression. Stomach short, quadrangular, with four simple lips. Two opposite marginal tentacles and two bulbs without tentacles; bulbs yellow with a single central strip of blue-black pigment. Marginal vesicles adradial, each with one concretion.

Notes on other Hydromedusae

Boreohydra simplex Westblad 1937.

Ten specimens of this interesting hydroid were collected on August 9 1937 at Ypsøsund, Herdla, at a depth of 70 m. The specimens were 1·0–1·75 mm. in length and the oral tentacles were four in number. Except for their slightly greater size, the specimens differed in no respect from the description given by Westblad (1937). He found the species in two localities on the Norwegian coast, in the Ramfjord and at Tromsö. Eleven specimens were found by Dr Jöran Hult in the Balsfjord, Tromsö; they were identical with my species from Herdla.

Stauridium productum Wright 1858.

Synonyms: *Coryne cerberus* Gosse 1853.
Perinema cerberus Stechow 1923.

A colony of this hydroid was grown from a stolon on a stem of *Tubularia indivisa* obtained at Bognøstrømmen on August 14 1937. The stem of the *Tubularia*, which also had other hydroids growing on it, was placed in a similar apparatus to that described by Rees & Russell (1937), which Professor Brinkmann had specially set up for my use. The polyps which I reared from this colony at Herdla and later at Plymouth* were very similar to those figured by Hartlaub (1895). The development of the hydranth is quite distinct from that of *Staurocoryne filiformis* Rees 1936. The developing hydranth first grows three or four capitate oral tentacles, and next the four or five filiform tentacles at the proximal end are developed (Fig. 11 *a*). At this stage the hydranths look exactly like *Coryne cerberus* Gosse, and I agree with Hartlaub that the two species are identical. The young hydranth corresponding to *C. cerberus* had a length of 0·25 mm. and a diameter of 0·11 mm. Additional whorls of tentacles (rarely more than one or two) are developed between the oral whorl and the filiform whorl. In the colony I reared, most hydranths never developed more

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* Three species of hydroid were brought back to Plymouth from Herdla in a thermos flask. These were *Bougainvillia muscoides*, *Stauridium productum* and a species of *Syncoryne*; they are still alive in my beakers (28. ii. 38).

than two whorls of capitate tentacles (Fig. 11 *b*). The oral whorl developed five or six tentacles in all; this agrees with Hartlaub's observations on this species. No medusa buds have developed to date (28. ii. 38).

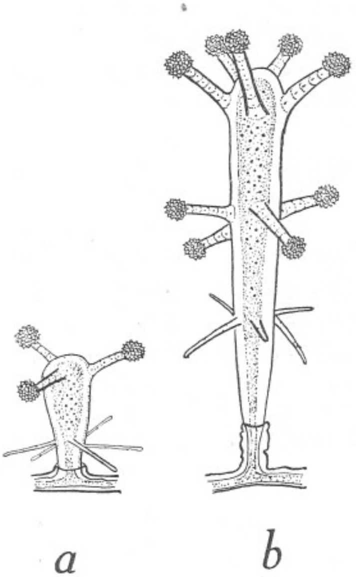

Fig. 11 *a*, *b*. *Stauridium productum*: *a*, young hydranth, Herdla, 20. viii. 37; *b*, fully developed hydranth, Herdla, 20. viii. 37.

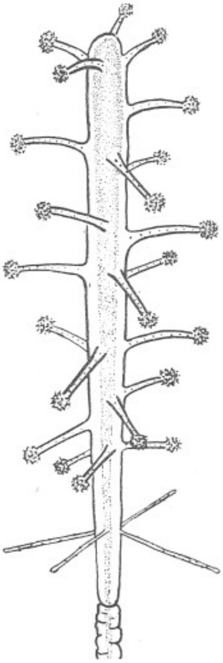

Fig. 12. *Staurocoryne filiformis*; single hydranth, Plymouth, 5. iv. 37.

Measurements of this colony are given below:

Measurements in mm.	
Length of hydranth	1·0 –1·8
Diameter of hydranth	0·15–0·23
Diameter of hydrocaulus	0·10
Diameter of stolon	0·15
Total length of oral tentacle	0·20–0·3

The trophosome of the hydroid can easily be distinguished from *Staurocoryne filiformis* by its more delicate growth, the smaller hydranths, the few whorls of tentacles and by the development of the whorl of filiform tentacles immediately after the oral whorl.

Staurocoryne filiformis Rees 1936.

A small colony of this hydroid was found on a *Pecten* shell dredged from New Grounds, Plymouth Sound, on March 16 1937. Previously this hydroid was only known from a colony reared in the Plymouth Laboratory (Rees, 1936). The colony from nature differed from that reared in the laboratory only in the slightly smaller size of the hydranths and in the more irregular distribution of the tentacles (Fig. 12). There were four filiform tentacles which later increased to five in number. They carried a few scattered nematocysts. Identification was verified when the colony developed styloid gonophores two months later.

SUMMARY

The newly liberated medusa of *Perigonimus muscoides* M. Sars has been found to be a *Bougainvillia*. A specimen from the plankton points to the extreme probability that it can be regarded as synonymous with a previously described medusa, *B. nordgaardi* (Browne). The name of both hydroid and medusa now becomes *B. muscoides* (M. Sars 1846).

The systematic importance of the above discovery is discussed, and the genus *Rhizorhagium* M. Sars 1877 is redefined to include all those species of "*Perigonimus*" with fixed gonophores, viz. *Rhizorhagium roseum*, *R. sarsi*, *R. antarcticum*, *R. formosum*, and a new species, *R. album*, from the Cornish coast.

Variations in the form of the hydroid of *Leuckartiara octona* are described. The newly liberated medusa of *Perigonimus abyssi* G. O. Sars is figured for the first time and the species referred to the genus *Leuckartiara*.

A new *Bimeria*-like hydroid, *Thamnostoma russelli*, is described. The characters of the medusa indicate that it belongs to the genus *Thamnostoma* Haeckel, and the characters of the hydroid show that the genera *Thamnitis* and *Thamnostoma* must be united.

Corymorpha annulicornis M. Sars is redescribed from living specimens and the medusa is shown to be *Euphysa aurata* Forbes. It must henceforth be known as *Corymorpha aurata* (Forbes).

A new species of *Campanulina*, *C. paracuminata*, with its young medusa is described from Plymouth.

Notes are included on *Boreohydra simplex*, *Stauridium productum* and *Staurocoryne filiformis*.

Certain points in the synonymy of all these species are discussed.

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THE SEASONAL OCCURRENCE OF MYSIDS OFF PLYMOUTH

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(Text-fig. 1)

In the course of his work on the plankton of the English Channel, Mr F. S. Russell (1928*b*) designed a special townet, made of stramin netting, to fish inside the Agassiz trawl as it was dragged along the bottom. The townet was so fixed as to fish a few inches above the bottom without actually stirring up bottom material. Mr Russell tells me that there was no indication that the net was catching bottom living forms, but that all the animals caught were plankton forms or animals swimming just above the bottom. The hauls, therefore, may be taken to present a picture of the fauna of the bottom layer of water, over a period of a year, and it may not be without interest to analyse the gatherings as far as mysids are concerned in an endeavour to glean information on the biology of the group.

The tow-nettings were taken at three stations in the neighbourhood of Plymouth, from June 1927 to May 1928. The three stations, referred to in the following pages as A, R, and L4, were situated as follows:

A = 2 miles east of Eddystone. Sand.
R = Off Rame Head. Mud.
L4 = Midway between the Breakwater Light and Eddystone. Mud and sand.

The Mysidacea include two groups of forms, those which are permanently planktonic and mostly oceanic, such as *Gnathophausia*, *Eucopia*, *Euchaetomera*, *Caesaromysis*, *Arachnomysis*, certain species of *Anchialina* and *Siriella*, and others, and the remainder which are normally bottom-living. It is to the latter group that the species in this collection belong. The members of this group may leave their bottom-haunting habits and undertake movements into the neighbouring water under the influence of varying stimuli and factors which may be briefly referred to.

In the first place it is almost certain that a large proportion of bottom-living forms spend part of their time in idly swimming just above the bottom. These movements are intermittent and their intensity varies with the operation of various factors in the environment. In shallow water, in suitable locations, I have often observed *Praunus flexuosus*, *P. neglectus* and *Neomysis integer* swimming about gently in 2 or 3 ft. of water in large numbers, especially on calm sunny days. The extent of their activity was seen to vary with such environmental factors as the intensity of light, the amount of water disturbance, temperature, and so on, but it was quite obvious that such idle swimming movements were a normal feature of their lives. It is not unreasonable to suppose that the majority of bottom-living forms have similar habits, and, in deeper water, where unfavourable conditions are minimized, one may suppose that idle swimming movements just above the bottom are a regular part of the normal life of the species. The fact that the present material includes fourteen out of the twenty-seven species known for the Plymouth fauna would lend support to this view, especially as the stations at which the plankton hauls were made were not suitable localities for most of the missing species, such as *Praunus flexuosus*, *P. neglectus*, *P. inermis*, *Neomysis integer* and the species of *Schistomysis*.

Mysids are also known to undergo diurnal movements in response to light intensity. Russell (1925, 1928*a*, 1931, 1933) has shown that, at Plymouth, certain mysids such as *Anchialina agilis*, *Leptomysis gracilis*, *Neomysis longicornis*, *Schistomysis*, *Erythrops* and *Gastrosaccus normani* move upwards from the bottom with the approach of darkness and may be taken at night in some numbers in mid-water. Some, such as *Anchialina agilis*, actually reach the surface in considerable numbers. I have shown (1936) that the same kind of thing happens in the waters inside the Great Barrier Reef. Fage (1933) suggests that these diurnal movements are dominated by the reproductive cycle and are more marked in the breeding season.

There is, further, evidence that in some Mysidacea at least, for example *Lophogaster typicus* (Tattersall, 1908), the breeding female becomes pelagic and rises to the surface at the time when the young are just ready to be liberated from the brood pouch, thereby ensuring the widest possible distribution for the young. A similar habit may be more generally characteristic of other species of the group, and introduces another factor which may influence movements.

Finally, Russell has called attention (1927) to the occurrence of immature mysids in plankton catches, taken in mid-water, suggesting that in the immature stages mysids are more planktonic in habit than in the adult condition.

A planktonic habit in mysids, therefore, may be either (i) permanent, or (ii) a temporary but normal and intermittent habit in the bottom-living forms, in the layers of water immediately over their haunts, varying in intensity with environmental factors such as light, wave action, temperature, and so on, or (iii) a breeding habit either during the actual processes of mating and egg laying, or to ensure a wide distribution for the young, or (iv) a habit characteristic of the immature phases.

In attempting to analyse the results of a series of tow-nettings such as the present one, it is difficult to assess the precise factor which was operating at the time of the catch or to estimate the degree to which one or more factors have combined to influence the result. Nevertheless some points of interest have emerged from this study.

THE MYSIDS AS A WHOLE

In Fig. 1 the total number of mysids caught in each tow-netting at each of the three stations has been plotted in graph form. The whole of the mysids were picked out and counted, and the figures reduced to 30 min. hauls so as to be strictly comparable.

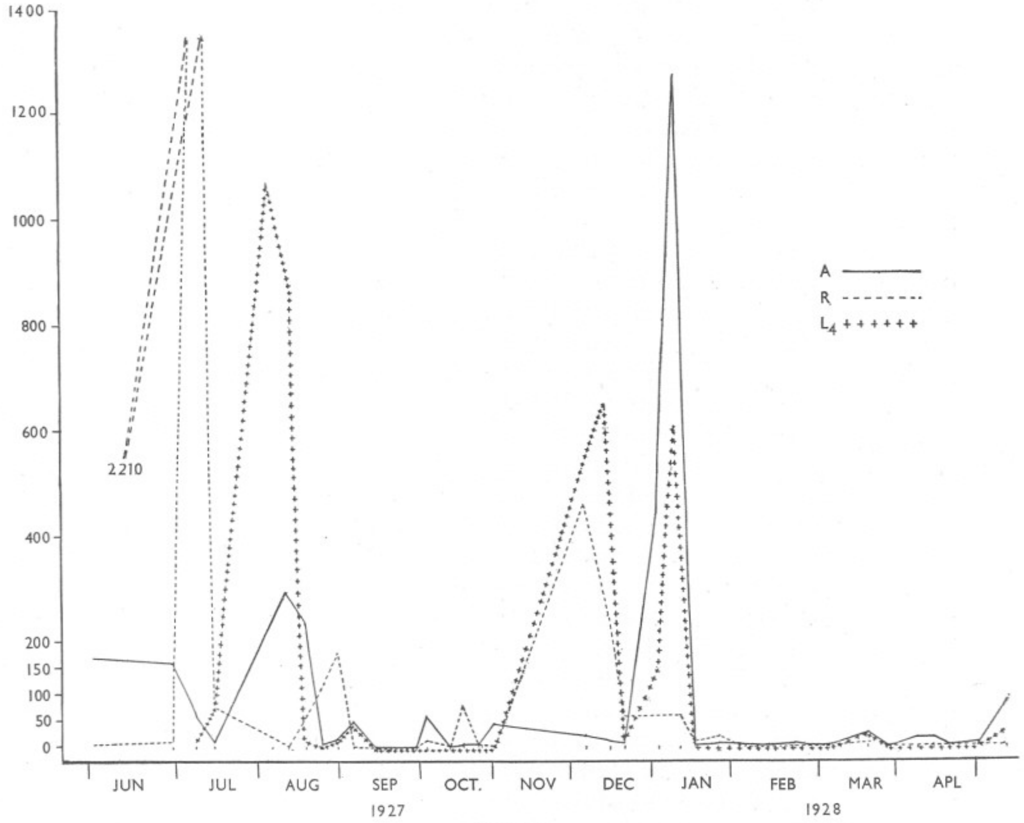

Fig. 1

From this graph it is apparent at once that, during two periods of the year, mysids appeared in the bottom plankton in very large numbers. These two periods are (i) from June to August 1927, and (ii) December 1927 and January 1928. At the other times of the year the number of mysids were small and probably represent a more or less normal picture of the idle and intermittent swimming movements of mysids in the bottom layer. The summer and winter maxima represent unusual activity for which an explanation must be sought. It is to be noted that the maxima did not always appear simultaneously at the three stations, but, taken as a whole, they are well marked.

Further analyses of the maxima show that the summer one is almost completely dominated by *Leptomysis gracilis* and that the high numbers in the catches at this period were almost entirely composed of this species. In the winter maximum, on the contrary, *L. gracilis* played a very insignificant part (negligible but for one haul of 209 specimens on 15. xii. 27) in the swarms of mysids which occurred. The dominant species was *Schistomysis ornata*, while *Anchialina agilis*, the two species of *Gastrosaccus*, and *Neomysis longicornis* also contributed considerably. The difference between the composition of the two maxima is brought out rather strikingly in Table I. In compiling this table I have selected *all* the hauls in which more than 100 specimens of mysids occurred. This is a purely arbitrary number chosen for convenience. There were sixteen such hauls, curiously enough eight in each maximum. I give the total number of mysids in each haul and the numbers of each species represented.

The occurrence of a summer maximum of *Leptomysis gracilis* is not a feature confined to the year 1927–8, but was further indicated in the year 1930 by an examination of the catches in oblique hauls above the bottom recorded by Russell (1933). Mr Russell kindly sent me the samples of the July and August hauls in that year on which the figures given in Table I of his paper are based. All the specimens submitted to me belong to *L. gracilis* except one specimen of *Neomysis longicornis*. Although these results are not strictly comparable with those of the bottom stramin net it is evident that, in 1930, *Leptomysis gracilis* was the most abundant species in the plankton in July and August, and produced a peak of the same nature, though less marked, as in the bottom catches in 1927. There is, however, much less evidence of a winter maximum in the plankton in 1930–1. On February 4 1930, 100 specimens of mysids were caught, and from November 13 1930 to April 16 1931, mysids occurred in only one haul, that on January 15 1931, when ten specimens were found.

A further difference between the two maxima must be noted. The summer maximum of *L. gracilis* is composed equally of adults of both sexes and immature forms. The precise details will be found under *L. gracilis* later in this paper, where it will be seen that, broadly speaking, immature specimens were abundant in June, and adults in July and August. Moreover, the adults were actively breeding, females with eggs or embryos in the brood pouch being present in considerable numbers. It would appear that *L. gracilis* becomes markedly planktonic during the breeding season and that the summer maximum of mysids is an expression of this reproductive activity.

On the other hand, the winter maximum of mysids was composed almost entirely of immature specimens, about half-grown or less. A few breeding females of *Schistomysis ornata*, and *Anchialina agilis*, and two breeding females of *Gastrosaccus spinifer* occurred in the winter hauls, but the number of adult specimens was very small and not at all comparable to the numbers of adult *Leptomysis gracilis* in the summer maximum. The winter maximum is obviously correlated with breeding activity among the species which compose

Table I. Composition of Mysid Fauna during Periods of Maximum Abundance

This includes the sixteen tow-nettings during the year in which the total number of mysids caught exceeded 100.

Summer maximum		Total no. of mysids	*Siriella jaltensis*	*S. clausi*	*S. armata*	*Gastrosaccus spinifer*	*G. normani*	*Anchialina agilis*	*Erythrops elegans*	*Mysidopsis angusta*	*M. gibbosa*	*Leptomysis gracilis*	*L. lingvura*	*Schistomysis ornata*	*Neomysis longicornis*
2. vi. 27	A	163	..	..	..	2	..	..	1	..	..	146	..	2	12
29. vi. 27	A	315	..	..	..	..	..	..	2	..	..	306	..	5	2
8. vii. 27	R	2210	..	..	..	..	..	9	2	..	..	2184	..	..	7
5. viii. 27	L4	1063	..	..	..	..	..	3	1	..	..	1011	..	4	44
12. viii. 27	A	294	..	..	..	..	..	..	..	..	..	284	..	3	7
	L4	885	..	..	..	..	..	2	..	1	..	875	..	2	5
19. viii. 27	A	235	..	..	..	..	1	6	1	4	3	166	..	47	7
25. viii. 27	R	108	..	..	..	..	..	2	..	..	..	94	..	6	6
Winter maximum															
6. xii. 27	R	450	2	..	..	..	2	116	1	1	2	3	1	326	1
	L4	527	..	..	..	..	7	195	6	14	7	8	..	285	5
15. xii. 27	R	233	1	..	..	..	4	6	4	3	..	1	3	209	2
	L4	643	1	..	..	18	238	30	2	3	1	209	..	56	85
3. i. 28	A	449	..	..	..	78	79	94	1	1	..	8	..	162	16
	L4	154	2	4	..	16	17	27	1	1	..	4	..	72	9
11. i. 28	A	1268	25	..	..	30	46	195	..	..	1	4	2	867	98
	L4	620	19	..	..	55	68	90	1	1	..	3	..	321	62

it, but these species do not appear to become markedly planktonic in the adult condition for breeding purposes, as does *L. gracilis*. In Table II, I have put together the data showing the months of the year in which the species dealt with in this paper are known to breed. A correlation of the data here presented with the analyses of the bottom plankton hauls will show that no other species of mysids behaves in the same way as *L. gracilis*. There is a suggestion of the same behaviour in *Schistomysis ornata* and *Anchialina agilis* but it is not nearly so definite.

TABLE II. BREEDING OF MYSIDS

Showing the months of the year in which the species dealt with in this paper have been recorded to breed. The table is compiled from data provided by the present material (T), the Plymouth Marine Fauna, 2nd edition, 1931 (P), and Colosi, 1929 for the Mediterranean (C).

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Siriella armata	..	..	..	P	..	P	..	T	..	P	..	..
S. jaltensis	..	..	C	..	..	P	..	..	C	..	..	..
S. clausi	..	..	C	C	..	..	..	C	C	C	..	..
Gastrosaccus spinifer	T	..	..	..	..	..	..	..	..	..	..	..
G. normani	..	..	..	..	..	..	..	T	P	PC	..	..
Anchialina agilis	T	T	TC	..	..	P	..	C	..	TC	..	T
Erythrops elegans	..	..	..	..	..	P	..	..	..	P	..	..
Mysidopsis angusta	..	T	..	..	..	P	P	P	P	PT	..	T
M. gibbosa	..	..	..	P	..	..	P	..	..	..	T	..
Leptomysis gracilis	..	..	..	..	..	PT	T	T	T	T	..	..
L. lingvura	..	..	C	CP	C	C	C	..	C	PC	..	..
Schistomysis ornata	T	P	..	PT	T	..	..	T	T	P	..	T
Neomysis longicornis	..	..	..	..	T	PT	P	PT	P	P	P	..
Heteromysis formosa	..	..	..	..	..	..	..	..	..	P	P	..

The further question arises as to why there should be large numbers of immature forms in the bottom plankton during the winter and not at other times. Table II shows that mysids were breeding at other times of the year yet immature specimens were not conspicuously abundant in the bottom plankton hauls. In *Schistomysis ornata*, for instance, one of the dominating species of the winter maximum, adult females carrying eggs or embryos occurred in August, September and October, but there was no corresponding large number of immature forms in the bottom plankton. *Anchialina agilis* was also breeding earlier in the year without any marked accession of immature forms to the plankton. The explanation of these facts is probably to be found in an observation made by Russell (1927). He there notes the appearance of numbers of immature mysids in mid-water tow-nettings in July. This observation suggests that immature forms are more planktonic in habit than the adults, and that for the greater part of the year the young forms are to be sought for higher up in the water than the immediate bottom layer. In winter, conditions (e.g. temperature) are less favourable to a mid-water habit and the young forms are driven into deeper water and become concentrated in the bottom layer. On this assumption the winter maximum in the bottom layer would be an expression of the operation of a different set of factors from that which brings about the summer maximum. At other times of the year the young forms might be scattered over a much greater range of depth of water. Moreover, the immature forms of the spring, summer and autumn broods rapidly become adult and sink to the bottom to take up their normal bottom-haunting life. The immature forms found in winter represent the overwintering stages of the species concerned and remain in the immature or non-breeding condition for a much longer period than is customary in the summer broods. If, as it appears, immature stages are more planktonic than adults, a greater concentration of young forms is to be expected in the winter months.

The winter of 1927–8 was not abnormal in respect to its winter maximum. Mr Russell has sent me some figures for bottom plankton hauls made in 1932–3 and these show markedly high numbers for December and January. I have not examined the material but the results suggest a winter maximum of the same nature as in the winter 1927–8.

NOTES ON THE SPECIES OF MYSIDS

Fourteen species in all were found in the collection, of which one, *Gastrosaccus spinifer*, has not been recorded previously from the Plymouth area, though known from other parts of Devonshire and Cornwall.

Siriella armata (M.-Ed.).

Cawsand Bay, 12. viii. 27, seven specimens including one adult ♀, carrying embryos. A, 18. x. 27, one immature specimen.

Breeding females have been recorded from the Plymouth area in April, June and October. The occurrence of a breeding female in August fills a gap in this series and suggests that the species has a continuous breeding period at Plymouth lasting at least from April to October. This does not agree with the results of Fage's work at Concarneau where he found that the breeding period of the species extended from September to March.

Siriella jaltensis Czern.

6. xii. 27, R, 2 juv.: 15. xii. 27, R, 1 juv.; L4, 1 juv.: 21. xii. 27, R, 1 ♂: 3. i. 28, A, 3 ♂, 4 juv.; L4, 2 juv.: 11. i. 28, A, 7 ♂, 2 ♀, 16 juv.; R, 2 juv.; L4, 6 ♂, 13 ♀: 26. i. 28, R, 1 ♂, 1 ♀; L4, 1 ♂.

The species only occurred during the time of the winter maximum and then only in small numbers. No breeding specimens were found and none of the specimens is fully mature. This material throws no new light on the breeding season. The only Plymouth records of the breeding season refer to specimens caught in June. Fage (1933) gives the early spring, March and April, and the late summer, August and September, as the breeding times of this species at Concarneau. The only Plymouth record is just midway between these two periods.

Siriella clausi G. O. Sars.

3. i. 28, A, 1 adult ♀; L4, 1 adult ♂, 3 juv.: 17. i. 28, R, 4 juv.; L4, 3 juv.

None of the specimens is breeding and all but two are immature. The species was only met with during the winter maximum. There are no records of breeding females for Plymouth. Fage (1933) gives the same breeding season at Concarneau for this species as for *S. jaltensis*.

Gastrosaccus spinifer (Goës).

2. vi. 27, A, 2 juv.: 15. xii. 27, L4, 18 juv.: 21. xii. 27, A, 1 juv.: 3. i. 28, A, 2 ♀, 78 juv.; L4, 16 juv.: 11. i. 28, A, 30 juv.; R, 5 juv.; L4, 1 ♂, 1 ♀, 51 juv.: 30. iv. 28, A, 1 juv.

This species is new to the Plymouth fauna. It has, however, been recorded from Starcross, the mouth of the R. Exe, and Padstow (Norman & Scott, 1906). The two females caught at St. A in January were carrying eggs in the brood pouch. Fage (1933) states that at Concarneau breeding females were found from February to May.

Gastrosaccus normani (G. O. Sars).

	A			R			L4		
	♂	♀	juv.	♂	♀	juv.	♂	♀	juv.
15. vii. 27	..	..	..	..	..	..	..	..	1
19. viii. 27	..	1	..	..	..	..	..	..	..
6. ix. 27	..	1	1	..	..	..	..	..	..
4. x. 27	2	1	..	..	..	..	..	..	..
1. xi. 27	..	..	1	..	..	..	..	..	..
6. xii. 27	..	..	2	..	..	2	..	..	7
15 xii. 27	..	..	2	..	..	4	..	..	238
21. xii. 27	..	..	3	..	..	2	..	..	..
3. i. 28	..	..	79	..	..	..	..	..	17
11. i. 28	..	..	46	..	..	8	..	..	68
26. i. 28	..	..	..	4	4	..	..	..	..
23. iii. 28	..	..	..	1	..	..	..	..	..

Only one female carrying eggs appears in the collection and that was taken at St. A in August. Fage (1933) notes that the species is more abundant in the night plankton from the end of the summer to the end of the autumn and that this is its breeding season. In the present collection large numbers of immature specimens appeared in the bottom plankton in December and January. Previous Plymouth records show that breeding females have been found in September and October. The Plymouth observations, therefore, support Fage's conclusions that the summer and autumn are the breeding season for this species. The large number of immature specimens found in December and January represent the last of the autumn broods which are overwintering in the immature condition and will probably breed early in the spring.

One further point should be mentioned. Some of the specimens caught on January 11 and all those caught on January 26 and March 23 1928, had forwardly directed lobes on the carapace exactly as is found in *G. sanctus*, but the pleopods of the males of such lobed specimens were clearly of the *G. normani* type. I have already called attention (1908) to the occurrence of lobed specimens captured by the "Huxley" in the Bay of Biscay in August 1906. I have never been able to solve this problem, but it does appear that the presence or absence of such lobes on the carapace is not infallible as a specific character.

Anchialina agilis (G. O. Sars).

	A			R			L4		
	♂	♀	juv.	♂	♀	juv.	♂	♀	juv.
8. vii. 27	..	..	..	..	..	18	..	..	..
5. viii. 27	..	..	..	..	..	..	3	..	..
12. viii. 27	..	..	..	..	..	..	2	..	..
19. viii. 27	2	4	..	..	..	..	..	..	..
25. viii. 27	..	..	..	1	1	..	1	..	..
31. viii. 27	..	..	..	4	1	..	..	..	..
6. ix. 27	..	2	..	..	..	..	..	..	..
15. ix. 27	..	..	..	1	..	..	..	..	..
4. x. 27	2	1	..	..	2	..	..	..	..
18. x. 27	2	..	..	..	..	..	..	..	..
25. x. 27	1	..	..	..	..	..	..	..	..
1. xi. 27	7	5	7	..	..	..	..	..	..
6. xii. 27	..	..	14	20	5	91	23	28	144
15. xii. 27	..	..	—	..	1	5	..	1	29
21. xii. 27	..	..	—	2	4	25	..	..	5
3. i. 28	21	24	51	..	..	..	3	2	22
11. i. 28	18	17	160	..	..	11	9	17	64
17. i. 28	..	..	..	..	1	3	..	..	..
26. i. 28	..	..	1	1	..	..	..	1	..
24. ii. 28	..	..	3	..	..	..	..	..	..
23. iii. 28	4	1	..	2	..	..	..	1	..

This species occurred sparingly in the adult condition during most of the year, but in December 1927 and January 1928 large numbers of immature specimens, accompanied by a good many adults contributed to the winter maximum. Breeding females occurred in October and December 1927, and January, February and March 1928. The large number of immature specimens in the winter is clearly correlated with active reproduction during the winter months. The increased number of adults in the winter also suggests that *Anchialina agilis*, like *Leptomysis gracilis*, becomes more planktonic and active in its movements during the breeding season. This reproductive planktonic phase in the adult is not so marked as in *L. gracilis*, but is perhaps more emphatic than in *Schistomysis ornata*. Other Plymouth records show that breeding females have been taken there in June. None of the specimens caught between July and October 1927 were actually carrying eggs or embryos, though some of them looked as if they had recently shed their brood.

Erythrops elegans (G. O. Sars).

2. vi. 27, A, 1 ♀; R, 1 ♂: 29. vi. 27, A, 2 ♀: 8. vii. 27, R, 3 ♀: 5. viii. 27, L4, 1 ♂: 19. viii. 27, A, 1 ♂: 18. x. 27, A, 1 ♀; R, 1 ♂: 1. xi. 27, A, 1 ♂: 6. xii. 27, R, 1 ♂; L4, 1 ♂, 5 ♀: 15. xii. 27, R, 1 ♂, 3 ♀; L4, 2 juv.: 3. i. 28, A, 1 ♂; L4, 1 ♀: 11. i. 28, L4, 1 ♀: 23. iii. 28, A, 2 ♀: 18. iv. 28, A, 2 ♂, 2 juv.

No breeding females occurred in the plankton, and the species made no contribution either to the summer or winter maximum.

Mysidopsis angusta G. O. Sars.

2. vi. 27, R, 1 ♂: 12. viii. 27, L4, 1 ♂: 19. viii. 27, A, 2 ♂, 2 ♀: 4. x. 27, A, 2 ♂, 1 ♀: 18. x. 27, A, 1 ♀: 25. x. 27, A, 1 ♂: 1. xi. 27, A, 1 ♂: 6. xii. 27, R, 1 ♂; L4, 3 ♂, 4 ♀, 7 juv.: 15. xii. 27, R, 1 ♂, 1 ♀, 1 juv.; L4, 1 ♂, 2 juv.: 21. xii. 27, R, 1 ♀, 4 juv.; L4, 1 juv.: 3. i. 28, A, 1 ♀; L4, 1 ♂: 11. i. 28, L4, 1 juv.: 23. ii. 28, A, 2 ♀: 23. iii. 28, L4, 2 ♂, 1 ♀: 23. iv. 28, A, 1 ♂; L4, 1 juv.: 30. iv. 28, A, 1 juv.: 11. v. 28, A, 1 ♀.

Breeding females occurred in October, December and February. The Plymouth records show a more or less continuous breeding season from June to February. The species contributes nothing to either the summer or winter maximum, but occurs as isolated specimens or in very small numbers all the year round in the bottom plankton.

Mysidopsis gibbosa G. O. Sars.

19. viii. 27, A, 3 ♀: 1. xi. 27, A, 1 ♀: 6. xii. 27, R, 2 juv.; L4, 1 juv.: 15. xii. 27, L4, 1 juv.: 11. i. 28, A, 1 ♀: 23. ii. 28, A, 1 ♂, 1 ♀.

The single specimen caught on November 1 1927, was a breeding female with embryos. Previous Plymouth records refer to breeding females caught in April and July. This suggests that the species has a continuous breeding season extending from April to November. The species is apparently a casual member of the bottom plankton fauna.

Leptomysis gracilis (G. O. Sars).

	A			R			L4		
	♂	♀	juv.	♂	♀	juv.	♂	♀	juv.
2. vi. 27	70	60	16	2	..	3	..	..	..
29. vi. 27	14	26	266	1	..	19	..	..	..
8. vii. 27	12	9	38	2180 (not sexed)			6	2	9
15. vii. 27	..	..	15	13	6	7	4	1	60
5. viii. 27	..	..	..	..	..	..	467	544	..
12. viii. 27	163	121	..	..	2	..	415	460	..
19. viii. 27	50	116	..	25	26	..	4	6	..
25. viii. 27	1	..	5	36	58	..	..	..	..
31. viii. 27	4	1	..	42	44	..	..	..	..
6. ix. 27	21	20	..	..	..	..	22	20	..
15. ix. 27	..	..	..	..	..	..	..	1	..
4. x. 27	28	15	3	5	1	..	2	..	1
18. x. 27	..	..	2	4	4	..	..	..	..
25. x. 27	2	..	..	..	..	..	..	..	..
1. xi. 27	4	5	..	2	..	..	..	..	..
6. xii. 27	..	..	2	..	..	3	2	..	6
15. xii. 27	..	..	7	..	..	1	..	1	208
21. xii. 27	..	..	..	..	..	2	..	..	..
3. i. 28	7	1	..	..	..	..	..	..	4
11. i. 28	..	..	4	..	..	8	1	..	2
17. i. 28	..	..	..	..	..	..	1	..	..
14. ii. 28	..	1	..	..	..	..	1	1	..
24. ii. 28	1	..	..	..	..	..	..	..	..
23. iii. 28	..	..	2	..	..	..	..	3	..
12. iv. 28	..	..	14	..	..	..	..	..	..
18. iv. 28	..	1	1	..	..	1	1	1	..
23. iv. 28	..	..	..	..	..	..	..	3	..
30. iv. 28	..	..	..	..	1	1	1	..	..
11. v. 28	25	55	..	..	..	..	11	13	..

This species is entirely responsible for the summer maximum of mysids in the bottom layer of water. Plymouth records, based mainly on the evidence of this collection, show that the species is actively breeding from June to October, females carrying eggs or embryos appearing in considerable numbers throughout that period. No breeding females were found after October and the numbers of specimens of the species in the bottom layers fell considerably for the remainder of the year from November to May. The only exception occurred on December 15 1927 at L4, when 208 immature specimens were caught. Adults again became numerous in the plankton in May and indicate that the species was again preparing for the breeding season.

The present material seems to suggest that *L. gracilis* becomes very active in the adult breeding condition, and leaves the actual bottom for a planktonic life at that time. They remain, however, in the bottom layer of water and here the young are liberated. It will be noticed from the table that during the breeding season the number of immature specimens in the bottom layer is not very large. The evidence supplied by Russell (1927) suggests that the immature forms at this time are to be found in the higher layers of water, about midway between the surface and bottom. In the winter months the immature stages are driven into deeper water, and the occurrence of 208 specimens at L4 in December 1927 seems to be explained on these grounds. In other words the depth position of the larvae in the plankton is influenced by environmental factors, probably by the temperature of the water.

This species therefore provides evidence of two types of movement, (i) a movement from a bottom living to a planktonic life in the adult condition for breeding purposes, and (ii) a migration of the immature forms to greater or lesser depths according to the season of the year, movements which are presumably influenced by temperature.

Leptomysis lingvura (G. O. Sars).

1. xi. 27, A, 1 ♂: 6. xii. 27, R, 1 juv.: 15. xii. 27, R, 3 juv.: 21. xii. 27, A, 2 juv.; R, 1 juv.: 11. i. 28, A, 2 juv.: 23. iii. 28, A, 1 juv.

All the specimens but one are immature and no breeding females were taken. Plymouth records refer to breeding females caught in April and October, but in the Mediterranean the breeding season appears to be a continuous one from March to October (Colosi, 1929).

Schistomysis ornata (G. O. Sars).

	A			R			L4		
	♂	♀	juv.	♂	♀	juv.	♂	♀	juv.
2. vi. 27	..	..	2	..	..	..	..	..	..
29. vi. 27	1	2	2	..	..	..	..	..	..
5. viii. 27	..	..	..	..	..	..	1	..	3
12. viii. 27	1	1	1	..	..	..	..	..	..
19. viii. 27	18	23	6	1	1	..	..	..	..
25. viii. 27	..	1	..	1	3	2	..	..	..

Schistomysis ornata (G. O. Sars) (*cont.*)

	A			R			L4		
31. viii. 27	6	1	..	..	..	..	..	..	..
30. ix. 27	..	..	..	..	1	..	..	..	..
4. x. 27	1	1	4	1	2	..	..	..	..
18. x. 27	..	..	..	1	3	2	..	..	..
1. xi. 27	2	3	9	..	..	..	..	..	1
6. xii. 27	..	..	1	..	..	326	..	..	285
15. xii. 27	..	..	1	8	17	184	1	1	54
21. xii. 27	..	..	..	1	3	6	1	..	..
3. i. 28	..	1	161	..	..	..	..	2	70
11. i. 28	..	..	867	..	..	20	..	..	321
26. i. 28	..	1	..	4	3	..	..	..	..
3. ii. 28	..	..	..	..	..	2	..	..	..
29. ii. 28	..	..	..	..	..	..	..	2	..
23. iii. 28	2	1	2	..	1	..	3	3	7
12. iv. 28	..	1	..	..	..	..	..	..	..
18. iv. 28	1	1	8	..	..	..	..	..	..
23. iv. 28	..	..	1	..	..	..	..	..	..
11. v. 28	..	1	1	..	..	..	..	..	..

The numbers of adult specimens in the bottom layer of water was never very large and may, for the most part, be accounted for as the result of a normal habit of swimming about idly near their bottom haunts. There is a faint suggestion that when breeding these movements are more marked, for on August 19 1927, when forty-one adults were caught at St. A, and on December 15 1927, when twenty-five adults were caught at St. R, the females in both hauls were carrying eggs or embryos. Such breeding movements are not nearly so well marked and definite as in *Leptomysis gracilis*, or in *Anchialina agilis*. On the other hand, immature specimens were largely responsible for the winter maximum of mysids in the bottom layer of water. The evidence from adult specimens shows that there was considerable breeding activity during December and January. From Table II, however, this species would appear to be breeding practically all the year round. In the present material breeding females occurred in January, April, May, August, September and December, and other Plymouth records show that breeding females have occurred in February and October. The question naturally arises as to what happens to the immature forms at other seasons of the year except the winter. The table of the occurrence of this species during 1927–8 shows no marked accession of immature forms to the bottom plankton at these times and there is no other evidence available. Russell (1927) does not mention this species when observing that immature mysids are to be found in mid-water hauls in considerable numbers. His remarks refer mainly to *Leptomysis gracilis*. It is possible, however, that at seasons of the year, other than winter, the immature forms may inhabit layers of water higher up than the bottom layer and that this may account for their absence in the bottom water at times other than winter when the adults are actively breeding.

To sum up, *Schistomysis ornata* does show some slight movements from its bottom living haunts to the bottom water for breeding purposes, but the movement is not nearly so marked or so definite as in *Leptomysis gracilis*. Large numbers of immature forms occur in the bottom layer of the plankton in the winter, but there is no evidence of what happens to these immature forms at other seasons of the year.

Neomysis longicornis (M.-Ed.).

	A			R			L4		
	♂	♀	juv.	♂	♀	juv.	♂	♀	juv.
2. vi. 27	6	4	2	..	..	..	..	..	..
29. vi. 27	1	1	..	..	..	..	..	..	..
8. vii. 27	..	..	..	8	6	..	..	..	..
15. vii. 27	1	1	..	..	..	..	..	..	..
5. viii. 27	..	..	..	..	..	..	15	29	..
12. viii. 27	6	1	..	..	..	..	1	2	1
19. viii. 27	5	1	1	4	2	..	..	..	..
25. viii. 27	..	..	..	4	2	..	..	..	..
31. viii. 27	2	2	1	..	..	..	..	..	..
6. ix. 27	6	..	..	..	..	..	..	..	..
4. x. 27	..	1	..	..	..	..	..	..	..
6. xii. 27	..	..	..	..	1	..	..	5	..
15. xii. 27	..	..	..	1	..	1	5	1	79
3. i. 28	6	2	8	..	..	..	6	1	2
11. i. 28	21	19	48	..	..	..	29	34	4
24. ii. 28	..	3	..	..	..	..	..	..	..
23. iii. 28	..	..	..	1	..	..	..	..	..
11. v. 28	..	3	..	..	..	..	..	..	..

This species appears to behave very much as *Schistomysis ornata*. It occurred in small numbers fairly regularly throughout the year. Breeding females were captured in May, June and August, and the Plymouth records indicate a continuous period of breeding activity from May to November. The species took part in the winter maximum of mysids, there being a small accession of immature and young forms to the bottom layer of water in December and January.

Heteromysis formosa S. J. Smith.

23. iii. 28, L4, 1 adult ♂.

SUMMARY

An analysis is made of the mysids which occurred in a series of bottom stramin net plankton hauls made at three stations in the Plymouth area in 1927–8.

There were two marked maxima in numbers of mysids, a summer one in July and August, and a winter one in December and January.

The summer maximum was due entirely to *Leptomysis gracilis*.

The winter maximum was due mainly to *Schistomysis ornata* and *Anchialina agilis*, but the two species of *Gastrosaccus*, and *Neomysis longicornis* also contributed to a lesser degree.

The summer maximum was composed mainly of adult males and breeding females of *Leptomysis gracilis* which appear to become markedly

planktonic in habit at the breeding season though keeping to the deeper layers. Immature specimens were present but the majority were probably higher up in the water (mid-water).

There is a suggestion that a similar planktonic habit is to be found in *Schistomysis ornata* and *Anchialina agilis* during their breeding period in the winter, but it is not nearly so marked as in *Leptomysis gracilis*.

The winter maximum is mainly due to large numbers of immature forms and it is suggested that environmental factors, probably temperature, cause a concentration of immature stages in the bottom water during winter. At other times of the year these immature forms are distributed over a much greater depth range of water.

Idle swimming movements just over the bottom are a normal habit of bottom living mysids.

The collection provides evidence of three types of movements in mysids: (i) idle swimming just over the bottom, (ii) definite and marked movements into the plankton in the adult condition during the breeding season, and (iii) movements of the immature forms to greater or lesser depths according to environmental conditions, probably temperature.

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THE BIOLOGY OF *PURPURA LAPILLUS*. PART II. GROWTH

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(Text-figs. 1–6)

In a previous paper (Moore, 1936) an account was given of certain variations in the shape and colour of the shell in *Purpura*, and it was pointed out that these variations are apparently controlled by diet. It was shown that growth ceases at the onset of sexual maturity, and at the same time other changes such as the thickening of the edge of the shell take place. It was shown also that both the proportion of the population exhibiting these changes, and the average size at which they occur, vary considerably from one locality to another, this variation also being apparently correlated with the nature of the animal's diet. The present paper consists of a study of the growth of the shell and soft parts and an attempt to show whether the observed differences in size at sexual maturity in different populations are to be accounted for by differences in the growth rate during the growing phase.

The growth rate of this species is difficult to determine for several reasons. In the first place, as will be shown later (Moore, 1938, p. 67), the young and the adults live in different habitats, thus rendering it impossible to obtain a representative sample of the whole population. Even were this possible, the animal breeds throughout the year, so that its size distribution does not show year groups from which growth can be determined. I was therefore forced to use a method of marking individual shells, which involved the marking of large numbers, their release on the shore, and the subsequent recapture at intervals of the small proportion which could be found. If a true picture is to be obtained of growth under normal conditions it is essential that the growth period under observation should be passed in the natural habitat on the shore; but the very small shells could not be found again after they had been marked, and the difficulties of marking them were considerable. In practice therefore it was found necessary to determine the growth of the very small sizes in a laboratory tank, and to assume that the results so obtained were at any rate some indication of what the growth would have been under normal conditions. By linking these figures with those for larger animals living under natural conditions on the shore an approximate picture of the total growth of the animal has been obtained.

The young *Purpura* were obtained from egg capsules brought in from the shore when on the point of hatching, or, on one occasion, from eggs laid in a tank in the laboratory. They were kept in sea water in finger bowls until they hatched, when they were transferred to stones well covered with the polychaete *Spirorbis borealis* and free from algae and sponges. The stones were placed in a tank in which tides consisting of 8¼ hr. immersion and 4¼ hr. emersion were maintained electrically, and the tank was screened from too bright light to avoid excessive algal growth. The young *Purpura* lived well in such a habitat on a diet of *Spirorbis*, and showed little tendency to climb out of the water as they do when no tide is supplied. It was found, however, that the duration of the tide was of little consequence so long as the animals were uncovered at intervals. In addition to the above experiments, a few very small *Purpura* were brought in from the shore and their shells painted with cellulose paint, so that new growth appeared as clean shell. As there was a suggestion of a normal change of diet with increasing size (see Moore, 1938, p. 67), some stones covered with small *Balanus balanoides* were included as an alternative diet.

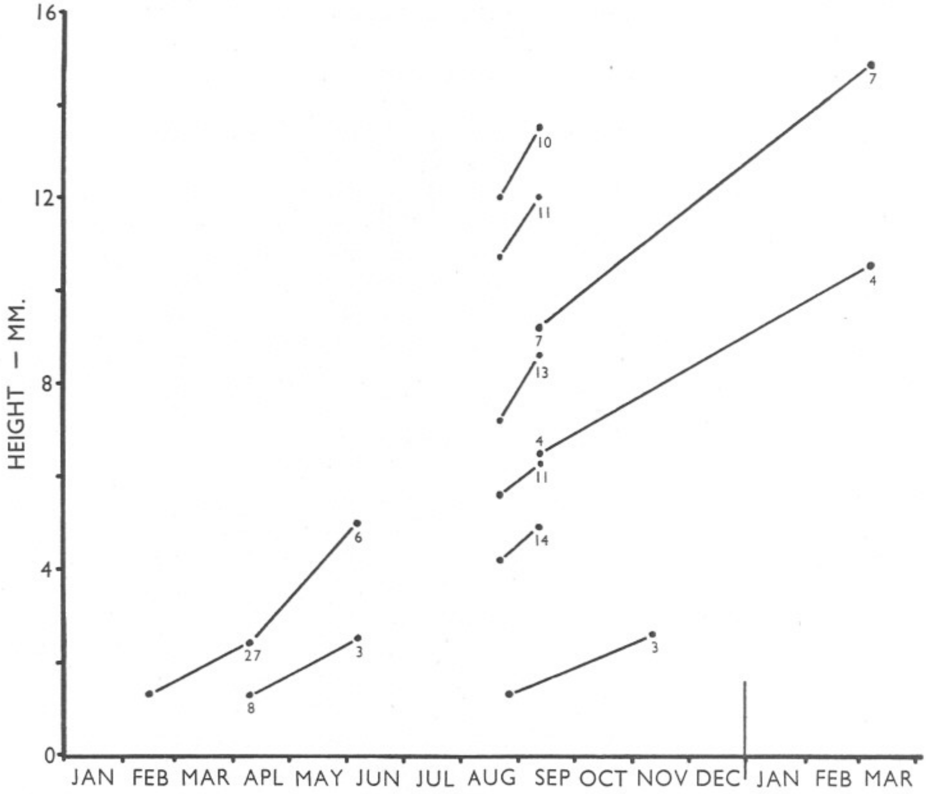

Fig. 1. Growth of batches of young *Purpura* in a tidal tank at Plymouth. Figures indicate numbers of individuals. Height at hatching approximately 1·3 mm.

The results from these experiments are brought together in Fig. 1. The series is incomplete, and the numbers of individuals are small, but the results may at least be taken as suggesting a growth of from 10 to 15 mm. in the first year. Laboratory conditions are probably very much closer to normal for these small *Purpura*, which live in sheltered crevices and under stones, than they would be for the larger animals which live in the open, and whose feeding is more dependent on weather conditions. Colton (1916) has attempted to estimate the growth of this species at Mount Desert Island from the number of rings on the shell, believing that these rings are formed each winter. He adduces no evidence to prove this, and as he makes no mention of the important matter of cessation of growth at sexual maturity, his results must remain open to doubt. If, however, his assumptions are correct, his figure of 11–15 mm. high at the first winter is comparable with the results obtained at Plymouth.

Drake's Island, in Plymouth Sound, was used for the main field experiments on the growth of the larger sizes. The method of marking was similar to that described for *Littorina littorea* (Moore, 1937, p. 723), the lip of the shell being notched with a carborundum wheel, and the apex of the shell dipped in cellulose paint. In September 1934, 2745 such marked shells were released on Drake's Island, on the same spot from which they were collected. Of these, the sex of 995 was determined and indicated by a different colour of paint, but as no difference of growth rate was found in the two sexes, and as it was later realized that growth occurs only while the animal is sexually immature, it was decided to combine the results from all the marked animals. The living shells were recaptured at intervals and taken back to the laboratory for measurement of growth. During this process, care was taken to keep them cool, and they were returned to the shore as soon as possible, either the same or the next day. The numbers of growing shells recaptured, together with the amounts of growth, are shown in Fig. 2. This figure also shows the results for a further 1500 shells which were released in May 1935 a short way from the first group, the numbers of the first group recaptured having by then dropped to so low a figure as to necessitate replacements.

The method of calculating the amount of increase in height of a shell corresponding to an observed increment to the lip has already been described for *Littorina littorea* (Moore, 1937, p. 727), and is applicable in the same way to *Purpura* once the necessary constants and their variation with size of shell have been determined for the population in question. The shells, when brought in to the laboratory, were sorted into millimetre groups according to their height, and the increment to the lip of the shell measured for each individual. From these figures the mean increment of height, and hence the mean initial height at marking, were determined for each group. Owing to the gap between the last measurement of the first group of animals on March 27, and the release of the second group on May 8, it was necessary to calculate what the growth would have been during that period on the assumption that the rate was the same as during the previous period of January 9 to March 27, the value so obtained being then used as a base line for the growth of the second group.

Although only growing, thin type, shells were used for the growth experiments, it is probable that the cessation of growth at the onset of sexual maturity is not instantaneous, so that at any rate some of the decrease in growth rate of the largest sizes is to be accounted for in this way. If we assume a height for the young shells of 10–15 mm. at the end of their first year, then they will grow about another 11 mm. in their second year, and a slightly smaller growth rate in their third year would bring them to sexual maturity (at a mean size of 29·5 mm. for this population) at from 2½ to 3 years old. The error due to abnormal conditions in the young stages is unlikely to be more than ±6 months at the outside.

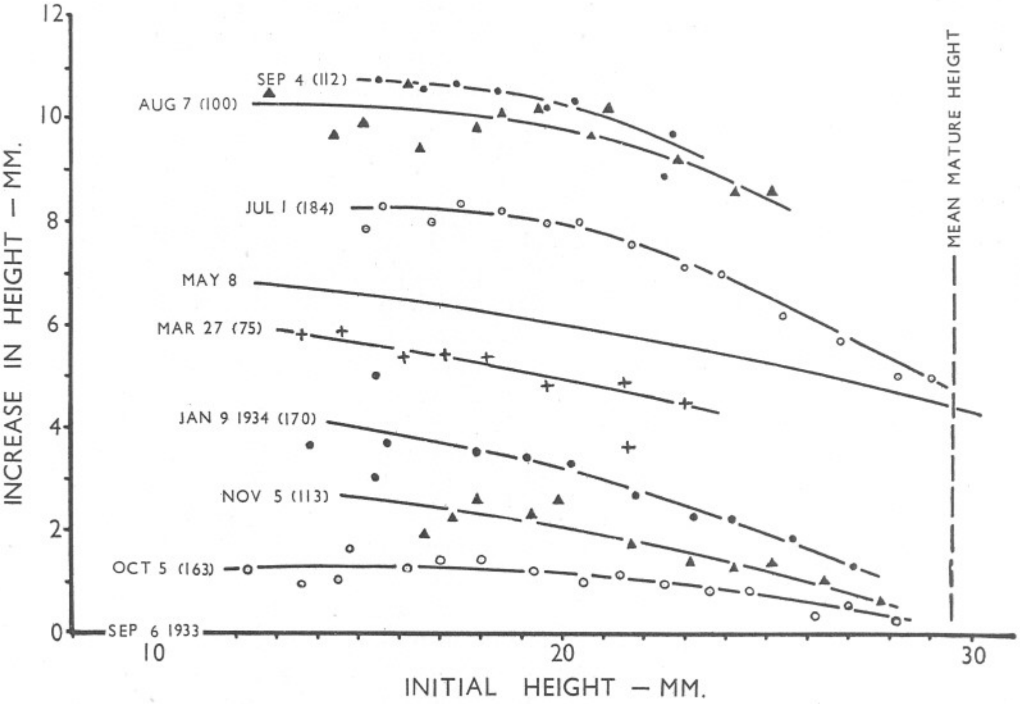

Fig. 2. Curves, at intervals up to one year, relating growth of large *Purpura* on the shore at Drake's Island, to initial height of shell. Each point represents the mean for a group of animals, and the total number for each curve is shown in brackets.

A small number of results are available also from shells kept on the shore at Port Erin, in the Isle of Man (Fig. 3); consecutive measurements of height were obtained from individual animals which had been marked with serially numbered silver tags wired to the lip of the shell. No data are available here for the growth rate of the young shells, but for the larger ones the average growth seems to be about 8–10 mm. per year. These curves show clearly the cessation of growth of the shell at sexual maturity. Colton's figures show an increase of two to five millimetres in height per year after the first year, but this may have included maturing or mature animals. Growth data for a short period during the summer from a number of localities in Devon and Cornwall (see below) show a growth of 0·5–4 mm. per hundred days, the localities having been chosen to represent extremes of certain environmental characters.

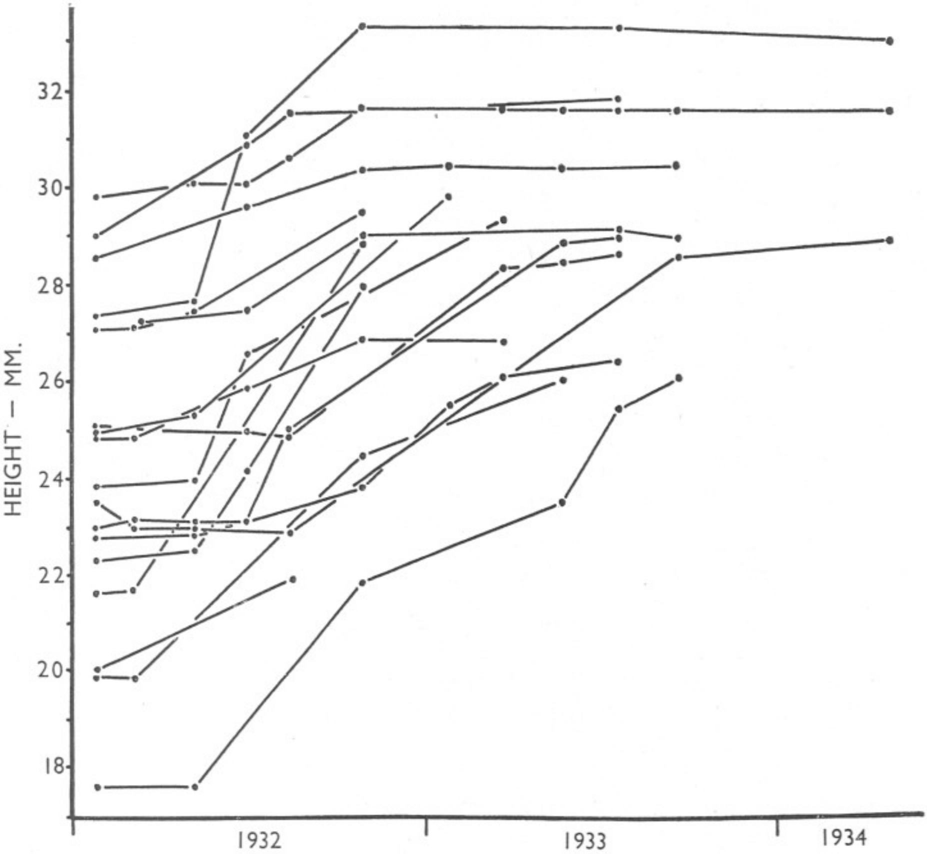

Fig. 3. Growth of individual *Purpura* on the shore at Port Erin, Isle of Man.

In comparing populations of *Purpura* from different localities, it was found (Moore, 1936) that there was a definite tendency for those which had fed on a diet of *Mytilus edulis*, in contradistinction to one of barnacles, to attain sexual maturity, with cessation of shell growth, at a greater size, but for there to be a smaller proportion of the mature, non-growing phase in the population. The percentage of these non-growing shells varied from 0 to 98 %, which seemed too wide a range to be accounted for by hastening or delay of maturity unless this were correlated with a considerable variation in growth rate. In the hope of testing the latter point, samples were taken in the summers of 1935 and

1936 from various selected localities in the west of England, marked in the usual way, and released in the places from which they were collected. After approximately three months these animals were recaptured, and the amounts of new shell growth measured. To obtain an adequate picture of the local growth conditions it would be essential to know the growth rate of all sizes of shells, but it was clearly impossible in the time available to deal with any but the larger sizes which could be found again on the shore. It would also have been desirable to work a larger number of localities, but the labour involved would have been too great. The principal characteristics of the populations and localities are shown in Table I. The localities are shown in the maps in my paper of 1936, where fuller details of the other characteristics are also given. The mean thick type height is the height at sexual maturity; the wave-exposure scale ranges from 0 = complete shelter, to 100 = exposure to all winds from all quarters; the abundance of *Mytilus* ranges from 0 = absent to + + + + = very abundant.

TABLE I

Locality	Mean thick type height (mm.)	Percentage of thick type in population	Wave exposure	Abundance of *Mytilus*
Porthcurno	18·9	88·6	9	0
Wanson Mouth	19·9	89·7	55	+
Bedruthan Steps	24·6	6·9	51	+ + + +
Trebarwith Sands	27·0	4·0	12	+ + + +
Salthouse	27·4	92·6	54	+ + + +
Biddle Head, Salcombe	28·7	81·8	6	0
Duckpool	29·4	3·6	45	+ + + +
Drake's Island	29·5	54·7	0	+ +

The results obtained are shown in Fig. 4, and unfortunately they are inconclusive so far as the original problem is concerned. It is true that the *Purpura* from Biddle Head, Salcombe, which attain the large size at maturity of 28·7 mm., also show the highest growth rate, while Wanson Mouth with the lowest growth rate shows the small size at maturity of 19·9 mm. It is possible that this is significant, but the localities with intermediate mature heights show very varying growth rates, and Porthcurno, which attains an even smaller height at maturity than Wanson Mouth, has not nearly so low a growth rate, at least in the sizes used in the experiment. More detailed experiments would be necessary to clear up these points, but certain facts of value emerge from the experiments. In the first place the rates of growth in different localities are very different. Individuals of two centimetres high from Salcombe, for example, grow at ten times the rate of those of similar height from Wanson Mouth. The other noteworthy point is the lack of constancy in the relation of growth rate to size of shell, some populations increasing in growth rate with increasing size while others decrease. This is perhaps to be accounted for by variations in the relative values of the food supply in the young, *Spirorbis*-fed, stages, and the older, *Mytilus*- or barnacle-fed, stages in the different localities.

The seasonal variation in tissue weight was determined in material from Misery Point, at the mouth of the river Yealm. Samples of the thick and thin types were taken at intervals and sorted into millimetre groups. Twenty individuals from each group were then dropped into boiling water for a minute, removed from their shells, and both animals and shells dried to a constant weight in a boiling water oven. The question of shell weight was dealt with in a previous paper, and it was found that it showed no seasonal variation. In

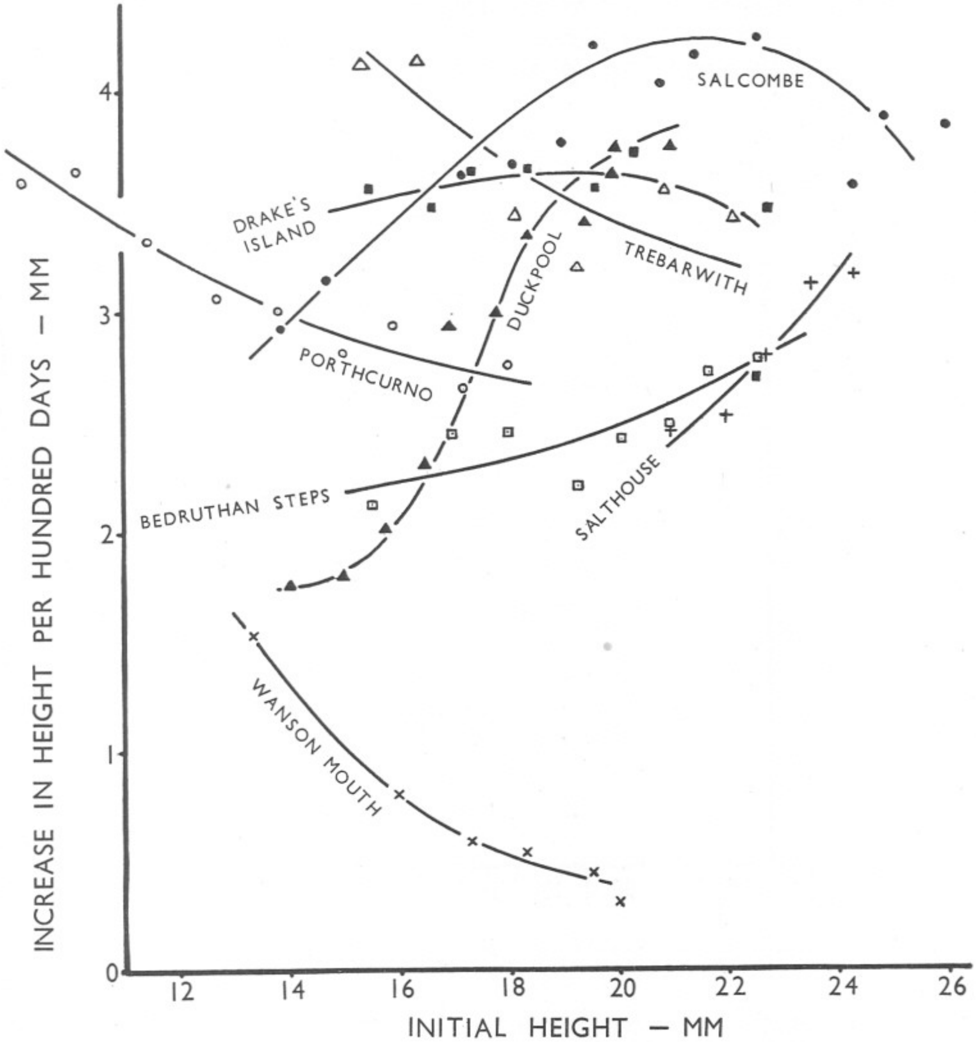

Fig. 4. The relation of growth to initial height in *Purpura* from different localities for a short period during the summer.

the thin-shelled immature animals, no significant seasonal variation in the tissue weight was found either, but the mature animals showed a considerable variation. Fig. 5 shows the seasonal changes in tissue weight of a *Purpura* 25·5 mm. in height, which is the mean size for mature shells for this locality. As will be seen, the tissue weight drops rapidly from October to the beginning of April, and then rises again up to July, when observations ceased. This drop in weight may be caused by spawning, or by inability of the animal to obtain adequate nourishment during the winter months when the weather is too stormy for it to come out onto the open rocks to obtain its food. This latter explanation is unlikely, however, as the locality is well sheltered from the open sea, and no such winter drop in weight is shown by the larger immature animals feeding on the same diet and side by side with those that were mature. Yet another possibility is that the drop in weight is not directly due to the loss of ova or sperm, but to cessation of feeding during the period when the

Fig. 5. Seasonal variation in tissue weight of mature (non-growing) *Purpura*, 25·5 mm. high, at Misery Point, Yealm.

animals congregate in crevices to deposit their eggs. In any case, however, the drop in weight appears to be associated in some way with spawning. Pelseneer (1935, p. 445) quotes Peach as giving January to April as the principal spawning season of this species, and Garstang as giving January to April and September. Colton (1916) says that the young are hatched throughout the greater part of the summer, but most in August, and, allowing for their taking four months to hatch, as stated by Pelseneer (1935, p. 527), they would have been laid about April. In the Plymouth neighbourhood, although egg capsules are to be found throughout the year, they seem to be most abundant in the early summer, and the tissue weight curves suggest that the main spawning period is during the winter and spring.

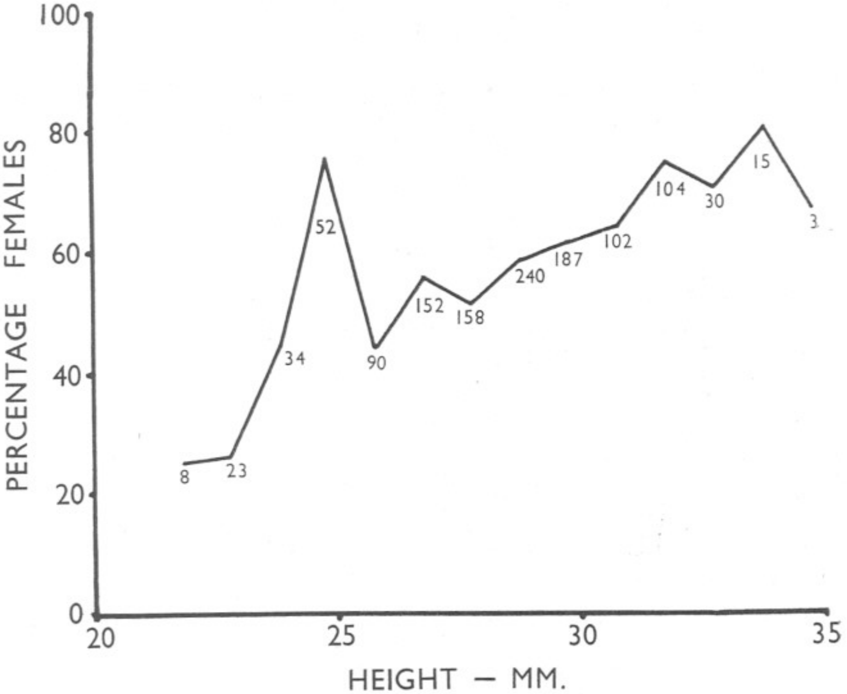

Fig. 6. Variation in the percentage of females in relation to size, in a sample of *Purpura* from Drake's Island. Figures indicate numbers examined.

Although the experiments with marked shells failed to show any difference in the rates of growth of males and females, a test was made to see whether the two sexes matured at the same size. The material was collected from Drake's Island in July 1935, and 1195 individuals of the mature, thick type, were examined. Sex was determined by the presence or absence of a penis. The size distribution for each sex was then determined in millimetre groups. Females were more abundant in the ratio of 700 to 498, and, as shown in Fig. 6, the proportion of females increases in the larger sizes. This increase could not be accounted for by protandrous hermaphroditism, since growth ceases at maturity in both sexes, and must be due to some inherent difference in growth rate or age at maturity of the two sexes. Actually this increase chiefly affects those individuals whose size departs far from the mean, the mean sizes of the two sexes being 28·77 ± 0·088 mm. for the females, and 28·18 ± 0·105 mm. for the males, the difference, 0·59 ± 0·137 mm., being small but significant. Pelseneer also (1935, pp. 414–15) notes the high proportion of females in this species, and that the proportion increases with age.

In conclusion I wish to express my great indebtedness to all those who have assisted in the collection of this material, and in particular the staff of the Plymouth Laboratory, Dr A. Gibson, Mr J. R. Bruce, and Messrs W. Searle and C. Haughton.

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THE BIOLOGY OF *PURPURA LAPILLUS*. PART III. LIFE HISTORY AND RELATION TO ENVIRONMENTAL FACTORS

By Hilary B. Moore, Ph.D.

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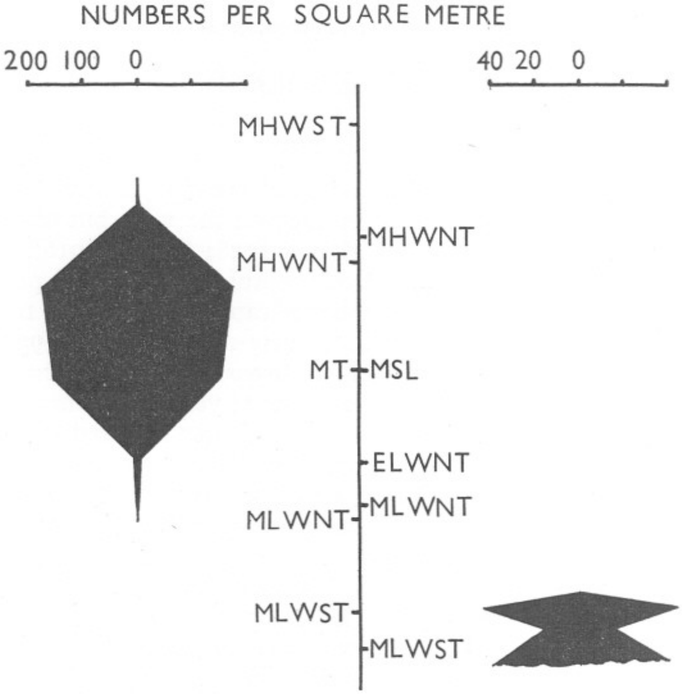
(Text-fig. 1 and Plate I)

Life History

The eggs of *Purpura* are laid in vase-shaped capsules, attached in clusters to the rocks. Spawning takes place throughout the year, but chiefly in the winter and spring (Pelseneer, 1935; Moore, 1938; Colton, 1916). It is said to take more than an hour to produce one capsule, and 24 hr to produce ten (Pelseneer, 1935, p. 508), and the number of capsules laid at one time is said to average fifteen, and to range from six to thirty-one (Pelseneer, 1935, p. 490). Cooke (1895, p. 124) states that a single *Purpura* produces as many as 245 capsules. The capsules contain a large number of yolky eggs, the estimates of the numbers of these per capsule varying from three hundred to a thousand (Colton, 1916; Pelseneer, 1935, p. 527). Most of these ova are unfertilized and serve as food for the few embryos which develop: five to forty according to Pelseneer (1935, p. 481), ten to twelve according to Colton (1916). The time of development is about 4 months (Pelseneer 1935, p. 527). The capsules are laid in crevices in the rocks, or sometimes under stones, but at the same tidal level as that inhabited by the adults. The young, when hatched, are generally supposed to retreat into cracks in the rocks, presumably at the same level, and Colton states that they feed there on small *Mytilus*. I myself have examined many such crevices close to hatching groups of *Purpura* eggs, but have rarely found young shells less than 5 mm. high in them. On the other hand I have frequently found numbers of young *Purpura* down to 2 mm. in height living among the tubicolous polychaete *Spirorbis borealis* on the underside of stones at a much lower tidal level than that inhabited by the adults, and have come to the conclusion that this is their normal habitat for the first few months. And, since the distance would be great for such small shells to walk, it seems probable that they are washed down there by wave action, from the capsules from which they have hatched. In experiments in a tidal tank (Moore, 1938), it was found that the newly hatched *Purpura* would not eat even very small barnacles, but lived well on a diet of *Spirorbis*. It was noticed further, that at a height of about 8–10 mm., they showed a tendency to climb out of the tank as if conditions there did not suit them, and that this tendency was stopped if they were provided with some stones covered with barnacles. It is probable therefore that at about this size they normally change their diet and begin to move up the shore on to the barnacle-covered rocks, and it is at about this size that they are first found there in any numbers. Probably even then they at first spend a good deal more of their time sheltering in crevices than do the larger individuals, a possibility which has already been suggested on the ground of shell coloration (Moore, 1936, p. 82). The difference in tidal level of the young and adult habitats is clearly brought out in Text-fig. 1.



Text-fig. 1. Vertical distribution of adult *Purpura* (> 10 mm.) at Òb Allt an Daraich, on barnacle-covered rocks (left), and of young (< 10 mm.) under *Spirorbis*-covered stones at Wembury (right). Note that, owing to tidal differences in the two localities, the relative tidal levels do not exactly coincide.

The diet which the adult *Purpura* seems to prefer is barnacles, either *Balanus balanoides* or *Chthamalus stellatus*. They do not bore the shells of the barnacles, but force the valves apart and then eat out the soft parts. Dubois (1909), in discussing the extremely toxic nature of purpurin, suggests that the animal may use it to kill and relax its prey so that it can force the valves apart and attack the exposed body. It is quite possible that this may happen with barnacles, although nothing can be seen of the process, since the greater part of the barnacle is covered by the foot of the *Purpura* attacking it. Various gastropods are attacked by *Purpura* including *Patella vulgata*, *Gibbula cinerarea* and *G. umbilicalis*, *Littorina littorea*, *L. obtusata* and even sometimes *Purpura* itself, although in the last-named I have never seen a shell which was bored right through. The hole has been shown to be bored entirely by the radula, unaided by any acid secretion (Pelseneer, 1935). The mollusc which is most subject to attack, and in some places comprises the entire diet of the *Purpura*, is the mussel *Mytilus edulis*. Fischer-Piette (1935) has given an extremely interesting account of the changes which took place on a piece of shore which was at first inhabited mainly by barnacles and by *Purpura* which fed on them. Over this shore there was an invasion of *Mytilus*, and gradually the *Purpura* ate all the available barnacles and found themselves forced to eat the mussels. Apparently they did this at first only when forced to, taking by preference their accustomed diet of barnacles. Their efforts to penetrate the mussels, which had never before been included in their diet, were at first clumsy. Some wasted time by boring holes in empty shells, and some even settled inside empty shells and bored a hole outwards. After a time these mistakes became less frequent and finally ceased, and later still the *Purpura* learned to force apart the valves of the smaller shells without having to bore them at all. Finally the *Purpura* killed so many mussels that the barnacles, which had been displaced from the rocks, were able to recolonize them, and eventually the *Purpura* returned to their original barnacle diet. This slowness of the *Purpura* in learning to utilize mussels when these first colonize a normally barnacle-covered rock has been noted elsewhere also, and may account for the fact that in some places where the barnacle-covered rocks have small patches of mussels growing on them, the latter are left completely untouched by the *Purpura* which are feeding all round them on the barnacles, while in other apparently similar situations the bulk of the *Purpura* are feeding on the mussels, and a few only are on the barnacles. Fischer-Piette noted that when the barnacles recolonized the rocks the *Purpura* did not attack them until they were some six months old and had attained a fair size.

The mortality which they cause is very great: as described by Fischer-Piette it was sufficient to change the whole balance of life on a piece of shore. An estimate for the mortality rate of *Balanus balanoides* made at Port Erin (Moore, 1934, p. 860) was 35 and 21 % per annum at the two lower stations worked, this being probably almost entirely due to *Purpura* although these particular rocks were frequently cleared of all *Purpura*, as they were wanted for experiments on the growth of the barnacles. The rate would no doubt be much greater on rocks habitually crowded with *Purpura* like those shown in Plate I, fig. 1.

The *Purpura* do not feed continuously, and are frequently found clustered in large numbers in crevices, either for shelter or for the purpose of breeding. According to Fischer-Piette (1935) they are driven to shelter by extreme cold or by the risk of drying up, and they then pass into a state of aestivation. Probably this also is liable to happen after a large meal, and he notes that those which are living among clusters of mussels are frequently trapped at such times by the mussels' byssus threads, which become attached to their shells and anchor them so firmly that they are unable to escape and so die.

Relation to Environmental Factors

There are very few observations available on the tolerance of this species to variation in the environment, although certain notes on limiting values have been made. With regard to tidal level, Colman (1933) says that *Purpura* occurs at Wembury from one foot above mean sea level to half way between mean and equinoctial low water of spring tides, that is from 55 to 10 % emersion. Fischer-Piette (1936) gives its upper limit as high water of neap tides. It certainly does not extend above the upper limit of barnacles, and this is usually about high water of neap tides, unless elevated by splash. Usually, however, *Purpura* becomes less abundant some way below the top of the barnacle zone. Its lower limit is less well defined and varies greatly from one place to another. It can certainly live in the sublittoral zone in some places, and even down to a depth of 10 fathoms (Moore, 1936, p. 84), but this is unusual; extreme low water of spring tides is probably its normal lower limit, and its occurrence even as low as this will depend on the presence of barnacles or other suitable food at that level. In sheltered waters barnacles may not go below half-tide level, and unless there are *Mytilus* present the *Purpura* also will stop at that level. The above statement applies only to the larger sizes, above about 10 mm. in height. The young, as has already been shown, live in the *Spirorbis* zone which frequently takes the place of the *Balanus* zone towards low water, and all those places where we have found very small *Purpura* in abundance have been about low water of spring tides. It is usually difficult to find sufficiently large unbroken surfaces on which to make comparative counts of the density of population of the larger *Purpura* at the different levels, but Text-fig. 1 shows the result of such a count made at Òb Allt an Daraich, in Skye, one of the levels being also shown in Pl. I, fig. 1. The distribution of small *Purpura*, at a stage when they are still feeding on *Spirorbis*, made in a stony gully at Wembury, Devon, is also shown in Text-fig. 1, for comparison with the zonation of the adults.

Gowanloch (1927) gives the upper lethal temperature for *Purpura* as 35–35·5° C.; and the proximity of its northern limit of distribution to the 0° C. winter isotherm (Moore, 1936) suggests the presence of ice as the limiting factor there. Colton (1916) also comments on its absence from places where ice accumulates, whilst Gislén (1930) states that in the Gullmar Fjord it descends below low water for the winter, presumably to avoid the ice. Caullery (1929) has noted it as one of the species which suffered from the coincidence of a very cold spell during the winter on the Boulogne coast with the occurrence of low water of spring tides, and Orton & Lewis (1931) record the effect of the unusually cold weather in January–February 1929 in greatly reducing the proportion of *Purpura* to *Urosalpinx* on the oyster beds of the Blackwater estuary. On the latter occasion, however, it is not possible to say whether the result was directly due to the low temperature or perhaps to a reduction of tolerance to low salinity produced by the lowering of the temperature, comparable with that recorded by Broekhuysen (1936) for *Carcinus maenas*.

Its tolerance to low salinity is probably low, despite Pelseneer's statement (1935, p. 323) that it can survive 9·5 days in fresh water. Fischer (1928) records it in the estuary of La Rance between the salinities of 35·0 and 22·8 °/₀₀; Alexander, Southgate & Bassindale (1935) also state that it is confined to the extreme mouth of the Tees estuary (which, however, is strongly polluted), and it certainly does not penetrate beyond the extreme mouths of the Tamar and Yealm estuaries at Plymouth. Ökland also (1933) has shown that round the island of Tromö, *Purpura* does not occur where the summer salinities fall below 20–25 °/₀₀, even where *Mytilus* and *Balanus balanoides* offer abundant food for it. Fischer (1928) states that the eggs are tolerant of the same salinity range as the adults, but he found (1931), during a winter drop in salinity in La Rance estuary, that the eggs were killed although the adults survived.

With regard to limiting values of other factors there are practically no data available. Fischer (1927) gives its upper limit of *p*H in pools as 9·3, and later (1931) gives its *p*H range in pools as 9·3 to 7·45. He also gives its oxygen range in pools as 26 to 5·8 mg. per l. These figures however mean little without a knowledge of how long such conditions can be endured. *Purpura* occurs occasionally, though not commonly, in muddy surroundings, where it has the appearance of having been introduced accidentally and not having bred there. At Blue Anchor Bay, near Minehead, just beyond the extreme eastern limit of penetration of *Chthamalus stellatus* up the south side of the Bristol Channel, no *Purpura* were found, although *Balanus balanoides* was present in small numbers. The limiting factor here was probably the muddiness of the shore.

ENEMIES

There are no data available at present as to the mortality rate or normal duration of life of *Purpura*. Several marked individuals lived on the shore at Port Erin for 2¼ years, and were probably 1½–2½ years old when first marked, but they can probably live much longer than this. If the rings found on the shells of *Purpura* by Colton were really annual, then the oldest specimens recorded by him were 7 years old, but these must have been much slower in maturing than is normal in England, since at maturity they would stop growing and form no more annual rings, that is if cessation of growth occurs at all in his communities.

Various animals are recorded as occasionally eating *Purpura*, although most of them probably do not take sufficient numbers to have any appreciable effect on the community as a whole. Colton (1916) suggests that they may be taken by *Gadus virens* at Mount Desert Island, and probably wrasse sometimes take them in English waters. Bauer (1913) has found that shells of *Nassa* inhabited by hermit crabs frequently show a fracture of the last whorl which suggests that they have been broken open by the crab and the animal eaten out of them. He further suggests that the thickening of the lip found in some species of *Nassa* is a protection against the attacks of hermit crabs. Since empty shells of *Purpura* also are frequently found inhabited by hermit crabs the same suggestions would presumably apply to them, but my own impression is that they occupy only shells which are already empty, and that the fractured shells found are the work of birds.

Probably the most serious enemies of *Purpura* are birds, and these in certain localities only. Dewar (1910) has given a detailed account of how *Purpura* shells are broken open by oyster-catchers (*Haematopus ostralegus*). The *Purpura* are removed from the rock and carried either to a crevice or to a patch of firm sand where they can be held steady. They are then turned with the opening up, the lower part of the bill inserted between the operculum and the outer lip, and a piece of this lip broken away either by pressure or by hammering. The shell is then turned slightly and a second chip broken away in a similar manner, by which time the animal is sufficiently exposed for the soft parts to be picked out of the shell. A good many shells resist the attacks of the birds. In a later paper (1913) Dewar records that out of 294 *Purpura* attacked by oyster-catchers, 1 % had only one chip removed, 21 % were completely opened (two chips), while 78 % remained undamaged. He states also (1910) that *Purpura* is an uneconomical food for the oyster-catcher as compared with mussels. In 20 min. a single bird attacked seven shells and opened three of them, whereas many more mussels could have been opened in the time, and he says further that they only eat the *Purpura* sporadically, having a habit of feeding on them for a few days and then leaving them again completely. Colton (1916) says that herring gulls (*Larus argentatus*) eat them, swallowing the smaller shells whole, but carrying the larger shells into the air and dropping them until they break. He says too that on certain islands where the gulls are particularly numerous, the *Purpura* are practically exterminated. In the British Isles gulls certainly take *Purpura* at times as shown in Plate I, fig. 2, which is a photograph of part of the contents of a herring gull's nest containing numerous *Purpura* shells; but an examination of numbers of heaps of shells regurgitated by herring gulls on different parts of the coast shows that, while they may at times be feeding almost entirely on molluscs, *Purpura* forms only a very small proportion of their food.

The *Nassa* shells with a chip out of the lip, attributed by Bauer to the action of hermit crabs, seem to be very similar to those chipped open by oyster-catchers, and similarly chipped shells of *Purpura* have been found by us on grounds where oyster-catchers were common. Quite frequently the animal escapes, although with a damaged shell, and the proportion of shells showing a repaired fracture is high in some populations. Probably a similar cause accounts for the populations in which many of the animals have a damaged operculum or none at all. Cooke (1917) records one such population in which, out of 121 animals examined, fifty-six had damaged opercula, and eleven had none. Other birds also may attack *Purpura* on occasions, and there is even a record by Venables (1936) of a song-thrush which was seen hammering a *Purpura* on a stone during a spell of very cold weather, with a heap of dead *Purpura* shells alongside.

The shells may be attacked by boring algae such as *Gomontia* and *Plectonema* (Moore, 1936), and even very seriously pitted by their action, and the shell may also be damaged by the boring sponge *Cliona cellata* and the polychaete *Polydora*; but it is unlikely that any of these ever kill the animal, since it is able to repair a damaged shell. Various trematode parasites infect the soft parts and may destroy the reproductive organs, but probably these also rarely kill the animal.

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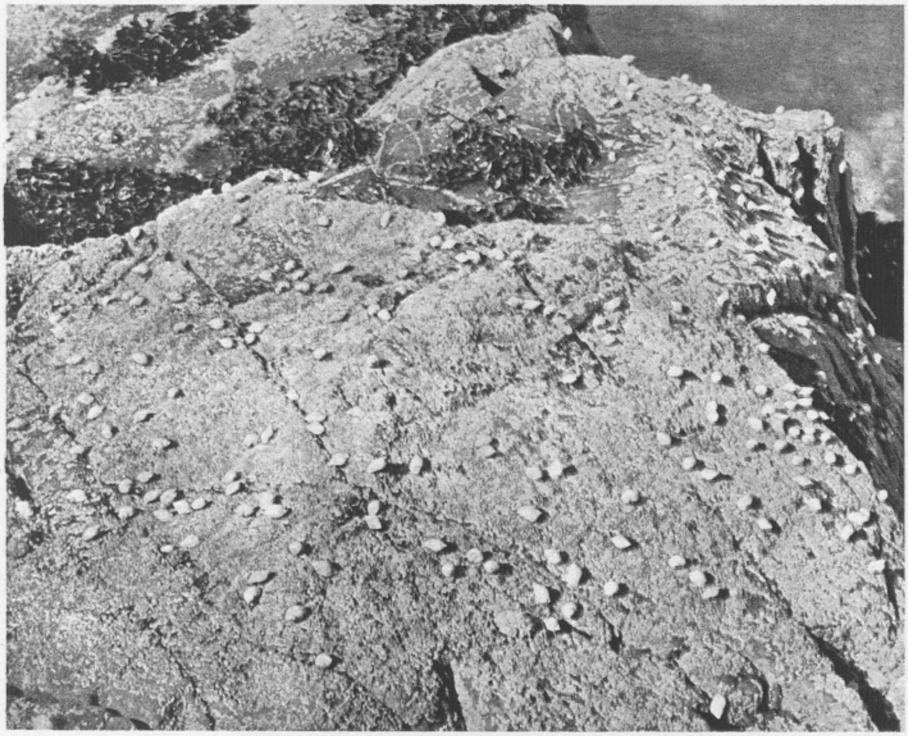
EXPLANATION OF PLATE I

Fig. 1. *Purpura* feeding on *Balanus balanoides* at Òb Allt an Daraich, Skye. 12. vi. 36.

Fig. 2. Part of the contents of a herring gull's nest, Geodha Chobhair, Sutherland, 24. vi. 36, showing fragments of *Purpura lapillus*, *Patella vulgata*, *Balanus balanoides*, *Cancer pagurus*, *Portunus puber* and egg shells. × 0·81.



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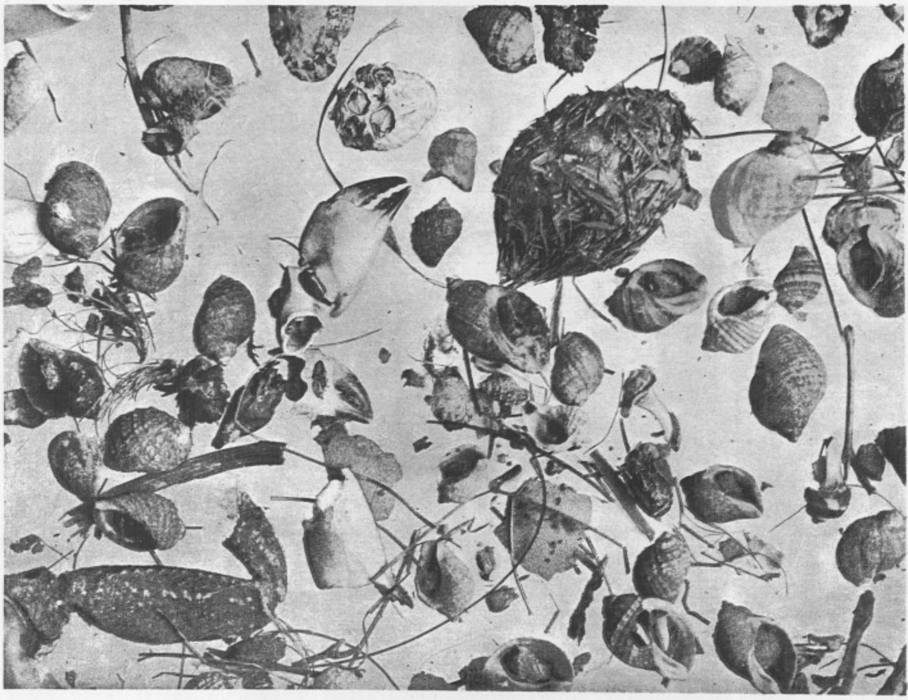

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AN INTERNAL FACTOR CONTROLLING POSTERIOR REGENERATION IN SYLLID POLYCHAETES

By Yô K. Okada

Kyoto Imperial University, Japan

(Text-figs. 1–3)

In a former paper (1929) it was stated that "regeneration takes place easily at the posterior end of divided syllids, but on cutting the most anterior part, the chitinous tube and massive proventriculus of the pharynx hinder the process of closing the wound and subsequent regeneration fails in most cases". The minimum length of so-called head pieces, in which regeneration of the tail can be effected, always comprises at least one or two more segments than those constituting the pharyngeal region. This length is internally occupied by a large chamber containing a series of highly specialized organs of ectodermal origin, extending as far as the first appearance of the moniliform intestine in a segmental cavity, which is separated from the previous one by a complete septum.

The peripharyngeal chamber is of different lengths in different species. The shortest length of the head pieces, which give caudal regeneration, also differs according to the species. The nature of this correlation between the anterior differentiation of segments and their physiological property of regeneration at the posterior end, is not yet elucidated. If, however, the cause of failure to regenerate at the posterior end in a head portion cut at the extreme anterior part of the body be assigned to the absence of certain internal structures in such an anterior portion, the formative factor of the posterior regeneration should then be correlated with the existence of such structures in the pieces and not with the physiological property of the segments involved.

Experiments with reference to this question were performed, during the summer of 1927 when I was working at the Plymouth Laboratory, on *Autolytus edwarsi*, which is very abundant in this district in close association with the hydroid *Obelia geniculata*. The anterior chamber of the species is composed of cavities corresponding to 9 or 10 anterior segments and the tail regenerates only beyond the 11th setigerous segment.

In the first series of experiments the animals were cut across at different levels of the pharyngeal part within the bounds of the region presumptively non-regenerative at the posterior end, after the intestine was forced into the anterior chamber. This was done by pressing the proventriculus forward forcibly with the back of a knife. This procedure made it possible, provided exceedingly anterior levels were not operated on, to retain a bit of the intestine in the isolated head pieces. The latter closed the wound more easily and the specimen lived longer than in the former experiments when the cut was made simply at the corresponding levels of the body. Moreover, some pieces were detected, when observed about 2 weeks later, regenerating more or less segments at the posterior end (see Fig. 1). The operation was repeated several times until a sufficient number of specimens was obtained to give conclusive results. From the results the following two facts emerged:

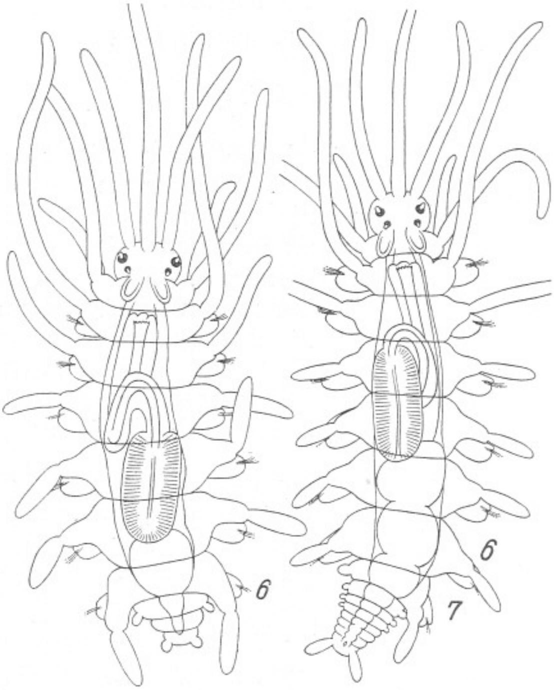

Fig. 1. Tail regeneration in short head pieces of *Autolytus edwarsi* in the presence of the intestine.

(1) Regeneration can take place posteriorly from any level after the 6th setigerous segment backwards, and this level at which posterior regeneration ceases is quite definite. For example, the anterior pieces isolated between the 5th and the 6th segments do not produce a tail, but if a small fragment of the 6th segment remains attached to the posterior end of the 5th segment, regeneration occurs at this end (see Fig. 2).

(2) Where regeneration occurs, the tail does not develop beyond the state of the pygidium, unless the intestine elongates and is in close contact with the body wall at the posterior end. It is only when the last mentioned condition

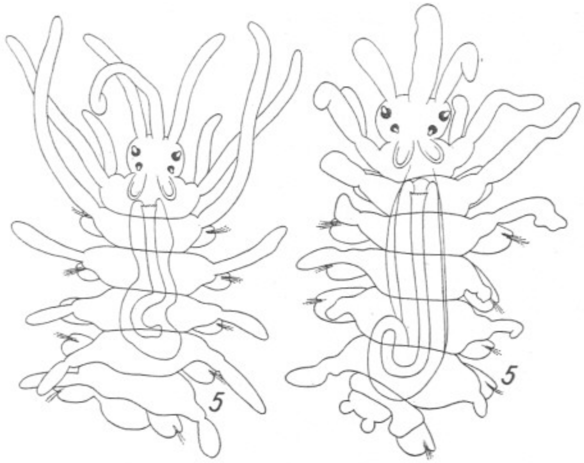

Fig. 2. Experimental demonstration of the anterior limit of tail regeneration of *Autolytus edwarsi*.

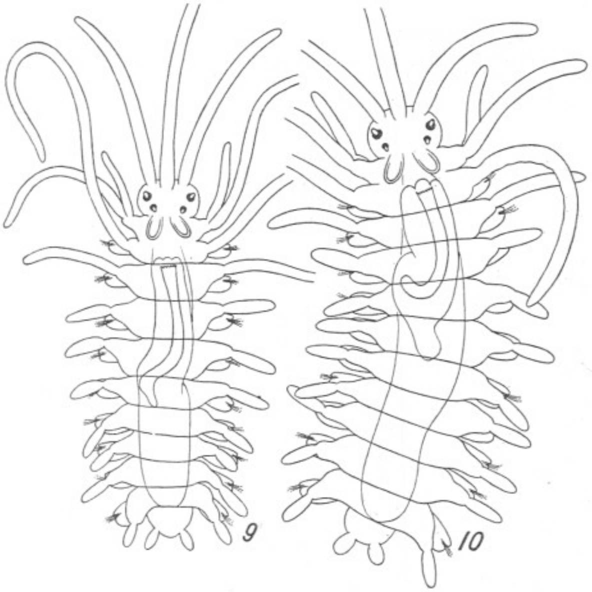

Fig. 3. Incomplete tail regeneration in long head pieces of *Autolytus edwarsi* in the absence of the intestine.

is fulfilled that the development proceeds further and a long tail is produced.

That the intestine plays an important role in the caudal regeneration of the syllid is obvious. But it remains for us to show what the role is.

Thereupon the intestine was removed from fairly long anterior pieces in which caudal regeneration is normally possible. This operation was done by pressing down the proventriculus with the back of a knife and drawing it out through the wound at the posterior end by a fine hooked needle. A cut was then made in front of the pushed-down proventriculus, and the more posterior part of the alimentary canal was removed including the intestine. The animals operated on lived well as in the preceding experiment. They closed the wound and most of them regenerated a tail, which, however, did no more than develop a caudal extremity (see Fig. 3). A pair of anal cirri was quite distinct but there appeared no other segments beside the pygidium.

From the second experiment it now becomes clear that the intestine is necessary for elongation and segmentation of the new tail. The intestine itself does not seem to modify the nature of regeneration. Nevertheless, none of these regenerates without the intestine produced a heteromorphic head.

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ON THE OCCURRENCE OF *JAXEA NOCTURNA* (CHIEREGHIN) NARDO OFF RAME HEAD, DEVON

By Ruth Rawlinson, M.Sc.

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(Plate II)

A single specimen of the rare thalassinid *Jaxea nocturna* was recently dredged from mud off Rame Head, Devon, by S.S. *Salpa* on September 3 1937 during the September Vacation Course at the Plymouth Laboratory. Prior to this there are only four records of the adults of this species in waters round the British Isles although they are abundant in the Adriatic Sea. Selbie (1915) summarizes the British records as far as 1914. The first individuals were taken as fragments from the stomachs of gurnards and *Pleuronectes cynoglossus* captured in the Firth of Clyde near Ailsa Craig (Scott, 1899); the next was from the Irish Sea, in mud, off Clogher Head, Co. Louth, at a depth of 32½ fathoms and in 1908 one was taken in Loch Fyne in 34 fathoms. The next record is a single specimen taken by Mr G. A. Stephen on March 26 1936 from the mud two miles south of Rame Head, and at a depth of 24 fathoms. Since September 3 1937 four more have been captured in the same locality, one on September 28 1937 and three on October 6 1937, using a new type of dredge.

The trachelifer larvae of *Jaxea nocturna* are quite widely distributed in British waters. They have been recorded from the Irish Sea and the west coast of Ireland (Selbie, 1915); the Clyde Estuary, and Tobermory, Mull (Scott, 1899); Barrow Channel, off Piel and Tremadoc Bay, Caernarvon (Scott, 1905); the English Channel between Looe and Eddystone (Bouvier, 1914); Plymouth Sound (Lebour, 1916) and Salcombe (Norman & Scott, 1906).

All the 1937 Plymouth adults, as far as one can judge without dissection, agree closely with the description of *J. nocturna* by Selbie (1915). One male and one female have been dissected for a careful examination of the body segments, appendages and gills. They show only minor points of difference from Selbie's account. Three teeth were present in the male on the anterior edge of the first pleura, as in Selbie's account, but they were absent from one side of the female and there was only one tooth on the other. The fifth pleura of two females were rather more rounded at the apex than figured by Selbie, but in the rest they were as figured by him. The second maxillipede is somewhat different. The epipodite has a distinct twist towards the proximal end and the merus bears long setae on its outer margin (Plate II, fig. 3).

Three of the Plymouth individuals were females and the other two males. The only obvious difference between the sexes is the absence of the first pair of pleopods from the male. Two of the specimens were approximately 36 mm. from the tip of the rostrum to the tip of the telson, and the others about 34 mm. The chelae, measured from the proximal end of the merus to the tip of the dactylopodite are about three-quarters the length of the body. Selbie's drawing gives the impression of a much longer chela than is present in the Plymouth specimens, but there is not really very much difference between them (see Plate II, fig. 1).

The specimen captured on September 3 1937 was kept alive in the laboratory until December 29 1937 at an average temperature of 57·1° F. in October, 52·7° F. in November, and 49·5° F. in December. During this time intermittent attempts were made to study its mode of feeding. It was kept in a square glass dish containing a layer of sand about an inch deep, and provided at various times with shreds of fish, *Mytilus*, living *Polystomella* and plankton. None of these were apparently eaten and, with the exception of the *Mytilus*, which was toyed with by the second peraeopods, all were ignored. The second pair of peraeopods are usually extended forwards beneath the head (Plate II, fig. 2), so that their tips are visible beneath the antennae when viewed from the dorsal surface. Their dactylopodites are flattened and may be folded back against the next segment. By their movements, fine particles are disturbed from the substratum and whisked towards the mouth. At intervals the third maxillipedes sweep downwards in a plane at right angles to the ground and may possibly capture particles disturbed by the second pair of walking legs. The chelae are held outstretched in front of the head and do not perform any definite movements apart from a regular swaying from side to side as the animal walks. The inner margin of their dactylopodites bears a fringe of long setae which are frequently thickly coated with fine particles. The animal did not make any attempt to burrow in the sand and unfortunately died before there was an opportunity of providing it with finer and deeper mud, as had been intended. The few observations which have been made on the movements of its appendages show resemblances to the burrowing and feeding movements described in *Callianassa californiensis* and *Upogebia pugettensis* by MacGinitie (1930, 1934). *Callianassa californiensis* uses its second and third pairs of legs as shovels, and also to sift the sand from the sides of the burrow for the detritus which accumulates on their setae; the detritus is scraped off by the third maxillipedes and then passed to the mouth. *Upogebia pugettensis* lives in mud burrows, feeding on suspended material. It holds its first and second walking legs so as to form a basket through which water is drawn from the entrance of the burrow by the movements of the swimmerets. The sieved particles are swept out of the basket at intervals by the outward and downward movements of the third maxillipedes and pass via the second maxillipedes to the mouth. If *Jaxea nocturna* lives in mud burrows, possibly between rocks, in places inaccessible to the usual dredging methods, the movements of the second pair of walking legs and the third maxillipedes suggest that its feeding mechanism is similar to that of the species described by MacGinitie. Whether *Jaxea* uses the fringed chelae to construct a basket like *Upogebia pugettensis*, scrapes sand like *Callianassa californiensis* Dana, or has some different, but probably very similar feeding method, is not known. These members of the Callianassidae, like some other detritus and suspension feeders of the tribe Anomura, use their third maxillipedes to sweep off food particles gathered by the anterior walking legs towards the mouth. One or more of the first three pairs of peraeopods is used by the three species described above. Among the Paguridae, *Eupagurus bernhardus* employs only the smaller claw of the first pair of peraeopods to gather food, which is passed on to the third maxillipedes (Orton, 1927), whereas other anomurans, for example *Galathea dispersa* and *Porcellana longicornis*, use their third maxillipedes to gather food particles from the substratum or from the water (Nicol, 1932).

My thanks are due to Dr Kemp for the loan of the four additional Plymouth specimens of *Jaxea nocturna*, and his permission to dissect one of them, and to Mr D. P. Wilson for the photograph published as fig. 1 in Plate II.

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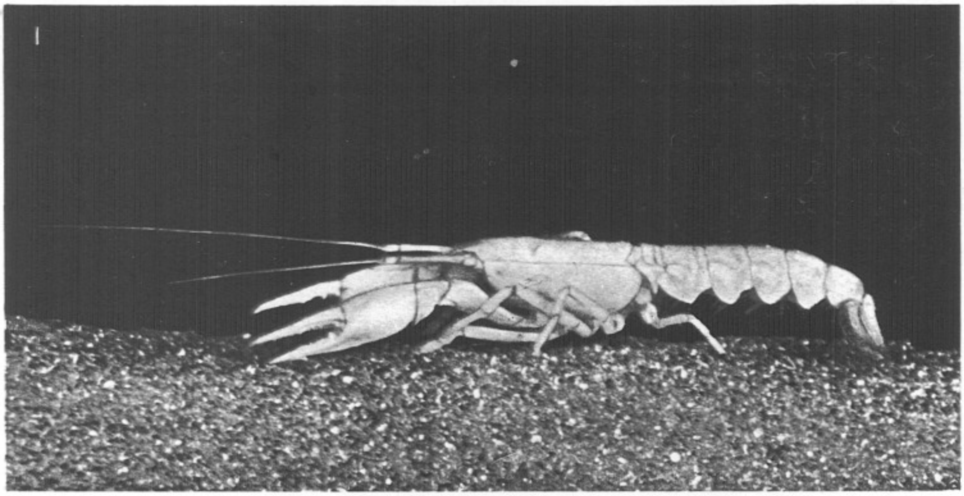
EXPLANATION OF PLATE II

Fig. 1. Side view of *Jaxea nocturna* ♂ (3. ix. 37). × 1·7. (Photograph by Mr D. P. Wilson.)

Fig. 2. *Jaxea nocturna* (♂), drawn from the living animal captured 3. ix. 37, from Rame mud, Plymouth. × 2·2.

Fig. 3. The second maxillipede of *Jaxea nocturna* showing the twisted epipodite. × 17.



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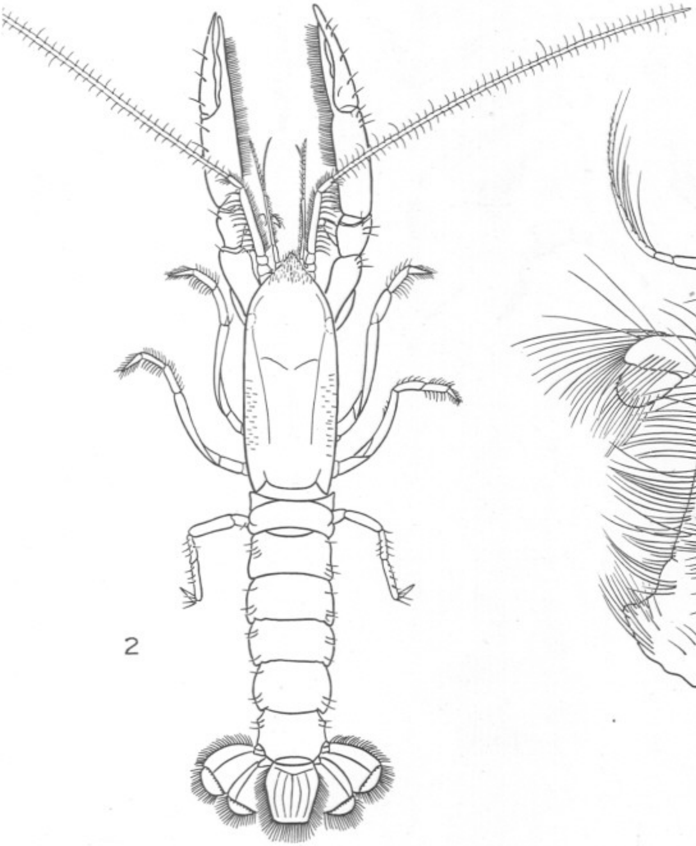

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THE INTERTIDAL FAUNA OF THE MERSEY ESTUARY

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(Plate III)

INTRODUCTION

During a general survey of the tidal banks of the Mersey Estuary observations on the nature of the banks and on the density of the burrowing animals inhabiting them were made and were supplemented by the identification of the more common macroscopic types found.

The positions of the different areas of mud and sand were determined by means of sextant angles and plotted by station pointers. These areas are shown in Plate III and reference to them in the text is made by means of the numbers shown on the Key Chart therein.

Specimens of the common macroscopic animals inhabiting the banks were preserved in formalin for subsequent identification.

The nature of the banks (whether mud or sand) and the abundance of the infauna were ascertained from inspection of the surface layers to a depth of about one foot. All the observations were made in the summer of 1933.

A detailed description of the topography and tidal conditions in the estuary, and the results of analyses of the water and of the material constituting the tidal banks and bed of the estuary, are given in *Water Pollution Research Technical Paper*, No. 7, issued by the Department of Scientific and Industrial Research (1937).

The estuary is divided into two natural divisions—the Outer Estuary or Liverpool Bay and the Upper Estuary. The Upper Estuary is that part of the estuary lying between Warrington and Rock Light. The Outer Estuary lies seaward of Rock Light and consists of a bay in which large areas of banks are exposed at low tide.

Of 37 sq. miles of tidal banks in the Outer and Upper Estuary as far as Runcorn Gap, approximately half occurs in the Outer and half in the Upper Estuary. Four-fifths (29 sq. miles) of the total area are banks of sand of which only 7½ sq. miles are inhabited (one-fifth of the total area). The remaining banks (one-fifth of the total or 7½ sq. miles) are of mud, and by far the greater area of mud occurs in the Upper Estuary, mainly along the Cheshire shore from Mount Manisty to the River Weaver. Densely inhabited mud is much commoner than sparsely inhabited or uninhabited mud, the former occupying approximately 6½ sq. miles and the two latter only 1 sq. mile.

The main bank of mud along the Cheshire shore is separated from the uninhabited sand banks, through which the channels run by a series of patches of sparsely inhabited sand or mud, and densely inhabited sand. The main mud bank is divided into two parts by the River Gowy which, entering the Upper Estuary at Stanlow, occupies a low sandy plain flanked on either side by high mud banks.

Much of the sand is formed into waves (presumably by current action), and these areas adjoin the main channels. The island banks in the Outer Estuary have a high peak directed towards the river mouth at Rock Lighthouse, and shelve away seawards.

GENERAL DESCRIPTION OF THE INFAUNA

The Upper (or Inner) Estuary

The Upper Estuary comprises the Narrows from Rock Light to Garston, a large basin extending from Garston to Runcorn and a smaller basin above Runcorn. Except at high spring tides Howley Weir (at Warrington) divides the tidal from the non-tidal reaches. Observations have not extended beyond Norton Marsh some 3 miles above Runcorn. As will be shown later in a comparison with other estuaries, this limits the collections to areas where freshwater animals are not normally found.

The most notable inhabitant of the banks is the brackish water polychaete *Nereis diversicolor*. This mud-living worm is found in the Upper Estuary from Norton Marsh to the Narrows wherever mud with a depth of more than a few inches occurs; it is also found in banks of mud in the Outer Estuary near the mouth of the River Alt. Large areas of the main mud bank (Areas Nos. 23 and 29, Pl. III) between Stanlow and the Weaver Sluices in the Upper Estuary are densely inhabited by this organism. At Stanlow a density of 440 per sq. m. was found from a count within a quarter metre square, and the difficulties of sieving the mud make it probable that the true figure is higher. The softer parts of the bank, in gulleys and near the Weaver Sluices, are not inhabited by *Nereis*. In these softer places a small red oligochaete, identified by Fraser (1932) at Dingle as *Clitellio arenarius*, is abundant and is the only inhabitant. In addition it usually occurs wherever *Nereis* is found. Both these forms appear to burrow more deeply into the mud when the surface has become dry and cracked during neap tides. *Clitellio* may then be found well below the surface in the form of balls containing large numbers of intertwined specimens.

At most times of the year, but particularly during the summer, the surface of the banks of mud in the Upper Estuary is covered by a green scum consisting mainly of *Euglena* sp., probably *Euglena limosa* (Fraser, 1932). The scum seems to develop most readily on the soft mud not inhabited by *Nereis*. Many species of diatoms are also found in the scum, and in places these are so abundant as to give the surface a dark green or brown colour. In certain areas, as on the mud-covered rocks at Runcorn Gap, Hale Head and Garston and occasionally on sand, there is a brown scum of diatoms without *Euglena*. Ghazzawi (1933) has identified the diatoms found on the Dingle foreshore, and in his list of some fifty species are to be found the names of fresh-water, marine and brackish-water species.

In addition to the scum of unicellular forms, the estuarine mud banks are frequently covered by a growth of a filamentous alga, *Vaucheria* sp. This alga covers the surface mud, and the tide frequently rolls up the blanket-like layer of mud and alga, and washes it away. In other parts (Area No. 33, on the foreshore near Speke) the growths appear as rounded tufts above the general level of the soft mud. *Clitellio* is the only recorded inhabitant of mud covered by *Vaucheria*.

The remaining outstanding feature of the mud banks in the Upper Estuary is the presence of the small crustacean, *Corophium volutator*, which builds small U-shaped burrows in the surface layers. It occurs over a large part of Areas Nos. 23 and 29 and in many other places. It is most abundant in the sandy mud of Area No. 27 near Stanlow and in the adjoining area of densely inhabited sand (Area No. 24) which contains a fair proportion of mud. It is in this neighbourhood that the small bivalve *Macoma balthica* is to be found, widespread and abundant in mud and muddy sand. Fraser (1932) found a maximum of 6000 *Macoma* per sq. m. at Dingle, and it is probable that the abundance in Areas Nos. 27 and 24 is similar or even greater than at Dingle. *Macoma* does not appear to tolerate soft mud nor the clayey mud of Areas Nos. 23 and 29.

The two other species of burrowing animals found commonly in the Upper Estuary are worms, and they are associated with fairly clean sand. *Arenicola marina* (the common lug-worm) is sparsely distributed in fairly large areas as far up as Area No. 22 on the bank between Dungeon Point and Hale Head. The tube-building form *Pygospio elegans* is abundant but patchy in its distribution and occurs as far up as Area No. 16.

In the Narrows at Wallasey, burrowing worms are found in greater variety than elsewhere in the Upper Estuary, seven species being recorded from Area No. 45.

The Outer Estuary (Liverpool Bay)

The Upper Estuary opens into Liverpool Bay at the corner of a right angle formed by the Cheshire and Lancashire coasts. At low tide extensive sand banks are exposed in Liverpool Bay (Pl. III). The variety of species in the Outer Estuary is much greater than in the Upper Estuary.

Of the species occurring commonly in the Upper Estuary *Nereis diversicolor* has a limited distribution in mud at the mouth of the River Alt. *Macoma balthica* and *Corophium volutator* also occur near the Alt and in mud at Hoylake. *Arenicola marina* is much more widespread and abundant and occurs over large areas. *Clitellio* was not recorded. *Pygospio elegans* occurs near the Alt but is not widespread. Of the plants recorded from the Upper Estuary *Vaucheria* and *Euglena* were not observed in Liverpool Bay. A diatom scum occurs in places but the species were not determined.

Two interesting low-lying areas of densely inhabited muddy sand occur on Taylor's Bank (Area No. 97) and on Spencer's Spit (Areas Nos. 60, 61 and 51).

At Taylor's Bank the cockle, *Cardium edule*, occurs in abundance with a few *Cardium rusticum*. The burrowing heart urchin, *Echinocardium cordatum*, with its attendant bivalve, *Montacuta ferruginosa*, and the large tube-building worm, *Lanice conchilega*, are fairly common. In addition, the molluscs *Chione striatula* and *Tornatella fasciata*, the worms *Nephthys hombergi* and *Arenicola marina* and hydroids growing on the cockles were found. Towards the edge of the cockle bed, cockles die away and *Lanice* becomes more abundant finally giving way in cleaner sand to another tube-building worm, *Owenia fusiformis*, at Areas Nos. 98, 99 and 100. The areas of sparsely inhabited sand shown in Plate III at Area No. 100 were actually more numerous than figured and consisted of gullies lying between the crests of long broad-fronted waves of sand. At Area No. 101, which consists of fine sand, the bivalve *Donax vittatus* occurs in small numbers.

The sand at Spencer's Spit has a different fauna. *Donax vittatus*, rare on Taylor's Bank, occurs at Area No. 61 in great abundance.

At Area No. 60, *Echinocardium*, with *Montacuta* and a tube-building worm, *Pectinaria koreni*, are extremely abundant. Rough estimates of the abundance of these three species gave for *Echinocardium* (mainly up to 1 in. in length) 150 per sq. m. and for *Donax* and *Pectinaria* about 300 per sq. m. Other species with *Donax* at Area No. 61 were *Echinocardium*, *Lanice*, *Arenicola* and a brittle star, *Ophiura texturata*, which was often partly buried in the sand. At Area No. 60, with *Echinocardium* and *Pectinaria*, were *Arenicola*, *Lanice* and *Donax*. In the less densely inhabited sand at Area No. 62, *Arenicola* and *Echinocardium* occurred occasionally, and, near the centre of this area, *Ophiura* occurred in enormous numbers. Numerous patches, each about 15 sq. m. in extent, were estimated to contain about 1600 individuals per sq. m. Intervening areas of similar extent contained only a few specimens. Isolated specimens of six species of burrowing worms and of the razor shell, *Ceratisolen legumen*, were also recorded from Spencer's Spit.

The adjacent area of the shore banks (Area No. 51) was similar to Area No. 60 and contained *Lanice*, *Pectinaria*, *Owenia*, *Echinocardium*, a few young *Ensis siliqua* (a razor shell), and a few *Ophiura*. A burrowing bivalve, the clam *Mya arenaria*, was common in small patches of very muddy sand.

The island banks known as the Great Burbo Bank (Areas Nos. 66–70) are composed almost entirely of coarse sand. The surface is waved and lakes occur. The North Bank is similar but does not attain the same height. It is connected to the shore banks at low water of a high spring tide. *Lanice* is sparsely distributed over low lying areas of fine rippled sand at Areas Nos. 63, 64, 66, 67 and 68. At Areas Nos. 63 and 64 *Chione* was also found, while at Area No. 65 *Chione* alone was found.

In 1933 along the Lancashire coast the shore banks were of fine sand with some mud. The sand near the Gladstone Docks contained a large amount of mud and Area No. 72 was covered by a thin layer of mud. As Formby Point was approached the sand became cleaner and only rare patches of inhabited fine sand were found at the Point. This general trend was much disturbed where the river Alt flowed across the shore. Mud inhabited by *Nereis diversicolor* occurred close to the channel of the Alt (Areas Nos. 79 and 80), and areas of muddy sand containing large numbers of *Corophium* with some *Macoma* (Areas Nos. 83 and 95) merged into the surrounding uninhabited clean sand.

A north-westerly gale covers the areas of mud and muddy sand near the Alt with a layer of clean blown sand and completely alters for a time the appearance of these banks. The channel of the Alt was artificially shortened in 1936, and the distribution of banks in this region has been completely altered.

In the fine muddy sand extending from Crosby to the Gladstone Dock, *Arenicola marina* occurred in abundance at Area No. 75 and sparsely in other areas. *Macoma* and a few species of burrowing worms were also found. A small gastropod, *Hydrobia ulvae*, occurred on the surface over most of this area of inhabited or otherwise uninhabited sand.

A patch of sand, gravel and stones overlying clay at Area No. 71 is of interest by reason of the abundance of the anemone *Sagartia troglodytes* in the sand. Another anemone, *Tealia felina*, occurred in the gravel and stones and large blue and red specimens of *Nereis virens* in the underlying clay. Hydroids and the barnacle *Balanus crenatus* were common on the stones.

The sparsely inhabited areas of sand near Formby Point contained *Arenicola* and *Cardium* with occasionally *Chione* and *Nephthys* sp.

Except near Hoylake the shore banks on the Cheshire coast are composed of cleaner and coarser sand than on the foreshore at Waterloo and they end in the East Hoyle Bank which, in the centre, attains the considerable height of 26 ft. above Liverpool Bay datum, falling away in all directions.

A low-lying bed of mussels, *Mytilus edulis*, on shingle and stones overlying clay occurs at Area No. 47. The large areas of sparsely inhabited sand at Areas Nos. 48 and 59 contain *Cardium* and *Lanice*; these species occur in larger numbers at Areas Nos. 49 and 50. Other species include *Echinocardium*, *Macoma*, *Mactra corallina*, *Spisula solida*, *Owenia* and *Arenicola*. The last named species is common at Area No. 50 and *Owenia* is common in parts of Area No. 59. Towards the tip of the East Hoyle Bank everything except *Mactra corallina* dies away. *Lanice* and *Owenia* reappear on the Dee side of the bank and these two species also inhabit Area No. 58. *Arenicola* alone occurs at Area No. 57.

At the inshore end of the East Hoyle Bank *Corophium*, *Cardium* and *Macoma* occur in gullies at Area No. 56. *Corophium* alone occurred in great abundance at Area No. 55. A reef of rock separates Areas Nos. 55 and 54. In mud at Area No. 54 *Corophium* lived in abundance together with *Macoma*, *Cardium*, *Hydrobia* and a few *Arenicola*. In the adjoining transitional area of muddy sand at Area No. 53 *Macoma* and *Arenicola* occurred in dense, alternating patches with a few *Corophium*. *Cardium* and clumps of a seaweed *Enteromorpha* sp. were present at the Meols end of Area No. 53 with *Scoloplos armiger* and *Donax*, which two species also occurred in the adjacent part of Area No. 52. Area No. 52, of fairly clean sand, was densely inhabited by *Arenicola* which died out as the cleaner and higher centre of the bank was approached.

Only a few observations were made below low-water mark; these indicated that *Donax* was widespread and abundant in fine sand around the tip of Taylor's Bank and that *Pectinaria* was abundant in sand of a more muddy character in the channels.

Discussion

An investigation of the fauna of the estuaries of the Tees and of other rivers (*Water Pollution Research Technical Paper*, No. 5, 1935) showed that marine animals were abundant near the mouth and became less common as the estuary was ascended until eventually no marine animals were found. Similarly, the fresh-water animals, common at the head of the estuary, were found to die out as the estuary was descended.

In order to compare different estuaries the Tees Estuary was divided into thirteen sections of equal length, and comparable sections were mapped out in other estuaries on the basis of similar salinities of the water at high and low tides.

An account of the salinity conditions in the Mersey Estuary has been published (*Water Pollution Research Technical Paper*, No. 7, 1937, p. 31) so that it is possible to compare points on the two estuaries which are subject to similar salinity conditions. From such a comparison it has been found that Section XIII in the Tees (from the mouth to 1½ miles above it) corresponds in the Mersey to the whole of Liverpool Bay and part of the Narrows, and that the highest point at which collections were made in the Mersey corresponds with Section V on the Tees. From these comparisons two points emerge.

(*a*) The absence of fresh-water forms from the Mersey collections (with the possible exception of fresh-water oligochaetes) is to be expected since, in the Tees and other estuaries, fresh-water animals are only represented as low as Section V by small red oligochaetes.

(*b*) There is no reason, on grounds of differences in salinity, why the fauna of the Narrows should not be as varied as that of Liverpool Bay. Of thirty species recorded from Liverpool Bay, however, only fifteen occur in the Narrows. It seems probable that this is due to the high speed of the tidal streams in the Narrows, the large amount of sediment in the water and the relatively small area of tidal banks.

Although the salinity in the whole of Liverpool Bay is similar to that of Section XIII in the estuary of the Tees, it seemed possible that some effect of estuarine conditions might be evident near Rock Light. Accordingly the Bay was divided by a circle with a radius of 6 miles and with the centre of the channel near Rock Light as its centre. Zone A (Key Map in Plate III) within the circle is subject to the discharge of the Mersey and Alt; zone B, including the East Hoyle Bank and Spencer's Spit, might be affected by the discharge of the Dee; and zone C (Formby Point and Taylor's Bank) should be least affected by any of these discharges. A list of all recorded species for each zone shows, however, that zone C had only fourteen species, while both A and B had twenty-eight species. Any influence of the estuary which may be felt in Liverpool Bay seems therefore to have no localized adverse effect on the fauna.

Returning to a consideration of the distribution of the common burrowing animals found in the Upper Estuary it is apparent from the account given earlier in this paper that, while *Nereis diversicolor* (a brackish-water species) occurs above Hale Head, the common marine burrowing species only appear below Hale Head and do so one by one as the Estuary is descended from this point. This distribution is similar to the distribution of marine animals in the Tees and other estuaries.

Previous work on the fauna of the Mersey Estuary has been applied mainly to the bottom fauna of the Outer Estuary (e.g. Fraser, 1935). In the Upper Estuary Fraser (1938) studied the fauna of the buoys and pontoons, and he has published a detailed account of the fauna and conditions at Dingle (Fraser, 1932).

The present survey has shown that the mud banks of both the Upper and Outer Estuary are inhabited by the same species, but that the sand banks of the Outer Estuary support not only the same species as those of the Upper Estuary but in addition a large number of other species. The abundance of burrowing animals throughout the estuary is therefore due to large numbers of a few species in the Upper Estuary (notably *Nereis*, *Macoma* and *Corophium*) and in the Outer Estuary to a large variety of species. The fauna of the buoys and pontoons shows a similar distribution (Fraser, 1938, pp. 19, 20). The similarity of the mud-living fauna throughout must be attributed to the fact that few species can tolerate conditions in tidal mud flats, and that these few species are all tolerant of varying salinity conditions. Since it is only on parts of the coast sheltered from strong wave action that tidal mud banks can develop, and since such inlets are most liable to be subject to land drainage, it appears natural that an animal evolved to tolerate conditions on a tidal mud flat should also tolerate the conditions of salinity found in estuaries.

The lack of variety of sand-living species in the Upper Estuary when compared with the variety found in Liverpool Bay is probably due to intolerance of strong currents, varying salinity, and large amounts of suspended matter in the water.

NOTES ON THE FLORA

Large plants, whether marsh plants or marine algae, do not form an important feature of the Mersey Estuary. In the following list such observations as were made during the zoological survey of the tidal banks are given.

FLOWERING PLANTS

(Marsh plants or aquatic land plants)

At one time large areas of land were flooded at high water of spring tides in the Mersey Estuary. These occurred noticeably at Wallasey, Stanlow, Frodsham, Hale Head to Runcorn, and on both sides of the river just above Runcorn. The development of Wallasey Pool as a dock area and the building of the Manchester Ship Canal led to a considerable reduction in the flood areas at Wallasey, Stanlow and Frodsham, whilst much land has been protected from flooding in the other areas. There are now limited areas subject to flooding at Frodsham Score, Hale Head to Runcorn, on each side above Runcorn, and at Norton Marsh. These areas consist of coarse grassland used for grazing sheep and are cut by drainage gullies. Other marsh plants occur spasmodically in different places, but nowhere do they occupy extensive areas. Some years ago small patches of *Spartina* grass were found growing on the mud at Stanlow, and to prevent their spreading and building up the mud banks, with a consequent reduction in the capacity of the estuary, the Mersey Docks and Harbour Board destroyed the plants.

ALGAE

Fucus vesiculosus L.

Growths occur on the dock walls in the Narrows and in places on each side of the river up to Hale Head and Eastham Locks. In the Outer Estuary the only notable growths occur on the Leasowe embankment and the promenades at Meols and Hoylake.

Enteromorpha sp.

Enteromorpha occurs a little higher on the walls than *Fucus* and has a similar distribution. In addition, tufts occur on the muddy sand at Hoylake (Area No. 53).

Porphyra sp.

A small growth occurs on the rocks at Rock Ferry and in the Manchester Ship Canal.

Vaucheria sp.

Vaucheria Thuretii Woron has been identified at Dingle (Fraser, 1932), and patches—doubtless of this species—are widespread on the mud flats and near high-water mark from Dingle and Mount Manisty to Norton Marsh. Clumps and small matted growths are common on the mud at Speke (Area No. 33) and from Stanlow to the Weaver (Area No. 23).

Desmids.

Closterium sp. has been identified from below Hale Head and doubtless occurs in other localities.

Euglena sp.

The most noticeable feature of the mud banks is the presence, over extensive areas, of a bright green colour caused by immense numbers of this microscopic organism, identified at Dingle as *Euglena limosa* Gard (Fraser, 1932). It occurs from Dingle and Eastham to Norton Marsh.

Diatoms.

A brownish tinge in the green colour caused by *Euglena* is frequently observed and is due to an admixture of diatoms. Growths of diatoms, unmixed with *Euglena*, occur in places, mainly on sand.

Throughout the estuary the scarcity of rocky foreshores at low levels in the tidal zone prevents the extensive development of weed and the growth of numbers of species of animals associated with this type of habitat. The absence of weed from some areas of rock may be attributed to the film of mud covering them. In the case of the training walls flanking the main channels in Liverpool Bay the absence of large algae from what seems to be an admirable habitat may be due to the scouring action of the sand carried by the strong currents, although Fraser (1938, p. 16) attributes this absence to a reduction in illumination caused by the suspended matter.

FAUNA LIST

All records were made between May and October 1933. Numbers refer to the Areas in the Key Map in Plate III. The names used are those of the *Plymouth Marine Fauna* (2nd edition) of the Marine Biological Association except where otherwise stated. Thanks are due to the Zoology Department of Liverpool University where some of the identifications were carried out.

COELENTERATA

Class HYDROZOA

Hydractinia echinata (Fleming).

Common on shells inhabited by hermit crabs, *Eupagurus bernhardus*. East Hoyle Bank, Spencer's Spit, Meols shore and Taylor's Bank.

Tubularia indivisa L.

Extremely abundant on the pontoons of the landing stages in the Narrows. On rocks at Gladstone Dock (71). An average of three counts of the growth on boats moored in the Narrows gave 1300 stalks of *T. indivisa* per sq. in. On one boat a growth, mainly $1\frac{1}{4}$–$1\frac{1}{2}$ in. long, had grown in 16 days and was reproducing. A count showed 1340 stalks per sq. in., of which 675 carried heads. Many heads had been knocked off in collecting and counting.

Laomedia gelatinosa (Pallas).

On Garston Rocks and on stones at Aigburth (36).

Class SCHYPHOMEDUSAE

Aurelia aurita (L).

During May and June 1933, the Upper Estuary water carried large numbers of *Aurelia aurita* and many were observed in July and August. Many stranded in May and June on the sand flats from Runcorn Gap to Dungeon Point.

Class ANTHOZOA

Tealia felina (L).

Common on stones near Gladstone dock (71).

Sagartia elegans (Dalyell) var. venusta (Gosse).

A single specimen taken near the Gladstone Dock (71).

Sagartia troglodytes (Price).

Abundant in gravel and sand near the Gladstone Dock (71).

ANNELIDA

Class CHAETOPODA

Order POLYCHAETA

Lagisca extenuata (Grube).

A single specimen at Wallasey (45).

Sigalion mathildae Audouin and Milne Edwards (Fauvel, 1923, p. 103).

A single specimen in sand on Spencer's Spit.

Nereis pelagica L.

In sand near Gladstone Dock (73), at low-water mark at Meols (51) and at Wallasey (45).

Nereis diversicolor O. F. Müller.

The commonest polychaete in the Estuary. It occurs in great abundance in the Upper Estuary from below Runcorn to Rock Ferry (7, 18, 23, 29, 33, 37, 42) and sparsely from Norton Marsh to Rock Ferry (2–5, 8–15, 17, 19, 20, 24, 26, 27, 28, 34, 38). In the Outer Estuary it is abundant in patches near the Alt (79 and 80) and occurs at 78 and 84. Usually in mud, it occurs in muddy sand (never abundantly) and occasional specimens have been taken in comparatively clean sand. These, however, may have been specimens washed out of mud which burrowed as soon as they settled.

Nereis fucata Savigny.

A single specimen from Spencer's Spit.

Nereis virens Sars. (Fauvel, 1923).

Burrowing in clay underlying sand and gravel near Gladstone Dock (71) and near Leasowe with *Pholas candida* (near 50).

Nephthys caeca (O. F. Müller).

A single specimen in sand at Spencer's Spit.

Nephthys hombergi Lamarck.

Sparsely but widely distributed in the Outer Estuary. Specimens recorded from Meols (52), Waterloo (75), near the Alt (93), Formby (89) and Taylor's Bank (97).

Nephthys hombergi var. ehlersi Heinen (Fauvel, 1923).

A single specimen from Waterloo beach in the *Arenicola* area (75).

Nephthys cirrosa Ehlers.

Single specimens obtained in sand from Wallasey (45), East Hoyle Sands (59) and Spencer's Spit.

Glycera convoluta Keferstein.

A single specimen in sand from Spencer's Spit, and one in mud at the Alt (77) with spat of *Macoma balthica* and *Cardium edule*.

Scoloplos armiger (O. F. Müller).

Common in muddy sand in a small patch at Meols (53).

Nerine cirratulus (Delle Chiaje).

Taken in sand or muddy sand at Wallasey (45), Gladstone Dock (73), Spencer's Spit and East Hoyle Sands (59).

Pygospio elegans Claparède.

Very abundant in parts of the Upper Estuary in sand (16, 17, 27 (top end near 17), 34, 35, 40, 45). Outer Estuary near the Alt (77, fringes of 80, 84, 92).

Arenicola marina L.

Sparse, but widely distributed in muddy sand in the Upper Estuary (15, 17, 22, 24, 27, 30, 32, 35, 40, 44, 45). The highest recorded specimens occurred at 15 and 22. Abundant in the Outer Estuary at Waterloo (72–75) and at Leasowe and Hoylake (50 and 52). It occurs sparsely all over the Outer Estuary (46, 48, 53, 57, 61, 62, 63, 84, 85, 86, 91, 93, 94, 96, 97) and two isolated specimens were taken on the Great Burbo Bank (69).

Owenia fusiformis Delle Chiaje.

Not taken in the Upper Estuary. Abundant in fairly clean sand in the Outer Estuary on Taylor's Bank (98, 99, 100), at Leasowe (48) and East Hoyle Sands (51, 58, 59).

Pectinaria koreni Malmgren.

Abundant in muddy sand on Spencer's Spit (60) and off Meols (51) at low-water mark. Fraser (1935) records shells of *P. belgica* at New Brighton and quotes records of *P. belgica* from Liverpool Bay.

Lanice conchilega (Pallas).

Found only on Wallasey beach (45) in the Upper Estuary. Common and widespread in sand and muddy sand in the Outer Estuary, occurring on Taylor's Bank (97), Great Burbo Bank (66, 67, 68), North Bank (63, 64), Cheshire shore banks (48, 49, 50, 51, 58, 59) and on Spencer's Spit (60, 61, 62). Not recorded from the Lancashire shore banks.

Hydroides norvegica Gunnerus.

Tubes were found on a dead shell on the East Hoyle Sands.

Pomatoceros triqueter (L).

Tubes found on the same shell as *Hydroides norvegica*.

Order OLIGOCHAETA

Clitellio arenarius O. F. Müller.

This species was identified by Fraser (1932) at Dingle (38). Small red oligochaetes occur in mud in all parts of the Upper Estuary, together with *Nereis diversicolor*, from Norton Marsh to Rock Ferry (2, 3, 18, 23, 29, 33, 37, 38, 42, 74).

ARTHROPODA

Class CRUSTACEA

Sub-class COPEPODA

Eurytemora affinis (Poppe) var. hirundoides Nordquist.

Two short plankton surveys in daylight showed this species to be present at high water in the zone above Hale Head to 2 miles above Runcorn Gap. More abundant near the bottom than at the surface.

Acartia spp.

Abundant in the plankton on two surveys to just above Hale Head. Most abundant near the bottom.

Sub-class CIRRIPEDIA

Balanus crenatus Brugière.

Fairly common on stones as far as Hale Head. Common near the Gladstone Dock (71) and on the mussels and stones at Rock Light (47). Also found on shells and stones cast up on Taylor's Bank, Spencer's Spit and the Meols shore.

Balanus balanoides (L).

Fairly common on the dock walls in the Narrows and on rocks as far as Eastham Locks. On occasional posts and rocks in the Outer Estuary.

Sub-class MALACOSTRACA

Order ISOPODA

Eurydice pulchra Leach.

Taken in clean sand on the Great Burbo Bank. Probably widespread in the Outer Estuary in similar situations.

Jaera marina (Fabricius).

Among weeds on the Garston Rocks.

Order AMPHIPODA

Gammarus marinus Leach.

Among weeds on the rocks at Rock Ferry (44).

Gammarus locusta (L).

In a pool near high-water mark at Crosby.

Gammarus duebeni Lilljeborg.

On the rocks at Garston and in gravel just above Garston (34). In pools at high-water mark just below Hale Head (near 20). Ship Canal near the Weaver.

Talitrus saltator (Montagu).

Local and widespread in clean sand at high-water mark. Found at Hale and Speke (18 and 33), Mount Manisty and Hightown.

Talorchestia deshayesei (Audouin).

A single specimen taken with *Talitrus saltator* at Hale Head.

Corophium volutator (Pallas)*.

Widespread and extremely abundant in muddy sand and mud with *Macoma balthica* and *Nereis diversicolor*. Also taken with *Arenicola marina*. Abundant at 24, 27, 42 and 44 and in parts of 23 and 29. Near high-water mark from Hale Head to Dingle (18, 33, 37). Abundant around the Alt (79, 80, 83, 84 and 95), at Hoylake (53–56) and common near the Gladstone Dock (72).

Order SCHIZOPODA

Mysids are apparently common in the Upper Estuary. Seen in abundance in shrimp nets at Garston Rocks and in a pool near Weston Locks. Taken in the plankton from Eastham to Runcorn Gap.

Order DECAPODA

Crangon vulgaris L.

The common shrimp forms the basis of a shrimp fishery, the inner grounds being fished mainly in the Eastham to Dungeon Point region, whilst shore nets are worked at and above Garston. In the Outer Estuary the main ground is the Formby Channel and along the Crosby Channel to Rock Lighthouse. The highest point at which shrimps have been observed is near the Weaver Sluices (12).

Eupagurus bernhardus (L).

Numerous specimens on the sand banks at Taylor's Bank, Spencer's Spit, East Hoyle Sands and Meols shore. Most of the shells carried a good growth of *Hydractinia echinata*.

Portunus sp.

Occasional specimens on Taylor's Bank and Spencer's Spit.

Carcinus maenas (Pennant).

Small specimens occur among rocks and gravel up to Hale Head.

Cancer pagurus L.

A specimen was taken on Taylor's Bank (97) in a pool.

Corystes cassivelaunus (Pennant).

Two females in berry were dug out of the sand near the tip of the East Hoyle Sands (59) on 20 October 1933.

MOLLUSCA

Class PELECYPODA

Mytilus edulis L.

The common mussel is abundant on buoys and pontoons in the river channels. On the shore it is abundant on the mussel bed at Rock Lighthouse (47) and at Wallasey (45); it has not been taken elsewhere. Fraser (1932) records it from Dingle.

Montacuta ferruginosa (Montagu).

Taken in the anal siphon of *Echinocardium cordatum* on Taylor's Bank (97) and Spencer's Spit (60).

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* Identified at the British Museum (Nat. Hist.) by Dr I. Gordon.

Tellina tenuis da Costa.*

A single young elongated specimen taken in sand near low-water mark at Leasowe (48).

Macoma balthica (L.).

The commonest bivalve of the Estuary. Found in great abundance in the mud at 27 and parts of 23 and 29. It occurs in muddy sand at 24, 26, 27 and 28. Also found at 16, 17, 30, 32, 34, 35 and 43. The highest recorded specimen was taken in clean sand near 10. In the Outer Estuary it occurs in abundance at the Alt (78, 79, 80, 84) and at Hoylake (53, 54, 56), and specimens have been taken at 46, 48, 74, 75 and 94. Spat were observed at 76 and in abundance (with spat of *Cardium edule*) at 77 in mud.

Donax vittatus (da Costa).

Found in extreme abundance on Spencer's Spit (61) at low water of spring tides. It also occurs at 52, 60 and 101. On Spencer's Spit small clusters of whole and broken specimens seemed to indicate that the gulls flocking on this bank were feeding to repletion and then regurgitating. The area is exposed only at spring tides.

Mactra corallina (L.).

Found in sand near low-water mark. Large specimens were sparsely distributed over the tip of the East Hoyle Sands (59). Broken shells indicated that gulls had been feeding on them. Smaller specimens were obtained along the Meols shore (51 and 48) and as far as Leasowe.

Spisula solida (L.).

Occasional on the East Hoyle sands (59) and near Leasowe (48).

Chione striatula (da Costa).

Nowhere abundant but widely distributed in the Outer Estuary. Recorded from Taylor's Bank (97), Formby shore (87 and 88) and North Bank (63, 64, 65).

Cardium echinatum L.

Dead shell picked up on the East Hoyle Sands (59).

Cardium edule L.

Common in the Outer Estuary. Abundant on Taylor's Bank (97) and common along the Leasowe shore (48, 49, 50) and at Hoylake (53, 54, 56). It occurs sparsely at 71, 85, 86, 89 and 96. Young specimens were abundant at 77 and 92. In the Upper Estuary they are found at Dingle (38) where dwarfing is apparent (Fraser, 1932).

Cardium rusticum L. (Forbes & Hanley, 1853, Vol. II, p. 11).

Dead shells are common along the Leasowe shore and at the Gladstone Dock. A few specimens occur on Taylor's Bank (97) among *C. edule*.

Mya arenaria L. (Forbes & Hanley, 1853, Vol. I, p. 168).

A large patch of small specimens occurs in mud near Stanlow (25). The species also occurs at Dingle (37, 38) where dwarfing is again apparent (Fraser, 1932). At Rock Ferry (43) the specimens are larger than at 25; in localized but abundant patches of very muddy sand at 51 off Meols, still larger specimens occur. These last, however, are considerably smaller than the dead shells common along the Hoylake and Meols shore.

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* Identified at the British Museum (Nat. Hist.) by Mr G. C. Robson.

Mya truncata L.

A dead shell was picked up on the Meols shore (59).

Ensis siliqua (L.).

A few young specimens were dug in muddy sand off Meols (51).

Ceratisolen legumen L. (Forbes & Hanley, 1853, Vol. I, p. 256).

A single living specimen was taken on Spencer's Spit (60) although dead shells are common along the Leasowe shore (49).

Pholas candida L. (Forbes & Hanley, 1853, Vol. I, p. 117).

Outcrops of clay occur in the sand in many parts of the estuary. At Moreton and Leasowe several patches at about half tide level are inhabited by small specimens of *Pholas candida*; large dead shells are abundant along the Leasowe shore (49, 50) and may be picked up anywhere in the Outer Estuary.

Class GASTROPODA

Littorina littorea (L.).

The periwinkle has been found on stones at Wallasey (45), Rock Ferry (43) and at Dingle (37 and 38). It is extremely abundant in patches.

Hydrobia ulvae (Pennant).*

This small snail occurs on the surface of sand or mud over wide areas at the Gladstone Dock (72 and 73), Waterloo (74 and parts of 75), Hightown (84) and Hoylake (53 and 54). It also occurs in vast numbers in long pools behind the Leasowe Embankment. In the Upper Estuary it has been recorded from Dingle beach by Fraser (1932).

Natica nitida Donovan (Forbes & Hanley, 1853, Vol. III, p. 330).

Rare. Taylor's Bank (97).

Tornatella fasciata L. (Forbes & Hanley, 1853, Vol. III, p. 523).

Occasional. Taylor's Bank (97).

Aeolidiidae.

Numerous Eolids were found spawning on slag on Taylor's Bank (97) (27 Aug. 1933) and feeding on *Tubularia indivisa* at Gladstone Dock (71).

ECHINODERMATA

Class OPHIUROIDEA

Ophiura texturata Lamarck.

A few specimens were observed near low-water mark off Meols (51). On Spencer's Spit the species was widely distributed near the centre of the bank. Numerous in patches in which the specimens formed a carpet over the surface of the sand. In an area of roughly 15 sq. yd. a count of the numbers in $\frac{1}{4}$ sq. ft. indicated that there were 20,400 individuals in the patch (1400 per sq. yd.). Many similar patches occurred.

Class ECHINOIDEA

Echinocardium cordatum (Pennant).

Abundant on Taylor's Bank (97) and Spencer's Spit (60 and 61). Less common at 62 and 51. Also found at 59 and 48 near low-water mark.

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* Identified at the British Museum (Nat. Hist.) by Mr H. M. Tomlin.

BRYOZOA

Class ECTOPROCTA

Triticella pedicillata Alder (Hincks, 1880, p. 547).

Common in pools near Mount Manisty (near 32) apparently broken off from the Dolphin piles at Eastham where the growths of this species are abundant.

SUMMARY

The 37 sq. miles of intertidal banks in the Mersey Estuary have been surveyed and classified according to their nature and fauna.

Half the banks occur in the Outer and half in the Upper Estuary. Four-fifths of the total area is composed of sand and most of the remaining one-fifth of mud occurs in the Upper Estuary.

The burrowing fauna of the Outer Estuary is abundant and varied; that of the Upper Estuary is abundant but not varied.

The distribution of species in the Mersey Estuary is similar to that in the estuaries of the River Tees and Tay, except that in the Mersey Estuary a sudden drop in the numbers of species occurs at Rock Light. This is attributed to the strong tidal streams in the Narrows.

The densely inhabited banks of the Upper Estuary are mainly composed of mud and are situated high in the shore zone. In the Outer Estuary the densely inhabited banks are of muddy sand with some banks of mud and are situated near the low-water mark in sheltered positions.

The burrowing species of the Upper Estuary also occur, with many others, in the Outer Estuary.

The observations described in this paper were made during an investigation of the estuary of the River Mersey by the Water Pollution Board of the Department of Scientific and Industrial Research and the results are published by permission of the Department.

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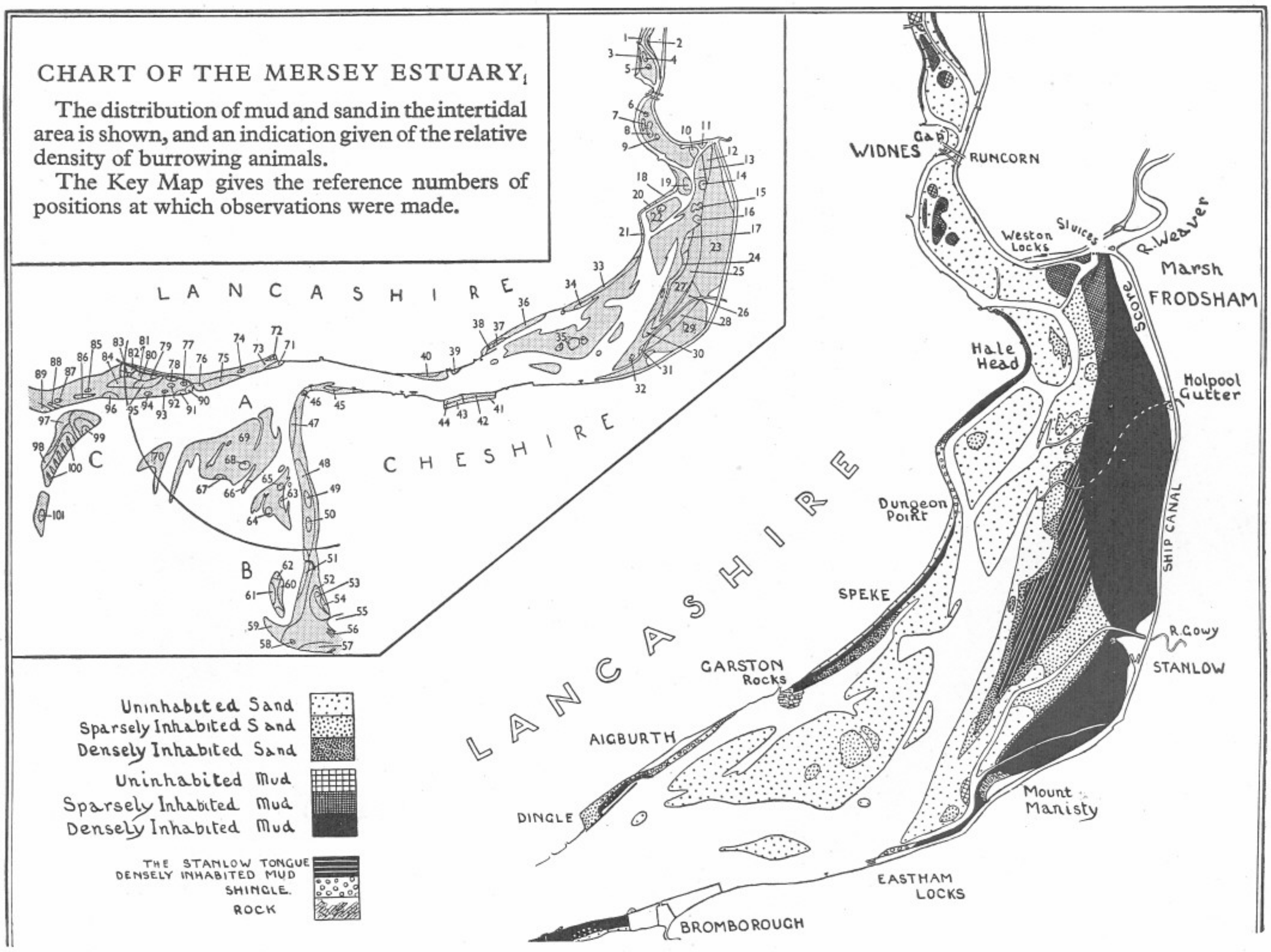

CHART OF THE MERSEY ESTUARY.

The distribution of mud and sand in the intertidal area is shown, and an indication given of the relative density of burrowing animals.

The Key Map gives the reference numbers of positions at which observations were made.

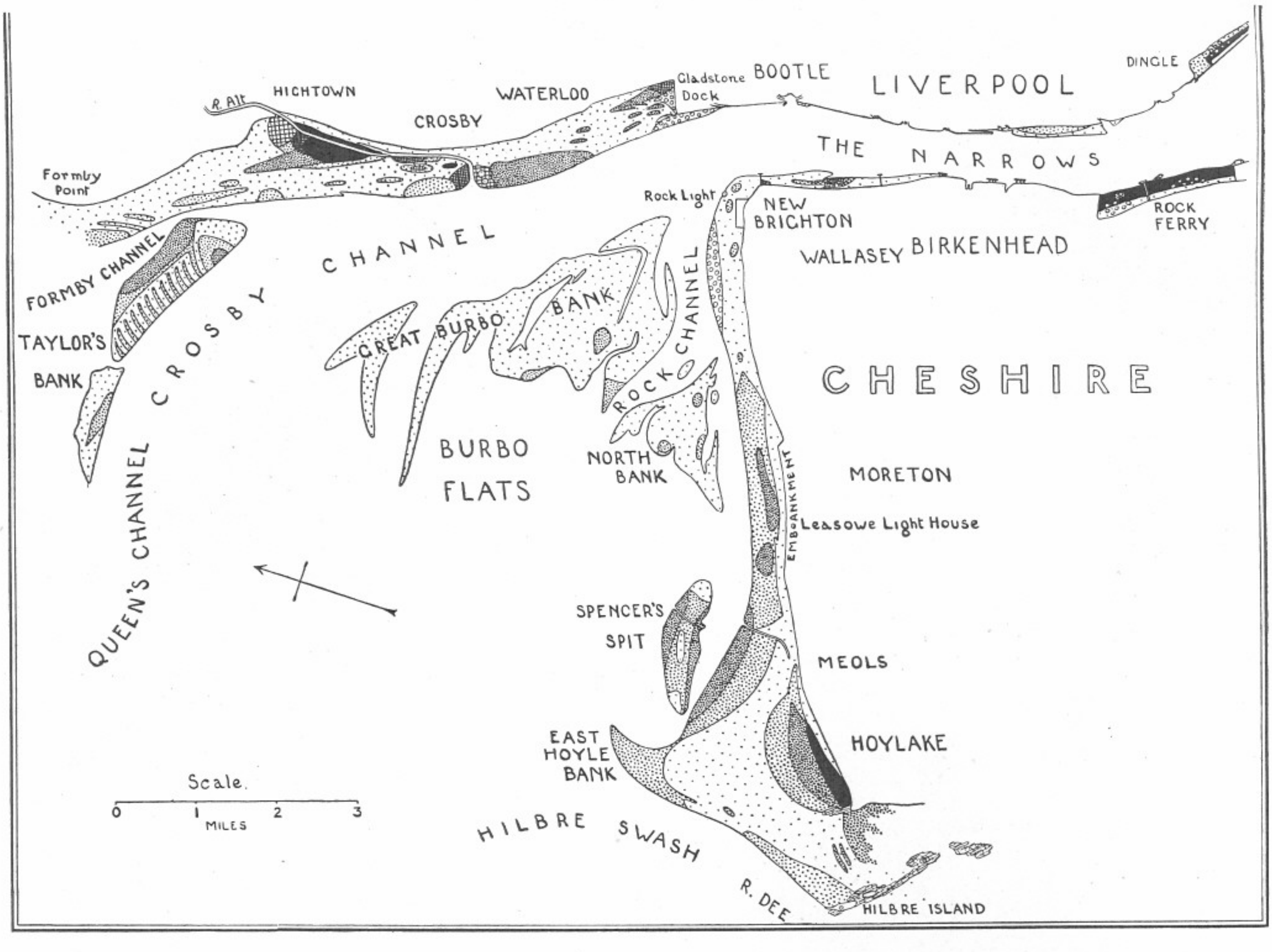

PLATE III

THE PHOTOGRAPHIC METHOD FOR RECORDING AVERAGE ILLUMINATIONS

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(Text-figs. 1–3)

The photo-electric cell is admirably suited for measuring instantaneous illuminations, but does not lend itself readily to the measurement of the total illumination received on a surface over a long period of time, or the average illumination received during that time, although it has been used for this purpose (Atkins & Poole, 1936*a*). The method used by these authors, however, would be difficult to use in the field and away from laboratory facilities. The photographic method, on the other hand, is admittedly not capable of yielding results of high precision, but the simplicity of operation, and absence of elaborate and bulky apparatus, make it suitable for use in the field.

In principle, the amount of blackening produced in a photo-sensitive emulsion is used as a measure of the total illumination received; in order to increase the range over which measurements can be made, a neutral tint wedge, of suitable slope, is placed in front of the emulsion, and the distance along the wedge at which a standard amount of blackening is produced is taken as a measure of the illumination. The standard amount of blackening is best defined as that amount which is produced, in the absence of the wedge, by a known illumination acting for a known time. The method has inherent limitations, particularly when used for long-period observations, which result from (*a*) the failure of the reciprocity law, (*b*) the uncertainty in the value of the wedge constant, and (*c*) the varying sensitivity of the emulsion to lights of different wave-lengths.

The use of the neutral tint wedge in photometry has been fully described by Hecht (1918) and Eder (1919, 1920*a*, *b*). These authors, however, do not appear to have considered in any detail the possible effects of the limitations just mentioned, although their existence is recognized. Gruber (1924) and Oberdorfer (1928) used the Eder-Hecht photometer for ascertaining the intensity of illumination at various depths below the surface of a lake, and Cooper & Sayce (1932) made continuous records of the intensity of daylight throughout the day, with the aid of a neutral tint wedge. Such observations, however, fail to make use of the innate integrating properties of the photographic emulsion.

Let the emulsion be exposed behind the wedge to a constant illumination I for a time t. Let the print of the wedge at a distance l from the zero end of the wedge have the same density (amount of blackening) as that produced by the standardizing light, of intensity I_s acting for the same time, t. Then the intensity of light actually reaching the emulsion must be the same during both exposures. Now, if $I^\star$ is the intensity of light emerging from the wedge, and striking the emulsion, we can write, from the known properties of the wedge,

$$\log I^\star = \log I - kl,$$

where k is the "wedge constant". Hence, in the particular case considered,

$$\log I = \log I_s + kl.$$

If, however, the duration of the standardizing exposure is not the same as that of the wedge exposure, or if the intensity of the illumination during the latter is not constant, complications arise.

THE FAILURE OF THE RECIPROCITY LAW

The total illumination received during any time t is given by $R = It$, if the intensity is constant. The amount of blackening produced in a photographic emulsion, however, by a constant illumination acting for a time, t, does not, in general, follow this "reciprocity law", but depends upon the product It^p, where p is the "Schwarzschild constant" (Schwarzschild, 1900). If, as before, $I^\star$ is the illumination actually reaching the emulsion, during the wedge exposure, at the point l, as previously defined,

$$R^\star = I^\star t,$$

whence $$\log R = \log R^\star + kl.$$

But at the point l the amount of blackening produced under the wedge is the same as that produced by the standardizing exposure of intensity I_s and of duration t_s. We can write, therefore,

$$I^\star t^p = I_s t_s^{\,p}$$

or $$R^\star t^{p-1} = R_s t_s^{\,p-1},$$

whence $$\log R = \log R_s + kl + (p-1)\log(t_s/t).$$

An extensive treatment of the law of blackening of the photographic emulsion, and the failure of the reciprocity law, is given in the monograph by Dobson, Griffith & Harrison (1926).

Clearly, then, a correction must be introduced whenever the standardizing exposure and the wedge exposure are of different durations, unless the value of p approximates sufficiently closely to unity.

TABLE I. CORRECTION TO BE APPLIED TO PHOTOGRAPHIC RECORDS DUE TO DEPARTURE FROM THE RECIPROCITY LAW

	t_s/t				
p	0·1	0·2	0·3	0·5	0·7
1·03	0·935	0·95	0·965	0·980	0·990
1·05	0·890	0·92	0·935	0·965	0·980
1·10	0·790	0·85	0·885	0·930	0·965

Values of this correction are given in Table I. Two points are of significance in connexion with these figures. (*a*) In many cases, the total illumination received over the whole period of daylight must be measured, while it is inconvenient to continue the standardizing exposure for more than 1 or 2 hr. (*b*) In such cases, the exact duration of the illumination under measurement is difficult, or impossible, to discover; this is usually of no importance, except that the exact value of the correction to be applied is also unknown, and so must be kept small. It will be shown in a later section that the inherent experimental uncertainty of the method is about $\pm 10\%$. The maximum tolerable departure of the value of p from unity is thus about $\pm 0{\cdot}05$.

Non-uniform illumination. The magnitude of the correction necessary when the illumination is fluctuating depends, obviously, on the nature of the fluctuation. Two special cases, however, may be considered.

(1) The exposure is made on a clear day from sunrise to sunset, so that we may write, approximately,

$$I = I_0 \sin \frac{\pi t}{12},$$

where t is the time in hours. The total radiation received is thus

$$R = \int_0^{12} I_0 \sin \frac{\pi t}{12}\, dt = \frac{24}{\pi} I_0.$$

The amount of blackening produced, however, depends upon the quantity S, where

$$S = \int_0^{12} \left(\frac{\partial S}{\partial t}\right) dt = \int_0^{12} p t^{p-1} I_0 \sin \frac{\pi}{12} t\, dt.$$

Graphic integration of this expression, putting $p = 1{\cdot}10$, gives

$$S = 10{\cdot}1\, I_0.$$

We will assume, for simplicity, that the standardizing exposure has the same duration as the wedge exposure, hence

$$S_s = (12)^{1{\cdot}10}\, I_s = 15{\cdot}4\, I_s.$$

Similarly

$$R = \frac{24}{\pi} I_0,$$

$$R_s = 12\, I_s.$$

If the amount of blackening produced in the two exposures is the same, then $S = S_s$, and

$$I_0 = \frac{15{\cdot}4}{10{\cdot}1} I_s = 1{\cdot}53\, I_s.$$

The fact that the unknown exposure produced the same amount of blackening as the standardizing exposure, however, would lead us to suppose that the total radiation received in both cases was the same, i.e. that

$$R_s = 12\, I_s = R_0 = \frac{24}{\pi}\, I_0$$

or that

$$I_0 = 1{\cdot}57\, I_s.$$

The estimate of the total illumination received, in terms of the amount of blackening produced, will thus be too high by about 3%.

(2) The illumination is fluctuating in a simple harmonic fashion about a fixed value. This approximates to the conditions in the neighbourhood of noon, with intermittent clouds. The intensity at any moment can now be written,

$$I = I_1 + I_2 \sin \omega t.$$

Since the greatest fluctuations, and hence the greatest possible discrepancy, will be when the illumination falls periodically to zero, we can simplify the expression, and write

$$I = I_0\,(1 + \sin \omega t)$$

and

$$R = I_0 \int_0^t (1 + \sin \omega t)\, dt.$$

If t is such as to occupy any whole number of waves, this reduces to $R = I_0 t$, i.e. the fluctuations do not affect the total illumination received.

Similarly

$$S = pI_0 \int_0^t t^{p-1}\,(1 + \sin \omega t)\, dt$$

$$= I_0 t^p + pI_0 \int_0^t t^{p-1} \sin \omega t\, dt.$$

The second term in this expression has the property that the area of any half-wave is greater than the area of the preceding half-wave. The area of successive whole waves, however, approaches zero as t becomes greater, so that the area of the first whole wave will give a measure of the maximum discrepancy introduced, which will not be exceeded however many subsequent waves are included in addition. Since, in general, any type of fluctuation can be reduced to a series of simple harmonic waves of suitable frequency, this discrepancy must also be the maximum which will be introduced by any type of fluctuation about a finite mean.

Graphic integration, with $p = 1{\cdot}10$ as before, over the first complete wave gives $I_0 = 1{\cdot}04\, I_s$ as the condition that the same amount of blackening shall be produced by the fluctuating light as by the standardizing light. We should be led to believe, however, that $I_0 = I_s$, and the discrepancy introduced is thus about 4%. The photographic measure of the illumination will be smaller or greater than the true measure according as the exposure was begun while the illumination was rising or falling.

In general, then, fluctuations in the illumination will not introduce any discrepancy greater than 2 or 3 % so long as the Schwarzschild constant does not differ from 1 by more than 0·10.

THE WEDGE CONSTANT

The wedge was of the Goldberg (1910) pattern and was supplied by Messrs Ilford, Ltd. It was 21 cm. long by 1·25 cm. wide, with a density of 3·0 at the dense end and was cut in the middle, the two halves being mounted side by side so as to form a rectangle 10·5 × 2·5 cm.; a wide range of densities was thus available in a compact form. The wedge itself was mounted between two pieces of glass, one of which was made as thin as possible (1 mm.) in order to reduce the shading effect of the edges, and the errors introduced by parallax between the wedge and the paper.

The makers of the wedge furnish a figure for the relation between the density of the wedge at any point, and the distance of this point from the end of the wedge; this is derived from measurements made in the photometer described by Benson, Ferguson & Renwick (1918) and will not necessarily be applicable in all circumstances. The disturbing factors are (1) the inclination of the incident light to the normal, and (2) the wave-length sensitivity of the photo-sensitive material with which the wedge is used. The first arises from the fact that a ray of light passing through the wedge obliquely has to traverse a greater thickness of absorbing material than one passing through normally. The second arises from the fact that the material of which the wedge is composed, while strictly "neutral" in that the density at any point is independent of the wave-length for all values greater than about $420\,m\mu$, becomes rapidly denser with decrease in wave-length below this figure, as has been shown by Toy & Ghosh (1920). In the Ferguson-Benson-Renwick photometer, the wedge is illuminated by diffuse light and the densities are measured visually, so that the effective wave-length is considerably larger than $420\,m\mu$.

THE EFFECT OF THE INCLINATION OF THE INCIDENT LIGHT

If the wedge is illuminated by light derived from a diffusing surface, which is itself illuminated by approximately parallel light incident nearly normally, the conditions will be identical with those in which it is calibrated, and the makers' figure may be used. It is of interest, however, to investigate what corrections would be needed in the following circumstances. (1) The degree of imperfection of the diffusing surface used differs from that of the diffuser used by the makers (a "perfect" diffusing surface is considered to be one from which the illumination emitted per unit solid angle is independent of the direction of emission, i.e. the illumination emitted per unit area is proportional to the cosine of the angle of emission). (2) Parallel light is incident obliquely on an imperfect diffusing surface. (3) Parallel light is incident obliquely on the wedge without interposition of a diffusing surface. (4) The wedge is illuminated by the system of two lamps and diffusing surface used in the measurement of the Schwarzschild constant (see below).

(1) *Calculation of the ratio of the wedge constant in diffuse light to that in parallel light.* Let the wedge be illuminated by an infinite diffusing surface. Consider the illumination received by any point on the wedge from an elementary annulus which subtends an angle θ at this point. Let the illumination emitted per unit solid angle be I_θ. I_θ is a measure of the imperfection of the diffusing surface, and is independent of θ if the illumination is perfectly diffuse. Then, the illumination emitted per unit surface in the direction θ is $I_\theta \cos\theta$.

The total illumination received at the point considered from the elementary annulus is $2\pi I_\theta \sin\theta\, d\theta$, and the vertical component is $2\pi I_\theta \sin\theta \cos\theta\, d\theta$. The total illumination falling on the wedge $= I = \int_0^\pi 2\pi I_\theta \sin\theta \cos\theta\, d\theta$. This expression reduces to πI_θ for perfectly diffuse light, and can be evaluated graphically if the relation between I_θ and θ is determined empirically for any given diffusing surface. But this illumination passes through the wedge at an angle ϕ, where $\sin\theta/\sin\phi = \mu$, the refractive index of the material of which the wedge is composed. Hence, if D is the density of the wedge at the point considered to light of normal incidence, the density to light incident at an angle θ is $D/\cos\phi$, and the vertical component transmitted is

$$\frac{2\pi I_\theta \sin\theta \cos\theta\, d\theta}{(10)^{D/\cos\phi}}.$$

The total illumination received on the paper after passing through the wedge is thus

$$\int_0^\pi \frac{2\pi I_\theta \sin\theta \cos\theta\, d\theta}{(10)^{D/\cos\phi}} = I^\star.$$

Integration can again be carried out graphically. The effective density of the wedge to light emitted from any given diffusing surface is given by $\log_{10} I^\star/I = D'$. For perfectly diffuse light, the ratio D'/D was calculated to be 1·135, while for light from two samples of surface-flashed opal glass, the ratio D'/D was found to be 1·120 and 1·125 respectively; the second of these was markedly more nearly "perfect" than the first. μ has been taken as 1·5, a value which is probably rather too large.

The "imperfection" of an actual diffuser was measured by projecting an image of an incandescent filament 2 mm. wide normally on one side; the intensity of the light emitted on the far side at a number of angles to the normal was then measured by means of a rectifier photo-cell behind a slit 2 mm. wide, and 45 mm. from the diffuser. The photo-cell and galvanometer used were calibrated by means of an inverse square law photometer.

It would appear that variations in the "perfection" of the diffuser over reasonable limits will not seriously affect the value of the wedge constant.

Atkins & Poole (1936*b*) remark that "a 1 mm. filter is about equivalent to a similar one 1·15 mm. thick, if it is used in diffuse light". The calculated figures are in adequate agreement with this observation.

(2) *The effect of parallel light incident obliquely on an imperfect diffuser.* In this case, the illumination emitted by the elementary annulus will not be uniform at all points, but will reach a maximum in the direction of the incident light. The distribution of intensity of the light emitted was measured by projecting the image of the incandescent filament on the diffusing surface at an angle to the normal, either in the plane of rotation of the photo-cell, or in a plane at right angles. From the approximate distribution curve so obtained, the mean circular intensity was derived, and used as the value of I_θ in the expression given in the previous section. For an angle of incidence of 60°, and the less perfect diffusing surface, the value of D'/D so obtained was 1·14. The distribution curve was very little affected by further increase in the angle of incidence, so that we may take it that for this particular diffusing surface, the value of D'/D would lie between 1·12 and 1·14 for all angles of incidence. Further, the figures are not likely to be altered significantly by considerable changes in the degree of imperfection of the diffusing surface.

(3) *Parallel light is incident obliquely on the wedge without the interposition of a diffusing surface.* Here, $D'=D/\cos\phi$, where $\sin\theta/\sin\phi=\mu$. If μ is taken as 1·5, the values given in Table II are obtained. In actual practice, however, if a wedge is exposed to bright sunlight, the value of D'/D will not vary to so great an extent with the altitude of the sun. In the first place, there is a considerable amount of scattering of light within the wedge itself, with the result that the observed value of D'/D for an imperfect diffuser was 1·09 ± 0·02 instead of the calculated 1·12. In the second place, the wedge is never exposed to pure sunlight, but to a mixture of sunlight and diffuse skylight. Atkins & Poole (1936*a*) give a large number of values for the ratio of the vertical component of sunlight to the vertical component of skylight, from which average values can be obtained for various altitudes of the sun. The estimated actual values of D'/D for sunlight + daylight are given in the last line in Table II. In addition, if a wedge recorder is exposed at sea, the random motion will largely average out the values of D'/D. The average of the figures for pure sunlight given above is 1·15, a value which differs little from that for diffuse light.

TABLE II. RELATIVE VALUES OF WEDGE CONSTANT IN LIGHTS OF VARYING OBLIQUITY

Angle of incidence	0°	30°	45°	60°	90°
D'/D calc.	1·00	1·06	1·135	1·22	1·34
D'/D daylight conditions	—	1·10	1·135	1·16	—

A second-order effect on the wedge constant produced by light incident obliquely in the plane of the long axis of the wedge arises from the fact that light reaching the photo-sensitive surface at a point distant l from the zero end of the wedge, will pass through the wedge at some point distant $l \pm \Delta l$ from the zero end. If d is the thickness of the glass between the wedge and the photo-sensitive surface, $\Delta l = d \tan \phi$. Now the maximum value of ϕ is $\sin^{-1} \mu$, where μ is the refractive index of the glass. If this is taken as 1·5, the maximum value of Δl, for $d = 1$ mm., becomes 0·9 mm., corresponding to a maximum increase or decrease in density of 3%. This effect, of course, will not be apparent in diffuse light, since the positive and negative corrections will be equal.

It is clear, therefore, that it is always advisable to place a sheet of diffusing material above the wedge. The extra uncertainty introduced by the omission of the diffuser, however, is not likely to be large except when the recorder is exposed on land to bright sunlight with the altitude of the sun greater than about 55° or less than about 35°. If the diffuser is used, care must be taken that the diffusing surface is large enough to allow the intensity of illumination at the ends of the wedge to be the same as that in the centre. It can easily be shown that the necessary minimum length of a perfect diffusing surface increases as its distance from the wedge increases. If the wedge is 10 cm. long, and the diffusing surface is 5 cm. from it, and 25 cm. long, the intensity at the ends of the wedge will be 3% less than that at the centre. If, on the other hand, the diffusing surface is only 0·5 cm. from the wedge, a 3% difference of intensity will be obtained with a diffusing surface only 11 cm. long. In both cases the illumination sensibly reaches the value at the centre at points 0·5 cm. from the ends.

It may be pointed out that any uncertainty in the value of the wedge constant only becomes significant if the illumination integrals to be compared differ considerably in magnitude. Thus while it may not be possible to determine with great accuracy the absolute value of, say, the total illumination received during one day, it is possible to compare this illumination with that received during another day with considerable accuracy.

(4) *The constant of the wedge when exposed to the source of light used for the measurement of the Schwarzschild constant*. The value was found by direct measurements to be identical with that for diffuse light, except when measurements were made at points immediately opposite one of the lamps. As was to be anticipated, owing to the imperfection of the diffusing arrangements, the wedge constant at these points was lower than at other points—actually by about 3·5%. This discrepancy is of no consequence, as the extreme ends of the wedge were always placed opposite the lamps, and no measurements were made on the corresponding parts of the prints.

The Effect of the Wave-length of the Light

The particular wedge examined by Toy & Ghosh (1920) had a density at 300 mμ. which was 2·2 times the density at 420 mμ. Now the photographic emulsion is mainly affected by light of short wave-lengths, and it is thus clearly necessary to inquire whether it is appropriate to use the "visual" wedge constant when calculating the effective intensity of light falling on the photographic paper.

In the case of gaslight paper, it is possible to determine the "photographic" wedge constant directly. The paper is exposed behind the wedge on a number of occasions for the same duration, but at different distances from a point source of light. If precautions are taken to avoid stray light, the inverse square law can be applied, and the wedge constant determined by the inverse of the method used to determine the intensity of an unknown illumination, as described above.

An automobile head-lamp bulb was used as source of light, and exposures were made at distances varying from 50 to 400 cm. The values obtained for the wedge constant were independent of the distance from the source of light, indicating the validity of the inverse square law, and the mean "photographic" value, so determined, was 38 % higher than the "visual" value for parallel light as measured by a rectifier type photo-cell; the correction, therefore, is clearly of great importance.

Unfortunately, it is hardly possible to make similar direct measurements with "P.O.P.", owing to the difficulty of obtaining a point source of light sufficiently intense to allow of reasonable durations of exposure. An estimate of the probable magnitude of the correction, however, can be obtained from the spectral sensitivity curves of the emulsion before and after interposing the wedge between the source of light and the spectrograph; details of the methods used are given in a later section. The curves are shown in Fig. 2. If A_0 and A_w are the areas below the curves obtained in the absence of the wedge, and in its presence, respectively, then it can be shown that $D' = \log A_0/A_w$, where D' is the "photographic" density of the wedge at the point used. For "Slogas" the photographic density calculated in this way agreed within the limits of error with that determined directly. No very great accuracy can be expected, since the result depends considerably on the value chosen for the Schwarzschild constant.

It was not possible to obtain a spectral sensitivity curve for P.O.P. with the wedge in position owing to the very long exposures that would have been necessary. The curve can, however, be constructed, since the density of the wedge for any given wave-length is known from the observations on the gaslight paper. The photographic density is thus found to be 3 % greater than the visual density, when tungsten filament light was used. For sunlight and daylight the corresponding corrections are 2 and 4 % respectively.

Choice of Emulsion

For general reasons, a relatively insensitive emulsion that requires the least amount of processing is desirable, and P.O.P. and gaslight paper appear to be the most suitable. A paper support for the emulsion also has some advantages over celluloid or glass. As there appear to be no records in the literature of measurements of the degree of failure of the reciprocity law in these emulsions, or of the spectral sensitivity of P.O.P., such measurements have had to be made.

The Applicability of the Reciprocity Law to P.O.P. and Gaslight Paper

The paper was exposed behind a neutral tint wedge to a uniform source of light for different times. In general, four exposures were made on each sheet of paper, of approximately 1, 3, 8 and 24 hr. respectively. The prints were processed in the usual way, and dried. The method was sensibly the same as that described by Mallett (1922, 1923). Two millimetres were then trimmed off the sides of each wedge print, in order to eliminate the effects of shading by the binding of the wedge, and two of the four strips so formed were placed beneath a slit 2 mm. wide in a piece of cardboard. One strip was then fixed so that the portion of the print beneath the slit was of a suitable density, and the other slid longitudinally until it also had the same density. Four such density matches were made, and then the two strips reversed in position, so as to eliminate as far as possible the effects of uneven illumination, accidental irregularities in the paper, and so forth, and four more matches made. The mean of the eight readings was then taken. If l_1 is the distance from the slit to the end of the print, corresponding to the zero end of the wedge, on the first strip, and l_2 the corresponding distance on the second strip, then, from the equation for the blackening of a photographic emulsion, given above,

$$\log I - kl_1 + p \log t_1 = \log I + kl_2 + p \log t_2,$$

where I is the intensity of the illumination during the exposure. Hence

$$p = \frac{k\,(l_1 - l_2)}{\log\,(t_1/t_2)}.$$

The comparison can, of course, be made at any desired density of the wedge prints, and, in general, four different densities were used whenever possible, defined arbitrarily as "very pale", "pale", "medium" and "dark". Such comparison at several different densities assists in eliminating the well-known unevenness in the response of different parts of the same emulsion. The use of a paper support, moreover, reduces this unevenness considerably, by allowing the processing solutions to reach the emulsion from both sides.

The Source of Light. It was necessary to obtain sensibly uniform illumination over a length of 10 cm. (about 3 mm. at each end of the wedge print were rejected in any case, owing to the shading by the binding which held the wedge between the glass plates), of sufficient intensity to produce an adequate density in the print in 1 hr., and free from random fluctuations over a period of at least 24 hr. Spatial uniformity was obtained in the case of gaslight paper by placing the wedge and paper a sufficient distance from the source of light, which was a 12 V. 36 W. automobile head-lamp bulb. A distance of

2·5 m. was found to give a suitable intensity. For P.O.P. a much greater intensity is required, and two such head-lamp bulbs were used, mounted about 10·5 cm. apart, and with a sheet of surface flashed glass in contact with the bulbs. The wedge and paper were then mounted as close as was possible without introducing sensible non-uniformity of the illumination; this was about 7 cm. from the lamp filaments. The uniformity of illumination was checked at intervals by means of a rectifier type photo-cell, and slight adjustments made if necessary. The two lamps usually had surprisingly equal emissions, but any small difference was eliminated by bringing one lamp closer to the wedge than the other.

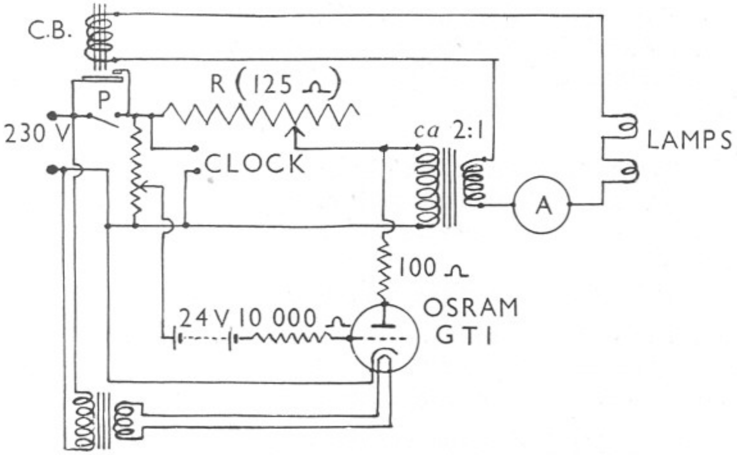

Fig. 1. Diagram of circuit used for current stabilization in lamps used as source of illumination. *R*, main voltage dropping resistance; *P*, bell-push for starting current through lamps; *CB*, no-load circuit breaker.

Temporal uniformity was obtained by running the lamps off the A.C. mains in conjunction with one of two types of current stabilizer. The first involves the use of a gas-filled relay (or thyratron—for characteristics, see Hull, 1929), and the circuit is shown in Fig. 1. If the line volts rise, the negative bias on the grid of the relay falls more during each positive half-wave, and the current taken by the relay rises more than in proportion to the rise in the line volts. The potential drop across the resistance *R* is increased, and the volts fed to the transformer, and hence the current in the lamps is reduced. A no-load circuit breaker was included as subsidiary equipment. If the current through the lamps fails, either through failure of the supply, or breakage of a filament, the circuit-breaker *CB* opens, and protects the gas-filled relay from the rise of anode potential that would otherwise follow. The circuit-breaker cannot be closed again except by deliberately closing the bell-push *P*. The current regulation obtained was such that a 1 % change in the lamp current was produced by a 5 % change in the line volts; considerably better regulation was obtained for smaller changes in the line voltage. The G.T. 1 gas-filled relay does not take quite a large enough anode current for perfect regulation; in particular, occasional large mains fluctuations would extinguish it entirely. It would have been better to have included a step-up transformer in front of the circuit shown, so that a larger value of *R* could have been used.

The second type of current stabilizer used depended upon the action of a barretter. Two type 304 Osram barretters were used in parallel, in the primary circuit of a Zenith regulating transformer, together with a variable resistance and the no-load circuit breaker, the lamps being connected in the secondary circuit. When two lamps were being used, it was necessary to step up the supply to about 350 V., in order to bring the barretters to the proper operating conditions. The degree of regulation obtained was rather better than with the circuit shown in Fig. 1 for slow fluctuations, a 1% change in lamp current being produced by a 10% change in line voltage. Owing to the slow response of the barretters, however, they were unable to take charge of rapid fluctuations.

In both circuits, an electric clock was connected in the circuit beyond the no-load circuit-breaker. This indicated the duration of the exposure in the event of the circuit-breaker opening for any reason.

The Value of the Schwarzschild Constant

A. *P.O.P.* (*Ilford matt white*). Seventeen experiments were performed involving sixty-eight exposures and 124 determinations of the Schwarzschild constant. The results are shown in Table III. Previous to these, ten experiments had been performed while the technique was being developed. The results of these were more erratic, but the general conclusions to be drawn are the same.

TABLE III. THE SCHWARZSCHILD CONSTANT FOR P.O.P.

Duration of exposure, hr.	Density of print			
	Very pale	Pale	Medium	Dark
1–3	1·05 ± 0·023	1·02 ± 0·013	1·04 ± 0·012	—
3–8	1·04 ± 0·033	1·03 ± 0·022	1·00 ± 0·020	0·83 ± 0·057
8–24	1·02 ± 0·015	1·05 ± 0·018	1·07 ± 0·010	1·01 ± 0·025

General mean 1·033 ± 0·007.
Standard deviation for single observation 0·075 ± 0·005.

Three general conclusions can be drawn. (1) The value of the Schwarzschild constant is independent of the duration of the exposure up to 24 hr. (2) The value of this constant is independent of the density of the print, except in the case of the exposures of medium duration, where there is a definite fall at high densities. It should be pointed out that in the limit, of course, the Schwarzschild constant must fall to 0 as the density increases, since there is a definite limit to the density which can be produced by any amount of illumination. The densities used were all well below this limit. (3) The departure from the reciprocity law is barely significant. In addition, it was shown that the value of the Schwarzschild constant is unaffected by changes, over wide limits, in the duration of fixation, or in the concentration or temperature of the hypo used. A few not very accurate measurements were made on unfixed prints; in these, the value of the constant was about 1·5.

The value of the standard deviation indicates an uncertainty of ±7·5% for a single measurement. This includes the uncertainty in the constancy of the illumination in two experiments, as well as the uncertainty in the matching of the densities, and the lack of uniformity of the emulsion, but does not include the uncertainty in the value of the wedge constant. The effect of this will become proportionately greater as the total illumination measured becomes greater. It may be expected, therefore, that the uncertainty in the determination of an unknown illumination will be between ±5 and ±10%.

B. *Gaslight paper* (*Illingworth Slogas matt soft*). A smaller number of determinations was made with gaslight paper, as it very soon became apparent that this emulsion is not suited for photometric work involving long durations of exposure. The value of the Schwarzschild constant as shown in Table IV is considerably less than 1 and appears to fall with increase in the duration of the exposure.

TABLE IV. THE SCHWARZSCHILD CONSTANT FOR GASLIGHT PAPER. (MEAN OF ALL PRINT DENSITIES)

Duration of exposure, hr.			
3/4	3/4–3	3–15	15–30
0·94 ± 0·01	0·88 ± 0·02	0·80 ± 0·02	0·81 ± 0·03

Jones & Huse (1923) give values of the Schwarzschild constant for three types of emulsion; at very low intensities (exposures lasting up to a few hours) they find values of 0·63 for a high speed emulsion, 0·88 for a medium speed emulsion, and 0·68 for a low-speed emulsion. In all cases the value of p fell as the intensity of illumination was reduced. Baker (1924), working on three brands of panchromatic emulsion and with exposure times up to 200 sec., reports values of 0·80–0·93. Again, the value fell as the exposure time was increased.

The Spectral Sensitivity of the Emulsions. In all photometric methods it is important to know at least approximately the limits of wave-length to which the method is sensitive. For biological work, moreover, it is desirable that these limits should at least be within the visible spectrum. Spectral sensitivity curves of various photographic emulsions to tungsten filament light are given by Davis & Walters (1922). These authors find that ordinary plates have a maximum sensitivity to light of wave-length between 450 and 475 mμ., while the slower transparency and lantern plates have a maximum sensitivity in the region 420–460 mμ. These curves, however, give little indication as to the spectral sensitivity to be expected from an emulsion such as P.O.P. which is not developed.

Accordingly, fresh observations were made with a Hilger quartz spectrograph, using an automobile head-lamp bulb as source of light; under the conditions of operation, the colour temperature would have been about 2800° K.; a slit width of 2 mm. had to be used to get a sufficiently high illumination to affect P.O.P. in a reasonable time. The approximate sensitivity curves shown in Fig. 2 were obtained by making a series of exposures of different durations and plotting the wave-length at which a standard amount of blackening had been produced, against $1/t^p$, where p is the Schwarzschild constant for the emulsion in use. Each ordinate was then corrected for the varying dispersion of the spectrograph and the varying obliquity of the light falling on the paper.

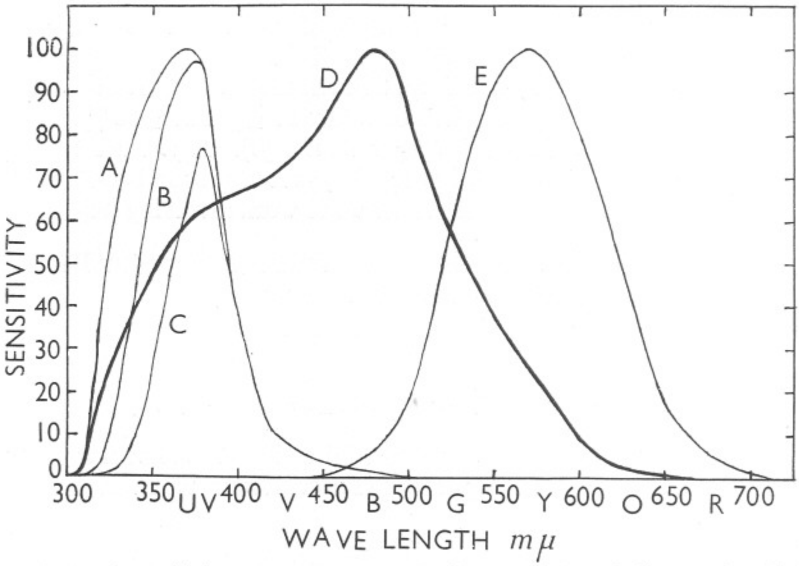

Fig. 2. Spectral sensitivity curves to tungsten filament light. *Ordinates*: Sensitivity in arbitrary units. *Abscissae*: Wave-length. (A) Illingworth Slogas. (B) The same with neutral tint wedge (zero end) in front of slit, i.e. showing the effect of absorption by the glass mounts. (C) The same with neutral tint wedge (density = 1·0) in front of slit, the ordinates being multiplied by 10. (D) Ilford P.O.P. (E) The human eye. Curve E is derived from the luminosity figures of Gibson & Tyndall (1923) and the distribution of energy with wave-length in tungsten filament light given by Priest (1922).

The curve for gaslight paper differs very markedly from that given by Davis & Walters for ordinary photographic plates, the maximum sensitivity being in the neighbourhood of 370 mμ. As a check, a series of exposures was made on an Imperial S.R. plate; the maximum sensitivity was found to be around 465 mμ., in good agreement with the observation of Davis & Walters. The shift of the maximum sensitivity towards the shorter wave-lengths in the case of gaslight paper is in agreement with the similar but smaller shift observed by Davis & Walters in the case of transparency and lantern slide plates.

The behaviour of P.O.P. is very different. If the unfixed print is examined (Fig. 3) it will be seen that the blackening begins at a wave-length of about 370 mμ. The density, however, does not increase at all rapidly in this region, but extends toward the red end of the spectrum, the maximum density after 32 hr. exposure being produced at about 520 mμ. It is to be supposed that the surface layers of the emulsion become blackened first, and that these then absorb the shorter wave-lengths more than the longer, and so prevent the former from penetrating to the deeper layers. On fixing, the density of the whole print is reduced, and the weak effects of the short wave-lengths in the short exposures are removed entirely. The most effective wave-length for the fixed print, i.e. that at which blackening is first produced, is thus shifted to about 485 mμ. Introduction of the dispersion correction, shifts this maximum to 480 mμ.

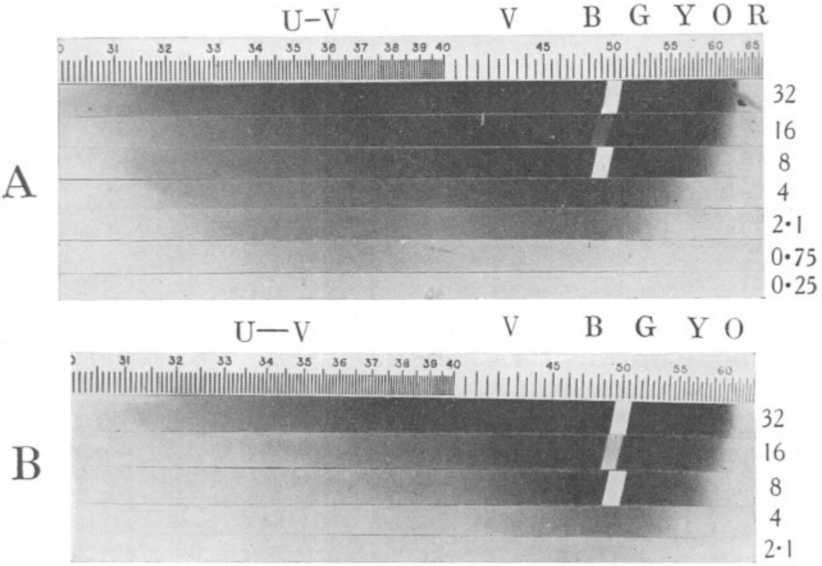

Fig. 3. Photographs of continuous spectrum of tungsten filament light taken on P.O.P. (A) Unfixed. (B) Fixed. The duration of each exposure is given in hours. The white mark across the upper three exposures in each case is due to the glass plate which was placed in front of the paper cracking during the 16 hr. exposure; this was made before the 8 hr. exposure.

It is clear, therefore, that for purposes of photometry in visible light, P.O.P. is greatly to be preferred to gaslight paper, or, in all probability, to any emulsion after development. Not only is it sensitive to a wider range of wave-lengths, but it has the added advantage of obeying the reciprocity law within the limits of experimental error.

STANDARDIZATION AND CALCULATION OF THE RESULTS

A 12 V., 36 W. automobile head-lamp bulb was used as standardizing light, operated from one of the current stabilizing circuits already described. An elaborate circuit of this kind is not necessary, as the exposure is only of a few hours' duration, and the current can easily be regulated by hand. The paper was exposed to this light at a distance of 30 cm., a sheet of flashed glass being placed in contact with the lamp bulb. Three exposures were usually made for about 2, 4 and 6 hr. respectively, giving three patches of different density. The wedge print was then compared with each of these patches in turn exactly as described above for the determination of the Schwarzschild constant. The mean of the three results was then taken. The method of calculation is indicated by the following example.

An exposure was made on the roof of the Plymouth laboratory from 20.30 G.M.T. 12 July 1934 to 20.30 13 July, say 17 hr. of daylight. The weather was mainly overcast. No diffusing screen was used and consequently the exact value of the wedge constant to be used is a little uncertain. The results are given in Table V, in terms of the intensity of the standardizing light. If this is measured in visual units, then the unknown illumination can also be directly expressed in visual units, provided that the distribution of energy with wave-length is the same in the unknown as in the standardizing source of light. For other sources of light—notably daylight—correction factors are necessary. The magnitude of these colour correction factors are subject to very considerable uncertainty since the methods used in their derivation fail to take more than an approximate account of the behaviour of photographic emulsions in lights of different intensities and different wave-lengths. Measurements made in any one quality of light, however, will be consistent among themselves even though their absolute magnitudes in visual or energy units are uncertain. The object of the standardizing exposure is primarily to eliminate random differences between one sheet of paper and another, arising from inherent differences of sensitivity, or from small differences in processing.

TABLE V. ANALYSIS OF A TYPICAL RECORD

Recorder on roof of Laboratory 20.30 12 July to 20.30 13 July

Duration of standardizing exposure, hr. (t_s)	Mean distance along wedge print to point of density match, mm. (l)	D ($=kl$) ($k=$wedge constant)	Log R/I_s ($=D+\log t_s$)	R/I_s corrected for $p=1{\cdot}03$
1·9	104	3·15	3·43	2580
3·0	86	2·90	3·37	2240
5·0	72	2·71	3·41	2480
				Mean 2435

These correction factors express the relative brightness of the two sources of light as measured by (1) the human eye, and (2) the photographic emulsion. The relative brightness to the human eye on the one hand, and to the photographic emulsion on the other hand, of tungsten filament light can be discovered from a knowledge of (*a*) the luminosity curve of a constant energy spectrum (Gibson & Tyndall, 1923), (*b*) the distribution of energy with wave-length in the tungsten filament light (Priest, 1922), and (*c*) the spectral sensitivity curve of the photographic emulsion to tungsten filament light, described in the previous section. The ratio between the area below the luminosity curve for tungsten filament light and that below the photographic spectral sensitivity curve for the same light, gives us the photographic effectiveness of each lux of this light; we will denote this by E_w. For daylight, a similar factor can be derived from (*a*) the luminosity curve as above, (*b*) the distribution of energy with wave-length in daylight (Davis & Gibson, 1931), and (*c*) the spectral sensitivity curve of the photographic emulsion to daylight, derived from the similar curve for tungsten filament light by means of the two energy distribution curves; we will denote this factor by E_d.

The figures used for daylight are those given by Davis & Gibson for the distribution of energy with wave-length in the sun's radiation outside the earth's atmosphere. These authors give reasons for believing that the colour temperature of an overcast sky is very closely equal to that of the sun outside the earth's atmosphere.

The figures given by Priest (1922) for the energy distribution with wave-length of a tungsten filament lamp, are for a lamp with an efficiency of 15·6 lumens per watt. The distribution of radiant energy in the plane of the filament used under normal operating conditions (11·6 V., 2·8 amp.) was measured approximately by means of a photo-cell, and the luminous efficiency calculated to be about 16 lumens per watt, a sufficiently close approximation for the present purposes.

The illumination on the photographic paper when exposed to the standardizing light was measured by means of a Holophane Lumeter, and found to be 550 lux. The value of E_w was found to be 0·26, so that the "photographic" intensity of the standardizing light was $550 \times 0{\cdot}26 = 143$ "photographic units". Similarly, the value of E_d was found to be 0·69, so that if we have a daylight illumination which is, photographically, A times the standard of 143 photographic units, its visual intensity will be $\frac{143 \times A}{0{\cdot}69}$. Thus in the example given in Table V, the total vertical illumination received becomes $2435 \times \frac{143}{0{\cdot}69} = 505$ kilolux-hours. The recorder, in this experiment was placed on a horizontal surface, and so the readings represent the vertical component only of the total illumination. There is no reason why a photographic recorder of this type should not be placed within a globe integrator, such as is described by Atkins & Poole (1936*a*), in which case the total illumination from all directions would be measured.

The question now arises as to the appropriate value to be used for the factor E_d during bright sunshine. Owing to the scattering in the upper atmosphere, sunlight at the earth's surface is relatively deficient in the blue end of the spectrum, the scattered light being apparent in the blueness of the clear sky. If the recorder is placed in a spherical integrator, so that it receives the whole radiation from the celestial hemisphere, the direct sunlight and the scattered skylight would be recombined, and the value 0·69 would still be appropriate for the factor E_d. When used to record the vertical component only, it will receive one-half of the scattered skylight, and a fraction of the direct sunlight depending on the altitude of the sun. From the figures given by Davis & Gibson (1931), it can be calculated that the photographic effectiveness (P.O.P.) of each lux of mean noon sunlight is 0·46, and the calculated values of E_d for various altitudes of the sun are given in Table VI. The low value for very low altitudes is only estimated; when the sun is very low, there will be a considerable amount of scattering by the thick layer of atmosphere, and the sunlight will be distinctly yellow. Moreover, this yellow light will be reflected by the under surfaces of clouds and mist, and so will not be compensated by the blueness of the sky. In view of the very great variability of light conditions at sunrise and sunset, it would be unwise to place any reliance on photographic observations made at these times.

TABLE VI. THE PHOTOGRAPHIC EFFECTIVENESS OF DAYLIGHT + SUNLIGHT FOR P.O.P.

Altitude of sun	75°	50°	38°	30°	10° and less
Value of E_d	0·62	0·64	0·665	0·69	0·60 and less*

* According to amount of mist and cloud.

It should, perhaps, be pointed out, to avoid misconceptions, that we are not concerned, here, with the relative intensity of the sunlight and the skylight. As is shown by the figures given by Atkins & Poole (1936*b*), this quantity varies very greatly according to the altitude of the sun, the time of year and type of sky. We are concerned only with the apparent colour temperature of the light falling on the photographic recorder. Two extreme examples will illustrate the difference between these two quantities. (1) Outside the earth's atmosphere, there is no skylight (to all intents and purposes), and the intensity ratio sun/sky is infinity. (3) When the sky is completely overcast, there is no sunlight, and the intensity ratio is zero. Yet the colour temperature in both cases is the same.

USE OF THE METHOD IN THE FIELD

The detailed technique must depend upon the exact nature of the measurements to be made, and the only essentials are some means of clamping the wedge in contact with the sensitive paper, and suitable protection from the weather. That part of the paper which is not underneath the wedge must be protected from the light, so that the standardizing exposure or exposures may be made on the same sheet. There is no necessity to perform the standardization in the field. The prints, if reasonably cool and dry, can be kept in the dark without deterioration certainly for a week, and probably for longer, before fixing. When used on land, and in bright sunlight, the recorder should be placed as far as possible so that the direction of the sun is at right angles to the long axis of the wedge; the small errors due to the parallax between the wedge and the emulsion are thus eliminated.

SUMMARY

1. The photographic neutral-tint wedge method of measuring the total illumination falling on an area over a long period of time is described.

2. A study is made of the chief sources of error inherent in photographic methods, i.e. (*a*) the uncertainty in the value of the wedge constant, and (*b*) the failure of the reciprocity law, in that the amount of blackening of the photographic emulsion is not, in general, strictly proportional to the product of the intensity of the illumination and the duration of the exposure.

3. It is shown that P.O.P. obeys the reciprocity law sufficiently closely for durations of exposure between 1 and 24 hr. Gaslight paper, on the other hand, can only be used when the duration of exposure is less than about 1 hr.

4. It is shown that when P.O.P. is used, and a sheet of diffusing glass is placed above the wedge, the value of the wedge constant is sensibly independent of the direction and quality of the incident light.

5. Spectral sensitivity curves to tungsten filament light for gaslight paper and P.O.P. have been evaluated. From these, and other data, correction factors have been calculated for converting the photographic measurements of illumination into visual units.

6. It is concluded that the method is sufficiently reliable for use in the field, where its simplicity and the small amount of apparatus required, make it specially suitable. The experimental uncertainty is about ±5 to ±10%.

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NOTES ON THE BREEDING OF SOME LAMELLIBRANCHS FROM PLYMOUTH AND THEIR LARVAE

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(Text-figs. 1–7)

CONTENTS

INTRODUCTION

A study of the larval stages of different lamellibranchs from Plymouth with a view to determining their importance in the plankton has brought out some interesting facts. It is well known that the free-swimming larvae are much simpler than most of the gastropod veligers, and that the velum is usually entire, having rarely a slight indentation, showing a tendency to be bilobed in the larger forms. They thus resemble in this respect the primitive gastropods. In many of them the velum is lost early in life, and usually the change in form of the shell takes place after metamorphosis. The post-larval growth is therefore an important part of the life history. The first shelled stage is so similar in all species that it is almost impossible to distinguish the different early veligers in the plankton, but in certain cases fertilizations have been made and the larvae reared until they have lost the velum and descend to the bottom when the species, or at least the genus, can usually be identified.

Fertilizations were found to be difficult. Those which were successful were made in finger-bowls in the usual way, in sterilized or filtered water, the free-swimming larvae being transferred to plunger jars or small bowls with minute flagellates for food. Veligers from the plankton were kept in bowls or plunger jars with flagellates or diatoms for food until they grew to a stage in which the species or genus was recognizable. In this way much useful knowledge has been gained. Adults of many species were examined to find the state of the gonads and the breeding seasons. This, together with the recognition of the larvae in the plankton, has shown many definite breeding periods, and certain veligers at times dominate the plankton, such as *Mytilus edulis* in late spring and early summer and *Ensis siliqua* in early spring.

Descriptions of the larvae and post-larvae of *Lima hians* and of *Kellia suborbicularis* have already been published (Lebour, 1937–1938). Notes on several other species are given below; though unfinished it is thought best to publish them now, since the work must be discontinued for a period owing to my absence from Plymouth.

Knowledge of the later lamellibranch larvae and post-larvae is slight except for those which are economically important. References to these latter are purposely omitted in the list of literature, and only a selection of the more important papers relating to lamellibranch larvae is here included. The bulk of the previous work has been done on the egg and newly hatched larva. We have, however, the researches of Drew (1901) on *Nucula* and *Yoldia*, Odhner (1914) on various larvae from Rovigno, Pelseneer (1926) on *Lucina*, and Kändler (1926), who reared several planktonic veligers to recognizable forms, his work being quoted extensively by Haas in Bronn's *Tierreich* (1929, 1937). Thorson (1935) described the eggs and young of *Musculus*, and Matthews (1913) reared *Mytilus edulis* from fertilization to the young sessile stages. All these papers deal with species which occur in Britain or with closely related forms. In Japan Miyazaki (1935, 1936) has reared several species from fertilizations to young sessile stages.

The descriptions show that most of the essential external changes take place after the velum is lost. This, however, does not by any means indicate that the free-swimming larvae are of no account in the plankton, for they are often present in very large numbers and are known to be eaten by many planktonic and other animals. They are found in very small herring before the loss of the yolk sac, and young sprat of whitebait size frequently have their stomachs full of early veligers (Lebour, 1921). The best food for rearing crab larvae was found to be the larvae of the common oyster taken from the gills of the parent, and *Teredo* larvae one day old, obtained from fertilizations, were also found useful for this purpose (Lebour, 1927). Many small invertebrates eat lamellibranch larvae; to quote but one instance, the larvae of the annelid *Magalona* is always found to be feeding on them (Lebour, 1922).

Most lamellibranch veligers are small, the largest being well under 0·5 mm. long. A striking fact shown in the present study is that some of the largest veligers belong to very small adults. Thus an unusually large larva is found in *Kellia suborbicularis*, reaching to 0·32 mm. in shell length, the outstretched velum being still larger (Lebour, 1938), and two only slightly smaller turn out to be closely related forms, *Mysella bidentata* and a species which is possibly undescribed (see below, p. 143). Both *Kellia* and *Mysella* are small when adult, *Kellia* breeding at a shell length of from 4 to 9 mm., while *Mysella* is still smaller. Both are viviparous; the larvae are retained in the gill pouch until an early shelled stage, and the remainder of the larval life is continued for some time freely in the sea. All of these veligers are round or roundish.

Lima is a striking member of the plankton in its larval stage (Lebour, 1937) at certain times of the year; it often occurs with *Kellia*, and is easily recognizable by its triangular wedge-shaped shell attaining a large size before losing the velum. *Hiatella arctica* also grows to a large size, the shell being triangular with its greatest diameter lengthways. *Kellia*, *Lima* and *Hiatella arctica* are the commonest large lamellibranch larvae at Plymouth. Of these *Kellia* may occur throughout the year, the others chiefly in late summer and autumn. *Hiatella gallicana* breeds in winter and its larva, smaller than that of *H. arctica*, occurs in winter and early spring. *Heteranomia squamula* is also easily recognizable in the plankton on account of its very conspicuous pedal sinus (see below, p. 140), *Anomia* being similar but without such a distinct sinus. Both occur irregularly throughout the year, *Heteranomia* especially in autumn and winter. *Ensis siliqua* characterizes the plankton in early spring, apparently its only breeding season; the larva can be recognized by its oval shell curving in dorsally behind and by its bright yellowish brown liver. The closely related larva of *Cultellus pellucidus* occurs in autumn and winter and is distinguishable from *Ensis* by the red colour near the siphons in the late larva (see below, p. 128). *Mytilus edulis* is by far the commonest larva in May and June, occurring also sparingly at other times; it is recognizable by its conspicuous eye and purplish tinge. *Pecten* larvae and their near relatives also have conspicuous eyes, but the shell is more oval and not tinged with purple; moreover, early post-larvae are often seen with the beginning of the shell sculpture peculiar to these forms. Closely related to *Mytilus* is the larva of *Musculus*. This is larger than *Mytilus*, coloured dark brown and purplish and with the shell rounder.

Cardium larvae are small and inconspicuous except those of *Cardium crassum*, which grow to a large size and are conspicuous members of the plankton in the summer months (see below, p. 132). Another easily recognizable veliger is *Teredo*, almost certainly *T. norvegica*, which is almost spherical and very globose, occurring at almost any time of year, sometimes in numbers. A second *Teredo* veliger, found inside the parent and swimming about round the wood in which it burrows, is probably closely related to *T. navalis* (see below, p. 136). *Pholadidea* and *Barnea* lose the velum at a very early stage and are difficult to recognize in the plankton (see below, p. 132). *Venus fasciata* has a small round veliger, and probably the other members of the genus have similarly shaped larvae difficult to distinguish. Among the numerous small roundish and oval veligers that of *Abra* sp. (probably *Abra alba*) can be recognized and a few others guessed at, but there are still very many not identified. *Nucula nucleus* and *N. nitida* have free-swimming larvae; the egg of *N. nucleus* has been reared from a fertilization to a barrel-shaped larva similar to that described by Drew for *N. proxima*. It has been shown by Drew

(1901) that there is no typical velum in the family, but that the velar cells enwrap the larva in a case. The free-swimming stage is apparently very short in these two British species, for perfectly formed shells similar to the adults occur at a very small size.

It is found that a large number of different species of lamellibranch veligers occur in late summer and autumn, apparently after the second large diatom outburst. Although there are always some larvae present in the plankton more species occur at this season. The winter months have the fewest species; in spring and summer they are plentiful, but the plankton is frequently characterized by one predominating species.

A few lamellibranchs retain the larvae in the gill pouch until they have the adult form. This occurs in *Lasaea rubra*. Certain species of *Musculus*, as is shown by Thorson (1935), deposit their eggs in gelatinous strings, the young emerging as miniature adults. Several species are viviparous, notably the Erycinidae and their near relatives.

A table is given showing the fertilizations which have been successful. All those which resulted in egg division are marked. *Cardium edule*, *Cardium scabrum* and *Pholadidea loscombiana* were reared until they lost the velum and descended to the bottom. *Ensis siliqua*, *Barnea parva*, *Teredo norvegica*, *Hiatella gallicana*, *Spisula solida* and *Heteranomia squamula* were reared to the shelled larva, *Nucula nucleus* to the free-swimming larval stage.

TABLE I. SUCCESSFUL FERTILIZATIONS

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Nucula nucleus	.	.	.	.	.	.	×	.	×	×	×	.
Nucula turgida	.	×	.	.	.	.	.	.	.	.	.	.
Heteranomia squamula	.	.	.	.	×	.	.	.	.	.	.	.
Mytilus edulis	.	.	.	.	×	.	.	.	.	.	.	.
Chlamys opercularis	.	.	.	.	×	.	.	.	.	.	.	.
Cardium scabrum	.	.	.	.	.	.	×	.	.	.	.	.
Cardium edule	.	.	.	×	×	×	×	×	×	.	.	.
Venus ovata	.	.	.	.	.	.	×	×	×	×	.	.
Venus fasciata	.	×	.	×	×	.	×	.	.	×	×	.
Venus striatula	.	×	.	.	×	.	.	.	.	.	.	.
Paphia rhomboides	.	×	.	.	.	.	.	.	.	.	.	.
Paphia pullastra	.	.	.	.	.	×	×	.	×	×	.	.
Tellina crassa	.	.	.	.	.	.	.	.	.	.	×	.
Scrobicularia plana	.	.	.	.	.	×	.	×	.	.	.	.
Abra alba	.	.	.	.	×	.	.	×	×	×	.	.
Cultellus pellucidus	.	.	.	.	.	.	.	.	.	×	.	.
Ensis siliqua	.	.	×	×	.	.	.	.	.	.	.	.
Spisula solida	×	×	.	.	.	.	.	.	.	.	.	.
Aloidis gibba	.	.	.	×	.	.	.	.	.	.	.	.
Hiatella gallicana	×	×	.	×	×	.	.	.	.	.	.	.
Gastrochaena dubia	×	.	.	.	.	.	.	.	.	.	.	.
Barnea parva	.	.	.	.	.	.	.	.	×	.	.	.
Pholadidea loscombiana	.	.	.	.	.	.	.	.	×	×	×	.
Teredo norvegica						Any month						
Thracia convexa	.	.	.	.	.	.	.	.	×	.	.	.
Viviparous species extruding larvae:												
Kellia suborbicularis	.	.	.	.	.	.	.	.	×	×	.	.
Galeomma turtoni	.	.	.	.	.	.	.	.	×	.	.	.

The study of the post-larval stages has shown that two species exist of certain forms. Thus it is conclusively proved that *Hiatella gallicana* and *H. arctica* are distinct species, a fact often denied, but recognized by Winckworth (1932) and others. One breeds in winter, the other in spring, and the shelled veligers, as already shown by Odhner (1914), are easily distinguished. From the study of the post-larvae it is found that besides *Mysella bidentata* there is another very closely related species. The post-larval growth, that is to say the growth after the loss of the velum, is most interesting in many species, especially in the Pholadidae and Teredinidae. In *Pholadidea loscombiana* certain phases occur which are intermediate between the veliger and adult and peculiar formations are found in *Teredo*. The post-larval phases in *Pholadidea* seem to indicate a habit of life intermediate between swimming and boring which apparently lasts for a long time. The very young *Pholadidea* are never seen in the rock, and it may be that there is a prolonged period of crawling before any boring takes place.

NOTES ON THE BREEDING SEASONS OF CERTAIN LAMELLIBRANCHS

(The names are according to Winckworth, 1932)

Nucula nucleus (L.). Fertilized successfully in July, September, October and November. Reared to barrel-shaped larvae in July. No eggs or ripe sperm seen from December to March. Breeding from spring to early autumn. Eggs 0·10 mm.

Nucula hanleyi Winckworth. Breeding at the same time as *Nucula nucleus*.

Nucula turgida Leckenby & Marshall. Fertilized successfully in February and reared to free-swimming early larvae. Breeding in winter. Eggs 0·09 mm.

Glycimeris glycimeris (L.). Ripe eggs obtained in January, March and October; ripe sperm in January and March.

Arca lactea L. Ripe eggs in September and October; ripe sperm in January, June, September and October.

Anomia ephippium L. Ripe eggs in June and October. Larvae of this species or *Monia* are found in the plankton at any time of year.

Heteranomia squamula (L.). Successful fertilizations obtained in May and the larvae grew to an early shelled stage. Ripe eggs and sperm found at any time of year. Larvae are common in the plankton throughout the year but especially in autumn and winter when the breeding season is more intense.

Mytilus edulis L. Successful fertilizations obtained in May and the larvae grew to the young shelled stage. Mrs Matthews (1913) grew them successfully to young mussels. The chief breeding season is from April to June, but some may be found ripe at almost any time.

Modiolus modiolus (L.). Ripe eggs and sperm in December.

Musculus sp. (probably *M. marmoratus* (Forbes)). Veligers common in the plankton in late summer and autumn. Thorson (1935) found the eggs of *M. discors* and *M. niger* from East Greenland in strings close to the parent in Ascidians; they hatched out after the loss of velum. He states that *M. marmoratus* has small eggs hatching as veligers and it is therefore probable that the present species is *M. marmoratus*.

Chlamys varia (L.). Ripe eggs in July.

Chlamys distorta (da Costa). Ripe eggs and sperm in March and July.

Chlamys opercularis (L.). Eggs and sperm were given out in the laboratory tanks on May 25 1936. The eggs were successfully fertilized and grew to the young shelled stage. Post-larval stages are found throughout the year.

Chlamys tigerina (Müller). Ripe eggs and sperm in January. Larvae of *Chlamys* spp. not identified occur in any month of the year.

Lima hians (Gm.). Breeding from late summer to early spring. Larvae are most frequent in late summer and early autumn and are common in the plankton.

Astarte sulcata (da Costa). Ripe eggs were obtained in July and October, and ripe sperm in January and July.

Phacoides borealis (L.). Ripe eggs and sperm in March and April. Pelseneer (1926 as *Lucina lactea*) describes stalked egg capsules deposited on the sand.

Kellia suborbicularis (Montagu). Viviparous, giving out small shelled larvae from the gill pouch. Embryos found developing in the gill pouch in May, July and August; ripe sperm in May and October. The species apparently breeds throughout the year, as the larvae are present in the plankton in any month; but they are specially common in late summer and early autumn. Post-larvae have been found crawling on red rock and in rock crevices.

Galeomma turtoni Sowerby. Viviparous. Free-swimming embryos at an early stage without a shell were given out in September (obtained by Miss M. L. Popham).

Mysella bidentata (Montagu). Viviparous. Late veligers are common in the plankton in summer and autumn. Post-larvae and young are found in shell sand in autumn.

Mysella sp. Veligers common in the plankton in summer and autumn.

Cardium echinatum L. Nearly ripe eggs and ripe sperm found in January, April, May and September. Larvae have been taken in the plankton at various times.

Cardium scabrum Philippi. Fertilized eggs were obtained in July and were reared until the loss of the velum.

Cardium edule L. Breeding from spring to early autumn, chiefly May to August. Successful fertilizations were obtained from April to October and the larvae reared until the loss of the velum.

Cardium crassum Gm. Hermaphrodite. Apparently ripe eggs and ripe sperm found in almost any month. Larvae are taken in the plankton through spring and summer, and are often very plentiful.

Dosinia exoleta (L.). Apparently ripe eggs and ripe sperm in February and July.

Venus verrucosa L. Ripe eggs and sperm in April.

Venus ovata (Penn.). Breeding from March to October. Successful fertilizations were obtained in September and October and the larvae reared to an early free-swimming stage.

Venus casina L. Breeding throughout the year.

Venus fasciata (da Costa). Breeding throughout the year. Successful fertilizations were obtained in July and November, and the larvae reared to an early free-swimming stage.

Venus striatula (da Costa). Breeding in February, March and May. Eggs were successfully fertilized in February and May and reared to an early free-swimming stage.

Paphia rhomboides (Penn.). Breeding in October, November, December, February and March.

Paphia pullastra (Montagu). The chief breeding season is in summer, but the species breeds also in autumn. Successful fertilizations were obtained in June and September, and the larvae reared to an early shelled stage.

Paphia decussata (Gm.). Ripe eggs and sperm were found in summer months and also in December.

Tellina tenuis da Costa. Ripe eggs and sperm in May.

Tellina crassa Penn. Usually breeding in summer, but ripe eggs and sperm were also found in January. Successful fertilizations were obtained in July and the larvae reared to an early free-swimming stage.

Macoma balthica (L.). Active sperm in July.

Scrobicularia plana (da Costa). Breeding in summer. Eggs were successfully fertilized in June and July, and the larvae reared to an early free-swimming stage.

Abra alba (S. Wood). Breeding in summer. Successful fertilizations were made in May, August and October, and the larvae reared to an early free-swimming stage.

Gari tellinella (Lam.). Breeding in summer.

Solecurtus chamasolen (da Costa). Breeding in summer.

Solecurtus scopula (Turton). Nearly ripe eggs and sperm in July.

Cultellus pellucidus (Penn.). Breeding in late summer and winter, especially in winter. Successful fertilizations were made in September, but the eggs were reared only to the gastrula. Larvae are found in the plankton in autumn and winter.

Ensis siliqua (L.). Breeding in early spring. Eggs successfully fertilized in March and April were reared to an early shelled stage. Larvae are taken in the plankton in early spring.

Spisula solida (L.). Breeding in winter and early spring. Successful fertilizations were obtained in January and February, and the larvae reared to an early shelled stage.

Spisula subtruncata (da Costa). Active sperm in November and January; nearly ripe eggs in November.

Mya truncata L. One hermaphrodite with nearly ripe eggs and active sperm in May.

Aloidis gibba (Olivi). Successful fertilizations in April were reared to the gastrula stage.

Hiatella gallicana (Lam.). Breeding chiefly in winter, but also in spring. Eggs successfully fertilized in January, February, April, May and December were reared to an early shelled stage. Larvae are taken in the plankton chiefly in winter. Post-larvae are found in winter, crawling on red rock, into which they bore.

Hiatella arctica (L.). Breeding in summer. Larvae are taken in the plankton throughout the summer and autumn. They are especially common in late summer and early autumn.

Gastrochaena dubia (Penn.). Successful fertilizations were made in January and the larvae reared to the gastrula.

Barnea parva (Penn.). Breeding in summer and early autumn. Successful fertilizations were made in October and the larvae reared to an early shelled stage. The post-larva was reared in a plunger-jar from planktonic veligers taken in May.

Pholadidea loscombiana Turton. Breeding in autumn. In December nearly all were found to be spent females or males, and later all males. Eggs fertilized in September, October and November were reared until the loss of the velum and the beginning of post-larval growth.

Teredo norvegica Spengler. Breeding throughout the year. Successful fertilizations can be made at any time and the eggs were reared to the early shelled larvae. Veligers, almost certainly belonging to this species, are taken in the plankton in any month, especially in autumn.

Teredo sp. Viviparous. Adults with late veliger larvae were found in spring, but probably occur at other times also.

Thracia phaseolina (Lam.). Four hermaphrodite specimens nearly ripe were taken in July.

Thracia convexa (W. Wood). One hermaphrodite. The eggs were fertilized successfully in September and reared to the gastrula.

THE LARVAE AND POST-LARVAE OF *ENSIS* AND *CULTELLUS*

We know little of the breeding and larval stages of the Solenidae. Kändler (1926) at Heligoland reared *Cultellus pellucidus* from a planktonic veliger, with the shell 0·37 mm. long or less, to a young stage 1 mm. in length. The larval shell has a characteristic shape, narrowing at the anterior end, with a very conspicuous golden brown liver. The same shape, but with the anterior end slightly blunter, and a similarly coloured liver distinguish the larva of *Ensis siliqua* at Plymouth, which I have reared in a similar way until the characteristic teeth of *Ensis* were seen. This larva is very like that of *Cultellus* but differs in certain constant features noted below.

Ensis siliqua (L.) (Figs. 1 *a–g*)

This species is very common in sandy shores in the neighbourhood of Plymouth, especially at Millbay, Salcombe, and at Whitsand Bay. It was breeding freely in March and April, and in the early spring months the larvae characterized the plankton. Since these larvae rapidly disappeared towards early summer and the *Ensis* examined at other times of year were never ripe, it may be assumed that early spring is the usual breeding season here. Successful fertilizations were effected in March and April, the larvae growing to the shelled stage (Fig. 1 *a*) and then dying. Later larvae in the plankton were reared until the genus could be recognized.

Ensis siliqua is the only really common species (it is confused with *Ensis ensis* in the Plymouth Fauna List, 1931) and since the presence of the larvae in the plankton naturally followed the breeding of the species it may be safely assumed that the larvae are those of *E. siliqua*. Numbers taken at Millbay and Salcombe in March and April were ripe, and at other seasons no specimen examined was found to be breeding. Both ovaries and testes are cream-coloured and in the breeding season are very full of eggs and sperm. The eggs are small, 0·07 mm. in diameter, with a very thin membrane and no gelatinous covering. Shelled larvae were obtained in bowls from the fertilizations in two days. The shells were 0·10 mm. in length and slightly less in depth, the hinge being almost straight but slightly hollowed in the centre (Fig. 1 *a*). The velum was about half the length of the shell, and was surrounded by long cilia, but no large central cilium could be seen. These larvae did not live. Larvae of all sizes, from 0·16 to 0·35 mm. in length, abound in the spring plankton (Fig. 1 *b–d*), and some are seen even as early as February, dwindling at the end of April and almost absent in May and later. They resemble very closely the larvae of *Cultellus pellucidus* described by Kändler (1926), but the late larval stages and post-larvae do not have the characteristic orange-red pigment round the posterior mantle edge found in that species. Both have a very conspicuous golden brown liver, the shell being irregularly oval, narrowing

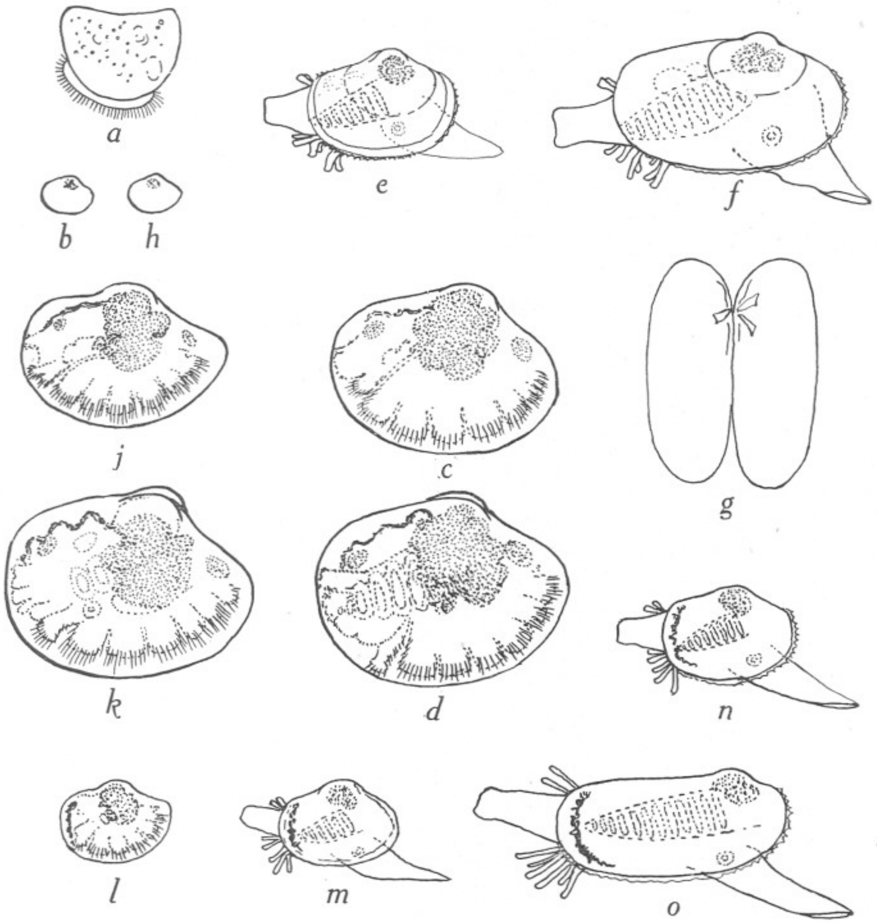

Fig. 1.

a–g, Ensis siliqua.

a, shelled larva from fertilization, 0·10 mm. long; *b*, smallest larva found in plankton, 0·16 mm. long; *c*, later larva from plankton, 0·28 mm. long; *d*, later larva just before losing velum, 0·35 mm. long; *e*, post-larva, grown in plunger-jar from planktonic veliger, 0·48 mm. long; *f*, post-larva, grown in plunger-jar from planktonic veliger, 0·72 mm. long; *g*, shell of post-larva, grown in plunger-jar from planktonic veliger, showing teeth, 0·72 mm. long.

h–o, Cultellus pellucidus.

h, smallest larva seen in plankton, 0·16 mm. long; *j*, later larva from plankton, 0·24 mm. long; *k*, later larva from plankton, nearly ready to metamorphose, 0·32 mm. long; *l*, later larva from plankton just before losing velum, 0·36 mm. long; *m*, post-larva grown in plunger-jar from planktonic veliger, 0·38 mm. long; *n*, post-larva grown in plunger-jar from planktonic veliger, 0·4 mm. long; *o*, post-larva grown in plunger-jar, 0·72 mm. long.

anteriorly, and rounded posteriorly, the umbo being prominent. The anterior end is sharper in *Cultellus* than in *Ensis*. In the larva of *Ensis siliqua* at 0·28 mm. long (Fig. 1 *c*) the velum is well developed and the animal is in much the same stage as Kändler's *Cultellus pellucidus* at 0·30 mm. At 0·35 mm. (Fig. 1 *d*), the largest larva seen, it is nearly ready to metamorphose but still retains a large velum. Five to seven gill slits may be present—a higher number than in Kändler's *Cultellus* at 0·36 mm. which has lost the velum—but the tentacles in the siphonal region have not yet appeared. There is, however, irregularity in the growth of the organs and in the size of the larva in both species at Plymouth.

These late larvae metamorphosed in a plunger-jar and became much elongated posteriorly, the original embryonic shell being still fairly conspicuous (Figs. 1 *e–g*). At 0·48 mm. the velum has completely disappeared, there are several gill slits and the siphons have developed with ciliated tentacles at their base, two above the dorsal siphon, which has a long extensile valve, and four below it, and two below the ventral siphon, as in *Cultellus* (Fig. 1 *e*). Later post-larvae were 0·72 mm. in length (Fig. 1 *f*, *g*) and showed the typical teeth of *Ensis* (Fig. 1 *g*), one cardinal in the right valve and two in the left, besides laterals. The foot is very large and powerful with a blunt flat tip and is capable of extensive jerky movements. Such older stages were in the plunger jars in January, having grown from the early spring veligers. It is probable, however, that they grew slowly and that in nature they would have attained this length much sooner.

Cultellus pellucidus (Pennant) (Figs. 1 *h–o*)

This species is often dredged in silty sand both inside and outside the breakwater, especially inside. It breeds in autumn and winter. Kändler found it breeding in Heligoland in November. Only one ripe female has so far been found at Plymouth at the same time as a male, and a partially successful fertilization was obtained at the end of September. All specimens examined in spring and summer were unripe except one male full of active sperm in July. The eggs from the fertilization only developed as far as a few segments.

Larvae attributable to this species and closely resembling those described by Kändler occur fairly commonly in the plankton in autumn and winter (November to January). The smallest seen was 0·16 mm. in length (Fig. 1 *h*), the largest 0·36 mm. (Fig. 1 *l*). They resemble very closely the larvae of *Ensis*, but the shell is more pointed anteriorly and the post-larvae are decidedly narrower in the shell. The orange-red pigment in the late larvae and post-larvae at the posterior end inside the mantle distinguishes them at once, as Kändler has already shown. Specimens grown in plunger-jars from the winter larvae in July measured 0·38 to 0·72 mm. (Figs. 1 *m–o*), the smallest being fully metamorphosed and agreeing well with Kändler's description.

THE LARVAE AND POST-LARVAE OF SOME SPECIES OF *CARDIUM*

It has been possible to differentiate between several *Cardium* larvae at Plymouth and to follow the growth of *Cardium edule* and *Cardium scabrum* from the egg to metamorphosis and post-larva.

The larva of *Cardium crassum* (*Laevicardium*) is easily recognized in the plankton and also another species which is almost certainly *C. echinatum*. *Cardium edule* and *C. scabrum* were reared from the fertilized egg to the time of metamorphosis and loss of velum. *Cardium crassum*, which is hermaphrodite, was not fertilized as up to the present it has not been possible to obtain really ripe eggs; but the larva, which is at times common in the plankton, was reared to a stage in which the species was recognizable. The veliger is much larger than that of either *Cardium edule* or *C. scabrum*, and the shell is smooth in the post-larva, even in those up to more than 1 mm. in length. *Cardium echinatum* was never obtained in a sufficiently ripe condition for successful fertilization, but the larva almost certainly attributable to this species is very unlike the others.

Cardium edule L. (Figs. 2 *a–j*)

Little is known of the late larval and post-larval stages of this species; it loses its velum very early and the ribs only appear after metamorphosis. At Plymouth it breeds in the late spring and summer months, although occasional exceptions may be found at other times. The veligers are chiefly found up the estuaries or in the sea near their openings in spring and summer. Successful fertilizations were made in April, May, June, July, August and September. The larvae were reared in bowls until the velum was lost, but they did not live to put on any ribs. Early and late veligers from the plankton corresponded with those reared, and post-larvae showing the same-sized embryonic shells were found in tow-nettings taken near the bottom in the estuaries. Later young stages were found in the estuaries. At Neal Point, in the Tamar Estuary, early in July, they were about 1 mm. in length, showing that spawning must have taken place some time before.

The eggs (Figs. 2 *a*, *b*) are covered with a thin membrane and a large gelatinous envelope in which development takes place until the veliger emerges. The unfertilized egg is 0·05 mm. across and is opaque with a large nucleus. It is surrounded by the closely fitting membrane which soon disappears, the large gelatinous covering being 0·16–0·18 mm. in diameter. The free-swimming veliger 3 days after fertilization measured 0·14 mm. in length; the hinge line of the shell was straight, the valves roundish and flat. The velum, armed with powerful cilia round the margin and a large central flagellum, was about half the length of the shell (Figs. 2 *c*, *d*). The internal organs were forming. In three weeks the shell was 0·16 mm. long (Fig. 2 *e*), the growth probably being slower than in natural conditions, and in five weeks it had increased to 0·30 mm. in length, the shell being nearly round and still perfectly smooth (Fig. 2 *f*). It now lost the velum and descended to the bottom. Although living for some time after this the reared larvae ceased to grow and eventually died.

Veligers of all sizes in the inshore plankton were similar to the reared specimen and none were larger than the largest reared. These, grown in plunger-jars and bowls, put on ribbed growth, the ribs at first being always very irregular. A growth of 0·05 mm. in three days was noticed in one. In all these post-larvae the embryonic shell can be recognized. Specimens 1 mm. in length from mud from the estuary show ribs more like the adult, but unarmed, and long tentacles in connexion with the siphons. The embryonic shell is still conspicuous (Figs. 2 *g–j*). Although so small the enormous numbers of these veligers must be very important in the plankton of the estuaries and inshore waters.

Cardium scabrum Philippi (Figs. 2 *k–q*)

This species is common in certain parts of the Sound and outside, especially on or in the crevice of the red rock dredged from Stoke Point grounds. Besides adults many post-larvae were found in this locality on the rock, often in small holes. Two adults were put together in a bowl and the next morning many eggs had been extruded. As these were all fertilized and beginning to segment, both a male and a female were probably present. The eggs lived and developed into larvae, some of which did well in bowls and reached the stage in which the velum was lost and the animal descended to the bottom. As with *Cardium edule* they grew no further, never putting on any ribs, and eventually they died.

Young *Cardium scabrum* are easily identified and many were reared from the planktonic veligers to a late post-larval stage in plunger-jars. The egg is similar to that of *C. edule* and almost the same size, the larva remaining in the gelatinous covering until it emerges as a free-swimming veliger (Fig. 2 *k*). The free-swimming shelled stage is at first very like that of *C. edule* but soon puts on concentric striations which are characteristic (Figs. 2 *l*, *m*). At 3 days old the shell is 0·08 mm. long, growing only to the small size of about 0·16 mm. long before losing the velum. The late larval shell is rather more oblong than in *C. edule*, and the concentric striae and small size at metamorphosis distinguish it. Post-larvae grown in plunger-jars from planktonic veligers put on irregular ribs, with the embryonic shell exactly similar to those reared from the egg showing very clearly (Figs. 2 *n*, *p*). The post-larvae are very much elongated posteriorly and nearly straight on the posterior dorsal margin which is highly spinous as are also the posterior ribs. Specimens about 1 mm. long are clearly distinguished from those of *Cardium edule* of the same size. At about 8 mm. the young shell is very like the adult and has become much rounder.

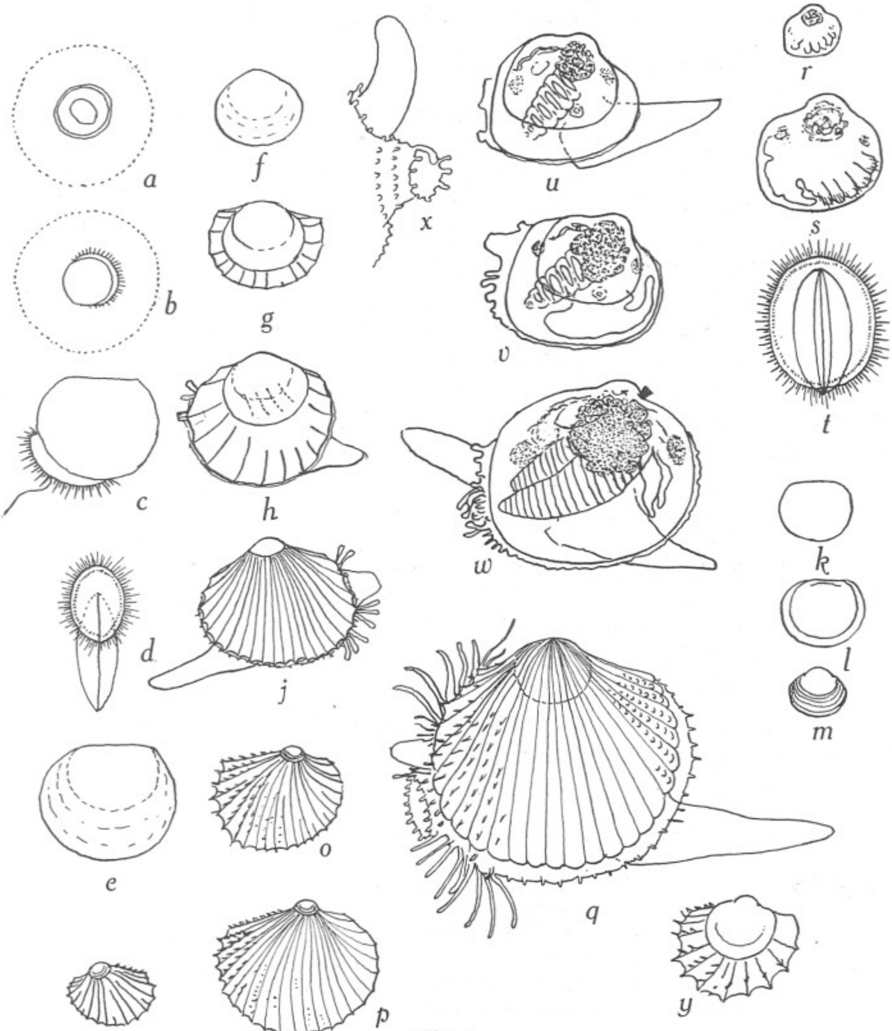

Fig. 2.

a–j, Cardium edule.

a, unfertilized egg, gelatinous covering, 0·18 mm. across; *b*, embryo in gelatinous covering, 24 hours old, from fertilization; *c*, free-swimming larva, 3 days old, reared from egg, shell 0·14 mm. long; *d*, the same swimming; *e*, older larva 0·16 mm., reared from egg; *f*, post-larva reared from egg, aged 5 weeks, 0·30 mm. long, having lost the velum; *g*, post-larva grown in bowl from planktonic veliger, 0·4 mm. long; *h*, later post-larva grown in plunger-jar from planktonic veliger, 0·48 mm. long; *j*, young *Cardium edule*, 1 mm. long from mud, Neal Point.

k–q, Cardium scabrum.

k, *l*, very young shells from fertilization, 0·07–0·08 mm. long; *m*, the same at loss of velum, 0·16 mm. long; *n*, post-larva grown in bowl from planktonic veliger, 0·56 mm. long; *o*, *p*, later post-larvae grown in plunger-jar from planktonic veliger, 0·8–1·12 mm. long; *q*, *Cardium scabrum*, 8 mm. long.

r–x, Cardium crassum.

r, smallest larva recognized from plankton, 0·2 mm. long; *s*, *t*, late veliger from plankton, ready to metamorphose, 0·44 mm. long; *u*, *v*, *w*, post-larvae reared from planktonic veligers in plunger-jars, 0·97–1·5 mm. long; *x*, siphons of a slightly older specimen.

y, post-larva of *Cardium echinatum* (?) reared from planktonic veliger in plunger-jar, 0·83 mm. long.

Cardium crassum Gmelin (Figs. 2 *r–x*)

Veligers of this species are common at times in the plankton in spring and summer, both inside and outside the breakwater. They are quite unlike those of *Cardium edule* and *C. scabrum*; they grow to a much greater size before losing the velum, and the shell is almost square posteriorly and in the post-larvae quite smooth in specimens up to at least a length of 2·5 mm. The smallest veliger recognized was 0·2 mm. in length (Fig. 2 *r*), and at metamorphosis and loss of velum it is about 0·4–0·45 mm. The velum is large and in the late stages overlaps the valves to a considerable extent (Figs. 2 *s*, *t*). Late larvae from the plankton reared in plunger-jars have the same square posterior end, the siphons gradually appearing with their tentacles, a very large and active foot, gill slits and conspicuous liver (Figs. 2 *u*, *v*, *w*). A specimen was reared in a plunger-jar to a shell length of 2·5 mm., showing the characters of this species.

Larva almost certainly attributable to *Cardium echinatum* L. (Fig. 2 *y*)

A veliger occurs at times in the plankton in spring, summer and autumn which almost certainly belongs to *Cardium echinatum*. The only other species it could be is *C. aculeatum*, and this is not nearly so common in the neighbourhood. Unlike the three larvae described above its valves are very much inflated, the shell with its two valves being almost globular. The veliger reaches a length of 0·48 mm. before metamorphosis. Specimens from the plankton reared in a plunger-jar put on growth with ribs and very sharp spines (Fig. 2 *y*).

KEY TO THE LARVAE OF THE ABOVE SPECIES OF *CARDIUM*

A. Larvae very small at metamorphosis, valves flat:
  (*a*) valves smooth (0·14–0·30 mm.) *C. edule*;
  (*b*) valves with concentric striations (0·07–0·16 mm.) *C. scabrum*.
B. Larvae large at metamorphosis:
  (*a*) valves fairly flat, square posteriorly (latest larva 0·44 mm.) *C. crassum*;
  (*b*) valves much inflated, round (latest larva 0·48 mm.) *C. echinatum* (?).

THE LARVAE AND POST-LARVAE OF *PHOLADIDEA LOSCOMBIANA* AND *BARNEA PARVA*

All the free-swimming larvae known which belong to the Pholadidae have a more or less round shell and lose the velum at a small size. Kändler (1926) reared a species of *Pholas* (the species not identified but he thinks it is probably *Pholas dactylus* or *P. crispata*) from the planktonic veliger to a post-larva beginning to elongate. Miyazaki (1935) reared the Japanese species *Parapholas quadrizonata* up to a fairly late veliger from an artificial fertilization. In all these the embryonic shell (that is to say up to the period of metamorphosis) is round or nearly round, the elongation coming on later.

At Plymouth successful fertilizations were made of *Pholadidea loscombiana* and of *Barnea parva*. Unknown veligers from the plankton reared in plunger-jars developed into post-larvae almost certainly attributable to these two species, and in all of these the embryonic shell was small and nearly round. The veligers are so small and inconspicuous even in the late stages that it is very difficult to recognize them in the plankton, but when post-larval growth begins there are characteristics by which members of the family can be recognized. *Pholadidea loscombiana* was reared from the egg to the metamorphosis when it lost the velum, and to a post-larval stage in which it put on some anterior growth, but the post-larvae did not live longer. Post-larvae in the plunger-jars reared from veligers taken from the plankton almost certainly belong to this species, as well as a post-larva found on the surface of the red rock from Stoke Point grounds. As none of these grew to a sufficiently late stage the identification is, however, not certain. The fertilization of *Barnea parva* grew only as far as the early shelled stage. A post-larva found in a plunger-jar almost certainly belongs to this species and shows that it assumes the adult form at an extremely small size. Shell growth in the post-larvae of Kändler's *Pholas* and of both the forms mentioned above is put on anteriorly and posteriorly, the anterior growth beginning first in *Pholadidea*.

Pholadidea loscombiana Turton (Figs. 3 *a–o*)

This species is common round Plymouth, boring in rocks, especially in the red rock dredged at Stoke Point grounds. It breeds in autumn and winter, and in spring and summer is always unripe, or there are only males. Eggs were fertilized successfully in February, the end of September, October and November. Active sperm and apparently ripe eggs were seen in January and March, but fertilizations were not successful. Sperm only was seen from May to July. November is the month when all appear to be ripe and when the most successful fertilizations were made. The proportion of the sexes at this time is about equal. Fertilizations were made in bowls of filtered water, the active larvae a day old being transferred to a plunger-jar containing outside sea-water. Minute flagellates were given as food.

The unfertilized egg is pear-shaped and is 0·08 mm. in length (Fig. 3 *a*). When ripe the eggs are loose in the ovary. Both male and female gonads are cream-coloured and very large when ripe. When fertilized the egg contracted and became round, and was surrounded by a membrane (Fig. 3 *b*). With the membrane it measured 0·05 mm. It quickly lost the membrane and developed by the next day into a round larva, ciliated all over, with long hairs at one end. In two days there was a shell, 0·07 mm. long, with a straight hinge (Fig. 3 *c*). The velum was about half as long as the shell and circular in outline, but no central flagellum was seen. The shell became rounder and the velum larger (Figs. 3 *d*, *e*). Growth in the plunger-jar was very slow, the shell at four weeks old was only 0·24 mm. long, although the organs were well developed and three gill slits present. At this size the shell was pointed at the anterior end and rounded posteriorly. The foot was large and active, the velum nearly as long as the shell, and the larva ready to metamorphose. The larva then lost the velum and descended to the bottom, putting on anterior shell growth (Figs. 3 *f–k*). This growth was in the form of a smooth border on each valve turning outwards. No further growth took place and the larvae all died.

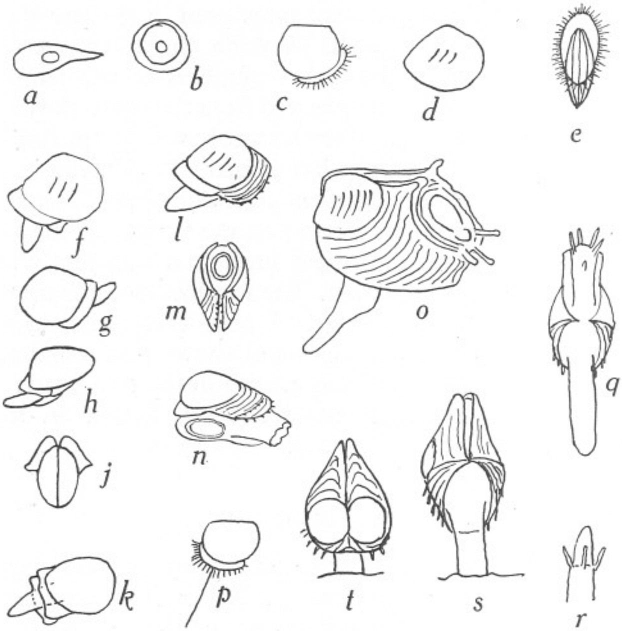

Fig. 3.

a–k, Pholadidea loscombiana.

a, unfertilized egg, 0·08 mm. long; *b*, fertilized egg, 0·05 mm. long; *c*, early shelled veliger, 0·07 mm. long, reared from egg; *d*, latest larva, 0·24 mm. long, reared from egg; *e*, the same swimming; *f–k*, post-larvae 0·24–0·26 mm. long, reared from egg.

l–o, probably *Pholadidea loscombiana.*

l, *m*, *n*, post-larvae from surface of red rock, 0·27–0·32 mm. long; *o*, post-larva reared from veliger in plunger-jar, 0·56 mm. long.

p–t, Barnea parva.

p, shelled larva 0·06 mm. long, reared from egg; *q*, *s*, *t*, young shell, 0·32 mm. long, reared from planktonic veliger in plunger-jar; *r*, extended siphon.

Post-larvae grown from unknown veligers in plunger-jars corresponded exactly with those reared from the egg, and having similar embryonic shells probably belong to this species (Fig. 3 *o*). The larvae reared from the egg were almost colourless until they lost the velum and then were yellowish with a purplish edge. The post-larvae from the plunger-jars were dark brown and purple and were possibly abnormal. A post-larval stage found on the surface of the red rock from Stoke Point grounds showed an anterior end very similar to that of the post-larva reared from fertilizations; it probably belongs to this species although it could not be kept alive long enough to be certain. It was 0·27 mm. in length. The embryonic shell was similar to that of *Pholadidea*; it had the form of one of the Pholadidae, small spines at the edge of the posterior elongated part, and a large siphon.

It is curious that no very young *Pholadidea* were found in the red rock, although careful search was made for them. It is possible that the post-larvae crawl about for a long time before settling down.

Barnea parva (Penn.) (Figs. 3 *p*–*t*)

Breeding of this species appears to be in summer and early autumn. It is common in the rocks at Rum Bay and, more rarely, with *Pholadidea* in the red rock of the Stoke Point grounds. A successful fertilization was obtained on September 15 1937, in a bowl of filtered water. The eggs are similar to *Pholadidea* but slightly smaller. The larvae lived only to the first shelled stages, 0·05–0·06 mm. across, and resembled *Pholadidea* but with a long central flagellum on the velum (Fig. 3 *p*). The later veligers were not recognized in the plankton, but a young stage grown from a mixture of planktonic veligers in a plunger-jar is almost certainly this species; it has the form of *Barnea* and young *Pholadidea*, but the embryonic shell is considerably smaller than it is in *Pholadidea*, being only 0·08 mm. in length and quite round. From the embryonic shell grow out two distinct portions, an anterior portion armed with spines and enclosing the foot, gaping very widely, and a posterior portion, the two parts of which can meet and enclose the siphon, but are also capable of gaping widely when the siphon is extended (Figs. 3 *q*, *r*, *s*, *t*). This specimen is only 0·32 mm. in its entire length, assuming the adult form very much earlier than does *Pholadidea*. The siphon is provided with tentacles surrounding a valve which is evertible.

THE LARVAE AND POST-LARVAE OF *TEREDO* AT PLYMOUTH

Two species of *Teredo* occur boring in the raft near the breakwater, a small one closely related to *Teredo navalis*, but differing from it in certain important points, and *Teredo norvegica*. The first, like *Teredo navalis*, is viviparous. It keeps the veligers inside its body until they have attained a large size, the free veligers settling down on the wood and metamorphosing almost immediately they have left the parent. The second extrudes its eggs into the water before development takes place. Fertilizations were frequently made of *Teredo norvegica*, the larvae living until the young shelled stage. Late veligers, probably belonging to this species, occur fairly frequently in the plankton. In one instance one of these metamorphosed in a plunger-jar, and although not attached to wood grew to a post-larval stage in which the genus could be recognized. The larvae of the two forms are quite distinct and there is a great difference in the post-larvae.

Teredo norvegica Spengler (Figs. 4 *a–l*)

This species breeds throughout the year, judging from its eggs and sperm, which are ripe at any time. Fertilizations were frequently made during spring and summer when the larvae were used for feeding crab zoeae. The eggs are about 0·04 mm. across. The early shelled larva is about 0·05 mm. long with a straight hinge line and the velum is rather more than half the length of the shell (Figs. 4 *a*, *b*). Later larvae, probably this species, from the plankton, are nearly spherical with a velum nearly as large as the shell and a long foot with which they sometimes swim; the shell is 0·32 mm. long (Fig. 4 *c*). The latest larva is about 0·38 mm. long with a very large velum reaching far beyond the shell (Figs. 4 *d*, *e*, *f*). The sample of veligers from which the larvae metamorphosed possessed no eyes and came from inshore plankton in January. All through the autumn and winter they had occurred more frequently than at other times, although a few specimens may be seen in any month. The shell at metamorphosis is spherical and the one specimen which changed to a post-larva (Figs. 4 *j*, *k*, *l*) became slightly larger before the growth anteriorly of four hook-like spines on each valve, and in the centre of the ventral margin a long pointed outgrowth ending in a long spine which prevents the valves from shutting. The foot is very large and powerful and the siphons projecting at the posterior end are armed with stout tentacles. Five pairs of gill slits are present. This specimen, reared from a late veliger in a plunger-jar, was unfortunately lost.

In the plankton there are found at times veligers very like those described above but possessing eyes, some in the shape of a crescent and some large and round (Figs. 4 *g*, *h*). These also had the large foot which helped in swimming and were so similar in other ways that it seems probable that they belong to the same species and that some develop eyes and some do not.

Teredo sp. (Figs. 4 *m–p*)

This species differs from the description of *Teredo navalis* in its small size, the adults with young measuring under an inch in length, and in the shape of the pallets. It is hoped to investigate this further. Veligers of all sizes may be seen inside the body, the largest being about 0·32 mm. in length. The shell is, however, not quite spherical and slightly broader than long. This is not apparent when the animal is swimming, for it then appears to be round, the velum being about the same size as the shell (Fig. 4 *m*). The veligers emerge from the parent by means of the upper siphon and swim actively round the wood in which the parent bores. I have never seen them in the plankton. Larvae kept in plunger-jars and bowls metamorphosed into post-larvae, some on the wood. The post-larva at the loss of the velum is only slightly larger than the largest inside the parent. Almost directly the velum is lost there is formed a row of fine marginal spines anteriorly, followed quickly by a second (Figs. 4 *n*, *o*, *p*). The siphons with blunt tentacles begin to form, and ventrally there is a central pointed projection in the same position as in the post-larvae of (presumably) *T. norvegica*, but without a distinct spine. The blades inside the shell are long, reaching nearly half way down the shell.

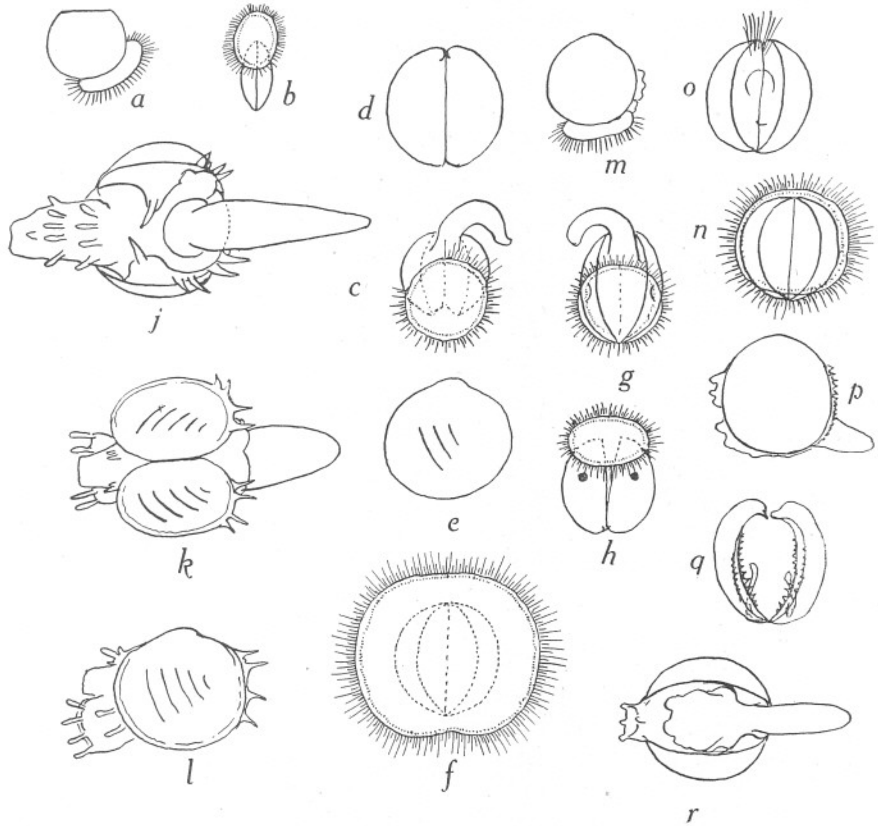

Fig. 4.

a–b, *Teredo norvegica*.

a, *b*, shelled larvae from fertilization, 0·05 mm. long.

c–l, almost certainly *Teredo norvegica*.

c–f, later veligers, 0·24–0·38 mm. long; *g*, *h*, veligers with eyes, probably this species; *j–l*, post-larvae reared from veliger in plunger-jar, shell 0·4 mm. long.

m–r, *Teredo* closely related to *Teredo navalis*.

m, young veliger, 0·24 mm. long; *n*, *o*, slightly older from parent, 0·32 mm. long; *p–r*, early post-larvae from wood.

The late larvae and post-larvae of this species are strikingly like those of *Xylotrya gouldi* described by Sigerfoos (1908), and are much more like them than those attributed to *Teredo norvegica*. Little has been done in the description of post-larval stages of Teredinidae and I have been unable to find in the literature any similar to those described above.

THE LARVAE OF *HIATELLA ARCTICA* AND *H. GALLICANA*

In the Plymouth Marine Fauna 1931, *Hiatella arctica* is listed as including *rugosa*. Winckworth (1932), however, again separates them. The larvae show that they are undoubtedly distinct species, as Odhner (1914) has already noted in specimens from Rovigno. Both species are common, *H. gallicana* (=*rugosa*) always or nearly always boring in stones, *H. arctica* usually free but occasionally found in holes in similar situations. *H. arctica* is not so common as *H. gallicana* and no fertilizations were made from it, but successful fertilizations were made from *H. gallicana*. They breed at different times: *H. gallicana* from autumn to early spring, *H. arctica* in summer. Larvae which developed into *H. gallicana* were present commonly in the plankton from autumn to spring, those of *H. arctica* being common in late summer and early autumn. The best locality for *H. gallicana* is in the red rock dredged from Stoke Point grounds, but the species is also found in the rocks at Rum Bay.

Hiatella arctica (L.) (Figs. 5 *k–q*)

The late larvae of this species are some of the commonest and largest veligers in the plankton, both inside and outside the breakwater at Plymouth, in summer and autumn, beginning about July and continuing to November or December. The late larva ready to metamorphose is about 0·36 mm. in length with a large velum about the length of the shell, the shell having concentric striae round the margin. It is usually a pinkish yellow, being redder towards the margin, but may be almost colourless. The liver is large and conspicuous, a dullish grey, and there are usually three gill slits present. The anterior end of the shell is more pointed than the posterior and the whole shell is somewhat triangular with the longest side ventrally (Figs. 5 *k*, *l*). At this size the velum is lost and layers of shell are formed all round, the anterior end being always more acute than the posterior, which is very square. At a length of 0·46 mm. there is one spine at the dorsal posterior end, the siphons have several blunt tentacles and there are five or six gill slits (Figs. 5 *m*, *n*). At a length of 0·56 mm. it has the same character, but there are two or more posterior dorsal spines (Fig. 5 *o*), whilst at 0·96 mm. there are two rows of large spines postero-dorsally (Fig. 5 *p*). A specimen reared in a plunger-jar grew to 1·44 mm. in length and had another row of spines dorsally (Fig. 5 *q*).

This late post-larva is very characteristic and grew many times from veligers in the plunger-jars. Similar specimens are to be found attached to weeds and hydroids in dredgings. The adults are often found in the neighbourhood of rocks.

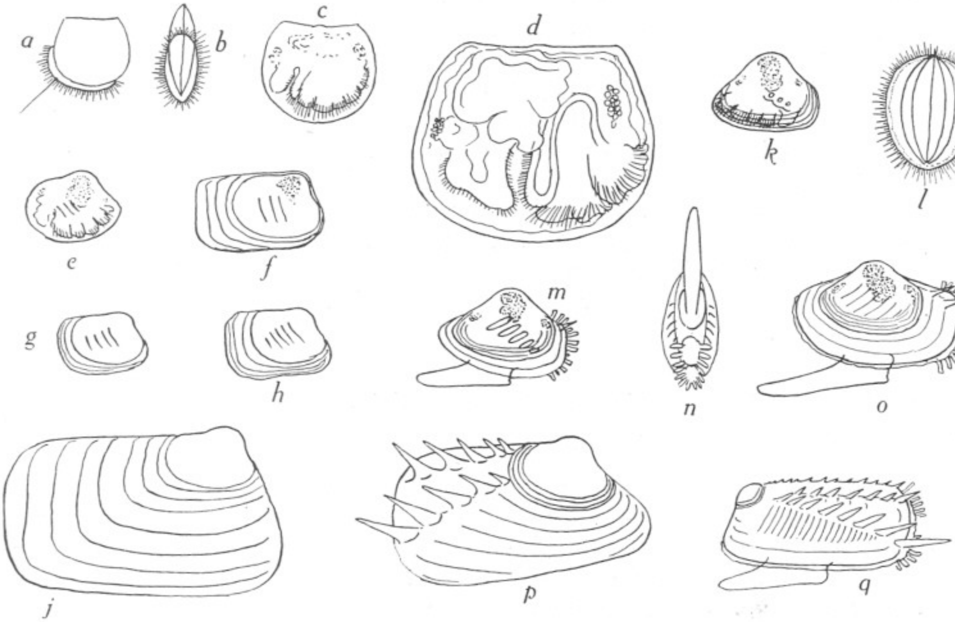

Fig. 5.

a–j, *Hiatella gallicana*.

a, *b*, shelled larvae reared from egg, 0·08 mm. long; *c*, *d*, the same, 0·12 mm. long; *e*, late larva from plankton, 0·32 mm. long; *f*, post-larva, 0·48 mm. long, grown from planktonic veliger in plunger-jar; *g*, *h*, post-larvae from red rock, 0·38–0·4 mm. long; *j*, young, 1 mm. long, reared from late veliger in plunger-jar.

k–q, *Hiatella arctica*.

k, *l*, late veliger from plankton, 0·36 mm. long; *m*, *n*, post-larvae grown from late planktonic veliger in plunger-jar, 0·46 mm. long; *o*, later post-larva grown from late planktonic veliger in plunger-jar, 0·56 mm. long; *p*, *q*, young reared from late planktonic veliger in plunger-jar, 0·96–1·44 mm. long.

Hiatella gallicana (Lam.) (Figs. 5 *a–j*)

Successful fertilizations of this species were obtained several times, particularly in winter and early spring. Late larvae from the plankton were reared in plunger-jars and bowls to the post-larval stages and young forms.

The eggs are pinkish although the ovary is usually a pinkish cream colour (Odhner (1914) states that the eggs of *Hiatella arctica* (= *Saxicava*) are red). The ripe egg is 0·05 mm. across, the free-swimming larva in less than 24 hours is about the same size, the shelled larva very soon after being about 0·08 mm. in length (Figs. 5 *a*, *b*) with the velum about two-thirds the length of the shell and provided with a large central flagellum. The shell has a straight hinge and the valves are slightly longer than broad.

In eight days the veliger was 0·12 mm. in length with the internal organs forming (Figs. 5 *c*, *d*). They did not grow after this and soon died. Late larvae from the plankton are roundish oval, more pointed anteriorly than posteriorly, 0·32 mm. in length (Fig. 5 *e*). At this size they lose the velum and put on anterior and posterior growth, especially posterior; usually they are without spines, but occasionally there are slight spines postero-dorsally in the same position as those of *H. arctica*. At a length of 0·48 mm. there are three gill slits in those grown in plunger-jars (Fig. 5 *f*). In some post-larvae found at the surface of the red rock in which the adult burrows there are four gill slits at a smaller size, the embryonic shell being smaller, and five at a length of 0·4 mm. (Figs. 5 *g*, *h*). Young stages reared from veligers in plunger-jars grew to 1 mm. and more, usually still without spines dorsally and of a squarish oblong shape, not so sharply pointed anteriorly as in *H. arctica* (Fig. 5 *j*).

THE LARVA AND POST-LARVA OF *HETERANOMIA SQUAMULA* (L.)

(Figs. 6 *a*–*f*)

This is the commonest species of the family Anomiidae at Plymouth. The adults abound on stones and other objects both inside and outside the breakwater, and the larvae are some of the commonest veligers in the plankton. Odhner (1914) has already described very similar larvae from Rovigno which he regards as *Anomia ephippium* and mentions another allied species.

Apparently the feature common to all anomiid larvae is the pedal sinus, which is very distinct in *Heteranomia*. This indentation is the beginning of the hole through which passes the byssus and eventually the plug for attachment. The lower (right) valve is flat, with the indentation; the upper (left) rounded, with a conspicuous umbo and a slight process ventrally which at first fits into the pedal sinus. Fertilizations were made in May and developed into shelled larvae, but the species may be ripe at any time. Specimens watched by Dr H. B. Moore in a situation in which he knew that the spat fall had occurred in February, were apparently ripe at a length of 5 and 6 mm. in March, active sperm being present and loose red eggs.

The early shelled larva (Fig. 6 *a*) was 0·05 mm. long with a slightly indented dorsal margin and the velum about two-thirds the length of the shell. No central flagellum was seen in the velum. The larvae from the fertilizations did not live, but the later veligers are very common in the plankton, both inside and outside the breakwater, at almost any time of year but especially in early autumn. The late larva nearly ready to metamorphose is about 0·18 mm. in length, the velum being large, slightly longer than the shell and the foot long and mobile. The larva swims actively shell downwards, the foot helping in the swimming (Figs. 6 *b*, *c*). The velum is soon lost, but specimens still retaining it with a shell length of 0·2 mm. may be seen (Fig. 6 *d*). The newly metamorphosed larva, from 0·2 to 0·23 mm. in length (Fig. 6 *e*) crawls on the bottom by means of a very long and contractile foot. At the umbo the early shell may still be seen. Specimens from the plankton which metamorphosed in plunger-jars grew to a large size and settled on the glass. At 0·45 mm. long the pedal sinus growing into the hole for the byssus is well shown (Fig. 6 *f*).

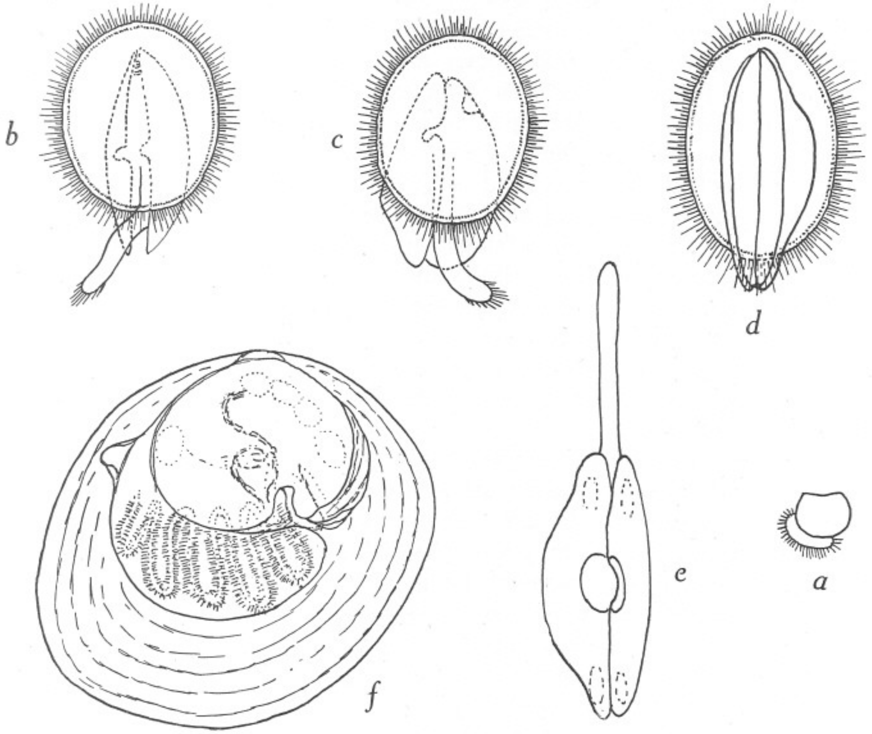

Fig. 6.

Heteranomia squamula.

a, early shelled larva from fertilization, 0·05 mm. long; *b*, *c*, later larvae, from plankton, swimming, 0·18 mm. long; *d*, late veliger, from plankton, ready to metamorphose, 0·2 mm. long; *e*, newly metamorphosed *Heteranomia*, grown in plunger-jar from planktonic veliger, 0·2 mm. long; *f*, young grown from planktonic veliger in plunger-jar, 0·45 mm. long.

Another species belonging to the family, which has a much less conspicuous pedal sinus, also occurs in the plankton. This resembles Odhner's specimen from Rovigno and may be *Anomia ephippium.*

THE LARVAE AND POST-LARVAE OF *MYSELLA BIDENTATA* AND A CLOSELY RELATED SPECIES

Certain large veligers often occur in the plankton, which when reared in plunger-jars grew into a species of *Mysella*. It was at first thought that these were *M. bidentata*; but another larva which was much less symmetrical was found which grew up into this species, and in shell gravel near the Eddystone all stages were found. As the first larva certainly belongs to the Montacutidae and the post-larva does not agree with other known species of *Mysella* or *Montacuta* it seems that there is a second species of *Mysella* occurring at Plymouth which is closely related to *Mysella bidentata* but distinct from it. Both species have the typical median cartilage with the lateral teeth forming a V enclosing it; the mantle is fringed with short processes, the siphons are hardly perceptible, the foot is large and very contractile and the posterior end of the shell is shorter than the anterior. The last character is much more marked both in the larva and post-larva of *M. bidentata*. The larva of the other form, here called *Mysella* sp., is nearly round, but slightly longer than broad, and the post-larva is oval with the posterior portion only slightly shorter than the anterior.

The larvae are comparable with the large veligers of *Kellia suborbicularis* (Lebour, 1938) and it is an interesting fact that the adults of both *Kellia* and of the known species of *Mysella* are viviparous, giving out their young as shelled larvae and yet attaining a large size before settling down.

Miyazaki (1936*a*) has described the larvae of *Mysella japonica* (Yokoyama). This species is also viviparous, the newly freed larvae being 122μ in length. The largest form reared was 306μ in length and this is very much like the Plymouth species at that stage. The same worker also reared another mollusc which he found commensal with the crustacean *Gebia major*. This he names *Erycina* sp. It is also viviparous, the larva at extrusion being 220μ in length and beginning to lose the velum at 351μ. It is thus seen that all these closely related genera apparently grow to a large size before settling down and that they probably remain a considerable time as planktonic veligers.

Mysella bidentata (Montagu) (Figs. 7 *a–c*)

Lovén (1848) has described and figured the newly ejected shelled larvae of this species, which are very like those of *Kellia* but slightly larger. The late larvae in the plankton, occurring chiefly from autumn to spring, are very flat and although nearly circular in outline have the anterior portion longer than the posterior. The velum is about the same size across its longest diameter as the shell. When ready to metamorphose the shell is 0·34 mm. long, with the lateral teeth already formed in a V and about four gill slits (Fig. 7 *a*). Slightly larger post-larvae were 0·4 mm. long and more oblique (Fig. 7 *b*). Young specimens about 0·5 mm. long had the adult form with the anterior end very much elongated. At a length of about 0·80 mm. the siphon and mantle processes were formed, and the teeth and cartilage were typical (Fig. 7 *c*).

Mysella sp. (Figs. 7 *d–g*)

Adults of this species have not yet been found, but young forms grown up from the plankton in plunger-jars show decided differences from the preceding species, the veliger differing much in form. Veligers from about 0·2 to 0·32 mm. across are very common in the plankton, especially in late summer and autumn, but they may also be found in spring. The velum is large and oval, reaching as far as the shell length (Figs. 7 *d*, *e*). At about 0·32 mm. the larva loses the velum (Fig. 7 *f*). The shell is very round in outline, the younger specimen being slightly longer than broad and at the time of metamorphosis both anterior and posterior ends are almost equal. Grown in plunger-jars these post-larvae grew into oval young with the posterior end rather shorter than the anterior and the mantle edged with fine processes (Fig. 7 *g*). The cartilage

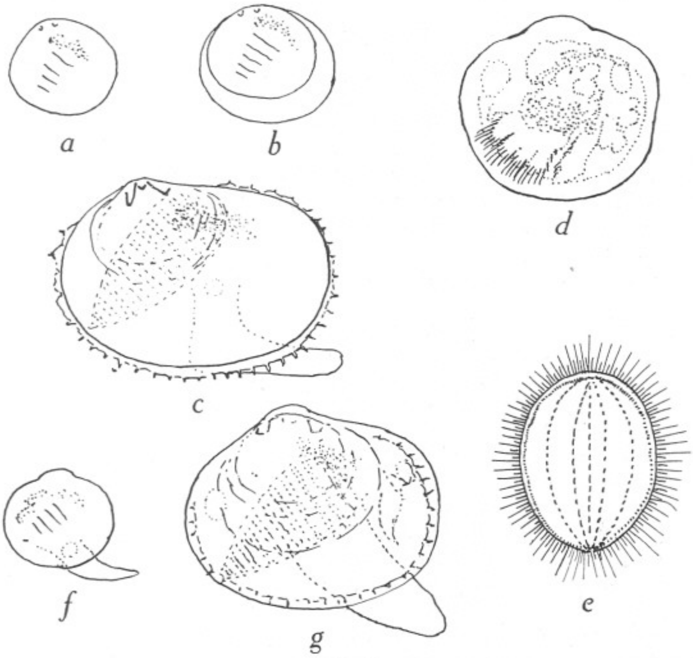

Fig. 7.

a–c, *Mysella bidentata.*

a, late veliger from plankton, 0·34 mm. long; *b*, post-larva from shell gravel, 0·4 mm. long; *c*, young from shell gravel, 0·82 mm. long.

d–g, *Mysella* sp.

d, *e*, veliger of *Mysella* sp. from plankton, 0·2 mm. long; *f*, newly metamorphosed form reared from planktonic veliger in plunger-jar, 0·32 mm. long; *g*, young reared from planktonic veliger in plunger-jar, 0·80 mm. long.

is well formed as well as the lateral teeth, the latter being blunter than those of *M. bidentata* and not forming such a distinct V. The foot is more pointed than in that species.

It was noticed in specimens of *Montacuta substriata* (Montagu) that the embryonic shell, visible in the adults, measured about 0·20 mm. in length, again showing a probable tendency to a large veliger in a viviparous form.

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ON THE NEMATOCYSTS OF HYDROMEDUSAE

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(Text-figs. 1–88)

In view of the possible use of nematocysts as characters for showing phylogenetic relationships among medusae (Weill, 1934), or even for the differentiation of species (Papenfuss, 1936), it is desirable that our knowledge of the nematocysts of medusae should be increased. I have accordingly examined the nematocysts in a number of species of Hydromedusae occurring at Plymouth.

Examination was always made on living material from which the portions to be examined, such as tentacles and mouth lips, were dissected. The dissected parts were placed on microscope slides, sometimes in sea water and sometimes in distilled water, and various stains such as magenta, methylene blue, and neutral red were used. Generally it was found that magenta and distilled water produced the best results for showing the minute structure of the nematocyst. The proportions of the nematocyst were first drawn under a monocular microscope with a camera lucida, and the slide was then transferred to a Leitz binocular microscope for more detailed examination. A 2 mm. apochromatic oil immersion objective was used, with × 10 eyepieces. Illumination was obtained with a "pointolite" and increased definition was helped by the use of a substage screen—a Wratten filter, Rheinberg No. 2 Blue Disc.

It is necessary to emphasize that observations were made on fresh material, since, as pointed out by Weill (1934, p. 30), fixation or desiccation may modify the form of the nematocyst. The nematocysts of most medusae are very small, the majority being less than 15μ in length, and certain difficulties may be experienced. One of the chief dangers is that if insufficient material is examined one type of nematocyst, at least, may be overlooked. I have on several occasions found an additional type of nematocyst, which I had not observed when examining previous medusae of the same species. This is generally due to the fact that different types of nematocysts may resemble one another in outline when in the undischarged* state. Unless, therefore, a very large number of nematocysts are discharged, that type which happens to be the least frequent may easily be overlooked if none are discharged. It was, for instance, only after I had examined a number of specimens of *Phialidium hemisphericum* that I found a few atrichous nematocysts among the very abundant mastigophores and later found that they were quite common.

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* The terms discharged and undischarged are used here in preference to exploded and unexploded.

Considerable difficulty was also experienced in this species, as in some other Leptomedusae, in deciding whether the nematocysts were microbasic mastigophores or basitrichous haplonemes, i.e. whether the basal portion of the discharged thread was thicker than the remainder of the thread. A number of *Phialidium* were examined at different times and the conclusion was reached that, immediately after the discharge of the nematocyst the basal portion of the thread was considerably thicker than the terminal portion. But there was often subsequent swelling of the terminal portion, whether through increased pressure of the coverglass, or for other reasons, and the terminal portion assumed the same thickness as the basal portion. There must, therefore, always be some doubt whether the classification of some Leptomedusan nematocysts into microbasic mastigophores and basitrichous haplonemes is reliable. A similar increase in diameter in the terminal portion of the thread is referred to on page 151 in the microbasic euryteles of *Zanclea costata*, and it was noticed in other species. Weill (1934, pp. 58, 153) says that the diameter of the thread can only be accurately seen after staining with neutral red, but I found that this frequently caused swelling.

Difficulties of rather a similar nature arose concerning the microbasic mastigophores of *Leuckartiara octona*. Weill (1934, p. 392) records that he only found microbasic mastigophores in this species. In the first specimens that I saw, however, there was no doubt that all the discharged nematocysts seen were not mastigophores but microbasic euryteles. But, on examining more specimens, I found some microbasic mastigophores, and I was then in some doubt whether these might not really have been microbasic euryteles in which the basal portion was abnormal and had not swollen to its full extent, or whether perhaps the nematocysts were incompletely developed. These doubts were enforced when I found among the microbasic euryteles of *Rathkea octopunctata* some in which the walls of the base were parallel, and also some intermediate stages between this and the typical euryteles. A subsequent examination of more *Leuckartiara* showed that, in this species at any rate, the mastigophores were of a very slightly different shape from the euryteles and could eventually be distinguished in the undischarged state.

It was found that in one species, *Amphinema dinema*, one of the nematocyst types was present in the medusa just liberated from the hydroid, but absent in the adult medusa. The newly liberated medusa possessed microbasic euryteles and desmonemes; the adult had only microbasic euryteles. The hydroid had, however, both kinds of nematocysts, and it is probable that the nematocysts of the hydroid migrate into the developing bud and that the medusa itself when liberated is only capable of making one kind. How exactly the desmonemes disappear in the medusa is uncertain, but it is just possible that they remain throughout the life of the medusa and were not noticed owing to their numbers being swamped by those of the nematocysts made by the medusa as it grew.

Another possibility of error is due to the occurrence in a medusa of nematocysts which are not its own. I have on several occasions found, in the manubrium and hollow basal portions of the tentacles, nematocysts of quite a different type from those typical of the species of medusa in question. Thus I have seen large stenoteles in both *Leuckartiara octona* and *Amphinema dinema*. These must undoubtedly have been ingested by the medusa with its food. Usually these foreign nematocysts are obvious on account of their collapsed condition, but if they have been recently ingested they may lead to a source of error.

The nematocysts typical of any one species of medusa sometimes showed considerable differences between their range of size from one specimen to another. This is probably usually a function of the size, or age of the medusa, or its state of nourishment. For instance, the microbasic euryteles in *Amphinema dinema* just liberated from its hydroid were $6\text{–}7 \times 2\,\mu$, whereas in the adult medusa they were $7\text{–}9{\cdot}5 \times 2\text{–}3{\cdot}5\,\mu$; in one specimen of *Saphenia* the basitrichous haplonemes were mostly $18\text{–}19\,\mu$ long, while in another specimen they ranged from 22 to $28\,\mu$ long.

In the following pages accounts are given of the nematocysts from twenty species of medusae. In this paper I have followed Weill's classification, which, in spite of such difficulties as I have mentioned above, is extremely serviceable. It is quite to be expected that with the great variety of structure shown by coelenterate nematocysts it is impossible to make a rigid classification and intergrading types are sure to be found (e.g. Weill, 1934, p. 59). But on the whole his classification does enable one quickly to place a nematocyst in its right category. I feel, however, a little doubtful about trying to discriminate between homotrichous and heterotrichous forms in such small nematocysts as those of most medusae. It should be realized that in the minute structure of many of these nematocysts we are reaching the limit of comfortable visual observation. It thus becomes extremely difficult, and perhaps impossible, to decide the comparative lengths of the smaller spines or barbs owing to the effects of foreshortening when each spine is lying in a different plane. I have therefore purposely omitted any reference to homotrichy or heterotrichy in the following accounts, since I was never able to satisfy myself as to their validity.

In the following descriptions I have generally given only the types of the nematocysts and their measurements and location. It seemed unnecessary to attempt to describe in words their various shapes, when this has been shown in the accompanying figures. As I have already stated, the outlines of these figures were drawn with a camera lucida, but in order to eliminate personal error in the interpretation of the minute structure in the discharged nematocysts I have, for almost every drawing, called upon the help of independent observers who checked my drawings against the originals. For their kind assistance in this way I have especially to thank Mr E. Ford, Mr W. J. Rees and Mr G. M. Spooner.

As far as I could see, the number of spirals, when these occurred, on all the nematocysts examined was always three; this is in agreement with the statements of most workers. I have, however, in some drawings, where the basal portion of the thread was very narrow, only indicated the general appearance, as it was difficult to draw three spirals without spoiling the effect by running the lines together. In the accompanying figures all nematocysts, except where stated otherwise, are drawn to the same scale, so that the sizes of the nematocysts of the different species can easily be compared.

Measurements are only given to 0·5 μ on account of the difficulty of making sure that the nematocysts were exactly orientated horizontally and showing their greatest width. Any attempt to do this by pressure is liable to distort the capsule.

No attempt has been made to depict accurately the course of the thread in the undischarged basitrichous haplonemes or mastigophores. They are shown merely as simple coils, whereas they are generally thrown into S-shaped loops. While the capsules are mostly drawn in lateral view, the coils thus shown give the impression produced when the capsule is looked at dorso-ventrally.

This work must be regarded merely as a preliminary survey of the types of nematocyst present. No attempt has been made to obtain average sizes for the different species; this would involve measurements on great numbers of medusae of different sizes.

ANTHOMEDUSAE

Steenstrupia nutans (M. Sars).

There appear to be at least four kinds, stenoteles, ? anisorhize heterotrichous haplonemes, ? microbasic mastigophores or microbasic euryteles, and desmonemes (Figs. 1–7).

Stenoteles: there is a large range of size shown by these nematocysts, which appear to be grouped roughly in two sizes:

Large: 11–16 × 9–13 μ undischarged, 11–13 × 9–11 μ discharged.

Small: 7–10 × 6–8 μ undischarged.

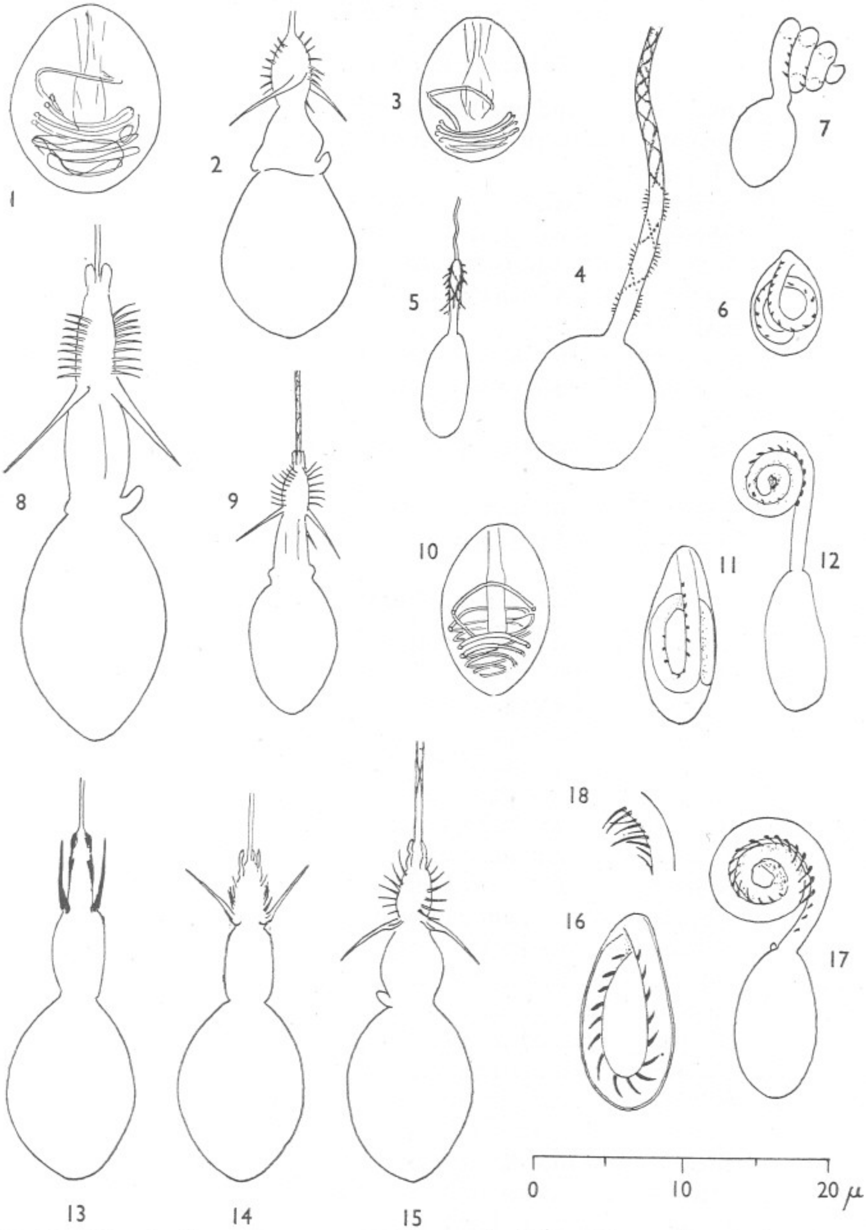
? *Anisorhize:* 11–12 × 9·5–10 μ undischarged, 9 × 8 μ discharged.

While these appeared to be anisorhize after first discharge, the thread later swelled up. There were definite spirals of short spines at the base, but the spirals on the rest of the thread appeared to have no spines.

? *Euryteles:* 8–12 × 3·5 μ undischarged.

I had the same difficulty with these as in *Rathkea*; in some specimens they appeared as euryteles and in others as mastigophores.

Desmonemes: 6–7·5 × 4·5–5·5 μ undischarged.



Figs. 1–7. *Steenstrupia nutans*: 1–3, stenoteles; 4, anisorhize; 5, ? eurytele; 6, 7, desmonemes. × *ca.* 2000.

Figs. 8–12. *Sarsia eximia*: 8, large stenotele from hydroid; 10, small stenotele from hydroid; 9, stenotele from newly liberated medusa; 11, 12, desmonemes from newly liberated medusa. × *ca.* 2000.

Figs. 13–18. *Purena gemmifera*: 13–15, stenoteles in process of discharge; 16, 17, desmonemes; 18, enlarged portion of desmoneme thread. × *ca.* 2000.

Sarsia eximia Allman.

In the hydroid I only found one kind of nematocyst, viz. stenoteles. In the newly liberated medusa there were, however, two kinds, stenoteles and desmonemes (Figs. 8–12).

HYDROID (*Syncoryne eximia*):

Stenoteles: these are of two sizes:

Large: 21·5–26 × 15–18 μ undischarged.

Small: 12–13 × 7·5–9 μ undischarged.

MEDUSA, newly liberated:

Stenoteles: these ranged in size from 9·5–16 × 6·5–10 μ undischarged. Most were *ca.* 13 × 9 μ undischarged; the smaller nematocysts may not have been fully developed.

Desmonemes: 9·5–12 × 4–5·5 μ undischarged. Most were *ca.* 12 × 4·5 μ undischarged.

I do not agree with Weill (1934, p. 385) as regards the structure of the stenoteles. I have discussed this below under *Purena gemmifera*.

Purena gemmifera Forbes.

Two kinds, stenoteles and desmonemes (Figs. 13–18).

Stenoteles: these are of two sizes:

Large: 16 × 12 μ undischarged.

Small: 13 × 9–10 μ undischarged.

Desmonemes: 13–14 × 6–7 μ undischarged.

While I agree with Weill (1934, p. 384) as regards the types of nematocysts present in this medusa, I cannot agree with him as regards the structure of the stenoteles in this species and in *Sarsia eximia*. Weill states that the small median spines are absent. They are in fact present and the stenotele is quite typical. The appearance or absence of the median spines is I think entirely due either to incomplete discharge of the nematocyst or to the incomplete development of the nematocyst. For instance, in a preparation in sea water and methylene blue, almost all the stenoteles were partially discharged with their posterior spines directed forwards. I was only able to find two fully discharged. In another preparation in distilled water and magenta, however, many were fully discharged with their basal spines directed backwards. In these the median spines were quite distinct. If the nematocysts are only partially discharged, the median spines all lie directed forwards over one another and each spiral appears only as a dark line. I have illustrated the various stages of discharge in Figs. 13–15. In many instances the whole armature of the hamp was broken away from the nematocyst, indicating that the nematocyst was not completely developed and the walls of the hamp had not reached their full thickness and strength.

Zanclea costata Gegenbaur (?).

I have examined a number of specimens newly liberated from the hydroid in the laboratory. The hydroid was the same as that described by Russell & Rees (1936). There were three kinds of nematocysts, stenoteles, macrobasic telotrichous euryteles and ? atrichous haplonemes.

Stenoteles: 7–13 × 6–12 μ undischarged, 6–11 × 5–9 μ discharged. These were present in the exumbrellar armature.

Macrobasic euryteles (Figs. 19–22):

Capsule: 7–7·5 × 4·5–5·5 μ undischarged, 5–6 × 3–4 μ discharged.

Length of hamp: *ca.* 25–30 μ discharged.

Ampulla: 4·5–5 × 1·5–2·5 μ.

The three spirals of barbs were present *on* the ampulla and extended for a short way down the hamp as in *Pteroclava krempfi* (Weill, 1934, p. 78). When first discharged the thread beyond the hamp is definitely thinner than the hamp itself. The thread, however, swells up later under pressure to the same thickness as the hamp. This increase in thickness of the thread under pressure possibly accounts for the differences in the observations of Weill and Allman (Weill, 1934, p. 78 *et seq.*), but both these authors describe the ampulla in this much discussed species as having no barbs. Both Weill and Allman also give the length of the hamp as being much greater than in my specimens. These nematocysts occur in the cnidophores of the tentacles.

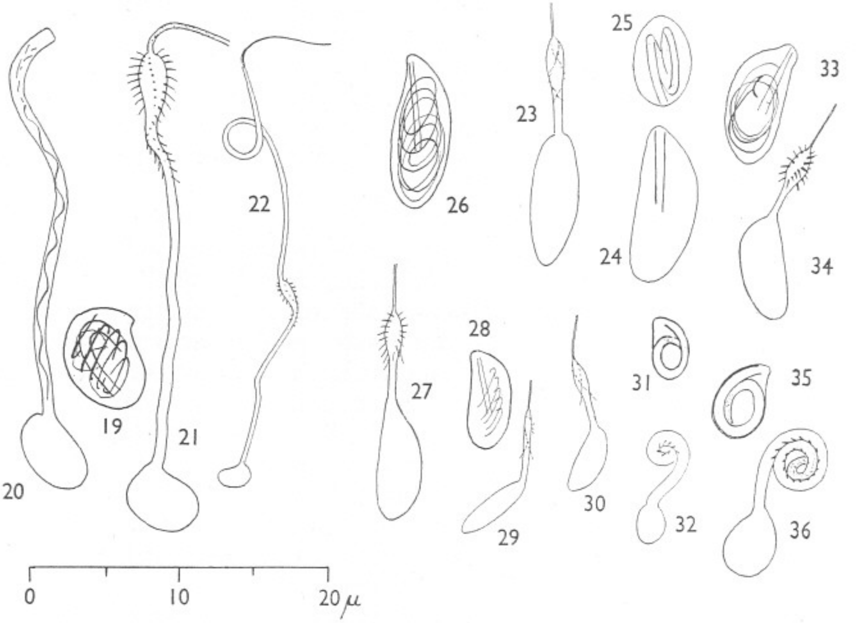
? *Atriches:* I only saw an occasional atriche and unfortunately obtained no measurements. They appeared to be extremely rare.

While discussing the nematocysts of *Zanclea* it will be convenient to answer a question raised by Weill (1936*a*) and Ranson (1937) concerning the nature of the exumbrellar nematocyst armature. The four exumbrellar groups of nematocysts are embedded in solid tissue and not in hollow sacs. This agrees with Weill's observation (1934, p. 420) on the American medusa. Allman (1871, p. 224) states that the nematocysts are immersed in a clear fluid; they certainly have this appearance unless highly magnified.

A comparison between the American medusa as described by Weill (1934, p. 418) and the Plymouth medusa as described by Russell & Rees (1936) is given below. Both descriptions refer to medusae just liberated from the hydroid:

	Plymouth	Woods Hole
Size	0·6–0·7 mm. high	1·8 mm. high
Cnidophores	18–20 × 13 μ	30 × 17 μ
Stenoteles	7–13 × 6–12 μ	12–17 μ
Euryteles	Telotrichous	Merotrichous
Capsule	7–7·5 × 4·5–5·5 μ	9 μ
Hamp	25–30 μ long	79 μ long
Ampulla	4·5 × 5 μ long	7 μ long

It can only remain a matter of opinion whether these differences should be regarded as of specific value, until a large number of medusae with two and four tentacles from different localities have been examined. Until we know what degree of constancy there is in these differences, any further discussion is at present valueless, but it should be borne in mind that mere size difference is of doubtful value.



Figs. 19–22. *Zanclea costata*, newly liberated: 19–21, macrobasic euryteles, × *ca.* 2000; 22, macrobasic eurytele after pressure, × *ca.* 900.

Figs. 23–25. *Bougainvillia britannica*: 23, 24, microbasic euryteles; 25, desmoneme (dorsal view). × *ca.* 2000.

Figs. 26–32. *Rathkea octopunctata*: 26, 27, microbasic euryteles from oral tentacles; 28, 30, microbasic euryteles from marginal tentacle; 29, ? microbasic mastigophore; 31, 32, desmonemes. × *ca.* 2000.

Figs. 33–36. *Lizzia blondina*: 33, 34, microbasic euryteles; 35, 36, desmonemes. × *ca.* 2000.

Bougainvillia ramosa (van Beneden).

One adult male only examined (2·2 mm. diameter).

Two kinds: microbasic euryteles and desmonemes.

Euryteles: 8–9×3·5–4μ undischarged.

Desmonemes: 4·5–5·5×3–3·5μ undischarged.

These nematocysts were similar in shape and appearance to those of *Lizzia blondina* (Figs. 33–36).

Bougainvillia britannica Forbes.

Two kinds, microbasic euryteles and desmonemes (Figs. 23–25).

Euryteles: 10–11×3·5–4μ undischarged, 9×3μ discharged.

Desmonemes: 6–6·5×3·5–4μ undischarged.

Of these the euryteles only occur in the mouth tentacles; both kinds of nematocysts are found in the marginal tentacles, the desmonemes being the more abundant.

Lizzia blondina Forbes.

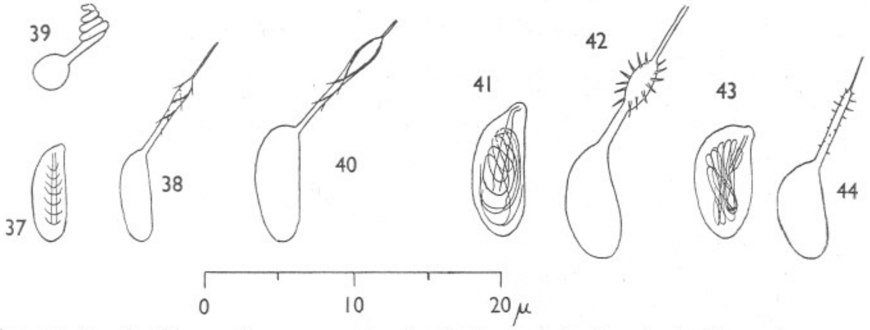
Two kinds: microbasic euryteles and desmonemes (Figs. 33–36).

Present in marginal tentacles and mouth tentacles:

Euryteles: 7–10 × 3–5 μ undischarged, 6–7·5 × 2·5–3·5 μ discharged.

Present in tentacles only:

Desmonemes: 4·5–6 × 2·5–3·5 μ undischarged.



Figs. 37–40. *Amphinema dinema*: 37, 38, microbasic euryteles from hydroid; 39, desmoneme from hydroid; 40, microbasic eurytele from medusa. × *ca.* 2000.

Figs. 41–44. *Leuckartiara octona*: 41, 42, microbasic euryteles; 43, 44, microbasic mastigophores. × *ca.* 2000.

Rathkea octopunctata (M. Sars).

Two kinds: microbasic euryteles and desmonemes (Figs. 26–32).

Present in marginal tentacles and oral tentacles:

Euryteles:

In oral tentacles: 10–12 × 3–4 μ undischarged, 8–9 × 2·5–3·2 μ discharged.

In marginal tentacles: 6–10·5 × 2·5–4 μ undischarged (mostly 6–8 μ), 5–7·5 × 1·5–3 μ discharged.

Present in marginal tentacles only:

Desmonemes: 3–5 × 2–3 μ undischarged.

Sometimes the microbasic euryteles appear as microbasic mastigophores (Fig. 29). This was especially so in one specimen in which the majority appeared to be microbasic mastigophores.

Amphinema dinema (Pér. & Les.).

In the hydroid and newly liberated medusa there are two kinds, microbasic euryteles and desmonemes. In the adult medusa there is only one kind, microbasic euryteles (Figs. 37–40).

HYDROID.
Euryteles: 6·5–7·5 × 2–2·5 μ undischarged.
Desmonemes: 3·5–4·5 × 2–2·5 μ undischarged, 2·5 × 2 μ discharged.
MEDUSA.
Newly liberated:
Euryteles: 6–7 × 2 μ undischarged.
Desmonemes: 3·5–4 × 2 μ undischarged.
Adult:
Present in marginal tentacles and mouth lips.
Euryteles: 7–9·5 × 2–3·5 μ undischarged, 6·5–7·5 × 2–2·5 μ discharged.

Amphinema rugosum (Mayer).

One specimen *ca.* 2 mm. high only seen. There was only one kind, microbasic eurytele (not figured).
Euryteles: 8–9 × 2 μ undischarged.

Leuckartiara octona (Fleming).

There appear to be quite definitely two kinds, microbasic euryteles and microbasic mastigophores (Figs. 41–44).
Present in tentacles and mouth lips:
Euryteles: 8–10·5 × 3–4·5 μ undischarged.
Present (?) only at base of tentacles or on umbrella margin:
Mastigophores: 7 × 3·5–4 μ undischarged.

At first I thought that there were only euryteles present, but subsequent examinations showed that there were undoubtedly also mastigophores, but these were much fewer. They appeared as small groups, and I was unable to make certain whether they were limited to the base of the tentacle or the umbrella margin. They were certainly not present in the main body of the tentacle. The mastigophores are shorter and more plump than the euryteles.

Weill (1934, p. 392) states that in *L. octona* from Wimereux there were only microbasic mastigophores, 10–12 μ long, present in the tentacles and mouth lips.

Willia stellata Forbes.

I have unfortunately been unable to obtain any living specimens of this interesting medusa. I have, however, had its hydroid, *Lar sabellarum*, and its nematocysts are sufficiently interesting to be described here. There were three kinds, macrobasic mastigophores, microbasic euryteles and desmonemes (Figs. 45 *a–j*).
Mastigophores: 24–33 × 9–13 μ undischarged.

In some specimens treated with acetic acid or distilled water the distal end of the hamp swelled into an ampulla, like that in the macrobasic eurytele of *Zanclea* (Fig. 45 *d*).

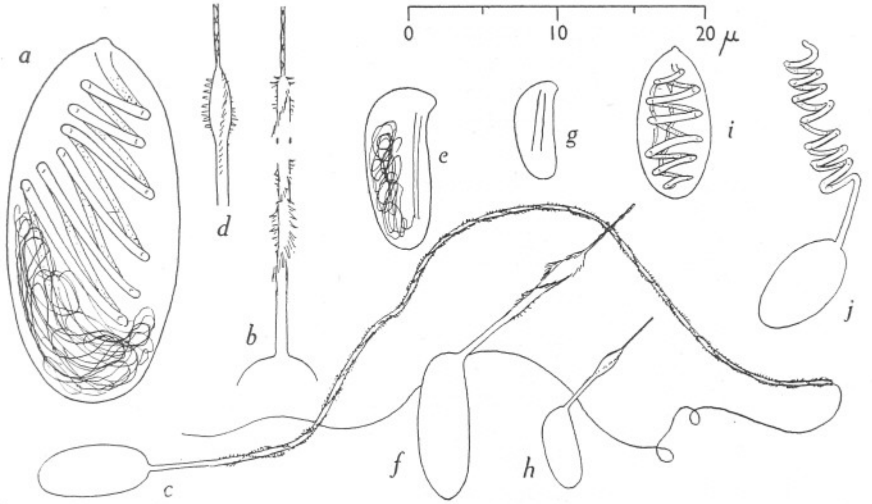
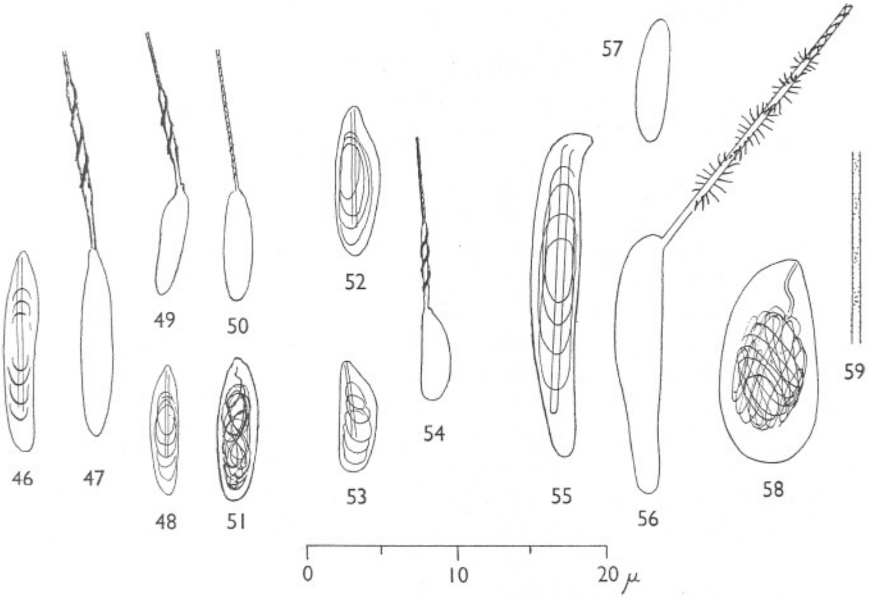


Fig. 45. *Lar sabellarum* hydroid: *a–d*, macrobasic mastigophores (*c*, × *ca*. 600); *e–h*, microbasic euryteles; *i–j*, desmonemes. × *ca*. 2000.



Figs. 46–51. *Phialidium hemisphericum*: 46, 47, large microbasic mastigophores from exumbrella; 48, 49, microbasic mastigophores from tentacle; 50, 51, atrichous haplonemes. × *ca*. 2000.

Figs. 52–54. *Phialella cymbaloides*: microbasic mastigophores. × *ca*. 2000.

Figs. 55–59. *Saphenia gracilis*: 55, 56, basitrichous haplonemes; 57, very small ? basitrichous haploneme from margin of umbrella; 58, atrichous haploneme, with portion of thread, 59. × *ca*. 2000.

Euryteles:

Large: 9–13 × 4–5 μ undischarged, 9·5–10 × 3–3·5 μ discharged.

Small: 6·5–7 × 2·5–3 μ undischarged, 5·5 × 2 μ discharged.

Desmonemes: 10 × 5 μ undischarged.

The desmonemes had unusually long threads for Anthomedusae, with as many as seven coils.

The macrobasic mastigophores were present only in the nematocyst pad on the proboscis.

LEPTOMEDUSAE

Mitrocomella brownei (Kramp).

One adult female only seen. There were two kinds, basitrichous haplonemes and atrichous haplonemes (Figs. 60–65).

Present in marginal tentacles and mouth lips:

Basitriches: two sizes.

Large: 14–16 × 4–5 μ undischarged, 13–14 × 3–3·5 μ discharged.

Small: 8·5–11 × 2–2·5 μ undischarged, 8–9 × 2 μ discharged.

Atriches: 11–12 × 4 μ undischarged, 10–11 × 3·5 μ discharged.

The armature on the base of the basitriches is very strong, the barbs being very long and pronounced.

Phialidium hemisphericum (L.).

There were two kinds, atrichous haplonemes and what appeared to be microbasic mastigophores. These were quite clearly mastigophores when first discharged, but, later, possibly due to pressure, the thread swells up so that they appear as basitrichous haplonemes (Figs. 46–51).

? *Mastigophores:* these were of two sizes:

Large: 12–14 × 2–3 μ undischarged, 11–13 × 1·5–2 μ discharged.

Small: 8–10 × 2 μ undischarged, 7 × 1·5 μ discharged.

The large mastigophores occurred on the umbrella. Some of the small mastigophores were mussel-shaped, but most were almond-shaped. The small ones were by far the most numerous.

Atriches: 9–10 × 2·5–3 μ undischarged.

It was only after I had examined a number of specimens that I found a discharged atriche. They can easily be confused with the others in their undischarged state, being of approximately the same size. In one of the later specimens I examined, when placed in distilled water and magenta, only the atriches discharged. They were then seen to be quite common, and were subsequently found in many specimens.

Weill (1934, p. 464) states that in this medusa from Wimereux there was only one type of nematocyst, a basitrichous haploneme, 10–12 μ long. He found, however, that in the hydroid of this species, *Clytia johnstoni*, there were both basitriches and microbasic mastigophores. It seems possible that he may have been misled by the swelling of the thread.

I examined medusae newly liberated from the hydroid and found both mastigophores and atriches present. In the hydroid I found mastigophores of two sizes but saw no atriches. I do not regard this as proof that they were not present.

When examining the mastigophores in this species and in *Phialella cymbaloides* I could never see for certain whether the spirals on the hamp were composed of spines. I imagined that this was so, for at the end of each dark diagonal line there was a slight projection. This may, however, have been an optical illusion due to the continuation of the spiral round the hamp. There are three spirals present, but I have not indicated these in Figs. 47 and 49 because it would not have been possible to draw them satisfactorily to so small a scale. I have therefore shown the appearance of the hamp when the upper surface is brought into focus. Thus in the small nematocysts there appear to be two dark diagonal lines and in the large nematocysts three diagonals.

Phialella cymbaloides (van Beneden).

One kind: ? microbasic mastigophores or basitrichous haplonemes (Figs. 52–54). I experienced the same swelling of the thread in these as in *Phialidium*. There were two sizes.

Small, in marginal tentacles: 6–9 × 2–3 μ undischarged.

Large, in mouth lips: 9–13 × 2·5–4 μ undischarged.

It is curious that I saw no atriches, for these seem to be present in most Leptomedusae.

Eucheilota clausa (Hincks).

There appear to be two kinds, atrichous haplonemes and possibly basitrichous haplonemes (Figs. 66–74). As with *Phialidium hemisphericum*, however, the basitriches in at least one specimen appeared as microbasic mastigophores immediately after discharge.

? *Basitriches:* these nematocysts occurred in two distinctly different shapes, (i) in the shape of an almond; (ii) in the shape of a mussel, *Mytilus*.

The almond-shaped basitriches were of two sizes and occurred in the tentacles and mouth lips: 12–19 × 3–4 μ undischarged, and 6·5–10·5 × 1·5–3 μ undischarged. The smaller of these were more numerous in the mouth lips than the larger.

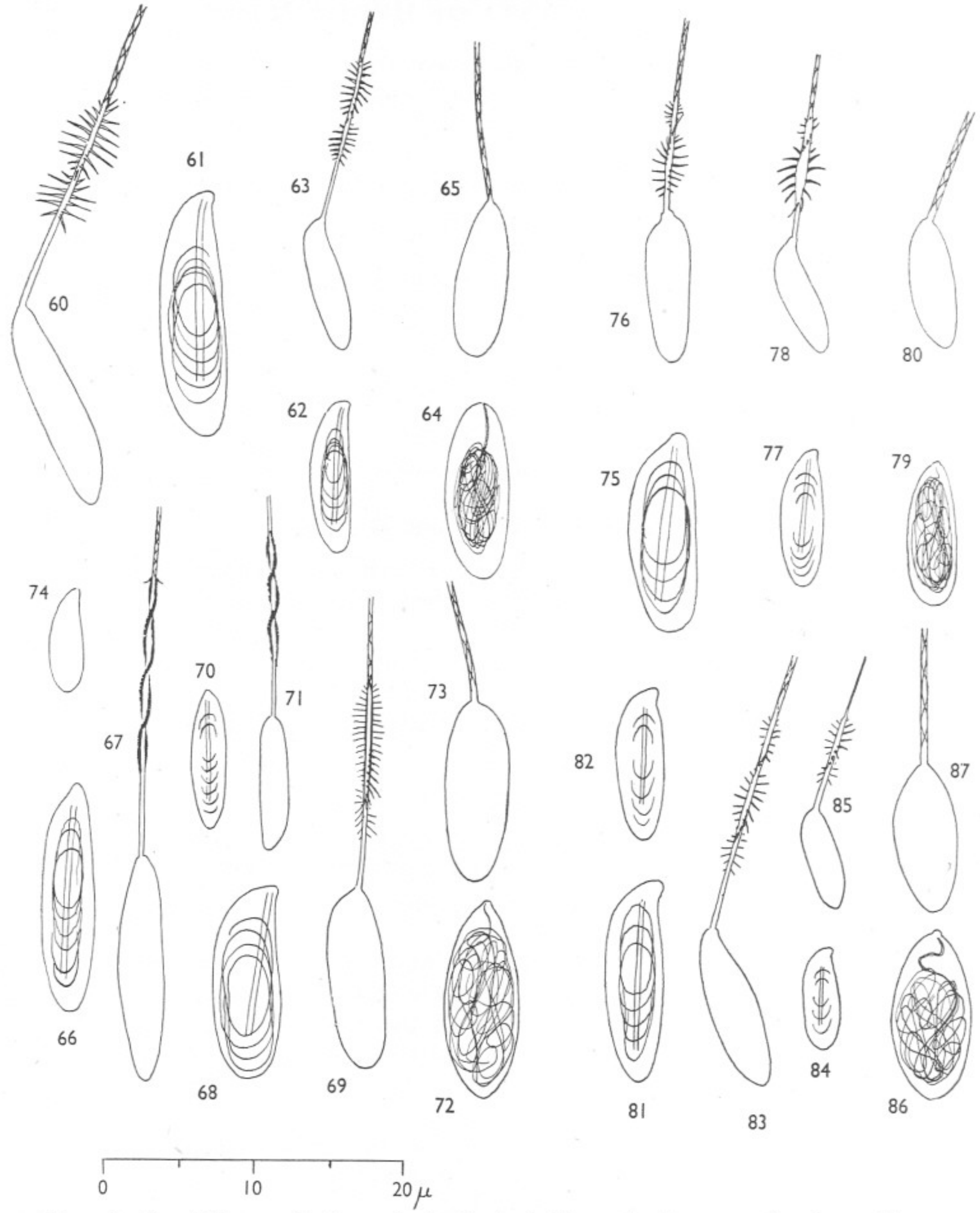
The mussel-shaped basitriches appeared to be confined to the umbrella margin and had longer barbs on their basal armature.

Atriches: ca. 12–13 × 4–5 μ undischarged.

Saphenia gracilis (Forbes & Goodsir).

There were three kinds, basitrichous haplonemes and atrichous haplonemes, and very small ? haplonemes or mastigophores (Figs. 55–59).

Basitriches: these were of two sizes.



Figs. 60–65. *Mitrocomella brownei*: 60–63, basitrichous haplonemes; 64, 65, atrichous haplonemes. × *ca*. 2000.

Figs. 66–74. *Eucheilota clausa*: 66–71, ? basitrichous haplonemes; 68, 69, mussel-shaped form; 72, 73, atrichous haploneme; 74, very small ? basitrichous haploneme. × *ca*. 2000.

Figs. 75–80. *Helgicirrha schulzei*: 75–78, basitrichous haplonemes; 79, 80, atrichous haplonemes. × *ca*. 2000.

Figs. 81–87. *Octorchis gegenbauri*: 81–85, ? microbasic mastigophores; 86, 87, atrichous haplonemes. × *ca*. 2000.

Large, in marginal tentacles: 18–28 × 3–4 μ undischarged.

Small, in mouth lips: 10–13 × 2·5–3 μ undischarged.

Atriches: 12–16 × 4–7 μ undischarged.

The very small nematocysts, 7–8 × 2–2·5 μ undischarged, were present on the umbrella margin. Unfortunately I was unable to see any discharged, so could not make certain of their type.

Weill (1934, p. 460) states that in *S. gracilis* from Wimereux there were two kinds, atriches 15 × 7 μ and basitriches 22 × 5 μ.

Octorchis gegenbauri Haeckel.

Two kinds, atrichous haplonemes and basitrichous haplonemes, the smaller of which may have been basitrichous mastigophores (Figs. 81–87).

Basitriches: these were of two sizes in the tentacles and margin:

Large: 12–15 × 3·5–5 μ undischarged.

Small: 7–8·5 × 2–2·5 μ undischarged.

In the mouth lips I saw only one size, 8·5–10 × 2·5–3 μ undischarged.

Atriches: 9–13 × 4–5·5 μ undischarged.

I could not make out for certain whether the smaller basitriche nematocysts were haplonemes or mastigophores.

Helgicirrha schulzei Hartlaub.

Two kinds: basitrichous haplonemes and atrichous haplonemes (Figs. 75–80).

Basitriches: 9–13·5 × 3–4 μ undischarged.

Atriches: 9–12 × 3–4 μ undischarged.

All types were present in the tentacles but I could see only small basitriches in the mouth lips.

SIPHONOPHORA

Muggiaea atlantica Cunningham.

On the tentilla there are three kinds, desmonemes on the terminal filament, and large microbasic mastigophores and atrichous haplonemes in the battery (Figs. 88 *a–f*).

Desmonemes: 7–10 × 4–6 μ undischarged.

Mastigophores: 36–43 × 6–7·5 μ undischarged, 33–36 × 6 μ discharged.

Atriches: 13–18 × 3–4 μ undischarged (often anisorhize in form).

Interspersed among the desmonemes on the terminal filament there are numerous so-called "anacrophores", 5–6 × 2 μ, arranged in pairs much as Weill (1934, fig. 111) has shown for *Diphyes spiralis*. Since the desmonemes show a range in size down to that of the "anacrophores" I am inclined to think that the "anacrophores" may be immature desmonemes at the stage before they become rounded; otherwise it is difficult to understand whence so many desmonemes originate. Similarly I observed that the immature atrichous

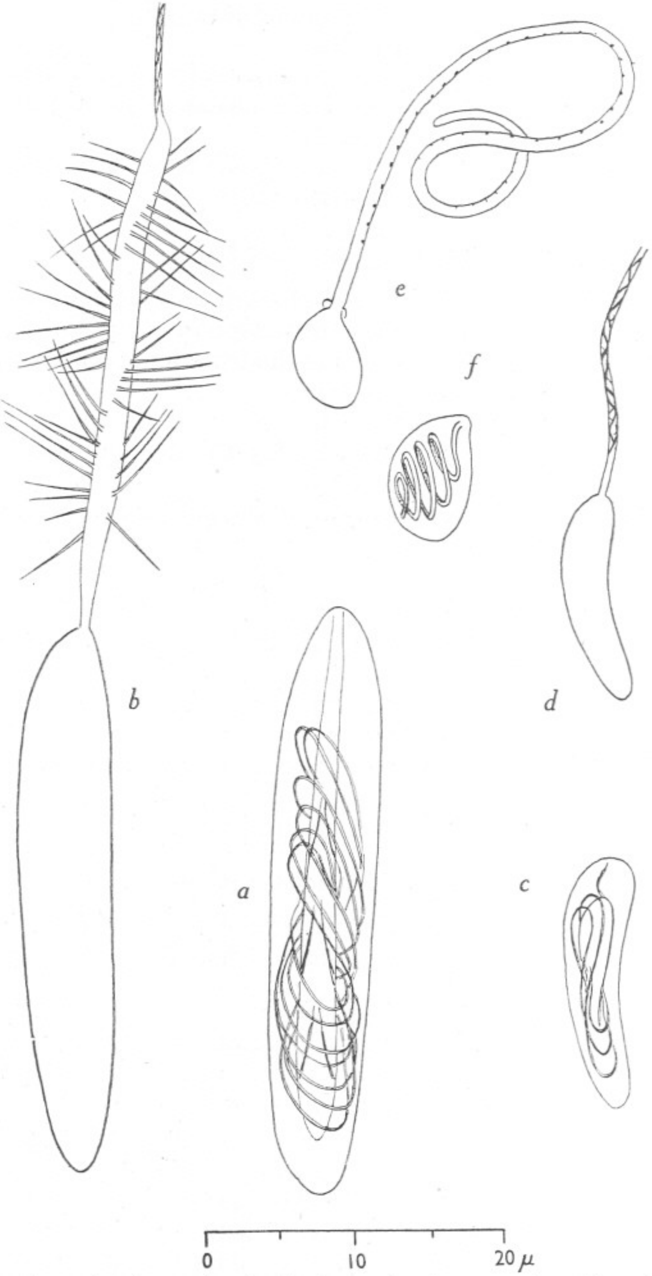


Fig. 88. *Muggiaea atlantica*: *a*, *b*, microbasic mastigophores; *c*, *d*, atrichous haplonemes; *e*, *f*, desmonemes(*e*, thread uncoiled). × *ca*. 2000.

haplonemes, 9–12 × 2 μ, would partly discharge and appear like "anacrophores", having a dilated basal portion with a terminal filament from the end of which the remaining un-everted portion of the thread could be traced back to the capsule in which it was coiled. On these grounds I suggest that the so-called "acrophores" and "anacrophores" recorded in Siphonophores may be merely stages in the development of other nematocysts.

DISCUSSION

The nematocysts may be regarded as characters of a medusa worthy of description, just as much as any of the other structures which are dealt with when a detailed description is made of any one species. But, apart from this aspect, it has been repeatedly urged that a knowledge of their structure may give a clue to the phylogenetic relationships of species of coelenterates whose relationships are not made clear by other known characters (e.g. Stephenson, 1929; Weill, 1934). With this further addition to our knowledge of the nematocysts of medusae, it is therefore not without interest to summarize the results for medusae alone, as Weill has done for so many groups. I have therefore given a table (p. 163) showing the distribution of the different types of nematocysts among a number of species of Anthomedusae and Leptomedusae. In this table a cross in brackets indicates that I was uncertain to which category a nematocyst should belong; the two alternative categories are therefore shown in this manner whenever I was in doubt. The medusae have been arranged in their order of classification into the different families that are more generally accepted at the present time.

A first glance at this table shows that most of these medusae fall into four main groups as regards their nematocyst characters. Of these the first, the Tubulariidae, are set apart by having four types of nematocysts.

The other three groups comprise the Corynidae and Eleutheriidae in which there are two kinds, desmonemes and stenoteles; the Clavidae and Bougainvilliidae or Margelidae with two kinds, desmonemes and microbasic euryteles; and thirdly the Leptomedusae as a whole which have two kinds, atrichous haplonemes and the basitrichous haploneme—microbasic mastigophore type (except *Phialella cymbaloides*). There is yet a fifth group, the Pandeidae, whose adults lack all types of nematocysts except the microbasic eurytele, with the addition of a microbasic mastigophore in *Leuckartiara*.

It can thus be seen that the distribution of nematocyst types fits very well with the accepted classification of the medusae based on other characters. Some reliance may therefore be placed on them as classificatory characters. Their value has been shown quite definitely for *Zanclea* and the Eleutheriidae by Weill (1934, 1936*b*). *Zanclea* has indeed been set apart from the Corynidae on account of its very remarkable tentacle structure and because its gonads do not surround the manubrium. Yet its hydroid is very corynid in appearance. Its nematocysts show its relationship with the tubularian and corynid groups in the stenoteles. It is separated from them, however, by the absence of desmonemes, which occur in both the other groups, and by the presence of the remarkable macrobasic euryteles. The position of the Eleutheriidae has long been a source of discussion, but their nematocysts show quite clearly a close relation with the Corynidae.

When we consider the other groupings we see that the hydroid of *Willia stellata* stands apart in having macrobasic mastigophores which are not found in any of the other medusae. This is further evidence justifying the formation of a separate family, the Williidae, to hold this medusa and its near relatives. It is also of great interest to find that in its nematocysts this species shows a relationship with the clavid-bougainvilliid group in the presence of desmonemes and absence of stenoteles. It is thus in its relationship to this group somewhat like *Zanclea* in its relationship to the tubulariid-corynid group. Both species possess a unique type of nematocyst and both have somewhat remarkable armature on the exumbrella. *Willia* shows no relationship to the Leptomedusae in its nematocysts and is thus probably correctly placed in the Anthomedusae.

There are other points of interest shown in the table, such as the apparent relationship between *Rathkea* and *Lizzia* and *Bougainvillia*, but until more species are studied it seems a little premature to discuss such relationships in detail.

It is a noticeable feature that while the Anthomedusae are thus divided into a number of distinct groups by their nematocyst characteristics, the Leptomedusae as a whole show no such division (cf. Weill, 1934, p. 478). This is in agreement with the great diversity of form shown by the Anthomedusae as compared with the Leptomedusae. It is unfortunate, because I had hoped that by examining a number of widely separated genera of Leptomedusae some of their relationships might have been shown by their nematocysts.

This preliminary review of medusan nematocysts has shown that the opinion that their study may be of value in showing phylogenetic relationships is justified and that more observations should be made. When we consider their value as specific characters, however, it is evident that a great deal more research will have to be done on the dimensions and variations of the nematocysts in individual species. It is true that a study of the accompanying illustrations of the nematocysts of Leptomedusae shows that a few of them are quite distinctive, but on the whole they are extraordinarily alike. All the species so far studied are quite easily distinguishable by other morphological characters, and the value of nematocysts as specific characters will have to be shown in species that are closely alike and in which as yet specific distinctions remain in considerable doubt. Typical examples of such medusae are the species of *Obelia* and of *Aequorea*. I have not myself examined such species yet. If the differences are small, as they are quite likely to be, it is necessary for the observer to have had considerable experience in observing

		Haplonemes			Heteronemes				
	Desmonemes	Atrichous	Basitrichous	Anisorhize	Microbasic mastigophores	Macrobasic mastigophores	Microbasic euryteles	Macrobasic euryteles	Stenoteles
ANTHOMEDUSAE									
Tubulariidae									
Steenstrupia nutans	×	..	..	×	(×)	..	(×)	..	×
*Ectopleura dumortieri**	×	..	..	×	×	..	..	..	×
Corynidae									
Sarsia eximia	×	..	..	..	..	..	..	..	×
*Sarsia prolifera**	×	..	..	..	..	..	..	..	×
Purena gemmifera	×	..	..	..	..	..	..	..	×
Eleutheriidae									
Eleutheria dichotoma†	×	..	..	..	..	..	..	..	×
Cladonema radiatum†	×	..	..	..	..	..	..	..	×
Pteronemidae									
Zanclea costata?	..	×	..	..	..	..	..	×	×
Clavidae									
*Oceania armata**	×	..	..	..	..	..	×	..	..
Bougainvilliidae-Margelidae									
Bougainvillia ramosa	×	..	..	..	..	..	×	..	..
Bougainvillia britannica	×	..	..	..	..	..	×	..	..
Lizzia blondina	×	..	..	..	..	..	×	..	..
Rathkea octopunctata	×	..	..	..	..	..	×	..	..
Pandeidae									
Amphinema dinema	‡	..	..	..	..	..	×	..	..
Amphinema rugosum	..	..	..	..	..	..	×	..	..
Leuckartiara octona	..	..	..	..	×	..	×	..	..
Williidae									
Willia stellata (Hydroid)	×	..	..	..	..	×	×	..	..
LEPTOMEDUSAE									
Mitrocomidae									
Mitrocomella brownei	..	×	×	..	..	..	..	..	..
Eucopidae									
Phialidium hemisphericum	..	×	(×)	..	(×)	..	..	..	..
Phialella cymbaloides	..	..	(×)	..	(×)	..	..	..	..
Eucheilota clausa	..	×	(×)	..	(×)	..	..	..	..
Saphenia gracilis	..	×	×	..	..	..	..	..	..
Octorchis gegenbauri	..	×	×	..	..	..	..	..	..
*Eirene viridula**	..	×	..	..	×	..	..	..	..
Helgicirrha schulzei	..	×	×	..	..	..	..	..	..
Aequoridae									
*Aequorea forskalia**	..	×	×	..	(×)	..	..	..	..

* Weill (1934). † Weill (1936*b*). ‡ Present only in medusa just liberated from hydroid.

nematocysts. Only then will he know what kind of differences to look for. Examination of closely related species must, also, be made by the same observer. There is liable to be a pronounced personal factor in observing these minute structures under high powers of the microscope. On this account interpretations of structure may be quite different by different observers, because the same kinds of nematocysts may appear so different unless examined in exactly the same positions. In this respect it seems rather significant that when I compare my results with those of so eminent a specialist as Dr Robert Weill I find that I differ from his conclusions in no less than five out of the six species that we have both studied.

SUMMARY

The nematocysts of twenty species of Hydromedusae occurring at Plymouth are described. Of these, twelve were Anthomedusae and seven were Leptomedusae, and one was the Siphonophore, *Muggiaea atlantica*. The medusae fit very well into the generally accepted classification as regards the types of nematocysts they possess.

Lar sabellarum, the hydroid of *Willia stellata*, has a type of nematocyst not found in the other species—a macrobasic mastigophore. This is a further justification for the formation of a separate family, the Williidae, to hold this species and its relations.

While the Anthomedusae are clearly split up into distinct groups as regards their types of nematocysts, the Leptomedusae form a single group.

It is suggested that the so-called acrophores and anacrophores recorded in siphonophores may be merely stages in the development of other nematocysts.

It is urged that much more research is required on variation in size and structure of nematocysts in individual species before they can be used as specific characters for separating doubtful species.

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LUCERNARIA DISCOIDEA, A NEW SPECIES FROM THE CHANNEL ISLANDS

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(Text-figs. 1–3)

While collecting on the *Zostera* beds at Grève d'Azette, Jersey, on August 23 1937 Mr R. B. Pike found fourteen specimens of an unknown lucernarian. These *Zostera* beds, made famous by the work of Mr J. Hornell, are now greatly impoverished, and at extreme low tide during the spring tide period only a few scattered patches of the weed remain. Hornell reported *Haliclystus octoradiatus* from this area, and it was while searching for it that the present species was found.

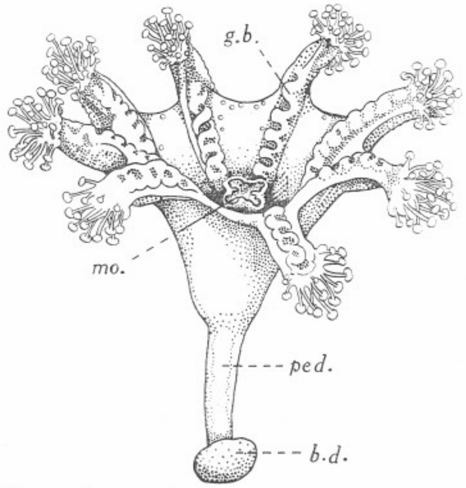

Fig. 1. *Lucernaria discoidea* n.sp.; an individual of medium size in lateral view. ×5. *b.d.* basal disk; *g.b.* genital band; *mo.* mouth; *ped.* peduncle.

The general form of the lucernarian is typical (Fig. 1), but more delicate than that of *L. campanulata*. When alive, the colour was greenish yellow, with numerous scattered, pale yellow, opaque spots all over the umbrella, and a few cerulean blue spots between the genital bands not far from the mouth. The yellow and blue colour rapidly disappeared in formalin. The specimens vary in size from 5 to 20 mm. high, and from 3 to 15 mm. across the bell. The basal disk is distinct and is broader than the peduncle, which is rather long and slender, and expands gradually into the umbrella. Of the fourteen specimens, one has twelve arms, twelve have eight arms, and one has seven arms, the odd arm in the last specimen being formed by the fusion of two arms. The normal number can therefore be taken as eight. In a fully expanded specimen the length of the free arm is about one-third of the radius of the umbrella, and the tentacles which crown the arm are the distinguishing feature of the species. In all other species of both *Lucernaria* and *Haliclystus* which I have been able to trace, the tentacles are rounded and button-like (capitate) at the tips, the nematocysts being confined to this area. In the species here described the fully formed tentacle has a *flat disk* at its apex, although young tentacles show that the discoid type is derived from the normal rounded one and the disk can be contracted to form a thick "cake". The number of tentacles in a bunch rarely exceeds twenty-five and is usually fewer (Fig. 2). Though all are slender, the size and shape vary, and three kinds can be distinguished:

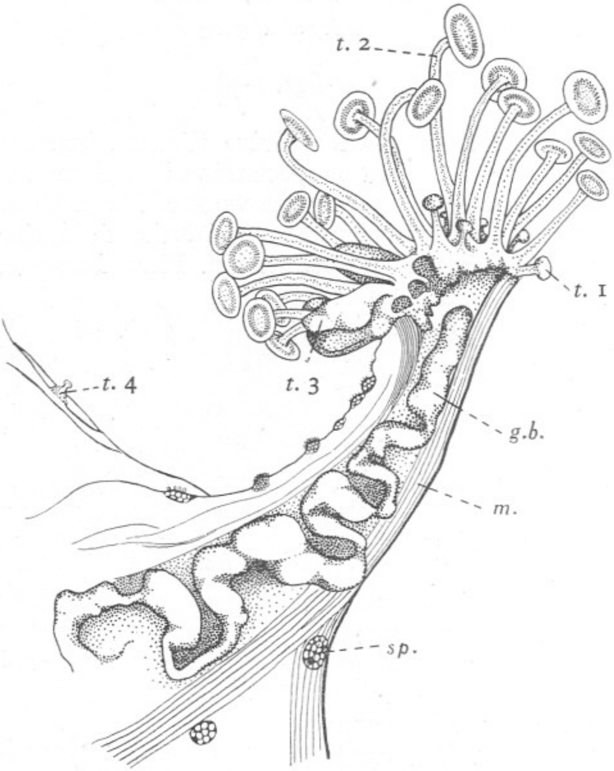

Fig. 2. The arm of *L. discoidea* n.sp. from the oral side. Its apex is twisted to the right to expose the aboral glandular tentacles. ×25. *g.b.* genital band; *m.* muscle; *sp.* opaque spot on umbrella; *t.* 1, capitate tentacle; *t.* 2, discoid tentacle; *t.* 3, glandular discoid tentacle; *t.* 4, vestigial per- or interradial tentacle.

(*a*) On the oral side of the arm are from four to six short capitate tentacles (Fig. 2, *t.* 1).

(*b*) On the extremity of the arm are situated about ten or twelve long slender tentacles, with disk-shaped heads set at right angles to the centrally placed stalk, somewhat like the podia of an *Echinus* (Fig. 2, *t.* 2).

(*c*) On the aboral side of the summit of the arm are from three to five tentacles with discoid heads, and rather short stalks expanded greatly on the aboral side of the base to form glandular adhesive organs. A bulbous prolongation of each swollen area is contained within the arm (Fig. 2, *t.* 3).

The cruciform mouth with frilled lips projects on a short manubrium from the centre of the umbrella, and is held in place by four perradial strips fastened to the umbrella between the adradially situated genital bands, as the latter diverge towards the arms. The interradial areas being free from such attachment are usually more widely expanded, so that the genital bands naturally fall into four groups of two each, although symmetry is regained on the umbrella margin. (Cf. *L. quadricornis*, where the arms are grouped in twos.) The genital bands are of characteristic shape, being sinuous and swollen, but continuous. They extend as far as the base of the tentacles, and appear to possess one aperture for each band near the tip. The gastric filaments are unbranched, the stalk is one-chambered, but four bands run downwards as continuations of the taenioles. On the inner surface of the disk these bands broaden out, are visible externally, and have the shape of a four-rayed clover-leaf.

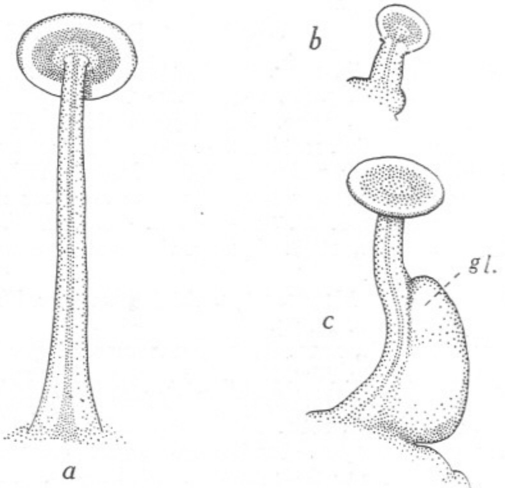

Fig. 3. Three types of tentacle from the arm of *L. discoidea* n.sp. × 60. *a*, tall discoid; *b*, short capitate; *c*, short glandular discoid: *gl.* glandular base of tentacle.

Young specimens exhibit two points of difference from adults. The tentacles tend to resemble the ordinary capitate type, and there is in some a single capitate tentacle on the umbrella edge in the centre of each bay between the arms. In older specimens these isolated perradial and interradial tentacles become reduced in size and may either disappear or persist in one or more of the bays. Elmhirst (1922) noted similar tentacles in *L. quadricornis*.

Although *L. discoidea* is here called a new species, it was discovered over eighty years ago by H. Milne Edwards at Langrune, east of Cherbourg, and accurately figured by him in the Disciples' Edition of Cuvier's *Règne Animal*, 1847. He found orange and greenish specimens, and gave a coloured figure of the former. He noted both the knob-shaped and disk-shaped tentacles, the opaque spots on the umbrella, the sinuous nature of the genital bands, the simple gastric filaments, and the swollen basal expansions of the peduncle supports. He did not see, however, the adhesive pads on the outer tentacles, or the attachment of the mouth angles. His specimens did not possess the blue spots. At the time two species of lucernarian were known, viz. Müller's *L. auricula* and *L. quadricornis*, the former a *Haliclystus* and the latter a *Lucernaria*. Milne Edwards called his specimens *L. auricula*, an obvious error in the light of present-day knowledge, since his specimens had no colletocystophores and Müller's had. Consequently a specific name is required for it, and *L. discoidea* is suggested, because of the peculiarity of the tentacles.

Specimens have been deposited in the British Museum of Natural History, and I should like to thank Dr A. K. Totton for his assistance with the literature, and Mr Pike for drawings of the animal.

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SALT ERROR IN DETERMINATIONS OF PHOSPHATE IN SEA WATER

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Investigations extending over several years have shown that the salt error in colorimetric determinations of phosphate in sea water may be dependent, not only upon the concentrations of reagents and to some extent on the temperature, but also on the method of making the comparison. Uncertainty had become acute since alterations in procedure had been made, which were found to invalidate comparison between results obtained before and after 1933. Since we possess much the longest series of phosphate records yet made and these show promise of close correlation with other biological phenomena, it became essential to ensure that all were on a comparable basis.

The Conditions of Formation of Phosphomolybdenum Blue

From a detailed study Tischer (1934) concluded that:

(1) To reduce one molecule of phosphomolybdic acid to phosphomolybdenum blue four stannous ions are required.

(2) The experimental solution should lie between 0·09 and $0{\cdot}17N\ H_2SO_4$. This agrees with Kalle's finding (1934), since 100 ml. of water treated with 1 ml. of the usual acid molybdate reagent contains $0{\cdot}14N\ H_2SO_4$. The optimum normality of acid is very dependent on the amount of molybdate present (cf. Kalle, 1934).

(3) The influence of *p*H is due to its effect on the competing oxidation-reduction systems, phosphomolybdic acid $\rightleftharpoons$ phosphomolybdenum blue, $Sn^{++++} \rightleftharpoons Sn^{++}$ and $H^+ \rightleftharpoons H$. Electrometric measurements showed that the colour intensifying effect of sulphate is due to an increase in the *p*H of the reaction mixture.

(4) The depth of colour in distilled water, reached after thirty minutes, is independent of temperature but electrolytes give rise to a temperature coefficient.

(5) Chloride, in contrast to sulphate, causes not only a diminution but also an alteration in the shade of the reduced solution so complicating the salt error problem in work with sea water (cf. also Robinson & Wirth, 1935).

Formation of Complex Molybdenyl Halides

Reduction of molybdic acid in solution in strong hydrochloric or hydrobromic acid, either with hydrogen iodide or electrolytically at a platinized platinum electrode, leads to the formation of complex molybdenyl halides,

$R_2[MoOX_5]$, where R is an alkali metal or an ammonium base and X is chlorine or bromine. Under suitable conditions these complexes may be crystallized, the chlorides being green and the bromides brown to yellow. They are all rapidly hydrolysed by water, the concentrated solutions being reddish brown passing through orange to bright yellow on dilution. The bromides are even more liable to hydrolysis than are the chlorides. The stages in the hydrolysis have been elucidated (James & Wardlaw, 1927; Angell, James & Wardlaw, 1929). This work agrees with the views put forward by Tischer (1934). In a sample of sea water submitted to colorimetric analysis of phosphate we have all the conditions required for the formation of these complexes—large amounts of chloride and some bromide, excess of molybdic acid, a degree of acidity sufficient to promote their formation and a reducing agent, present only in small quantity it is true, but more powerful than hydrogen iodide.

This formation of molybdenyl halides and their yellow hydrolytic products may be readily shown by adding a solution of stannous chloride, drop by drop, to a resting sample of sea water containing acid molybdate reagent. Bright yellow streaks will be seen slowly falling towards the bottom of the flask. Complete suppression of the complex molybdenyl halide formation is difficult, but it may be much reduced by rotating the solutions rapidly whilst the stannous chloride solution is being added, so avoiding a temporarily high local concentration of the reducing agent. It may also be reduced by cutting down the amount of stannous chloride added (Atkins, 1928 p. 202). Controls are necessary to ensure that this is not cut down too much.

Between five and ten minutes after the addition, a slight development of yellow tint need not prevent an experienced analyst making a reproducible colour match. Since the yellow colour then develops more rapidly, comparison after half an hour or more is undesirable.

When colour filters are used a very serious source of error may arise. The formation of molybdenyl chlorides is accompanied by absorption not only in the blue and green but also in the red. This absorption in the red would be attributed to the presence of phosphate. In any one group of experiments where "yellowing" is taking place, it may be uniform and very difficult to detect by ordinary methods of control, using a photometer in a dimly lit room. When this happens the results may appear excellent; the colour increment for the addition of a given amount of phosphate may be uniform throughout a long series of determinations; blank measurements may appear in perfect order, and yet the content of phosphate found may be as much as 75% too high. The unsuitability of the solutions for analysis is at once evident when they are examined in bright daylight. The colour increment is also greater than is found when a good blue has developed.

STRENGTH OF MOLYBDATE REAGENT

Kalle (1933, 1934, 1935*a*, *b*) has made a detailed investigation of the optimum conditions for the analytical determination of phosphate in artificial sea water. He found (1934) that the usual molybdate reagent is blended in the right proportions, but that if the amount used were reduced by one-half the intensity of colour development was always increased and the salt error diminished. From Kalle's results with the Pulfrich photometer (S72 filter), using 1 ml. of molybdate reagent per 100 ml. of water, a correction factor, 1·13, was found, and agreed closely with determinations then made by the writer using Hehner cylinders and natural sea water—1·11 and 1·12.

The reduced quantity of molybdate reagent (1 : 100) was adopted as standard practice in April 1934, but comparison in Hehner cylinders was continued in preference to the Pulfrich photometer.

THE EFFECT OF COPPER

Subsequently Kalle (1935*a*) suggested that minute traces of copper affect the development of blue colour and are mainly responsible for the salt error. To overcome this he suggested adding copper to all standards and sea water samples, so that results would then not require correction for salt error. Tischer and Kalle agree that the depressing effect of increasing quantities of copper is represented by a curve with a flat inflection but do not agree as to its position. They both used 1 ml. of molybdate reagent per 100 ml. of water. The flat part of the curve, where increase in the amount of copper leads to no further decrease in colour, lies between 120 and 1200 mg./m.^{3} according to Kalle and between 1460 and 8560 mg./m.^{3} according to Tischer. With 250 mg./m.^{3}, the decrease in colour in distilled water is about 3% according to Tischer, about 5% according to Kalle and about 10% according to extensive experiments made by the writer. It is clear from Tischer's discussion that the effect of copper will be the greater the less the quantity of stannous chloride used.

As much copper as 30 mg./m.^{3} has been shown to have a negligible effect on colour development by Tischer, Kalle and the writer. With this the investigations of Robinson & Wirth (1935) and Brambel & Cowles (1937) agree. Such an amount of copper has never been found in our distilled water nor in our sea-water samples, so that we feel that no phosphate analyses here are likely to be affected in this way. Since our Nansen-Pettersson sampling bottle is made of a copper alloy which has corroded badly, a number of tests have been made for contamination of the samples by copper. During the few minutes of a routine haul from less than 100 m. contamination is not serious, but when water had been left in the sampling bottle for four hours during the journey back to the laboratory it was found to have been enriched with 500 mg./m.^{3} Thus in working at greater depths or with less attention to washing the bottle with fresh water after the day's work, there is an ever present risk of serious contamination. The alloy used in the hydrographical bottles is unsatisfactory and an effort should be made to build them of incorrodible components such as stainless steel and ebonite, or silver-lined bottles of the *Discovery* Expedition type should be used.

From June 1936 to October 1937 copper was added to all our standards and sea-water samples prior to analysis (25 μg. Cu and 1 ml. of molybdate reagent per 100 ml.). The development of colour was diminished but to the same extent in both sea water and standards (Tables I and II). The phosphate results required the same correction factor as though no copper had been added.

DETERMINATION OF SALT ERROR

The method of phosphate analysis is that of Denigès as applied to sea water by Atkins (1923). The reagent blank, which includes colour due to impurities in the reagents, natural colour of the water and any colour due to slight reduction of molybdic acid in absence of phosphate, was evaluated as described by Cooper (1933, p. 715).

TABLE I. EFFECT OF COPPER ON SALT ERROR CORRECTION FACTOR.

Waters compared (D.W. = distilled water; S.W. = sea water)		Comparison by daylight in Hehner cylinders		Comparison with S72 filter in Pulfrich photometer	
		No. of Determinations	Mean Factor	No. of Determinations	Mean Factor
		2 ml. molybdate reagent/100 ml.			
D.W. + no added Cu	D.W. + 4 mg.-atom/m.^{3} added Cu	—	—	2	1·15
D.W. + no added Cu	S.W. + no added Cu	2	1·36	2	1·23
D.W. + no added Cu	S.W. + 4 mg.-atom/m.^{3} added Cu	—	—	1	1·25
D.W. + 4 mg.-atom/m.^{3} added Cu	S.W. + 4 mg.-atom/m.^{3} added Cu	1	1·25(?)	2	1·13
		1 ml. molybdate reagent/100 ml.			
D.W. + no added Cu	D.W. + 4 mg.-atom/m.^{3} added Cu	—	—	9	1·11
D.W. + no added Cu	S.W. + no added Cu	3	1·11	5	1·07
D.W. + no added Cu	S.W. + 4 mg.-atom/m.^{3} added Cu	—	—	4	1·23
D.W. + 4 mg.-atom/m.^{3} added Cu	S.W. + 4 mg.-atom/m.^{3} added Cu	2	1·10	8	1·10

In certain experiments the amount of acid molybdate was reduced from 2 to 1 ml. per 100 ml. of water (cf. Kalle 1935*b*; Tischer 1934). No attempt was made exactly to control temperature. In winter during the day the laboratory temperature ranged from 11 to 15° C. During the experiments of June 1936 it was 17° C. The acid ammonium molybdate reagent was prepared as described by Atkins (1923). The solution of stannous chloride was freshly made by dissolving 0·10–0·15 g. $SnCl_2.2H_2O$ in 25 ml. 4*N* hydrochloric acid. A solution made by dissolving metallic tin in hydrochloric acid in presence of a little copper sulphate (Atkins 1923) is equally effective.

One drop of the stannous chloride solution added to 100 ml. of water containing 0·5 mg.-atom/m.^{3} P (15 mg./m.^{3} P) gives a sixfold excess of stannous ions. Stronger solutions of phosphate require more stannous chloride but the same amount must be added to standards as well. If there should be any doubt as to whether sufficient stannous chloride has been added, the increment of colour due to, say, 0·3 mg.-atom/m.^{3} P should be determined.

Direct visual comparison was usually made in Hehner cylinders 20 cm. high. In work with the Pulfrich photometer, absorption tubes 15 cm. long and holding about 90 ml. of liquid were used in conjunction with the red S72 filter. This shows maximum absorption above 700 mμ. (see Cooper and Milne, 1938, Fig. 1).

TABLE II. SALT ERROR CORRECTION FACTOR FOR PHOSPHATE IN SEA WATER UNDER DIFFERENT CONDITIONS OF DETERMINATION

Comparison by daylight in Hehner cylinders		Comparison in Pulfrich photometer with S72 filter	
Date	Factor	Date	Factor
I. Using 1 ml. of molybdate reagent per 100 ml. of water.			
(*a*) No copper added to either sea water or standard.			
June 1934*a*	1·11	Jan. 1936*a*	1.05
June 1934*b*	1·12	Jan. 1936*b*	1·09
March 1936	1·09	June 1936	1·13
Jan. 1938	1·15	Sept. 1936	(1·00?)
Feb. 1938	1·17	Jan. 1937	1·13
		Jan. 1938	1·11*
Mean	1·13		1·11
(*b*) 0·4 ml. *M*/1000 CuSO$_4$ added to sea water and standards.			
March 1936	1·09	Jan. 1936	1·13
Dec. 1937	1·10	Sept. 1936	1·04
		Jan. 1937	1·10
		Dec. 1937	1·10
Mean	1·10		1·10
II. Using 2 ml. of molybdate reagent per 100 ml. of water.			
No copper added to either sea water or standard.			
March 1936	1·37	June 1936	1·23
Feb. 1938	1·35	Jan. 1937	1·22
Mean	1·36		1·22

* Result of an experiment with extensive cross-checks and controls; has been given the weight of four experiments.

In Tables I and II are collected determinations of the correction factor for salt error in sea water under different experimental conditions; in Table III may be found those by other workers.

When 1 ml. of molybdate reagent is used per 100 ml. of water the method of comparison is immaterial. The correction factor, 1·12, has been adopted for all the writer's determinations with 1 ml. molybdate per 100 ml. of water, no matter whether comparison had been made by direct comparison of the blue colour in Hehner cylinders or by means of the red S72 filter in the Pulfrich photometer, or whether or not extra copper had been added to both sea water and standards.

However, when double the concentration of reagent is used (2 : 100, as in Atkins' original method), the correction factor is considerably greater for comparison by daylight (1·35) than when a red filter is used in some kind of photometer (1·19). It is evident that the spectral composition of the blue colour differs somewhat according to the amount of reagent used. The factor 1·35 has been adopted for correcting all direct visual determinations made by Atkins and the writer, using 2 ml. of molybdate reagent per 100 ml. of water.

TABLE III. CORRECTION FACTOR FOR SALT ERROR FOR SEA WATER OF 35 ‰ SALINITY

Method	Author	Factor
(a) When 2 ml. of acid molybdate reagent is used per 100 ml. of sea water.		Factor (a)
Spectrophotometer with filters having maxima at 660 and 684 mμ	Buch (1929)	1·17*
Photoelectric colorimeter; 650 mμ	Brambel & Clowes (1937)	1·17†
Pulfrich Photometer and S72 filter	Robinson & Wirth (1935)	1·15
,, ,, ,,	Cooper (this paper)	1·22
Mean of measurements with filters		1·18
Comparison by daylight	Ibañez	1·29‡
,, ,, ,,	Brujewicz & Krasnowa (1933)	1·35
,, ,, ,,	Redfield, Smith & Ketchum (1937)	1·35
,, ,, ,,	Cooper (this paper)	1·36
,, ,, ,,	Igelsrud, Robinson & Thompson (1936)	1·25§
(b) When 1 ml. of acid molybdate reagent is used per 100 ml. of sea water.		Factor (b)
Pulfrich photometer and S72 filter	Kalle (1934)	1·13
,, ,, ,, ,,	Cooper (this paper)	1·11
Mean of measurements with filters		1·12
Comparison by daylight	Cooper (this paper)	1·13

* Buch found that the salt error varied with the concentration of phosphate. The figure given is taken from his Tables and graphs for amounts of phosphate up to about 1 mg.-atom/m.^{3} P.

† From graph.

‡ For waters containing less than 1·1 mg.-atom/m.^{3} P.

§ For water of 29 ‰ salinity.

Small variations in these factors arise from variations in the concentration of stannous chloride and in temperature. The correction factor must not be assumed to be a true constant. It is desirable therefore that each worker should establish the factor afresh for the precise conditions applying to his own work.

There is some evidence (Table I) that, when 2 ml. of molybdate reagent is used per 100 ml. the presence of copper (*ca.* 200 mg./m.^{3}) affects differentially the development of colour in distilled water standards and in sea water. In presence of copper the salt error factor for comparison by daylight may be about 1·25, but this figure is the result of one determination only.

Analyses here are now carried out by the procedure described by Wattenberg (1937), except that only 0·05 or 0·10 g. of stannous chloride dissolved in 25 ml. 4*N* hydrochloric acid is used since hydrolysis is thereby more completely suppressed. They are invariably made within 24 hours of collection.

SUMMARY

The yellowing which may occur during phosphate determinations in sea water is attributed to hydrolytic products of complex molybdenum halides.

When 1 ml. of the usual acid molybdate reagent is used per 100 ml. of water, addition of copper as recommended by Kalle reduces the development of colour in sea water samples and in distilled water standards to the same extent. The correction factor 1·12 applies to comparison by daylight in Hehner cylinders and to photometric determinations with a red filter.

When 2 ml. of reagent is used per 100 ml. of water, the factor depends on the method of comparison. With comparison by daylight in Hehner cylinders it is 1·35, whereas if a photometer with a red filter is used it is only 1·19.

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APPENDIX

On 13 April 1938, after this paper had been prepared, a fresh batch of acid molybdate reagent was made up. Using 1 ml. of this per 100 ml. of water, the salt error correction factor was found to be 1·39 instead of 1·12 as anticipated. Moreover the factor decreased with time:

April 14	1·39
April 19	1·33
May 13	1·29
June 8	1·29
July 24	1·25.

To remove a slight yellow tint, the 50% (by volume) sulphuric acid had been treated with a few drops of *N*/10 permanganate as suggested by Kalle (1934) (0·4 mg. Mn per litre of acid molybdate reagent). The resulting manganous salt, although very small, provided a possible explanation of the anomalous correction factor. To test this view, two fresh 400 ml. batches of acid molybdate reagent were prepared on July 28, one treated with permanganate as above, the other not. The same samples of ammonium molybdate and sulphuric acid were used as in April. The salt error correction factor, determined by direct visual comparison in Hehner cylinders, was, in each case, 1·11, in agreement with the value established on p. 176. The anomalous factor cannot therefore be attributed to the presence of manganese. Further search for the cause of the anomaly has not been made but, nevertheless, this experience emphasizes the need for care if accurate results are to be had.

REDEFINITION OF THE ANOMALY OF THE NITRATE-PHOSPHATE RATIO

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The paper on the ratio of nitrogen to phosphorus in the sea (Cooper, 1937) was written before it was realized that in phosphate determinations, using *two* ml. of molybdate reagent per 100 ml. of water, the magnitude of the salt error correction factor is changed by the use of a spectral filter. Due to the resulting uncertainty it was felt better to use uncorrected figures for phosphate content rather than to risk a correction which might later prove to be wrong. We now know (Cooper, 1938) that the factor, 1·35, can be applied to all Plymouth data given in the 1937 paper and presumably to the results of the *Dana* and *Discovery II* there cited. The ideal ratio of 20 : 1, for nitrate-N/phosphate-P expressed as milligram-atoms, therefore becomes 20 : 1·35 = 14·8, or, say, 15 : 1. Most of Redfield's figures are probably amenable to the same correction. The revised nitrate-N/phosphate-P ratio agrees even better with the mean ratio of the thirteen sets of nitrogen and phosphorus analyses of plankton taken off Plymouth, viz. 16·3.

I suggest therefore that the "anomaly of the nitrate-phosphate ratio" be redefined as the amount by which the nitrate-phosphate ratio differs from fifteen, each salt being expressed in milligram-atoms and phosphate being corrected for salt error by the appropriate factor (see Cooper, 1938).

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PHOSPHATE IN THE ENGLISH CHANNEL, 1933–8, WITH A COMPARISON WITH EARLIER YEARS, 1916 AND 1923–32

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(Text-fig. 1)

Continued observations of dissolved inorganic phosphate at International Hydrographic Station E 1, 22 miles S. 37° W. from Plymouth, started by Atkins in 1923, support the accepted picture of the seasonal cycle (Matthews, 1917; Atkins, 1923–30; Harvey, 1928, 1934; Cooper, 1933*a*, *c*; Harvey *et al.*, 1935), but fresh points of interest have emerged, their significance lying in the contrast they offer to earlier years. Difficulties due to the uncertainty as to the salt error have now been overcome (Cooper, 1938).

Numerical records for phosphate have not been published for 1930, 1931, 1933 and 1937 whilst the results for January to April 9 1934, given in the *Bulletin Hydrographique*, have been corrected by too low a factor. Those for April 20–December 1934 and for 1935 and 1936 in that *Bulletin* are correct.

There is a strong case for publishing nutrient salt results in terms of the milligram-atom of the element concerned (Cooper, 1933*d*; Carter, Moberg, Skogsberg & Thompson, 1933), and this has been endorsed by a subcommittee of the International Council. The milligram-atom of phosphorus per cubic metre corrected for salt error has therefore been adopted as the unit of measurement for this paper and for future work here. To facilitate comparison all my results since 1930 for Station E 1 expressed in this unit are brought together in Table I. Each is corrected by the salt error factor appropriate to the conditions of analysis (Cooper, 1938). In 1938 and sometimes in earlier years, the factor has been accurately determined at the time of analysis. There must always be a little uncertainty unless the factors are so determined since they are not true constants. Records for Station E 2 are similarly presented in Table II.

The salt error correction factor for all Atkins' (1923, 1925, 1926, 1928, 1930) phosphate results is 1·35 so that, to convert these to mg.-atoms P per cubic metre corrected for salt error, it is necessary to multiply by $1{\cdot}35/71 = 0{\cdot}0190$.

To compare production of phytoplankton for different years, as deduced from phosphate records, Table III has been prepared to show the average content of the water column down to 20 m. (including the region of active photo-synthesis) and down to the bottom at 70 m. for every cruise to E 1 between March 1923 and August 1938. Furthermore, to establish whether

TABLE I. COMPLETE PHOSPHATE RECORDS AT STATION E 1 AUGUST 1930 TO AUGUST 1938; MG.-ATOM/M.³ P

All corrected for salt error.

Depth	1930					1931								
m.	12/8	10/9	9/10	11/11	4/12	13/1	4/2	19/2	23/3	7/4	22/4	18/5	10/7	26/8
0	0·10	0·00	0·33	0·50	0·53	0·53	0·58	0·46	0·25	0·42	0·23	0·11	0·07	0·03
5	0·06	0·00	...	...	...	...	...	...	0·21	0·28	0·17	0·11	0·07	0·04
10	0·05	0·05	...	...	...	...	...	...	0·26	0·24	0·18	0·14	0·08	0·08
15	...	0·18	...	...	...	...	...	...	...	...	0·20	...	0·09	0·04
20	0·13	0·18	...	...	...	...	...	...	...	...	...	...	0·12	...
25	0·24	0·20	0·27	0·51	0·48	0·48	0·49	0·49	0·25	0·25	0·19	0·13	0·15	0·04*
50	...	...	...	0·52	0·51	0·48	0·38	0·39	0·23	0·24	0·17	0·11	0·14	0·07
70†	0·23	0·20	0·33	0·48	0·60	0·49	0·40	0·47	0·26	0·25	0·16	0·10	0·17	0·07

Depth	1931					1932‡							1933	
m.	8/9	25/9	20/10	30/11	31/12	28/1	15/6	16/8	12/9	27/10	15/11	20/12	11/1	14/2
0	0·16	0·19	0·19	0·31	0·39	0·46	0·24	0·00	0·00	0·46	0·41	0·42	0·54	0·46
5	0·17	0·19	0·19	0·44	0·43	0·45	0·02	0·00	0·08	...	0·42	0·44	0·55	0·46
10	...	...	...	...	...	...	...	...	...	...	...	...	...	...
15	0·17	0·19	...	...	...	...	0·10	0·00	0·09	...	...	...	...	...
20	...	...	...	...	...	...	...	...	...	...	...	...	...	...
25	0·18	0·17	0·20	0·44	0·43	0·47	0·10	0·05	0·22	...	0·42	0·47	0·55	0·46
50	0·19	0·16	0·20	0·47	0·43	0·48	...	0·03	0·22	...	0·40	0·50	0·51	0·48
70†	0·26	0·20	0·18	0·45	0·43	0·46	0·24	...	0·28	...	0·42	0·57	0·51	0·48

Depth	1933									1934				
m.	13/3	4/4	11/5	18/7§	9/8	19/9	23/10	15/11	15/12	22/1	12/2	20/3	1/5	30/5‖
0	0·31	0·31	0·02	0·00	0·00	0·16	0·17	0·28	0·48	0·36	0·32	0·39	0·09	0·13
5	...	0·30	0·08	0·02	0·02	0·32	0·18	0·26	0·48	0·36	0·36	0·38	0·08	0·05
10	0·40	0·29	...	0·02	...	0·21	...	...	...	...	...	...	...	...
15	...	0·33	0·14	0·03	0·04	0·17	...	...	...	...	...	...	0·20	...
20	...	...	...	0·02	...	...	...	...	...	...	...	...	...	...
25	0·42	0·33	0·19	0·03	0·05	0·21	0·18	0·28	0·48	0·36	0·35	0·39	0·21	0·20
50	0·44	0·38	...	0·14	0·04	0·34	0·17	0·27	0·48	0·38	0·35	0·41	0·20	...
70†	0·48	0·35	0·22	0·15	0·06	0·33	0·23	0·27	0·48	0·38	0·35	0·39	0·21	0·20

Depth	1934						1935							
m.	9/7	15/8	21/9	18/10	14/11	20/12	15/1	26/2	22/3	2/5	4/7	8/8	16/10	21/11
0	0·00	0·00	0·09	0·21	0·23	0·35	0·41	0·44	0·54	...	0·07	0·02	0·20	0·43
5	0·03	0·00	0·09	0·21	0·26	0·33	0·41	0·44	0·39	0·11	0·06	0·03	...	...
10	...	...	...	...	...	...	...	...	...	...	...	...	...	...
15	0·14	0·00	...	...	...	...	...	...	...	...	0·07	0·12	0·25	0·41
20	...	...	...	...	...	...	...	...	...	...	...	...	...	...
25	0·13	0·19	0·10	0·22	0·24	0·33	0·43	0·42	0·42	0·24	0·13	0·15	0·25	0·41
50	0·16	0·19	0·24	0·19	0·24	0·33	0·42	0·42	0·37	0·25	0·23	0·16	0·25	0·41
70†	0·25	0·21	0·27	0·18	0·24	0·33	0·42	0·41	0·37	0·25	0·25	0·16	0·25	0·41

Depth	1935	1936								1937					
m.	13/12	23/1	10/3	28/4	12/5	18/6	22/7¶	30/9		14/1	18/2	19/5	17/6	22/7	21/9
0	0·45	0·58	0·24	0·10	0·29	0·07	0·06	0·13		0·48	0·47	0·05	0·03	0·05	0·10
5	0·45	0·44	0·22	0·10	0·05	0·01	0·06	0·14		0·49	0·48	0·00	0·04	0·05	0·10
10	...	...	...	...	...	...	0·07	...		...	...	...	...	...	...
15	...	0·46	0·22	0·13	0·18	0·05	...	...		...	...	0·06	0·05	0·06	0·10
20	...	...	...	...	...	...	...	...		...	...	...	...	...	...
25	0·46	0·47	0·31	0·19	0·22	0·10	0·24	0·25		0·47	0·49	0·10	0·22	0·30	0·13
50	0·46	0·47	0·41	0·24	0·27	0·26	0·24	0·34		0·49	0·49	0·26	0·28	0·33	0·26
70†	0·46	0·48	0·43	0·20	0·27	0·26	0·24	0·34		0·48	0·49	0·28	0·28	0·35	0·26

Depth	1937		1938								
m.	14/10	8/12	24/1	22/2	29/3	14/4	18/4	13/5	8/6	24/7	12/8
0	0·21	0·39	0·52	0·46	0·35	0·25	0·17	††	0·22	0·05	0·00
5	0·24	0·38	(0·66?)	0·46	0·30	0·26	0·15	0·22	0·06	0·04	0·00
10	...	...	...	...	...	...	...	...	...	0·06	...
15	0·21	...	...	0·46	...	0·26	...	0·19	0·09	0·04	0·01
20	...	...	...	...	...	...	...	0·19	...	0·09	...
25	0·21	0·38	0·45	0·49	0·41	0·28	0·17	0·29	0·11	0·12	0·04
50	0·21	0·39	0·45	0·48	0·42	0·32	0·18	0·24	0·20	0·26	0·18
70†	0·21	0·37	0·47	0·44	0·45	0·30	0·18	0·24	0·20	0·26	0·18

* 35 m., 0·04.
† Samples from 2–4 m. above the bottom.
‡ Interval February–May due to illness.
§ Station L 6.
‖ Station L 6, bottom sample at 55 m.
¶ Near E 1, 11 miles S.W. × W. of Eddystone.
†† See Table X.

any particular year was early or late, the maximum, minimum and average values that have been found for each of the twelve calendar months between March 1923 and February 1938 have been set out in Table IV. The differences between the averages for any two spring months gives the average monthly consumption at that time. It will be seen that by April, on an average, half of the year's supply of phosphate has been used up.

TABLE II. COMPLETE PHOSPHATE RECORDS AT STATION E 2, 1930 TO 1936. MG.-ATOM/M.^{3} P

All corrected for salt error.

Depth	1930	1931				1932	1933			1934				1935				1936
m.	9/10	4/2	22/4	26/8	30/11	15/11	14/2	9/8	13/11	12/2*	1/5	15/8	14/11	26/2*	2/5	4/7	21/11	12/5
0	0·42	0·42	0·58	0·01	0·27	0·50	0·36	0·00	0·52	0·52	0·22	0·00	0·25	0·39	...	0·00	0·37	0·11
5	...	...	0·34	0·02	0·38	0·50	0·36	0·00	0·53	...	0·27	0·00	0·27	0·40	0·32	0·02	...	0·10
10	...	...	0·33	0·04	...	...	...	...	...	...	...	...	...	...	...	...	...	...
15	...	...	0·29	0·04	...	...	...	0·00	...	...	0·27	0·00	...	...	...	...	0·37	0·12
25	...	0·40	0·30	0·05†	0·50	0·51	0·37	0·27	0·52	0·45	0·27	0·37	0·27	0·41	0·35	0·29	0·37	0·13
50	...	0·46	0·34	0·13	0·48	...	0·37	0·27	0·48	0·43	0·26	0·33	0·30	0·43	0·36	0·31	0·37	0·17
70–75	...	0·60	...	0·16	...	0·51	...	0·29	...	...	...	...	...	...	...	...	...	...
80–90	0·44	0·52	0·34	0·18	0·50	0·50	0·40	0·29	0·52	0·40	0·28	0·37	0·31	0·42	0·37	0·31	0·37	0·17

* Midway E 1–E 2; 33 miles S.W. of Eddystone. † 35 m., 0·05; 40 m., 0·07; 45 m., 0·13.

The consumption of phosphate as a measurement of plant production is affected by the length of time elapsing between two cruises. A more useful criterion of the intensity of an outburst is the consumption of phosphate per day (Fig. 1). Even here it should be recognized that the highest consumption may appear when cruises are very frequent (e.g. April 1938). Since a high intensity of production is unlikely to persist for a month or more, within that time a period of intense production may be partially masked by a preceding or following quiescent one. This comment applies with especial force in the years 1932 and 1937.

THE WINTER MAXIMUM OF PHOSPHATE

The maximum amount of phosphate is usually found at E 1 towards the end of December or beginning of January. This winter maximum is a measure of the amount of phosphate available for the following season's crop of phytoplankton and indirectly may control the survival of the larval planktonic stages of many marine animals.

Organically combined phosphorus, after allowing for the presence of arsenic, may amount to about 0·25 mg.-atom/m.^{3} (Cooper, 1937). There is evidence that organic phosphorus may become available fairly quickly (Cooper, 1935; Redfield, Smith & Ketchum, 1937; Seiwell & Seiwell, 1938). Since organic phosphorus is formed by the breakdown of living matter, at midwinter it is likely to be proportional to the inorganic phosphate available in a given area for plant growth. Deductions from records of the winter maximum of inorganic phosphate are therefore unlikely to be invalidated by vagaries of organic phosphorus.

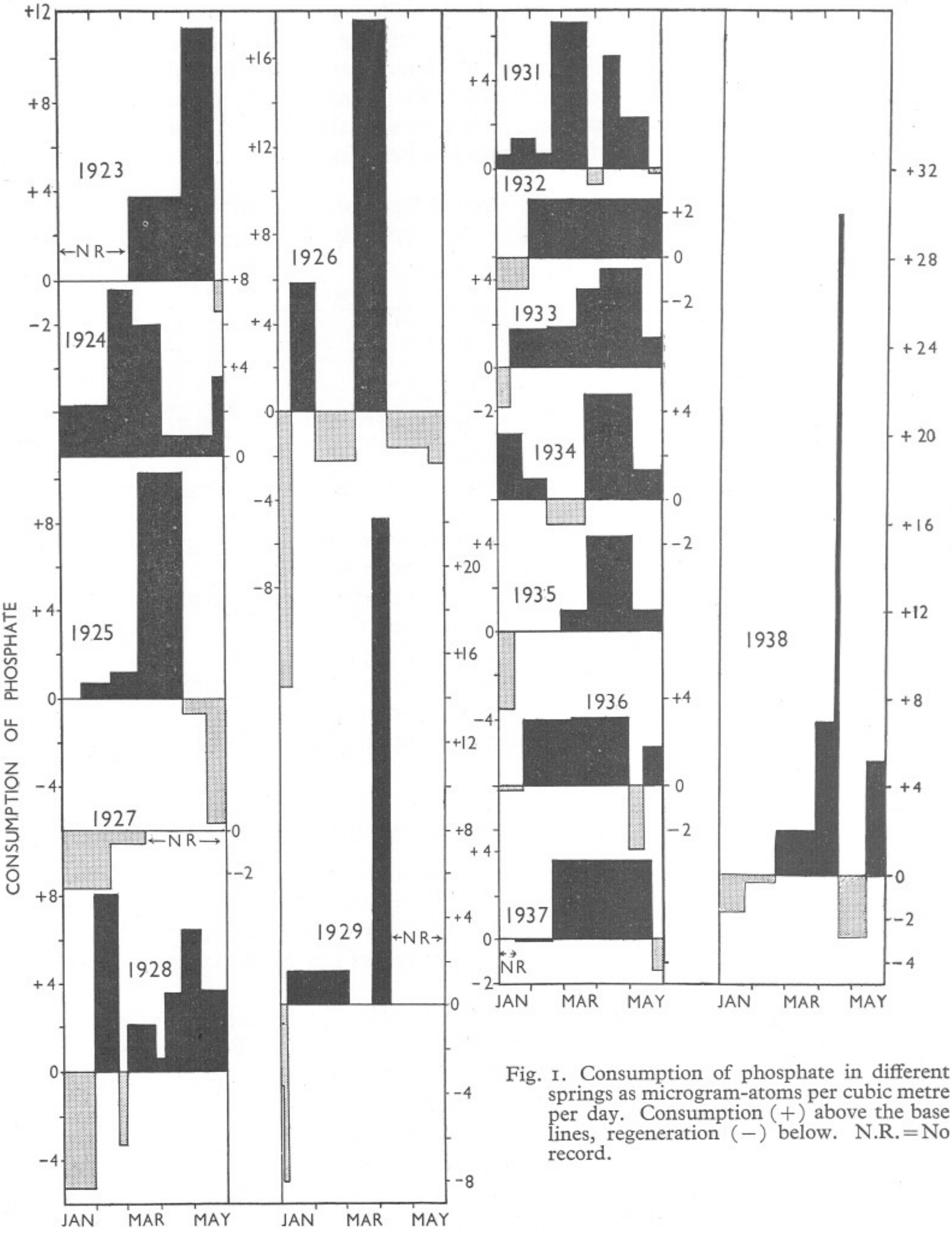

Fig. 1. Consumption of phosphate in different springs as microgram-atoms per cubic metre per day. Consumption (+) above the base lines, regeneration (−) below. N.R. = No record.

Table III. Average Phosphate Content between the Surface and 20 m. and between the Surface and Bottom at Station E 1

All corrected for salt error; mg.-atom/m.^{3} P.

	January			February			March			April			May			June		
	Day of month	0–20 m.	0–70 m.	Day of month	0–20 m.	0–70 m.	Day of month	0–20 m.	0–70 m.	Day of month	0–20 m.	0–70 m.	Day of month	0–20 m.	0–70 m.	Day of month	0–20 m.	0–70 m.
1923	...	...	...	...	...	...	7	0·70	0·71	24	0·49	0·53	22	0·14	0·21	19	0·09	0·25
1924	2	0·73	0·715	15	0·615	0·615	10	0·37	0·44	4	0·28	0·29	20	0·19	0·25	17	0·08	0·17
1925	19	0·59	0·61	17	0·59	0·59	14	0·56	0·56	22	0·05	0·16	13	0·09	0·175	3	0·13	0·30
1926	12*	0·76	0·76	3	0·63	0·63	11†	0·68	0·71	10†	0·19	0·18	17†	0·21	0·24	24	0·18	0·33
1927	...	...	...	15	0·53	0·53	21	0·53	0·55	...	...	...	...	...	...	...	...	...
1928	31	0·71	0·69	21	0·52	0·52	1	0·55	0·55	5	0·47	0·49	7	0·26	0·325	4	0·175	0·210
							27	0·49	0·495	19	0·44	0·44				13	0·09	0·17
1929	2	0·68	0·66	...	...	...	4	0·61	0·61	11	0·24	0·27	...	...	...	...	...	...
	7	0·715	0·70				26	0·51	0·61									
1930	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
1931	13	0·50	0·49	4	0·53	0·46	23	0·25	0·24	7	0·26	0·25	18	0·125	0·12	...	...	...
				19	0·475	0·45				22	0·19	0·18						
1932	28	0·46	0·47	...	...	...	...	...	...	...	...	...	...	...	...	15	0·09	0·135
1933	11	0·55	0·53	14	0·46	0·47	13	0·38	0·42	4	0·31	0·34	11	0·11	0·175	...	...	...
1934	22	0·36	0·37	12	0·35	0·35	20	0·385	0·39	...	...	...	1	0·14	0·19	...	...	...
1935	15	0·42	0·42	26	0·43	0·42	22	0·42	0·395	...	...	...	2	0·18	0·22	...	...	...
1936	23	0·47	0·47	...	...	...	10	0·23	0·23	28	0·12	0·18	12	0·15	0·22	18	0·04	0·155
1937	14	0·48	0·48	18	0·48	0·48	...	...	...	...	...	...	19	0·04	0·16	17	0·05	0·20
1938	24	0·48	0·46	22	0·46	0·47	29	0·34	0·40	14	0·26	0·29	13	c. 0·20	0·24	8	0·10	0·14
										18	0·16	0·17						

	July			August			September			October			November			December		
	Day of month	0–20 m.	0–70 m.	Day of month	0–20 m.	0–70 m.	Day of month	0–20 m.	0–70 m.	Day of month	0–20 m.	0–70 m.	Day of month	0–20 m.	0–70 m.	Day of month	0–20 m.	0–70 m.
1923	12	0·07	0·16	15	0·185	0·32	13	0·10	0·27	15	0·36	0·31	8	0·38	0·38	10	0·65	0·65
1924	9	0·09	0·19	7	0·06	0·20	3	0·28	0·34	1	0·25	0·28	12	0·37	0·38	9	0·615	0·615
1925	8	0·08	0·13	5	0·165	0·37	...	...	...	1	0·23	0·325	11	0·50	0·50	11	0·33	0·36
				31	0·05	0·09												
1926	8	0·115	0·20	16	0·03	0·195	22	0·06	0·16	19	0·35	0·35	24	0·495	0·49	14	0·52	0·54
																31	0·425	0·41
1927	...	...	...	...	...	...	...	...	...	...	...	...	4	0·38	0·44	9	0·59	0·59
1928	4	0·10	0·265	9	0·01	0·18	18	0·115	0·37	2	0·24	0·25	30	0·52	0·54	...	...	...
	11	0·06	0·27	16	0·12	0·23												
	23	0·03	0·20	29	0·20	0·30												
1929	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
1930	...	...	...	12	0·08	0·185	10	0·08	0·165	9	0·30	0·30	11	0·51	0·51	4	0·50	0·515
1931	10	0·075	0·13	26	0·05	0·06	8	0·17	0·19	20	0·195	0·195	30	0·43	0·445	31	0·425	0·43
							25	0·19	0·18									
1932	...	...	...	16	0·01	0·03	12	0·09	0·19	27	0·46	0·46	15	0·42	0·41	20	0·45	0·49
1933	18*	0·02	0·08	9	0·03	0·04	19	0·22	0·27	23	0·18	0·18	13	0·27	0·27	15	0·475	0·475
1934	9	0·08	0·14	15	0·00	0·14	21	0·09	0·18	18	0·21	0·20	14	0·25	0·24	20	0·33	0·33
1935	4	0·07	0·16	8	0·08	0·12	...	...	...	16	0·23	0·245	21	0·42	0·41	13	0·455	0·46
1936	22	0·09	0·20	...	...	...	30	0·17	0·27	...	...	...	...	...	...	...	...	...
1937	27	0·07	0·25	...	...	...	21	0·10	0·18	14	0·22	0·21	...	...	...	8	0·38	0·38
1938	24	0·05	0·17	12	0·02	0·09	...	...	...	...	...	...	...	...	...	...	...	...

* Station L 6. † All values in March, April and May 1926 may be high as the standard had deteriorated and the correction applied was only an approximation.

A fall in the winter maximum, from the level of earlier years of about 0·7 mg.-atom/m.^{3}, was noticed in 1930–1 and 1931–2. Since then it has remained within narrow limits—around 0·47 mg.-atom/m.^{3} (Table V).

The influx of warm saline Atlantic water into the English Channel in the autumn of 1921 and its marked effect on the climate of the south-west of England is well attested (Harvey, 1925). It is quite possible that this influx brought with it the relatively rich supply of nutrient salts which was found when the routine determinations of phosphate started in 1923. Atkins (1938) has suggested that the 1921 influx may be related to the remarkable maximum in the constant of solar radiation found by Abbot (1935) in the autumn of that year. Abbot has analysed his records of the solar constant and has found that the resulting periodicities, which are integral multiples or sub-multiples of 23 years, may be correlated with fluctuations in weather in different parts of the world. Such attempts to relate terrestrial weather to astronomical periodicities have occupied others, in particular, O. Pettersson (1914*a*, *b*). As to the shorter periods there is no general agreement but Pettersson has arrived at two long lunar periodicities of 92 and 111 years. Of these the first is an exact multiple of Abbot's 23-year period and the second is reasonably close to Abbot's period of $115 = 5 \times 23$ years. Since terrestrial weather appears to be the result of a large number of periodic astronomical functions closely interwoven, any speculative attempt to link up our results more closely with these would be premature. Meanwhile, it is essential that our routine determinations of phosphate shall be continued and that special attention be devoted to the autumn and winter of 1944–5 when a period of 23 years from the notable influx of 1921 will have elapsed.

TABLE IV. AVERAGE PHOSPHATE CONTENT OF WATER COLUMN

Showing the maximum, minimum and "normal" or mean values found between March 1923 and February 1938 at the International Hydrographic Station E 1; mg.-atom/m.^{3} P, corrected for salt error.

Month	No. of years for which data are available	Average content between 0 and 20 m.			Average content of whole water column (70 m.)		
		Max.	Min.	Normal	Max.	Min.	Normal
Winter max.	13	..	..	..	0·76	0·42	0·559
January	13	0·76	0·36	0·554	0·76	0·37	0·548
February	11	0·63	0·35	0·506	0·63	0·35	0·503
March	12	0·70	0·23	0·465	0·71	0·24	0·490
April	9	0·49	0·05	0·262	0·53	0·16	0·292
May	11	0·26	0·04	0·149	0·32	0·12	0·208
June	8	0·18	0·04	0·100	0·33	0·135	0·216
July	11	0·115	0·02	0·075	0·27	0·08	0·171
August	11	0·20	0·00	0·068	0·37	0·03	0·160
September	11	0·28	0·06	0·126	0·37	0·16	0·235
October	12	0·46	0·18	0·269	0·46	0·18	0·275
November	12	0·52	0·25	0·412	0·54	0·24	0·418
December	12	0·65	0·33	0·473	0·65	0·33	0·481

Evidence in support of the view that the English Channel was enriched with phosphate during the 1921 influx of Atlantic water may be found in Matthews' pioneer phosphate determinations in 1916–17 (Matthews, 1917). His control experiments suggest that the method is free from salt error and the results appear to be accurate to within ± 0·04 mg.-atom P/m.³ Due to war-time restrictions his samples were taken at the Knap Buoy which lies outside Plymouth Breakwater between stations L 2 and L 3. Admixture of estuarine water is liable to increase the amount of phosphate so that only waters having salinities greater than about 33·4 ‰ may be legitimately compared with station E 1. In 1916 on January 14, 18 and 24, he found respectively 0·45, 0·48 and 0·52 mg.-atom phosphate-P/m.³ In 1917 on January 10 the amount was somewhat higher, 0·62 mg.-atom P. In 1922, on February 12, when the winter maximum had almost certainly been passed, the Government Chemist using the same method found as much as 0·72 mg.-atom P (Atkins, 1923), agreeing closely with Atkins' own corrected analyses at that time and season. Our more recent records show that at midwinter, the phosphate content at stations L 2 and L 3, in waters more saline than 33·4 ‰, lies on an average about 0·05 mg.-atom P/m.³ higher than at E 1.

TABLE V. WINTER PHOSPHATE MAXIMA FOR WHOLE WATER COLUMN AT E 1

Calculated minimum production of phytoplankton and actual production of young fish.

					Minimum production of phytoplankton. Metric tons wet weight per sq. km. and depth of 72 m.		
Winter	Phosphate maximum, mg.-atom/m.³	Deviation from mean, mg.-atom/m.³	Percentage deviation from mean	Year	Between winter phosphate max. and May	Between winter phosphate max. and summer min.	Young fish summer spawners (Russell)
1921–22	> 0·65*	> +0·09	> +16	1922	..	..	..
1922–23	> 0·71†	> +0·15	> +27	1923	> 1700	> 1850	..
1923–24	0·71	+0·15	+27	1924	1600	1850	696
1924–25	0·61	+0·05	+ 9	1925	1500	1600	140
1925–26	0·76	+0·20	+36	1926	> 1750	> 2000	909
1926–27	0·55	−0·01	− 2	1927	..	..	170
1927–28	0·69	+0·13	+23	1928	1250	1750	..
1928–29	0·69	+0·13	+23	1929	> 1400	..	321
1929–30	..	..	..	1930	..	..	403
1930–31	0·52	−0·04	− 7	1931	1450	1650	230
1931–32	0·47	−0·09	−16	1932	1150	1500	197
1932–33	0·53	−0·03	− 5	1933	1200	1650	117
1933–34	0·48	−0·08	−14	1934	1000	1150	79
1934–35	0·42	−0·14	−25	1935	700	1000	37
1935–36	0·47	−0·09	−16	1936	800	1050	115
1936–37	0·48	−0·08	−14	1937	1100	1100	174
1937–38	0·47	−0·09	−16	1938	1050	1350	..
Mean 1923–24–1937–38	0·56	..	..	..	..	..	..

* March 1922 by Matthews' method.

† March 15 1923, 0·71 mg.-atom; maximum probably higher.

Although these investigations were the first to give even the right order of magnitude of the phosphate content of sea water, we may place considerable confidence in them. They suggest, firstly, that the phosphate content of the English Channel in 1916 and 1917 was similar to that in the 1930's and, secondly, that the increase took place between January 1917 and February 1922.

Table V shows also that in the winters of 1923–4 to 1928–9, the phosphate maximum averaged 0·67 mg.-atom/m.^{3}, whereas for the winters 1930–1 to 1937–8 it averaged only 0·48 mg.-atom. The high catches of young fish in the summer of 1930 suggest that the winter of 1929–30 was also one of high phosphate. The winter 1930–1 was therefore probably the first of low phosphate. Our results show a correlation with the direction of the residual current at the Varne lightship in the Straits of Dover (Carruthers, 1935). I am greatly indebted to Dr Carruthers for providing unpublished records required to bring the comparison up to date (Table VI). The records are arranged in order of decreasing easting of the current. In the four calendar years 1927–30 the average set of the current always lay between 25° and 40° east of north. In 1932–7, years of low phosphate, the average set lay between 8° west and 10° east of north. This comparison suggests that water of higher phosphate content is unlikely to work into the western end of the English Channel until the average residual current at the Varne lightship shows greater easting.

TABLE VI. COMPARISON BETWEEN WINTER PHOSPHATE MAXIMA AND REPRESENTATIVE DAILY WATER-FLOW PAST THE VARNE LIGHT VESSEL IN THE PRECEDING YEARS

			Phosphate maximum at E 1	
Year Jan.–Dec.	Residual current at Varne; miles per lunar day towards a true direction	Winter	mg.-atom/m.^{3}	Deviation from mean (%)
1927	3·1 N 40° E	1927–28	0·69	+33
1930	3·8 N 33° E	1930–31	0·52	0
1928	3·3 N 26° E	1928–29	0·69	+33
1929	3·2 N 25° E	1929–30	..	..
1931	3·2 N 18° E	1931–32	0·47	−10
1935	4·2 N 10° E	1935–36	0·47	−12
1936	4·1 N 9° E	1936–37	0·48	− 8
1934	3·9 N 7° E	1934–35	0·42	−19
1932	3·5 N 6° E	1932–33	0·53	+ 2
1937	3·5 N 6° E	1937–38	0·47	−10
1933	2·9 N 8° W	1933–34	0·48	− 8
		Mean*	0·52	..

* Mean of winters 1927–8–1937–8, except 1929–30 for which no records are available. This mean is not the same as that in Table V.

THE RELATION BETWEEN THE WINTER PHOSPHATE MAXIMA AND ABUNDANCE AND COMPOSITION OF PLANKTON AND YOUNG FISH

Russell (1935, 1936) has found that fluctuations in the phosphate content at E 1 are closely correlated with fluctuations in numbers and changes in composition of the plankton population. Broadly speaking water poor in phosphate as judged by the winter maximum, is characterized by the presence of *Sagitta setosa*, scarcity of all other holoplanktonic organisms, and poor production of the young of summer spawning fish. Water rich in phosphate is associated with *S. elegans* and other indicators of "Atlantic" water, a rich and varied zooplankton population and successful production of young fish. For a more detailed account of this topic Russell's papers must be consulted.

In any study of the impoverished state of the fisheries in the western end of the English Channel, the question of overfishing must take pride of place. If the intensity of fishing exceeds the natural recovery rate of the stock, the chemical and biological conditions governing that recovery rate are of lesser importance. Even so the evidence is growing ever stronger that the impoverishment, at least in part, may work back to the depletion of inorganic phosphate available in the first place for the growth of phytoplankton and ultimately for that of all animals living in our waters. As yet we are unable to say whether the richer conditions of the 1920's or the poorer ones of the 1930's are the more normal or whether both form part of some cyclical process which will recur. Even so it would appear that any considerable improvement in the fisheries is likely to be preceded, not only by a lesser intensity of fishing, but by an increase in the available inorganic phosphate and with predominance of *Sagitta elegans* over *S. setosa* in the western end of the Channel.

More detailed Comparison of the Years 1923 to 1937

The interval between the time of the winter maximum for phosphate and mid-May (Table III) covers the vernal outburst of diatoms and the consumption of phosphate is an index of the quantity of phytoplankton produced. The years may be grouped in order of productivity:

★★★★★	1923	1926		
★★★★	1924	1925	1929	1931
★★★	1928	1933		
★★	1932	1934	1937	1938
★	1935	1936		

In several of the earlier years much of the phosphate was used up in short periods of intensive plant production. Nevertheless 1932, 1934, 1937 and 1938 were probably poor survival years and 1935 and 1936 must have been exceptionally bad. In 1935 not only was the winter maximum the lowest on record but of this phosphate only 49 % was used between January and May, the lowest percentage utilization yet recorded. The entire consumption during these five months was considerably less than during several periods of a few weeks in earlier years. These conditions were mirrored in the exceedingly low production of young fish in that year, also the lowest recorded (see Table V).

Due no doubt to different degrees of vertical mixing in different years (cf. Atkins, 1930, p. 825), the percentage consumption of the total inorganic phosphate content of the water column fluctuates between 49 and 81 % for the spring period and between 63 and 93 % for the period between winter maximum and summer minimum. Although some phosphate may be regenerated and used more than once in one growing season, these fluctuations are probably highly significant. For example although the maximum in the winter 1930–1 was only 0·52 mg.-atom/m.³, the efficiency of phosphate utilization in the following spring and early summer was so high that the year 1931 is placed in the "four star" class in the list on p. 189. If other periods be studied in Table III similar variations will be found between the different years which may be of significance for the survival of young fish.

In 1931 (Cooper, 1933*b*) calculations of minimum crop production were made on the basis of the fall in several nutrient salts between the winter maximum and summer minimum at station E 1 (Table VII). The figure for phosphorus has now been corrected for salt error. The oxygen calculation is almost certainly too low and the nitrate-nitrogen took no account of other available forms of nitrogen such as ammonia. Such a calculation based on total inorganic nitrogen has been added to Table VII. Even this is rather uncertain since we know nothing of the amounts of urea, amino-acids and other simple organic nitrogen compounds which may quickly become available. The agreement is good and a figure of about 1650 metric tons for a water column one sq. kilometre in area and 72 m. deep seems representative. This was associated with a consumption of 0·46 mg.-atom P/m.³ (corrected). On this basis crop figures have been calculated for all the years for which data are available (Table V). A summarized account of phytoplankton production follows:

TABLE VII

1931 Between	On basis of change in	Phytoplankton produced, wet weight. Metric tons per sq. km. of surface for a depth of 72 m.
4/12 and 26/8	Phosphorus	1650
19/2 and 10/7	CO_2	1730
23/3 and 10/7	Nitrate-N (incl. nitrite-N)	1270
23/3 and 18/5	Total inorganic N	1350
19/2 and 26/8	O_2 lost to atmosphere	1000

PRODUCTION OF PHYTOPLANKTON 1923–38, AS DEDUCED SOLELY FROM NUTRIENT SALT DATA

(In this account "available phosphate" means the winter maximum available for the following year's production.)

1923 No data until March 7. Probably little production until then. Average consumption of phosphate during April. Very heavy consumption during May. A late year.

1924 Production started in January and continued steadily until June. Although definitely an early year, conditions were good throughout for the survival of young fish dependent on phytoplankton. The water was, however, very cold.

1925 Production was crowded into the 6 weeks between March 14 and April 22 when two-thirds of the available phosphate and also silica were consumed. Possibly a poor survival year for all organisms other than those able to use this concentrated production of diatoms. Much of this may have gone to waste.

1926 Three-quarters of the available phosphorus was used in the four weeks, March 11–April 10. In this period the consumption was greater than the total amounts available for use in the springs of 1932, 1934, 1935, 1936, 1937 and 1938 and equal to those of 1931 and 1933.

1927 A very late year. Regeneration of phosphate preponderated up to March 21 after which no phosphate data are available. Nitrate results show considerable production in April and May.

1928 "Early and late." Periods of strong production: January 31–February 21; March 27–April 5; April 19–May 5. The first two were periods of diatom production, the last one of *Phaeocystis* or other non-siliceous phytoplankton. The period February 21–March 27 was one of regeneration and conditions were then unfavourable.

1929 On the whole an average year. Although some production occurred between January 7 and March 4, the vernal outburst cannot be said to have got under way before March 26. In the fortnight following, one half of the available phosphate was consumed. Records cease on April 11. Such intense short period production as occurred in 1925, 1926 and 1929 is not likely to be of great value to the herbivores since these are thought to avoid dense growths of phytoplankton.

1930 No records.

1931 An early year. Production started in December and was well spread out. The month February 19–March 23 was the peak period during which 40 % of the available phosphate was used.

1932 Inadequate data.

1933 A late year but even so has much in common with 1931.

1934 "Early and late." Greatest production occurred in January and April. February and March were poor months.

1935 Very late and exceptionally poor. April was the only month with production of any consequence, consumption of phosphate being then about average. Not only was the initial stock of phosphate very low, but it was very inadequately used.

1936 A poor year. Some consumption of phosphate occurred throughout February, March and April.

1937 In mid-February no sign of any vernal outburst was apparent. No further records are available until mid-May when surface phosphate was nearly exhausted.

1938 A late year and poor; 25 % of the total phosphate was used up in four days, April 14–18, and 50 % during the first three weeks of April. This represented four-fifths of the spring minimum production.

N.B. All the years after 1930 are affected by the marked fall in the winter maximum for phosphate which took place about then.

Autumn Diatom Outbursts

In the late summer and autumn the chemical evidence is difficult to interpret owing to the uncertain balance between consumption by plants and regeneration from dead material. The evidence suggests that outbursts occurred as follows:

1923	August, September.
1924	September.
1925	August.
1926	None.
1927	(No records.)
1928	September (1st fortnight).
1929	(No records.)
1930	None.
1931	August?
1932	None.
1933	End September–mid-October.
1934	None.
1935	?
1936	?
1937	August?

THE SPRING OUTBURSTS AT STATIONS E 1 AND E 2

Attention has been drawn (Atkins, 1930; Cooper, 1933*a*) to the quite different behaviour of the water masses at these stations between the February and May cruises. Three further years' work has added more data which repay examination (Tables VIII and IX). In only one year has more phosphate been found in February at E 2 than at E 1 and in five out of nine years the amount has been much less. Either the spring outburst regularly starts earlier in the more southerly waters, or, equally regularly, Station E 2 is occupied by a body of water quite different from that at E 1. The salinities shed no light on this. However, when the February results are examined in conjunction with the next cruise in May, it is seen that for every year except 1934 production at E 1 has far outstripped that at E 2 (Table IX). For the nine years for which we have phosphate records, the mean production in the upper layers at E 1 was twice as great as that at E 2. It is difficult to allow for the different depths at the two stations but, if the calculations are based on the changes in the whole water column to the bottom, the same general picture emerges. There is probably

TABLE VIII. AVERAGE CONTENT OF WATER COLUMN BETWEEN THE SURFACE AND 20 M. DEPTH AT STATIONS E 1 AND E 2 IN FEBRUARY; MG.-ATOM/M.^{3} P

Date	E 1	E 2
4/2/31	0·53	0·41
12/2/34	0·35	0·48*
14/2/33	0·46	0·365
15/2/27	0·53	0·51
15/2/24	0·615	0·59
17/2/25	0·59	0·37
21/2/28	0·52	0·42
26/2/35	0·43	0·40*
Mean	0·50	0·44
Also 11/3/26	0·68	0·47

* Station midway E 1–E 2.

TABLE IX. FALL IN THE AVERAGE PHOSPHATE CONTENT OF THE WATER COLUMN BETWEEN THE SURFACE AND 20 M. DEPTH AT STATIONS E 1 AND E 2 BETWEEN THE FEBRUARY AND MAY CRUISES; MG.-ATOM/M.^{3} P

Year	Between cruises of	Fall at E 1	Fall at E 2
1929	Jan. 7–Mar. 26	0·20	0·17
1931	Feb. 4–Apr. 22	0·34	0·06
1934	Feb. 12–May 1	0·21	0·21
1924	Feb. 15–May 20	0·42	0·32
1925	Feb. 17–May 13	0·50	0·18
1928	Feb. 21–May 7	0·26	0·20
1935	Feb. 26–May 2	0·25	0·07
1923	Mar. 7–14–May 22–25	0·56	0·28
1926	Mar. 11–May 17	0·47	0·05
	Mean for nine years	0·36	0·17

more vertical mixing of the water in mid-Channel, but while this may tend to keep down multiplication of the diatoms in stormy weather, it should also help to bring up the bottom store of phosphate into the optimum photosynthetic zone. Cruises to E 2 were discontinued in 1936.

SURFACE REGENERATION OF PHOSPHATE

Atkins (1930) found large quantities of phosphate, up to 3 mg.-atom/m.^{3}, at the L series of stations on January 2 1929 and attributed them to regeneration of phosphorus from organic material at the surface. Supporting evidence for this view is set out in Table X which includes all occasions when the phosphate content of the surface water was at least 0·1 mg.-atom/m.^{3} greater than at 5 m.

TABLE X. SURFACE REGENERATION OF PHOSPHATE AT STATION E 1

Depth (m.)	2/1/29	23/1/36	31/1/28	1/3/28	21/3/27	22/3/34	7/4/31	12/5/36	13/5/38
0	0·91	0·58	0·82	0·63	0·78	0·54	0·42	0·58	*
5	0·64	0·44	0·67	0·49	0·51	0·39	0·28	0·44	0·22
Average 5–25	0·64	0·46	0·68	0·53	0·52	0·41	0·25	0·46	0·22

Depth (m.)	8/6/38	15/6/32	4/7/28	11/7/28	16/8/28	29/8/28	23/9/26	19/10/26	24/11/26
0	0·22	0·24	0·23	0·16	0·65	0·46	0·29	0·49	0·78
5	0·06	0·02	0·09	0·03	0·02	0·07	0·10	0·32	0·46
Average 5–25	0·09	0·06	0·08	0·05	0·10	0·21	0·09	0·32	0·48

* Triplicate analyses on three samples taken in one routine haul, 1·10, 1·10, 1·13; analysis on sample collected half an hour later, 0·44.

Occasionally, as in the four cruises in June and July, this might be attributed to the light at the surface being too intense for active photosynthesis, depletion of phosphate occurring at the optimum depth around 5 or 10 m. This explanation cannot hold at other seasons. On May 13 1938, analyses showed a large change in surface phosphate whilst the ship was drifting freely at Station E 1. Since this type of irregularity is confined to surface samples, contamination only of these is highly unlikely. The phenomenon is not confined to any one season of the year and appears to be independent of weather conditions. High surface phosphate values have been found following calm and stormy weather and with winds from all points of the compass. It is true that winds from the southerly and westerly quadrants have predominated, but these are the prevailing winds of the district. Regeneration of phosphate from decomposing floating organic material, as suggested by Atkins, provides the only reasonable explanation.

I am indebted to Dr H. W. Harvey for collecting the greater part of the water samples used in this work, also to Mr C. F. Hickling and Mr P. G. Corbin for some in 1937 and 1938.

Summary

At Station E 1, 22 sea miles south-west from Plymouth, the winter maximum for phosphate, representing the stock available for plant growth in the following spring, averaged 0·67 mg.-atom/$m.^3$ for the winters 1923–4 to 1928–9 and only 0·47 mg.-atom for 1930–1 to 1937–8. This fall in phosphate shows a close correlation with the abundance of summer-spawning young fish (Russell). Since water containing similar low phosphate appeared to occupy the English Channel in 1916 (Matthews), the inflow of warm Atlantic water in the autumn of 1921 may well have brought with it the relatively rich phosphate found in the 1920's.

The impoverishment of phosphate around 1930 runs parallel with a decrease in the easting of the residual current at the Varne lightship in the Straits of Dover (Carruthers).

On the basis of spring phosphate consumption, the years may be classified in order of productivity:

★★★★★	1923	1926		
★★★★	1924	1925	1929	1931
★★★	1928	1933		
★★	1932	1934	1937	1938
★	1935	1936		

The efficiency of utilization of the total stock of phosphate varies from year to year. In 1935 it was only 63 % whereas a much higher percentage, 93 %, placed 1931 in the four star class.

Between February and May, the phosphate consumption in the upper layers at E 1, averaged over nine years, is twice as great as that at E 2 in mid-Channel.

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THE DISTRIBUTION OF PHOSPHATES IN THE SOUTH-WESTERN AREA IN APRIL 1938

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(Text-fig. 1)

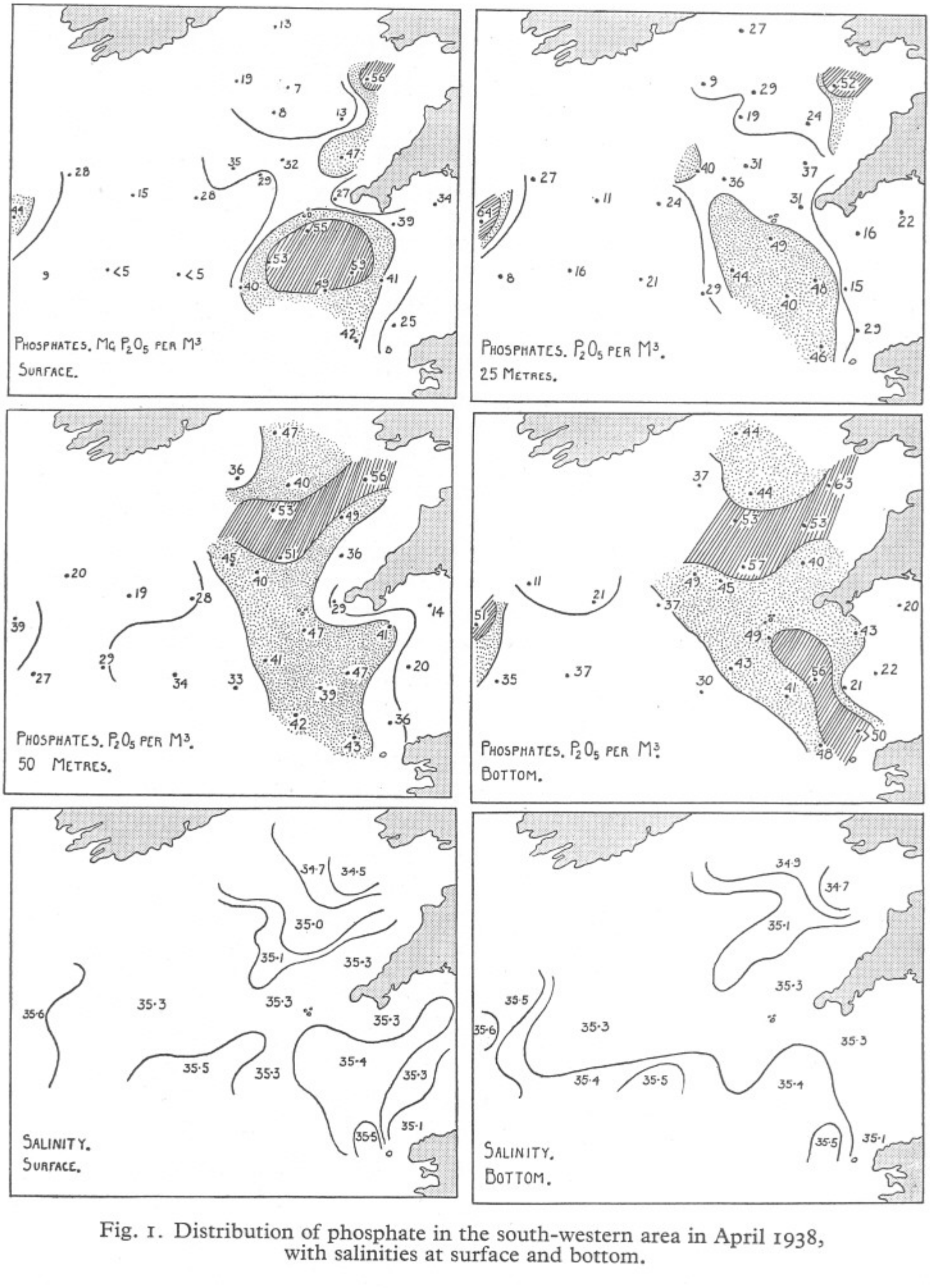
In April 1938 the Ministry of Agriculture and Fisheries research-vessel, *George Bligh*, surveyed, in connexion with a programme of mackerel research, a large area of sea in the western English Channel, St George's Channel, and to the west of Cornwall. The opportunity was taken of estimating the distribution of the phosphate in this area by means of the "Lowestoft Photometer". This instrument has been described by Graham (1936). In preparing the samples for use in the photometer, 3 c.c. of molybdate reagent were added to about 140 c.c. of the sample to be tested, and 4–6 drops of $SnCl_2$ solution.

In the first four charts in Fig. 1 are given the values of phosphate found at each station, at four depths, namely, at the surface, at 25, and 50 m., and at the bottom. The values are expressed as mg. P_2O_5 per cu. m., and have been raised by the factor 1·3 to allow for salt error. Contours have been inserted in the charts as follows: a hatched contour to include values greater than 50, a stippled contour to include values of from 40–50, and a contour to include values of 30–40 mg. per $m.^3$

No high degree of accuracy is claimed for these observations, for, as Graham points out, at high concentrations of phosphate the instrument is less reliable than at low concentrations; further, certain stations have been rejected because the instrument appeared to be faulty. There is, however, some internal evidence that the determinations are at least consistent, for when the itinerary of the ship brought her back into regions visited shortly before, the phosphate values were found to be in good agreement with those found previously.

The season in which the cruise was made was unfavourable for a survey of the distribution of the phosphates, for Cooper (1938) shows that, on an average, the consumption of phosphate by the phytoplankton has so far advanced, by April, that about half the year's supply has been used up. Nevertheless, in view of the scarcity of observations on the distribution of phosphates in the south-western area, it has been thought worth while to present the results obtained.

The charts show that, generally speaking, there was much more phosphate in the deeper water than at the surface. At the sea bottom, values greater than 30 mg. per cu. m. were found almost everywhere, whereas, at the surface, they



PHOSPHATES. MG P_2O_5 PER M^3
SURFACE.

PHOSPHATES. P_2O_5 PER M^3.
25 METRES.

PHOSPHATES. P_2O_5 PER M^3.
50 METRES.

PHOSPHATES. P_2O_5 PER M^3.
BOTTOM.

SALINITY.
SURFACE.

SALINITY.
BOTTOM.

Fig. 1. Distribution of phosphate in the south-western area in April 1938, with salinities at surface and bottom.

were restricted. But at all depths there were three regions where phosphate was especially abundant, namely, off the Bristol Channel, off the English Channel, and on the edge of the Continental Shelf west of Cornwall.

Variations in the distribution of phosphate in the sea are, of course, due not only to water movements, which may carry water rich in phosphate into regions poorer in phosphate, but also to the consumption and regeneration of phosphate *in situ* by living organisms. The first factor named may perhaps be traced, in the present data, by a comparison with the salinity of the water. In Fig. 1, in addition to the four charts of phosphate distribution, are given two charts showing the salinity at the surface and at the bottom.

A tongue of water of low salinity appeared to spread westwards from the Bristol Channel, and this tongue of low salinity is closely associated with the area rich in phosphate lying off the Bristol Channel. It may be that this phosphate-rich water was derived from the extensive watershed draining into the Bristol Channel. Kalle (1937) showed that the sea in the neighbourhood of the great rivers draining into the North Sea was rich in phosphate, and Graham (1938) shows that an area rich in phosphate may be associated with the drainage from the Thames, including, of course, the output of phosphates from the London sewage.

More saline water appeared to spread from the south across and into the English Channel, and also to be present on the edge of the Continental Shelf. Probably this more oceanic water carried with it a richer supply of phosphate, derived from the upwelling of deeper water, and would in part account for the areas richer in phosphate lying at the mouth of the English Channel, and at the edge of the Continental Shelf.

As to the biological factors affecting the distribution of the phosphate, these may be seen in the scarcity of phosphate in the surface water, as compared with the deeper water. Further, stations in certain regions were markedly rich in phytoplankton. This was, in many cases, shown by the colour and smell of the water, as well as by the observed presence of the larger diatoms in the reagent tubes. Through the kindness of Mr Corbin I have had a list of the stations at which phytoplankton was plentiful in the plankton catches; and it is clear that the area comparatively poor in phosphates, which lay between the richer areas off the English Channel and at the edge of the Continental Shelf, was an area in which the phytoplankton was developing rapidly.

SUMMARY

The results of a survey of the distribution of phosphates in the south-western area in April 1938 show that there were three regions exceptionally rich in phosphate. These regions appeared to be associated respectively with the outflow of the Bristol Channel, with the flow of more oceanic water across the entrance of the English Channel, and with upwelling of deeper water at the edge of the Continental Shelf.

The surface water was poorer in phosphate than the deeper water, and regions poorer in phosphate were in some cases associated with a crop of phytoplankton.

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SOME OBSERVATIONS OF THE HYDROLOGY AND PLANKTON OF THE NORTH SEA AND ENGLISH CHANNEL

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(Text-figs. 1–4)

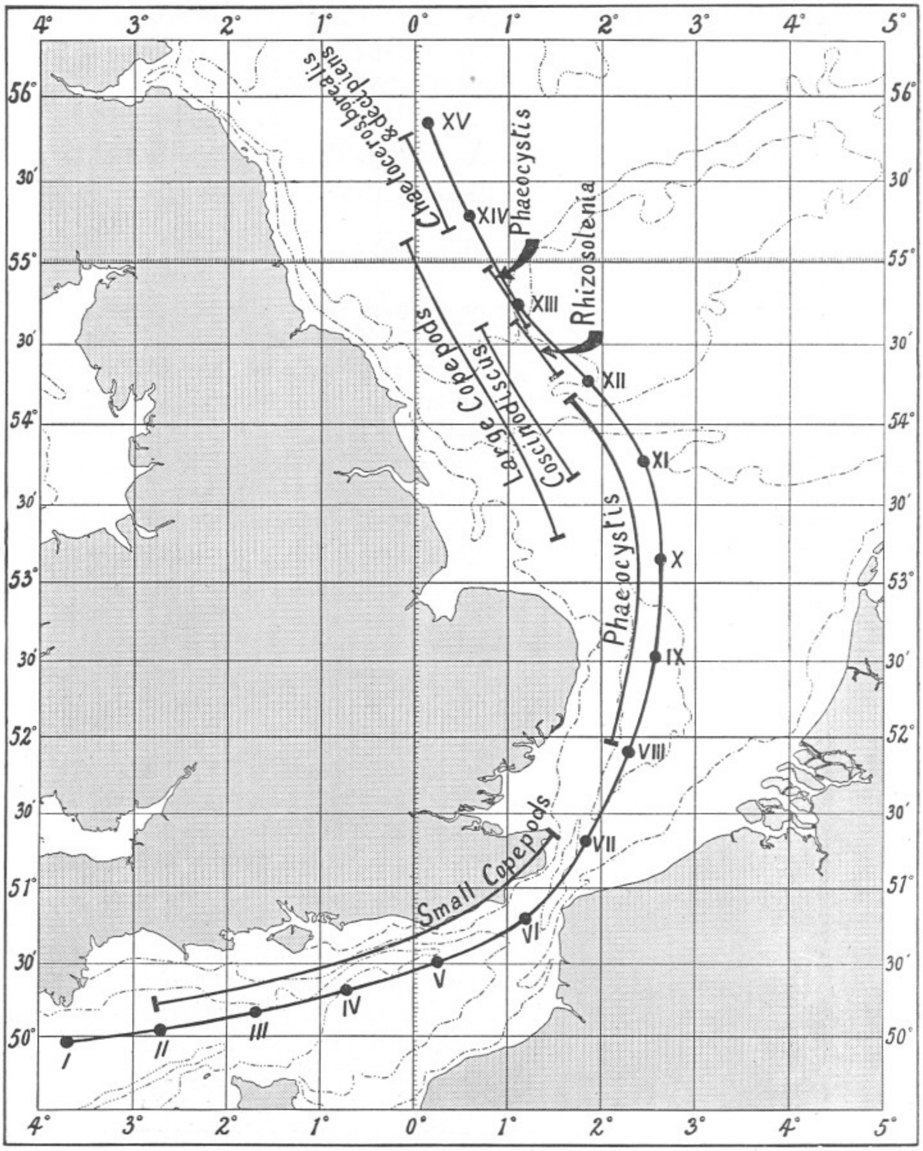
In April 1935 a vacant period in the programme of the research vessel *George Bligh* was occupied in determining the phosphate content of the waters of a selected line of stations in the North Sea and English Channel. The object was to extend the usual observations of phosphate in the North Sea, which form the subject of a separate paper (Graham, 1938), in the directions from which the southern North Sea receives its more oceanic water. It was thought in particular that observations between the southern North Sea and the area regularly examined from the laboratory at Plymouth would have an intrinsic interest. The distribution of the phosphate found in 1935 seemed to be of sufficient interest to warrant repetition of the experiment in 1936 and again in 1937.

Observations were made along the line drawn on the chart (Fig. 1). The positions marked I–XV on this chart correspond to the vertical lines I–XV in Figs. 2–4. The stations at which the observations were actually made lie near this line in positions indicated by circles in Figs. 2–4. The exact positions have been published in the *Bulletin Hydrographique* of the International Council for the cruises of the *George Bligh* April 26–30 1935, and May 13–18 1936, and will be published for the cruise April 8–15 1937.

Temperature, salinity and phosphate determinations were recorded at 10 m. intervals from surface to near bottom at each station, and samples of the plankton were taken with Hensen's net.

The phosphate content was determined in 1935 by the Atkins-Denigés method, as recommended by the conference which met in Oslo in 1928, recorded in the *Rapports et Procés-Verbaux des Réunions du Conseil International*, Vol. LIII, pp. 96–100. In 1936 and 1937 the phosphate was determined with the "Lowestoft Photometer" (Graham, 1936).

The season at which it was possible to do this work was not particularly suitable because the phosphate content of the water was changing rapidly near the spring outburst of diatoms. Nevertheless, certain features have been repeated. There is a tendency for areas of high phosphate content to be associated with extremes of salinity and temperature, and three sources of phosphate are recognized: (i) A trough of cool deep water connecting the


4°
3°
2°
1°
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4°
5°
56°
30'
55°
30'
54°
30'
53°
30'
52°
30'
51°
30'
50°
Chaetoceros borealis & decipiens
Phaeocystis
Rhizosolenia
Large Copepods
Coscinodiscus
Phaeocystis
Small Copepods
I
II
III
IV
V
VI
VII
VIII
IX
X
XI
XII
XIII
XIV
XV

Fig. 1.

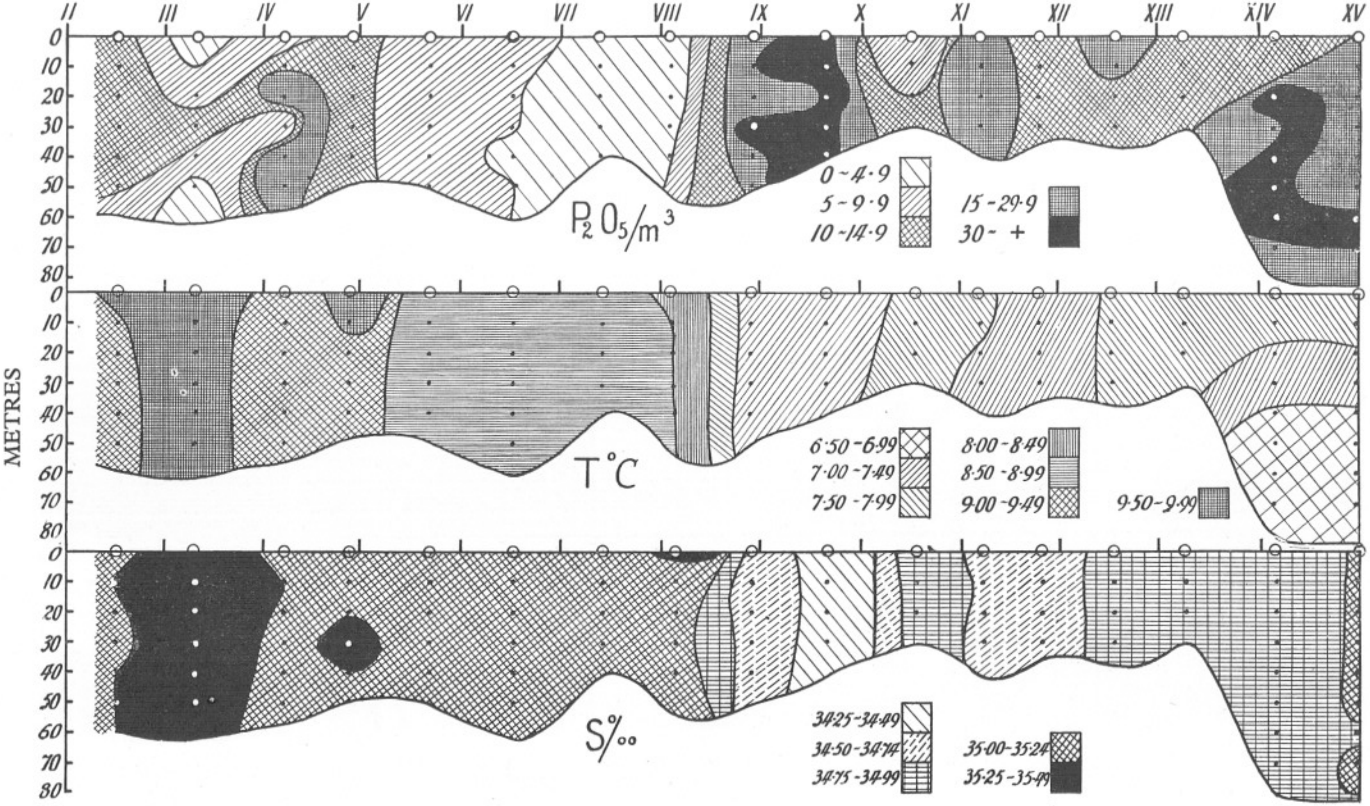
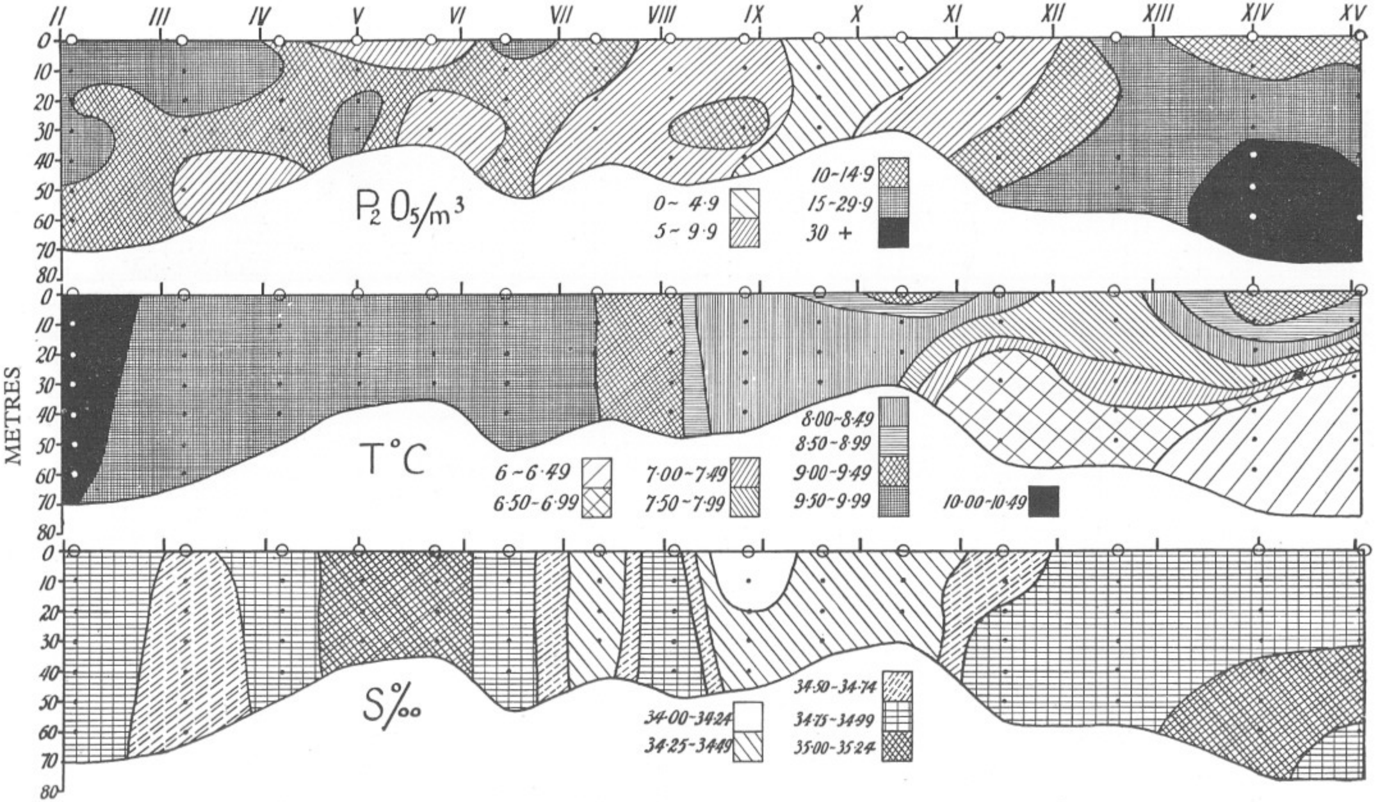

II
III
IV
V
VI
VII
VIII
IX
X
XI
XII
XIII
XIV
XV
METRES
0
10
20
30
40
50
60
70
80
P_2O_5/m^3
0 - 4·9
5 - 9·9
10 - 14·9
15 - 29·9
30 - +
T °C
6·50 - 6·99
7·00 - 7·49
7·50 - 7·99
8·00 - 8·49
8·50 - 8·99
9·00 - 9·49
9·50 - 9·99
S‰
34·25 - 34·49
34·50 - 34·74
34·75 - 34·99
35·00 - 35·24
35·25 - 35·49

Fig. 2. 1935.


II
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VII
VIII
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XI
XII
XIII
XIV
XV
METRES
0
10
20
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40
50
60
70
80
P2 O5/m3
0~ 4·9
5~ 9·9
10-14·9
15-29·9
30 +
T°C
6 ~6·49
6·50-6·99
7·00~7·49
7·50~7·99
8·00~8·49
8·50-8·99
9·00-9·49
9·50-9·99
10·00-10·49
S‰
34·00-34·24
34·25-34·49
34·50-34·74
34·75-34·99
35·00-35·24

Fig. 3. 1936.

southern North Sea with the more oceanic water of the northern North Sea, which was found to have a high phosphate content; (ii) Irregular areas of high phosphate content in the warmer Channel waters, which may be assumed to be oceanic in origin; and (iii) An area of low salinity about position IX, which was found to have a high phosphate content. This area was most pronounced in April 1935 and April 1937, and there was some indication of it in May 1936. The water here tended to be a little cooler than the surrounding water. The interpretation of these features is helped by the observations of other cruises. The high phosphate content of the northern part is ascribed to accumulation of phosphate under the thermocline, indications of which are present even at this early season. In the same way the high phosphate associated with low salinity in part of the southern North Sea is recognized as similar to areas of high phosphate found in other cruises and ascribed to the sewage of the River Thames. In regard to the Channel, the records from Plymouth for the International hydrographic station E 1 (Atkins, 1930; Cooper, 1933; and Harvey *et al.* 1935, and more recent records from the *Bulletin Hydrographique*) show that the phosphate near the bottom of this part of the Channel is rarely less than 10 mg. $P_2O_5/m.^3$ This condition is found to extend up the Channel but is lost near the Straits of Dover, where the water tends to

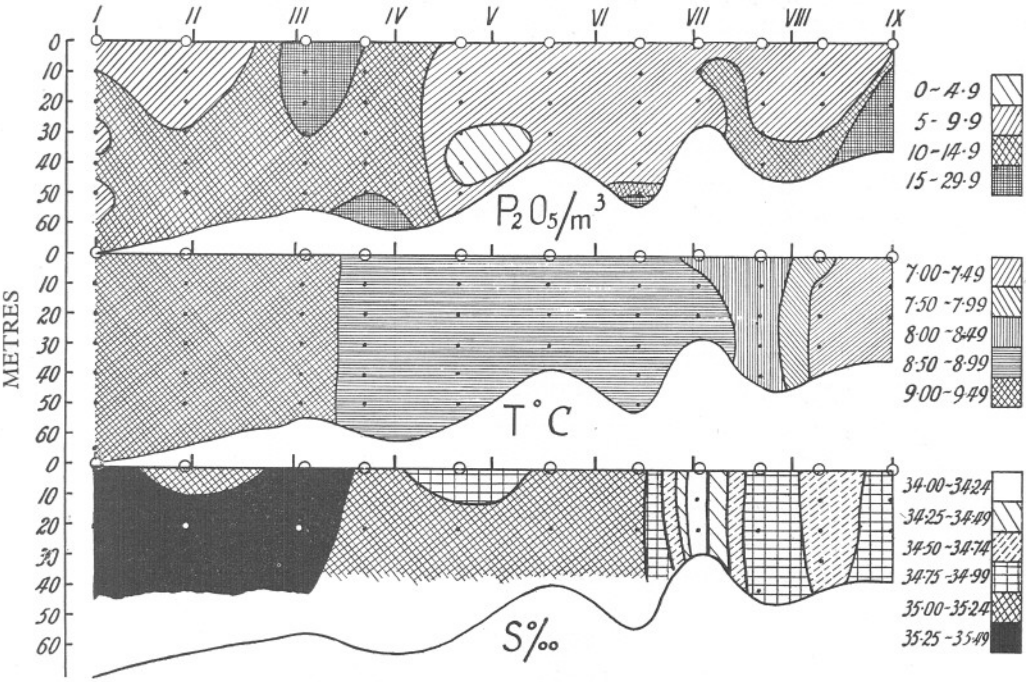

Fig. 4. 1937.

have very low concentration. There is no obvious explanation of why phosphate in the Channel does not reach the North Sea.

In regard to the larger plankton organisms that are taken in Hensen's net, the main features were also repeated in all three years. The distribution found in the 1935 Hensen samples is shown in Fig. 1. It is seen that the Channel, Southern Bight and the more northern part of the section have characteristic plankton populations. This distribution was repeated in 1936 and 1937 with the following modifications: in 1936, small copepods were found in the northern positions XI–XV as well as in the Channel positions II–VII. Small copepods were also found in all stations in 1937, but owing to pressure on the ship's time these stations did not extend farther north than position IX. *Phaeocystis* was found farther south in 1936 than in 1935 in positions V–XII, and in 1937 it was practically absent, traces only being found in position VIII. The area of large copepods was restricted to position XV in 1936, though it had extended as far south as position X in 1935.

SUMMARY

Phosphate, salinity and temperature records of waters of the North Sea and English Channel have been compared for April or May in the years 1935, 1936 and 1937, and the plankton distribution has been noted. Attention is called to the appearance of stability in certain features.

Thus, a high phosphate content was found to be associated with extremes of salinity and temperature, in similar areas in each year. The phosphate appears to be brought into the North Sea and Channel by oceanic water and by drainage from the land.

The plankton organisms were also similarly distributed in each year.

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THE DISAPPEARANCE OF *ZOSTERA MARINA*

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In his paper on "The autecology of *Zostera marina* in relation to its wasting disease", Tutin (1938) states that "In the British Isles the year 1931–2 showed a sunshine deficiency of about 20 % below normal, and no other year in the past ten showed a deficiency approaching this. The scanty figures available for other countries suggest that this unusual lack of sunshine was a general phenomenon, though in some countries it was less pronounced but of longer duration." His enquiries showed that about 1931 there was extensive mortality on the Atlantic coast of the U.S.A., though there was some evidence of a local decline in 1930. A year later, in 1932, *Zostera* had practically disappeared at Beaufort, North Carolina and as far north as Nova Scotia. In 1933 scarcity spread still farther northward to all localities in Canada. At Plymouth, England, the plant is believed to have begun to decrease towards the end of 1931. In § 6 of his summary Tutin writes: "It is suggested that the enfeeblement of the plant due to lack of sunshine in 1931–2 is the fundamental cause of the epidemic, and that recovery depends on the regeneration of the plant from seed and is therefore likely to proceed slowly."

It appeared desirable that this interesting suggestion should be tested by an extension of the examination of the meteorological records beyond ten years, as far as they go, namely back to 1897, and that the alleged 20 % deficiency should be checked. Accordingly, taking the sunshine normals as revised up to 1928, the amounts of sunshine received each year in each of the twelve districts of the British Isles were tabulated as percentages of the normal. As is customary mean values were obtained for the districts 1–10, namely excluding the north of Scotland (0) with adjacent islands, and the English Channel Islands (11). It appears unnecessary to give all the figures, especially as since 1928 such percentages have been published by the Meteorological Office on the 1928 basis, but the following comments may be made upon the records from 1897–1937 inclusive. The most striking thing in the series is the uniformity of the results. As regards low values, in 1898 Ireland S. had 81 % of its normal sunshine. In 1900 and 1902 England N.E. had 84 %, as had also Scotland E. in 1902. The year 1912 gave conspicuously low values, and averaged 83 % for the ten districts, Scotland E. and England N.E. showing 76 and 78 % respectively. In 1916 districts 0–4 inclusive showed 83–86 %. In 1920 England Midland, Scotland W. and Ireland S. had 84–86 %, and in 1924 Ireland S. had 84 %. In 1927 England M. had 82 %. In 1931, the year supposed to have been destructive for *Zostera*, England S.W. had 83 and England M. 85 %, both districts had 85 % in 1932 and England E.

had 85 %. In 1936 England S.W. had 85 % and in 1937 England E. had 84 %. There is obviously nothing very unusual in the low values which occurred in some districts in 1931 and 1932.

Turning to the high values, in 1899 England S.W. had 122 % of the normal sunshine with an average of 114, and in 1901 England N.W. had 119. England E. had 115 % in 1906 and England N.W. had 120 % in 1911, which averaged 115 %, the maximum average, followed by the minimum in 1912. England M. had 115 % in 1921 and England S.E. had 116 % in 1929 and 115 % in 1933.

Table I puts on record the values for the district including Plymouth, namely England S.W. and S. Wales, and the mean values for the ten British Isles districts as usually taken by the Meteorological Office. For neither are the low values of 1931–2 outstandingly low. They have been equalled or surpassed in earlier years.

TABLE I. PERCENTAGE OF NORMAL SUNSHINE

a, England S.W. and S. Wales (district No. 8) calculated on the normal value to 1928, namely 4·28 hr. a day.
b, The ten districts of the British Isles, calculated on the normal, 3·95 hr. a day.

	1897	1898	1899	1900	1901	1902	1903
a	106	109	122	111	111	97	98
b	104	97	114	100	111	93	94
	1904	1905	1906	1907	1908	1909	1910
a	99	101	110	98	102	109	98
b	99	104	111	98	99	104	97
	1911	1912	1913	1914	1915	1916	1917
a	118	81	91	104	101	96	99
b	115	83	91	104	102	89	98
	1918	1919	1920	1921	1922	1923	1924
a	104	105	85	111	97	95	89
b	100	103	90	111	98	96	91
	1925	1926	1927	1928	1929	1930	1931
a	105	93	91	99	113	90	83
b	101	94	93	101	109	95	89
	1932	1933	1934	1935	1936	1937	
a	85	107	100	97	85	88	
b	89	106	102	104	93	90	

Table II shows the normal values for the hours of sunshine for the ten districts and the corresponding percentages calculated with respect to the maximum, England S.E., and to the mean. The value for the north of Ireland 3·51 hr. is only 78 % of the maximum, and only 89 % of the mean. In spite of this *Zostera* formerly grew well in the north of Ireland, though a reduction of sunshine to 89 % of the mean is suggested as having been the cause of the fatal nature of the *Zostera* disease.

Furthermore, the illumination due to sunshine in the north of Ireland or of Scotland is on the average less than that in the south of England in which with a midsummer maximum solar altitude of 63°, for latitude 50°, the vertical component of the light from sun and sky is about 122 kilolux (Atkins, Ball & Poole, 1937); for the north of Ireland, around latitude 55°, the maximum altitude is 58°, so the illumination is about 117 kl., similarly with altitude 55° in the north of Scotland the maximum illumination is around 110 kl. This is to some extent offset by the longer duration of daylight during the summer, though the vertical illumination from a low angle sun is small. *Zostera* has been reported as growing (Börgesen, 1903) as far north as 61° 28′ N. in 2–4 m. of water in Vaagfjord in Syderö, the most southerly of the Faeröes. The mean sea temperature at the adjacent Thorshaven is 7·8° C. with minimum 5·4° and maximum 10·6°. No sunshine records are available for the Faeröes.

TABLE II. NORMAL SUNSHINE (1928) AND PERCENTAGES CALCULATED ON THE MAXIMUM AND MEAN VALUES

District	Hours	%	%
Scotland E.	3·63	81	92
England N.E.	3·93	87	100
England E.	4·32	96	109
England M.	3·82	85	97
England S.E.	**4·49**	100	114
Scotland W.	3·70	82	94
England N.W. and N. Wales	3·89	87	99
England S.W. and S. Wales	4·28	95	108
Ireland N.	*3·51*	78	89
Ireland S.	3·96	88	100
Mean	3·95	88	100

But the assumption that a greater duration of sunlight necessarily means a greater amount of light is not correct. It has been shown (Atkins, 1938) that though the relation usually holds over a year, it does not always do so, for the altitude of the sun when clear is of great importance. According to photo-electric measurements made at Plymouth the year 1931 stood third on the list of eight years 1930–7, as regards the amount of light received, and 1932 was almost identical with four of the other years. Furthermore, the radiation records at London show that in 1931 the amount received was not unusually low but rather above normal.

Finally, with a water plant, one has to consider the extinction coefficient of the water. In estuarine and coastal waters this is subject to large variations, from about 0·2 to 2·5 even in June, thus introducing more than a tenfold variation in the amount of light reaching the plants (Poole & Atkins, 1937; Cooper & Milne, 1938).

At Plymouth *Zostera* has been under observation since the opening of the laboratory, as it was always exhibited in one of the aquarium tanks. I am indebted to Dr E. J. Allen for the information that never within his 42 years' experience was there a scarcity of *Zostera* in any way comparable to the shortage of the last few years. There is certainly no ground for attributing its disappearance to any decrease in illumination leaving the plant, thus weakened, an easier prey to disease.

SUMMARY

The suggestion that the enfeeblement of *Zostera marina* due to lack of sunshine in 1931–2 is the fundamental cause of the epidemic is not supported by the meteorological data available from 1897 onwards, or by the known extinction coefficients of the water.

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A REVISION OF THE AMPHIPOD GENUS *BATHYPOREIA* LINDSTRÖM

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(Text-figs. 1–6)

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HISTORY OF THE GENUS

The genus *Bathyporeia* was established by Lindström (1855, p. 59) on specimens collected in the Baltic at Wisby and Landskrona. His description is based, apart from a reference to the epimera as small and beset with hairs, on the form of the appendages. He assigned to the genus one species, *pilosa*, in which the segments of the body are described as smooth, the form generally rounded, the eyes black, small and somewhat reniform, and the length under three lines. He gives a detailed description and drawing of the appendages. From the description of the antennae and of the eyes it may be assumed that the specimens were females.

Spence Bate in 1856 (p. 59), and again in 1857*a* (p. 146), unaware of Lindström's paper, described a new genus, *Thersites*, as follows: "The upper antennae with the second joint of the peduncle produced from the inferior side of the first. Second gnathopod terminating in a bush. Telson double." He assigned to the genus two species, namely, *guilliamsoniana* with "the inferior antenna as long again as the superior" and *pelagica* with "the inferior antenna six times as long as the superior". Thus Bate was describing a female specimen in *guilliamsoniana* and a male in *pelagica*. Later (1857*b*, p. 271) he pointed out that his genus *Thersites* lapsed in favour of *Bathy-*

poreia, and that his species *guilliamsoniana* was probably the same as the *pilosa* of Lindström.

In 1862 (p. 174) Bate gave more extensive descriptions of the two species *pilosa* and *pelagica*, based on imperfect specimens, and added a third species, *robertsoni*, based on imperfect male specimens obtained in February at Cumbrae from low-water pools. The distinction between *pelagica* and *robertsoni* is based mainly on the length of the flagellum of the antenna which in the former is "longer than the animal", and in the latter about "half as long as the animal", and in the diagram shown as having twenty-four articulations bearing calceoli. Bate and Westwood in 1863 (pp. 304–10) gave further descriptions of these three forms.

Stebbing (1875, p. 74), on an examination of living specimens from the north Wales coast and from the English Channel coast, came to the conclusion that all three of Bate's species were referable to one species, the *pilosa* of Lindström, with *pilosa* as the adult female, *pelagica* as the adult male and *robertsoni* as the young male. He collected specimens indiscriminately over the whole intertidal area; evidence is now available to show that the various species are definitely zoned in relation to tide levels. Stebbing further commented on the scarcity of forms with long antennae, i.e. the adult males; this is a feature common to all the species in the genus.

Meinert (1877, p. 201) also expressed the opinion that the *pelagica* and *robertsoni* of Bate should be referred to the *pilosa* of Lindström. However, he described a new species, *tenuipes*, which Sars later (1891, p. 129) regarded as a synonym of *pelagica*.

Blanc (1884) agreed with Stebbing and Meinert, but Chevreux (1887) upheld *robertsoni* as a distinct species.

Sars (1891, pp. 127–34) gave detailed descriptions of five species of this genus, four of which occur in the fauna of Norway, namely *norvegica*, *pelagica*, *gracilis* and *robertsoni*. *B. norvegica* is described as a new species occurring in fine sand at a depth of 2–6 m. in south Norway, *pelagica* as occurring along the whole of the Norwegian coast within the littoral zone and associated with *norvegica*; *gracilis* as a new species of which he had one male and one female specimen occurring in deep water off the west coast; *robertsoni* from three male specimens obtained on the west coast of Finmark. He further described *pilosa* from specimens in the Stockholm museum, and this is referred to as a Baltic species with no known ex-Scandinavian distribution. Sars pointed out the taxonomic value of the coxal plates, of the third epimeral plate and of the armature of the fourth pleon segment on which later Stebbing established a key for the separation of the species.

Della Valle (1893, pp. 751–54) accepted *norvegica* as a distinct species but referred *pelagica*, *robertsoni* and *gracilis* to the *pilosa* of Lindström.

Scott (1893, p. 213) referred to *norvegica*, *pelagica* and *robertsoni* as occurring in the fauna of the Firth of Forth, thus accepting the species as described by Sars.

Walker (1895*a*) examined the specimens of this genus in the British

Museum collections which were presumably determined by Spence Bate. His remarks are as follows:

> "*Bathyporeia pilosa* (Lindström).
>
> "Two tubes so labelled, of these No. 50 contains two females of *B. norvegica* (Sars); the other No. 85 contains eleven specimens, all of which have dark eyes; some have dorsal spinules on the fourth pleon segment, others have not; one (a large female) has a rudimentary tooth slightly in front of the rounded hind margin of the third pleon segment.
>
> "*Bathyporeia pelagica* (Bate). One adult male 5 millim. long.
>
> "This agrees with the form described by Sars under the above name. It must be confessed that, of the five species of *Bathyporeia* given by Sars, only *B. norvegica* (Sars) seems to be distinct, owing to its having the hinder angle of the third pleon segment produced to a point, instead of being rounded, as in the other species."

Walker later (1895*b*, p. 295) expressed the opinion that the species *pelagica*, *robertsoni* and *gracilis* should be referred to the *pilosa* of Lindström.

Norman (1900, p. 326) stated that he could not "regard some of the forms as entitled to specific, indeed they seem hardly worthy of varietal, separation". He refers to the species *norvegica*, *pelagica*, *robertsoni* and *gracilis* but does not state which he regards as specific. In a later paper (1905, p. 82) he assigns *norvegica* as a synonym of *guilliamsoniana*.

Stebbing (1906, pp. 119–22) accepted the five species as described by Sars and added a sixth doubtful species, *lindströmi*, based on Della Valle's description of the Mediterranean forms. He accepts *norvegica* as a synonym of *guilliamsoniana*, based on Walker's statement that the finest specimens in the Spence Bate collection are similar to the *norvegica* of Sars.

Chevreux & Fage (1925, pp. 91–5) described and referred to *guilliamsoniana*, *pelagica* and *robertsoni* as occurring on the coast of France.

Stephensen (1928, p. 130–32) described and referred to *guilliamsoniana*, *pelagica* and *robertsoni* as occurring in the fauna of Denmark, with *pilosa* as a Baltic species.

In the above survey of the history of the genus, reference is made only to those papers which have contributed to the morphology and nomenclature of the species. In the survey of the species which follows reference is also restricted to those papers which describe or figure specimens I have had the opportunity of examining. A reference is omitted if I have not examined the specimens or cannot satisfy myself as to the identity of the species referred to. The survey of the geographical distribution of the species is based almost entirely on the examination of specimens in various collections and on personal collection; it is not based on reference to the species in the literature.

This genus is abundant in the intertidal sands around all the shores of Britain and occurs generally distributed around the coasts of Europe extending into comparatively deep water. Raitt (1937, p. 249) has shown that it is abundant in the Petersen grab hauls taken in the north-western North Sea and adjacent waters and in the stomachs of haddock, forming a considerable item in their diet.

The genus is easily identified by the geniculate character of the first antenna and the spatulate nature of the second gnathopod. Sars (1891, p. 127), Stebbing (1906, p. 119), Chevreux & Fage (1925, p. 91) give adequate descriptions of the genus. I hope to publish shortly a description of the feeding mechanism and burrowing habits of some of the species.

NOTES ON THE STRUCTURAL CHARACTERS OF THE GENUS

The species in the genus are remarkably similar in their structural characters, a fact which has led to their confusion one with another. The chief distinguishing characters are relatively minor ones, the form of the coxal and epimeral plates, the presence or absence of spines on the fourth pleon segment, the shape of certain joints of the appendages and their relative size in relation to succeeding joints, the form of the body, the colour of the eyes and of the eggs, and the extent of the body pigmentation. The sensory armature of the species follows very closely that described by Sexton (1925, pp. 358–60) for *Gammarus chevreuxi* and is remarkably constant in the various species. It affords little of specific value so that a generalized description will serve for all the species. Only the armatures of those parts of the body used in the identification of the species is given. The differences between the sexes, apart from the brood plates, are well marked in the adult stages, particularly in the characters of the antennules and antennae.

ANTENNULE. The large truncated basal joint shows a considerable degree of variation in the shape of its apex, which character may be used as specific. The dorsal surface of this joint carries a sensory groove in which lies a group of plumose hairs which Sexton (1925) regards as probably analogous to the auditory sac of *Anaspides* and many Decapoda. On the ventral surface is a group of feathered hairs varying in number from two to five in the various species, and two plumose hairs set at an angle of 90° to each other with a series of bristles immediately dorsal to them. On the ventral surface at the apex is a group of spines, each with a bifid tip and a small flagellum near the apex. No attempt is here made to distinguish between pointed spines, slender spines and spines. The second joint is characteristically elbowed in relation to the first joint and bears distally a group of spines dorsally and a group of spines or of bristles ventrally. The third joint is like the second. The number of joints in the flagellum is of some specific value and it shows distinct "secondary sexual characteristics".

In the male each joint carries distally a calceolus with an associated group of setae dorsally and a group of aesthetascs ventrally, however, the last one or two joints do not bear calceoli. In the female the number of joints is less, and the number of aesthetascs per joint is less. The accessory flagellum has two joints, the basal of which bears up to four groups of two spines each on the inner margin, with a single spine at the distal dorsal apex in both male and female; the male in addition has a tuft of setae on the middle of the outer margin. The size relation of the basal joint to the second joint is of specific value; the second joint is unarmed apart from a tuft of setae at the apex.

ANTENNA. The third joint is short and broad and carries two groups of bristles on its anterior margin. The fourth joint is twice as long as the third and bears groups of bristles on both anterior and posterior margins; the third and fourth joints may bear an occasional plumose hair. The fifth joint is less than the fourth and with bristles on the anterior and posterior margins. The flagellum shows secondary sexual characteristics in the male. The flagellum of the adult male is considerably elongated, its length in relation to the size of the body is of specific value. Each joint apart from the last one or two carries at the apex a calceolus and a tuft of setae. In the female the number of joints is few, and they are not modified in any way; the length of the flagellum in relation to the last two joints of the peduncle is of some specific value.

GNATHOPOD I. The shape of the propodus is of some specific value. Generally it is oval in outline with the posterior border carrying a long series of hairs and the anterior border some groups of bristles. The inner surface bears a row of spines diagonally placed, and the outer surface a few scattered bristles. The shape, size and armature of the propodus in male and female are alike. The dactylus is claw-like and larger in the male than the female; its anterior border carries a bristle which is modified in the fully adult form to a serrated bristle; the posterior border has an unmodified bristle.

PERAEOPOD III. The basis is much expanded with a row of bristles along the anterior and posterior margins and with five groups of spines on the outer surface near the anterior margin. The bristles of the anterior margin gradually change to feathered bristles near the ischium. The ischium is small and bears a group of bristles distally and feathered bristles on its anterior margin. The merus is characteristically expanded and its shape is of specific value. Its anterior margin is heavily clothed with a row of feathered bristles which become modified to serrated feathered bristles near the carpus. The number of feathered bristles is usually greater in the female than in the male. The outer surface near the anterior edge carries a row of spines. The carpus and propodus are reduced and the dactylus is absent. The carpus bears a number of spines along the anterior edge, the propodus a number of bristles along its anterior edge and one spine on the outer surface apically.

PERAEOPOD V. The size relation of the carpus and propodus is of some specific value. The dactylus is much reduced and is surrounded by a group of spines from the apex of the propodus. The carpus carries groups of bristles and spines on its anterior and posterior margins. The propodus carries groups of spines on the anterior margin and on the outer face.

UROPOD III. The basal joint carries groups of bristles along its outer margin and a row of spines at the apex. The inner ramus is much reduced, with a few serrated spines at its apex. The outer ramus carries numerous feathered bristles along the inner margin and in some species an ordinary bristle associated with some of the groups of feathered bristles; the outer margin carries groups of spines. The terminal joint has the same armature as the basal joint. The shape of the first joint of the outer ramus and its size in relation to the second is of specific value.

Telson. In all species the telson is cleft almost to the base. The armature is remarkably constant and gives little of specific value. Each half carries at the apex, from within outwards, a group of bristles which vary in number from two to six according to age and species, a group of usually two spines, a group of one or two serrated spines, and finally a group of one to three bristles. The dorsal surface carries one plumose hair apically, one a third of the distance from the apex and one nearer the base. The outer margin carries a further group of serrated spines and bristles, which increase in number with age. The variation in the number of bristles and spines with age in each species is such that this character, which has previously been given specific value, cannot be a determining one.

Pleon segment IV. This segment is grooved dorsally, the groove in the adult male is considerably deeper than in the adult female. The posterior edge of the groove carries a pair of forwardly directed bristles which are better developed in the male than in the female. In some species this segment also carries a pair of backwardly directed spines.

Description of the Species

B. guilliamsoniana (Bate) (Fig. 1 *a–g*)

Thersites guilliamsonia Bate, 1856, p. 59.
T. guilliamsoniana Bate, 1857*a*, p. 146.
Bathyporeia guilliamsonia Bate, 1857*b*, p. 271.
B. pilosa Bate, 1862, p. 172, pl. 31, f. 4; Bate & Westwood, 1863, p. 304.
B. norvegica Sars, 1891, p. 128, pl. 43; Della Valle, 1893, p. 754; Scott, 1893, p. 213, pl. 5, f. 22; Walker, 1895*a*, p. 470; Walker, 1895*b*, p. 295.
B. guilliamsoniana Norman, 1905, p. 82; Stebbing, 1906, p. 120; Chevreux & Fage, 1925, p. 92, f. 84, 85; Stephensen, 1928, p. 130, f. 25.

It is now impossible to be certain if the two female specimens in tube no. 50 of the Spence Bate collection are the type specimens (see p. 213). Bate refers to the type specimens as having a length of $\frac{2}{20}$ inch, this is either an error or the above two female specimens are not the type specimens.

The description and drawings of this form as given by Sars are reasonably adequate, so that a brief description of certain appendages only is required.

Male. First pair of coxal plates with a pointed tip and carrying a group of up to six bristles on the posterior margin; the origin of a smaller bristle is marked by a well-defined tooth. Second and third pair of coxal plates with a well-defined tooth at the posterior corners, marked by a distinct sulcus; the ventral margin bears a row of about fifteen to twenty bristles. Fourth pair of coxal plates rounded as in the other species but carrying up to forty-eight bristles on the ventral margin. Last pair of epimeral plates (pleon segment III) with a distinct tooth at the posterior corner which projects beyond the posterior vertical margin of the plate; in fully adult males this tooth is considerably reduced and traces of it only remain; the outer margin bears four or five groups of spines which may be serrated in fully adult forms. Pleon segment IV deeply depressed with a pair of forwardly curving bristles and a pair of backwardly directed spines. The basal joint of the antennule is evenly rounded at the tip, its lower border with four or five feathered hairs; the flagellum is of ten to twelve joints of which the first eight to ten carry a calceolus and a dense tuft of aesthetascs; the basal joint of the accessory flagellum is long and narrow, as 100 : 14, with the second joint about a third the length of the first, with five groups of spines on the inner margin and a tuft of bristles on the outer margin. The antenna and first gnathopod are as described by Sars. Peraeopod III with the merus twice as long as broad, as 100 : 50, with the relation of the length of the merus to carpus plus propodus combined as 100 : 75. The propodus and carpus of peraeopod V are of equal length, robust and very spiny, dactylus short. Uropod III with the second joint of the outer ramus less than a third the length of the basal, as 30 : 100, with fifteen to seventeen feathered bristles on the inner margin of the basal joint and three to four on the second joint, with nine groups of spines on the outer margin. Telson with the typical arrangement of apical armature of which an average condition is, reading from within outwards, five or six bristles, two spines, one plumose hair (inset on dorsal surface), one or two serrated bristles, one to three bristles; laterally four serrated bristles and two bristles.

FEMALE. The female differs from the male in the following points: flagellum of antennule with seven or eight joints, the accessory flagellum without a tuft of setae on outer margin; flagellum of the antenna with eight or nine joints, considerably shorter than the fourth and fifth joints of the peduncle combined, as 71 : 100. The merus of peraeopod III may carry up to forty feathered bristles on its anterior border. Uropod III with a less number of feathered bristles, usually ten to twelve. Pleon segment IV less deeply depressed.

This species attains a length of 8 mm., and is the largest and most robust in the genus. It is translucent without any trace of pigment apart from the eyes which are a bright red. Eggs with a yellowish tinge.

Geographically this species is probably distributed around all the shores of Europe apart from the Baltic. Chevreux & Fage (1925, p. 92) have recorded it from numerous localities in the English Channel and Mediterranean waters; Stephensen (1926, p. 53 and 1928, p. 130) from numerous localities around the Danish coasts; Elmhirst (1931, p. 170) from numerous localities around the Scottish coasts; Raitt (1937, p. 249) as present in many of the Petersen grab hauls from the north-western North Sea to a depth of 75 m. and in the stomachs of haddock to a depth of 35 m.; Crawford (1937*a*,

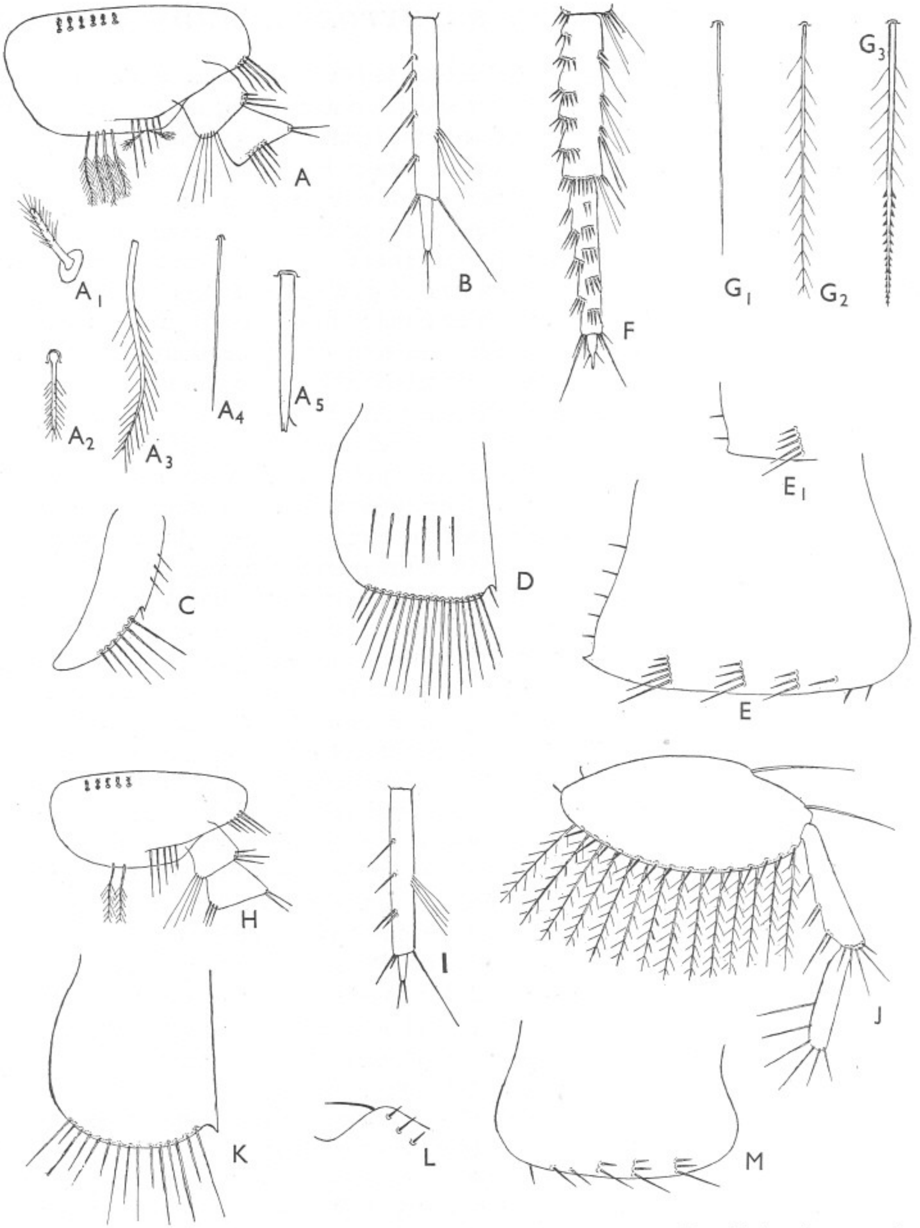

Fig. 1. *a–g*, *B. guilliamsoniana* ♂. *h–m*, *B. gracilis* ♂ type specimen. *a*, Basal joint of antennule; a_1, Plumose hair from dorsal groove; a_2, a_3 and a_4, Plumose hair, feathered hair and bristle from ventral margin; a_5, Spine from apex of joint. *b*, Accessory flagellum of antennule. *c*, First coxal plate. *d*, Second coxal plate. *e*, Third epimeral plate in adult ♀ and young ♂. e_1, Third epimeral plate in adult ♂. *f*, Carpus, propodus and dactylus of peraeopod V. g_1, g_2, g_3, To show change from bristle to feathered bristle to feathered serrated bristle along anterior margin of basis, ischus and merus of peraeopod III. *h*, basal joint of antennule. *i*, Accessory flagellum of antennule. *j*, Merus, carpus and propodus of paraeopod III. *k*, Second coxal plate. *l*, Fourth pleon segment. *m*, third epimeral plate.

p. 637) from Plymouth waters; Moore (1937, p. 118) from Isle of Man waters. In the Norman collection in the British Museum there are specimens from the Moray Firth (register numbers 13762–781 and 13803), from Ilfracombe (13792) and from Guernsey (13782–791). As *B. norvegica* Sars (1891, p. 128) has recorded it from a single locality in the south of Norway; Della Valle (1893, p. 754) from the Bay of Naples; Scott (1893, p. 213) from the Firth of Forth; Walker (1895*b*, p. 295) from the north Wales and Isle of Man coasts. Spence Bate (1863, p. 306) gives the type locality as Weymouth "on a fine sandy bottom", and Tenby. This species may be collected at the low-water mark of spring tides and in shallow water at many localities around the British coasts.

B. pelagica (Bate) (Fig. 2)

Thersites pelagica Bate, 1856, p. 59; 1857*a*, p. 146.
Bathyporeia pelagica Bate, 1862, p. 174, pl. 31, f. 6; Bate & Westwood, 1863, p. 309.

Type specimen, a male, 5 mm. long, in the Spence Bate collection, British Museum, tube no. 86. Locality, Bate (1863, p. 309), Moray Firth.

MALE. This description is based partly on the type specimen (as far as possible without dissection) and partly on specimens collected at Aberystwyth and Kames Bay, Millport, and compared with specimens from other localities.

Body robust. First pair of coxal plates with a rounded tip and carrying a row of three to four bristles on the posterior margin; the origin of a more dorsally situated bristle is not marked by a tooth. Coxal plates II, III and IV as deep as the corresponding segments. Second pair of coxal plates rounded anteriorly without a tooth at the posterior corner; this corner is marked by a rounded projection not defined by a sulcus; the ventral margin carries a row of six to nine bristles. Third pair of coxal plates rectangular in outline, otherwise much as the second pair. Fourth pair of coxal plates rounded as in the other species with about 24 bristles on ventral margin. Last pair of epimeral plates (pleon segment III) unevenly rounded at the posterior corner in the adult male but with a small tooth marked by a well-defined sulcus some little distance from the apex in the young male; the ventral border carries about four groups of spines, the number of spines per row decreasing anteriorly. Pleon segment IV deeply depressed dorsally and carrying a pair of stout spines directed posteriorly and a pair of bristles directed anteriorly. Antennules with the basal joint produced to a point dorsally—the somewhat triangular apex is characteristic of this species and of *tenuipes*—lower border with three feathered hairs. The flagellum is of nine to eleven joints of which the first eight to ten carry calceoli and each a dense tuft of aesthetascs; accessory flagellum with the second joint about a quarter the length of the basal, as 27 : 100; the basal carries three or four groups of two spines each on the inner margin and a tuft of setae on the outer margin. The flagellum of the antenna is longer than the body; all the joints except the last one or two carry calceoli. The propodus of the first gnathopod is an oblong oval as in the other species,

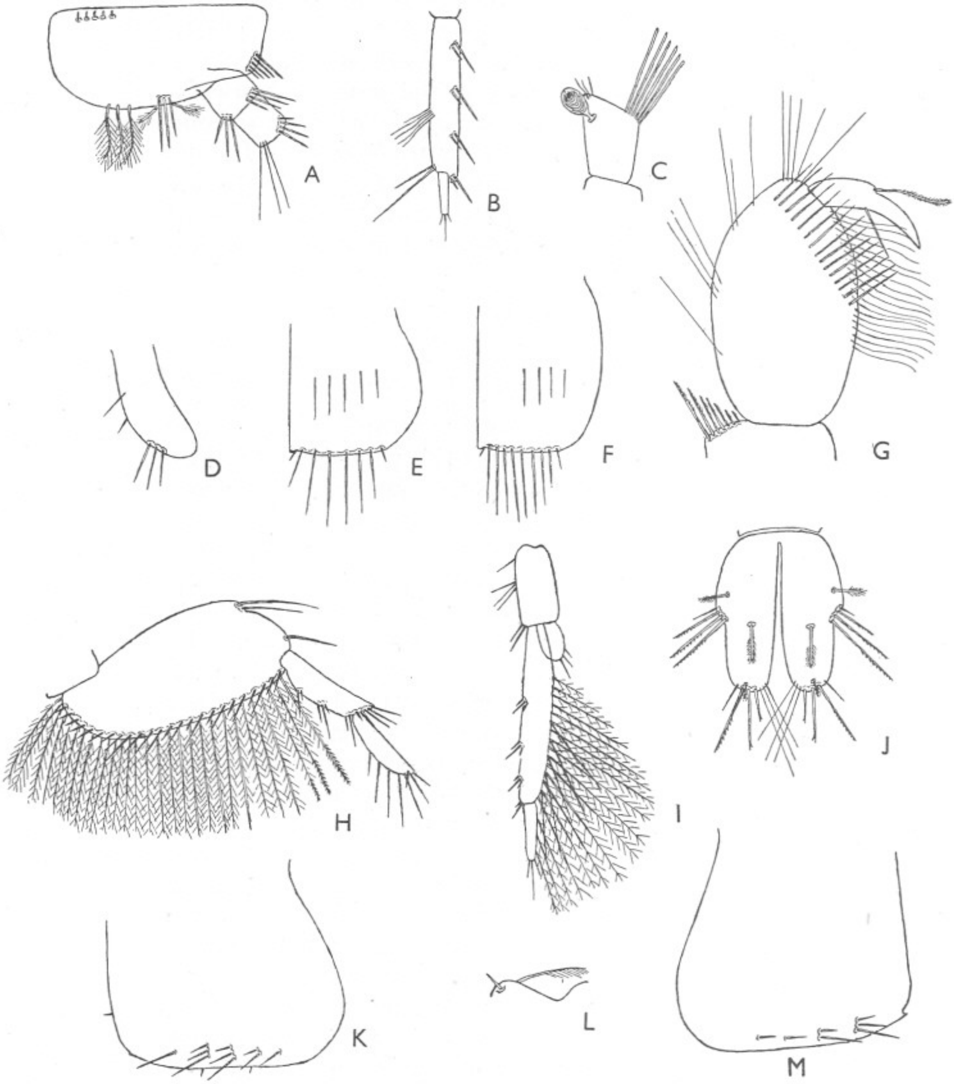

Fig. 2. *B. pelagica* ♂. *a*, Basal joint of antennule. *b*, Accessory flagellum of antennule. *c*, Typical joint from middle of flagellum of antennule. *d*, First coxal plate. *e*, Second coxal plate. *f*, Third coxal plate. *g*, Propodus and dactylus of first gnathopod. *h*, Merus, ischus and propodus of peraeopod III. *i*, Third uropod. *j*, Telson. *k*, Third epimeral plate in adult ♂. *l*, Fourth pleon segment in adult ♂. *m*, Third epimeral plate in adult ♀ and young ♂.

except *elegans*; the dactylus is sharply pointed and carries a feathered bristle on its anterior margin in fully developed males but a simple seta in mature but not fully developed males. Peraeopod III with the merus more than twice as long as broad, as 100 : 44, the relation of the length of the merus to carpus and propodus combined being as 100 : 74; the anterior border of the merus carries up to thirty feathered bristles on its edge with up to twenty-four spines on the outer face. Peraeopods IV and V elongate, the relation of the length of the carpus to propodus in peraeopod V as 81 : 100. The outer ramus of uropod III with the second joint about a third the length of the basal, as 37 : 100, with fourteen to sixteen feathered bristles on inner margin of basal joint and two to four on the second joint; an ordinary bristle is associated with several of the feathered bristles, outer margin with four or five groups of spines. Telson with the typical arrangement of apical armature of which the usual condition is, reading from within outwards, three to five bristles, two spines, one plumose hair, one serrated bristle, one bristle; laterally with two or three serrated bristles and one or two bristles. Eyes reniform with dark red pigment.

FEMALE. The female differs from the male in the following points: the flagellum of the antennule with six or seven joints, the accessory flagellum without a tuft of setae on its outer margin. The flagellum of the antenna with eight to eleven joints and a little less in length than the fourth and fifth joints of the peduncle combines, as 92 : 100. The merus of peraeopod III may carry up to thirty-four feathered bristles on its anterior margin, although this number is exceedingly variable in egg-bearing females, the minimum count was twenty-one. The outer ramus of uropod III carries a less number of feathered bristles, usually seven to ten. Last pair of epimeral plates as in the young male and with a variable number of groups of spines and spines per group, an examination of ten individuals gave the following readings: 2.2.1, 2.2.2, 3.2, 3.2.1 (twice), 3.3.2, 3.2.2.1, 3.3.1.1, 3.3.2.1, 3.3.1. The number of bristles on the ventral margin of the coxal plates is greater than in the male. The fourth pleon segment is less deeply depressed. Eyes rounded with dark red pigment.

The body pigment is abundant, particularly in the pleon and its appendages, but this is variable in specimens from various localities. Eggs deep blue in colour.

The distribution of this species is, as far as my present records are concerned, restricted to the intertidal sandy shores of the coasts of Britain. It is found to occupy a definite tidal level below the high-water mark of neap tides. It has been found at numerous points on the west coast of Wales, at Redcar (Yorkshire) and the extensive collections of the Scottish Marine Biological Station show it to be common in many localities around the Scottish coast. It has not appeared in the collections of the Copenhagen, Stockholm and Oslo Museums.

B. elegans*, nom.nov. (Fig. 3)

B. pelagica Sars, 1891, p. 129, pl. 44, f. 1.

Type specimens, numerous adult males and females, and young forms in the Zoological Museum, Oslo. Locality "in the Ognebugt off Jaederen", South Norway (Sars, 1891, p. 45).

The description given by Sars may be modified and amplified in the following particulars. Of the species in this genus this is the smallest and finest. The body is narrow and elongate; occasional specimens may reach a length of 6 mm., although 4–5 mm. is much more usual.

MALE. First pair of coxal plates with an obtusely pointed tip; the posterior margin carries a row of four to five bristles with a single bristle dorsal to the row, the origin of which is marked by a distinct but small tooth. The second, third and fourth pairs of coxal plates as deep as the corresponding segments. Second pair of coxal plates with a tooth on the posterior corner which is not as well developed as in *guilliamsoniana* and *tenuipes*; the tooth does not reach to the level of the base of the plate, but is variable in the degree of its development; the ventral margin carries a row of about twelve bristles. Third pair of coxal plates rectangular in outline, otherwise as the second pair. Fourth pair of coxal plates rounded as in the other species with about twenty-four bristles on the ventral margin. Last pair of epimeral plates (pleon segment III) rounded, without a tooth at the posterior corner; the outer edge carries about four groups of setae decreasing in number anteriorly. Pleon segment IV deeply depressed dorsally with one pair of bristles directed anteriorly and one pair of spines posteriorly. The basal joint of the antennule is evenly rounded at the tip, the lower border with two or three feathered hairs. Flagellum of nine to eleven joints of which the first seven to nine carry calceoli and a dense tuft of aesthetascs. Accessory flagellum with the second joint about a third the length of the basal, as 33 : 100; the basal carries up to four groups of spines on the inner margin and a tuft of setae on the middle of the outer margin. The flagellum of the antenna is longer than the body. The propodus of the first gnathopod is an oblong oval about twice as long as broad, longer than in the other species. The merus of peraeopod III is more than twice as long as broad, as 100 : 46, the relation of the length of the merus to carpus and propodus combined being as 100 : 87; anterior border of the merus with about twenty-four feathered bristles and with about twenty-four spines on the outer face. Peraeopod V with the carpus not so long as the propodus, as 90 : 100, dactylus pointed as a spine. The second joint of the outer ramus of uropod III is a little more than a third the length of the basal, as 100 : 38; the basal carries nine to eleven feathered bristles on its inner margin with an accessory seta associated with some of the bristles, the second joint

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* Mr G. I. Crawford desires me to state that his reference to *B. elegans*, this *Journal*, Vol. XXI, p. 639, line 4, is an error and should read *B. gracilis*.

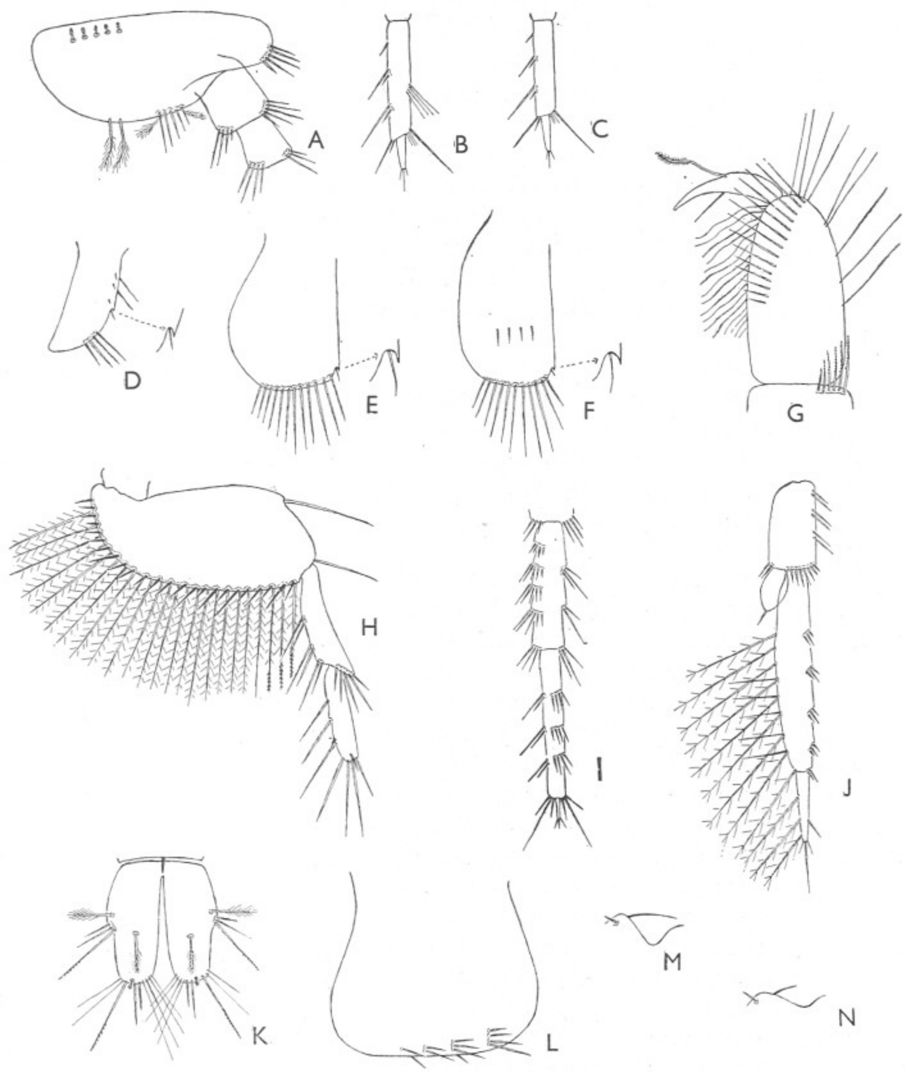

Fig. 3. *B. elegans* ♂. *a*, Basal joint of antennule. *b*, accessory flagellum of ♂. *c*, Accessory flagellum of ♀. *d*, First coxal plate. *e*, Second coxal plate. *f*, Third coxal plate. *g*, Propodus and dactylus of first gnathopod. *h*, Merus, carpus and propodus of peraeopod III. *i*, Carpus, propodus and dactylus of peraeopod V. *j*, Third uropod. *k*, Telson. *l*, Third epimeral plate. *m*, Fourth pleon segment in ♂. *n*, Fourth pleon segment in ♀.

with two or three feathered bristles; the outer margin bears four to six groups of spines. Telson with the typical arrangement of apical armature of which a usual condition is, reading from within outwards, two to four bristles, two spines, one plumose hair, one to three bristles, and laterally one or two serrated bristles and two or three bristles. Eyes large and reniform with bright red pigment.

FEMALE. The female differs from the male in the following points: the flagellum of the antennule with six joints, occasionally five, accessory flagellum with the basal joint shorter and broader, giving a relation with the second joint as 100 : 42 and without a tuft of setae on its outer margin. The flagellum of the antenna has eight or nine joints, occasionally ten, the relation of the length of the flagellum to the fourth and fifth joints of the peduncle being as 88 : 100.

The feathered bristles on the inner margin of uropod III are about equal in number to those in the male but are not so well developed. The merus of peraeopod III has up to thirty feathered bristles on the ventral margin. The third epimeral plate gave the following readings for spine groups: 4.2.1 (twice), 4.2.2, 4.3.1 (twice), 4.3.2, 4.1.1.1, 5.3.2 (twice). The fourth pleon segment is less deeply depressed. Eyes rounded with bright red pigment.

The body in both male and female is translucent with practically no pigment. The colour of the eggs is yellowish.

Thus the main points in which *elegans* differs from *pelagica* are (i) the shape of the basal joint of the antennule, (ii) the presence of a small tooth on the coxal plates, (iii) the rounded posterior border of epimeral plate III, (iv) the general lack of pigmentation, (v) the colour of the eggs and of the ovary in the female, and (vi) the distribution in relation to tide level.

This species may be collected at low-water mark of spring tides in several localities around the coasts of Britain. It is in general a shallow-water form. The collections of the Oslo Museum show it to be present in several localities along the whole Norwegian coast, the Copenhagen Museum collections contain specimens from the Kattegat and from the North Sea coast of Denmark. In the Norman collection in the British Museum there are specimens from the Moray Firth (register numbers 13762–781 and 13826–827), from "25 miles off the Isle of May" (13813–816), from Whitsand Bay (13828–842), from Shetland (13843–845), and from Cumbrae (13846–855). Crawford (1937*a*, p. 637) records it as *B. pelagica* from Plymouth waters. The extensive collections of the Scottish Marine Biological Station show it to occur in several localities on the east and west coasts of Scotland and I have found it in one locality on the west coast of Wales. Stephensen (1928, p. 131) records *B. pelagica* as far south as Madeira, but this record needs confirmation in view of its possible confusion with *tenuipes*. Thus it may be stated to have a general distribution around all the Atlantic coasts of Europe.

B. tenuipes Meinert (Fig. 4)

B. tenuipes Meinert, 1877, p. 201.
B. gracilis Norman, 1900, p. 326.
B. elegans Crawford, 1937 *a*, p. 639.

Type specimen, an adult male in the Zoological Museum, Copenhagen. Locality given on label in tube as Anholt, Kattegat. Meinert's description is as follows: "Antennae superiores subundae, flagello appendiculari biarticulato. Antennae inferiores articulo tertio et quarto longis atque tenuibus. Angulus capitis acutus productus. Pedes omnes tenues, modice hirsuti; pedes saltatorii ultimi paris setis simplicibus instructi."

Through the kindness of Dr K. Stephensen of Copenhagen I have been able to examine the type specimen of *tenuipes* and find it sufficiently different from *B. pelagica* (Bate) and *B. elegans* to justify specific rank.

MALE. The type specimen may be redescribed as follows: Length 6 mm. Body elongate and narrow. First pair of coxal plates narrow with an obtusely pointed tip; the posterior margin possesses a row of about six setae with a single seta on the middle of the margin the origin of which is not marked by a tooth; dorsally there is a row of about eight setae on the outer face. Coxal plates II, III and IV deeper than the corresponding segments. Second pair of coxal plates triangular in outline with a pronounced tooth posteriorly defined by a deep sulcus, and carrying a row of about twenty-one bristles ventrally. Third pair of coxal plates rectangular in outline, otherwise as the second pair. Last pair of epimeral plates (pleon segment III) evenly rounded at the posterior corner without any trace of a tooth; the lower edge carries numerous groups of spines with one to three spines per group, reading 2.2.3.1.2.2.2.1.1.1, the posterior edge with three hairs. Pleon segment IV deeply depressed dorsally with a pair of anteriorly directed bristles and a pair of posteriorly directed spines; an additional pair of spines may be present in some specimens. The basal joint of the antennule is produced into a triangular point (N.B. "Angulus capitis acutus productus"), lower border with five feathered hairs. Flagellum of eleven joints of which the first nine carry calceoli and a dense tuft of aesthetascs. Accessory flagellum long and narrow with the second joint a little less than a third the length of the basal, as 31 : 100; the basal carries four groups of spines on the inner margin and a tuft of setae on the outer margin. The flagellum of the antenna is longer than the body. The propodus of the first gnathopod is an oblong oval as in the other species except *elegans*. Peraeopod III with the merus twice as long as broad, as 100 : 50, the relation of the length of the merus to carpus plus propodus combined as 100 : 84, the anterior border carries an edge row of about twenty-six feathered bristles with a row of about twenty-five spines on the outer face. Peraeopods IV and V elongate and narrow, peraeopod V with the carpus longer than the propodus, as 100 : 85, dactylus pointed as a spine. The outer ramus of uropod III is long and narrow with the second joint more than a

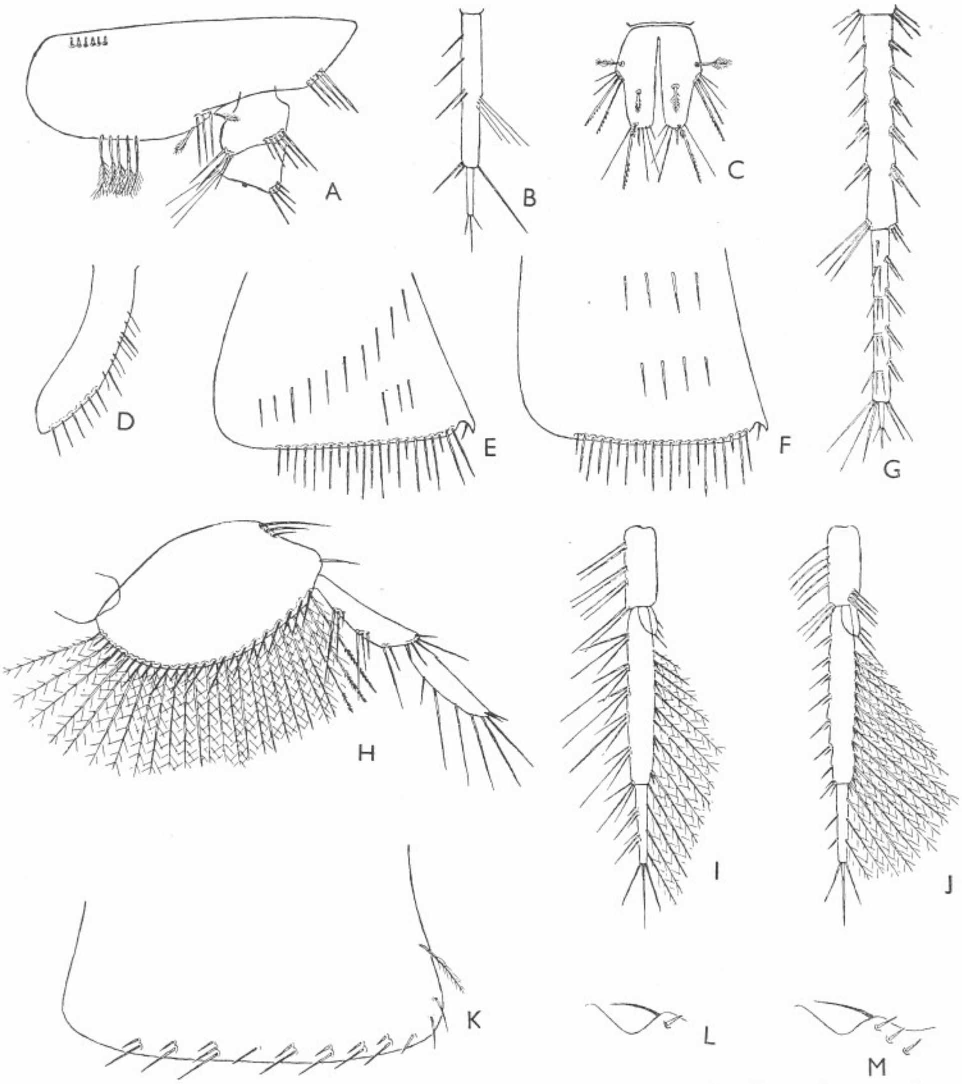

Fig. 4. *B. tenuipes* ♂. *a*, Basal joint of antennule. *b*, Accessory flagellum of antennule. *c*, Telson. *d*, First coxal plate. *e*, Second coxal plate. *f*, Third coxal plate. *g*, Carpus, propodus and dactylus of peraeopod V. *h*, Merus, carpus and propodus of peraeopod III. *i*, Third uropod of ♀. *j*, Third uropod of ♂. *k*, Third epimeral plate. *l*, Fourth pleon segment of type specimen. *m*, Fourth pleon segment of male from unrecorded locality in Kattegat.

third the length of the basal, as 45 : 100; the basal joint carries thirteen and the second joint three feathered bristles on the inner margin, each with an associated short seta; the outer margin with eight groups of spines. Telson with an apical armature of two or three bristles, one spine, one plumose hair, two or three bristles one of which may be modified to a serrated bristle, two bristles, laterally with two serrated bristles, two bristles. Eyes large and reniform. Colour unknown. A comparison of other adult males with the type shows but little variation.

FEMALE. The female differs from the male in the following points: the flagellum of the antennule with six or seven joints, accessory flagellum without a tuft of setae on the outer margin, the second joint from a quarter to more than a third the length of the basal. The flagellum of the antenna with eight to ten joints, the relation of the length of the flagellum to fourth and fifth joints of the peduncle combined as 84 : 100, but somewhat variable. The outer ramus of uropod III with about seven feathered bristles on the inner margin with the accessory bristles well developed, the outer margin with ten groups of well-developed spines, the spines almost as long as the feathered bristles. The anterior border of the merus of peraeopod III carries a greater number of feathered bristles. The ventral margin of the second and third coxal plates a greater number of bristles. The fourth pleon segment is less deeply depressed.

Thus the main points in which *tenuipes* differs from *elegans* are (i) the triangular end to the basal joint of the antennule with four or five feathered hairs on the lower margin, (ii) the well-developed tooth at the posterior corner of coxal plates II and III, (iii) the numerous rows of spines on the third epimeral plates, and (iv) the length of the second joint of the outer ramus of uropod III which is more than a third the length of the basal.

Geographically this species has a wide distribution, but due to its previous confusion with *elegans* the number of records are few. The author has examined the collections of *B. pelagica* of the Copenhagen Museum, which show *tenuipes* as occurring at five stations in the Kattegat; the Stockholm Museum collections contain one tube of this species labelled as from the Kristiniberg Biological Station without exact locality. In the Norman collection in the British Museum there are specimens from Guernsey (register numbers 13782–791 and 13808–812), from Start Bay, Devon (13817–821), from the Kattegat (13859), from the Scilly Isles (13875) and from two stations of the *Porcupine* Expedition, 1869, namely St. 6, west of the Shannon, Ireland, 90 fathoms (13871–874), and St. 18, west of Clew Bay, Ireland, 183 fathoms (13856–858). Crawford (1937*a*, p. 639) records it as *B. elegans* (see footnote, p. 222) from Cawsand Bay, Plymouth.

B. gracilis Sars (Fig. 1, *h–m*)

This is a somewhat doubtful species described by Sars (1891, p. 132, pl. 45, f. 1) from an adult male and female collected from comparatively deep water off the Norwegian coast. The male specimen only is extant.

An examination of the male specimen shows that it agrees in certain features with *tenuipes*, to which it seems most nearly related. It agrees with *tenuipes* in possessing (i) a well-developed tooth at the posterior corner of coxal plates II and III; the shape of the first coxal plate was not ascertained, but Sars describes it as obtusely pointed. (ii) Peraeopods IV and V are long and narrow, (iii) the third epimeral plate is evenly rounded at the posterior corners and carries numerous groups of spines, (iv) the pleon segment IV carries more than one pair of backwardly directed spines. (v) The third uropod is missing in the specimen, but Sars' drawing of this appendage in the female shows its agreement with *tenuipes*. It differs from *tenuipes* in (i) the rounded end to the basal joint of the antennule with two feathered hairs on the lower margin; (ii) the second joint of the accessory flagellum is short and about a fifth the length of the basal; (iii) the merus of peraeopod III is not expanded, it is more than twice as long as broad. It is unlike any other species in the character of the flagellum of the antenna in the male, which is short and composed of thirteen joints of which the first five carry calceoli. It seems advisable to retain this species until further specimens are available.

B. pilosa Lindström (Fig. 5)

B. pilosa Lindström, 1855, p. 59, pl. 2, f. 1–11; Sars, 1891, p. 133, pl. 45, f. 2; Stebbing, 1906, p. 121; Stephensen, 1928, p. 132, f. 25.
B. robertsoni Bate, 1862, p. 173, pl. 31, f. 5; Bate & Westwood, 1863, p. 307.

Type specimen, a female, not extant. Locality, off the island of Gottland, Baltic. A brief description of specimens collected at Kames Bay, Millport, which have been compared with specimens from the Baltic kindly loaned by Dr Sixten Bock of the Zoological Museum, Stockholm, follows:

MALE. Length not exceeding 6 mm. Body robust. First pair of coxal plates with a pointed tip and with a group of three or four bristles on the posterior margin; the origin of a single bristle dorsal to this group is not marked by a tooth. Coxal plates II, III and IV are not as deep as the corresponding segments and thus are smaller than in the other species. Second pair of coxal plates rounded but narrowing towards the base; the ventral margin carries a row of about five to six bristles and the posterior corner is not marked by a tooth. Third pair of coxal plates rectangular, but narrowing towards the base, otherwise as the second pair. Last pair of epimeral plates (pleon segment III) evenly rounded at the posterior corner without any trace of a tooth; the number of groups of spines is less than in the other species, a typical arrangement is 2.1 or 3.1. Pleon segment IV deeply depressed dorsally with a pair of anteriorly directed bristles. The basal joint of the antennule is evenly rounded at the tip which is narrower than in the other species; lower margin with two feathered hairs; the number of joints in the flagellum varies from ten to fourteen of which the first eight to twelve carry calceoli and a small group of three to four aesthetascs, the flagellum is longer than in the other

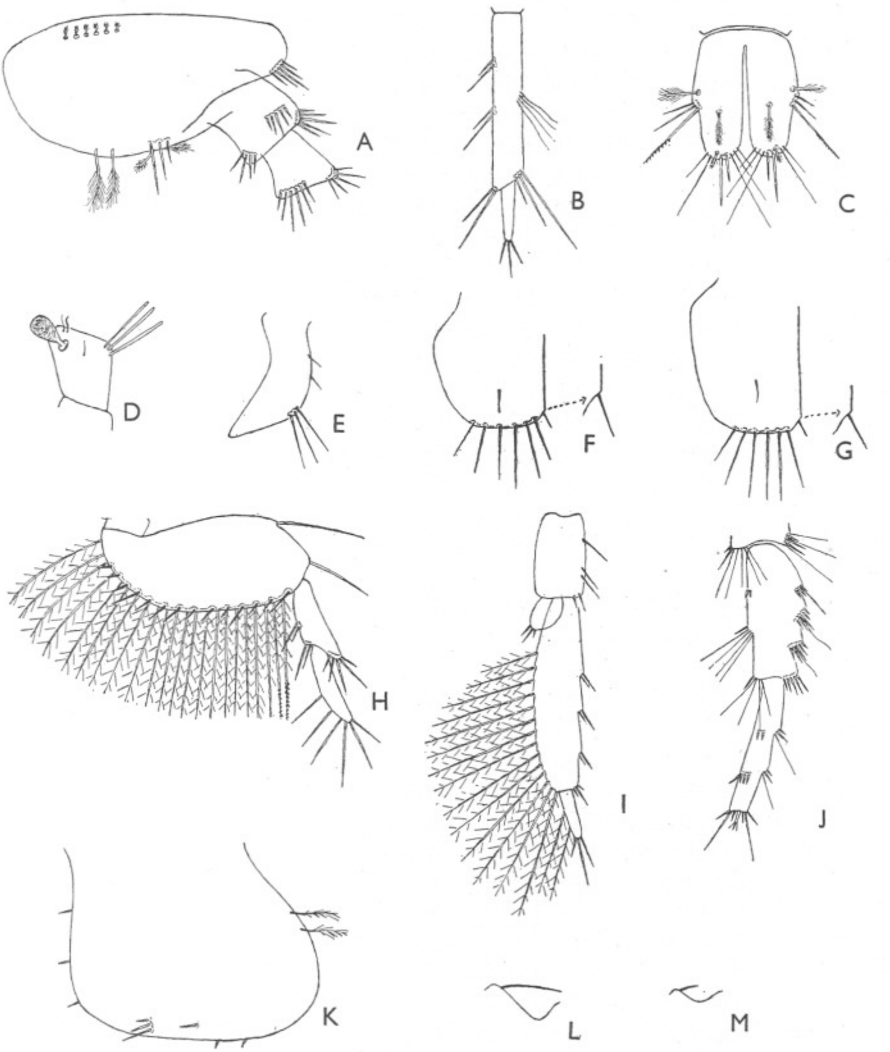

Fig. 5. *B. pilosa* ♂. *a*, Basal joint of antennule. *b*, Accessory flagellum of antennule. *c*, Telson. *d*, Typical joint from middle of flagellum of antennule. *e*, First coxal plate. *f*, Second coxal plate. *g*, Third coxal plate. *h*, Merus, carpus and propodus of peraeopod III. *i*, Third uropod. *j*, Carpus, propodus and dactylus of peraeopod V. *k*, Third epimeral plate. *l*, Fourth pleon segment in ♂. *m*, Fourth pleon segment in ♀.

species and the number of aesthetascs fewer. Accessory flagellum with the second joint less than a third the length of the basal, as 29 : 100, with three groups of spines on the inner margin and a tuft of setae on the outer margin. The flagellum of the antenna is about one-half to two-thirds the length of the body, the number of joints varying from seventeen to over thirty, all of which apart from the last one or two carry calceoli. The propodus of the first gnathopod as in the other species except *elegans*. The merus of peraeopod III is more than twice as long as broad, as 100 : 46; its anterior margin carries a row of from eighteen to twenty-four feathered bristles, and is much longer than the carpus plus propodus combined, as 100 : 71. The carpus and propodus of peraeopod V are of equal length, the carpus is broad and more robust than in the other species. The basal joint of the outer ramus of the third uropod is expended along the middle of its length, with from twelve to eighteen feathered bristles on the inner margin and three to four groups of spines on the outer margin; the second joint is less than a third the length of the basal as 26 : 100, with one to three feathered bristles on its inner margin. A typical arrangement of the armature at the apex of the telson is, reading from within outwards, two or three bristles, two spines, one plumose hair which may be absent, two to four bristles, the inner one of which may be modified to a serrated bristle, laterally one serrated bristle and two bristles. Eyes reniform with dark red pigment.

FEMALE. The female differs from the male in the following points: the flagellum of the antennule with six or seven joints, accessory flagellum without a tuft of setae on the outer margin and with the second joint on an average more than a third the length of the basal, as 37 : 100. The flagellum of the antenna with eight or nine joints and in length less than the fourth and fifth joints of the peduncle combined, as 83 : 100. The number of feathered bristles on the anterior border of peraeopod III varies from twenty-three to thirty, on the inner margin of the third uropod from five to ten. The number of groups of spines and spines per group on the third epimeral plate of ten specimens gave the following readings: 1 (twice), 1.1 (twice), 1.1.1, 2.1 (four), 2.1.1. Eyes round with dark red pigment. Eggs blue.

Colour of body variable; in the reddish sands of Kames Bay the amount of red pigment in the pleon is considerable, in the lighter coloured sands of the Welsh coast pigment it is much less.

Geographically this species occurs in numerous localities in the Baltic from the Danish coast to the island of Gottland (Oldevig, 1933), in the Kattegat and on the North Sea coast of Denmark (specimens in the Zoological Museum, Copenhagen), in the Oslo fjord (specimens in the Zoological Museum, Oslo). My only records of it from the east coast of England and Scotland are Leigh-on-Sea (Essex) collected by Crawford (specimens in the British Museum) and from Amble (Northumberland), specimens supplied by Professor A. D. Hobson, Newcastle, who also collected it in the Hebrides in 1937. Further collecting in the estuaries on the east coast will probably add many records.

I have no records from the English Channel. On the west coast of Britain it is abundant in several localities. I have collected it in the estuaries and sandy beaches of the west coast of Wales, at Kames Bay, Millport, and on the Ayrshire coast; in these localities it occurs above the high-water mark of neap tides, occasionally in water of somewhat reduced salinity. Crawford (1937*b*, p. 652) records it as *Bathyporeia* sp. from the River Taw, North Devon.

B. sarsi, nom.nov. (Fig. 6)

B. robertsoni Sars, 1891, p. 131, pl. 44, f. 2; Scott, 1893, p. 213, pl. 5, f. 26–9; Stebbing, 1906, p. 121; Chevreux & Fage, 1925, p. 94, Stephensen, 1928, p. 132, f. 25.
B. pilosa Elmhirst, 1931, p. 170.

Type specimens, three adult males, two of which are extant, in the Zoological Museum, Oslo. Locality (Sars, 1891, p. 132) Sorvaer, west coast of Finmark, northern Norway.

The specimens described by Bate as *B. robertsoni* were collected by Robertson on "Cumbrae...in sand pools, near low water mark, numerous darting hither and thither". Bate gave two somewhat meagre descriptions and two contradictory drawings of these specimens, the first (1862, p. 173, pl. 31, f. 5) shows fourteen joints in the flagellum of the antennule and twenty-four joints with calceoli in the flagellum of the antenna; the second (1863, p. 307, with figure) shows ten joints in the flagellum of the antennule and eighteen joints in the flagellum of the antenna. Sars in his description of the Norwegian specimens states "inferior antennae...composed of seventeen articulations each except the last two bearing calceoli". Thus Sars seems to have based his identification of the Norwegian specimens on the second of Bate's drawings. An examination of the type locality of *B. robertsoni* Bate during April 1936, 1937 (Watkin, 1937) and 1938 failed to show a single specimen of this species as described by Sars, but *B. pilosa* Lindström was abundant and an occasional specimen was found with as few as seventeen calceoli-bearing joints in the flagellum of the antenna.

I am myself confident that the *robertsoni* of Bate was *pilosa*, and it thus follows that Sars was dealing with a new species which is here named "sarsi" in compliment to him. The following description is based partly on the two type specimens and partly on specimens from other localities.

MALE. Length not exceeding 6 mm. Body robust. First pair of coxal plates with a rounded tip, the posterior margin with a row of three to four bristles; the origin of a single bristle dorsal to this row is not marked by a tooth. Coxal plates II, III and IV as deep as the corresponding segments. Second pair of coxal plates square in outline with about four to five bristles on the ventral margin; the posterior corner is not marked by a tooth but a definite ridge may occur in some specimens. Third pair of coxal plates rectangular in outline, otherwise much as the second pair. Last pair of epimeral plates (pleon segment III) with the posterior corner rounded, the lower edge

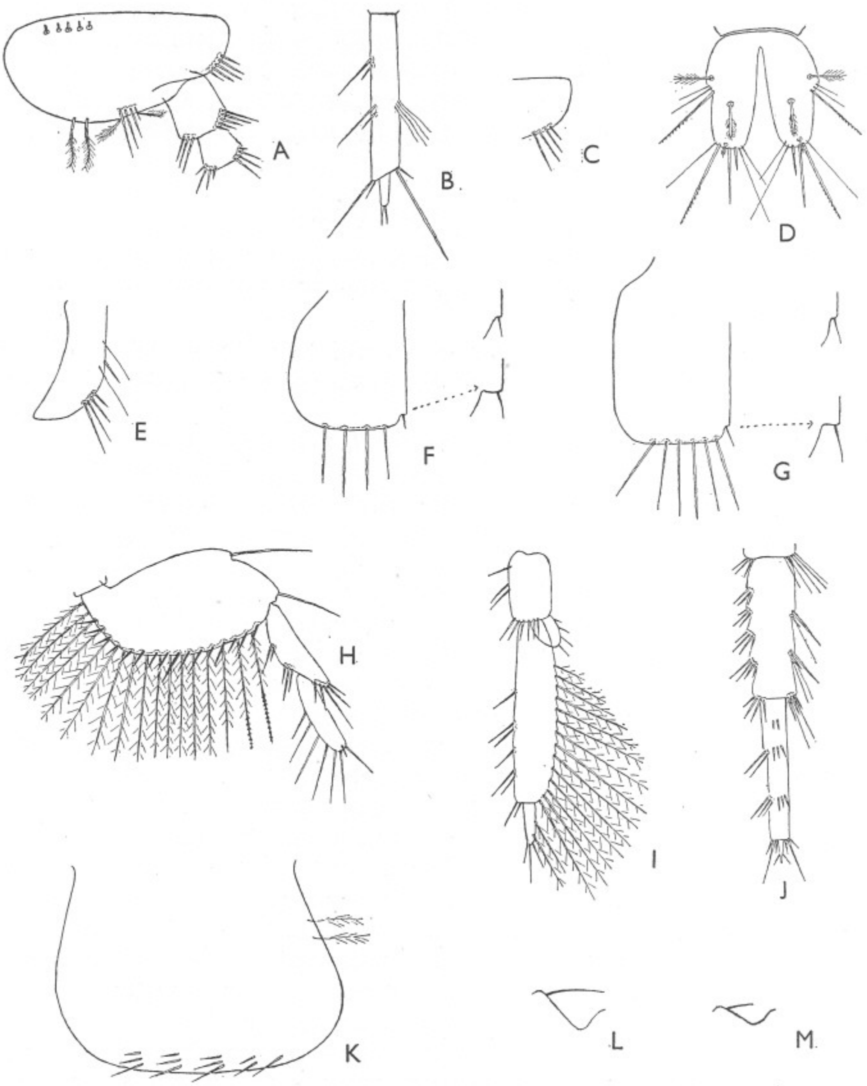

Fig. 6. *B. sarsi* ♂. *a*, Basal joint of antennule. *b*, accessory flagellum of antennule. *c*, Apex of basal joint of antennule in ♀. *d*, Telson. *e*, First coxal plate. *f*, Second coxal plate. *g*, Third coxal plate. *h*, Merus, carpus and propodus of peraeopod III. *i*, third uropod. *j*, Carpus, propodus and dactylus of peraeopod V. *k*, Third epimeral plate. *l*, Fourth pleon segment in ♂. *m*, Fourth pleon segment in ♀.

carried four to five groups of spines, typical arrangements are 3.3.3.2.1, or 3.3.2.1. Pleon segment IV deeply depressed dorsally with a pair of anteriorly curved bristles only. The basal joint of the antennule with an evenly rounded tip, with two or three plumose hairs ventrally; the flagellum is of ten or eleven joints of which the first eight or nine carry calceoli and a dense tuft of aesthetascs. The accessory flagellum with the second joint less than a fifth the length of the first, as 19 : 100, with three or four groups of spines on the inner border and a tuft of setae on the outer border. The flagellum of the antenna is shorter than in any other species, not exceeding one-half the length of the body, and is composed of fifteen to twenty-two joints each of which carries a calceolus with one or two joints without a calceolus. Eyes reniform. Colour unknown.

The propodus of the first gnathopod a rounded oval as in the other species except *elegans*. The merus of peraeopod III is about twice as long as broad, as 100 : 51, the anterior border with seventeen to twenty-two feathered bristles. Peraeopod V with the propodus longer than the carpus, as 100 : 90, dactylus pointed as a spine. The second joint of the outer ramus of the third uropod is about a quarter the length of the basal, as 24 : 100, the basal joint is expanded along the middle of its length with twelve to sixteen feathered bristles on the inner margin and four groups of spines on the outer margin, second joint with two to three feathered bristles. A typical arrangement of the armature at the apex of the telson is as follows, reading from within outwards: two or three bristles, two spines, one plumose hair, one or two bristles the inner of which may be modified as a serrated bristle; laterally one serrated bristle, one or two bristles.

FEMALE. The female differs from the male in the following points: Length 7–8 mm. The basal joint of the antennule has a more square tip; the number of joints in the flagellum is seven or eight; accessory flagellum without a tuft of setae on the outer margin of the basal joint. The number of joints in the flagellum of the antenna is eight to ten, the relation of its length to the fourth and fifth joints of the peduncle being as 78 : 100. The second and third coxal plates carry numerous bristles on their ventral margins, the number increasing with age up to about twenty-four. The anterior margin of the merus of peraeopod III carries many more feathered bristles: counts of up to forty were recorded. The number of groups of spines on the third epimeral plate is greater, a typical arrangement is 3.3.2.2.1.1. The number of feathered bristles on the inner margin of the outer ramus of the third uropod is less, varying from ten to fourteen. Pleon segment IV is less deeply depressed.

Geographically this species occurs along the whole of the Norwegian and Danish coasts, on the French and English sides of the English Channel, and in several localities along the east coast of Scotland and England. Its absence from the west coast of Britain is peculiar, but extensive collecting failed to record its occurrence. It is usually an intertidal or shallow water form.

B. lindströmi Stebbing

B. lindströmi Stebbing, 1906, p. 122.
B. pilosa (part), Della Valle, 1893, p. 752, pl. 5, f. 1; pl. 36, f. 19–32.

Della Valle referred *pelagica*, *robertsoni* and *gracilis* to the synonymy of *pilosa*, and described and figured specimens collected from sand in the Bay of Naples at a depth of 10–20 m. as *pilosa*. Stebbing formed the doubtful species *lindströmi* on the description and figures of *pilosa* as given by Della Valle. This form is obviously different from *pilosa* and *sarsi* in that the coxal plates are toothed and the fourth pleon segment carries a pair of backwardly directed spines. The third epimeral plate is rounded at the posterior corner, and thus it may agree with *elegans*, *tenuipes* or *gracilis*, but the description and figures are insufficient for correct determination. The absence of the dactylus in peraeopod V and the lack of armature at the apex of the telson are probably incorrect. The original specimens described by Della Valle are lost and no further specimens are at the moment available. The Norman collection in the British Museum contains two tubes labelled as from Naples, but the specimens are somewhat damaged and brittle and unreliable for detailed description. This species must remain a doubtful one until further specimens are available. It is omitted from the key given below.

KEY TO THE IDENTIFICATION OF THE SPECIES

1. Fourth segment of pleon with spines directed posteriorly and bristles anteriorly 2
   Fourth segment of pleon with anteriorly directed bristles only ... 5

2. Third epimeral plate, in adult females and young males, with tooth at or near the posterior corner. In adult males the tooth is reduced, its reduction being indicated by an uneven border... 3
   Third epimeral plate evenly rounded at posterior corner 4

3. Third epimeral plate with well-developed tooth at posterior corner which extends beyond the vertical margin of the posterior border (reduced in adult males). Second and third coxal plates with tooth at posterior corner ... ... *guilliamsoniana*
   Third epimeral plate with small tooth almost at the posterior corner, not extending beyond the vertical margin of posterior border (reduced in adult males). Second and third coxal plates without tooth at posterior corner ... ... *pelagica*

4. Basal joint of the antennule rounded at tip; coxal plates II and III with small tooth on posterior corner... ... ... *elegans*
   Basal joint of the antennule produced to a point; coxal plates II and III with well-developed tooth at posterior corner ... *tenuipes*
   Basal joint of the antennule rounded at the tip; coxal plates II and III with well-developed tooth at posterior corner ... ... *gracilis*

5. Third epimeral plate with not more than three groups of spines; basal joint of antennule with a rounded but narrow tip ... ... *pilosa*
Third epimeral plate with from four to six groups of spines; basal joint of antennule with a rounded but broad tip ... ... *sarsi*

ACKNOWLEDGEMENTS

The author desires to acknowledge his indebtedness to Dr K. Stephensen, Dr Sixten Bock and Dr Johan Huus, of the Zoological Museums of Copenhagen, Stockholm and Oslo respectively, for forwarding their collections of the species in this genus for examination; to Dr I. Gordon, of the British Museum, for permission to examine the Spence Bate and Norman collections; to Dr S. Kemp, of the Marine Biological Association, for the loan of the Plymouth collections; to Professor A. D. Hobson, Newcastle, for the loan of specimens from the North East coast and the Hebrides; to Mr G. I. Crawford, of the British Museum, for specimens from the Hampshire coast and information regarding his collections of this genus.

This work was in part carried out at the Laboratory of the Scottish Marine Biological Station, Millport, and my thanks are due to the Director, Mr R. Elmhirst, for facilities afforded me there in collecting specimens and for permission to examine the Robertson collection and the numerous tubes of specimens from many localities around the Scottish coast. Finally, I have to thank Professor R. D. Laurie for his interest in the progress of this research which was undertaken mainly in the Department of Zoology, University College of Wales, Aberystwyth.

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ABSTRACTS OF MEMOIRS

RECORDING WORK DONE AT THE PLYMOUTH LABORATORY

ON THE CILIARY MECHANISMS AND INTERRELATIONSHIPS OF LAMELLIBRANCHS

PART II. SORTING DEVICES ON THE GILLS

By D. Atkins

Quart. Journ. Micr. Sci., Vol. 79, 1937, *pp.* 339–73

The following mechanisms are described: (1) Utilization of plicae for sorting in two ways, (*a*) the frontal currents are in opposite directions in the grooves and on the crests, and particles intended for consumption are carried in the grooves to the safe dorsal channels, e.g. in *Pecten*, (*b*) the plical grooves open into the safe channel at the bottom of the deep marginal groove, while the crests lead to a superficial path along the lobes of the marginal groove, e.g. in *Pinna*. (2) Acceptance and rejection of material by the opening and closing of a deep marginal groove, e.g. in *Solecurtus scopula*. (3) Presence of guarding cilia on the lobes of the marginal groove, preventing the entry of large masses, but allowing that of small particles, e.g. in *Musculus marmoratus*. (4) Presence of cirri (in addition to the usual frontal cilia), which remove grains of sand and rock from the gills, e.g. in *Mactra corallina*, *Barnea parva*.

Small gills and large palps are found in certain deposit feeding bivalves with long free siphons, and forwardly beating cirri on the ends of the gills provide extra help to draw the current down the long inhalent siphon.

Certain of the ciliary structures are clearly adaptive, correlated with feeding difficulties incidental to the habitat. A preliminary sorting of material on the gills, before it is passed on to the palps, is far from unusual in lamellibranchs.

D. A.

ON THE CILIARY MECHANISMS AND INTERRELATIONSHIPS OF LAMELLIBRANCHS

PART III. TYPES OF LAMELLIBRANCH GILLS AND THEIR FOOD CURRENTS

By D. Atkins

Quart. Journ. Micr. Sci., Vol. 79, 1937, *pp.* 375–421

The gills of some ninety odd species (chiefly marine), belonging to sixty genera and forty-one families, have been investigated and grouped under seven main types (with subtypes) according to structure and ciliary currents.

D. A.

ON THE CILIARY MECHANISMS AND INTERRELATIONSHIPS OF LAMELLIBRANCHS

PART IV. CUTICULAR FUSION, WITH SPECIAL REFERENCE TO THE FOURTH APERTURE IN CERTAIN LAMELLIBRANCHS

By D. Atkins

Quart. Journ. Micr. Sci., Vol. 79, 1937, *pp.* 423–45

A form of fusion involving only the cuticle has been found between the dorsal edges of the ascending lamellae of the outer demibranchs and the mantle or visceral mass in *Solen marginatus* Montagu, *Ensis siliqua* (L.), *E. arcuatus* (Jeffreys), *Cultellus pellucidus* (Pennant), *Solecurtus scopula* (Turton), *Lutraria lutraria* (L.), and *Tellina tenuis* da Costa; between the dorsal edges of the ascending lamellae of the two inner demibranchs in *Barnea parva* (Pennant); and between the mantle lobes in the mid-ventral line between the pedal and fourth apertures in *Ensis siliqua*, *E. arcuatus* and *Cultellus pellucidus*. A more advanced stage of fusion occurs in this last position in *Lutraria lutraria*. The histological structure of the junction is described, and is especially considered in relation to the condition of the fourth aperture in the Solenidae.

D. A.

CHOLINESTERASE IN INVERTEBRATE MUSCLES

By Z. M. Bacq and D. Nachmansohn

Journal of Physiology, Vol. 89, *No.* 4, 1937, *p.* 368

The rate of hydrolysis of acetylcholine by muscle is the same in crustaceans (*Homarus vulgaris*), molluscs (*Eusepia officinalis*) and echinoderms (*Holothuria nigra*). The hydrolysis by the muscle of a sea-leech is apparently a little slower.

Cholinesterase is absent from the sphincter muscle of the sea-anemone.

The hydrolysis of acetylcholine by the brain ganglion of *Eusepia* is more than ten times quicker than by muscle.

Z. M. B.

STUDIES IN TUNICATE DEVELOPMENT. III

DIFFERENTIAL RETARDATION AND ACCELERATION

By N. J. Berrill

Phil. Trans. Roy. Soc. B, Vol. 225, 1935, *pp.* 255–326

The development of forty-four species was investigated. The rate of cleavage, gastrulation and of differentiation of larval tissues varies directly with the (volume)/(free surface-area) of the egg and embryo. Cell division ceases at an early stage in the larval structures, cell numbers remaining constant, cell sizes varying with the egg volume. In the permanent organs and tissues cell division continues until a minimal size is reached, so that cell numbers vary with the egg volume.

An increase in proportion of yolk to cytoplasm retards the rate of development up to and including gastrulation. After gastrulation cell division in tadpole tissues has in any case ceased and differentiation is in progress. The rate of this differentiation is retarded to the same degree as early development. But the rate of cleavage and development of permanent tissues becomes progressively accelerated.

Increase in egg volume or increase in proportion of yolk to cytoplasm induces a telescoping of development. The development of larval chordate (tadpole) structure and that of the permanent ascidian structure are virtually independent of one another. N. J. B.

STUDIES IN TUNICATE DEVELOPMENT. IV

By N. J. Berrill

Phil. Trans. Roy. Soc. B, Vol. 225, 1935, *pp.* 327–79

An investigation of budding in *Diazona*, *Tylobranchion*, *Morchellium*, *Enherdmania*, *Endistoma*, *Archidistoma*, *Pycnoclavella*, *Chondrostachys*, *Distaplia*, *Colella*, *Clavelina*, *Diplosoma*, *Perophora*, *Ecteinascidia*, *Stolonica*, *Distomus*, *Polyandrocarpa*, *Symplegina*, *Botryllus* and *Botrylloides*.

Budding is usually correlated with autolysis or antero-posterior regression of the zooid. Regression results from the migration posteriorly of yolk-laden trophocytes. The extent of the migration depends upon the nature of the zooid. Where there is no post-abdomen nor enlarged ventral vessel, the abdomen regresses. Where the ventral vessel is enlarged it becomes congested, forming the buds and allowing the rest of the zooid to regress. Isolation of buds is effected by transverse epidermal constriction. The tissues within the bud depend upon the region constricted by the epidermis. When part of the digestive tube persists, bud development is primarily a regeneration, when absent, a reorganization. Highly specialized tissue can survive but is unable to proliferate. Moderately specialized tissue can proliferate to form more of its own kind but no other. Unspecialized tissues, such as epicardial, septal, or atrial, alone are multipotent. The vascular septum of the ventral stolon has no connexion at any time with the epicardium and cannot be considered as an extension of the epicardium into the stolon for purposes of budding.

N. J. B.

STUDIES IN TUNICATE DEVELOPMENT. V.
THE EVOLUTION AND CLASSIFICATION OF ASCIDIANS

By N. J. Berrill

Phil. Trans. Roy. Soc. B, Vol. 226, 1936, *pp.* 43–70

The morphology and development of the heart and epicardium is described of *Ciona*, *Diazona*, *Phopalea*, *Tylobranchion*, *Enherdmania*, *Sidnyum*, *Endistoma*, *Archidistoma*, *Distaplia*, *Colella*, *Diplosoma*, *Pycnoclavella*, *Clavelina*, *Perophora*, *Ecteinascidia*, *Ascidia* and *Molgula*. A new classification of the Ascidiacea is proposed, based on the nature of the epicardium. The function of the epicardium is found in its most primitive condition in *Ciona*, where it is of a coelomic nature. The importance of the epicardium in the budding stolons of *Diplosoma*, *Aplidium* and the Thaliacea, and as an excretory organ in the Ascidiidae, Styclidae, Pyuridae, and Molgulidae is the result of extreme specialization in different directions of functions present, though poorly developed, in *Ciona*. N. J. B.

CELL DIVISION AND DIFFERENTIATION IN ASEXUAL AND SEXUAL DEVELOPMENT

By N. J. Berrill

Journ. Morph., Vol. 57, 1935, *pp.* 353–427

In ascidians the development of eggs and of buds are in sharp contrast. In bud development cell sizes are minimal throughout. Gross differentiation of form becomes apparent from the beginning, histological differentiation only when cell division is ending. The position of a cell relative to the whole determines its nature. Multiplication of cells continues until sufficient have been formed for the expression of all specific and other characters. In sexual development the egg is a large cell which divides until the minimal cell sizes characteristic of the species are obtained. The course of cleavage is a curve suggesting the attainment of a state of equilibrium. Commencing before fertilization and continuing during cleavage is a precocious differentiation of certain parts that inhibits further cell division and results in the formation of special larval structures that function when a mere fraction of the whole developmental period has elapsed. This differentiation may be suppressed, or may be retarded, without affecting the development of the rest of the egg. In the remaining parts cell division continues until minimal cell sizes are reached, and only then does histological differentiation become apparent, as in sexual development. The number of cells thus formed is very small compared with that necessary for the expression of the full character of the species, and the newly functional post-larval organism is necessarily peculiar in structure. N. J. B.

REGENERATION IN *CLAVELINA LEPODIFORMIS*

By **N. J. Berrill** and **A. Cohen**

Journ. Exp. Biol., Vol. XIII, 1936, *pp.* 352–62

The number of rows of stigmata formed during the development of a stolon fragment varies directly with the size of the fragment. In very small pieces development may become arrested at almost any stage, depending upon the quantity of mesenchyme contained in the proximal region of the stolon piece. If sufficient is present to enable development to proceed to the formation of a functional heart, a circulation is established that includes food reserves in the distal part of the stolon, and development proceeds to completion. In shorter pieces, less than 0·4 mm. long, development or regeneration does not begin. Total failure to develop is correlated with the absence of a region of relatively columnar epidermis. N. J. B.

REORGANIZATION AND REGENERATION IN *SABELLA*. I. NATURE OF GRADIENT, SUMMATION, AND POSTERIOR REORGANIZATION. II. THE INFLUENCE OF TEMPERATURE. III. THE INFLUENCE OF LIGHT

By **N. J. Berrill** and **D. M. Mees**

(I) Journ. Exp. Zool., Vol. 73, 1936, *pp.* 67–83. *(II and III) Ibid., Vol.* 74, 1937, *pp.* 61–89

I. When abdominal parapodia are reorganized to form thoracic parapodia during regeneration of a head, a whole thoracic field is imposed at the same time. Failure of regeneration is correlated with a loss of ciliary polarization of original segments. The gradient in time of reorganization of successive segments is due to difference in time of commencement and not to differing rates. Successive decapitations produce a summation of effect. A mixed type of parapodia may appear at the junction of reorganized and normal segments. Posterior thoracic parapodia may appear next to a posterior cut surface. They are to be correlated with a delayed outgrowth of the intestine. Removal of an abdominal parapodium results in the regeneration of a thoracic parapodium.

II. The *rate* of anterior regeneration and that of reorganization have each a temperature coefficient (Q_{10}) of about 2·4. The *range* of reorganization under standard conditions in the dark is about four segments. The range is not affected by temperature, $Q_{10} = 1{\cdot}0$.

III. Light is responsible for reorganization of segments averaging more than four in number. It may increase by twentyfold the number reorganized in the dark. The effective light is within the visible range. It has a threshold intensity of about 15,000 metre-candles below which reorganization is at a minimum. It is most effective during the period of most active morphogenesis, and it acts upon anterior regenerating tissue or tissue adjacent to it.

It is concluded that a photochemical reaction liberates electrical energy rather than a chemical evocator, as a reorganizing force. N. J. B.

The Early Development of Ascidian Eggs

By Arthur Cohen and N. J. Berrill

Biological Bulletin, Vol. 70, 1936, *pp.* 78–88

When unfertilized nude eggs of *Ascidiella aspersa* are stained with Nile Blue it is found that the periphery stains more heavily and is clearly defined from the central region. A tiny peripheral area—the polar pit—remains unstained. Dalcq's statement that the latter is the site of polar body formation could not be confirmed; evidence to the contrary is presented. In the young tadpole the stain becomes confined to the endoderm (gut) and notochord.

Observation on the membraneless nude egg shows that it undergoes a series of changes in shape from the time of polar body formation to first cleavage.

A. C.

A Relation between the Lyotropic Series and Free Energies

By L. H. N. Cooper

Nature, Vol. cxxxix, 1937, *p.* 284

A relationship is traced between the lyotropic series of anions, which summarizes their behaviour in many physico-chemical reactions, with their free energies of formation.

The position in the series of ions less commonly investigated is forecast together with the probable value for the free energy of formation of the thiocyanate ion. It is suggested that a more quantitative examination of the series from the thermodynamic standpoint may lead to results of value.

L. H. N. C.

Some Conditions Governing the Solubility of Iron

By L. H. N. Cooper

Proc. Roy. Soc., Ser. B, Vol. 124, 1937, *pp.* 299–307.

Since experiment had shown that the amount of ionic iron in true solution in sea water is extremely small, theoretical methods were invoked to calculate the maximum activities of the ions, Fe^{++}, $FeOH^{++}$ and Fe^{+++}, which can exist in sea water at equilibrium. The activity of ferrous ion is controlled by that of ferric ion and by the oxidation-reduction potential of the water, reversible or irreversible. Maximum activities, expressed as mg.-atom/m.^{3} Fe, may be summarized:

			$a_{Fe^{++}}$	
*p*H	$a_{Fe^{+++}}$	$a_{FeOH^{++}}$	Governed by $a_{Fe^{+++}}$ and reversible oxygen potential	Governed by $a_{Fe^{+++}}$ and irreversible oxygen potential
8·5	4×10^{-16}	5×10^{-10}	2×10^{-15}	1×10^{-10}
8·0	$1·3 \times 10^{-14}$	5×10^{-9}	2×10^{-14}	$1·5 \times 10^{-9}$
6·0	$1·3 \times 10^{-8}$	5×10^{-5}	2×10^{-10}	4×10^{-5}

These amounts are all far less than could be detected by the most delicate methods of analysis. Other tables and equations show the effect on the iron system of change in *p*H and oxidation-reduction potential. The results are applicable to all natural waters and to many physiological fluids where equilibrium is attained. L. H. N. C.

ON THE FEEDING MECHANISM OF *APSEUDES TALPA*, AND THE EVOLUTION OF THE PERACARIDAN FEEDING MECHANISMS

By Ralph Dennell

Trans. Roy. Soc. Edin., Vol. LIX, *Pt. I, No.* 2, 1937, *pp.* 57–78

The respiratory current of *Apseudes* is produced mainly by the movements of the pedunculate hemispherical epipodite, which closely invests the rounded and swollen base of the second thoracic limb. The oscillation of the epipodite is effected by the alternate action of the peduncular muscles and fluid pressure within the peduncle. Movements of the second and third thoracic limb exopodite produce currents assisting the respiratory current.

An anterior membranous flap on the epipodite margin controls the filter exit—the lateral gap between maxillule and maxilla—and enables the epipodite to draw a current of water—the filter current—through the filter chamber. The maxilla is thus a passive filter. It bears typical filtratory setae, but the maxillipedal brushing setae are prevented from scraping them effectively by a second row of stouter maxillary setae. True maxillary filter-feeding is therefore of little importance. In addition to raptatory feeding, food particles are retained directly by the maxillipedal brushing setae.

The feeding of *Apseudes* is compared with that of other Peracarida, and the functional evolution of the peracaridan feeding mechanisms is discussed.

R. D.

THE ACTION OF A SINGLE VAGAL VOLLEY ON THE HEART OF THE EEL AND THE TURTLE

By Ernst Fischer

Amer. Journ. Physiol., Vol. 117, 1936, *p.* 596

The chronotropic effect of a single vagal volley is markedly dependent on the cycle phase at which the volley reaches the pacemaker. The experimental results can be explained by the assumption that around the pacemaker there are two mechanisms of liberation of an acetylcholine-like substance (A.C.): a quick mechanism with a short latent period, and a slow mechanism with a long latent period. Vagal fatigue or small doses of atropine depress the quick chronotropic A.C. liberation process more than the slow one. Neither the dromotropic nor the inotropic vagal action is dependent on the cycle phase.

Eserine and acetylcholine act more strongly on the inotropic and dromotropic mechanism than on the chronotropic. The results are interpreted as indicating that the different vagal fibres affecting the heart are not only functionally distinct, but that there exist several chemical transmitters for the vagal action.

E. F.

THE STRUCTURE AND FUNCTION OF THE ALIMENTARY CANAL OF SOME SPECIES OF POLYPLACOPHORA (MOLLUSCA)

By Vera Fretter

Proc. Roy. Soc. Edin., Vol. LIX, 1937, *pp.* 119–64

The anatomy and histology of the alimentary canal of *Lepidochitona cinereus* are described in detail and compared with that of *Acanthochitona crinitus*, *Ischnochiton magdalenensis* and *Cryptochiton stelleri*. All agree in the most important points. The physiology of the gut is studied in *Lepidochitona cinereus* and *Acanthochitona crinitus*.

The buccal cavity containing the odontophore, the openings of a pair of salivary glands and the subradular sac, leads into the oesophagus which expands laterally into a pair of anterior pouches and receives the ducts of a pair of posterior pouches or "sugar glands". The "sugar glands" secrete a diastatic enzyme which passes with the food into the stomach, where it is also mixed with a proteolytic enzyme secreted by the digestive gland. The products of digestion and the undigested food are passed into the anterior intestine whence the soluble products are squeezed into the liver ducts by the action of an intestinal valve or sphincter. The valve regulates the passage of food through the gut and also shapes the oval faecal pellets, which are further moulded and coated with secretion from the gland cells in the extensive coils of the posterior intestine.

Structurally the alimentary canal shows remarkable similarity to that of the lower gastropods.

V. F.

I. AMPHIPODA. II. DECAPOD LARVAE FROM NEWFOUNDLAND WATERS

By Nancy Frost

Reps. Faunistic Series No. 1, *Div. Fish. Res. Nfld.*, 1936

The Amphipoda and decapod larvae collected in Newfoundland waters during the period beginning fall 1931 and ending fall 1935 are listed. Of the twenty-eight species of Amphipoda, eight belong to the Hyperidea and twenty to the Gammaridea. Of the latter, one is a new species of the genus *Hippomedon*. This is described and figured.

Decapod larvae of sixteen species are recorded with detailed descriptions where necessary. The most common were found to belong to the genera

Pandalus, *Spirontocaris*, and *Hyas*. Of these the megalopa attributed to *Hyas araneus* (Linn.), apparently, has not been described before. Among the less common decapod larvae are species belonging to the genera *Caridion*, *Pontophilus*, *Sabinea*, *Cancer* and *Latreillia*. In addition a description is given for the first time of a young stage of *Latreutes fucorum* Stimpson. N. F.

THE LIFE HISTORY OF SOME MARINE PLANKTON DIATOMS

By F. Gross

Phil. Trans. Roy. Soc. B, Vol. 228, 1937, *pp.* 1–47

The observations and experiments described were made on cultures of *Ditylum Brightwelli* and several other species.

Mitosis was found to be very similar to that of other algae. Resting spores occurred regularly in *Ditylum* cultures during autumn, winter and early spring, not in summer. They are spherical bodies formed inside the parental shell by contraction of the protoplast.

The interaction of three factors was found to cause the formation of resting spores: (1) changes of the medium due to crowding; (2) low temperature; (3) low light intensity. Before the density of the cultures reaches such a degree that persistent resting spores are formed, their formation takes place for some time overnight, followed by germination in the course of the next day. The process of germination is described.

A continuous decrease of the average cell diameter could be established in all the species investigated. When the diameter of the diatoms reaches a certain minimum size no further division is possible and they perish unless they form auxospores which develop into big cells. Formation and development of auxospores are described. It only takes place in diatoms of a certain diameter, and may be induced by environmental factors.

Cytological observations support the view that reduction division and an autogamic sexual process precede auxospore formation. No microspores take part in this process. F. G.

THE NERVE NET OF THE ACTINOZOA. V. TEMPERATURE AND FACILITATION IN *METRIDIUM SENILE*

By D. M. Hall and C. F. A. Pantin

Journ. Exp. Biol., Vol. XIV, 1937, *pp.* 71–8

The chief protective response of *Metridium* is due to the contraction of the longitudinal mesenteric muscles and not to contraction of the sphincter as in *Calliactis*.

A simple apparatus for electrical stimulation of Actinozoa is described.

As in *Calliactis*, the response to electrical stimulation in *Metridium* does not depend on the intensity of individual shocks but on their number and frequency; moreover, *Metridium* obeys the rule that a stimulus produces no effect. As in *Calliactis*, graded responses can be produced in *Metridium* by varying the frequency of stimulation. The longitudinal mesenterics require the highest frequency for a facilitated response, the parietals require a lower frequency and the sphincter requires a relatively high frequency but its action is delayed owing to its slow rate of contraction. The graded responses of different muscles to stimulation are controlled by facilitation; they are not connected with differences in threshold.

Both contraction and relaxation of *Metridium* are slowed at low temperatures ($Q_{10} = 2$). The facilitating effect of a stimulus endures more than three times longer for a fall in temperature of 10° C. Temperature thus greatly influences the decay of the facilitation process. D. M. H.

A Study of the Histology of the Pituitary Gland of the Skate

By N. H. Howes

Quart. Journ. Micr. Sci., Vol. 78, *Pt.* 4, 1936, *pp.* 637–51

A study has been made of the pituitaries of young and adult *Raia maculata* Mont., *R. clavata* L., and *R. brachyura* Laf.

The gland shows two distinct regions of growth whose size can be correlated with the size of the animal. These are situated at the anterior and posterior end of the pars anterior.

The pars anterior can be subdivided into three regions differing by the staining reactions of their constituent cells: (*a*) an anterior region where deep purple chromaphil cells are found; (*b*) a middle, where they are faintly basiphil; and (*c*) a posterior, where they are mainly acidophil.

It is suggested that these regions are homologous with the pars tuberalis, basiphil, and oxyphil areas respectively of the pars anterior of the mammalian pituitary.

The ventral lobe is a completely separate structure from the pars intermedia, although it may run along the ventral surface of the latter for some distance.
N. H. H.

On the Protozoan Parasites of *Calanus finmarchicus* in the Clyde Sea Area

By Margaret W. Jepps

Quart. Journ. Micr. Sci., Vol. 79, 1937, *pp.* 589–658

An account is given of the parasites reputed to be of protozoan nature which where observed in *Calanus finmarchicus* in the Clyde Sea Area during the years 1933 to 1936. These comprise *Blastodinium*, *Syndinium*, some gregarines, an ectoparasitic ciliate new to science, *Paradinium*, *Ellobiopsis*, and *Ichthyo-*

sporidium, besides early stages in the development of some platyhelminth worms. A special study is made of *Paradinium*, which was plentiful throughout the summer months, and of the effect of the plasmodial parasites on their hosts.

M. W. J.

STUDIES IN SUBLITTORAL ECOLOGY. II. RECOLONIZATION AT THE UPPER MARGIN OF THE SUBLITTORAL REGION; WITH A NOTE ON THE DENUDATION OF *LAMINARIA* FOREST BY STORMS

By J. A. Kitching

Journ. Ecol., Vol. XXV, 1937, *pp.* 482–95

Recolonization of artificially denuded rock surfaces at the upper margin of the sublittoral region was followed during a period of two years. On an upward-facing horizontal surface at Dancing Ledge, Dorset, an area originally densely populated by *Corallina squamata* was colonized in the first year by *Himanthalia lorea* and various non-calcareous red algae. *Corallina* reappeared in the second year. It was concluded that normally *Corallina* excluded these early colonists by occupying all the available space. The motile fauna was little affected by changes in the algal population, but sedentary molluscs did not become established on the non-calcareous red algae.

On a denuded overhanging rock surface at a similar level in Wembury Bay, Devon, for an area originally populated by *Distomus variolosus* (Tunicate) and sponges, the sequence of recolonization was (1) *Balanus* spp. within the first half year, (2) *Lomentaria articulata* (red alga), various hydroids, *Halichondria panicea*, and *Diplosoma listerianum* (Tunicate) within the first year, (3) *Distomus variolosus* in the second year. It was concluded that *Distomus* normally restricts the earlier colonists by occupying most of the available space, but that hydroids and *Lomentaria* might remain projecting through the carpet of *Distomus*.

From an examination of *Laminaria* plants cast up by storms, it was concluded that—for the occasions in question—neither overloading of the stipes with epiphytes nor the depradations of the limpet *Patina pellucida* had contributed materially to the uprooting of the *Laminaria*. It was also concluded that in the sublittoral region *Balanus crenatus* was an early colonist of storm-denuded rock surfaces, but that this barnacle was eventually overgrown by *Laminaria*.

J. A. K.

COLOUR CHANGES IN *HIPPOLYTE VARIANS*

By L. H. Kleinholz and J. H. Welsh

Nature, Vol. 140, 1937, *p.* 851

A repetition of certain of the observations of Keeble and Gamble on colour changes of *Hippolyte varians* confirmed most of their findings. There is a distinct nocturnal blue phase and a darker day phase and these are due to changes in light conditions accompanying day and night. These phases persist, to some extent, when the eyes and eye-stalks are removed due to a direct effect of light on the chromatophores. There is in this species, however, no persisting diurnal rhythm in colour change under constant illumination or in constant darkness as claimed by Keeble and Gamble.

The crustacean eye-stalk hormone, when injected into *Hippolyte* in which the dark chromatophore pigments are dispersed, causes a concentration of these pigments and the appearance of the diffuse blue in the surrounding tissues; hence, in this respect, *Hippolyte* is like other members of the group Natantia which have been studied. J. H. W.

The Activity of the Horizontal Semicircular Canal of the Dogfish, *Scyllium canicula*

By Otto Löwenstein and A. Sand

Journ. Exp. Biol., Vol. XIII, 1936, *pp.* 416–28

The responses of the ampullary sense organ of the horizontal semicircular canal of *Scyllium* were investigated with an amplifier and oscillograph. The organ was stimulated by rotating the fish on a large turntable in the horizontal plane. It was found that these receptors, like the receptors of the lateral line, display a spontaneous activity which gives rise to a persistent discharge of impulses in the nerve. The discharge is increased during ipsilateral rotation.

During contralateral rotation the discharge is abolished or reduced. This is a type of sensory effect which has not been hitherto described. It shows how a sense organ can discriminate the two phases of a two-way stimulation. The observation helps to account for the way in which an operated animal with only one functional labyrinth can still perform reflex responses to both clockwise and anticlockwise rotation. A. S.

A Coccidian from the Eggs of *Thalassema neptuni* Gaertner

By D. L. Mackinnon and H. N. Ray

Parasitology, Vol. XXIX, *No.* 4, 1937, *pp.* 457–67

A certain percentage of female echiurid worms of the species *Thalassema neptuni* at Plymouth have their eggs parasitized by a large sporozoan which Ray Lankester (1885) named *Monocystis thalassemae.*

The organism, although vermiform when adult, is not a gregarine. Gametogenesis and sporogony are those of a typical coccidian. The number of chromosomes is seven and the reduction division is zygotic.

The schizogonic phase occurs in the same situation as do the sexual forms, i.e. in the eggs of the host, as these lie in the genital pouches.

A new genus, *Ovivora*, is created for this sporozoan, which should now be named *Ovivora thalassemae* (Lankester). Its affinities seem to be with the Aggregatinae. D. L. M.

ON THE NERVOUS SYSTEM OF THE STARFISH *MARTHASTERIAS GLACIALIS* (L.)

By J. E. Smith

Phil. Trans. Roy. Soc., B, Vol. 227, 1937, *pp.* 111–73

This account of the distribution of the nervous elements, sensory and motor, in the starfish *Marthasterias glacialis* shows that the sensory elements are primary sense cells distributed throughout the entire ectoderm (4000 or more per sq. mm. of surface), but especially numerous in the tube feet and around the bases of the spines and pedicellariae. Below the ectoderm is a plexus of neurofibrils constituted by the central fibres of the sense cells and by the fibrillae of association ganglion cells. The subepithelial plexus is especially well developed in the radial cords, the circumoral nerve ring, and in the tube feet, where it exhibits a zoning which has been interpreted as indicating a polarity of the nervous system in that impulses are conveyed via the tube feet and radial cords to the co-ordinating centres of the circumoral nerve ring.

The motor system is represented by fibrils situated internal to the subepithelial plexus and separated from it by a boundary zone of connective tissue. The latter is, however, penetrated by neurofibrils so that the sensory and motor divisions of the system are in intercommunication.

The motor system consists of Lange's nerves—below the radial cords and nerve ring—and of a lateral motor system. The latter is made up of segmentally arranged nerves which arise at points lateral to the tube feet and opposite the adambulacral ossicles. These nerves enter the perivisceral cavity of the arms and run in the coelomic epithelium where they innervate the circular, longitudinal and apical musculature of the arms.

An account is also given of the histology of the nervous elements of the optic pits and of the sensory-motor arcs of the pedicellariae.

J. E. S.

STUDIES ON THE PHYSIOLOGY OF *ARENICOLA MARINA* L.

PART I. THE PACE-MAKER ACTION OF THE OESOPHAGUS, AND THE ACTION OF ADRENALINE AND ACETYLCHOLINE

By G. P. Wells

Journ. Exp. Biol., Vol. XIV, 1937, *p.* 117

Lugworms were placed in glass tubes, designed to resemble the burrow, and watched. The majority showed a well-marked activity cycle, periods of anterior end activity (either proboscis extrusion or acts similar in nature but less vigorous in execution) alternating with periods of rest. Each activity cycle occupies $6{\cdot}6 \pm 2{\cdot}13$ minutes. It is suggested that *Arenicola* normally feeds in periodic outbursts, corresponding to this activity cycle.

By considering a series of dissected preparations, it can be shown that the activity cycle is due to a pace-maker action of the oesophagus. Outbursts of rhythmic activity originate in the oesophageal wall, and the excitations travel, via the neuromuscular structures in the wall of the proboscis, to the nerve ring and nerve cord, and thence to the body-wall musculature of the anterior end of the worm.

Application of adrenaline excites the oesophagus, which now discharges a continuous series of rhythmic excitations forwards into the proboscis and body wall. If intact worms are injected with adrenaline, they continue, for half an hour or longer, to show vigorous rhythmic burrowing movements. Acetylcholine causes partial contracture of the oesophagus, but does not significantly modify its normal rhythmic pattern.

Some biological implications of these results are discussed.

G. P. W.

NOTICES OF BOOKS

Marine Algae of the North-eastern Coast of North America

By William Randolph Taylor

Illustrated by Chin-Chih Jao. Ann Arbor: University of
Michigan Press, 1937. Price $5.

The book opens with a brief discussion of the geographical distribution and habitats of the algae, and useful directions as to methods of collection and preservation. There then follows a systematic list and key to the orders. Save for a casual mention in the introduction, the Myxophyceae have not been considered at all, though their description occupies over one-tenth of Prof. Newton's book on British Seaweeds. The bulk of the book consists of a description of the Chlorophyceae, Phaeophyceae and Rhodophyceae; the space they occupy is in the respective percentage proportions 19, 32 and 49. This is all excellently done, and reveals the author's intimate knowledge of his subject. In cases of doubt the type specimens have been consulted, and certain early identifications of European species have been rejected. But the author admits that certain of these have appeared and disappeared, probably several times over.

There is an ample bibliography and the sixty plates, each with numerous figures, are well chosen and well executed. The illustrations range from reductions to high magnifications.

The book is clearly printed and the price extremely reasonable. It can be warmly recommended. W. R. G. Atkins.

An Abridged Check List and Bibliography of West North American Marine Mollusca

By A. Myra Keen. Stanford University Press

Oxford University Press: Humphrey Milford. Price 7*s*. net.

This small book includes an enormous amount of information and is extremely useful to every conchologist. Its purpose is twofold: "to systematize published information on West American Mollusca and to supply biostatigraphers with a list of midpoints-of-range corrected to date". Anyone who masters the preliminaries of the system employed, which is simple, can use this list with advantage. Those who are not statisticians will be grateful for the bibliographical information. The list is printed in imitation typewriting, but the whole volume is compact and neat. M. V. L.

MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM

Report of the Council for 1937

Patron.

The Council has been informed that His Majesty the King has been graciously pleased to continue the Patronage granted by King Edward VIII to the Marine Biological Association of the United Kingdom.

The Council and Officers.

Four ordinary meetings of the Council have been held during the year in the rooms of the Royal Society, London, at which the average attendance was fifteen. The thanks of the Association are due to the President and Council of the Royal Society for allowing their rooms to be used.

The Council has learnt with very deep regret of the death of Mr E. T. Browne, a Governor of the Association. For many years and through times of much difficulty Mr Browne has been a staunch supporter of the Plymouth Laboratory and his death deprives the Association of one of its most generous benefactors. An obituary notice is being published in the Journal.

The Council also regrets to record the death of Mr R. L. Newman, a Governor representing the Fishmongers' Company. For a number of years Mr Newman has been a regular attendant at Council meetings and actively assisted each year in the work of the Visiting Committee appointed annually by Council to inspect the Laboratory.

The Allen Tablet.

A tablet commemorating Dr E. J. Allen's long service with the Association has been erected in the entrance hall of the Laboratory. It was unveiled by the Chairman of Council on July 8. The ceremony was attended by some members of Council, by all the Laboratory staff and visiting research workers, and by a number of Dr Allen's personal friends.

The Plymouth Laboratory.

The exterior of the Laboratory premises has been painted where needed. In the main building, at the west end, alterations and repairs effected at comparatively low cost have provided a well-equipped plunger-jar room on the first floor, improved office accommodation next door, a cloak room for laboratory attendants on the second floor, and a small store on the landing between the ground and first floors. At the same time the entrance hall and passage to the tank room, the staircase to the first floor and the passage to the main laboratory have been repainted and renovated. Plans have been approved and an order placed with G. Little and Co., Plymouth, for the replacement of certain worn-out sections of the pipe plant conveying sea water to the tank room and laboratory. Flanged glass-lined pipes and stainless steel cocks are being used throughout.

Work on the erection of a constant temperature building, situated between the north building and the Citadel wall, has been begun. The cost of the building and its equipment has been defrayed by a grant of £600 from the Rockefeller Foundation, a bequest of £150 from the estate of the late Dr Florence Buchanan and an anonymous contribution of £50.

The Aquarium.

The Aquarium has been particularly well stocked with both fish and invertebrates throughout the year and the general conditions of health have been very good. A reflector arranged above the mackerel tank has made some improvement to the lighting in what is the darkest corner of the aquarium. A shoal of over forty mackerel has recently been caught and is doing well. The number of visitors has been well up to the average of approximately 32,000 per annum, and the usual parties of school children in charge of their teachers have taken advantage of the educational value of the exhibits.

The Ship and Motor Boat.

The steam-drifter *Salpa* has given regular and satisfactory service since the completion of Lloyds' full-time survey at the end of last year. The Council is pleased to be able to report that the unforeseen expenditure incurred in the survey has been generously met by His Majesty's Treasury on the recommendation of the Development Commissioners.

The motor-boat *Gammarus* has also been in continuous commission throughout the year, although with the increasing age of the engines minor breakdowns have become more frequent.

The Staff.

Dr M. V. Lebour resumed full-time duty in April. Mr G. A. Steven was promoted to the grade of Naturalist as from April 1, 1937. In other respects the Staff remains the same as in the previous year.

Jewish Scholarship.

Dr Fabius Gross left the Laboratory at the end of September to take up an appointment as Lecturer in Experimental Zoology in the University of Edinburgh. Some of his cultures of phytoplankton organisms have been entrusted to Mr D. P. Wilson for care and maintenance. The Council have to thank the Development Commission for providing half of Dr Gross's salary for the months of August and September.

Ray Lankester Investigator.

Dr S. Ochoa, University of Madrid, was appointed Ray Lankester Investigator during the year. He commenced work at the Laboratory on July 5, for a period of five months, the subject of his research being phosphorylations in invertebrate muscle and the role of cozymase therein.

Dr Hilary B. Moore.

Dr Moore left the Laboratory at the beginning of November to take up an appointment as Assistant to the Director of the Bermuda Biological Station. He has presented to the Laboratory named collections of marine algae and barnacles and preparations showing the forms of the faecal pellets in a large number of marine animals.

Occupation of Tables.

The following investigators have occupied tables at the Plymouth Laboratory during the year:

Dr E. Baldwin, Cambridge (Biochemistry of the electric organ of *Raia*).
Dr E. J. W. Barrington, Nottingham (Digestion in *Amphioxus*).
Dr A. M. Bidder, Cambridge (Cephalopod digestion).
Dr J. Y. Bogue, London (Library).
Dr D. Brown, New York (The respiratory rhythm and activity of the electric organ in *Raia*).
The late Mr E. T. Browne, Berkhamsted (Medusae).
J. S. Colman, Farnham (*Idotea*).
L. R. Crawshay, lately Officer for Sponge Research, British Honduras (Sponges).
P. R. Crimp, Sheffield (Microfauna).
Capt. G. C. C. Damant, Cowes (Swim bladder gases).
Dr J. F. Danielli, London (Library).
Miss M. J. Dibb, London (Life history of protozoan parasites in Polychaete worms).
E. Downing, London (Calcification of tissue).
J. E. Forrest, London (Anatomy and physiology of *Archidoris* and other Nudibranchs).
Dr Vera Fretter, London (Food storage and excretion in Molluscs. Physiology and structure of the alimentary canal in *Philine*).
Miss E. G. Geiler, Southport (*Talitrus*).
Prof. Pol Gerard, Brussels (Excretion of dyes in the Selachians).
R. Goode, Cambridge (Nerve-net in sea anemones).
Prof. E. S. Goodrich, Oxford (*Phascolosoma* and Sponges).
Mrs H. Pixell-Goodrich, Oxford (Parasites of *Phascolosoma*).
Dr F. Gross, Vienna and Berlin (Rearing of marine organisms).
Prof. A. C. Hardy, Hull (Vertical migration of plankton).
Dr F. R. Hayes, Halifax, N.S. (A quantitative study of the electrolytes in molluscan blood and muscle).
Miss P. M. Jenkin, Bristol (Diatoms).
R. R. M. Jones, Anglesey (*Littorina rudis*. Chironomid larvae. Trematode parasites of *Cardium*).
Dr B. Katz, London (Excitability of crab-nerve).
Dr J. A. Kitching, Bristol (Library).
Dr L. H. Kleinholz, Cambridge, Mass., U.S.A. (Colour change in crustaceans and fishes).
J. Ledingham, London (Nerve excitation in crabs).
Dr A. M. Lysaght, New Zealand (Breeding of *Littorina neritoides*).
Dr R. J. Lythgoe, London (Visual purple of fishes).
E. G. MacGregor, Cambridge (Nerve-net in sea anemones).
Miss M. F. Mare, Cambridge (*Upogebia*).
Dr H. Maresquelle, Strasbourg (Marine algae).
H. D. Metten, London (Ovulation in dogfish).
A. Milne, Aberdeen (Estuarine fauna).

Dr H. B. Moore, Plymouth (Littoral ecology).
Dr A. G. Nicholls, Millport (Herring biometrics).
J. A. Nicholson, Bristol (Ecology of a mud flat at Wiveliscombe).
Dr E. Steemann Nielsen, Copenhagen (Plankton).
Dr C. L. Oakley, London (Parasitic copepods from fishes).
Dr S. Ochoa, Ray Lankester Investigator (Phosphorylations in invertebrate and fish muscle).
Miss G. M. Osborne, London (Library).
Dr C. F. A. Pantin, Cambridge (Nerve-net in sea anemones).
Mrs C. F. A. Pantin, Cambridge (Feeding in sea anemones).
D. A. Parry, Bristol (Feeding and digestion in *Sagitta* and *Spadella*).
Miss D. Pelluet, Halifax, N.S. (A quantitative study of the electrolytes in molluscan blood and muscle).
E. L. Pierce, Jr., Florida (Marine plankton).
Miss M. Leyborne Popham, Bristol (Studies in the Leptonidae).
Dr R. J. Pumphrey, Cambridge (Physiology of the central nervous system of Lamellibranchs).
R. D. Purchon, Bristol (Byssus of bivalves and ciliary mechanisms in *Teredo*).
M. Ramadan, Cairo (Library. Plankton).
E. C. Reeve, Oxford (Statistical methods in allometry).
D. M. Ross, Cambridge (Nerve-net in sea anemones).
Miss A. Rothschild, London (Life cycle of Cercariae).
Miss M. Rothschild, London (Parasitic Trematodes).
A. Sandison, Cambridge (Proprioceptive reflexes in *Carcinus*).
Dr D. L. Serventy, Australia (Library).
J. E. Smith, Sheffield (Library).
J. F. Spalding, Bristol (Sexual physiology of *Carcinus*).
Miss F. A. Stanbury, Plymouth (Silica in Diatoms).
Dr E. Stauffer, Switzerland (General Zoology).
Prof. and Mrs T. A. Stephenson, Cape Town (Intertidal ecology).
Dr S. Suneson, Lund, Sweden (Life history of red algae).
Dr W. F. Thompson, Seattle, U.S.A. (General).
Miss V. Waldes, Prague (Chemical influences on barnacles).
D. A. Webb, Cambridge (Chemical relations between marine invertebrates and their environment).
G. P. Wells, London (Physiology of *Arenicola*).
Dr J. H. Welsh, Cambridge, Mass., U.S.A. (Diurnal rhythms in Crustacea).
Prof. and Mrs C. M. Yonge, Bristol (Biology of *Nucula*).
J. Z. Young, Oxford (Physiology of the nervous system of Cephalopods).
O. Zammit, Malta (General fishery work).

The usual Easter Vacation Course in Marine Biology was conducted by Mr D. P. Wilson and Mr G. A. Steven, and was attended by forty students from Oxford, Cambridge, London, Edinburgh, Dublin, Sheffield, Birmingham and Bristol.

During the Summer Vacation, a Course of Marine Biology was conducted by Prof. J. H. Orton, assisted by Miss Ruth Rawlinson. Sixteen students attended from Cambridge, London, Dublin, Liverpool, Southampton, Bristol, Aberystwyth, Plymouth and Paris.

During the Easter Vacation, Mr J. M. Branfoot brought nine students from Oundle School, Mr P. H. F. White two from Harrow, Mr A. H. Lewis three from Wellington College, Dr W. L. Francis two from Repton School, Mr C. B. Owen two from Malvern College, and Mr A. H. Pott five from Stowe School. A Botanical Class from Oxford was also held by Dr A. R. Clapham at Easter, and was attended by twelve students.

The R.R.S. *Discovery II* visited Plymouth on her homeward passage from the Antarctic on May 24, providing an opportunity for inspection by the staff of the Laboratory and visiting workers.

The Scientific Work of the Plymouth Laboratory Staff.

Physics and Chemistry of the Environment

Dr W. R. G. Atkins, in collaboration with Dr H. H. Poole, continued the photo-electric measurement of illumination and assisted in the work of the subcommittee of the International Council for the Exploration of the Sea. Provisional recommendations have been made as to the methods and aims of measurements of under-water illumination. Photo-electric cells have also been standardized for other workers.

The results published in collaboration with Prof. N. G. Ball of Colombo, using cells standardized at Plymouth, show the variation in illumination, as the sun's altitude increases up to 90°. For the spectrum as a whole the intensity is much the same at Plymouth and at Colombo, when the altitude of the sun is the same; in the violet, however, the intensity is rather less in Ceylon.

The work at sea has also been published. This was carried out with a much improved zero-resistance circuit and the usual potentiometer-amplifier-telephone null-method, using selenium rectifier cells. Extinction coefficients were obtained for infra-red, six regions in the visible spectrum, and for the ultra-violet.

Much of Dr Atkins's time has been devoted to measuring the daily light records in continuation of those already published for 1930. The first nine months of the year are now complete up to 1937, and of the eight years the sum of the daily values is closely the same for 1932, 1933, 1935, 1936 with 1937 and 1931 slightly lower and higher respectively. For 1934 appreciably higher results were obtained, and for 1930 the values are 37% higher than for 1937.

The routine determinations of phosphate in the English Channel, started by Dr Atkins in 1923, have been continued by Dr L. H. N. Cooper. For some time it has been recognized that the ratio of nitrogen to phosphorus in the sea lies within quite narrow limits. Deviations from a standard ratio of 20 : 1 are termed "anomalies of the nitrate-phosphate ratio" and may prove of value in helping to characterize different bodies of water. Thus Mediterranean water has a high positive anomaly which can be traced for some hundreds of miles after such water has flowed into the Atlantic at a depth of about 800 metres.

A critical review of the nitrogen cycle in the sea, incorporating unpublished work, has been published in the Journal. Evidence has been produced that the oxidation of ammonia and nitrite takes place not only near the sea bottom, as is sometimes supposed, but in mid-water as well.

In collaboration with Dr Harvey, Dr Cooper has continued his studies on the iron cycle in the sea. A considerable number of measurements was made on the reactivity of various iron preparations in sea water. These were really velocity measurements and interpretation was made difficult by absence of precise knowledge of the rate at which ferrous ion reacts with dipyridyl. The work is still in progress.

Theoretical studies on the oxidation-reduction potential of sea water have been completed and published in the Journal. They made possible a further theoretical study on the solubility of different forms of iron which will appear in the Proceedings of the Royal Society. The maximum amount of ferrous ion which can exist in sea water is controlled by the amount of ferric ion and the oxidation-reduction potential of the water. The total amount of iron in true solution at equilibrium does not exceed 4×10^{-7} mg. Fe per cubic metre and of this the greater part consists of $FeOH^{++}$ and ferrous ions.

In the course of other thermodynamical studies it was observed that the order of the anions in the lyotropic series runs closely parallel with the order of their free energies of formation, and this observation was recorded in a letter to *Nature*.

Hydrographic observations have been made throughout the year. The water of exceptionally low salinity which filled the mouth of the English Channel in 1936 has now been replaced by waters of higher and more usual salinities. The winter values of phosphate, as in recent years, are still abnormally low.

Plankton

Dr H. W. Harvey has, during the year, finished and published part of an investigation on the occurrence of iron in sea water and its utilization by diatoms. The remaining question, whether iron in stable organic combination occurs in sea water, and can be utilized, is postponed, since Dr Cooper's research on the dissociation of ferrous dipyridyl should lead to more certain methods of estimating the minute traces of iron expected.

Experiments, made during the course of this investigation on the part played by iron in the sea, have indicated that the growth rate of diatoms and the ability of their auxospores to develop are profoundly influenced by some substance or substances in the water other than phosphate, nitrate, silicate and available iron. The influence of a boiling water extract of soil on the growth of diatoms and of various larvae is known. The growth of the diatom *Thalassiosira* in artificial sea water was found (Allen, 1914) to require the addition of either natural sea water or an infusion of *Ulva*. Dr Harvey has obtained evidence that the active principle of "bios" occurring in soil and in *Ulva* is an organic acid, or mixture of acids, insoluble in alcohol and ether. The ethyl ester is soluble in ether, and when this, after it had been reconverted to the acid, was added to cultures of *Ditylum Brightwelli* and *Chlamydomonas* sp., it caused greatly increased growth. It is hoped to separate the active principle or "bios". It has properties which differ from those of α and β auxin and heteroauxin. It is stable and very resistant to bacterial decomposition and in consequence it is likely to be present in sea water.

It has also been found that cystine has a marked effect on the growth of *Ditylum*.

An experiment on the rate at which *Calanus* eat diatoms has also been made by Dr Harvey, in order to link the results of some previous experiments with observations made subsequently by other observers. The results have now been published and the investigation is being pursued further at Wood's Hole.

Mr F. S. Russell has continued the weekly examination of ring-trawl collections with reference to the occurrence of *Sagitta elegans* and *S. setosa* and associated plankton indicators of water movements. The results for 1936 have been published, and the 1937 collections have been worked through to date. The unusual conditions as regards the *Sagitta* population noticed in 1936 have continued, both species being extremely scarce until September when *S. setosa* became abundant. The autumn of 1937 was characterized by the reappearance of *Salpa fusiformis* after a period of five years.

Miss M. V. Lebour has continued her work on lamellibranch larvae and has published an account of the larva and post-larva of *Lima hians* in the Journal. A paper on prosobranch larvae has also been published in the Journal. This brings together what is known of the eggs and larvae of the British Prosobranchs with special reference to their importance in the plankton. The survey shows that our knowledge is by no means complete and many gaps have still to be filled. A very interesting new discovery is the fact that the larva of *Capulus ungaricus*, which was hatched from the egg, possesses an Echinospira larva. The Echinospira shell is much like that of *Velutina*, and it may indicate that *Capulus* is allied to the Lamellariidae and Triviinae, to which this form of larva is apparently restricted, rather than to *Calyptraea* and *Crepidula*. A paper on the larvae of *Kellia suborbicularis* is ready to be published. This mollusc is viviparous and the larvae though minute when they are set free attain a very large size in the plankton before losing the velum, thus differing widely from those of such species as the oyster which live only a few days in the free-swimming stage. Many other lamellibranch larvae have been identified by rearing them for a time. Amongst these are *Ensis* and *Cultellus*, the larvae of which can be distinguished from one another, and *Pholadidea loscombiana*, reared from artificial fertilizations until it lost the velum. The breeding seasons of many species have been ascertained, and it is noteworthy that many breed in autumn and winter.

Among the Crustacea the larvae of the two species of *Porcellana* are being specially studied as they have not as yet been distinguished. A third larva occurs in the Plymouth plankton which must belong to another species, hitherto undetected, and this is probably a *Polyonyx*. A paper on the newly hatched larva of *Spirontocaris spinus*, which differs considerably from those of related species, has been published.

Mr Russell continued his work in collaboration with the late Mr E. T. Browne on a monograph of British medusae and the preliminary typescripts of thirty-two species of Anthomedusae and three species of Leptomedusae have now been completed. Attention has again been paid to the occurrence of medusae in the weekly ring-trawl catches and a paper is now in the press reviewing the medusa population in offshore waters for the last eight years, together with notes on the biology and structure of certain species. In September the early stages of the siphonophore *Muggiaea atlantica* were reared and a short account is now ready for publication.

Mr Russell and Mr W. J. Rees have continued their research on the rearing of hydroids from medusae. They have succeeded in rearing the hydroids of *Amphinema dinema*, *Rathkea octopunctata* and *Mitrocomella brownei*, and have found the hydroid of *Amphinema rugosum*. The results of this work have been published in the Journal.

Mr Rees has in addition made a number of observations on other species. By rearing the medusae from *Clytia gracilis* he has shown that this species is in all probability only a variation of *Clytia johnstoni*. He has found a new species of *Campanulina* which, while itself indistinguishable from *C. acuminata*, produces medusae quite distinct from those of the latter species.

A close study has been made of the genus *Perigonimus*, and in this connexion Mr Rees went for a month to work at the Marine Biological Station at Herdla, near Bergen. The main object of this journey was to obtain *Perigonimus muscoides*, which is the genotype of the genus *Perigonimus*. He was fortunate in obtaining specimens of this species from which the medusae were liberated. The medusa proved to be a species of *Bougainvillia*, a discovery of considerable importance to nomenclature. A number of other interesting specimens was obtained including a hydroid which liberated a medusa which is possibly a new species of *Thamnostoma*. Many specimens of the hydroid *Heterostephanus annulicornis* were found liberating medusae which are almost certainly *Euphysa aurata*. Mr Rees had previously published in the Journal an account of a young specimen of this hydroid found at Plymouth and he has since found other specimens here.

Mr Rees received a grant from the Challenger Society to cover his expenses while working at Bergen.

Fauna of the Sea Floor (Ecology, Physiology, Genetics)

The examination of the inter-tidal estuarine fauna, particularly that of mud-flats, has made considerable progress this year. Attention has been concentrated on the Tamar Estuary, from St John's Lake to the upper reaches, and Dr H. B. Moore, Mr P. H. T. Hartley and Mr G. M. Spooner have worked in collaboration. The value of the purely biological work has been considerably enhanced by parallel investigations of various physical and chemical conditions in the estuary, conducted by other workers in the laboratory. It has become possible to envisage an ecological survey of considerable scope, and it has been agreed that various contributions shall be published in a series, with a view to bringing the results of different lines of work in as close relation to each other as possible.

Mr Spooner has paid special attention to the estimates of numbers and the general biology of the various animals encountered; he has collected material for a reference collection of estuarine bottom-living forms supplemented, where necessary, from other localities. It is hoped that a paper on the macrofauna of the inter-tidal zone will be ready before long, dealing with the density and zoning of the dominant species, such as *Nereis diversicolor*, *Nephthys hombergi*, *Scrobicularia plana*, *Cardium edule* and *Hydrobia ulvae*. While in quiet situations the mud carries an abundant fauna, it has been found that in areas subject to strong current action there is almost none at all. As is well known, the variety of species decreases rapidly up river, but the total numbers of individuals per unit area in comparable situations show no similar decline. The data are now becoming adequate for an approximate estimate of the total productivity of mudflats as a source of food for estuarine fish and wading birds, though more precise information on the rate of growth of certain species would be desirable before the calculations are put in a final form.

In connexion with this ecological survey of the estuary, Dr Cooper has collaborated with Mr A. Milne in a study of under-water illumination. They used the Pulfrich photometer with filters which divide the visible spectrum into eight approximately equal parts. Extinction coefficients in the estuary are always higher than in the English Channel. In the very turbid water red light penetrates best. They have prepared their work for publication in the Journal, where they will show the relative energy composition of under-water light and suggest ways in which this affects plant life in the estuary.

In the spring Mr D. P. Wilson studied experimentally the settling reactions of the larvae of *Notomastus latericeus*, a worm found in mud or sand. Earlier tentative results were fully confirmed. The new experiments clearly showed that larvae of this species, when provided with mud or sand, metamorphose several days before those left in clean glass vessels or with clean shell gravel. Mud perhaps induces slightly more rapid settling than does sand. A paper has been published which records these results and discusses their bearing on problems concerning the distribution of the bottom fauna.

A description of an unusual specimen of *Eulalia* with a secondary tail has been published. In the majority of known examples of bifurcation in annelids the forking has been lateral, whereas in this specimen it was dorso-ventral, originating probably through injury to the ventral nerve cord.

During the past three years Mr Wilson has been keeping a regular record of tank temperatures and the habits and death rate in the aquarium of *Sepia officinalis*. Deaths tend to occur during or shortly after falls in temperature such as are brought about by frosty weather. Owing, however, to the present impossibility of controlling the temperature of a large tank results are sometimes difficult to interpret. It is nevertheless clear that below about 11° C.

little or no feeding takes place and the *Sepia* are relatively sluggish and in poor health.

Continuing his experiments on the physiology of the sense organs of fishes Dr A. Sand has completed the first part of an investigation on the lateral line, and this has been published in the Proceedings of the Royal Society. The main results of this work were obtained by a special technique for recording the discharge of impulses in single fibres of the lateral-line nerves when a portion of a lateral-line canal of the ray was perfused with elasmobranch ringer at a controlled rate of flow. This procedure has revealed the great sensitivity of the sense organs to movement of fluid in the canal, and has established the exact proportionality between the rate of flow and the frequency of impulse discharge. The behaviour of this sensory system with reference to displacement of the fluid in the lateral-line canals turns out to be fundamentally the same as that of the sense organs of the semicircular canals of the labyrinth with respect to angular accelerations, as studied last year by Löwenstein and Sand. But whereas in the semicircular canals the sensory mechanism serves to record angular displacement in space, in the lateral-line canals it serves for the perception of vibrations coming from a distance, and the way in which the impulse discharges follow the frequency of low tones, audible to the human ear, produced in the neighbourhood of the fish, justifies the description of the lateral-line system as a form of auditory organ.

Closely associated with the lateral-line organs in elasmobranch fishes are the ampullary canals of Lorenzini. Practically nothing is known concerning their function and Dr Sand has recently begun to study them. So far it has been established that, like the organs of the lateral line and of the labyrinth, they exhibit the property of spontaneous rhythmical nervous activity, and that their specific sensory function is entirely different from that of the other two sensory systems. This work is being continued.

In the course of the year the joint paper by Fessard and Sand on the muscle proprioceptors of the ray has been published in the Journal of Experimental Biology.

Mrs E. W. Sexton and Miss A. R. Clark have continued the experimental work on *Gammarus chevreuxi*, designed to determine the frequency of heterozygosis in the wild.

A sample of 5000 black-eyed animals was taken from a new locality at the head of the tidal water of the River Tavy. Owing probably to the continuous high temperatures during the summer there has been a great mortality in the bowls in the laboratory, and the numbers obtained are not sufficient for satisfactory conclusions. It has, however, been demonstrated that heterozygotes can be obtained from this population, similar to those previously found in Chelson Meadow, and the work is still being carried on.

Considerable progress has been made during the year in putting the charts and records of the whole work on a permanent basis, so that they can be made available for reference and further study at any time in the future.

Fish and Fisheries

Mr E. Ford has completed his first paper on Vertebral Variation in Teleostean Fishes. Thanks to a grant from the Royal Society it has been possible to publish this in the Journal, together with 16 Plates reproducing photographs. The work takes the form of a broad survey of the many interesting and important problems arising from the study of the teleostean backbone, exemplified by extensive data on upwards of one hundred species. Material has been collected for a detailed report on vertebral variation in clupeoid fishes, including the herring.

Mr Ford carried out a routine survey of the winter herring drift-net fishery at Plymouth during the season 1936–37 as in former years. As was to be feared from a knowledge of the condition of the fishery stock during recent years, the yield was again very disappointing. Only 56 East Country steam drifters and 26 Cornish motor drifters participated, and the combined catch for the two fleets during the two months of December 1936 and January 1937 was no more than 3040 cwt. How serious the position has become is shown by a comparison with corresponding figures for the season 1930–31 when 75 Lowestoft steamers and 177 Cornish motors landed a total of 94,811 cwt. valued at £52,973. Indeed, in a number of seasons in the past, landings on a single day have frequently exceeded the total catch for the season 1936–37. As stated in the Report of Council for 1935 and 1936, the paucity of fish on the grounds seems to be the result of the absence of young fish in the visiting shoals since about 1931–32. Why this should be, and when a change for the better may be expected, are questions of the greatest concern. Unfortunately it is not yet possible to answer them.

The lectures on the Nation's Sea-Fish Supply which were delivered by Mr Ford as Buckland Professor for 1936, were published in book form in June.

Mr G. A. Steven, assisted by Mr P. G. Corbin, has continued throughout the year his researches into the biology of the mackerel in western waters. With a view to ascertaining ages and growth rates otoliths have now been collected from 3561 fish. As mentioned in last year's report it is impossible to collect scales from ordinary samples of fish landed on the fishmarkets owing to the extreme smallness of the scales, which are very easily dislodged when one fish rubs against another. As, however, it has been highly desirable to supplement otolith readings with scale readings in as many fish as possible, suitable envelopes have been made into which fish for examination are placed immediately on capture; these have been supplied to selected fishermen. This method has been found to work well with line-caught fish which can be placed straight into the envelopes without handling. It is less successful with drift-net samples as each fish has to be grasped in the hand in order to remove it from the net. In this way most of the scales are rubbed off and other scales which do not belong to the fish become attached to it. Trawl and seine caught fish are always completely devoid of scales.

This year's work has confirmed last year's preliminary finding that the otoliths are readable in the younger fish—i.e. in those having up to three or four broad (? summer) zones in the otoliths. Where unadulterated scale samples have been obtained they agree with the otolith readings. The data thus acquired, though still insufficient for the precise determination of ages and growth rates, are already producing encouraging results.

Examination of the gonads of some 1600 female fish has shown that the mackerel does not get rid of all of one season's eggs in one brief spawning period, as does the herring. The eggs ripen in successive batches. Thus the spawning period of each individual fish and therefore of the population as a whole, is a lengthy one, extending, it appears, over several months of the spring and early summer. This successive ripening of the eggs in the mackerel ovary renders the already established scales of maturity stages inapplicable to this fish. Efforts are being made to devise some other method which can successfully be applied.

One of the major difficulties encountered in elucidating the life-history of the mackerel is the difficulty in obtaining young post-larval fish from 2 to 15 cm. in length. In all the history of fishery investigations only a very few isolated individuals between these sizes have been caught. It is therefore encouraging to report that large numbers of young stages from 9 cm. in length upwards have been obtained during the present year.

Some three thousand skeletons have been prepared and examined with a view to ascertaining whether distinctive racial characters exist. The total number of vertebrae is remarkably constant at 31. It has been found, however, that the number of thoracic vertebrae without haemal arches is variable—9 or 10; rarely 8 or 11—but further data are required before it can be established whether or not this variant has any significance.

Three cruises have been made this year in search of mackerel eggs and larvae, and for the collection of general plankton samples from the mackerel fishing and spawning grounds. One cruise took place in April in the Ministry's research ship *George Bligh*, one in May in a steam drifter, and one in July in a steam trawler. These cruises covered a considerably larger area than could be sampled last year. Examination of the material collected is not yet complete, but will show something of the distribution in space and time of the spawning activities of the mackerel and of the dispersal of the larvae. Last year larval mackerel were collected west of the Channel mouth as early as April 29, which pointed to the probability of spawning activities at least as early as mid-April. This probability was confirmed in April of this year when the westerly plankton samples were found to contain large numbers of mackerel eggs.

The material so far collected has been examined for a possible Sagitta-mackerel correlation.

Plankton samples have also been collected on the fishing grounds by selected commercial drifters working from Newlyn, but these samples have yet to be examined.

The International Council for the Exploration of the Sea, acting on the recommendation of their Atlantic Slope Committee, has appointed a subcommittee for the study of technical methods in mackerel researches. This subcommittee, which comprised representatives of Denmark, France, Germany, Portugal, the Irish Free State and England, met at the Plymouth Laboratory on December 8 and 9.

The observations on the seasonal abundance of the pelagic stages of young fishes have been continued by Mr F. S. Russell throughout the year 1937. The results for the year 1936 have been published in the Journal. In 1937 there has been a repetition of the conditions shown in 1936. The normal peak of the young of spring spawners has been almost completely absent, while there has been a slight improvement in the numbers of young of summer spawners. The year, like 1936, has been remarkable for the numbers of pilchard eggs in the plankton which have continued without interruption from April to November.

Mr P. H. T. Hartley has continued his investigation of the tuck-net fishery in the river Tamar. Monthly examinations have been made of the food of all species of fish taken in the net.

The flounder has been the subject of a special study. In addition to the length and stomach contents of each fish, the weight, sex, gonad condition and otolith reading were recorded. The fish were then handed to Mr D. P. Wilson for examination of the fat content. Mature flounders leave the river at the end of January and go down to the sea to spawn on muddy grounds a few miles offshore. Some females return to brackish water after spawning; but no spent males have been taken in the estuary. Few flounders are taken in the tuck-net during the summer months. The local fishermen say that they wander away among the saltings of the tidal creeks. Attempts were made to catch them there, with fish-spears at low tide, but with little success.

In order to obtain some exact data on growth rates and to investigate the movements of flounders within the estuary, a marking scheme was begun in September, 1937. By November 15, 813 fish had been marked and released at six stations. Several recoveries have already been made, the most remarkable being an 18 cm. female caught in a surface drift-net in 40 feet of water.

For plaice and dabs the estuary is largely a nursery ground. In 1937 the number of O-group fishes of these two species which came into the river mouth was much smaller than in the previous year. O-group flounders are rarely taken in the tuck-net.

Mr Hartley gave some assistance in the Mackerel Investigations in connexion with the vertebral counts and has cooperated with Mr Spooner and Dr Moore in an enquiry into the distribution and ecology of the fauna of the Tamar estuary. During the winter 1937–38 it is hoped to investigate the food of the wading birds by the examination of crop contents.

In his investigations into the histologically stainable fat in the muscular body regions of fishes Mr D. P. Wilson has been paying particular attention to the flounder. This species was chosen for detailed study because of the possibility of utilizing Mr Hartley's material from the River Tamar after the stomach contents etc. had been recorded. Information would thus be available which might in due course be correlated with the fat content. This expectation has to some extent been realized.

In the flounder, as in probably most fishes, there is undoubtedly considerable variation in fatness between individuals irrespective of size, sex or season; it seems evident that some naturally tend to fatness and others to leanness. However, the examination of four to five hundred flounders throughout the year has shown that in general they are lean about February, after a period of slack feeding during the winter, and are fattest in September and October after good summer feeding. A fact of interest is the discovery in some specimens of minute drops of intracellular fat in the fibres of the superficial lateral muscle. It is possible that their presence may eventually be correlated with a stage in the reproductive cycle. At the moment the matter is still being investigated, but results so far point to the deposition of this fat in maturing fish prior to spawning and its loss at or shortly after that event.

Dr Atkins was called upon to advise upon a number of questions in connexion with the preservation of nets and ropes. The clearance of the outlet of the Cawsand fish-pond rendered this again available for immersion tests. Herring-nets treated by about three dozen methods showed that a mixture of copper oleate and coal tar and a new modification of the old cutch bichromate treatment were the best. The tests are being continued to ascertain which of the two is the better. Similar tests with trawl twines are in progress and the herring-net results suggested further modifications which have still to be tested. Two rafts have been constructed and moored in the Sound for anti-fouling tests which are being carried out on behalf of the Admiralty and a firm of paint manufacturers.

The Library.

The thanks of the Association are again due to numerous Foreign Departments, and to Universities and other Institutions at home and abroad for copies of books and current numbers of periodicals presented to the Library, or received in exchange for the Journal. Thanks are also due to those authors who have sent copies of their books or papers, which are much appreciated.

In accordance with a decision of the Council the printing and publication of the Journal has been transferred to the Cambridge University Press. The change took effect from Vol. XXII, No. 1, which was issued in November. The width of the page has been increased in order to give more space for plates and tables, the height remaining unaltered. The revised lay-out of the cover includes a new drawing of the Laboratory.

Published Memoirs.

The following papers, the outcome of work done at the Laboratory, have been published elsewhere than in the Journal of the Association.

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Wykes, Ursula. The photic control of pigmentary responses in teleost fishes. *Journ. Exp. Biol.*, Vol. XIV, pp. 79–86.

Membership of the Association.

Governors. Two of the Governors appointed by the Fishmongers' Company have changed during the year. The new Prime Warden is Col. The Hon. Angus McDonnell, C.B., and the place of the late Mr R. L. Newman has been taken by Admiral Sir Aubrey C. H. Smith, K.B.E., C.B., M.V.O.

Founders. As last year, the number of Founders has been 44, of whom 18 are living.

Vice-Presidents. The Council regret to record the death of two Vice-Presidents, Sir Austen Chamberlain and Dr G. A. Boulenger. Mr Walter E. Elliott on leaving the Ministry of Agriculture and Fisheries has resigned from the Association, and Mr W. S. Morrison, who has succeeded him as Minister, has been proposed in his place as a Vice-President.

Annual Members. The total number of annual members on Jan. 1 1938 was 284, of whom 15 were elected during the year. This is a net increase of 6 over the total of 278 annual members on Jan. 1 1937.

Associate Members. The number of Associate Members has been increased to 4 by the election of Miss Maude Delap.

Finance.

The Council have this year to express their thanks to the Development Commissioners, not only for their continued support of the general work of the Laboratory, but for special assistance to meet unforeseen contingencies, such as the heavy additional cost of the repairs to the *Salpa*. They are also grateful for generous grants from the Fishmongers' Company (£600), the Royal Society (£100 + £55 towards cost of publication of Mr Ford's paper in Vol. XXII, No. 1, of the Journal), the British Association (£50), the Physiological Society (£30), the Ray Lankester Trustees (£20), the Universities of Cambridge (£105), Oxford (£52. 10*s.*), London (£52. 10*s.*), Bristol (£25), Birmingham (£15. 15*s.*), Manchester (£10. 10*s.*), Leeds (£10. 10*s.*), Sheffield (£5. 5*s.*), the Imperial College of Science and Technology (£10), and the Cornwall Sea Fisheries Committee (£10).

The Council are also deeply appreciative of the generous benefactions of £600 from the Rockefeller Foundation, £150 from the estate of the late Miss Florence Buchanan and an anonymous donation of £50, which have made possible the provision of a constant temperature plant at the Laboratory.

Vice-Presidents, Officers and Council.

The following is the list of gentlemen proposed by the Council for election for the year 1938–39.

President

The Lord MOYNE, P.C., D.S.O.

Vice-Presidents

The Duke of BEDFORD, K.G.
The Earl of STRADBROKE, K.C.M.G., C.B., C.V.O.
The Earl of IVEAGH, C.B., C.M.G.
Viscount ASTOR
Lord ST LEVAN, C.B., C.V.O.
The Right Hon. W. S. MORRISON, M.C., K.C., M.P.
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Sir NICHOLAS WATERHOUSE, K.B.E.
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J. O. BORLEY, Esq., O.B.E.
Col. E. T. PEEL, D.S.O., M.C.

COUNCIL

To retire in 1939
- Sir Joseph Barcroft, C.B.E., F.R.S.
- M. Burton, Esq., D.Sc.
- E. S. Russell, Esq., O.B.E., D.Sc.
- J. M. Tabor, Esq.

To retire in 1940
- Prof. H. Graham Cannon, Sc.D., F.R.S.
- Capt. G. C. C. Damant, R.N., C.B.E.
- H. Muir Evans, Esq., M.D.
- Prof. F. E. Fritsch, D.Sc., F.R.S.
- C. F. A. Pantin, Esq., Sc.D., F.R.S.
- J. Z. Young, Esq.

To retire in 1941
- R. S. Clark, Esq., D.Sc.
- A. C. Gardiner, Esq.
- Prof. A. C. Hardy, D.Sc.
- Prof. A. V. Hill, O.B.E., Sc.D., F.R.S.
- Prof. D. L. Mackinnon, D.Sc.

Chairman of Council

Prof. E. W. MacBride, D.Sc., F.R.S.

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Secretary

Stanley Kemp, Esq., Sc.D., F.R.S., The Laboratory, Citadel Hill, Plymouth

The following Governors are also members of the Council:

- G. P. Bidder, Esq., Sc.D.
- The Lord Moyne, P.C., D.S.O.
- H. G. Maurice, Esq., C.B. (Ministry of Agriculture and Fisheries)
- Col. The Hon. Angus McDonnell, C.B. (Prime Warden of the Fishmongers' Company)
- Guy Wood, Esq., M.B., M.R.C.P. (Fishmongers' Company)
- Admiral Sir Aubrey C. H. Smith, K.B.E., C.B., M.V.O. (Fishmongers' Company)
- Prof. E. S. Goodrich, D.Sc., F.R.S. (Oxford University)
- Prof. J. Gray, M.C., Sc.D., F.R.S. (Cambridge University)
- Sir P. Chalmers Mitchell, Kt., C.B.E., D.Sc., F.R.S. (British Association)
- Prof. E. W. MacBride, D.Sc., F.R.S. (Zoological Society)
- Sir Sidney Harmer, K.B.E., Sc.D., F.R.S. (Royal Society)
- E. J. Allen, Esq., C.B.E., D.Sc., F.R.S. (*Honorary*)

LIST OF ANNUAL SUBSCRIPTIONS

Paid during the year, April 1 1937 to March 31 1938

	£	s.	d.
E. J. Allen, Esq., C.B.E., D.SC., F.R.S.	1	1	0
Dr I. Amemiya	1	1	0
Miss D. Atkins	1	1	0
E. Baldwin, Esq.	1	1	0
Prof. Sir Joseph Barcroft, F.R.S.	1	1	0
Miss M. G. Barnes	1	1	0
W. H. Barrett, Esq.	1	1	0
Dr J. B. Bateman	1	1	0
L. C. Beadle, Esq.	1	1	0
R. L. A. Beauchamp, Esq.	1	1	0
G. R. de Beer, Esq.	1	1	0
Miss C. R. Begg	1	1	0
J. Bělehrádek, Esq., M.D.	1	1	0
N. J. Berrill, Esq., D.SC. (1932, 1933, 1934, 1935, 1936)	5	4	0
D. M. Bickmore, Esq.	1	1	0
Birkbeck College	1	1	0
W. Birtwistle, Esq.	1	1	0
Dr H. Blaschko (1937 and 1938)	2	2	0
H. H. Bloomer, Esq.	1	1	0
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	£313	16	0

DONATION TO THE GENERAL FUND

For the year April 1 1937 to March 31 1938

	s.	d.
Jewish Scholarship Fund	14	10
	14	10

THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM

INCOME AND EXPENDITURE ACCOUNT FOR THE YEAR ENDED 31 MARCH 1938

	£	s.	d.	£	s.	d.
To Salaries, including Institution's Contributions to Superannuation				7945	15	8
,, Laboratory Wages, including National Insurance and Institution's Contributions to Superannuation				2498	16	3
,, Depreciation of Library				473	10	8
,, Scientific Publications, *Less* Sales and Grant				392	0	11
,, Upkeep of Laboratories and Tank Rooms:						
Buildings and Machinery	434	15	1			
Electricity, Gas, Coal, Oil and Water	359	2	3			
Chemicals and Apparatus	406	15	6			
Rates, Taxes and Insurance	114	12	11			
Travelling Expenses	94	3	0			
Stationery, Postages, Telephone, Carriage and Sundries	356	0	4			
Specimens	107	4	6			
				1872	13	7
,, Maintenance and Hire of Boats:						
Wages, including Diet Allowance, National Insurance and Casual Labour	1715	8	3			
Coal, Water, Oil, Petrol, etc.	325	2	1			
Maintenance and Repairs with Nets, Gear and Apparatus	484	6	8			
Purchase of Material for Nets for Sale, excluding Labour	468	11	1			
Boat Hire and Collecting Expenses	38	18	5			
Insurance	252	3	8			
				3284	10	2
,, Transfer to Depreciation Reserve Account				290	14	0
,, Transfer to Mackerel Research Fund				15	4	3
,, Transfer to Director's House Reconditioning Fund				225	11	6
,, Transfer to E. T. Browne—Scholarship Grant Fund				100	0	0
,, Balance, being Surplus for the Year				169	10	4
				£17,268	7	4

	£	s.	d.	£	s.	d.
By Grants:						
Ministry of Agriculture and Fisheries Grant from Development Fund	13,204	0	8			
Fishmongers' Company	600	0	0			
British Association	50	0	0			
Royal Society	100	0	0			
Physiological Society	30	0	0			
Cornwall Sea Fisheries Committee	10	0	0			
				13,994	0	8
,, Subscriptions (excluding Subscriptions received in advance)				305	19	3
,, Donation—Jewish Scholarship Fund					14	10
,, Sales:						
Specimens	1098	3	6			
Fish (*less* Expenses)	120	11	5			
Nets, Gear and Hydrographical Apparatus	615	10	9			
				1834	5	8
,, Table Rents (including University of Cambridge £105; Oxford £52. 10*s.*; London £52. 10*s.*; Bristol £25; Birmingham £15. 15*s.*; Manchester £10. 10*s.*; Imperial College £10; Trustees of Ray Lankester Fund £20; Leeds £10. 10*s.*; Sheffield £10. 10*s.*)				471	11	6
,, Tank Room Receipts				580	3	3
,, Interest on Investments, Less Tax:						
General Fund	7	18	8			
Depreciation Fund	40	14	0			
Composition Fee Fund	2	17	6			
,, Interest on Bank Deposit Account (*less* Bank Charges)	1	4	8			
				52	14	10
,, Sale of Dr M. V. Lebour's Book				4	15	4
,, Sale of "Marine Fauna of Plymouth"				6	19	0
,, Income Tax Recoverable				17	3	0
				£17,268	7	4

THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM

BALANCE SHEET 31 MARCH 1938

	£	s.	d.	£	s.	d.	£	s.	d.
SUNDRY CREDITORS:									
On Open Account							650	9	1
PROPORTION OF SUBSCRIPTIONS RECEIVED IN ADVANCE							136	19	9
JEWISH SCHOLARSHIP FUND:									
As at March 31 1937					14	10			
Add: Fifth Instalment received				62	1	8			
Grant received				35	2	6			
	£	s.	d.	97	19	0			
Less: Expenditure	97	4	2						
Donation transferred to Income and Expenditure Account		14	10						
				97	19	0	–	–	–
E. T. BROWNE—SCHOLARSHIP GRANT FUND:									
As at March 31 1937				132	8	4			
Interest on Bank Deposit					7	10			
Transfer from Income and Expenditure Account				100	0	0			
				232	16	2			
Less: Expenditure				208	16	0			
							24	0	2
AQUARIUM GUIDE PRINTING FUND:									
As at March 31 1937				20	0	0			
Sale of Aquarium Guides				8	4	6			
				28	4	6			
Less: Expenditure				1	10	0			
							26	14	6
DR H. B. MOORE—SPECIAL GRANT FUND:									
Grant received				175	0	0			
Less: Expenditure				175	0	0			
							–	–	–

	£	s.	d.	£	s.	d.
BOATS AND EQUIPMENT, as per Valuation as estimated by the Director at March 31 1931						
S.S. *Salpa*	2000	0	0			
Motor Boat	150	0	0			
Nets, Gear and General Equipment	27	0	0			
				2177	0	0
LABORATORY APPARATUS, ENGINES AND PUMPS:						
As per Valuation as estimated by the Director at March 31 1931, plus additions at Cost						
As at March 31 1937	1023	2	5			
Additions during the year (Net)	127	4	0			
				1150	6	5
LIBRARY:						
As per Valuation as estimated by the Director at March 31 1931, plus additions at Cost, *less* Depreciation						
As at March 31 1937	2277	2	4			
Additions during the year	491	13	3			
	2768	15	7			
Less: Depreciation	473	10	8			
				2295	4	11
STOCK OF SPECIMENS, CHEMICALS AND JOURNALS:						
As estimated by the Director				510	0	0
SUNDRY DEBTORS:						
Sale of Specimens, Journals, Nets, Gear and Apparatus				187	7	6
INCOME TAX RECOVERABLE				39	1	11
PREPAYMENTS				114	9	11
GENERAL FUND INVESTMENT at Market Value as at March 31 1931:						
£352. 2*s*. 3*d*. Local Loans 3% ... ... (Market value at date £302. 16*s*. 4*d*.)				232	7	10

MACKEREL RESEARCH FUND:						
As at March 31 1937	56	11	11			
Grant received	543	8	1			
Transfer from Income and Expenditure Account	15	4	3			
	615	4	3			
Less: Expenditure	615	4	3	–	–	–
RESERVE FOR DEPRECIATION OF BOATS AND MACHINERY:						
As at March 31 1937	1744	6	7			
Add: Transfer from Income and Expenditure Account	290	14	0	2035	0	7
COMPOSITION FEE FUND:						
As at March 31 1937				126	0	0
CONSTANT TEMPERATURE ROOMS FUND:						
Special Donations received	800	0	0			
Less: Expenditure	666	15	4	133	4	8
DIRECTOR'S HOUSE RECONDITIONING FUND:						
Grant received	350	0	0			
Transfer from Income and Expenditure Account	225	11	6			
	575	11	6			
Less: Expenditure	575	11	6	–	–	–
SURPLUS:						
As at March 31 1937	6152	16	3			
Add: Surplus for the year as per Income and Expenditure Account	169	10	4	6322	6	7
				£9454	15	4

DEPRECIATION FUND INVESTMENTS at Cost:						
£590. 6*s.* Local Loans 3%	506	10	9			
£1502. 1*s.* 10*d.* Conversion Loan 3%	1528	9	10			
(Market value at date £2017. 5*s.* 2*d.*)				2035	0	7
COMPOSITION FUND INVESTMENTS at Cost:						
£18. 8*s.* 6*d.* Local Loans 3%	15	15	0			
£108. 6*s.* 5*d.* Conversion Loan 3%	110	5	0			
(Market value at date £124. 14*s.* 2*d.*)				126	0	0
CASH AT BANK AND IN HAND:						
Coutts & Company—Current Account	476	10	6			
Lloyds Bank Limited—Current Account	169	7	8			
Cash in Hand	41	18	1			
	687	16	3			
Less: Coutts & Company—Loan Account E. T. Browne—Scholarship Grant Fund	100	0	0	587	16	3
				£9454	15	4

E. J. ALLEN } *Members of Council.*
M. BURTON }

TO THE MEMBERS OF THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM:

We report that we have examined the above Balance Sheet with the books of the Association and have obtained all the information and explanations we have required. Capital expenditure on erection of Buildings on Land held on Lease from the War Department is excluded. Subject to this remark we are of opinion that the Balance Sheet is properly drawn up so as to exhibit a true and correct view of the state of the Association's affairs according to the best of our information and the explanations given to us and as shown by the books of the Association.

34 *and* 35 *Bedford Street,*
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The Journal of
Experimental Biology
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ASSISTED BY
The Hon. Secs. Society for Experimental Biology

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CONTENTS OF No. 320—*New Series*

Volume 80, Part IV, September 1938

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THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM

THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM is a corporate body of subscribing members founded 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 members.

The Association was founded in 1884 at a meeting held in the rooms of the Royal Society of London with Professor T. H. Huxley in the chair. Amongst distinguished scientific men present on that occasion were Sir John Lubbock (afterwards Lord Avebury), Sir Joseph Hooker, Professor H. N. Moseley, Mr G. J. Romanes, and Sir E. Ray Lankester, who 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 £16,000.

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 Resident 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 in September, and marine animals and plants are supplied to educational institutions.

Research work at sea is undertaken by the steam drifter "Salpa" and by a motor boat, which 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.; and 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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LONDON
CAMBRIDGE UNIVERSITY PRESS

PRINTED IN GREAT BRITAIN BY WALTER LEWIS, M.A., AT THE UNIVERSITY PRESS, CAMBRIDGE