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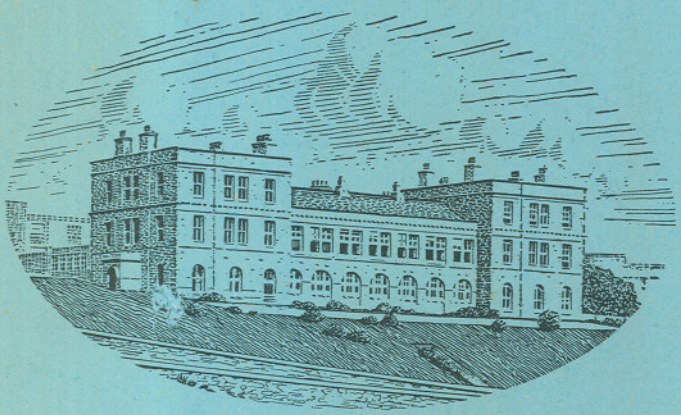

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A NEW BOTTOM-SAMPLER

By N. A. Holme, B.A.
Zoologist at the Plymouth Laboratory

(Plate I and Text-figs. 1–4)

INTRODUCTION

At Plymouth the bottom-fauna is usually sampled by the trawl and dredge, but for quantitative work the $\frac{1}{10}$ m.^{2} Petersen grab is sometimes used. Allen (1899) surveyed the bottom-fauna, on grounds between the Eddystone and Start Point, by means of trawling and dredging only. Ford (1923) has made collections of the bottom-communities near Plymouth, and gives lists showing the densities of species taken with the Petersen grab. Steven (1930) also used this grab for a survey of a limited area, but Smith (1932) resorted to a conical dredge with canvas bag, having found the grab ineffective in shell-gravel.

Davis (1925) has attempted to analyse some of the inaccuracies due to sampling with the grab. To some extent variations in the fauna in successive hauls are due to a patchiness of the fauna in any one soil, and also to the patchy distribution of soils in any one area. Rolling of the ship affects the size of the sample by altering the rate at which the grab hits the bottom and hence the size of the 'bite'. Drifting of the ship tends to decrease the size of the sample, as the grab must be pulled vertically from the soil to take its maximum 'bite'. The volume of the sample also depends on the consistency of the soil, which will affect not only the depth to which the jaws penetrate, but also the amount of material lost during hauling. Thus Smith (1932) found that when sampling on shell-gravel the grab frequently came up almost empty, the jaws having failed to close because of pieces of shell wedged between the teeth.

A further source of error is emphasized by Steven (1930): this is the ability of certain species to evade the grab, either by active burrowing or by normally living at a depth beyond its reach.

Thamdrup (1938) gives an account of the van Veen bottom-sampler, which differs from the Petersen grab by having long arms to the ends of which are attached the cables actuating the closing movement. A considerable leverage effect is thus exerted to close the jaws. In addition, the instrument is probably less likely to leave the bottom prematurely if there is a sudden jerk on the cable due to rolling of the ship. On a sandy bottom the van Veen sampler takes two or three times as much soil per unit area as does the Petersen grab.

Knudsen (1927) describes an ingenious sampler capable of digging to a depth of 30 cm. in sand. Comparable hauls against the Petersen grab (see Johansen,

1927) showed that it brought up ten to twenty times as much soil and four to five times as much animal tissue (by weight) as the latter. This instrument would hardly be suitable for use in the open sea in its present form owing to the risk of loss of material during hauling.

A new sampler has been designed to overcome some of the difficulties of bottom-sampling in the Plymouth area. These may be summarized as: the coarseness of the deposits, which makes penetration difficult and tends to result in considerable loss while hauling; Atlantic swell which makes perfectly calm days rare, so that the speed with which the sampler hits the bottom is variable; and currents which cause the sampler to descend rather obliquely, whether the ship is anchored or not.

I am indebted to Dr H. W. Harvey, F.R.S., and Mr G. A. Steven for suggestions and criticism in the design of the apparatus, and to Mr F. G. C. Ryder for constructing a working model of the grab and for help in many ways. I am also grateful to Captain C. Hoodless and the crew of R.V. *Sabella* for their skill in working the sampler at sea.

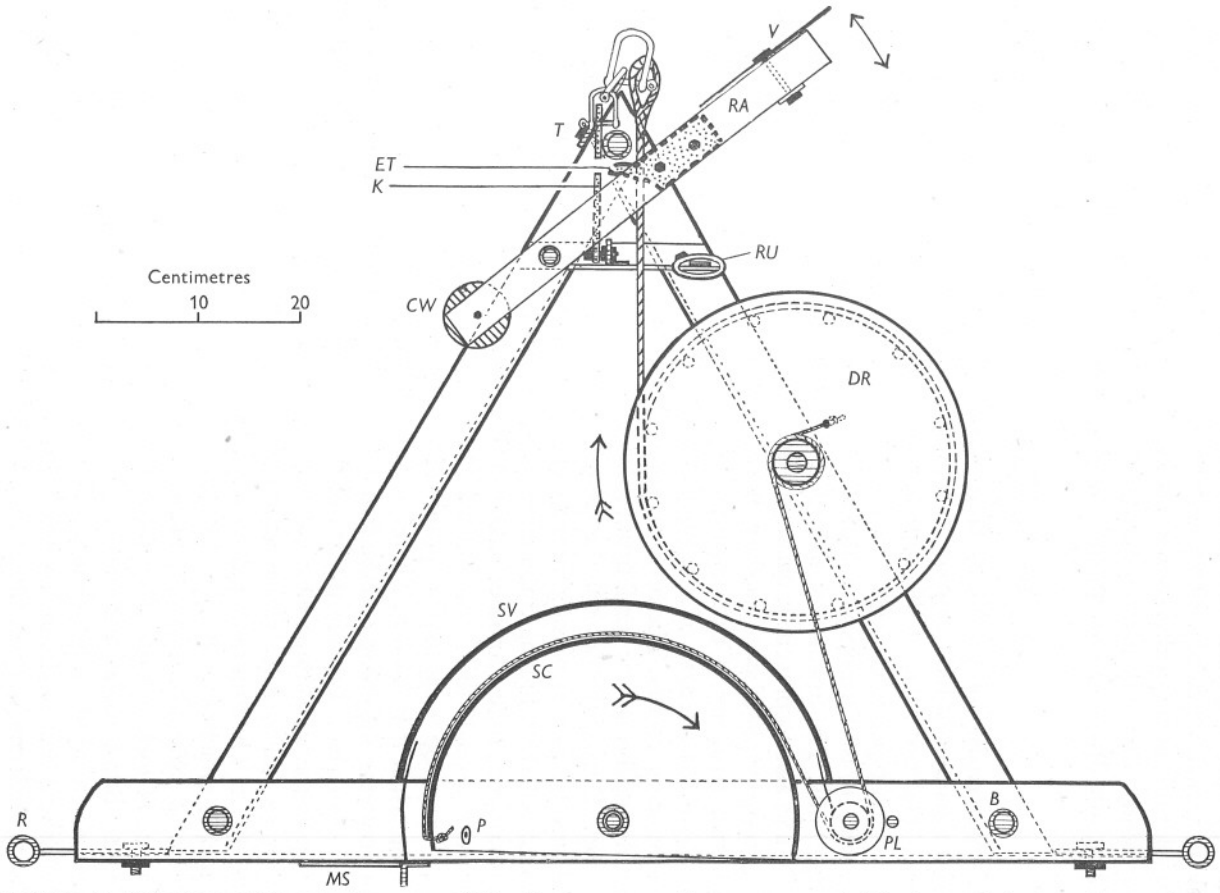
This work was accomplished during the term of a D.S.I.R. Research Grant at the Plymouth Laboratory and I am grateful to the Director and staff for facilities offered me during this period.

Mr F. S. Russell, F.R.S., Mr G. A. Steven and Mr E. Ford have kindly read the manuscript and have made a number of helpful suggestions.

The echinoderms shown in Table I were kindly identified by Mr H. G. Vevers, and some of the molluscs by Miss U. M. Grigg.

The Sampler

This is shown in Text-fig. 1 and in Pl. I, fig. 2. It consists of a frame supporting a semicircular scoop (SC), which rotates through 180° to take a sample. The scoop is actuated by unwinding cable from a large drum (DR) by the side of which is a smaller drum, which winds in a thin cable attached to the scoop. By this means a considerable mechanical advantage is obtained, so that the upward pull on the cable required to close the apparatus is small. Since there is only a single scoop there is no risk of the jaws not closing, and washing out during hauling is probably small, judging by the appearance of the sampler when it is coming up just beneath the surface. The sample is protected by a semicircular cover (SV), but there is a slight loss of soil when the grab breaks the surface and water empties from it. The sampler weighs rather more than 45 kg., and in use it is weighted to about 110 kg. The theoretical size of the 'bite' is a rectangle of $\frac{1}{20}$ m.^{2} surface area, semicircular in section, with a maximum depth of 15 cm. Some animals undoubtedly live below this depth, but observations on the shore and in baths of sand indicate that a very much greater force is required to dig deeper than this.



Text-fig. 1. Side view of the sampler, seen as if the frame on one side were removed. The key and the engaging tooth are stippled. B, frame bolt and distance piece; CW, counterweight; DR, drum; ET, engaging tooth; K, key; MS, transverse metal sheet; P, hole for wooden peg; PL, pulley; R, ring; RA, release arm; RU, metal strip protected by rubber hose; SC, scoop; S V, scoop cover; T, cross-piece holding key in position; V, vane.

The apparatus resembles in some respects the dredge used by Stetson (1938) for taking a small semicircular core of bottom-sediments. Since the design of the sampler was liable to alteration it was largely constructed by bolting rather than welding. The only parts requiring to be made professionally were the large ring, the drum, the scoop, and the scoop cover.

Details of Construction

The frame consists of six pieces of heavy angle-iron, bolted to form two triangles separated at their bases by 17 cm. and at the top by a slightly greater distance. The two sides of the apparatus are joined by bolts and distance-pieces of iron piping ('gas-pipe').

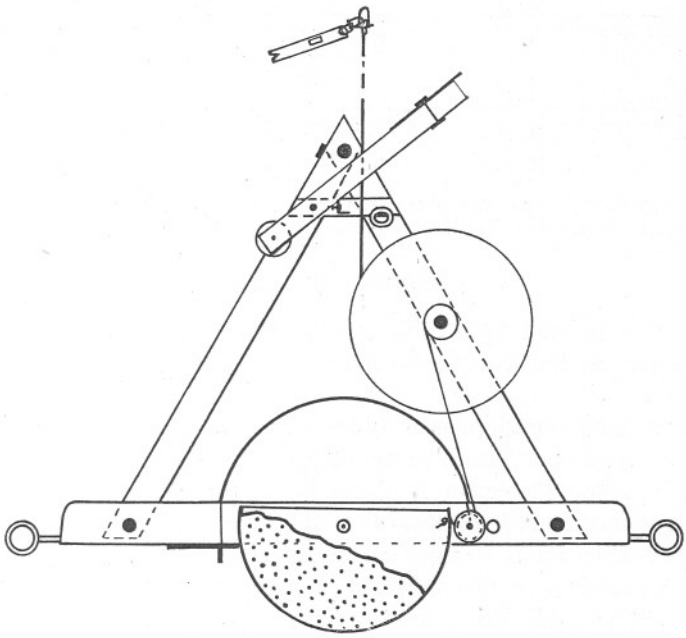
The ring (R) is of iron piping, attached to the base of the frame by welded lugs and bolts. The function of the ring is to keep the grab level on the sea-bottom, and also to prevent it damaging the ship's side.

The scoop (SC) is of steel plate 3 mm. thick welded to form a parallel-sided semicircular structure of external radius 17·5 cm. and width 15 cm. At the centre is welded a length of iron pipe through which passes an iron bar on which the scoop rotates. The bar is removed when the scoop is to be emptied. The cable attached to the small drum is fastened through a hole at one end of the scoop. During the descent the scoop is kept in an inverted position by a small wooden peg (P) passing through a hole in the scoop and the frame: this is sheared off when digging commences. The cutting end of the scoop is filed to a rather blunt edge. (Another scoop is being tested which has a pair of long teeth which precede the scoop and may help to anchor it in the soil.) While digging, the scoop tends to pile up soil in front of itself, but this falls back into the scoop when it is closing. There may be a slight loss of this soil through the gap between the scoop and the frame. Thus any stratification in the soil is partially disrupted. Outside the arc of the scoop the soil is prevented from piling up by the wide frame-base and a transverse sheet of metal (MS) pressing down on the soil surface. The arrangement of parts during hauling is shown in Text-fig. 2. The thin cable passes over the top of the scoop, round a pulley (PL), and is attached to the small drum on to which it is wound when the scoop closes. Should the scoop be unable to close, owing perhaps to catching on a piece of rock, a force of over 500 kg. is exerted on this cable, which is sufficiently thin to break and thus free the scoop. In practice the axle of the pulley tends to bend owing to the force exerted on it when the scoop is cutting through shells, etc., and this has had to be replaced by a thicker bar.

The large drum (DR) consists of two circular sheets of iron between which are welded short lengths of iron bar on which the large cable is wound. The latter is 3·5 m. in length and 25·5 mm. circumference. It is secured at one end to the centre of the drum by a shackle and short length of chain (these are not shown in Text-fig. 1). During hauling the cable has completely unwound from the large drum (to which it is still attached by the chain) so that there is

no longer any tension on the thin cable. The upper end of the cable passes between the top bolt of the frame and a metal strip protected by a piece of rubber hose (RU). It is attached to the 'key' (K) of the release through three shackles and to a cable from the ship of 32 mm. circumference.

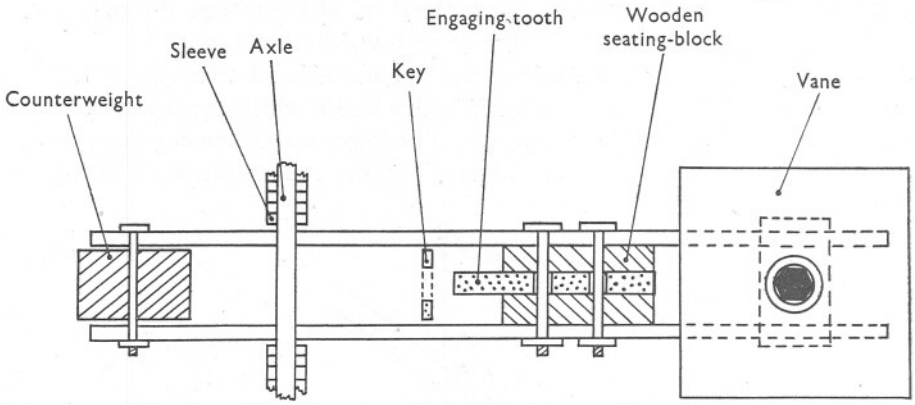
During the descent the weight of the apparatus is taken by the key. The key is a short length of thick metal strip with a slot in which the engaging tooth on the release arm grips during descent. The lower end of the key has a notch which slides on to a bolt head, thereby keeping it in position. The key is



Text-fig. 2. Position of parts when the instrument is closed. The soil sample is stippled.

prevented from lateral movement in one direction by the sides of the release arm, and in the other by the top bolt of the frame and a transverse metal strip (T). The release arm (RA), shown also in Text-fig. 3, consists of two metal strips separated by about 45 mm. internally. The engaging tooth (ET) is held between the strips, gripped between two blocks of hard wood. The base of the engaging tooth is slotted to allow adjustment of its position relative to the arm. The release arm pivots on an axle, being counterweighted so that the long arm just tends to drop. During descent it is kept in the upward position by the force exerted on the engaging tooth. When the sampler reaches the bottom the cable slackens, the arm drops and the key can slide out while cable is unwound from the drum. A vane (V) has been fitted to one end of the arm, as was done by Stetson (1938), to minimize the chances of release if the cable should momentarily slacken while the grab is descending. The release has proved

most successful, and only occasionally fails to work. The key is kept to a minimum size as it has to pass over a roller-sheave while hauling.



Text-fig. 3. Top view of the release arm. Transverse bolts are shown in section. The key and engaging tooth are stippled. The sleeves prevent lateral movement of the arm on its axle.

Method of Use

The sampler is hoisted by a cable attached to the winch and passing over a roller-sheave on the boom, the latter being swung over the ship's side (Pl. I, fig. 1).

The routine while sampling is as follows. The cable is wound on to the large drum and the release set, strain being maintained by taking some of the weight on the ship's cable. The scoop is placed in the 'closed' position, and its axle inserted. It is then rotated backwards to the 'open' position, care being taken that the thin cable winds straight across its top. The peg is inserted and the apparatus lowered over the side. As soon as the cable slackens, hauling commences. The cable need not be vertical while the sampler is closing, as the latter is extremely stable on the bottom. Since the efficiency of the sampler does not depend on the force with which it strikes the bottom, it may be lowered at any speed.

When the sampler is on board again, the cable is immediately rewound on to the large drum and the release set. The scoop is then removed and emptied. This is less damaging to the animals than merely inverting the scoop *in situ*.

In a depth of 30 m. a sample can be taken every three minutes.

A 'safety rope' is often used to minimize the risk of loss. This is attached from the end of the ship's cable to the ring. In common with all heavy gear, the sampler is difficult to work in a moderate sea.

Results

During 1948 the new sampler has been used at sea on a number of occasions, and in August a total of 100 hauls were made at thirty-seven stations during a cruise in Great West Bay. This provided a fair test of the instrument in

continuous use under favourable sea conditions. On the whole the instrument has worked successfully, and has taken good samples on sands, fine gravels and muds: adequate hauls have been taken at nearly all stations so far attempted.

The maximum volume of a sample is about $5\frac{1}{2}$ l. In practice the scoop is seldom quite full, usually bringing up 3–4 l. of soil. A number of hauls with this instrument and with the Petersen grab have been made to show the comparative increase in sampling efficiency. Sample volumes were:

Muddy gravel off Mewstone. Ship anchored.

New sampler: 5·25, 5·6, 5·25 l. in successive dips, i.e. average of 10·7 l./$\frac{1}{10}$ m.^{2}.
Petersen grab: total of 8 l. in three dips, i.e. 2·67 l./$\frac{1}{10}$ m.^{2}.

Muddy sand in Bigbury Bay. Ship anchored.

New sampler: first five dips—12+l., i.e. *c.* 4·8 l./$\frac{1}{10}$ m.^{2}; second five dips—11+l., i.e. *c.* 4·4 l./$\frac{1}{10}$ m.^{2}.
Petersen grab: five dips—1 l., i.e. 0·2 l./$\frac{1}{10}$ m.^{2}.

Muddy sand in Cawsand Bay. Ship anchored.

New sampler: first five dips—10·75 l., i.e. 4·3 l./$\frac{1}{10}$ m.^{2}; second five dips—10·5 l., i.e. 4·2 l./$\frac{1}{10}$ m.^{2}.
Petersen grab: five dips—1·75 l., i.e. 0·35 l./$\frac{1}{10}$ m.^{2}.

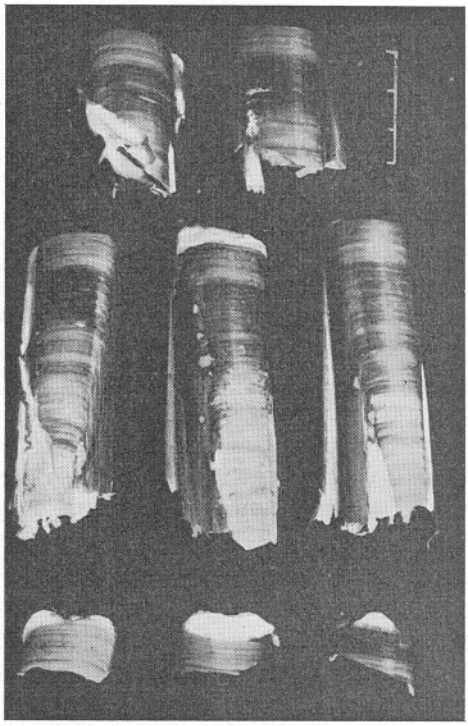
Johansen (1927) made a similar comparison between the Knudsen and Petersen grabs. On sand the former brought up an average of 25·6 l., whereas the Petersen grab only collected an average of 1·2 l./$\frac{1}{10}$ m.^{2}.

Thamdrup (1938) gives a number of comparisons of the van Veen and Petersen grabs. In a typical haul, in sand, the former brought up 3·4 and the latter 1·7 l./$\frac{1}{10}$ m.^{2}.

The collections made in Bigbury Bay show that the new instrument samples the bottom-fauna more efficiently than does the Petersen grab. The results of collections of 0·5 m.^{2} area are given in Table I. It will be seen that for nearly all species the Petersen grab gives too low a figure. In addition, only five species were recorded as against thirteen with the new sampler. It must be emphasized that this soil, being very tightly packed, is most unfavourable for bottom-sampling, and that on other grounds the differences in sampling efficiency would be rather less. The depth to which the various instruments were digging is indicated by fragments of *Ensis* shells taken (Text-fig. 4). The Petersen grab failed to capture any individuals, possibly because its jaws were not powerful enough to cut through the shell; while the new sampler cut off three individuals about 8 cm. from their upper ends, and shorter lengths of two other specimens. A dredge haul over the same ground cut off the top 2 cm. of three individuals. Assuming that the tops of the shells lie near or at the surface of the sand, and that the animal burrows nearly vertically,

TABLE I. COMPARISON OF HAULS MADE IN BIGBURY BAY, 18 MAY 1948. MUDDY SAND, SHIP ANCHORED

Instrument ...	New sampler	New sampler	Petersen grab
No. of dips	5	5	5
Total area (m.²)	0·25	0·25	0·5
Nephthys sp.	2	*c.* 4	1
Magelona papillicornis	*c.* 73	*c.* 50	2
Cirratulid	—	—	1
Gephyrea	1	—	—
Annelids *indet.*	10	7	—
Cellaria sp.	—	—	1
Cumacea	3	4	—
Bathyporeia elegans	71	27	28
Amphipods *indet.*	2	1	—
Natica alderi	1	3	—
Cylichna cylindracea	4	—	—
Mactra corallina	—	1	—
Ensis ? *siliqua*	4	1	—
Amphipholis squamata	2	—	—
Echinocardium cordatum	1	—	—



Text-fig. 4. *Ensis* from Bigbury Bay. Top two rows: individuals caught in new sampler; bottom row: individuals caught in dredge. For further explanation see text. The scale is 3 cm. long

the new sampler would seem to be digging about 8 cm., which is consistent with the volume of sand (*c.* $2\frac{1}{2}$ l.) brought up.

Discussion

In the last section it was shown that the new sampler is very much more efficient than the Petersen grab as a quantitative sampler on certain grounds in the Plymouth area. Other workers have compared the Knudsen and van Veen samplers against the Petersen grab and have also found that better results were obtained, when working on a sandy bottom.

While the Petersen grab is no doubt suitable for working in sheltered waters and on a soft muddy bottom, it is clearly relatively inefficient on a hard bottom. It has, however, been used by a number of workers under the latter conditions and has been found a useful instrument for semi-quantitative evaluation of the benthos. The variability in the size of sample taken on any one ground and on different grounds is in itself sufficient to show its unreliability in making an accurate estimate of biomass.

The Knudsen sampler, which digs to a depth of 30 cm., has shown the need for sampling to a considerable depth in order to capture the deeper-burrowing invertebrates. The use of the Knudsen sampler is, however, restricted on account of its weight (about 200 kg.), and its inability to dig into deposits other than sand.

The van Veen sampler is a considerable improvement on the ordinary type of grab, as judged by the volume of sample brought up. But there is still some risk of losing material through stones becoming wedged in the jaws.

The new sampler was designed to take a sample of sand or gravel which should be subject to the minimum of loss during hauling. In addition, it has been shown to dig considerably deeper than the Petersen grab, and to the same order of depth as the van Veen sampler. The area sampled ($\frac{1}{20}$ m.^{2}) is, however, rather small, and the apparatus rather heavy, and so difficult to work except in calm weather.

One of the most serious drawbacks to maximum efficiency appears to be the lateral shifting of the frame while the scoop is digging; this causes a decrease in sample volume. The addition of extra weights appears to be of little advantage in stopping this movement, and it is suggested that the only solution is a grab with two scoops working independently and rotating in opposite directions. The alternative of spikes or cross-pieces of angle iron on the base of the frame, to increase the grip on the soil, has not been very successful, as these tend to damage the ship's rail and do not seem to increase the size of the sample appreciably.

A half-scale model made in wood proved to be successful and took samples of about 300 c.c., being worked by hand from R.L. *Gammarus*. It is suggested that a sampler of this size might be used for survey purposes where a rather larger volume than that obtained by the 'snapper' is required.

Summary

A bottom-sampler is described for use under open-sea conditions, particularly where the bottom is of sand or coarser material.

It takes a sample of $\frac{1}{20}$ m.^{2} area of semicircular cross-section and maximum depth 15 cm. There is probably little loss of material while hauling and no danger of the apparatus losing soil through being wedged open by shell fragments, etc. The instrument weighs over 45 kg. and is weighted to 110 kg. in use.

Comparable hauls have been made against a Petersen grab: the new sampler digs four or five times as deep on a sandy bottom, and is thus of similar efficiency to the van Veen sampler. It is probably more efficient, however, than either of these on a bottom of fine gravel.

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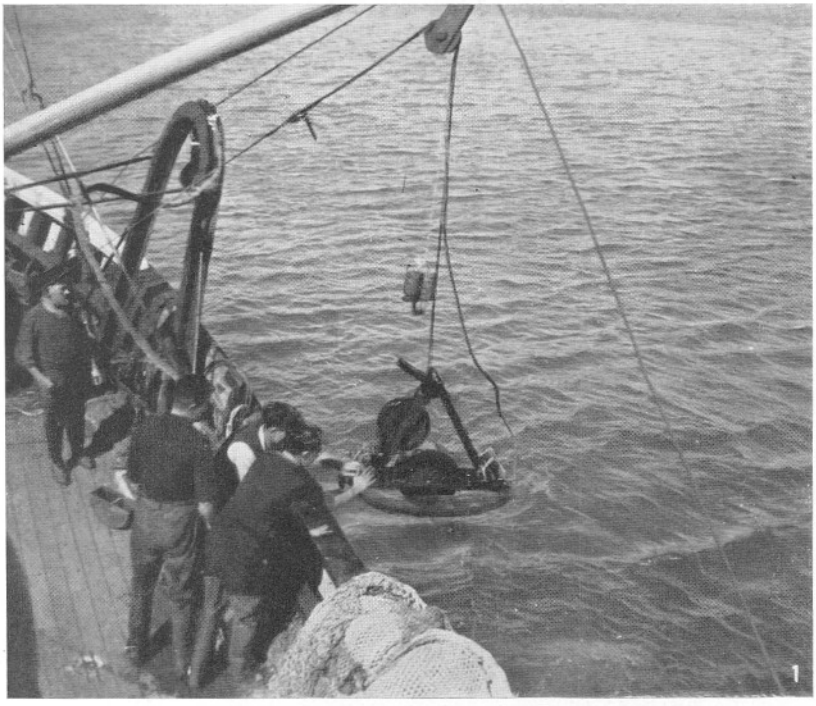
EXPLANATION OF PLATE I

Fig. 1. Working the sampler on R.V. *Sabella*. The instrument is being hauled up. Note that cable has unwound from the drum so that the key has passed over the sheave. The safety rope may be seen on the right of this cable. A toothed scoop is being tested; the type normally used is seen on the deck. Note the weights attached at either end of the frame.

Fig. 2. Photograph of the new sampler. The scoop may be seen under the frame. The two jars of sand together represent the volume of one sample.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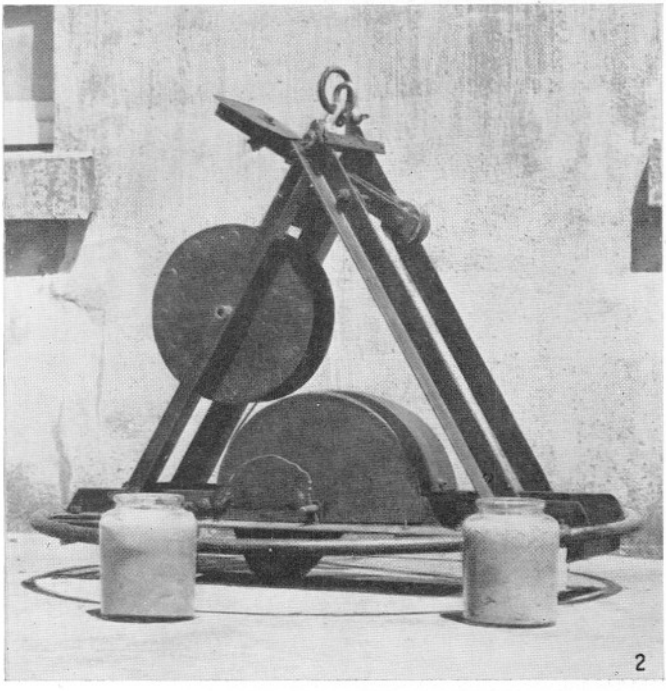
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THE RATE OF FEEDING BY *MYTILUS* IN DIFFERENT KINDS OF SUSPENSION

By C. Barker Jørgensen

From the Plymouth Laboratory, and the Laboratory of Zoophysiology, University of Copenhagen

(Text-figs. 1–3)

Introduction

Most lamellibranchs obtain their food from the particulate matter, micro-organisms or fine dispersed detritus, suspended in the surrounding water. The lamellibranchs transport water through the gills which serve as filters and retain the suspended particles. By means of cilia the material held back on the gill surfaces may be transported towards the mouth opening and ingested. In the quantitative feeding biology of this type of lamellibranch it is therefore of interest to know the water transportation capacity of the gills and also their efficiency in retaining particles from the filtered water. The amount of water transported through the gills has been measured by several investigators. Both direct and indirect methods have been employed. In the direct methods, for example that by Loosanoff & Engle (1947) on oysters, the water leaving the experimental animals through the exhalant siphon was separated from the surrounding water, collected, and measured. In the most frequently used indirect methods, the water transport was estimated from the rate of disappearance of particles from the surrounding water. However, the indirect method will measure the total amount of water transported only if the particles present in that water are all retained by the gills. If only a certain percentage is retained the value obtained will be lower, representing a certain volume cleared from particles. These particles may or may not be of any value as food and may or may not be ingested. The volume of water cleared from particles represents the potential feeding rate of the animal in question, or, more simply, the feeding rate.

If the size of food particles in the water is of importance for their retention by the gills, the indirect method offers information of greater importance concerning the feeding biology of the lamellibranchs than does the direct method. It is therefore of interest to investigate the efficiency of the gills in keeping back particles from the inhaled water. Only very few quantitative experiments dealing with this problem are available: they were performed on *Ostrea* and *Mytilus*. Galtsoff (1928) found that the oyster keeps back only a small fraction of *Bacterium coli* added to the water; 70–90% escaped the gill filter and could be recovered in the exhaled water. Loosanoff & Engle (1947),

likewise working on oysters (*Ostrea virginica*), determined the percentage retention of cells of *Chlorella*, *Nitzschia*, and *Euglena* in the gills. For *Chlorella* cells (about 5 μ in diameter) the value obtained varied from 0 to 92%. Apparently the gills function more efficiently at smaller concentrations than at larger ones. *Nitzschia* and even *Euglena viridis* (about 60 μ) were also found to pass through the gills, only 15–80% of *Euglena* cells being retained. In these experiments no correlation was found between the number of cells present in the water and the percentage removed. ZoBell & Landon (1937) stated that the gills of the California mussel retain bacteria very efficiently, although these authors do not mention directly the degree of retention. Therefore it seems possible that the pore sizes of the gills of *Mytilus* are smaller than those of oysters. However, the question arises whether the efficiency of the gills in retaining particles is always the same in one and the same animal. This is probably not so. Apart from possible changes in pore sizes of the gill filters arising from changed contraction of muscle fibres in the gill filaments, the animals seem to have other means of changing the efficiency of the gills. MacGinitie (1941) observed the gills through glass windows in the shells and he found that lamellibranchs, when quite undisturbed, can produce a layer of mucus covering the gill surfaces. This sheet of mucus most probably retains particulate matter present in the water down to very small particles, in any case far below bacterial sizes. The mucus including the particles is transported towards the mouth opening by means of the cilia and ingested. MacGinitie holds the view that lamellibranchs are feeding, i.e. ingesting the collected food material, only when they are producing the sheet of mucus. Furthermore, he states that they will only secrete the mucus layer when they are quite undisturbed and have been so for some time, and only if they accept particulate matter in the water as food. According to this view, perhaps all earlier experiments on feeding rates of lamellibranchs are open to criticism in the sense that under the experimental conditions the animals have not really been feeding. Against this assumption it may be said that in many of the experiments mentioned an uptake of particles in the alimentary tract has actually been demonstrated. The possibility thus exists that lamellibranchs may feed both with and without formation of a mucus layer. It was therefore thought worth while to investigate further the feeding behaviour of the lamellibranchs under conditions as natural as possible, using suspensions of both 'natural' (micro-organisms) and 'artificial' (graphite) particles as medium.

Since the NH_2-N content of an animal is a more satisfactory measure of the amount of living tissue than are length or weight, the feeding rate has been expressed per NH_2-N unit in the experimental animals.

The experimental part of the present investigation has been performed at the Plymouth Laboratory. I wish to express my sincere thanks to the Director,

Mr F. S. Russell, for the great interest he has taken in the work and for providing all the necessary working facilities. My most cordial thanks are due to Dr Mary Parke who prepared the gallons of culture used. I am greatly indebted to Dr W. R. G. Atkins who suggested the use of the colloidal graphite, and to E. G. Acheson Ltd., London, who placed the graphite at my disposal. The work has been made possible through a grant from the Rask-Ørsted Foundation.

Technique

Since small mussels seem to be less sensitive to handling and to changes in environment than larger individuals, the experiments were performed on small specimens of *Mytilus edulis* (L.) varying in length from about 1 to 5 cm. The mussels were collected from the piles of the old Plymouth pier. They were found to be most active when they remained in the naturally occurring clusters. To make sure that mussels of approximately the same size were used in the single experiments, the average size of the animals in the individual cluster was given preference, and animals of extreme sizes were removed together with those completely covered by their neighbours. Moreover, only those animals were chosen which were oriented so that their siphons were freely exposed to the surrounding medium. The resulting clusters contained between fifteen and fifty individuals, depending on the size of the individuals. The experimental vessels were of such shape and size that the mussels were able to keep the total water volume well mixed. Prior to the experiments, the mussels were adapted for several days to the running water from the circulation system of the laboratory. During that period the animals arranged themselves in an almost globular mass and moreover attached themselves to the bottom of the vessel by means of byssus threads. At the start of an experiment the water was replaced by the desired suspension, either freshly neutralized alga culture in vigorous growth diluted with tank water, or suspensions of graphite. A dilution of one part of alga culture with two to four parts of tank water was mostly used. Between subsequent experiments the animals were kept in running water. The temperature during the experiments varied between 17 and 20° C. The rate of feeding was computed from the formula

$$P_t = P_0 \exp\left[-\frac{m}{M}t\right],$$

where M is the quantity of water used for the experiment, and m the quantity 'cleared' from particles per unit time, while P_t and P_0 are the concentrations of the suspended material at the time t and 0, respectively (Jørgensen, 1943).

As suspended material *Nitzschia closterium* forma *minutissima*, and flagellates 'B', 'I' and 'J', which were kept in permanent culture in the Plymouth Laboratory, were employed. The first two of these have now been described by Parke (1949) and named *Dicrateria inornata* and *Isochrysis galbana*

respectively. Colloidal graphite was also used, from two different samples, viz. 'Prodag', grade 'C', and 'Aquadag', grade 'S', both supplied by E. G. Acheson Ltd., London. They are here referred to as graphite 'C' and graphite 'S'. The concentrations of the suspensions were determined photometrically by means of a portable 'Eel' photometer. NH_2-N determinations were made according to Parnas' (1938) micro-modification of the Kjeldahl analysis.

Results

The results obtained on the feeding behaviour of *Mytilus* differed according to the kind of suspensions used. The experiments with suspensions of graphite, flagellates, and *Nitzschia*, respectively, will be dealt with separately.

Experiments with graphite suspensions. When suspensions of graphite were used the values of the feeding rates decreased during the experiments. Some typical examples are given for graphite 'S' in Fig. 1, and for graphite 'C' in Fig. 2. Tables I and II summarize the numerical material obtained in experiments with graphite suspensions. Only the first and last values of feeding rates measured during one single experiment are recorded in the Tables (columns (iii) and (iv)). In column (v) the end value is expressed as a percentage of the value at the start. It is seen that at the time the experiments were concluded the feeding rates were often less than 10% of the feeding rates at the start. Sometimes, however, the decrease in feeding rate was only slight.

Two different mechanisms may be responsible for a decrease in feeding rate, viz. either a decreasing rate of transport of water through the gills, or a decrease in the percentage of suspended particles retained by the gills. Alternatively, both processes might occur simultaneously. Probably both mechanisms are of importance, as will appear from the following considerations.

During the experiments the general behaviour of the experimental animals was also studied. From observing the positions of the valves, the degree of extension of the siphons, and especially the movements on the surface of the water caused by the water currents produced by the animals, a rather rough measure for changes of the amount of water transported through the animals could be obtained. It was found that when the mussels were transferred from pure sea water to graphite suspensions they sometimes showed decreasing activity in the course of the experiment. This occurred in five out of seventeen experiments. In the twelve other experiments, however, there was no visible change in the activity of the mussels throughout the experimental period. Nevertheless, even under such circumtances the feeding rates were often much lower at the end of the experiment than at the start. Figs. 1 and 2 show two such examples; the same may be seen also from Tables I and II, column (vi), where notes have been made on such activity of the mussels as could be directly observed. In these mussels the percentage of particles retained by the gills decreased during the experiments.

The particles in the graphite suspensions were not all of equal size, as the

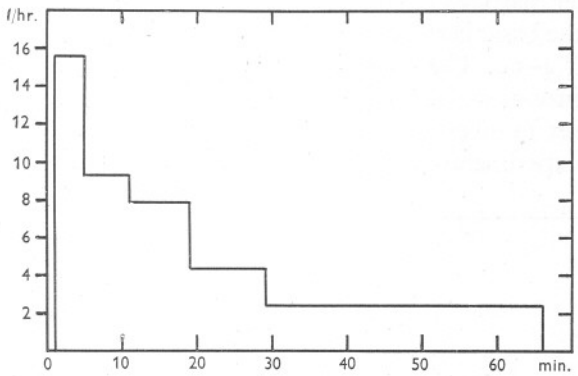

Fig. 1. Feeding rates in l./hr. of *Mytilus edulis* in suspensions of graphite 'S'.

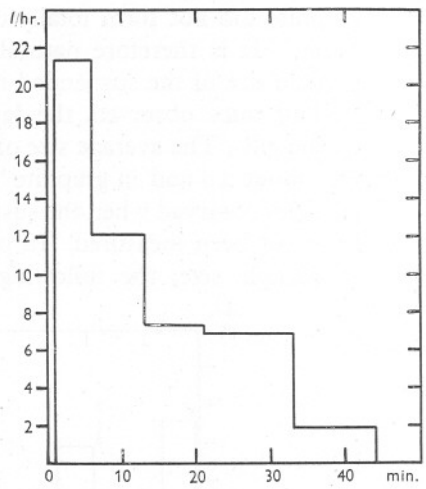

Fig. 2. Feeding rates in l./hr. of *Mytilus edulis* in suspensions of graphite 'C'.

TABLE I. EXPERIMENTS WITH SUSPENSIONS OF GRAPHITE 'S'

c means that the activity of the animals remained high and unchanged during the experiment, whereas *d* indicates that a decreasing activity was observed.

Mytilus (specimen no.)	Date	Feeding rate (l./hr.) Initial value	Feeding rate (l./hr.) End value	End value as percentage of initial value	
(i)	(ii)	(iii)	(iv)	(v)	(vi)
11	17. vi.	9·4	0·9	10	—
14	21. vi.	3·7	1·6	43	*c*
14	21. vi.	4·2	0·4	10	*d*
14	23. vi.	8·4	3·6	43	*c*
14	23. vi.	9·4	4·7	50	*c*
16	30. vi.	28·7	16·5	58	*c*
16	1. vii.	5·1	0·9	18	*c*
16	1. vii.	7·6	1·9	25	*c*
16	3. vii.	22·6	19·0	84	*c*
16	3. vii.	11·2	1·7	15	*d*
16	3. vii.	15·6	2·7	15	*c*
16	6. vii.	6·4	0·4	6	*c*
16	8. vii.	12·5	1·0	8	—

TABLE II. EXPERIMENTS WITH SUSPENSIONS OF GRAPHITE 'C'

Mytilus (specimen no.)	Date	Feeding rate (l./hr.) Initial value	Feeding rate (l./hr.) End value	End value as percentage of initial value	
(i)	(ii)	(iii)	(iv)	(v)	(vi)
11	17. vi.	5·8	1·8	31	*d*
11	18. vi.	13·1	2·4	18	—
11	18. vi.	9·4	2·2	21	—
11	18. vi.	21·3	1·9	9	*c*
16	3. vii.	26·2	24·5	94	*c*
16	3. vii.	33·5	31·0	93	*c*
16	7. vii.	6·5	2·5	38	*d*
16	8. vii.	12·5	1·0	8	*d*

graphite did not form totally dispersed and quite stable suspensions in sea water.[1] It is therefore natural to assume that the heterogeneity as regards particle size of the suspended material may be responsible for the decreasing feeding rates observed, the larger particles being more selectively retained by the gills. The average size of the basic particle in graphite 'S' suspensions was about 2 μ and in graphite 'C' 4–5 μ. The sizes of the aggregates of basic particles observed when the suspensions were examined under the microscope have not been measured. In order to investigate more closely the influence of particle size, the following experiments were made. In each of four

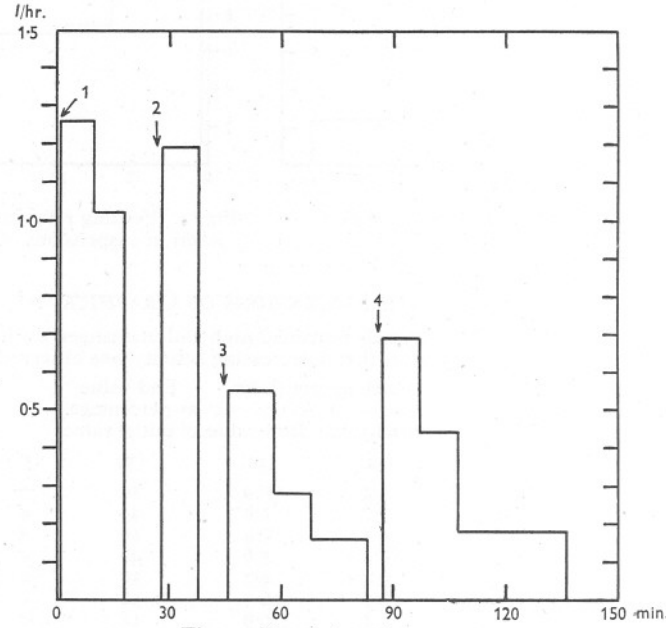

Fig. 3. For explanation, see text.

finger bowls were placed two mussels about 3 cm. in length. At the start of the experiment 250 ml. of graphite suspension were added to each of the bowls and the experiments were run until the concentration of the suspensions in each was reduced to about one-third. During this period, two determinations on the feeding rates were made. The second determination was always lower than the first. This is seen in Fig. 3, which represents the average

[1] A curve representing measurements of the light absorption (ampèremeter readings) at different dilutions of a standard suspension was used to determine the concentration of the suspensions during the experiments. Strictly speaking, this method is of course not admissible where the ratio between larger and smaller particles changes during an experiment, as most certainly occurred in the graphite experiments. With decreasing average particle size the densities of particles measured from the curve will be lower than the real densities, which means that the amount of water measured as cleared from particles will be too large. In fact, the decreases in feeding rates have been still larger than stated in the tables. This error will, however, not effect the conclusions to be drawn from the experiments.

of the four experiments. At the end of the period the suspension was decanted and stored for later use, and replaced by fresh graphite suspension taken from the same standard suspension as used previously. This time one determination of the feeding rate was made at the time when the concentration of the suspension was reduced to about one-half. Immediately after, the rest of the suspension was decanted and replaced by the suspension used initially. The feeding rates after the second addition of fresh suspension were always higher than the preceding ones. During the third period of the experiment the animals once more filtered the suspensions in which they had started until the concentration of the suspensions was about one-eighth of the initial value. It is seen that the values of the feeding rates decrease with time, and even at the start are lower than the preceding figures in fresh graphite suspension. Finally, the suspension left from the second period of the experiment was used once more. Immediately after addition of the suspension the feeding rates are relatively high, but they decrease later. This experiment, further, gives strong evidence for the view that under the prevailing experimental conditions *Mytilus* retained larger particles more efficiently than smaller ones.

Experiments with suspensions of flagellates. Of the three flagellates used in the experiments, *Dicrateria inornata* ('B') is spheroidal, about 3–5·5 μ in diameter; *Isochrysis galbana* ('I') is ellipsoidal, 5–6 μ long, 3–4 μ broad and 2·5–3 μ thick; whereas flagellate 'J' is ovoid, about 6–8 μ long and 3–4 μ broad. The results of the experiments are given in Table III. When using suspensions

TABLE III. EXPERIMENTS WITH SUSPENSIONS OF DIFFERENT FLAGELLATES

Mytilus (specimen no.)	Date	Feeding rate (l./hr.)		End value as percentage of initial value	
		Initial value	End value		
(i)	(ii)	(iii)	(iv)	(v)	(vi)
		Flagellate 'J'			
2	13. vi.	1·0	0·11	11	—
8	13. vi.	0·21	0·44	209	—
9	13. vi.	0·23	0·29	126	—
11	19. vi.	6·6	14·5	219	—
11	19. vi.	29·5	29·0	98	—
11	19. vi.	29·5	29·5	100	—
		Isochrysis galbana			
14	23. vi.	3·3	5·4	163	—
14	23. vi.	3·4	2·8	82	—
16	30. vi.	9·0	10·1	112	—
16	30. vi.	7·2	9·7	135	—
16	6. vii.	11·4	21·3	187	—
		Dicrateria inornata			
2	14. vi.	0·28	0·26	93	—
8	14. vi.	0·38	0·10	26	—
9	14. vi.	0·17	0·17	100	—
11	19. vi.	19·4	3·5	18	—
11	19. vi.	28·0	1·1	4	*c*
14	23. vi.	10·0	4·4	44	*c*
16	26. vi.	13·5	15·0	111	—

of the two last, the feeding rates measured were usually constant or increasing during the experiment. Only in one experiment out of eleven a pronounced decrease was observed. With *Dicrateria*, four experiments out of seven showed a pronounced decrease in feeding rates with time. In some of these at least the transport of water through the animals did not change noticeably, as judged from the direct observations of the behaviour of the mussels and the movements of the water. The decreasing feeding rates must therefore be caused by a decreasing retention of flagellates in the gills. As the particle size of the suspension is rather uniform, this factor cannot explain the decreasing rate. It seems that the 'pore' sizes of the gills can be changed so that the gill filter may be more or less permeable to particles of the same size. Furthermore, a comparison of Tables I, II and III shows that when suspensions of flagellates are used the feeding rates obtained are usually much higher than the feeding rates found with graphite suspensions in the later parts of the experiments when the smaller particle sizes most certainly dominate. This holds especially when the flagellate 'J' experiments are compared with the graphite experiments. See, for example, the experiments on *Mytilus* specimen no. 11 from 17 to 18 June (graphite) and from 19 June (flagellate 'J'). This means that the gills of the mussels may, and normally do, retain flagellates much more effectively than graphite particles even when these two kinds of particles are of about the same size.

Experiments with Nitzschia. The experiments with suspensions of *Nitzschia* lead to rather uniform results (Table IV). The feeding rates were found to be

TABLE IV. EXPERIMENTS WITH SUSPENSIONS OF *NITZSCHIA*

Mytilus (specimen no.)	Date	Feeding rate (l./hr.)		End value as percentage of initial value	
		Initial value	End value		
(i)	(ii)	(iii)	(iv)	(v)	(vi)
11	18. vi.	6·2	11·9	192	—
14	21. vi.	6·0	7·8	130	—
16	26. vi.	15·0	19·0	127	—
16	27. vi.	9·5	13·2	125	—
16	27. vi.	13·4	13·7	102	—
16	30. vi.	10·4	13·5	130	—
16	30. vi.	10·4	14·3	137	—
16	1. vii.	28·0	29·0	103	—
16	3. vii.	12·7	21·6	170	—
16	3. vii.	19·1	25·1	131	—
16	3. vii.	27·5	28·4	103	—
16	5. vii.	12·0	20·3	169	—
16	5. vii.	17·2	23·9	139	—
16	5. vii.	21·2	20·4	96	—
16	5. vii.	19·4	9·0	46	*d*
16	7. vii.	8·5	10·8	127	—
16	8. vii.	5·3	10·9	206	—

constant or, most often, to increase during the experiments. Only in one experiment out of seventeen was there observed a pronounced decrease in the

rate of feeding, when it was very conspicuous that the water propulsion from the mussels had also diminished towards the end of the experiment. The pronounced tendency to lower feeding rates, which was found at the start of the experiments with *Nitzschia* as well as in many of the experiments with flagellate 'J', is most probably caused by the heavy load of micro-organisms deposited on the gills at the start of the experiments. The suspensions used were comparatively thick, as could be estimated from the large amounts of pseudo-faeces formed by the mussels.

Discussion

The results from the experiments on the feeding rate of *Mytilus* in different suspensions seem rather divergent. In graphite suspensions containing particles ranging from about 2 μ and 4–5 μ to much larger ones, the larger particles were most frequently found to be retained more effectively than the smaller ones. Occasionally, however, the feeding rates were found to be high and almost constant during the experiments, thus indicating that the percentage of graphite particles retained by the gills had been high and independent of particle size (e.g., Table II, specimen no. 16, 3 July). In suspensions of flagellates with an average particle size close to the minimum size of particles in suspensions of graphite 'C', the percentage of micro-organisms retained by the gills was usually high and remained constant during the experiment, but in some instances it decreased. Once, indeed, the last measured feeding rate was only 4% of the feeding rate found in the beginning of the experiment (Table III, specimen no. 11, 19 June). In the later periods of the graphite experiments, when most of the bigger particles had presumably been removed from the suspension, the feeding rates were often found to be less than 10% of the feeding rates in suspensions of flagellates. This was observed even when there was no indication of a lower rate of water transport through the experimental animals. It must therefore be concluded that, under certain conditions, the gills of *M. edulis* retain only a small fraction of particles about 5 μ in diameter, whereas, at other times and under different conditions, particles of the same size are retained much more efficiently. This observation concerning the ability of the gills is in good agreement with the investigations of MacGinitie (1941) on the feeding behaviour of lamellibranchs referred to on p. 334. If MacGinitie's observations are taken into account the present experiments may be interpreted in the following way. In graphite suspensions *Mytilus* must be assumed normally not to accept the particles as food. Consequently they will not produce a mucus cover on the gills, and the efficiency with which particles are retained will depend entirely upon the particle size. That the mussels were genuinely disturbed in graphite suspensions could be seen from the fact that in five out of seventeen experiments with graphite decreasing activity during the experiments manifested itself in the general behaviour of the animals. On the other

hand, presentation of flagellate suspensions to the mussels clearly as a rule had no depressing effect on the formation of the mucus layer. In this event the retention of micro-organisms by the gills must have been approximately complete. It is difficult to imagine how flagellates should be able to penetrate a layer of mucus. In the experiments with *Nitzschia* it must be assumed, too, that the retention of cells in the gills was almost complete, as the feeding rates found were of the same order of magnitude as in the flagellate experiments. Moreover, only in four experiments out of twenty-nine with suspensions of flagellates or *Nitzschia* was decreasing activity of the mussels, with respect to the transport of water, observed during the experiments. This also indicates that the mussels tolerated and accepted the suspended material.

From the above considerations it must be assumed that the constant feeding rates found in suspensions of flagellates and *Nitzschia* probably give the total volume of water transported through the gills. Table V collates the values of

TABLE V

Mytilus (specimen no.)	Date	Average length (cm.)	No. of animals	NH_2-N (mg.) Total	NH_2-N (mg.) Average per animal	Suspension	Feeding rate in ml. per hr. per mg. N
14	21. vi.	1·5	56	110	2	*Nitzschia*	63
14	23. vi.	1·5	56	110	2	*Dicrateria*	94
14	23. vi.	1·5	56	110	2	*Isochrysis*	81
14	23. vi.	1·5	56	110	2	*Dicrateria*	86
14	23. vi.	1·5	56	110	2	*Dicrateria*	74
						Average	80
16	26. vi.	2·9	25	555	22	*Nitzschia*	31
16	27. vi.	2·9	25	555	22	*Nitzschia*	24
16	30. vi.	2·9	25	555	22	*Isochrysis*	16
16	30. vi.	2·9	25	555	22	*Nitzschia*	22
16	30. vi.	2·9	25	555	22	*Nitzschia*	23
16	1. vii.	2·9	25	555	22	*Nitzschia*	51
16	3. vii.	2·9	25	555	22	*Nitzschia*	37
16	3. vii.	2·9	25	555	22	*Nitzschia*	47
16	5. vii.	2·9	25	555	22	*Nitzschia*	37
11	19. vi.	3·2	24	657	27	Flagellate 'J'	23
11	19. vi.	3·2	24	657	27	Flagellate 'J'	44
11	19. vi.	3·2	24	657	27	Flagellate 'J'	45
11	19. vi.	3·2	24	657	27	*Isochrysis*	48
						Average	34

the feeding rate (=water transport) from experiments with flagellates and *Nitzschia*. All experiments performed are included in it, except for those in which the mussels were not fully open and active during the experimental period. The feeding rates are shown to be comparatively larger in the smaller animals than in the bigger ones. *Mytilus* containing about 2 mg. NH_2-N per animal filtered about 80 ml. water per hr. per mg. NH_2-N, whereas the value was about 30–40 ml. for animals containing about 20–30 mg. NH_2-N.

In order to compute the diurnal feeding rate from these values it is necessary to know the ratio between rest and activity in the course of 24 hr. Loosanoff (1942) found that, within a wide range of temperature, *Mytilus edulis* is most probably almost constantly active. Between 5° and 18° C. the valves were open throughout 97–99% of the time, and food was always found in the stomach. It therefore seems justified to consider *Mytilus* feeding almost permanently when undisturbed. This behaviour may apply generally to plankton-feeding lamellibranchs (Loosanoff, 1939; Loosanoff & Nomeiko, 1946).

MacGinitie (1941) states that lamellibranchs normally ingest food only when they are forming the sheet of mucus on the gills. If the mucus layer is not being formed particles collected on the gills and transported by the ciliary mechanisms to the labial palps will be rejected there without entering the mouth. These statements are in disagreement with the observations made in the present investigations. In the graphite experiments, the mussels frequently could not have secreted a sheet of mucus, as they were unable to retain the smaller graphite particles. Nevertheless, they were very often found to be ingesting all the graphite which had been retained by the gills. Formation of pseudo-faeces did not necessarily occur, but, *c.* 30–60 min. after the addition of the graphite suspension, large amounts of real faeces were rejected through the exhalant siphon. Several examples may also be found in the literature describing ingestion of food without formation of the 'feeding mucus'. Loosanoff & Engle (1947), for example, observed formation of large quantities of true faeces in *Ostrea virginica* fed on suspensions of *Chlorella* which were only partly retained by the gills. When feeding proceeds by means of the mucus sheet on the surface of the gills, no selection according to particle size is possible of particles imbedded in the mucus. On the other hand, we know, for instance through the very accurate and comprehensive work of Atkins (1936–38), that the gill surface possesses a very elaborate pattern of cilia which are able to sort and transport particles according to size for the purpose of either rejection or ingestion. It is difficult to believe that this complicated system of cilia should have nothing whatsoever to do with the normal feeding mechanisms of the lamellibranchs. Therefore it may be necessary to include in the normal feeding behaviour of lamellibranchs feeding *ad modum* MacGinitie as well as feeding by means of the filtering and sorting mechanisms provided by the cilia of the gills.

Summary

The feeding rate of small specimens of *Mytilus edulis* (L.) has been determined in suspensions of colloidal graphite ('Prodag', grade 'C', and 'Aquadag', grade 'S'), of flagellates, and of *Nitzschia closterium*. The feeding rate was measured as the volume of water cleared from particles per unit time. In graphite suspensions, with particle size of about 4–5 μ, as a rule only a small

percentage of the particles was retained by the gills, whereas flagellates of about the same size were normally nearly all retained. This difference in behaviour of the animals when kept in suspensions of graphite and flagellates, respectively, is discussed in the light of MacGinitie's observations. This author found that lamellibranchs, when feeding, secrete a continuous layer of mucus on the gills which are then able to retain even very small particles suspended in the water. When the animals are disturbed, or dislike the 'food', the formation of 'feeding mucus' is interrupted and small particles may pass and escape between the gill filaments. Therefore, it can be assumed that the mussels, when transferred to graphite suspensions, will stop forming the mucus sheet, with the result that only a small fraction of the 4–5 μ graphite particles are retained by the gills. On the other hand, the layer of mucus is secreted in suspensions of flagellates, which consequently are retained in bulk by the gills. Complete retention was normally also observed in suspensions of *Nitzschia*. The feeding rate in suspensions of flagellates and *Nitzschia* was found to be *c.* 80 ml. per hr. per mg. NH_2-N in mussels containing about 2 mg. NH_2-N per animal, and about 30–40 ml. in mussels containing about 20 mg. NH_2-N.

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NOTES FROM THE PLYMOUTH AQUARIUM

By Douglas P. Wilson, D.Sc., F.R.P.S.
Zoologist at the Plymouth Laboratory

(Plate I)

CONTENTS

During the daily maintenance work of a large aquarium many casual observations are made on the habits of the inmates. These are sometimes worthy of record, though too slight in themselves to justify separate papers each under its own distinctive title. It has, however, been thought fit to bring together in the form of a series of notes some of the more interesting of these observations. It is not intended to discuss each with full reference to the comparable literature; rather are they presented as raw material for the use of other investigators in their own specialized fields. Most of these observations have been made since the re-establishment of the Plymouth aquarium in 1946 (after its war damage), and up to the date of writing, November 1948.

A Disease of *Adamsia palliata* (Bohadsch)

In a shallow table tank strewn with shell-gravel there are regularly displayed a varying number of small hermit-crabs, *Eupagurus prideauxi* (Leach), with their cloak anemones, *Adamsia palliata* (Bohadsch). Normally the hermit-crabs die before the anemones, necessitating the removal from time to time of an accumulation of the latter from the bottom of the tank. It was therefore an unprecedented happening when on 17 March 1947 all the cloak anemones were found to be dead or almost dead, with most of the colour gone and the soft tissues shrunk away from their cuticular bases. Many had dropped off altogether to lie decaying on the gravel. The hermit-crabs themselves were alive and well but they looked peculiarly naked, their abdomens covered only with the thin brown cuticles of their late companions and the now absurdly small gastropod shells of their earlier youth.

Whatever it was that had killed the anemones had acted quickly. Two days before it had been noticed that the anemones were sickly, though previously there had been nothing unusual about their appearance, the tank having been looked over daily. About half the hermit-crabs and anemones present had come in straight from the sea less than a week before the catastrophe; others had been in the aquarium much longer, some perhaps for several weeks. The disease was probably introduced with the latest arrivals. There was no evidence of protozoan or other obvious parasites. (I am indebted to Mr Y. R. Tripathi for assisting me in the search for parasites.) The disease may therefore have been caused by some extremely small micro-organism.

On 20 March six hermit-crabs with cloak anemones newly brought in from the sea were put into the tank. Four days later the anemones were very ill and had begun to shrink away from their cuticular bases. On the next day their columns showed ugly lesions, and on the following day they were even worse, being almost detached from the basal cuticle. On this day (27 March) the tank was cleared of all hermit-crabs, anemones and visible traces of them and a new lot, procured by trawling, put in. In a few days these too had the disease and further batches also caught it soon after arrival. All this time there were a few hermit-crabs and anemones of the same species in another tank elsewhere in the building and these continued to be healthy, although the water running into their tank was supplied by the reservoir into which water from the diseased tank was draining.

On 2 May the entire contents of the diseased tank were removed and got rid of. The tank was emptied and swilled with antiseptic (Dettol) for 20 min. The antiseptic was washed away and the tank swabbed dry. It was then reflooded with sea water, new and well-washed shell gravel was strewn over the bottom, and a new lot of hermit-crabs with cloak anemones were put in. These had been caught a few days previously and acclimatized in another tank. There was no further trouble and there has been no recurrence of the disease.

Longevity of Sabellids

Many animals, once they have become accustomed to life in an aquarium, survive for many years. This is especially true of hardy fishes like grey mullet and bass for which a period of twelve or fifteen years in one tank is nothing unusual. Some invertebrates also reach and may exceed these figures (e.g. some sea-anemones) but only rarely are individual invertebrates kept sufficiently well isolated from others of their kind for definite records to be established.

In a tank containing grey mullet there had been for at least several months before the war one solitary *Sabella pavonina* Savigny var. *bicornata* Hornell (Ewer, 1946). This particular tank was one of the few to escape serious damage by enemy action, and throughout the war this sabellid maintained its position in the bottom gravel close to one side—and it is still there. The tank was emptied

and cleaned in 1946, but the worm was saved and replaced in its old position. It has therefore been alive for at least 10 years and during that period it has not been known to renew its crown, though this may have happened during periods when I have been away from the Laboratory.

In the same tank, close to the *Sabella*, is a piece of limestone dredged from the Sound; it also has been in the tank since before the war. It was selected for exhibition because of the large number of the boring sabellid *Potamilla torelli* Malmgren which it contained. To-day there are fewer of these worms to be seen than there were originally, but the stone is still a beautiful sight when all have expanded their crowns. It is not known whether the worms still living were present in the stone when it was dredged ten years or so ago, or whether they are newcomers. Some may be newcomers, for it is known that sabellids can breed in the aquarium system. Lately several *Branchiomma vesiculosum* (Montagu) have appeared in several tanks, particularly those with sandy bottoms, which had never had any of these worms put into them. The species is kept in other tanks in the same circulatory system, and the free-swimming larvae must have been carried round through the pump.

An Apparent Example of Learning in *Palinurus vulgaris* Latreille

In 1947 there were together in a large tank four or five *Palinurus vulgaris* Latreille and twenty or more large hermit-crabs, *Eupagurus bernhardus* (L.), in whelk shells on which were usually one or more parasitic anemones, *Calliactis parasitica* (Couch). The only other inhabitants of the tank were a few flounders. For some months these lived together peacefully and then, at a time when food was scarce, the *Palinurus* attacked the hermit-crabs, pulled them out of their shells and ate the soft abdomens. They continued this habit even when well fed. Any new hermit-crabs put into this tank were soon found and eaten and it was no longer possible to keep hermit-crabs with these particular rock lobsters. The latter were therefore removed and replaced by a similar number from another tank. The new *Palinurus* did not attack the hermit-crabs though kept with them for several months, and though they too sometimes went short of food during periods of scarcity.

Regeneration of Arms in *Marthasterias glacialis* (L.)

In May 1947 a specimen of *Marthasterias glacialis* (L.) regenerating four arms was brought in from the sea. The four regenerating arms were relatively short, about 2 cm. long, the fifth and unregenerated arm being about 15 cm. in length. This starfish was photographed shortly after arrival and was then kept in a small tank apart from any others of the same species. From time to time it was fed on mussels or on pieces of squid, but feeding was irregular and there were often long periods without food. The four regenerating arms slowly increased in size but they were still only a fraction of the length of the fifth arm when in

July 1948 the latter broke off at the disk and died. It may be that irregular and insufficient feeding had brought about some wastage of tissues, perhaps to supply materials to the regenerating arms. However that may be, there was soon to be seen on the side of the disk at the place where the old arm had been severed the rudiment of a new one. Now, in November 1948, the starfish consists of a disk about 2 cm. in diameter, four arms 6–7 cm. long and one arm 1·5 cm. long. There is some difference in appearance between the tissues of various ages, especially as regards colour, the disk being darkest and the newest arm lightest in tone. Thus had the specimen come in from the sea in its present condition, careful examination would have revealed the history of these events. Presumably in time the colour differences between the tissues of three distinct ages will become less and when the arms reach sizes commensurate with the disk there will be produced a starfish showing little or no trace of its history. The age of such a starfish is the age of its disk. In the sea such accidents to the arms may well delay growth of the disk and result—when the new arms have grown to match the disk—in a starfish, apparently normal and complete, but considerably smaller than others of the same species and age living under identical feeding conditions.

Regeneration of Fins in *Trigla hirundo* Bloch and *Mugil chelo* Cuvier

There are comparatively few references in the literature to the regeneration of fins in fishes. Aquarium keepers know that in due course torn fins usually heal to show no signs of injury, but actual records are not numerous.

In the autumn of 1946, not long after the reconstruction and reopening of the aquarium, a sapphirine gurnard, *Trigla hirundo* Bloch, about a foot long, was brought in from the sea and put into a tank with some others. It had been damaged in the trawl and for several days was very ill. Almost the whole of the upper lobe of the caudal fin showed extensive bruising and before long the tissues died and rotted away. The 'fingers' of both pectoral fins were likewise bruised, and similarly rotted away for about half their lengths. The condition of the fish was such that it was expected to die and there was some intention of removing it from the tank before it did so. However, some signs of recovery were noticed and it was allowed to remain, although for several weeks suppuration of the fingers was marked and the lesion of the caudal fin was inflamed. Slowly the wounds healed and eventually it was seen that the upper lobe of the caudal fin was being regenerated. For several months this regenerating lobe was darker in colour than the lower and it was, of course, much smaller. By the end of the first year it had by no means reached the dimensions of the lower lobe and even now, two years after the event, the upper lobe is still a little smaller than the lower. The fingers were also regenerated, some of them abnormally, the new growths being directed ventrally at various angles to the

old proximal parts. On the third finger of the left pectoral the angle is so acute that this particular finger is bent right back on itself. Some of the less acutely bent fingers are now straightening out.

In mid-June 1947 thirty or forty medium-sized grey mullet (*Mugil chelo* Cuvier) were caught in a seine-net in the estuary of the River Yealm and transported to a large reserve tank outside the main aquarium building. Within two or three days all the fish showed extensive bruises and each one had a mark around the head, or forepart of the body, where a mesh of the net had encircled it. Almost all the fins were torn and lacerated, particularly the caudal and paired fins which were extensively frayed with bared fin rays; in some instances only the stumps of the pectorals were left. Some of the fish died but more than half survived, their lesions becoming covered with thick brown scabs, often extensive, on head and body. In this condition they remained for several weeks, eventually feeding well. Towards the end of July and during August the scabs were reduced and disappeared entirely. At the same time the fins were regenerated and by September the fish were clean and fit for exhibition. Two or three of them were put with the grey mullet we have had for many years but most of them were sent by rail to the London Zoo aquarium where they are still living. The few kept in Plymouth still show marks, apparently scabless, where the deeper bruises had been.

Partial Burying of *Trigla hirundo* Bloch

Before the war *Trigla hirundo* Bloch were kept in a tank strewn with small pebbles; they are now kept on a sandy bottom and this has led to the observation that they can bury themselves, at least partially (Pl. I). The burying habit was most noticeable during the winter of 1947–48, especially did it take place late in the evening after the aquarium had been in darkness for a few hours. Burying has also been noticed during the daytime, particularly in the autumn of 1948 when the temperature of the water was falling rapidly. The observations are insufficient to associate the habit with low or falling temperatures, or with low light intensity, but they do at least indicate that it is usual for these fishes partially to bury themselves in the sea-bottom from time to time. The closely allied sea robins (*Prionotus*) are stated to bury themselves up to the eyes when disturbed (Romer, 1941).

The sand in the tank is not very deep and it seems likely that the fish would have covered themselves more completely had they been able to do so. The closed caudal fin was sometimes completely buried and the sand was heaped up on each side of the body towards the lateral line. Except for the fingers the pectoral fins were out of sight under the sand; the fingers emerged from it and were visible. The head was never covered in any way and the gill-slits were free from sand, respiration taking place in the usual manner and being unimpeded.

Shoaling of *Gobius flavescens* Fabricius

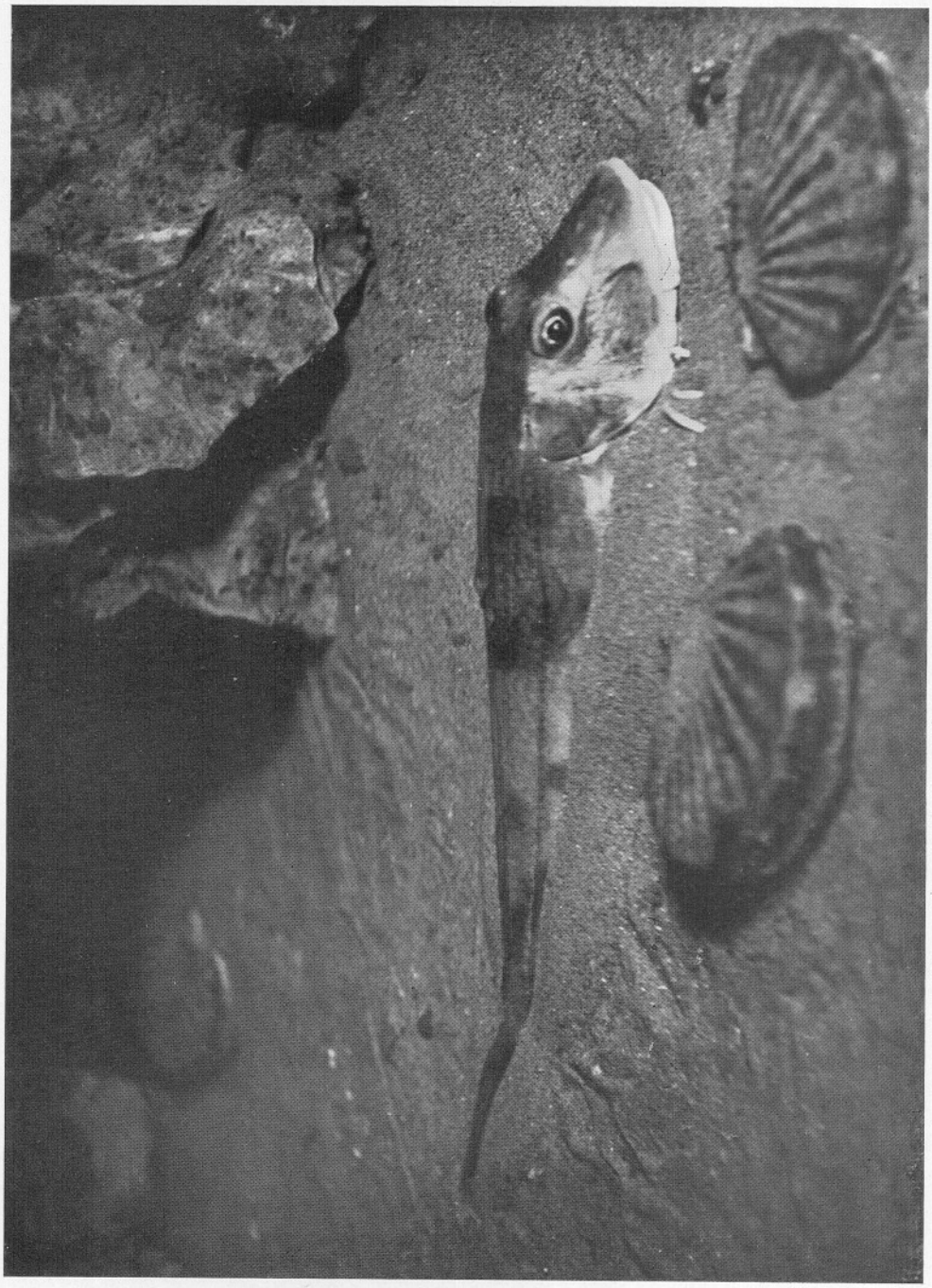
It has been the practice for some years to keep *Gobius flavescens* Fabricius in the largest tank in the aquarium, together with conger eels, dogfishes, nurse-hounds and large turbot. They swim about in the tank and are but little inclined to rest on the bottom or on the rocks, their habit being pelagic rather than demersal. The larger fishes take no notice of them, presumably because they are too small to tempt their appetites. The gobies normally swim about individually with no tendency to shoal. They progress with jerky forward motions produced by the beating of the pectoral fins, their chief organs of locomotion.

In the summer of 1948 two or three hundred young fishes of this species, each an inch or less long, were netted in shore pools and placed in the tank. Instead of dispersing immediately they kept together in compact rather globular shoals, each consisting of fifty or a hundred fishes. For one or two days these shoals moved slowly through the tank keeping more or less in mid-water. The jerky forward motions of the fishes were out of step and gave a curious scintillating appearance to the shoals. Gradually the shoals became less compact and in a few days each little fish was swimming about its business without reference to its neighbours. The gobies scattered throughout the tank, mainly in the lower levels but a few swam well up near the surface. Since then there has been no tendency to shoal, although occasionally the fishes gather into straggling groups. Perhaps the shoaling was a fear reaction induced by capture and by strange surroundings; perhaps it takes place in the sea when the gobies are very young, or when alarmed.

Blennius gattorugine Bloch Guarding Eggs

Early in April 1946 a *Blennius gattorugine* Bloch spawned in a corner at the back of a medium-sized tank in the research laboratories. There was some sandy gravel on the bottom of the tank but no rockwork, and the eggs were attached in a single layer to the vertical slate. They were assiduously guarded by what was presumably the male parent, and his devotion continued for many weeks although the eggs soon died and therefore did not hatch. It was the end of June before he ceased to guard them. It would be of some interest to know whether the hatching of the eggs would have been a signal for the guarding fish to cease his duties and whether this long and fruitless devotion was due to the signal not having been given.

There were several other specimens of the same species in the tank, but at the time there seemed no doubt at all that it was the same fish on guard the whole time. Any other fish approaching the vicinity of the eggs was vigorously chased away.



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EXPLANATION OF PLATE I

Trigla hirundo Bloch, partially buried in sand, about 8.30 p.m. in December 1947. The tracks in the sand were produced by the lower lobe of the caudal fin dragging along the bottom as the fish walked on its 'fingers'. Photograph by flashlight.

SHORT-PERIOD FLUCTUATIONS IN THE NUMBERS OF BARNACLE LARVAE, WITH NOTES ON COMPARISONS BETWEEN PUMP AND NET PLANKTON HAULS

By K. A. Pyefinch

Formerly Biologist to the Corrosion Committee,
British Iron and Steel Research Association.
From the Marine Station, Millport

(Text-figs. 1–7)

CONTENTS

INTRODUCTION

In the course of a series of daily plankton hauls, made over a period of over four years (Pyefinch, 1948), indications had been noted of variations in the numbers of barnacle larvae at different phases of the tide. It was also possible that diurnal variations occurred in the numbers of these larvae present near the water surface, and an attempt was therefore made to discover the extent of these variations.

It is clearly essential that an investigation of this character should be quantitative, and hauls were therefore made by pumping water through plankton nets. Hauls made by allowing plankton nets to fish from Keppel Pier during the ebb tide were, however, maintained throughout the period over which the pump hauls were made, so that comparisons could be made between the results obtained by the two methods.

Though the results of the investigation of the possible occurrence of tidal and diurnal variations in the numbers of barnacle larvae in the surface waters cannot be considered to be more than suggestive, the comparisons between pump and net hauls have revealed a number of points of interest, which it seems useful to place on record.

Acknowledgement is made to the Marine Corrosion Sub-Committee of the British Iron and Steel Research Association for their permission to publish

this work. Grateful acknowledgement is also due to the Scottish Marine Biological Association for the loan of the equipment used, and the author is especially indebted to Dr H. J. Thomas for his share in the labour of the serial hauls.

Methods

Hauls were made using a Standard-Gwynne centrifugal pump, fitted with an armoured suction hose approximately $3\frac{1}{2}$ in. in external diameter; the delivery hose was also armoured and was approximately $2\frac{1}{4}$ in. in external diameter. A cylindrical copper rose was fitted to the suction hose; this rose was approximately 7 in. long and 4 in. in diameter (external dimensions) and was drilled with $\frac{3}{8}$ in. holes, $\frac{1}{2}$ in. between centres.

The suction hose hung over the seaward end of the landing stage of Keppel Pier and the water pumped was directed into a plankton net supported over a tank situated on the pier. The rose of the suction hose was adjusted to a constant depth before each haul was made. For the earlier hauls this was 3 ft. below the water surface, but for the later hauls (those made from 29 March onwards) the rose was adjusted to a depth of 2 ft. below the surface before each haul. This adjustment could only be made approximately, especially when heavy seas were breaking. Hauls made at various depths showed little variation in the numbers of larvae, over the range possible with this pump, so that it is unlikely that the alteration in depth of rose from 3 to 2 ft. mid-way through the series of readings described below caused any significant difference in the results obtained.

The capacity of the receiving tank was 350 l., but the volume of water filtered through the net was usually 333 l. (0·3 m.^{3}). The volume of water which was pumped through the net was measured and the time taken to pump this volume of water was also recorded. This was done to ensure that approximately the same rate of pumping was maintained throughout, to minimize errors which might arise if gross variations in rate occurred. By adjustment of the water outlet valve and the throttle a reasonably uniform rate of pumping was achieved, of the order of 200 l./min. This is the minimum rate recommended by Wiborg (1948).

Most of the larvae collected were intact and so were readily identified, but there was evidence of some damage during passage through the pump, as isolated naupliar and cyprid appendages occurred occasionally in the hauls; these are rarely seen in hauls made by fishing a net from the pier. Larger planktonic forms (e.g. *Calanus*) were usually damaged, though it is not impossible to obtain samples of such larger forms using a pump, as Gibbons & Fraser (1937), using a different type of centrifugal pump, have obtained hauls of much larger planktonic forms than barnacle larvae in an undamaged state.

The site chosen for collecting these pump hauls was by no means ideal, but it was the best possible within reasonable working distance of the laboratory.

The chief disadvantage was that the rose was immersed very near to a barnacle-covered surface, so that there was a danger that larvae liberated from these barnacles could be taken directly into the suction hose; this seems likely to have occurred on at least one occasion during the sampling. On the other hand, the pump samples were taken as near as possible to the point from which plankton nets are usually fished, so that comparisons between the two types of haul could reasonably be made. It should be pointed out, however, that the currents flowing through the pier are undoubtedly complex, due to the obstruction of the piles, so that conditions cannot, in all probability, be regarded as strictly comparable. Any investigation of inshore planktonic forms seems bound to encounter difficulties of this nature, since hauls must be taken at sites where the hydrodynamic conditions are complex, due to the irregularities of the neighbouring shore.

Serial Hauls

Three sets of serial hauls, each extending over 24 hr. or longer, were made and these were supplemented by other series carried out over shorter periods. The first set of serial hauls was made on 11 and 12 March, the second set on 23 and 24 March, and the final set from 29 March to 1 April 1948.

Table I shows the average numbers of the larval stages of *Balanus balanoides*, *B. crenatus* and *Verruca stroemia* during these three periods, as averages for the 3-day period most closely corresponding to the period of the serial haul. These were obtained in hauls made from the pier in the usual way, by fishing a net for 1 hr. during the ebb tide. The first set of serial pump hauls was thus made during a period when early-stage nauplii predominated, the second set at a time when later-stage nauplii were more abundant, and the third set just when cyprids (particularly those of *Balanus balanoides*) were beginning to be plentiful.

Table I. Average Numbers of Barnacle Larvae occurring in Net Plankton Hauls during the Periods when Serial Pump Hauls were made

		Average numbers of larvae present						
		Nauplius						
Period	Species	I	II	III	IV	V	VI	Cyprid
10–12 March	*B. balanoides*	3845	20925	1460	260	40	0	0
	B. crenatus	565	4390	360	120	40	0	0
	V. stroemia	4320	5090	1075	600	20	0	0
22–24 March	*B. balanoides*	10	175	1065	3290	3235	4620	215
	B. crenatus	10	120	80	560	615	743	240
	V. stroemia	10	200	125	470	4120	35	0
29–31 March	*B. balanoides*	0	190	405	1745	1115	2895	9885
	B. crenatus	25	185	675	1705	1705	1490	205
	V. stroemia	5	20	35	415	4245	515	105

It was originally hoped that it would be possible to carry out further sets of serial hauls, but the numbers of larvae decreased so considerably after 9 April, that further series showed no promise of profitable results.

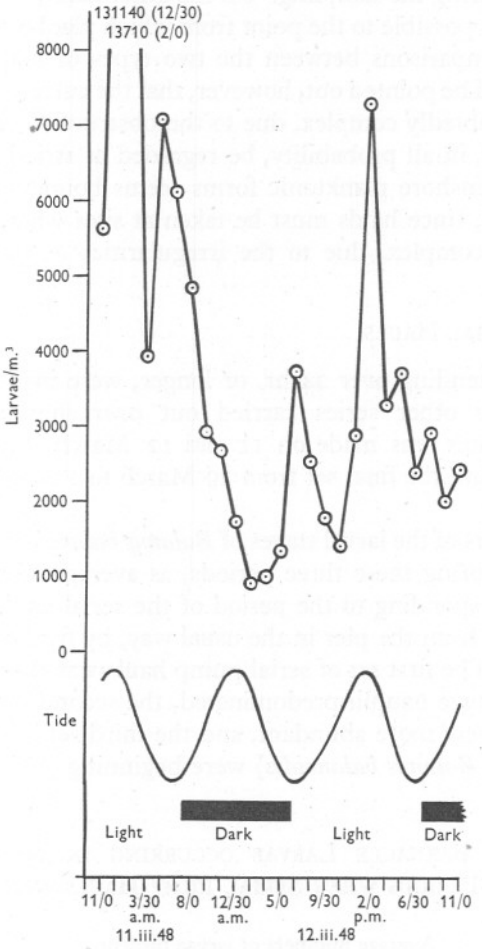

Fig. 1. Total barnacle larvae in the serial hauls of 11–12 March.

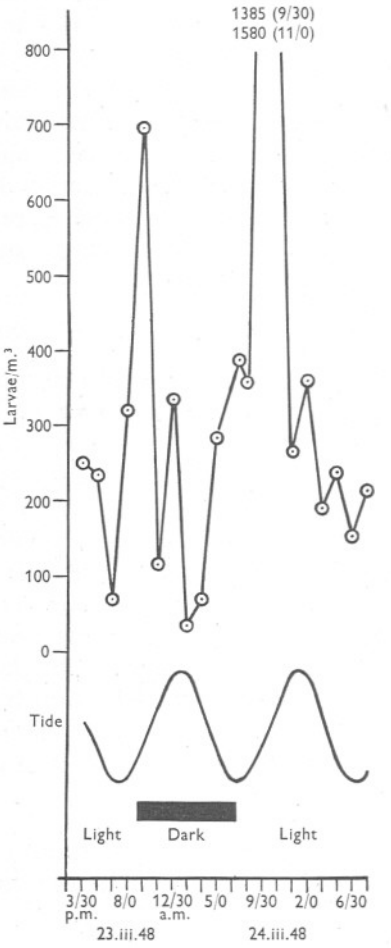

Fig. 2. Total barnacle larvae in the serial hauls of 23–24 March.

Series of 11–12 *March.* The results of this series are shown in Fig. 1. It would appear that the numbers of larvae present in the surface waters are reduced during the hours of darkness and, further, that maximum numbers of larvae are present at high water during the day, but not at high water during the night.

It will be noted that this graph is drawn for 'total nauplii', i.e. all stages present of the three species. A further analysis of these data suggests that the

generalizations just quoted are too clear cut. The exceptionally heavy haul taken at high water on 11 March consisted chiefly of the 1st-stage nauplius of *B. balanoides* (86% of the haul), whereas the maximum shown at high water the following day contained no 1st-stage nauplii of *B. balanoides*, but considerable numbers of the 2nd-stage nauplius, supplemented by 1st- and 2nd-stage nauplii of *B. crenatus*. It would seem reasonable to suggest that the maximum which occurred on 11 March was unusual; it may well have been produced by the liberation of nauplii from a small number of *B. balanoides* followed immediately by their uptake into the suction. Moore (1935) states that a single individual of *B. balanoides* can produce 13,000 nauplii, so that the product of only a few individuals would be needed to give the number of these larvae recorded in this haul.

Series of 23–24 *March*. The results of these hauls are shown in Fig. 2. The general outline of this curve is less regular than that shown in Fig. 1, fluctuations between successive hauls being more marked. This may well be due to the smaller numbers of larvae taken during this series, as it will be noted that the vertical scale of Fig. 2 is ten times that of Fig. 1.

Apart from the fact that the numbers of larvae taken during the hours of darkness were again rather smaller than those taken during the day, there is little correspondence between Figs. 1 and 2. In the present series there is no suggestion of a significant maximum at high water, the largest numbers of larvae being taken during the flood tide, both at night and during the day. The constitution of these two maximum hauls was similar, i.e. roughly the same proportion of the naupliar stages of each of the three species occurred in each haul. It is thus possible that, as this series of hauls was taken at a time when later-stage nauplii were abundant, this difference in behaviour is genuine and that the migrations of these stages differ from those of the earlier stages. In view, however, of the results obtained from the third series (see pp. 357–60) and of the considerable fluctuations that can occur in larval numbers over short periods of time (see p. 362), this suggestion does not seem likely to be correct.

Though cyprids (particularly those of *B. balanoides*) were obtained in these hauls, the records of their occurrence have been omitted from Fig. 2, as the numbers obtained were so small.

Series of 29 *March–1 April*. This series of hauls was made at the time when the cyprids of *B. balanoides* were beginning to become abundant; separate graphs have therefore been given of the total nauplii (Fig. 3) and the total cyprids (Fig. 5).

Fig. 3 presents a record which is even less regular than that of Figs. 1 and 2. The numbers of larvae present during the night were again rather lower than those present by day, but otherwise maxima seem to be irregular in their incidence. During the first night of the series a maximum occurred just after darkness had fallen, at the time of low water, whereas at the corresponding time 24 hr. later, naupliar numbers were practically at their minimum, but

there were signs of a maximum near the time of low water during the third night. During the day two maxima occurred at low water, two during the flood tide and one when the tide was ebbing.

Further analysis into naupliar stages does not reveal any regularity. Fig. 4 shows the occurrence of later-stage nauplii over the same period (naupliar stages III–VI inclusive were counted as 'later-stage' nauplii for *B. balanoides*

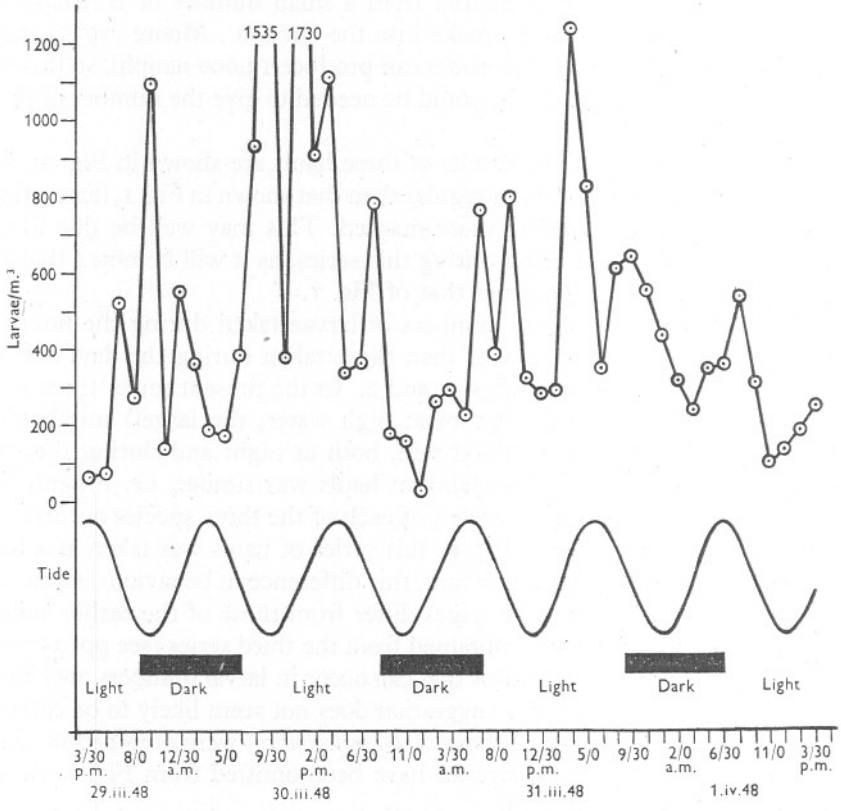

Fig. 3. Total barnacle larvae in the serial hauls of 29 March–1 April.

and *B. crenatus* and naupliar stages IV–VI for *Verruca stroemia*). The only point of interest about this figure is that the numbers of *Balanus balanoides* and *B. crenatus* larvae tend to decrease over the later part of the period, whereas the larvae of *Verruca stroemia* are then definitely more abundant. It is possible that the weather may have been an important factor in producing this result. For the last 24 hr. of this series of hauls, there was a gale from the south and west and it is possible that this churned the water sufficiently to bring numbers of *Verruca* larvae into the surface layers.

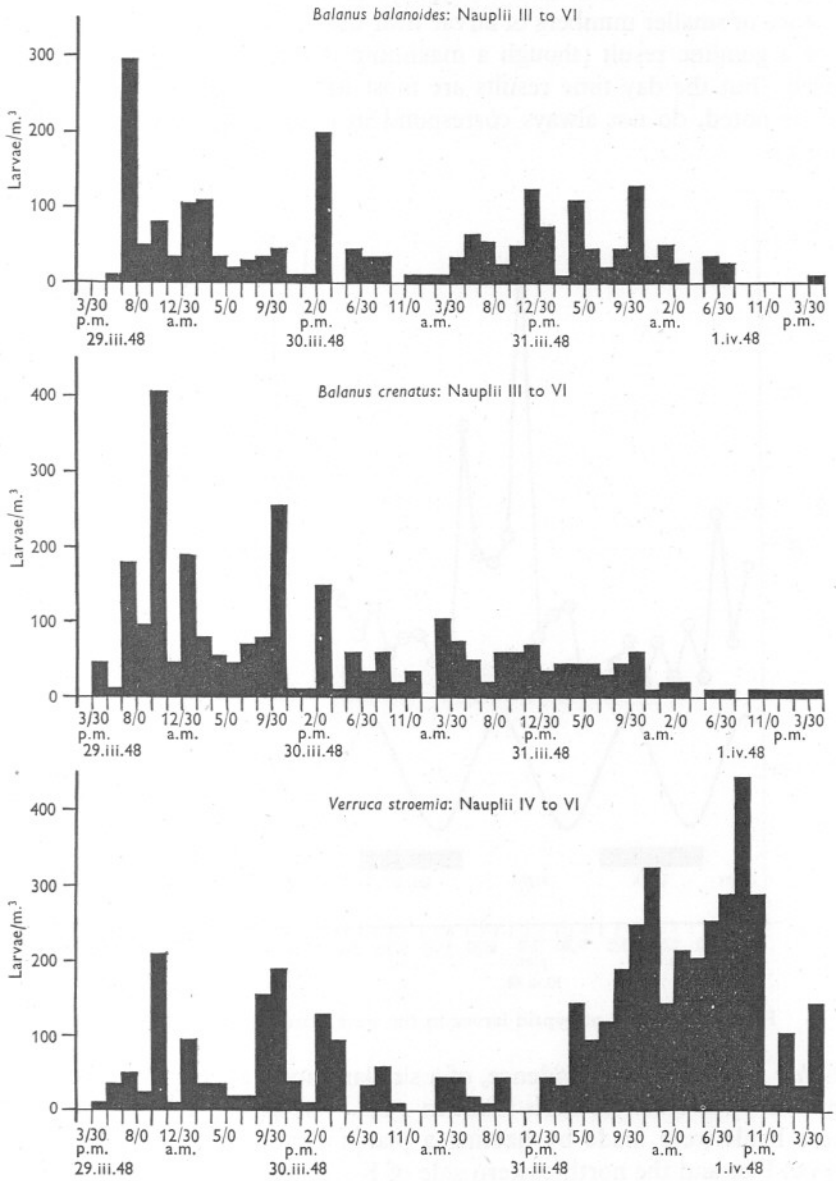

Fig. 4. Numbers of later-stage nauplii, separated into species, for the third set of serial hauls.

Fig. 5 shows the numbers of cyprids obtained in each haul. Here the presence of smaller numbers of larvae near the surface during the night seems to be a genuine result (though a maximum did occur just after dark on 31 March), but the day-time results are most irregular. The cyprid maxima, it will be noted, do not always correspond in time with the naupliar maxima (Fig. 3).

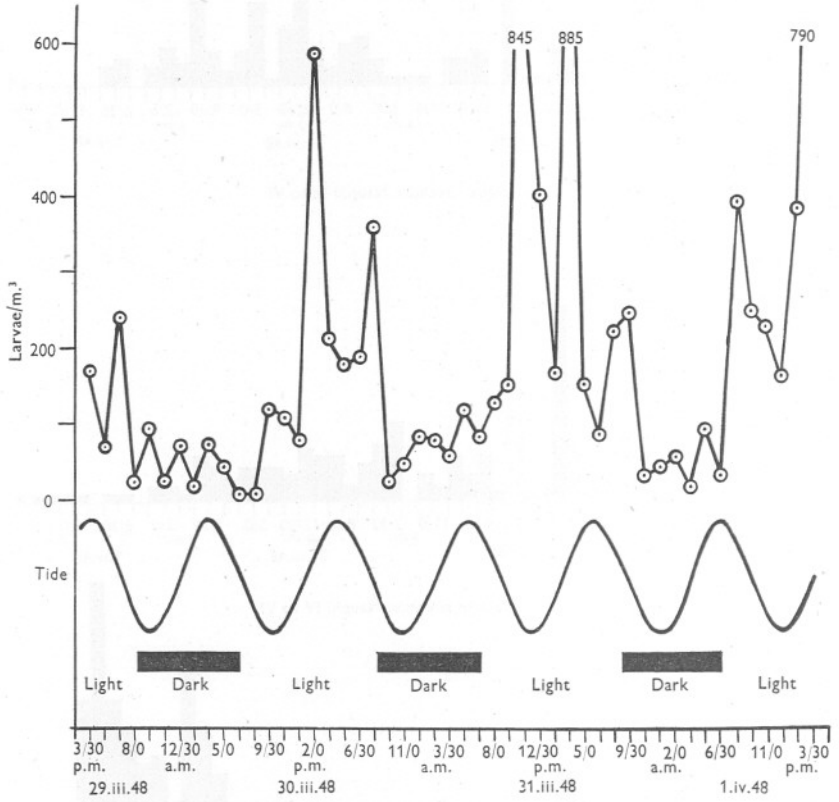

Fig. 5. Numbers of cyprid larvae in the serial hauls of 29 March–1 April.

Other series. Further evidence, of a similar nature to that just described, is provided by two sets of hauls made in 1944. The results are shown in Fig 6. These hauls were made by hauling a plankton net across the bay between Keppel Pier and the north-eastern side of Keppel Point, a distance of roughly 500 ft. The numbers of larvae recorded are not given as numbers/m.^{3} as these hauls cannot be considered as quantitative. The towing speed used was roughly one knot, but the relative speed of the net varied with the state of the tide. This factor was important because the towing speed was roughly the same as that of the ebb tidal current. An attempt was made to convert the figures

obtained to numbers/m.^{3}, assuming that the fishing efficiency of the net was 100% throughout and that the mouth of the net remained normal to the current throughout the run. The results obtained, however, were so low in comparison with those recorded from the pump hauls just described, as to indicate that these assumptions were not valid.

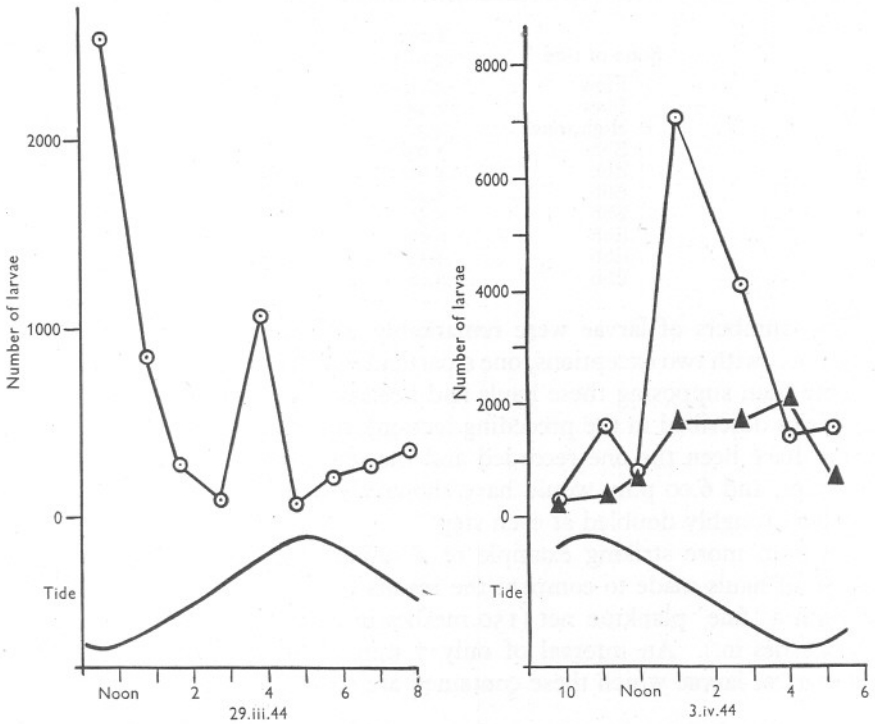

Fig. 6. Total barnacle larvae in the serial hauls of 29 March 1944 and 3 April 1944. ⊙ — ⊙ Stages I–VI, ▲ — ▲ Cyprid.

The first of this series of hauls was made on 29 March, when many late-stage nauplii and a few cyprids were present; the second was made 5 days later, when cyprids were more abundant. The results obtained on 29 March suggest a maximum number of nauplii at low water and possibly a minimum at high water, but they were contradicted by those obtained on 3 April, when numbers were low both at high and at low water, and a maximum occurred during the ebb. The cyprid maximum, which was ill-defined, occurred at low water.

Supplementary Hauls

In the intervals between the sets of serial hauls described in the last section, a number of other hauls were made, to test the reproducibility of the samples obtained.

One test of this kind was made on 16 March and the results are shown in Table II. It was designed both to investigate how much the larval population varied over very short periods and to compare the results of pump hauls with those of hauls made simultaneously from the pier.

TABLE II. VARIATION IN NAUPLIAR NUMBERS OVER VERY SHORT PERIODS

State of tide	Time (p.m.)	Nauplii/m.³
Flow	3.00	455
Flow	3.45	715
High water	4.32	905
Ebb	5.03	910
Ebb	5.36	930
Ebb	5.42	610
Ebb	5.57	2060
Ebb	6.08	925
Ebb	6.18	935
Ebb	6.26	910

The numbers of larvae were remarkably uniform after the haul made at 4.32 p.m., with two exceptions, one a particularly striking one. It is interesting to note that, supposing these hauls had been taken at 90 min. intervals (as in the series described in the preceding section), the exceptional haul (5.57 p.m.) would have been the one recorded and the sequence of readings, 3.00 p.m., 4.30 p.m. and 6.00 p.m. would have shown a convincing rise, with the larval numbers roughly doubled at each step.

An even more striking example of a sudden variation was found in the course of hauls made to compare the results obtained by pumping the water through a 'fine' plankton net (150 meshes/in.) and through a 'medium' net (50 meshes/in.). An interval of only 7 min. separated the two hauls; the numbers of larvae which these contained are shown in Table III.

TABLE III. NUMBERS OF NAUPLII FROM WATER PUMPED THROUGH 'FINE' AND 'MEDIUM' NETS (17 MARCH)

	Naupliar stages/m.³											
	I		II		III		IV		V		VI	
Species	*F*	*M*	*F*	*M*	*F*	*M*	*F*	*M*	*F*	*M*	*F*	*M*
B. balanoides	35	0	120	35	35	235	5	95	0	10	0	0
B. crenatus	1710	25	55	0	0	55	5	100	0	20	0	0
V. stroemia	25	0	85	0	40	0	30	80	20	55	0	0

F indicates 'fine' net (150 meshes/in.). *M* indicates 'medium' net (50 meshes/in.).

It was to be expected that the numbers of the early-stage nauplii would be greater from the 'fine' than from the 'medium' net, but there would seem no reason, except a variation in the larval population, why the numbers of later-stage larvae should vary so markedly, since they should be retained by both nets. It should be added that, as only an aliquot part of each haul was counted,

the smaller variations shown in Table III are probably not significant, but some of the variations (e.g. those of the 4th-stage nauplii) seem great enough to be independent of a sampling error.

Other hauls made in rapid succession indicate that sudden variations can also occur in the numbers of cyprid larvae (Table IV).

TABLE IV. VARIATION IN CYPRID NUMBERS OVER VERY SHORT PERIODS (2 APRIL)

Time of haul (p.m.)	Cyprids/m.^{3}
3.24	845
3.30	1305
3.35	730
3.39	1350
3.43	1490

As many of the maxima shown in Figs. 1–5 are isolated points, unsupported by a graded series of records on either side, it is evident that the results just quoted suggest that any maximum should be regarded with considerable suspicion, since its occurrence may merely be a matter of chance rather than an indication of diurnal or tidal variation. Though it would therefore seem reasonable to discount many of the maxima recorded in these figures, the situation is possibly not the same for the evidence of diurnal variation in the numbers of larval stages in the surface water. There is some consistent evidence for the reduction in the numbers of all the larval stages in the surface waters during the hours of darkness and this effect is perhaps most strikingly shown for the cyprids of *Balanus balanoides*.

It is possible that the sudden variations just discussed are due to sampling errors rather than to a true variation in larval numbers. The water was pumped through a net and errors may have arisen because all the catch was not always transferred to the collecting jar. Every effort was made to adopt a similar procedure at each collection, so a significant error would appear to be unlikely. A number of hauls were made in which 1 m.^{3} was pumped through the net in successive thirds. The variations in the numbers of larvae from these hauls were of a similar order to those from hauls in which only 0·3 m.^{3} of water was passed through the net. If the cause of the sudden variations had been a sampling error, this grouping of hauls into threes should have accentuated this effect, whereas no indications of accentuation were found.

It must therefore be concluded that sudden variations in the numbers of barnacle larvae do occur and that therefore the results of single hauls may be misleading.

Comparisons of Net and Pump Hauls

Plankton nets, both 'fine' and 'medium', were fished from Keppel Pier whenever an opportunity arose during the course of these series of pump hauls. A number of instances are thus available for comparisons between the two methods.

Qualitative comparisons are set out in Table V, in which the percentage composition of the net haul is compared with that of pump hauls made immediately before and immediately after the period for which the nets were fished.

There is evidently a rough qualitative equivalence between the pump and net hauls in spite of the sudden variations which may exist between successive pump hauls. Sometimes considerable differences between the two methods of collection do occur, however (e.g. those on 31 March), and these may be due to the incidence of this factor.

Table V. Qualitative Comparisons between Pump and Net Hauls

	Percentage composition of haul								
	B. balanoides			*B. crenatus*			*V. stroemia*		
Date	P_1	N	P_2	P_1	N	P_2	P_1	N	P_2
11 March	81·7	73·6	72·7	6·3	8·7	9·2	12·0	17·7	18·1
12 March	55·0	40·9	37·0	23·1	2·4	27·0	21·9	56·7	36·0
24 March	76·8	77·2	72·5	18·5	11·9	17·5	4·6	10·9	10·0
29 March	62·0	63·9	66·6	13·8	19·8	26·9	24·2	16·3	6·5
30 March	59·6	51·1	66·6	36·6	25·9	25·2	3·8	23·0	8·2
31 March	16·4	72·1	41·3	78·3	10·9	50·0	5·3	16·1	8·7
6 April	83·7	86·1	44·6	17·3	13·9	54·7	0	0	0·7
8 April	51·6	51·0	41·6	43·4	47·1	54·0	5·0	1·9	4·4
Average	60·9	64·5	55·4	29·7	17·6	33·1	9·6	17·8	11·6

P_1 indicates the pump haul made just before the net haul (N), P_2 the pump haul made just after the net haul.

These qualitative comparisons are taken a stage further in Fig. 7, which shows the analyses of the net and pump hauls for 11 March and 8 April into the larval stages represented. The set for 11 March is more closely comparable than that for 8 April, but as the numbers of larvae present in the pump hauls for 11 March were considerably greater than those for 8 April, a closer correspondence in the former set was perhaps to be expected.

Quantitative comparisons indicate considerable differences between the numbers of larvae collected by the pump and by nets fished from the pier. It is not possible accurately to estimate the volume of water that passes, or could pass, through a net fished from the pier, but if it is assumed that the current through the pier during the ebb runs at a speed of 1 knot and that all this water passes through the net, then the volume filtered is approximately 365 m.^{3}. It is probable that all the water does not pass through the net, but as

the estimate of current speed is a conservative one (a good ebb will run at a speed of just over 2 knots at Keppel Pier) this allows for some error in the assumption that all the water is filtered through the net.

On these assumptions, comparisons between pump and net hauls have been made and the results are shown in Table VI. The first two estimates in this table were made at a time when *Skeletonema* was very abundant; this was probably an important factor in producing the low fishing efficiencies recorded.

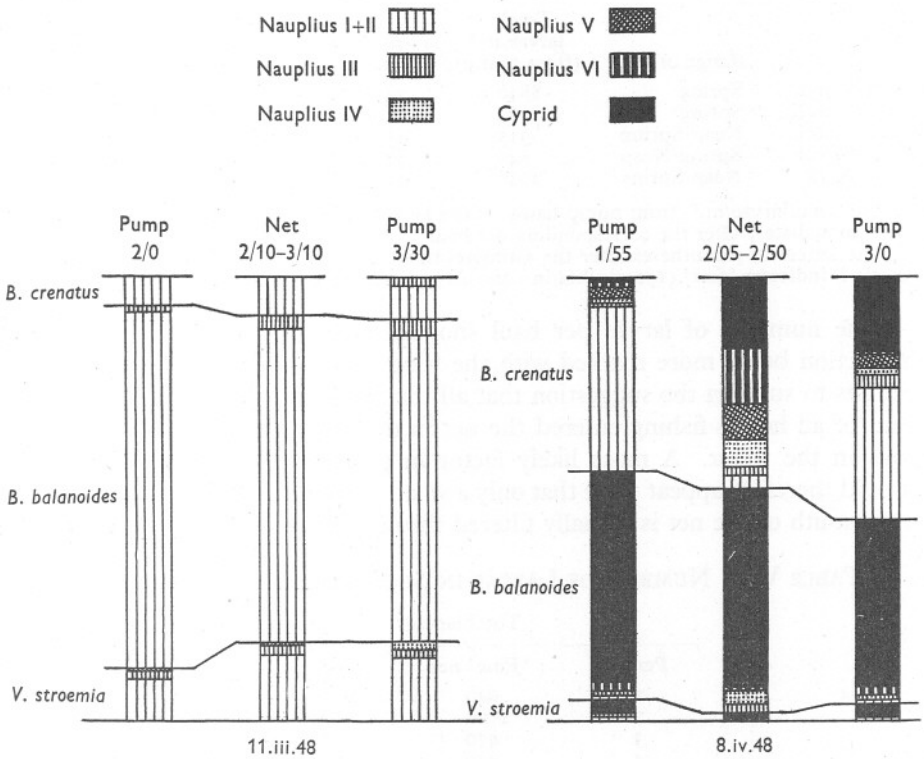

Fig. 7. Analysis of net and pump hauls on 11 March and 8 April.

Though the last three estimates are based on the net hauls from both 'fine' and 'medium' nets, roughly 95% or more of the larvae recorded came from the 'medium' net, so that the fishing efficiencies given may be taken as those of the latter net only.

During a period when diatoms are abundant in the water, clogging of the mesh of the net is doubtless an important factor in reducing fishing efficiency, but at other times clogging of the mesh does not seem to be the most important factor in reducing this efficiency. Nets have usually been fished from the pier for 1 hr. and if clogging were a significant factor the numbers of larvae caught,

for example, during the first 10 min. should be much greater than those caught during the last 10 min. of this immersion period. The experiment was therefore made of subdividing the fishing period into five periods, each of 10 min. duration. At the end of each fishing period, the net was carefully withdrawn and the collecting jar changed with the minimum of disturbance. The results of these hauls are shown in Table VII.

TABLE VI. FISHING EFFICIENCY OF PLANKTON NETS

Date	Range of tide	Total larvae/m.^{3} (from pump)	Total larvae (from net)	Theoretical total larvae from net	Fishing efficiency (%)
11 March	Spring	8820	24,200	3,220,000	0·75(F)
12 March	Spring	5270	5,870	1,923,000	0·30(F)
24 March	Neap/Spring	315	45,460	229,900	24·9 ($F+M$)
30 March	Spring/Neap	540	47,400	394,200	12·0 ($F+M$)
6 April	Neap/Spring	1040	38,980	759,100	5·1 ($F+M$)

The total larvae/m.^{3} (from pump hauls) is the average of the haul immediately before and that immediately after the corresponding net haul.

The letters in parentheses after the estimates of fishing efficiency indicate the type of net used; F indicates 'fine' (150 meshes/in.) and M indicates a 'medium' net (50 meshes/in.).

The numbers of larvae per haul showed a decrease with both nets, the reduction being more marked with the 'fine' net, but there is little in these results to support the suggestion that all the larvae which are recorded at the end of an hour's fishing entered the net in the first few minutes that the net was in the water. A more likely factor in producing low fishing efficiency would therefore appear to be that only a small proportion of the water reaching the mouth of the net is actually filtered through its mesh.

TABLE VII. NUMBERS OF LARVAE IN SUCCESSIVE 10 MIN. NET HAULS

	Total larvae	
Period	'Fine' net	'Medium' net
1	940	3370
2	1700	3160
3	470	3460
4	420	2960
5	360	2220

DISCUSSION

Weiss (1947) has recently investigated the rate of attachment of the cyprids of *Balanus improvisus* and finds that, for this species, there is a definite diurnal variation, attachment taking place more by day than by night. If the number of attachments over a given period is proportional to the number of larvae present in the surface water, then the results of the present study would suggest that the same was true for *B. balanoides*, as the cyprids of this species were more plentiful in the surface waters during the day. It was hoped that it

would be possible to supplement these planktonic investigations by observations on the amount of settlement on collectors exposed on Keppel Pier, but the numbers which attached were too small to allow this direct test to be made.

Diurnal variations in the numbers of cyprids in the surface water is one of the few definite results that have emerged from this investigation as it was originally planned, though it seems likely that all the larval stages, at least of *B. balanoides* and *B. crenatus*, also show some diurnal variation. Weiss (1947) also found that, during the day, the greatest numbers of cyprids attached during the low tide period. No regular variation with tidal state was found for the occurrence of the three species present in the hauls made in the present series, but this difference does not necessarily imply a difference in habit, since Weiss makes it clear that the variation he found seemed to be due to the geographical conditions of his experimental site.

The sudden variations which occur in larval numbers have been clearly shown by these counts of pump hauls; this phenomenon seems to be common to all the stages of the three species of barnacles. Fluctuations between hauls taken in rapid succession have, in the present investigation, probably been emphasized because the volume of water filtered was so small, but their persistence when the volume filtered was trebled and their occurrence in the early stages of the investigation, when the numbers of larvae present were much greater, suggests that the phenomenon cannot wholly be attributed to inadequacy of sampling.

The hauls collected by nets from the pier seem to give a reasonable qualitative impression of the various species and stages of barnacle larvae present in the plankton. As these nets are fished for periods much longer than those required to take a pump haul, the results they give are, in one respect, more reliable than those given by the pump hauls, namely that the longer fishing period will tend to obliterate the sudden fluctuations which characterize the shorter fishing periods. This advantage is certainly outweighed by the low fishing efficiency of the nets themselves.

The low fishing efficiency of the nets seems likely to be produced because only a small proportion of the water which is carried to the mouth actually enters the net. The low fishing efficiencies recorded suggest that the speed of the ebb tidal current may be reduced, near the mouth of the net, to a value which is not far removed from the rate of swimming of the larvae. This may mean that certain stages, or certain species, may be able to avoid capture. In this connexion, it is of interest to note the results presented in Table V (p. 364). The numbers of *B. crenatus* larvae caught in the net are less than those taken by the pump (this difference is mainly due to the increased numbers of 1st- and 2nd-stage nauplii in the latter hauls) and the numbers of *Verruca stroemia* larvae caught by the net are greater than those taken in the pump. No significant differences, however, occur between the pump and net hauls of the larvae of *Balanus balanoides*. These differences may be due to biological factors

such as differences in the rate of swimming or differences in rheotropism; further work on this point may well be interesting.

It should be added that the estimates of fishing efficiency quoted earlier, as they have been expressed numerically, probably give too definite an impression of the results achieved. Considerable variations in fishing efficiency are possible between two successive immersions of the same net, so that an extended series of determinations would have to be made to establish the fishing efficiency of a given net at all firmly.

Biologically, the difference in fishing efficiency between the fine and medium nets is important because it obscures the numerical differences between the various larval stages. The early-stage nauplii chiefly appear in fine net hauls, whereas the later-stage nauplii and cyprids chiefly appear in the hauls made with the medium net. As the fishing efficiency of a medium net appears to be as much as eighty times greater than that of a fine net, an incorrect impression of larval mortality and dispersal during the sequence from hatching to settlement is obtained. Table VIII, below, gives the highest numbers of each larval stage of each species recorded during the present series of pump hauls.

TABLE VIII. HIGHEST NUMBERS OF LARVAL STAGES (NUMBER/M.^{3}) FROM PUMP HAULS

	Larval stage						
	Nauplius						
Species	I	II	III	IV	V	VI	Cyprid
B. balanoides	112,570	10,285	235	230	350	230	1085
B. crenatus	3,430	2,000	70	190	70	70	145
V. stroemia	2,285	915	995	285	430	60	65

These results suggest that roughly 1% of the larvae of *B. balanoides* which are hatched survive to become cyprids, roughly 9% of the larvae of *B. crenatus* and roughly 3% of the larvae of *Verruca stroemia* complete the larval sequence. This is, however, only the crudest approximation, since it leaves out of account the life period of each larval stage (this is possibly the reason why the cyprid numbers are higher than those of the 6th-stage nauplii), and it also assumes that the three species can be fairly compared. This is probably not true, as these pump hauls were started at a time when the larvae of *Balanus balanoides* were hatching, and thus very large numbers of the early-stage larvae of this species were recorded, but the pump hauls were started too late to record the corresponding hauls of the early-stage larvae of *B. crenatus* and *Verruca stroemia*.

SUMMARY

Records are given of the numbers of barnacle larvae obtained from samples of water pumped through a plankton net. Several series of hauls were made at intervals over the time of year when barnacle larvae are abundant.

The numbers of the cyprid larvae of *Balanus balanoides* in the surface waters show a diurnal variation, being markedly less during the hours of darkness. This conclusion may also apply to the cyprids of *B. crenatus* and *Verruca stroemia*, but the numbers of these larvae were too small to permit reliable conclusions to be drawn. There is some evidence that similar diurnal variations occur in larval stages other than the cyprid.

The numbers of larvae present in the surface waters during the day showed marked variations which were not correlated with tidal state. Pump hauls made within a few minutes of each other showed comparable variations.

Comparison of the hauls made using the pump and those from nets fished in the ebb tide suggest that the latter give an adequate qualitative record of the barnacle larval stages present, but are inadequate quantitatively. The fishing efficiency of a 'fine' net (150 meshes/in.) is very low, values of less than 1% being recorded, and that of a 'medium' net (50 meshes/in.) is not high, the maximum value recorded for this type of net being roughly 25%. There are indications that loss of fishing efficiency is produced by water not entering the net rather than by clogging of the mesh. The latter factor is undoubtedly important, however, in producing the very low fishing efficiency of a 'fine' net during a period of diatom abundance.

The difference in fishing efficiency between 'fine' and 'medium' nets affects estimates of the numbers of each of the larval stages present, since most of the early-stage nauplii appear in 'fine' net hauls, whereas most of the later-stage nauplii appear in 'medium' net hauls. Pump hauls seem likely to present a more accurate record and estimates of the success of the larval sequence based on these hauls suggests that only 1% of the first-stage nauplii may complete the full sequence of development to the cyprid stage.

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CERTAIN EFFECTS OF AGITATION UPON THE RELEASE OF PHOSPHATE FROM MUD

By William Stephenson, Ph.D.

Dove Marine Laboratory, University of Durham,
Cullercoats, Northumberland*

Introduction

Studies of the phosphate concentration of sea water are of primary importance in assessing the potential productivity of the sea (Sverdrup, Johnson & Fleming, 1942; Harvey, 1945). Amongst the factors governing these concentrations, the role of the bottom deposits has been largely neglected. There is an impression (Marshall, 1947) based upon analyses of marine muds by Moore (1930) and estuarine deposits by Stockfisch & Benade (1930), that the surface layers of bottom deposits contain large amounts of phosphate. If so, the factors controlling the exchange of phosphate between mud and sea water are of interest. This investigation concerns one of these factors, and later papers will deal with others.

The work has been carried out in the laboratory because, although conditions are artificial, they are relatively controllable, and it is easier to distinguish the significant factors. Estuarine muds have been used in preference to offshore deposits because of their accessibility and because they are more likely to withstand laboratory conditions without catastrophic biological change. Analyses were made throughout upon sea water in contact with mud, thereby avoiding the difficulties of determinations upon mud itself.

Methods

Phosphate determinations. Atkins's (1923) modification of Denigès method was used, employing Atkins's original reagents. Molybdate solution (1 ml.) and two drops of stannous chloride solution were used per 100 ml. sample, and colours compared visually using Hehner or Nessler tubes. Comparisons were initially made in daylight, but it was suspected that variations in spectral composition were altering the salt errors (Cooper, 1938) and so all results below were determined in artificial light in a dark room. Tubes were viewed with standards alternatively right and left of the unknown (Matthews, 1916) and each time a value just above and just below the 'true' value was recorded. Finally the mean of the four values was noted. Salt errors were determined as described by Ibañez (1933), and the factor varied between 1·33 and 1·37 for

* Now at Dept. of Zoology, University of Queensland, Brisbane.

sea water, and between 1·15 and 1·18 for samples diluted with an equal volume of distilled water. Reagent blanks were determined as described by Cooper (1933) and allowances were made for salt errors in these blanks. Harvey (1948) has shown, in a paper published since this work was completed, that with stored reagents, blanks are largely due to silicomolybdate formation, and are not subject to salt errors. The results are thus too low by amounts up to about 2 mg. P_2O_5/m.^{3}. The experimental error is estimated at about ± 2 mg./m.^{3}, and any arsenate present is included as phosphate (Atkins & Wilson, 1927).

Mud. A scraping of the top centimetre of mud, containing *Corophium*, was collected on 11 December 1946 from mid-tide level on the south bank of the River Blyth, close to the Fever Hospital. Sand and grit were removed by washing, and sea water, mud, silt, and *Corophium* were added to a greenish glass tank ($35 \times 27 \times 35$ cm.) in a shaded corner of the laboratory. The solids settled as a loose brown layer about 7 mm. thick, and were kept for about a month before the experiments started.

Filtration. With turbid liquids, filtration was essential. Whatman No. 542 papers were used and the first 20 ml. of filtrate discarded. Distilled water, sodium chloride solution, and dilute sodium bicarbonate solution extracted no phosphate from these papers or from the glassware.

pH *determinations* were performed colorimetrically, and the results, after correction for salt errors, are accurate to about the nearest 0·05.

Results

Preliminary experiments

Sea water in contact with settled mud was analysed. After stirring for 5 min., samples were pipetted at intervals from the middle of the water column, filtered, and analysed. Typical results are given in Table 1, and these show, first,

Table I

8/9 January 1947; P_2O_5 at 23.00 hr. G.M.T., 125 mg./m.^{3}; stirred 23.15–23.20 hr.

Interval between stirring and collection of sample (min.)	Duration of filtration (min.)	P_2O_5 (mg./m.^{3})
0	15	111
75	15	110
120	10	120
195	15	122
240	15	109
265	15	123
460	15	112

considerable variation in phosphate concentration, and secondly that this concentration has decreased. Later experiments gave both increases (Table III) and decreases (Table II) in concentration.

Ultrafiltration

In the above experiment only the original sample was unfiltered, and particulate or colloidal material may have increased its phosphate concentration. To evaluate the significance of a colloidal fraction, sea water and mud were stirred, then filtered, and then ultrafiltered through a collodion membrane. After ultrafiltration the phosphate should be reduced by an amount equivalent to that released from the colloids.

Collodion ultrafilters were prepared round a 2·5 cm. boiling tube from the following mixture: 7·0 g. dry pyroxylin, 100 ml. absolute alcohol, 100 ml. ether, 4·8 g. ethylene glycol. A first coat was applied at 20° C. and dried for approximately 3 min., and a second similar coat added. A third coat was allowed to dry at 20° C. for about 10 min., and then at 15° C. for about $2\frac{1}{2}$ hr. The membrane was removed from the tube after standing in water for 1 hr. Many membranes were made similarly, but mostly burst under high pressures. Those finally selected withstood a pressure of 600 mm. Hg and filtered Congo Red from aqueous solution. During ultrafiltration, a pressure of 500–550 mm. Hg was used.

Sea water and mud were stirred, and two samples collected, one for normal filtration, and the second for normal filtration followed by ultrafiltration. Analyses showed (see Table II) that the ultrafiltered samples gave the *greater* phosphate concentrations. These increases were not due to evaporation of water, as chlorinities increased only by 0·5% during ultrafiltration.

TABLE II

9/10 January 1947; P_2O_5 at 23.00 hr. G.M.T., on unfiltered unstirred sea water, 123 mg./m.^{3}; stirred 23.15–23.20 hr.

Interval between stirring and collection of sample (min.)	Duration filtration (min.)	P_2O_5 (mg./m.^{3})	Duration ultrafiltration (min.)	P_2O_5 (mg./m.^{3})
0	15	115	—	—
0	40	—	125	149
2	10	120	—	—
2	35	—	139	145

In the next experiment, sea water was stirred with mud, filtered, and analysed. Half the filtrate was ultrafiltered, and the remainder left standing in a covered beaker for the duration of ultrafiltration. The results (Table III) confirm the increase in phosphate on ultrafiltration, and show that when filtered samples stand in glassware, a marked reduction in phosphate concentration may occur. The anomalous effects of ultrafiltration might be complicated by changes on storage, and these were therefore investigated.

TABLE III

10/11 January 1947; P_2O_5 at 23.00 hr. G.M.T., 118 mg./m.^{3}; stirred 23.15–23.20 hr.

Interval between stirring and collection of sample (min.)	Duration filtration etc. (min.)	P_2O_5 (mg./m.^{3})	Duration ultrafiltration (min.)	P_2O_5 (mg./m.^{3})
0	45	150	420	155
	as last, stood for 420 min.	138	—	—
465	105	145	180	175
	as last, stood for 180 min.	126	—	—

Phosphate Changes in Stored Filtrates of Muddy Sea Water

General Nature of Changes and Effects of Bactericidal Agents

A litre of filtrate was analysed, and three samples of 250 ml. set aside in 350 ml. conical flasks. One was kept as control, while to the others were added 1 ml. of 40% formaldehyde and 1 ml. of chloroform respectively. Analyses were performed at intervals, and the results (Table IV) show that storage in glassware produces an increase in phosphate concentration, followed by a decrease to the original value or even lower. These changes are prevented by formalin or chloroform.

TABLE IV

15/16 January 1947; stirred 21.30 hr. G.M.T.; filtered 21.35–02.15 hr.; P_2O_5 of filtrate then 111 mg./m.^{3}; bottles below filled 02.20 hr.

Time from filling bottle (min.)	P_2O_5 (mg./m.^{3})		
	Control	1/250 formalin	1/250 chloroform
40	117	109	111
100	127	111	109
160	122	108	109
220	115	108	109
280	108	109	110

Similar results were obtained in an experiment of longer duration using 500 ml. samples in 1 l. bottles (Table V). These results confirm the increase in phosphate concentration, and also show that on prolonged standing the phosphate concentration decreases to below the original value. It should be noted that while the results given in Tables IV and V are similar, the changes are less marked in the latter. Further experiments confirmed both the initial increase and subsequent decrease, for example in one experiment phosphates increased from 111 to 144 mg./m.^{3} on standing for an hour, and in another they decreased from 100 to 2 mg./m.^{3} on standing for 18 hr. The results in Table V also confirm that both formalin and chloroform prevent both the increase and decrease in values, and further work showed that a 1/250 concentration of toluene had a similar effect.

TABLE V

17 January 1947; stirred 09.30 hr. G.M.T.; filtered 09.30–10.10 hr.; P_2O_5 of filtrate then 97 mg./m.^{3}; bottles filled 10.30 hr.

Time from filling bottles (hr.)	P_2O_5 (mg./m.^{3})		
	Control	1/250 formalin	1/250 chloroform
1	104	98	97
2	101	98	99
3	101	99	98
4½	98	97	98
5½	98	96	95
6½	90	96	96
7½	86	95	95
8½	84	95	96
9½	84	94	95

The increase in concentration probably explains the high values after ultrafiltration because this process takes about the same time as the attainment of maximum values on standing. Rise and fall are prevented by bactericidal agents, and this suggests that living organisms in the filtered samples are responsible.

Changes in the Physico-Chemical Environment

Both rise and fall in phosphate concentration can occur during night or day, and when temperatures are either rising or falling (within the range 11·0–17·5° C.). The phenomena are not independent of temperature, since the fall at least is greatly retarded by low temperatures. For example, an original phosphate concentration of 105 mg./m.^{3} immediately after filtration was reduced after 19 hr. at 13–14° C. to 2 mg./m.^{3}, but a parallel sample at 0° C. was only reduced to 87 mg./m.^{3}.

The phosphate increase on storage is accompanied by a small increase in pH, but the subsequent decrease occurs without further pH change (Table VI).

TABLE VI

17 January 1947; stirred 09.30 hr. G.M.T.; filtration 09.30–11.10 hr.; solution stored in Winchester.

Time elapsed after filtration (min.)	P_2O_5 (mg./m.^{3})	pH
10	91	7·4
70	118	7·5
130	109	7·55
190	109	7·6
250	108	7·6
310	108	7·6
370	107	7·6

A filtrate of muddy sea water was poured into bottles, hydrochloric acid or sodium bicarbonate solution added, and the whole thoroughly shaken. (The

acid and bicarbonate contained negligible quantities of phosphate.) The results of a short experiment (Table VII) show that increasing the pH augments the rise in phosphate, while decreasing it has virtually no effect.

TABLE VII

20 January 1947; stirred 10.50–10.55 hr. G.M.T.; filtration 10.55–12.10 hr.

Interval between filtration and collection of sample (min.)	Alkaline		Control		Acid (1)		Acid (2)	
	P_2O_5 (mg./m.^{3})	pH	P_2O_5 (mg./m.^{3})	pH	P_2O_5 (mg./m.^{3})	pH	P_2O_5 (mg./m.^{3})	pH
5	—	—	121	7·4	—	—	—	—
10	—	8·8	—	7·45	—	6·6	—	6·4
110	141	8·8	126	7·8	128	6·7	129	6·5

For longer experiments, considerable volumes of filtrates are needed, and filtration takes so long that most of the rise in phosphate concentration has passed. When filtered samples are stored overnight, however, and the phosphate accordingly reduced, this can be regenerated by shaking. Vessels half full of liquid were shaken by hand for 5 min., and the subsequent changes in phosphate concentration were exactly similar to those observed after filtration (see control sample, Table VIII). This is of great interest, and suggests that the normal initial rise in phosphate may be due to mechanical agitation of the mud and sea water.

Further work upon the effect of pH was performed upon the changes occurring when filtered stored sea water is reshaken by hand for 5 min. Results are given in Table VIII, and these, in addition to demonstrating the effects of agitation, show that: (*a*) increases in pH augment the initial phosphate rise, but decreases have only a very slight effect; (*b*) pH changes have little effect on the subsequent fall in phosphate concentration.

TABLE VIII

20 January 1947; stirred 10.50–10.55 hr. G.M.T.; filtered 14.30–18.00 hr.; stored overnight at 8° C. At 09.35 hr. 21 January, P_2O_5, 98 mg./m.^{3}. At 09.40 hr. poured into flasks, acid and alkali added except to control; all shaken till 09.45 hr.

Interval between shaking and collection of sample (min.)	Alkaline		Control		Acid (1)		Acid (2)	
	P_2O_5 (mg./m.^{3})	pH	P_2O_5 (mg./m.^{3})	pH	P_2O_5 (mg./m.^{3})	pH	P_2O_5 (mg./m.^{3})	pH
5	—	9·1	—	7·9	—	6·8	—	6·2
65	125	9·01	102	7·9	103	6·8	103	6·2
125	148	9·1	115	7·9	120	6·8	125	6·2
185	119	9·05	104	7·9	116	6·9	125	6·3
305	103	9·05	78	7·8	100	6·9	102	6·3
365	94	9·05	70	7·8	85	6·9	88	6·25
After 385 min. (at 16.10 hr. G.M.T.) all shaken for 15 min.								
25	119	9·05	89	7·85	95	6·9	87	6·3
85	105	9·05	74	7·8	89	6·9	104	6·2

Size of the Containing Vessel

At various times, different-sized bottles of different types of glass were used for storage. The changes were similar for all types, but seemed greater with small vessels. (Compare, for example, the results in Tables IV and VI.) The effect of the size of the bottle was therefore investigated, using bottles of similar shape, and made of similar (white) glass. The results (Table IX) show that both rise and fall in phosphate values are greater in smaller vessels.

Recovery of Phosphate after Disappearance on Long Standing

After standing overnight at 14° C. the phosphate concentration of a filtered sample of muddy sea water was reduced from 105 to 2 mg./m.^{3}. About one-third of the phosphate which had disappeared was recovered from the containing vessel after treatment with distilled water on a water-bath for 1½ hr. None was obtained from the liquid after boiling for 1½ hr.

TABLE IX

4 January 1947; stirred 09.20–09.25 hr. G.M.T.; filtered 09.25–11.10 hr. At 11.40 hr. P_2O_5, 97 mg./m.^{3}. At 11.45 hr. all bottles filled to depth of 7 cm. and shaken vigorously till 11.50 hr.

	P_2O_5 in mg./m.^{3} in bottles of different sizes (diameter, cm.)			
	5·6	7·1	8·0	9·7
Interval between filling bottle and collection of sample (hr.)	Area in contact with liquid (cm.^{2})			
	c. 148	*c.* 196	*c.* 226	*c.* 291
1	107	101	99	97
3	105	102	98	98
5	100	100	96	94
23	75	81	92	92

DISCUSSION

Preliminary experiments on the effect of agitation upon the exchange of phosphate between estuarine mud and sea water gave variable results. Sometimes phosphate was evolved, and sometimes absorbed by the mud. It was suspected that colloidal material in the samples was introducing complications, and that removal of colloids would reduce the apparent amounts of inorganic phosphate present. On the contrary, removing the colloids was accompanied by an *increase* in phosphate concentration.

A similar increase occurs, however, when filtered sea water stands in glassware for the duration of ultrafiltration, and this obscures any possible effects of colloids. The increase is not due to phosphate leaching from the glassware, and implies the conversion of a precursor into 'Denigès active phosphate'. This process is more obvious in small containing vessels, which is reminiscent of the effects of size of the containing vessel upon the growth of bacterial populations in stored sea water (ZoBell & Anderson, 1936; Lloyd, 1937; ZoBell, 1946, p. 83). It is also prevented by bactericides. Redfield, Smith & Ketchum (1937) have shown that bacteria will pass extremely fine filters, and

Dr H. W. Harvey also informs me (personal communication) that cells up to 3μ in diameter can pass the filters here employed. It appears, therefore, that the above liberation of phosphate is due to the activity of living organisms, but work at present in progress shows that large quantities of phosphate can be freed from animal tissues solely as a result of enzymes in the tissues themselves.

On more prolonged storage, phosphate disappears from solution, and is probably mainly immobilized on the walls of the containing vessel. This removal is slowed by cold and bactericides, and depends on the size of the vessel. This suggests that living organisms are also responsible for the removal of phosphate. After this removal, phosphate can be regenerated by shaking the vessel, and if the previous reduction in concentration is due to removal by bacteria, regeneration is likely to be due to destruction of bacteria, and release of phosphorus-containing compounds.

The similarity between the phosphate release on shaking a filtrate and the initial release when muddy water is filtered suggests that, in the latter process, phosphate is also derived from the protoplasm of destroyed organisms. It is impossible to say whether these are destroyed by the stirring of the mud and water or by the filtration which follows. Probably both processes assist in phosphate release.

Waksman, Stokes & Butler (1937) and Renn (1937) have shown that phosphate is rapidly regenerated from autolysing bacteria, but as they dealt with large bacterial populations, with different proportions cytolysing at any given time, there is no indication of how long it takes for an individual cell to free its phosphate. Under present conditions this process seems to take about 2 hr. to be completed.

The following hypothesis explains the observed facts:

(i) When mud and sea water are mixed by stirring, or when muddy sea water is filtered, or when the filtrates are agitated, bacteria are destroyed.

(ii) Their protoplasm, rich in phosphorus, is broken down by living bacteria, with release of phosphate.

(iii) The bacteria grow, using the remaining organic matter, now poor in phosphorus.

(iv) During growth, they reabsorb the phosphate previously released.

The overall effect is therefore of phosphate absorption by the bacteria. Renn (1937) and Waksman *et al.* (1937) have already shown that when sea water is incubated in the dark, for the first day or two phosphate is absorbed. Work at present in progress has often given similar results.

This work has been solely concerned with exchange of phosphate between a surface scraping of aerated mud and sea water. Similar results have been obtained with several samples of aerated muds and silts, but there are preliminary indications that oxygen-free muds give different results.

SUMMARY

When sea water is stirred with mud and then filtered, its phosphate concentration may either increase or decrease. When the filtrate is ultrafiltered, the concentration increases.

Similar increases occur when the filtrate is stored in glassware, and these obscure any effects of the presence of colloidal material. On storage concentrations rise for about 2 hr., and then fall to as low as 2 mg./m.^{3} P_2O_5 in 18 hr.

Rise and fall are both prevented by the addition of formalin, chloroform or toluene, and are more noticeable in small containing vessels. Both occur during either day or night, and when temperatures are either rising or falling.

The increase in phosphate is accompanied by a small increase in pH and is augmented by an increase in pH value.

When a filtrate of muddy sea water is kept overnight, and the phosphate concentration reduced, phosphate can be regenerated by shaking.

The phosphate which disappears on long-standing is largely immobilized on the walls of the vessel.

It is suggested that these changes are due to: (i) destruction of organisms by agitation with release of protoplasm; (ii) breakdown of this protoplasm by bacteria with release of phosphate; (iii) absorption of phosphate by bacteria growing on the walls of the vessel.

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BRITISH FOLLICULINIDAE (CILIATA, HETEROTRICHA)

By S. M. Das, D.Sc., F.Z.S.

From the Plymouth Laboratory and Cullercoats Marine Laboratory, England*

(Text-figures 1–3)

CONTENTS

Introduction

The Folliculinidae are a well-marked family of heterotrichan ciliates, most of which are marine and have a world-wide distribution. They are abundant in most marine aquaria, while in the sea they are usually found attached to Algae, Polyzoa, Crustacea, Mollusca, tube-building Annelida or tests of Tunicata, down to a depth of about 5 fathoms. The family is characterized by: (*a*) the blue or bottle-green colour of the body; (*b*) the large bilobed peristomial field; (*c*) secretion of a case in the form of a bottle or flask; (*d*) the two phases in its life, one sedentary and the other migratory; and (*e*) dedifferentiation of the adult to form the migratory phase and its reorganization into the sedentary phase.

Since the latest publication on British Folliculinidae (Das, 1947*b*), the present author had the opportunity of examining six species of Folliculinidae during his stay in Great Britain. If the records by other workers of *Folliculinopsis ampulla* (Müller) be correct, and if *Parafolliculina hirundo* (Kent) be included, we now have eight definite species of British folliculinids; whereas until 1946 only three species were known. An attempt has been made in this paper to give complete, and for most revised, descriptions of these eight species. The classification followed here is after Fauré-Fremiet (1936*b*), who has shown that many of the genera listed by Kahl (1932, 1933) are not based on well-marked anatomical characters but on the case or lorica alone. Besides, many of the original descriptions by Kent (1881–82) require revision on the basis of work done since then. The characters used for differentiation of species

* Present address: Central Marine Fisheries Station, West Hill, S. India.

are: (i) the size and shape of the case and the body; (ii) the nature of the macronucleus; (iii) the structure of the cell-body; (iv) the colour and nature of pigment; (v) the ciliary bands; (vi) the peristomial lobes; and (vii) the shape and structure of the larva along with the nature of metamorphosis.

History of our Knowledge of British Species

Our knowledge of British Folliculinidae dates back to 1880, when Wright (1858–9, 1862) described a species as *Lagotia viridis*. Stein (1867) showed that the *Folliculina* of Lamarck (1816), *Lagotia* of Wright (1858), and *Freia* of Claparède & Lachmann (1858), were identical; and thus the prior name *Folliculina* was finally adopted. Wright's species were mostly from Ireland, and it is doubtful if any definite species from England, Scotland or Wales was described by him. Saville Kent (1881–82, pp. 596–601) listed six species, of which only one is definitely British, viz. *F. ampulla* Müller from Falmouth. If, however, we include the Channel Islands then another species, *Parafolliculina hirundo* (Kent, 1882), may be added. Little work was done on the family in Great Britain for the next 50 years. Orton (1930) recorded *Folliculina ampulla* from Plymouth, Fowell (1944) *F. viridis* from Swansea, and Bruce (1935) *F. ampulla* and *F. elegans* from the Isle of Man. The only recent additions to our knowledge of British Folliculinidae are two notes in *Nature* by Das (1947*a*) and by Fowell (1947), and a paper on the biology of some folliculinids by Das (1947*b*) in which a tentative key of the British species is added at the end. Only six British species are listed in the last-mentioned paper, whereas sixteen species are known from the continent (Fauré-Fremiet, 1936*b*) and ten from U.S.A. (Andrews, 1944). Besides the six species already recorded (*Folliculinopsis producta*, *F. ampulla*, *Folliculina simplex*, *F. elegans*, *F. viridis*, and *Parafolliculina hirundo*), two further species, *Folliculinopsis elongata* n.sp. and *F. andrewsi*, can now be added to the list of British species.

Descriptions of Species

Genus *FOLLICULINOPSIS* Fauré-Fremiet, 1936

The genus *Folliculinopsis* was erected by Fauré-Fremiet (1936*b*) to include those folliculinids which have a multiple macronucleus (i.e. like a string of beads). Before this genus was constituted the different species of *Folliculina* were distinguished with difficulty, as forms with simple and with multiple macronucleus were both included in the same species. Then, again, the delineation of species according to shape, size and colour of the case and of the body led to confusion amongst different workers. Individuals of the same protozoan species do not vary with regard to the simple or multiple character of the nucleus, but Kahl (1932) lists multinucleate forms under three separate genera—*Folliculina*, *Pebrilla* and *Mirofolliculina*—while, on the other hand,

both uni- and multinucleate forms are lumped together in *Folliculina ampulla*. I consider the erection of the genus *Folliculinopsis* as an important step forward in the classification of Folliculinidae.

Folliculinopsis producta (Wright) (Fig. 1A)

Folliculina producta Wright, 1858
Folliculinopsis producta Fauré-Fremiet, 1936*b*

DIAGNOSIS

Size and case: large size, total length of extended animal 1000–1500 μ; tube of case 500–600 μ long, not more than three times the length of the ampulla and having about eight to fourteen spiral thickenings on its wall. *Nucleus* multiple; consisting of a string of about fourteen beads, extending from near the cytopharynx to the junction of the body with the peduncle in the retracted condition of animal. *Cell-body* with peduncle long and narrow, tapering gradually up to its attachment on the ampulla; cell-body broadening in the proximal half and remaining of the same width up to base of peristomial lobes. *Pigment:* colour of animal deep greenish blue (inky, blue predominating); pigment as granules arranged in definite rows throughout body, alternating with the ciliary bands. *Ciliary bands*: about fifty on body, eight on peduncle, and six on each peristomial lobe. *Peristomial lobes* are slender attenuated ribbons, tapering at the free end but without a sharp point; V-shaped process at junction of lobes; each lobe is about half as long as the tube. *Larva* elongated and vermiform; posterior extremity rounded; size 200 × 75 μ; dark blue colour concentrated at oral extremity.

LOCALITY

Plymouth (first record); Cullercoats (Das, 1947*b*); attached to Algae and dead *Pecten* shells from sublittoral region.

REMARKS

See remarks on the next species.

Folliculinopsis elongata n.sp. (Fig. 1B)

Foliculina producta Wright, 1858, *in part*
Folliculinopsis producta Wright var. *elongata* Das, 1947*b*

DIAGNOSIS

Size and case: gigantic size, length 2000–3000 μ when fully extended; shape of case resembles a hockey-stick; tube 1000–15000 μ long and not less than four times the length of the ampulla; eighteen to thirty spiral thickenings on wall of tube. *Nucleus* multiple; consisting of a string of about sixteen to twenty beads. *Cell-body* attached to ampulla by a distinct narrow peduncle which extends beyond the ampulla in the relaxed condition; body fairly broad at free end. *Pigment:* colour of animal deep bluish green (green predomi-

nating); pigment granules arranged uniformly in rows alternating with ciliary bands throughout body. *Ciliary bands:* about fifty on body, eight on peduncle and six or less on peristomial lobes. *Peristomial lobes* are slender attenuated

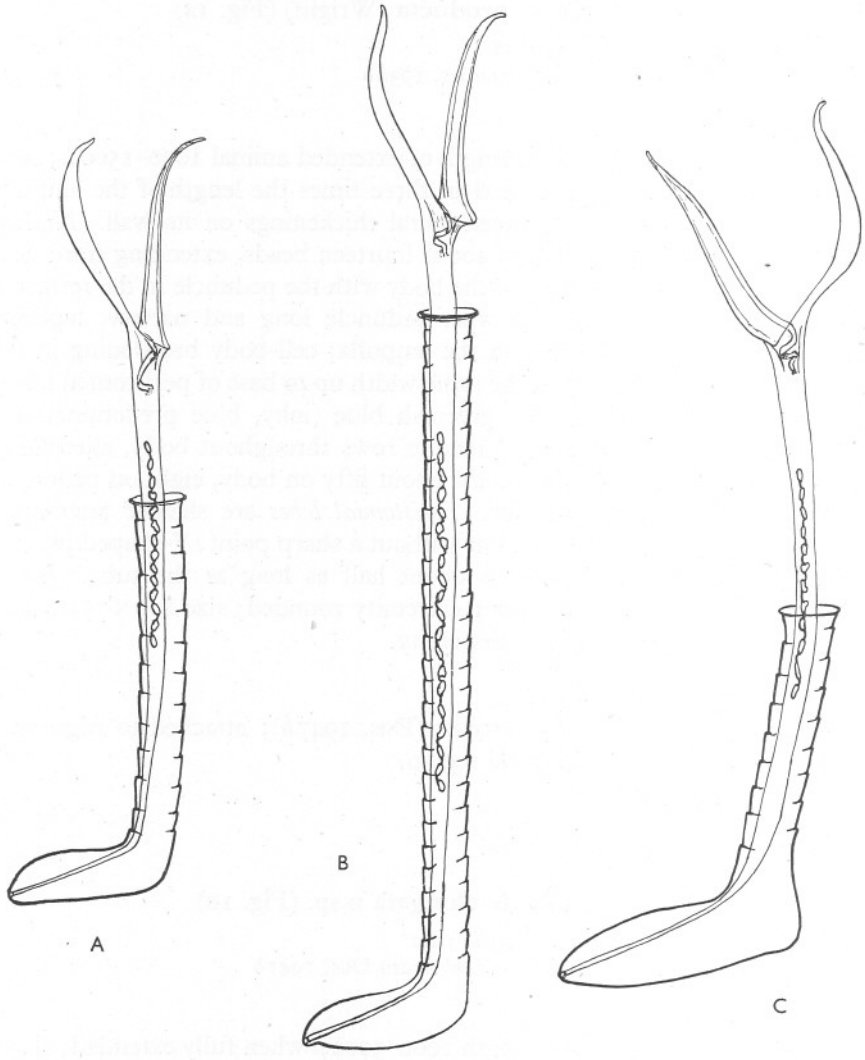

Fig. 1. A, *Folliculinopsis producta* (Wright), × 100. B, *F. elongata* n.sp., × 70. C, *F. andrewsi* (Hadži), × 150.

ribbons, tapering but without a sharp point at tip; V-shaped process at junction of the two lobes much exaggerated; each lobe is less than one-third the length of the tube. *Larva* pear-shaped with posterior end bluntly pointed; size 300 × 150 μ; dark opaque green colour at oral extremity; secretion of case

by attached, elongated larva with three regions—a head, a neck, and an elongated body; the spiral thickenings of the tube are formed by a special spiral band of cilia on the neck of the larva.

LOCALITY

Cullercoats (Das, 1947*b*); attached to tests of *Ciona intestinalis* and to various algae.

REMARKS

The present species was described by me (1947*b*) as *Folliculinopsis producta* Wright var. *elongata*. Since then I have had the opportunity of examining large numbers of specimens resembling *F. producta*, both at Cullercoats and at Plymouth. I can now definitely state that the differences tabulated by me (1947*b*, p. 443) are of a constant character. For example, I examined over a hundred specimens of *F. producta* at Plymouth, and not one of them showed more than fourteen or less than eight spiral thickenings of the case, while almost all the Cullercoats specimens had eighteen to thirty spiral thickenings, the average number being twenty-four. The *F. elongata* forms have been found only at Cullercoats, and I believe this to be a definitely northern species. The differences between *F. producta* and the new species *F. elongata* are even more marked than those between *F. producta* and *F. andrewsi*, the species described next, which has only five to eight turns of the spiral. It may be pointed out here that the gigantic *F. elongata* has not been reported by Andrews (1942, 1944) from U.S.A., and that some of the sketches of Kent (1882) which resemble this species, are superimposed tubes of two successive larvae and not one individual lorica. Both *producta* and *elongata* are multinucleate and thus they must be placed in the genus *Folliculinopsis*.

Folliculinopsis andrewsi (Hadži) (Fig. 1C)

Folliculina producta Wright, 1858, *in part*
F. producta Andrews, 1923
Metafolliculina andrewsi Hadži, 1938
Folliculinopsis producta Andrews, 1942

DIAGNOSIS

Size and case: fully extended animal 600–1000 μ long; case shaped like a sock; tube a little longer than ampulla and having five to eight spiral thickenings on its walls. *Nucleus* multiple; string of about twelve beads. *Cell-body* with peduncle long, narrow and tapering proximally, body ribbon-shaped when extended and about double the length of the tube. *Pigment*: greenish blue colour (much lighter than in *F. producta*): pigment granules uniformly distributed in rows. *Ciliary bands:* peduncle with nine to ten, body with 100, and peristomial lobes with seven to eight bands. *Peristomial lobes* are elongated, ribbon-shaped, tapering distally into a pointed but not sharp tip;

each lobe is only a little shorter than the tube. *Larva* elongated, vermiform, size 200 × 50μ; posterior end rounded; bluish pigment concentrated at anterior end.

LOCALITY

Plymouth and Cullercoats (first record for Great Britain); attached to dead *Pecten* shells from 3 fathoms, and on test of *Ascidiella aspersa*.

REMARKS

The *Folliculina* described by Andrews (1923, 1942) was referred to Hadži (1938), who described it as a species distinct from *Folliculinopsis producta* Wright, and named it *Metafolliculina andrewsi*. As this species is multinucleate the name *Metafolliculina* should give place to *Folliculinopsis*. I have compared the specimens from Plymouth and Cullercoats, with those described by Andrews and Hadži and have no hesitation in placing them in this species.

If we take the test or case alone into consideration, the present three species of *Folliculinopsis* appear to form a progressive evolutionary series. *F. andrewsi* is the simplest with only five to eight spiral turns on the tube; *F. producta* comes next with its eight to fourteen spirals; and finally the *F. elongata* tube is not only enormous in length, but has eighteen to thirty spiral turns on its walls. Similarly, the number of beads in the nucleus also shows progressive increase.

Folliculinopsis ampulla (Müller) (Fig. 2)

Folliculina ampulla Müller, 1854, *in part*
Folliculinopsis ampulla Fauré-Fremiet, 1936*b*

DIAGNOSIS

Size and case: length of extended animal about 600μ; case 300–500μ long and usually ridged at its mouth; ampulla flask-shaped, swollen, and large; tube plain and much shorter than ampulla. *Nucleus* multiple; string of twelve to fourteen beads. *Cell-body* with peduncle short and thin, body proper stout in middle and narrowed proximally as well as distally. *Pigment:* blue-green in colour. *Ciliary bands* not known. *Peristomial lobes* of two equal lobes, each leaf-like with short pointed tips. *Larva:* characters unverified.

LOCALITY

Plymouth (Orton, 1930); Port Erin (Bruce, 1935); Cullercoats (Bull, unpublished record, Dove Marine Laboratory); attached to submerged plates and tests of *Ascidiella aspersa*.

REMARKS

There is no gainsaying the fact that many different species of Folliculinidae have been recorded as *Folliculina ampulla* by past workers. A look at Fig. 2 will show that Laackmann's sketches (1910) depict four different species; similarly Stein's figures (1867) of *F. ampulla* show specimens of at least

two species; finally, Müller's sketches (1854) of his smaller specimens (200 μ) of *F. ampulla* really depict the separate species *F. simplex* Dons. I have made a thorough search for *F. ampulla* both at Plymouth and at Cullercoats, but have failed to collect a single specimen of this species. Fauré-Fremiet (1936*a*) also states that he could not find them on the Breton coast. I have a strong suspicion that the species *Folliculinopsis ampulla* (multinucleate) is really non-existent. The uninucleate *F. ampulla* of past workers will on examination turn out to be *F. simplex* or *F. viridis*; while the multinucleate forms, named as *F. ampulla* in the past, would probably be *F. andrewsi*, or *F. producta*. However, I leave the abolition of this species to future workers.

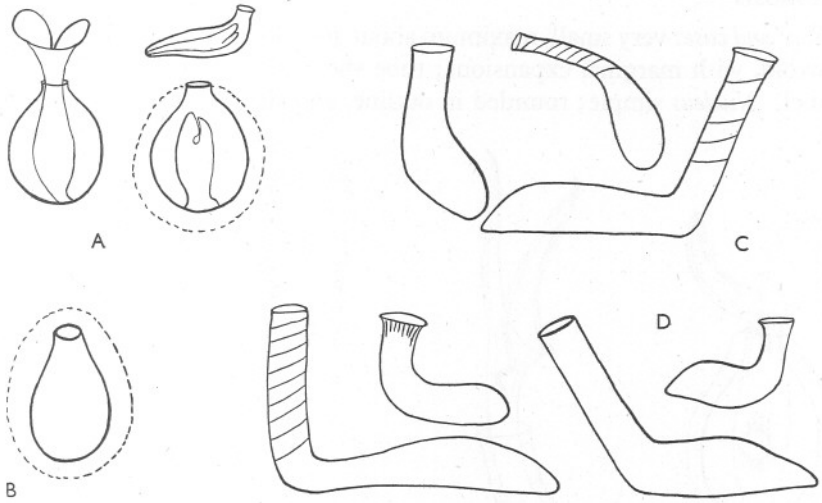

Fig. 2. *Folliculina ampulla* of various authors, some of which may be true *Folliculinopsis ampulla* (Müller). A, *Folliculina ampulla* Müller, the uninucleate small variety, × 125. B, *F. simplex* Dons, as sketched by Dons, to show that it is the same species as that sketched and named *F. ampulla* by Müller, × 125. C, *F. ampulla*: cases as sketched by Stein: there are at least two species represented here, × 50. D, *F. ampulla*: cases as sketched by Laackmann: all four of them appear to belong to different species, × 50.

Genus *FOLLICULINA* Lamarck, 1816

The genus should now be restricted to those forms that show a simple macronucleus and a single case (not divided by a constriction). The genera listed by Kahl (1932, 1933)—*Folliculina*, *Metafolliculina*, *Mirofolliculina*, *Parafolliculina*, *Pseudofolliculina* and *Pebrilla*—were founded by various workers and based mainly on the characters of the case. It has been shown by Fauré-Fremiet (1936*b*) and Das (1947*b*) that the case alone, when considered as a generic or even a specific character, causes endless confusion, if it is not taken in conjunction with other anatomical structures. The present genus *Folliculina*, from which the multinucleate forms have been removed, presents a well-knit group of species, and no useful purpose will be served by splitting

it up further. All the multinucleate forms can be included in *Folliculinopsis*, while the species with a 'double' case (divided into chambers), but simple nucleus, may be put in the genus *Parafolliculina*.

Folliculina simplex Dons (Fig. 3A)

Folliculina ampulla Müller, 1854, *in part*
F. elegans Stein, 1867
F. boltoni Kent, 1882
F. lentus Henneguy, 1884
F. simplex Dons, 1912

DIAGNOSIS

Size and case: very small, maximum about 200μ long; case patulous, rounded or ovoid, with marginal expansions; tube short or absent and without lipped funnel. *Nucleus* simple; rounded in outline, and situated in the proximal half

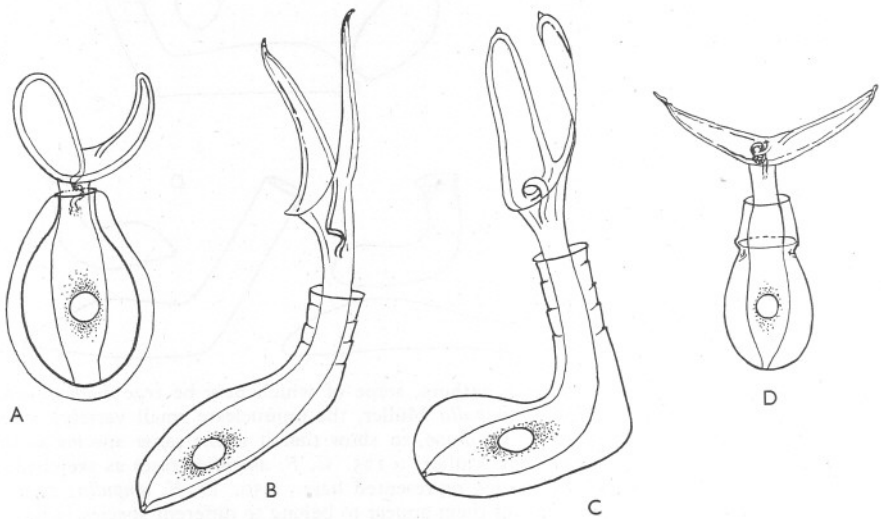

Fig. 3. A, *Folliculina simplex* Dons, ×200. B, *F. elegans* Clap. & Lach., ×125. C, *F. viridis* Wright, ×175. D, *Parafolliculina hirundo* (Kent), ×200.

of the body. *Cell-body* with peduncle absent; body short and cylindrical; attached by a broad base to the case. *Pigment:* body light bluish green generally and bottle-green only about the nucleus. *Ciliary bands:* about twenty-four on body and five on the peristomial lobes. *Peristomial lobes:* short and broad, the two appearing as one bilobed structure; left lobe larger and rounded and right one smaller and narrow throughout. *Larva* cylindrical and elongated, 150×25μ; narrowed and truncated anteriorly.

LOCALITY

Cullercoats (Das, 1947*a*, *b*); attached to tests of *Ciona intestinalis* and to submerged plates in aquarium.

REMARKS

On comparing the figures and descriptions of Müller (1854), Stein (1867), Kent (1882), and Henneguy (1884), it appears that *Folliculina elegans*, *F. boltoni*, and *F. lentus*, are all one and the same species, and that they are identical with *F. simplex* Dons, 1912. As *F. simplex* is the first well-defined species, the later name by Dons is retained.

Folliculina elegans Clap. & Lach. (Fig. 3B)

Folliculina elegans Clap. & Lach., 1858
F. ampulla Laackmann, 1910, *in part*

DIAGNOSIS

Size and case: fairly large, extended animal about 600 μ long; case about 450 μ; ampulla 250 μ; tube shorter than ampulla (150–200 μ) and with three turns of the spiral thickening; ampulla lies horizontally on substratum and the tube placed at an angle of about 45° (never 90°); funnel with expanded collar. *Nucleus* simple; ovoid or oblong, situated at basal end of body. *Cell-body* with short thin peduncle; proximal half of extended animal stouter than distal half. *Pigment:* body of light green colour generally; green pigment concentrated around nucleus. *Ciliary bands:* about forty on the body and five to six on the peristomial lobes. *Peristomial lobes:* flat, ribbon-shaped, tapering distally into a sharp tip. *Larva:* elongated, vermiform; 300 × 50 μ; oral ciliary disk broad and well-marked; after attachment the larva puts forth a long proboscis-like projection, which helps in making the tube of the case.

LOCALITY

Port Erin (Bruce, 1935); Plymouth (first record); Cullercoats (first record); attached to green algae and *Flustra*.

REMARKS

One must be very careful in distinguishing the three species: *Folliculina elegans* Clap. & Lach., *F. viridis* Wright, and *F. aculeata* Clap. & Lach. All three are uninucleate species, all of them have a comparatively short tube which is never longer than the ampulla, and all have only three spiral turns of the thickening on the tube. Looking at the case, the ampulla of *F. viridis* is the stoutest, although this is the smallest of the three species, and the tube is always shorter in length than the ampulla. The ampulla of *F. elegans* is probably the longest with the tube again shorter than ampulla; while the case of *F. aculeata* is characterized by the ampulla and tube being of about the same length. The peristomial lobes are, however, the main differentiating structures.

In *F. viridis* each lobe is leaf-like, non-acuminate and ends abruptly in a short, sharp tip; in *F. elegans* each lobe is ribbon-shaped, tapering, and ends in a somewhat elongated point; while in *F. aculeata* each lobe is acuminate and ends in an accentuated pointed tip. The three species thus form a progressive evolutionary series, so far as the peristomial lobes are concerned. The colour may be distinctive, but I have always found it difficult to distinguish them merely by colour, as variations are quite common in all three species.

Folliculina viridis Wright (Fig. 3C)

Folliculina ampulla Müller, 1854, *in part*
F. viridis Wright, 1862
F. ampulla Laackmann, 1910, *in part* (one of his sketches)

DIAGNOSIS

Size and case: smaller than *F. elegans*, not more than 400 μ when extended; case only 250 μ in length; tube a little more than half the length of the stout quadrangular ampulla, and usually at right angles to it. *Nucleus* simple; large, ovoid, and situated at about middle of ampulla. *Cell-body* stout in the middle and tapering at both ends; peduncle short and narrow. *Pigment:* yellow-green colour (yellow predominating); pigment more concentrated around nucleus. *Ciliary bands:* about fifty on the body, and five to six on the peristomial lobes. *Peristomial lobes* flat, leaf-like, with tips rounded; each lobe terminates abruptly in a sharp point of ectoplasm. *Larva* elongated, vermiform, about 200 $\times$ 40 μ; colour yellowish with yellow-green pigment concentrated near the oral ciliary disk; as in *F. elegans* the larva after attachment puts forth a long proboscis-like projection.

LOCALITY

Swansea (Fowell, 1944); Plymouth (first record); Cullercoats (first record). Attached to various green algae.

REMARKS

F. viridis can be easily confused with *F. elegans*; but, as mentioned by Das (1947*b*), the smaller size, yellow-green colour, erect tube, quadrangular ampulla, and non-acuminate peristomial lobes, should suffice to distinguish it from *F. elegans*.

Genus *PARAFOLLICULINA* Dons, 1914

Parafolliculina hirundo (Kent) (Fig. 3D)

Folliculina hirundo Kent, 1882

DIAGNOSIS

Size and case: very small size, about 180 μ when extended; case horizontal and 130 μ long; annular constriction at base of free end of the case (i.e. a short chamber, the neck, is present). *Nucleus* simple; ovoidal, situated at about the

middle of the cell-body. *Cell-body* short and cylindrical; peduncle absent, attachment by a broad base. *Pigment:* very feebly coloured; bluish green; colour somewhat dark around nucleus. *Ciliary bands:* about twenty on the body and five on the peristomial lobes. *Peristomial lobes* narrow, tapering, nearly symmetrical and lying far apart, so as to create the impression of a single flat T-shaped structure. *Larva:* resembles that of *F. simplex*, except that it is broadly rounded anteriorly.

LOCALITY

Channel Islands (Kent, 1882).

REMARKS

I have not been able to find specimens of this species either at Plymouth or at Cullercoats. It is common on the Breton coast of France and should occur on the south coast of England. The distinctive collar-like band at the free end of the case, and the symmetrical peristomial lobes should immediately distinguish it from the similar *F. simplex*.

KEY TO BRITISH FOLLICULINIDAE

(After Das, 1947*b*)

Macronucleus consisting of a string of beads

Tube not longer than ampulla — *Folliculinopsis ampulla* (Müller)

Tube longer than ampulla and spirally ridged

Tube with five to eight spirals; maximum size of animal 1000 μ; peristomial lobes a little shorter than tube. — *F. andrewsi* (Hadži)

Tube with eight to fourteen spirals; maximum size 1500 μ; peristomial lobes about half as long as tube. — *F. producta* (Wright)

Tube with eighteen to thirty spirals; maximum size up to 3000 μ; peristomial lobes less than one-third the tube. — *F. elongata* n.sp.

Macronucleus simple

Case divided by annular constriction — *Parafolliculina hirundo* (Kent)

Case entire, not constricted

Tube absent; maximum size 200 μ; peristomial lobes asymmetrical, short and broad. — *Folliculina simplex* Dons

Tube shorter than ampulla, with three spirals, and at 135° to ampulla; maximum size 600 μ; peristomial lobes tapering. — *F. elegans* Clap. & Lach.

Tube shorter than ampulla, but at 90° to it; maximum size 400 μ; peristomial lobes rounded at tip. — *F. viridis* Wright

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Summary

A brief résumé is given of the work done on British Folliculinidae up to the present time.

Descriptions follow of eight British species, many of which are revised accounts based on personal observations.

A new species, *Folliculinopsis elongata*, is described.

A revised key for the identification of British Folliculinidae is given.

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THE DECLINE OF *ZOSTERA MARINA* L. AT SALCOMBE AND ITS EFFECTS ON THE SHORE

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

Zoologist at the Plymouth Laboratory

(Plates I–IV and Text-fig. 1)

The history of the almost total disappearance of the eel-grass, *Zostera marina* L., from the Atlantic coasts of North America and a little later along the Atlantic coasts of Europe, in the early 1930's, is fairly well known (for references see Butcher, 1934 and Tutin, 1938, 1942), though the cause has never been satisfactorily determined. The symptoms of the 'wasting disease', with which it was stricken, are brown spots on the leaves which spread and darken until much of the leaf is covered, the leaf then becoming detached from the plant. Of the variety of factors to which this destruction of the living green tissues has been attributed a fungus, *Ophiobolus halimus* Mounce & Diehl (Mounce & Diehl, 1934; Petersen, 1935), and a species of *Labyrinthula* (Renn, 1936; Young, 1943) both rank high in probability as the chief causative agents. Atkins (1938) has strongly criticized the suggestion by Tutin (1938) that the fundamental cause of the epidemic was lack of sunshine in 1931–32 which led to enfeeblement of the plant with a lowering of its resistance to the parasites.

In the Plymouth district and at Salcombe a weakening of the growth of *Zostera* (locally known as 'gravit') was first noticed in the spring of 1932. During the summer of that year very little *Zostera* could be obtained, and that consisted of short pieces. Blackening and rotting at the ends of the leaves was usual. At Salcombe there was a slight growth during the early autumn but it did not result in restoring the beds, or banks, to their old condition and it died down during the following winter. By early 1933 the *Zostera* banks at Salcombe were almost entirely devoid of green leaves and presented a blackish appearance, though here and there were small green patches due to a sparse growth of a few plants with leaves about a foot long. A few of these leaves, however, showed blackened and slightly rotted tips, for they still had the disease. These growing plants were situated at the edges of the old banks and seemed to be colonizing new areas of sand. The years that have passed since then have seen little or no extension of these patches, which for a time became even further reduced. Their present extent is discussed below.

Soon after the disease had reached Salcombe the appearance of the shore at the lowest levels exposed by spring tides was markedly changed. In the late 1920's the mud flats north of the town, and the sandy muddy flats on each side

of the harbour between the ferry and the rocks at the seaward end near Biddlehead and Fort Charles (see Text-fig. 1), were green at low-water spring tides, so thickly did the *Zostera* cover them. Now there is little to be seen except grey mud above the town and shingly muddy sand and some seaweed below the ferry, for algae occupy some positions formerly covered with *Zostera*, especially on the south-east side between Small's Cove and Mill Bay, the area I know best of all. It is about this region of the harbour that I am here chiefly concerned, for I have followed its changes year by year, with the students' classes in the spring and when collecting polychaetes in the summer. Memory and notes are aided by old photographs; the latter are especially valuable in bringing to light changes in level which might otherwise have gone almost unnoticed. It seems well to publish some record of these changes whilst memories of past events are still fairly vivid, especially as the younger workers of to-day are almost unaware of the conditions that prevailed at Salcombe nearly twenty years ago.

The fauna of Salcombe was thoroughly investigated at the beginning of the present century by Allen & Todd (1900). Much of this account still holds good: the rocks, the Salstone region, indeed any of the areas where *Zostera* did not flourish are not very different to-day than they were then. The *Zostera* areas were also much the same until 1931; after that, with the death of so many of the plants, changes set in. The first animals to become scarce were those whose habitat was the leaves of the *Zostera* itself; such species as *Rissoa membranacea* (J. Adams), *Cantharidus striatus* (L.) and *Haliclystus auricula* (Rathke). Some of these seemed to disappear entirely, for they have not, so far as is known, been taken in this locality since. For a time the roots and rhizomes, though dead, still bound the sand in the raised mounds so characteristic of *Zostera* beds. Even as late as 1935, when there was very little living *Zostera* to be seen, the mounds or banks were still more or less unchanged and the buried fauna revealed by digging was much as before. The eventual decay of the roots and rhizomes, which in the later stages were often dug up in a soft and blackened condition, loosened the sand and the tidal currents flattened the mounds and washed them away. The level of the shore fell and in some places the substratum became much more stony through a concentration of stones which had previously been much diluted with, or covered by, sand. Thus the character of the substratum was changed, making it less suitable for some species and more suitable for others, and certainly making it much harder to dig into. These changes in fauna and flora will be discussed later.

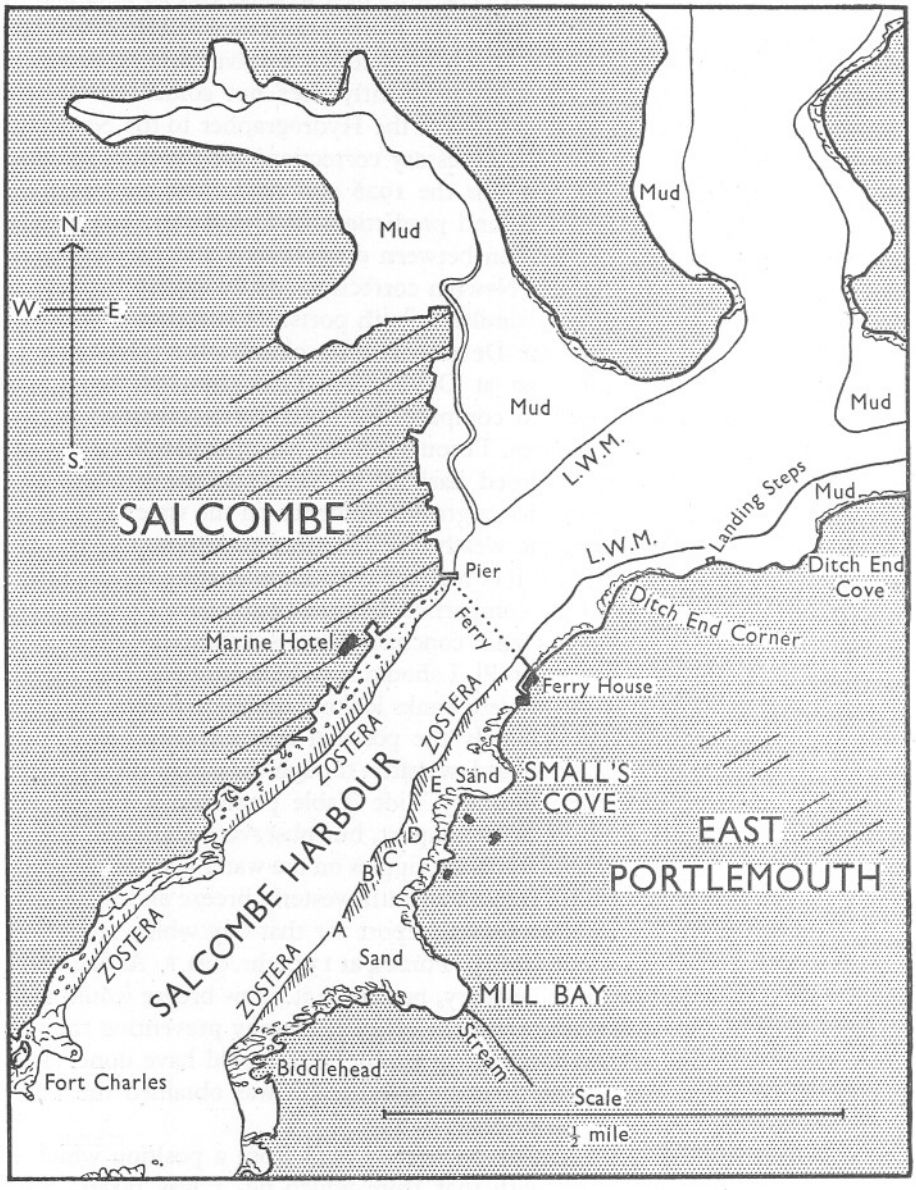
The Disappearance of Banks near Low-Water Mark

Much of the following argument is based on comparisons of photographs taken on various dates at, or about, low water. It is necessary in making the comparisons to know fairly closely the actual heights with reference to chart

datum of the water levels depicted. The level of low water can be obtained in the first place from the Admiralty Tide Table predictions, using those for Devonport, the nearest port for which predictions are available. The actual observed height of a tide, however, frequently does not coincide with the prediction, and I am therefore grateful to the Hydrographer to the Navy and his Department for supplying the necessary corrections for the tides referred to in this paper. The corrections for the 1926 and 1935 tides are based on comparison between observations and predictions at Devonport, but for the 1947 and 1948 tides by comparison between observations and predictions at Newlyn. It is assumed that the Newlyn corrections apply closely to Devonport, the tidal range being very similar at both ports. It is assumed also that the tides at Salcombe follow the Devonport tides closely; the tidal range at Salcombe is very similar to that at Devonport. Thus the corrected levels for Devonport are here used to compare the water levels recorded in the photographs on the different dates. Throughout the paper all datum references are to Devonport. In the enclosed harbour of Salcombe the strength and direction of the wind probably has a greater influence on the water level than at Devonport, and therefore the weather at the time the photographs were taken is considered here. Whilst it is realized that this and other factors introduce some uncertainty into the comparison between water levels on different dates it is not believed that the main conclusions are substantially affected.

The photographs reproduced in Pl. I should now be examined. Fig. 1 gives a general view of the decaying *Zostera* banks looking north-east from Mill Bay on 18 July 1935 from approximately the position marked A in Text-fig. 1. It must have been taken at or about low water, though the actual time was not recorded. On that date the Admiralty Tide Table predicted a low tide of 0·0 ft., Admiralty chart datum, at Devonport, but observation showed that it was 1·0 ft. higher. In the photograph the ripples on the water and the direction in which the seagull faces both suggest a south-westerly breeze and this seems to be confirmed by the meteorological report for that day which records at Plymouth a south-west by west wind of Force 4 at 13.00 hr. G.M.T. At Salcombe such a wind would blow up the estuary, not down it. This breeze would tend to hold back the water draining from the estuary, thereby preventing the tide from falling to quite such a low level as it otherwise would have done. It is assumed, therefore, that at the time the photograph was obtained the water level was not less than 1 ft. *above* chart datum.

Fig. 2 is a photograph taken on 26 March 1948 from a position which is identical, or almost identical, with that from which fig. 1 was taken. This position for the second picture was obtained by careful sighting of landmarks shown in the first one. These are: first, the mast, chimneys and roofs of the buildings near the ferry landing, seen in the middle distance to the left centre of the picture, and the manner in which they align with the hedges of the fields on the hillside far behind them; secondly the alignment of a chimney on the



Text-fig. 1. Sketch-map of Salcombe harbour and vicinity showing very approximately positions of *Zostera* beds (close hatched) on both sides below the ferry as they existed about 1926. *Zostera* also grew on the lower levels of the exposed mud above the ferry, but as the extent of the areas it covered is more doubtful they are not indicated. A, B, etc. mark the approximate positions from which the photographs reproduced in Pls. I–IV were taken, the camera always facing the Ferry House. A, Pl. I, figs. 1, 2; B, Pl. II, fig. 1; C, Pl. II, fig. 2; D, Pl. IV; E, Pl. III, figs. 1, 2.

lower of the two houses on the right with a corner and chimney of the house above and behind. These landmarks fix the position to within a yard, as was determined at the time the second photograph was obtained. On that occasion the distant hillside was slightly obscured by mist and hence is not so clearly rendered in the second photograph as in the first.

On 26 March 1948 the predicted low-water level was 1·9 ft. *below* datum at Devonport. However, observation at Newlyn showed that there the tide was 2·5 ft. higher than the prediction. If we apply an equal correction to the Devonport prediction we assume that the level there was actually 0·6 ft. *above* datum. From this we can further assume that the Salcombe low water on that day was 0·4 ft. below low water of 18 July 1935 and that there is at least this difference in the level of the water shown in the photographs, for whilst that of 26 March 1948 was taken at dead low water that of 18 July 1935 may have been taken a little before or after. However, on 26 March 1948 a fresh breeze blew down the estuary towards the open sea; at Plymouth an east wind of Force 4 was recorded at 12.00 hr. G.M.T., an hour before low water at Salcombe. By 18.00 hr. G.M.T. the wind had increased to Force 5. This wind at Salcombe would have aided the outflowing tide and tended to depress, not raise, the level. At Newlyn the same wind (the Lizard record also shows an east wind of Force 4 at 12.00 hr. G.M.T.) would not have this effect but rather the reverse.

Certainly at Salcombe the tide exposed ground not often uncovered, and in the opinion of the local ferry men made 'a big out', an opinion with which our experienced collector, Mr William Searle, concurred. Thus in accepting the Newlyn correction as being applicable to Salcombe on this particular day we are more likely to be overcorrecting than otherwise, and it therefore seems reasonable to assume that the level of the water shown in Pl. I, fig. 2 is not only lower than that shown in fig. 1, but is likely to be at least 6 in. lower and may well be lower still. If, for the purpose of what follows, this figure of 6 in. is taken, any estimated differences in ground level based on it can be regarded as minimal.

With these facts in mind the photographs may be compared. In the July 1935 picture there is in the near distance a low mound whose seaward edge slopes fairly steeply down to the main channel. This mound of sand, bound by dead roots and rhizomes of *Zostera*, stretches into the distance beyond the left-hand boat stranded on top of it and as far as the figure in a white jersey. The steepness of the seaward slope can be judged by the bathers waist deep within a few yards of the edge and by the boat being rowed close inshore. (Details of bathers, oars of boat, etc., which are clearly visible in the original print, may not be discernible in the reproduction.) Very little living *Zostera* is to be seen, but the position chosen for this photograph includes a few plants in the foreground. A few also still grew in small patches here and there on the mound, whose greater area was, however, bare. It may be noted now that at no time did the *Zostera* completely disappear, a little always being present—this matter will be considered later on.

The photograph of March 1948 shows a very different state of affairs. Where the mound previously existed there is now only water. The whole of the sandy foreground in Fig. 1 has been washed away and the change is strikingly evident if a comparison be made of the conditions around the site of the cross marked on each photograph to indicate the position from which the photograph reproduced in Pl. II, fig. 2, was taken a few minutes earlier. The water covering the site of the former mound was about a foot deep, in some places deeper, and this, it should be remembered, with what was almost certainly a lower tide; the general ground level must therefore be lower by 2 ft., perhaps even 3 ft. The 1935 photograph was taken from a tripod set on sandy ground above water level, whereas to obtain the 1948 photograph from the same position I was forced to wade almost up to the knees in water, again a difference in ground level of 2 or 3 ft. The slope to the main channel in 1948 is irregular but on the whole less sudden and steep than in 1935, at least at the water's edge, for it deepens again farther out. Collectors of to-day have less ground to work over than in 1935, and it needs a lower tide than before to get on to what is left.

A few words of explanation about the piles which appear in the 1948 picture are needed. They formed the seaward extension of a repair base for damaged landing craft which was built in Mill Bay by United States forces during the war. Apparently the craft were brought in between the two groups of piles and hauled up a slipway the lower end of which may be seen as a dark line on the right of the photograph. The base occupied a portion of the north-east side of Mill Bay; it is now derelict, an ugly eyesore in a lovely setting. There is no reason to suppose that the existence of this base has had any material effect on the sandbanks of the lower levels, changes in which were very marked before the Americans came. Moreover, these changes have occurred over a very much wider area than that affected by the activities of the base.

So far, levels in 1935 have been compared with levels in March 1948, but it is possible to go back another nine years. When in March 1926 a class in marine biology conducted by Dr (now Prof.) J. H. Orton at Plymouth was taken one day to Salcombe, I obtained the photograph reproduced in Pl. II, fig. 1. The collectors are busy on the steep seaward edge of a *Zostera* bed in the heyday of its development. The thick covering of plants is clearly seen and it should be remembered that the growth would be thicker still in the summer. The steep slope at the seaward edge is even more strongly marked than in the 1935 photograph when the beds were already beginning to disintegrate. This steep slope is very evident on the well-developed beds in the middle distance as well as in the foreground, in spite of the poor quality of the camera lens whose definition at the sides and in the distance left much to be desired. Nevertheless, landmarks are sufficiently clear for the camera position to be determined, and on 26 March 1948 an attempt was made to reach the same viewpoint (B in Text-fig. 1). The landmarks used were the same or similar to

those already described during the comparison of the photographs in Pl. I. The mast and buildings near the ferry landing and their parallax with the hedges of the hillside behind them fixed the position in one direction, whilst the tall white mast on the right and the gable of the house close by gave another. It is true that the gable in the 1926 photograph is partly obscured by trees since cut down but its position can be made out. As it happened, however, I was unable to reach the proper position, for after wading half-way up to the knees in water at the lowest ebb of the tide the ground began to drop away fairly steeply and I was unable to get out farther without flooding my rubber knee-high boots. I judged that in the true position I should be well over the knees in water and the camera held at eye-level would have been lower than the waist-level camera of 1926. Thus the photograph reproduced in Pl. II, fig. 2 was actually taken several feet landward of the 1926 position and closer, along the same straight line, to the house and flag-pole on the right (position C in Text-fig. 1). This landward position has resulted in the amount of shore exposed in the middle distance being apparently greater in 1948 than in 1926, but a consideration of the difference in viewpoints will show that this idea is erroneous. The viewpoint of 1948 must have been close to the cross marked on the 1926 photograph, and this same viewpoint is marked, as we have already seen, on the photographs in Pl. I. Actually the seaward edge of the shore at low-water mark extreme spring tides is not very much changed for the area shown in Pl. II, fig. 2, though it is a little nearer the land on the whole than before, but the ground is lower and it takes a lower tide to uncover it than it did. It is this part of the shore that is so much more stony than it was years ago. The large *Zostera* bank in the foreground of the 1926 photograph has completely disappeared and the level here must have dropped 2 or 3 ft. This bed in dead and dying condition was still in existence in 1935, for it was none other than the low mound in the near distance seen in Pl. I, fig. 1. That this is so is immediately apparent when it is remembered that the cross on that photograph and the cross on Pl. II, fig. 1, both indicate the same position as closely as can now be determined.

So far the tidal level of the 1926 photograph has not been considered. The picture most probably was obtained on 16 March for which the tidal prediction was 1·7 ft. *below* datum, but the observed height at Devonport was actually only 0·7 ft. *below* datum. The prediction for the previous day's tide had been a little lower but the class on that day was definitely not at Salcombe. No other tide in March 1926 was predicted as low or lower than that on 16th. For that day the weather report records a light westerly breeze of Force 2 and it will be seen that the water in the picture is but lightly rippled. This breeze would scarcely affect the water level which can, therefore, be assumed to have been about a foot lower than that seen in the 26 March 1948 photographs (Pl. I, fig. 2, and Pl. II, fig. 2—but see remark concerning this day's wind, on p. 399), and was lower than in the photograph taken in July 1935 (Pl. I, fig. 1).

The extensive *Zostera* banks which previously existed on the west side of the harbour, under the Marine Hotel and extending towards the harbour mouth, have similarly disappeared, and only a few sparse patches of *Zostera* remain. These banks were much more muddy than those on the east side and there were variations in the fauna to correspond. My visits to the west side have been less frequent than to the eastern shore and no photographs showing past conditions have been traced. Mr William Searle ('Bill'), the Laboratory's veteran collector, who has regularly worked under the Marine Hotel, informs me that the ground where the *Zostera* banks formerly existed is more stony and more difficult to dig into than the banks themselves used to be, and there is no longer a seaward edge where the ground suddenly sloped steeply downwards. To-day the collecting ground is uncovered by the tide for a shorter period than before, and with the tide at its lowest the water's edge is closer inshore.

It seems certain that the *Zostera* beds on this western side, south of the Marine Hotel, were considerably broader than indicated on the sketch map (Text-fig. 1), extending out beyond low water spring tides, as they do to-day.

The Accumulation of Sand near High-Water Mark

A consideration of four photographs has shown that the ground near low-water mark, on the east shore, has been lowered 2 ft. or more since most of the *Zostera* died, and the question now arises as to what has become of the sand which has been washed away. This question is answered, apparently, by a comparison of two more photographs which will now be considered.

The photograph of the north-west corner of Small's Cove reproduced in Pl. III, fig. 1, was taken in 1926 on the same day as that in Pl. II, fig. 1. On 21 May 1947 the photograph shown in Pl. III, fig. 2, was taken from the same viewpoint (E in Text-fig. 1), obtained by getting the lower left-hand buildings by the ferry slip in the same alignment with the distant hillside as shown in the earlier photograph. It was found that a very small displacement was sufficient to give appreciable parallax, and it can therefore be asserted with confidence that the camera in 1947 occupied a position in space almost identical with that of the camera of 1926, and that any variation could not have exceeded more than a few inches in any direction. The 1947 photograph was taken $1\frac{1}{2}$ hr. before low water; the tide when the 1926 photograph was obtained seems to have been a little lower. Differences in definition between the photographs are due partly to different atmospheric conditions and to the much better lens used in 1947.

Two features shown by the photographs call for first comment. The high jetty seen at the ferry landing in 1947 was not in existence in 1926. The end section of the drain pipe, so conspicuous in 1926, was accidentally broken off at a later date but the remainder of the pipe, which I am assured has not been repaired or rebuilt, had by 1947 disappeared under a covering of sand and it is still so buried to-day. The natural rocks, however, show most clearly the rise

in sand level, for it is plainly evident that in 1947 the sand was much more banked up at the foot of the cliff than in 1926, especially on the right towards high-water mark, the rise being some 3 or 4 ft. In the 1926 photograph high-water mark spring tides is out of sight beyond the right-hand edge of the picture, but in the 1947 photograph a thin dark line of stranded weed stretches from the right-hand edge to the cliff rocks near the centre of the picture and marks the highest level reached by the previous high tide, a moderately high spring. The tongue of dark fucus-covered rocks near half-tide mark in the middle distance was more submerged by sand in 1947 than in 1926 and it is obvious that the sand beyond them, towards the ferry house, had also been banked up. At the top of this little bay, out of sight beyond the right-hand edge of these photographs, sand has been steadily accumulating year by year, raising the height of the beach near high-water mark, until an appreciable area is no longer inundated by spring tides. At that place I have watched with interest the slow but steady formation of a small sand dune colonized by *Honckenya peploides* Ehrb. and maritime grasses (*Festuca*, *Agropyrum*). The sand level is much the same to-day (December 1948) as it was in May 1947.

Sand has also accumulated in the upper part of the larger Mill Bay, but of this I have no definite records of my own. I am much indebted, however, to local inhabitants for various information, particularly to Mr and Mrs R. C. Tyler who, since 1916, have occupied the house next to the ferry landing on the East Portlemouth side, and to Mr Harry Cook and son, boatmen of Salcombe. They all agree that sand began to accumulate on the east side of the harbour at least as early as 1920, long before there was any reduction in the growth of the *Zostera*. This accumulation steadily increased and still goes on. Material washed and blown up from the old *Zostera* mounds therefore does not by itself fully account for the banking up of the sand on the higher shore levels; it has merely added to a process due to other causes. These causes lie outside the scope of the present paper, but it is worth recording that Salcombe was formerly much visited by sailing vessels which took away from Mill Bay large quantities of sand for ballast. Sand for building purposes was also removed in barges to Kingsbridge; according to Mr Harry Cook hardly a day went by without one or more barges visiting Mill Bay for this purpose. During the early years of the present century this traffic decreased and the last barge load for Kingsbridge was taken, so I am informed, shortly after the end of the 1914–18 war. About this time the high tide reached a wall by the roadway at the inner end of Mill Bay; but to-day this wall is silted over and the high-tide mark is about half-way down the bay.

The removal of so much sand in years gone by must have kept the level down—assuming that sand was accumulating all the time—and it seems therefore reasonable to suppose that the present silting may in some measure be due to the cessation of these activities. It should be noted that at the time this sand was being taken there were extensive *Zostera* beds on both sides of

the harbour; some description of these will be found in Allen & Todd (1900).

On the eastern shore the sand in general drifts to the north-east (prevailing winds come from points between south and north-west), and at the present time is piling up, especially on the rocks at Ditch End Corner, north-east of the ferry. It has turned the corner and has already travelled along the south shore as far as the old steamer landing steps just west of Ditch End Cove, covering muddy shingle and rocks.

It should be noted that in this sheltered harbour really big waves are not generated and the great transport of sand from one locality to another, such as is of common occurrence during stormy weather on exposed beaches like those of north Cornwall, is unlikely to take place. However, Mr Tyler told me that in a gale the sand banked up against the sea wall by the ferry house is sometimes washed away but it always comes back again, often on the next tide.

The sand slopes steeply down from high-water mark for most of the tidal range. It is loose, well drained and devoid of any obvious buried fauna. At the bottom of the slope the ground levels off, and in the firmer and wetter sand *Arenicola*, *Lanice* and other members of a normal sand fauna appear.

The Effect on the Fauna

The death of the *Zostera*, and the consequent modification of the physical character of the areas it occupied, have had a noticeable effect on the fauna and flora. This has been most marked between Small's Cove and Mill Bay where the washing away of the sand has produced a stony ground with many of the stones exposed on the surface. This stony ground occupies a position where the most landward extensions of the *Zostera* lay; part indeed may not have been covered by *Zostera* at all. The stones give attachment to several species of algae, particularly *Enteromorpha* sp., *Ulva* sp., *Fucus serratus* Linn., *Laminaria saccharina* Lamour., and species of *Ectocarpus*, *Ceramium*, *Polysiphonia*, etc. Previously there had been growths of these seaweeds on a number of large stones which were scattered here and there, especially on this landward side of the *Zostera* beds, but the growths were nothing like as abundant as they are now. The photograph reproduced in Pl. IV shows the present seaweed-covered stony area very well. It was taken on 21 May 1947, 15–20 min. after dead low water when the tide had risen 2–3 in., as can be determined from another photograph, not reproduced, which gives a closer view of part of the same region at dead low water. The Admiralty Tide Table prediction for that day gives low tide as being 0·7 ft. *below* datum, but the observed height at Newlyn was 2·0 ft. above the prediction, from which we conclude that the water level when the exposure was made would be about 1·5 ft. *above* datum. There was no wind. The viewpoint for this picture is indicated, approximately, by the cross on Pl. II, fig. 2 (when the tide was lower) and at D in Text-fig. 1. The

view includes the only *Zostera* bed visible on that day; on the picture a dotted line has been drawn around it. The *Zostera* extended a little way under water at the lowest ebb of the tide. In 1948, conditions were still much the same as when this picture was obtained.

The extension of algal cover has very likely brought about an increase of animal life normally associated with stones and seaweed (e.g. *Littorina littorea* (L.), *L. littoralis* (L.), etc.), but no comparable figures exist and the surface fauna of this area has not been specially investigated. It appears to be much as would be expected in such a situation and it certainly lacks the interest of the specialized buried fauna for which this part of the Salcombe estuary has long been noteworthy. This is, of course, the remarkable and seemingly unmatched concentration of commensal animals in the ground on both sides of the harbour.

At the bottom of the slope down from Small's Cove there is still a large colony of *Lanice conchilega* (Pallas) and an abundance of *Arenicola marina* L. In the galleries of some of the *Arenicola* fairly large specimens of *Harmothoë lunulata* var. *marphysae* McIntosh may be found. Part of this area is uncovered in the near distance in Pl. III, fig. 1. *Zostera* beds occupied the lower levels of this cove and stretched in a nearly continuous bank to Mill Bay[1] and beyond (see Text-fig. 1 and Pl. II, fig. 1). It was in this bank that *Acrocnida brachiata* (Montagu), with its commensals *Mysella bidentata* (Montagu) and small specimens of *Harmothoë lunulata* var. *marphysae*, were abundant. The brittle-star is still common in the stony soil, but is not as numerous as formerly and seems less frequently accompanied by its commensals which, since the war, have been appreciably more difficult to find with it. This may, of course, be merely a passing phase, but it seems hardly likely that the brittle-star will again reach its former abundance in ground less suitable for it. The ground itself is relatively barren and but few animals of any kind are found for much hard digging, for there has taken place a very marked diminution in the number of species and individuals turned up by the fork. Thus *Phascolosoma elongatum* Keferstein, with which was often *Mysella bidentata*, was formerly common but is now infrequently found, while *Amphitrite edwardsi* Quatrefages with its large handsome commensal *Lepidasthenia argus* Hodgson have become very rare. These two associated polychaetes were not uncommon, although always less numerous here than in the muddier opposite shore of the harbour where they are also less abundant than before. The synaptids, *Leptosynapta inhaerens* (O. F. Müller) and *Labidoplax digitata* (Montagu), and their commensals, were previously present in small numbers on the Mill Bay side but are now rarely turned up when digging, and the same remark applies to *Upogebia deltaura* Leach and *U. stellata* (Montagu), while *Lepton squamosum* (Montagu), an inhabitant of

[1] The gap in the bed opposite Mill Bay, indicated in Text-fig. 1, is seen in photographs taken in 1926, and it forms the immediate foreground in Pl. I, fig. 1. It may have been caused by the freshwater stream which ran down the beach and at low tide discharged through it.

their burrows, has not been obtained here for several years. *Callianassa subterranea* (Montagu), always uncommon, is less frequently found than formerly, and this is true also of a number of other non-commensal species such as *Owenia fusiformis* Delle Chiaje and *Notomastus latericeus* Sars.

Towards Mill Bay, where there are still patches of sand with but few stones, *Echinocardium cordatum* (Pennant) and its commensal *Montacuta ferruginosa* (Montagu) are as common as ever, and some other inhabitants of clean sand such as *Caesicirrus neglectus* Arwidsson and one or two species of *Magelona* are also abundant. These species were always to be found here in the sand where *Zostera* did not grow, as well as occasionally in the beds themselves.

In this account no attempt is made to give a complete description of the buried fauna of the area under review, rather is it the intention to record the more obvious changes, or absence of change. The region is still of very considerable interest, but much of its former richness and diversity has been lost and this can be directly attributed to the physical changes following the disappearance of the *Zostera*. In my opinion overcollecting is not the cause. It would have been possible to overcollect on this shore but care was taken that this should not happen. During the war very little collecting was done[1] (there were no students' classes at Plymouth during the years 1941–45 inclusive), but the fauna has shown no sign of recuperation, for, on the contrary, it was definitely poorer after the war than before. It has become more than ever necessary to avoid excessive digging over the smaller area now uncovered and it is sincerely to be hoped that future collectors will do their utmost to conserve what remains.

The Surviving *Zostera*

There remains for consideration the *Zostera* itself. Of the three British species of *Zostera* there is only one likely to be confused with *Z. marina*. This is *Z. Hornemanniana* Tutin, which can grow from half-tide mark down to 1–2 fathoms and it has been seen at Salcombe (Tutin, 1936). The species is distinguished by the smaller stigmas relative to the length of the style and by the smaller seed (Tutin, 1938). It was thought necessary, therefore, to determine the species of the *Zostera* still growing in small quantity at Salcombe.

On 19 July 1947, during the flowering season, my wife aided me in going over all the *Zostera* we could find. On that day the small *Zostera* bed seen in the photograph on Pl. IV was not uncovered, the shallowest part being submerged by a few inches of water and most of it was covered by 6–9 in. at the lowest ebb. Between us we managed to cover most of the ground and obtain flowers and seeds. Without exception the plants proved to be *Z. marina* L.

Although the specific identity of the *Zostera* at Salcombe is the same now

[1] A local informant tells me that Americans stationed at the repair base in Mill Bay collected for eating all the *Ensis* they could find. These were always most numerous near the south-west corner of Mill Bay. *Ensis* was certainly very scarce at that place in 1946 and 1947 but by 1948 small ones were again fairly plentiful.

as it was always supposed to have been, I have a strong impression that present-day plants are shorter and a little narrower in the leaf than they used to be, and that they do not show as vigorous a growth. In this I am supported by the local people whose names have already been mentioned. It seems to be generally agreed that in the summer a length of 5 or 6 ft. was quite usual, though all plants did not attain these dimensions and they were longer in some parts of the estuary than in others. In July 1947 the tallest plants my wife and I could find did not exceed 3 ft. (about 90 cm.) and most were considerably shorter. The breadth of their leaves was $\frac{1}{4}$ in. and less (approx. 5–7 mm.) and the colour a good bright green. On the longer leaves some epiphytic red algae were growing, as is usual; we did not see any *Haliclystus*. In the previous May the plants had been less than 2 ft. long (about 60 cm.) and they had certainly not been longer than this in March. In March 1948 the tallest plants were only 18 in. (about 46 cm.) My memory assigns a length in March and April of 2–3 ft. to the longest leaves and Mr William Searle agrees with this. Prof. J. H. Orton writes 'my impression is that they might have been two feet about'. This would make them one and a half times or even twice their present length for that time of year. The plants in the photograph of March 1926 (Pl. II, fig. 1) look to have been of moderate length, and the appearance suggests that a good many exceeded the 18 in. maximum of March 1948, though the definition is too poor for certainty on this point. Some photographs taken at low tide near Ditch End Cove in 1927 show quite distinctly that the plants there growing on sticky mud were only about 9 in. (or 23 cm.) long, estimated with reference to a collecting basket also in the pictures. The time of year when they were taken is uncertain, but various indications point to January or February as the most likely months. There seems to be no *Zostera* at Ditch End now, and it was probably always shorter there than in the harbour below the ferry. There is, too, the possibility that it was *Z. Hornemanniana* (Tutin, 1942), which seems to grow best on a soft mud substratum, a possibility that is increased when the widths of the leaves, seen in the photographs, are compared with the wicker-work of the collecting basket. The same type and make of basket is still in use and the thin canes of which it is woven have an average diameter of 3·5 mm. with a variation either way of 0·5 mm. The basket in the photographs has an almost identical number of strands and the same general dimensions as present-day ones, therefore its canes must have been of similar cross-section. Now the *Zostera* leaves appear distinctly narrower than the cane strands, and such measurements as are possible on the photograph confirm this impression. One of the characters of *Z. Hornemanniana* is that its leaves are only about 2 mm. broad; those of *Z. marina* are mainly 5–10 mm. broad (Tutin, 1942), although there is said to be a very narrow-leaved variety, *Z. marina* var. *stenophylla* Asch. & Graebn. about which little definite information is available. In the photograph of the *Zostera* bed in Pl. II, fig. 1, the leaves seem distinctly broader than the woven strands of the baskets, thus agreeing with normal *Z. marina*.

If we accept a length of 2 or 3 ft. as the former length for *Zostera marina* in the Mill Bay region in March, it follows that a summer length of 5 or 6 ft. might very well have been attained. Summer *Zostera* obtained near Plymouth when trawling for pipe-fishes in the estuary of the River Yealm or in Cawsand Bay must have reached this length. It was the usual practice to tie bunches of this *Zostera* to stones which were then dropped into the pipe-fish tank in the aquarium. The tank is 3 ft. 4 in. deep, and I well remember how most of the leaves reached the surface and spread out floating horizontally for a foot or more, and this after some of the older and longer leaves most heavily covered with epiphytes had been removed. The *Zostera* in the River Yealm to-day is nothing like that length; there has been very little at all in Cawsand Bay for years, and what is there is short.

Whilst from the above considerations it seems quite definite that much of the *Z. marina* existing before the disease appeared had considerably longer leaves than any of the plants now living in the Plymouth district, it is more difficult to establish that the leaves were also wider. Most of those who remember the plants prior to 1930, and whom I have questioned, agree that the leaves were wider than any seen at present and it has already been stated that that is my own impression. Some equally good observers, however, are not so certain. In the absence of specimens (I have not been able to trace any in herbaria[1]) it is impossible to establish the truth, and the only photograph showing the leaves at all clearly is an old picture of pipe-fishes in one of the aquarium tanks among *Zostera* which had almost certainly come from the River Yealm. This photograph, made before 1931, is reproduced elsewhere (Wilson, 1935, fig. 83). By comparing the widths of the leaves with the lengths of the heads of the pipe-fishes in the photograph an estimate of the actual widths can be made when the dimensions of the heads of the pipe-fishes are known. This can be closely determined from museum specimens of the same species. Simple calculations based on the smallest probable lengths of the heads of the pipe-fishes photographed give the widths of the most clearly defined leaves as being over 8 mm.; this can be regarded as a conservative estimate. These leaves were thus considerably wider than any seen recently.

The conclusion that the leaves of *Zostera* were generally wider, as well as longer, is in agreement with earlier discussion on this subject (Blackburn, 1934; Cottam, 1935; Butcher, 1934, 1935) before *Z. Hornemanniana* Tutin (1936) had been recognized. It seemed then generally agreed that the *Zostera* remaining on the beds was of narrower leaf than many of the plants had formerly been. It is well known that the stature of individual plants, terrestrial and aquatic, is much influenced by the environmental conditions under which they grow and it has been suggested (Cottam, 1935, 1938; and see also Setchell, 1929)

[1] Miss E. Pearse, Paignton, has very kindly sent me a dried specimen of *Z. marina* collected in Cawsand Bay in August 1900. It has a length, exclusive of rhizome, of 3 ft. 4 in. (about 1 m). and a leaf width of about 5 mm.

that the different forms of *Z. marina* are but an expression of a varying environment. But apart from the washing away of the sand of the old banks it seems improbable that the physical and chemical conditions of the River Yealm and Plymouth Sound, to mention only localities near this laboratory, have so changed in character that the plant can no longer form broad and lengthy leaves. The hydrographic changes known to have taken place in the western English Channel might have been suspected had the phenomenon been purely local, but it was not. Everywhere, or almost everywhere, it was the broad long-leaf form which suffered most severely, leaving narrow short-leaved forms of which one subsequently proved to be a hitherto unrecognized species, *Z. Hornemanniana*. It would be interesting to know whether the broad-leaved and formerly vigorously growing variety was a definite morphological or physiological strain, which in the event proved more susceptible to the disease than did other strains.

The *Zostera* at Salcombe is, I think, spreading slowly, very slowly. No measurements are available but my impression is that there is a little more present than in the years immediately before the war when there was very little to show to the students attending the annual classes held during the Easter Vacation. To-day rather more is to be seen; it should be carefully conserved and the temptation to dig into it resisted. If left alone it may in the years to come re-establish itself and its specialized fauna with it. Unhappily, brown patches on many of the leaves can still be found, indicating that the disease is still present. It is to be hoped that the disease will become less virulent, or that a strain of *Z. marina* vigorous in growth but with high resistance to disease will some day appear to repopulate the estuaries and other sheltered waters where this useful plant was formerly abundant. On the American coast a trend toward restoration of the plant in favourable areas has been reported by Cottam (1945).

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Pl. I, fig. 1. Special acknowledgement is due to the Hydrographer to the Navy and his Department for tidal corrections for several dates. The Director, Mr F. S. Russell, has taken a kindly interest in this work throughout for which I am very grateful.

Summary

A comparison of photographs taken on the eastern shore of Salcombe harbour before and after the disappearance of much of the *Zostera marina* L. shows that where previously there existed extensive sand banks, stabilized by the growth of this plant, there has been a lowering of ground level of 2 ft. or more, due to the washing away of the sand where the *Zostera* has died. Much of the ground is more stony than before and has become largely covered with seaweed attached to the stones. The buried fauna is not as rich as it was and some species previously common are rare or have disappeared altogether. A few small patches of *Zostera* still survive, but the plants are shorter with narrower leaves than before.

On the west side of the harbour there also seems to have been a similar drop in shore level at about low-water mark spring tides following the disappearance of much of the *Zostera*, and the buried fauna is also poorer than previously, but for this side no photographs and fewer data are available.

On the east side the sand washed away from the old *Zostera* banks has apparently been carried on to the higher levels to add to sand which has been steadily accumulating there for many years, especially near high-tide mark.

Plants of *Z. marina* now growing at Salcombe reach a height of about 3 ft. (about 90 cm.) in summer and have a maximum leaf width of about $\frac{1}{4}$ in. (5–7 mm.), whereas previously the plants were longer, possibly reaching 5 or 6 ft. (150–180 cm.) and had wider leaves. Plants from the estuary of the River Yealm near Plymouth certainly reached a length of 5 ft. or more, prior to 1931, and a calculation from an old photograph indicates that their leaves attained a width of at least 8 mm.

Old photographs of *Zostera* growing on soft mud near Ditch End Cove, above Salcombe harbour, show short very narrow-leaved plants which may have been *Z. Hornemanniana* Tutin.

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ADDENDA

1

Since this paper went to press the following information has been received from Major Arthur A. Dorrien Smith, Tresco Abbey, Isles of Scilly, and this seems a suitable place to record it. He has kindly given permission for this to be done.

In the Isles of Scilly *Zostera marina* was formerly abundant, covering hundreds of acres of tidal flats between the Islands, but now in 1949 scarcely any remains. The eel-grass died away about the same time as at Salcombe and elsewhere round the British coast. After its death the mud in which it grew, and which was bound by its roots and rhizomes, was loosened and washed away leaving behind nothing but sand. The drift of the tide has carried the mud into the eastern approach to the Islands, known as Crow Sound, and it has come to rest in that area. This was once an excellent trawling ground for flat fish, but it is now ruined by the mud.

2

My wife finds additional evidence of former extensive removal of sand from Salcombe in 'Kingsbridge and Salcombe, with the intermediate Estuary, historically and topographically depicted' (Kingsbridge, 1819). The anonymous author (Abraham Hawkins) says (p. 82) that 'from the bar sand

is dredged up and carried in barges to various parts of the shores of the estuary for manure. Such was the practice in husbandry formerly, that many persons recollect to have numbered thirtytwo (*sic*) of these barges on the bar at once in the years 1775–6 & 7. At present however they rarely exceed three or four.' Futhermore (p. 101), from the South Sand 'large quantities of sea-sand...are...taken at will by the occupiers of farms throughout the parish of Malborough, and carried for manure. The right is founded upon an unvarying custom time immemorial, undenied and uninterrupted, and consequently cannot now be shaken.'

EXPLANATION OF PLATES

PLATE I

Fig. 1. Decaying *Zostera* banks at about low water on 18 July 1935. Predicted level at Devonport 0·0 ft., Admiralty chart datum; observed level at Devonport 1·0 ft. higher. The approximate position from which the photograph was taken is indicated by the letter A in Text-fig. 1. The white cross occupies the same relative position as that seen on Fig. 2 below. Photograph by M. A. Wilson.

Fig. 2. View from the same position as that from which Fig. 1 above was taken, photographed at dead low water on 26 March 1948. Predicted level at Devonport 1·9 ft. *below* Admiralty chart datum; observed level at Newlyn 2·5 ft. higher than prediction for that port. The white cross marks the position from which the photograph reproduced in Pl. II, fig. 2 was taken.

PLATE II

Fig. 1. Collecting on a *Zostera* bank at about low water on 16 March 1926. Predicted level at Devonport 1·7 ft. *below* Admiralty chart datum; observed level at Devonport 1·0 ft. higher. View from position B in Text-fig. 1. The white cross marks the approximate position from which was obtained the photograph reproduced as Fig. 2 below and it therefore indicates a position on the shore identical, or almost identical, with that marked by the white crosses on Pl. I, figs. 1, 2.

Fig. 2. Collecting on the same shore at about dead low water on 26 March 1948. Predicted level at Devonport 1·9 ft. *below* Admiralty chart datum; observed level at Newlyn 2·5 ft. higher than prediction for that port. The position from which the photograph was taken is indicated by the white cross on Pl. I, fig. 2 and by the letter C in Text-fig. 1. It is estimated that this position would be close to the white cross on Fig. 1 above. The white cross on this photograph marks the approximate position from which the photograph reproduced in Pl. IV was obtained.

PLATE III

Fig. 1. The Ferry House and north-west corner of Small's Cove viewed from the south-west corner (position E in Text-fig. 1) on 16 March 1926.

Fig. 2. The same view as Fig. 1 on 21 May 1947, 1½ hr. before low water.

PLATE IV

View of stony and algal covered area and of residual *Zostera* beds between Small's Cove and Mill Bay, 15–20 min. after dead low water on 21 May 1947. Predicted level of low water at Devonport was 0·7 ft. *below* Admiralty chart datum; observed level at Newlyn 2·0 ft. higher than prediction for that port but the tide had already risen about 3 in. The area enclosed by the white dots comprised the only *Z. marina* beds exposed anywhere between the ferry and the rocks at Biddlehead. The position from which this photograph was taken is indicated by a white cross in Pl. II, fig. 2, and by the letter D in Text-fig. 1

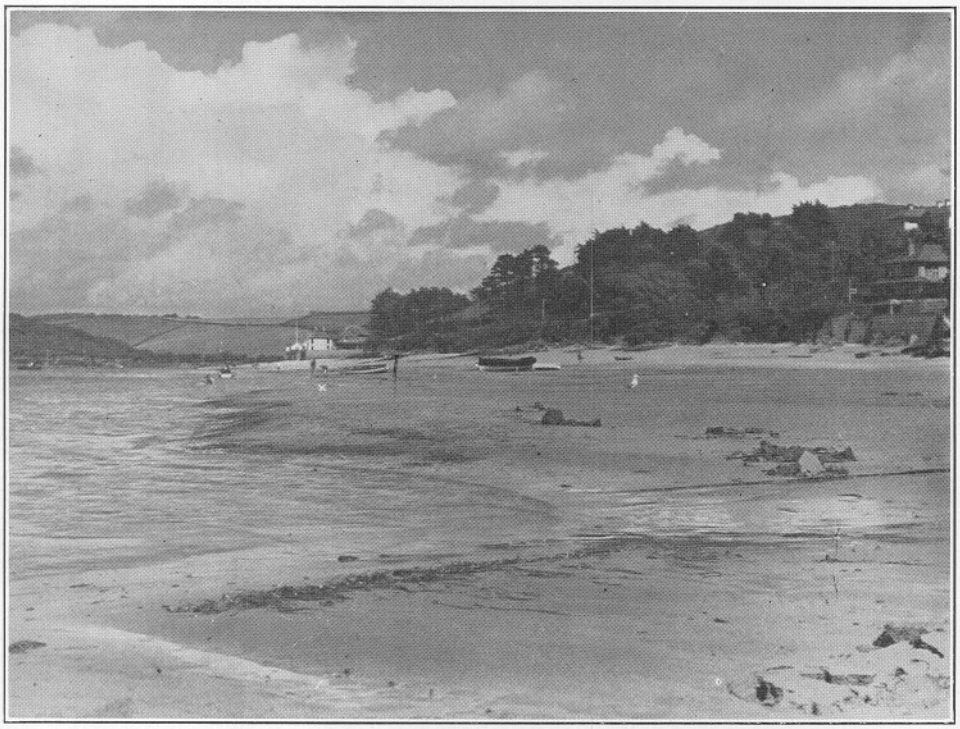


Fig. 1.

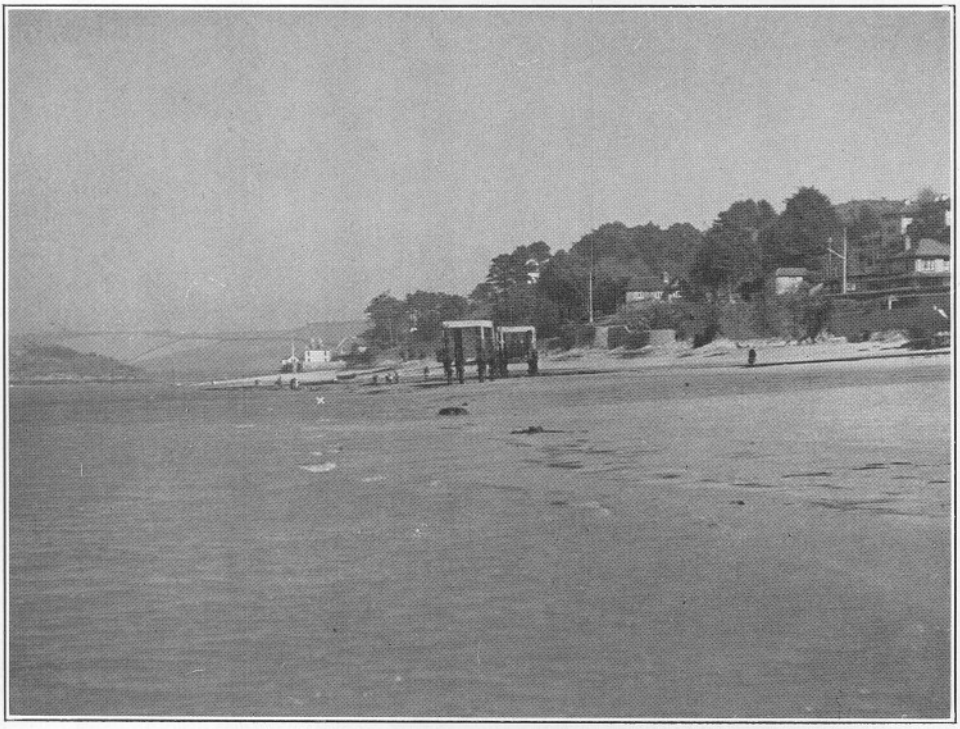


Fig. 2.

Fig. 1.

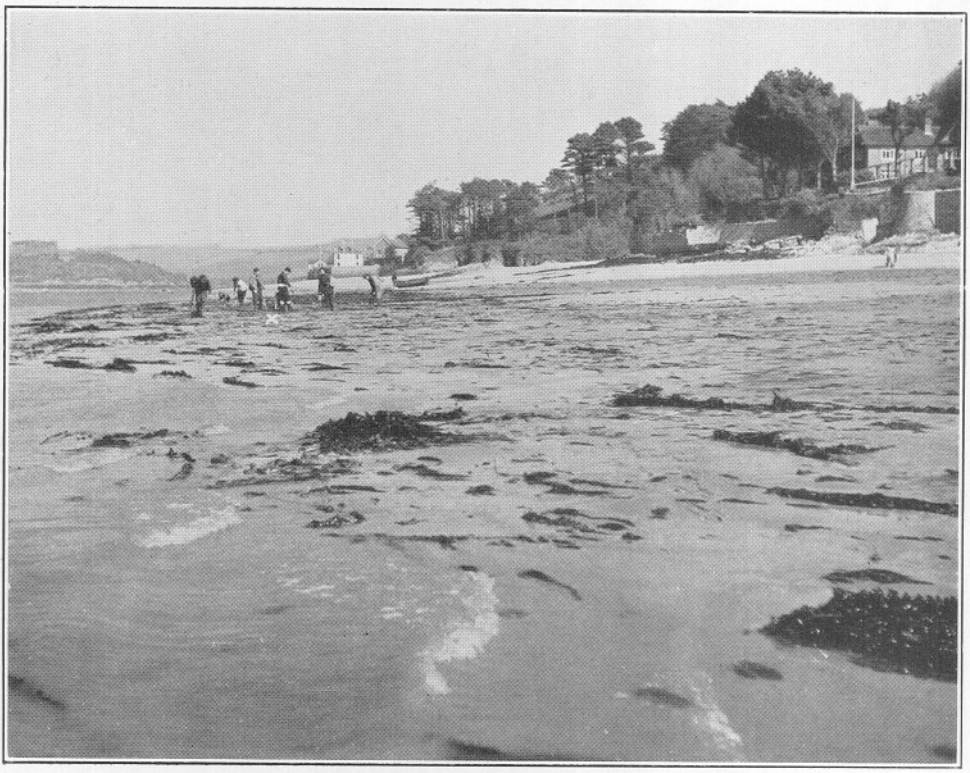


Fig. 2.

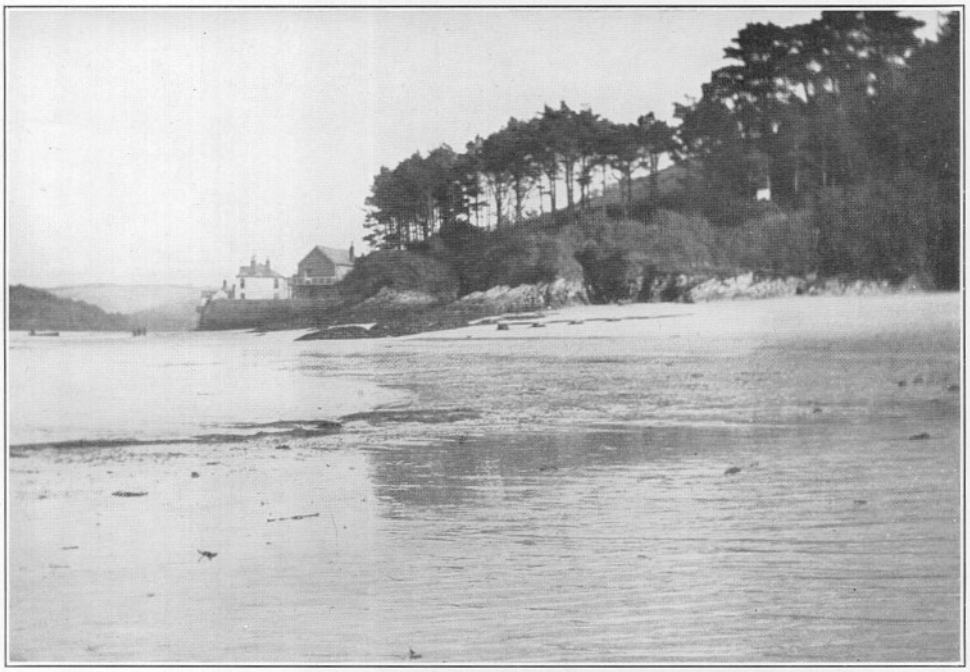
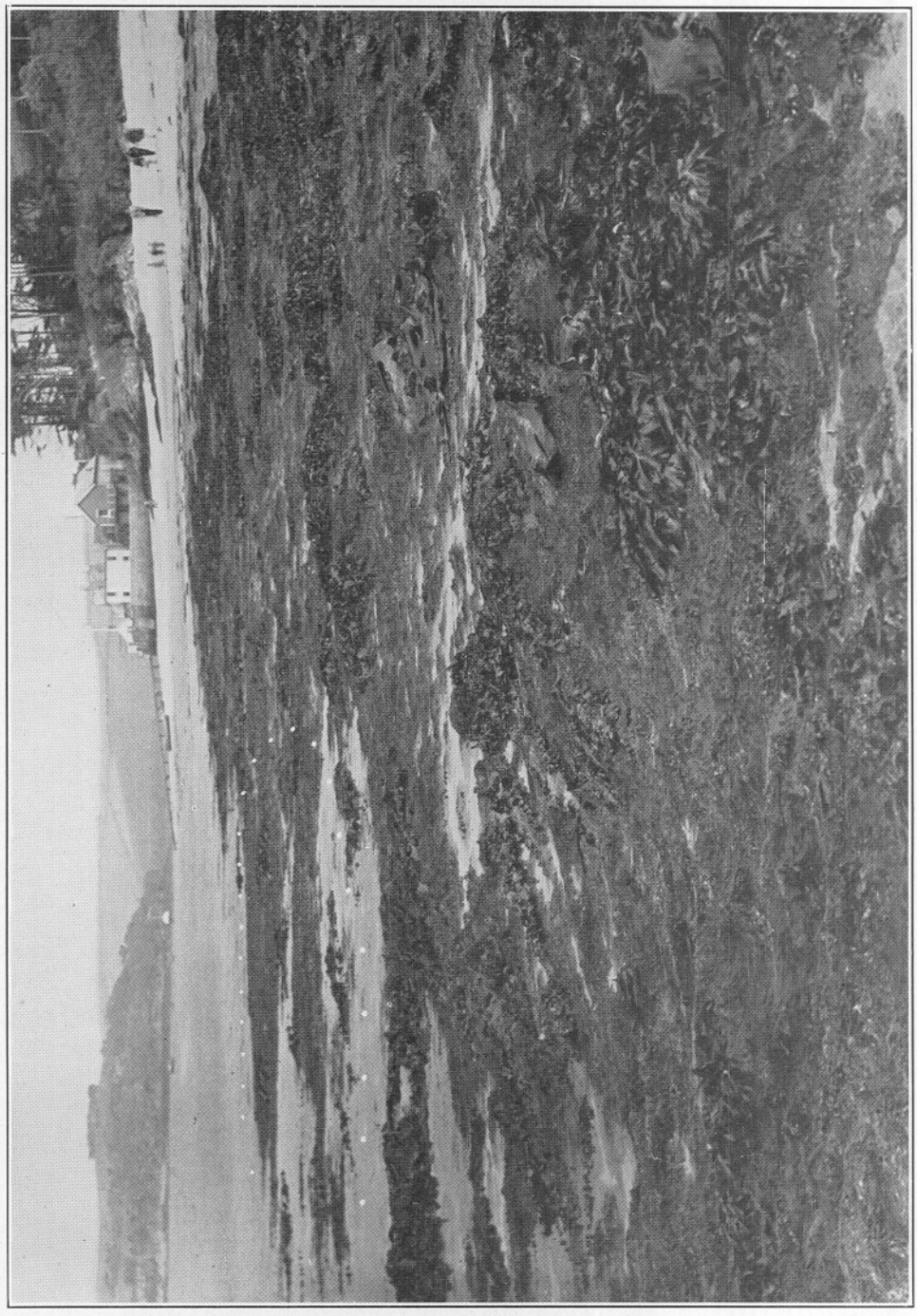


Fig. 1.

Fig. 2.



ON THE LARVAL DEVELOPMENT OF *ELMINIUS MODESTUS* DARWIN

By E. W. Knight-Jones and G. Duncan Waugh

Ministry of Agriculture and Fisheries, Burnham-on-Crouch, Essex

(Text-figs. 1–6)

CONTENTS

Introduction and Methods

Since its introduction to this country (see Bishop, 1947; Crisp & Chipperfield, 1948) the barnacle *Elminius modestus* Darwin has become numerous on Essex oyster beds. Owing to its remarkably long season of settlement and great fecundity it competes with young oyster spat for space and food more keenly than any other sessile form (Knight-Jones, 1948). It is also a dominant fouling organism of coastal craft in Essex. Workers investigating ships' fouling and oyster problems may therefore need to identify its larval stages in the plankton. These stages have not hitherto been described.

Routine plankton sampling to record the abundance and growth of oyster larvae has been carried out in the Rivers Crouch and Roach during the summers of 1947 and 1948. The standard sample used was obtained by filtering 100 l. of water, drawn from a depth of 2 m. by a $1\frac{1}{2}$ in. centrifugal pump. In 1948 cirripede nauplii were abundant in these samples throughout June and July. There were often several hundred per 100 l. Bassindale (1936) recorded that nauplii which were abundant in the Plymouth plankton during the late summer were *Chthamalus stellatus* and *Balanus perforatus*. In the Burnham-on-Crouch district, however, these two species appear to be absent. We have observed only four species of barnacles, *B. balanoides*, *B. crenatus*, *B. improvisus* and *Elminius modestus*. In 1948 the main settlement of both *Balanus balanoides* and *B. crenatus* occurred in April and neither species was observed to settle after 5 June. Settlement of *Elminius modestus* and *Balanus improvisus* occurred with varying intensity from May to September, and the great majority of barnacles settling during this period were *Elminius*. Evidently the majority of the larvae which were so numerous in the plankton during the summer were *Elminius*, so the

routine 100 l. samples provided ample material for the present study. It was necessary only to distinguish larvae of *Elminius* from those of *Balanus improvisus*.

This did not prove difficult (see pp. 424–6) and of over 300 nauplii obtained from June samples and examined, no more than eighteen proved to be *B. improvisus*. All these nauplii, together with some young larvae obtained in the laboratory from adult *Elminius*, were measured by means of an eyepiece micrometer. The number of naupliar stages in the development was deduced from their size distribution. The limb setation was then studied by the method advocated by Bassindale (1936). For this purpose several nauplii of each stage were dismembered under the binocular microscope by means of fine glass needles. All drawings were made with the aid of a camera lucida.

The Number of Naupliar Stages

Stage I nauplii were obtained by opening adult *Elminius* during June and by keeping others in aquaria. Nauplii of this stage were liberated by adults which had been living undisturbed for several days in a tank, the water of which was continually stirred. It is probable, therefore, that larvae are liberated at this stage under natural conditions. The first moult invariably occurred within 24 hr., however, and doubtless it is for this reason that very few Stage I nauplii were observed in the plankton. All batches kept in aquaria completed the first moult successfully, and Stage II nauplii were thus obtained. These and subsequent stages were also obtained from the plankton.

At the beginning of the work all cirripede nauplii which were seen in a selected plankton sample were measured. The measurements made included total length, greatest breadth and, in larvae in which the carapace fold had appeared, the length of the carapace. All measurements were taken to 0·01 of a millimetre. As work progressed it became possible to identify the larvae of *Balanus improvisus* and to judge which of those already measured belonged to this species. The data relating to these are not included here.

Presumably because of a high death-rate there were always far more younger larvae than older larvae in the samples. After measuring about 150 *Elminius* larvae it was clear that a greater proportion of early stages had been obtained and from then on only medium- and larger-sized nauplii were measured, except that occasional small specimens were measured to check that there was no appreciable difference in size between those liberated during the earlier and later parts of the season.

On examining the data it was decided that greatest breadth was the most useful measurement for identifying the various naupliar stages, since total length was affected by the degree of flexure of the abdomen, which varied considerably in different individuals, whilst carapace length could not be determined in early stages. The numbers of larvae which fell into each milli-

metre size group are given in Table I. These figures are shown graphically in Fig. 1. As already indicated, the larvae measured did not constitute a single random sample. Larvae measuring 0·14 mm. or less were obtained only from batches liberated in aquaria. A few of those measuring 0·15–0·17 mm. were obtained in the same way. The plankton samples from which the remainder were obtained were taken on several different dates during June and July, and

TABLE I

Greatest breadth (mm.)	No. of larvae	Greatest breadth (mm.)	No. of larvae	Greatest breadth (mm.)	No. of larvae	Greatest breadth (mm.)	No. of larvae
0·11	2	0·19	23	0·27	5	0·35	9
0·12	11	0·20	10	0·28	10	0·36	13
0·13	10	0·21	0	0·29	9	0·37	3
0·14	2	0·22	5	0·30	10	0·38	3
0·15	4	0·23	9	0·31	12	0·39	2
0·16	25	0·24	27	0·32	0	0·40	2
0·17	10	0·25	7	0·33	3	0·41	1
0·18	8	0·26	2	0·34	8		

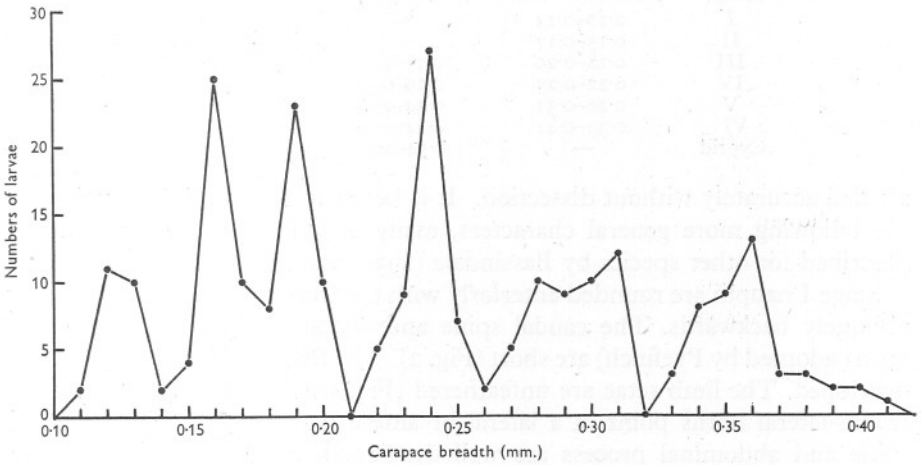


Fig. 1. The size distribution, in 0·1 mm. groups, of all *Elminius* nauplii measured (245). The larvae did not constitute a single random sample, but such general selection as was exercised in obtaining them cannot account for the presence on this graph of six distinct peaks. These indicate that there are six naupliar stages in the development. This was corroborated by morphological study. The naupliar stage to which each size group belonged can be seen from Table II. In respect of this measurement (carapace breadth) no overlapping in size between successive stages was observed.

often only the larger larvae seen in a sample were measured. This selection was exercised only in a general way, to ensure that all sizes of larvae were adequately represented in the sample. Such general selection cannot account for the presence on this graph of six distinct peaks. These indicate that there are six naupliar stages in the development and that the later stages are much more

variable in size than the earlier stages. The graphic evidence for six naupliar stages is corroborated by the determination of six distinct setation formulae (Table III, p. 420).

The Identification of the Naupliar Stages

The size limits observed for each stage are given in Table II. The measurements of carapace length included the length of the carapace spines, which varied rather widely between 0·015 and 0·045 mm., but was usually 0·02 or 0·03 mm. The measurements of total length showed much overlapping between successive stages, since the degree of flexure varied and was sometimes extreme, but other measurements afforded a fairly reliable means of identifying the stages. The limb setation of each stage is also characteristic, but this cannot be

Table II. Measurements of Larval Stages of *Elminius modestus* in mm.

Stage	Carapace		Full length
	Greatest width	Length	
I	0·11–0·14	—	0·24–0·26
II	0·15–0·17	—	0·36–0·43
III	0·18–0·20	0·21–0·25	0·35–0·43
IV	0·22–0·25	0·29–0·35	0·39–0·50
V	0·26–0·31	0·34–0·44	0·45–0·57
VI	0·33–0·41	0·42–0·55	0·48–0·71
Cyprid	—	0·54–0·56	—

studied accurately without dissection. It is better to rely for identification on the following more general characters, many of which are similar to those described for other species by Bassindale (1936) and Pyefinch (1948).

Stage I nauplii are rounded anteriorly with the fronto-lateral horns pointing obliquely backwards. The caudal spine and abdominal process (to use the terms adopted by Pyefinch) are short (Fig. 2). The frontal filaments are not yet developed. The limb setae are unfeathered (Fig. 5). In subsequent stages the fronto-lateral horns point in a lateral or antero-lateral direction, the caudal spine and abdominal process are well developed, the frontal filaments are obvious and many of the limb setae are feathered.

Stage II nauplii are characteristically slender with a particularly long caudal spine and a shorter, narrow abdominal process. The prongs of the forked abdominal process are proportionately longer than in the other stages. There is no sign of a posterior edge to the carapace.

Stage III nauplii are of the same total length as those of Stage II but are of stouter build. The posterior edge of the carapace is well defined and bears a carapace spine on each side of the mid-dorsal line. There is no projecting carapace fold, however, so the carapace spines are closely applied to the body and often difficult to distinguish at this stage. The abdominal process is slightly swollen at the base and is about the same length as the caudal spine. In both

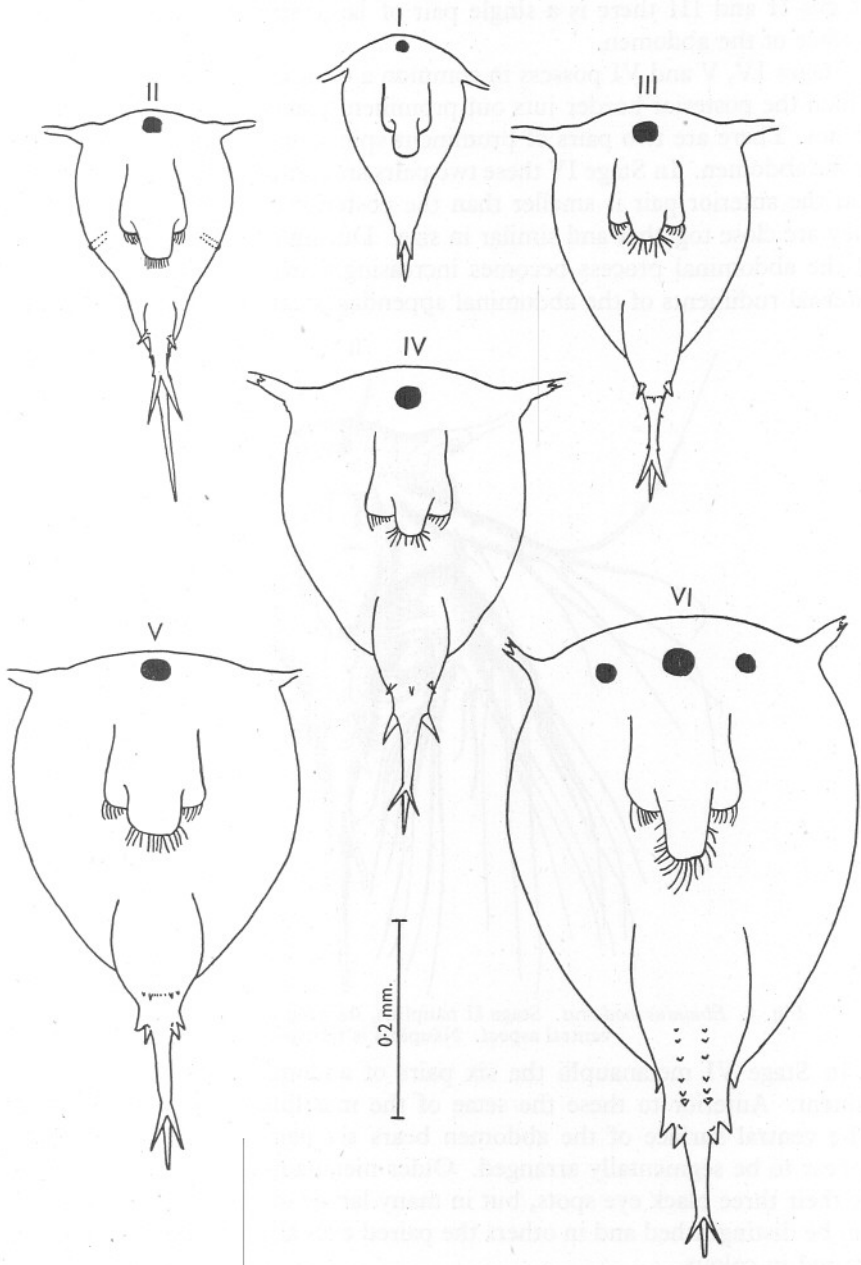


Fig. 2. *Elminius modestus*. Outline drawings of the six naupliar stages, showing the labrum, all to same scale.

Stages II and III there is a single pair of large spines on the latero-ventral surface of the abdomen.

Stages IV, V and VI possess in common a rounded shape and a carapace of which the posterior border juts out prominently and bears a pair of carapace spines. There are two pairs of prominent spines on the latero-ventral surface of the abdomen. In Stage IV these two pairs are comparatively widely separated and the anterior pair is smaller than the posterior pair. In Stages V and VI they are close together and similar in size. During these three stages the base of the abdominal process becomes increasingly swollen, and in Stage V the internal rudiments of the abdominal appendages can be distinguished.

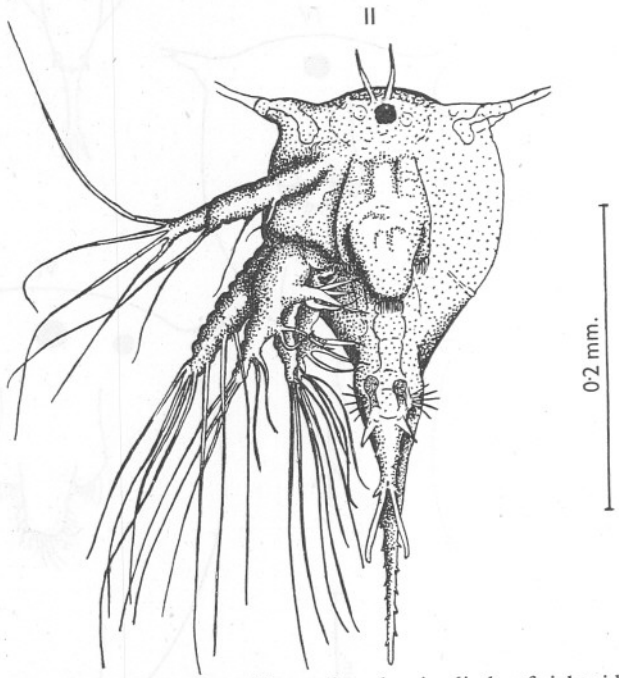


Fig. 3. *Elminius modestus*. Stage II nauplius, showing limbs of right side only, ventral aspect. Nauplius is transparent.

In Stage VI metanauplii the six pairs of abdominal appendages are prominent. Anterior to these the setae of the maxillulae can be distinguished. The ventral surface of the abdomen bears six pairs of small spines, which appear to be segmentally arranged. Older metanauplii are readily recognized by their three black eye spots, but in many larvae of this stage no paired eyes can be distinguished and in others the paired eyes are not fully pigmented and are red in colour.

Fig. 2 gives outline drawings of typical specimens of each stage all drawn to the same scale. Fig. 3 shows a Stage II nauplius in greater detail. Fig. 4 is a side view of a Stage VI nauplius and a cyprid.

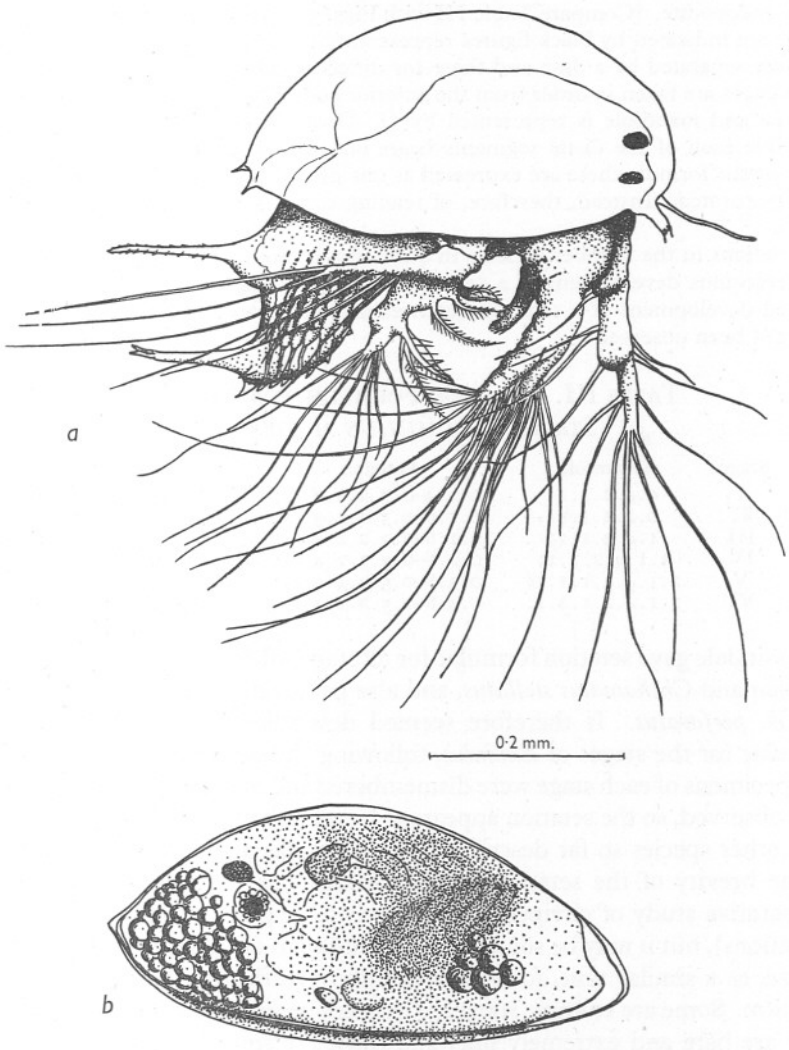


Fig. 4. *Elminius modestus*. *a*, Stage VI nauplius, right side; *b*, cyprid larva, left side.

Limb Setation

Bassindale (1936) wrote as follows:

In order to facilitate a comparison of barnacle nauplii a setation formula has been elaborated. The setae on the appendages of cirripede nauplii occur in groups along the dorsal and ventral sides of the appendages. Each group has been represented by a figure giving the actual number of setae present. The formula is obtained by arranging these numbers in order, reading from the base of each appendage along the dorsal edge of the exopodite, down its ventral edge, and then up the dorsal and down the ventral edges

of the endopodite. [Compare Table III with Figs. 5 and 6.] The setae at the tip of each ramus are indicated by black figures representing the group; the formulae for the two rami are separated by a dash and those for different appendages by a semicolon. The appendages are taken in order from the anterior end. The gnathobase occurring on the antenna and mandible is represented by G. On the exopodites of the antenna and mandible each of the distal segments bears one strong swimming-seta. In order to contract the formula these are expressed as one group, the terminal seta or setae alone being separated. Instead, therefore, of reading 0.1.1.1.1.1.1. the formula reads 0.1.6.

Variations in the number of setae in some groups are found. This is usually due to the precocious development of a seta normally appearing at the next stage or to the delayed development of a seta. Differences of more than one seta in any one group have not been observed.

TABLE III. SETATION FORMULAE FOR THE LARVAL STAGES OF *ELMINIUS MODESTUS*

Stage	Antennule	Antenna	Mandible
I	0.4.2.1.1;	0.1.4–0.3.2.2.2.G;	0.1.3–0.3.2.2.2.G
II	0.4.2.1.1;	0.1.6–0.3.2.2.3.G;	0.1.3–0.3.2.3.2.G
III	1.4.2.1.1;	0.1.6–0.3.2.2.4.G;	0.1.4–0.3.3.3.3.G
IV	1.1.4.2.1.1;	0.2.7–0.5.3.2.4.G;	0.1.4–0.4.3.3.3.G
V	2.1.4.2.1.1.1;	0.3.8–0.5.3.2.4.G;	0.1.5–0.4.4.4.3.G
VI	2.1.4.2.1.2.1;	0.4.8–0.5.3.2.4.G;	0.1.5–0.4.4.4.3.G

Bassindale gave setation formulae for all stages of *Balanus balanoides*, *Verruca stroemia* and *Chthamalus stellatus*, and also gave some data for *Balanus crenatus* and *B. perforatus*. It therefore seemed desirable to work out the setation formulae for the stages of *Elminius*, following the same method. From five to ten specimens of each stage were dismembered and examined. No discrepancies were observed, so the setation appears to be remarkably constant for each stage, as in other species so far described. The formulae are given in Table III.

The brevity of the setation formula makes it a useful instrument for the comparative study of cirripede nauplii (see p. 424 for a brief discussion of its limitations), but it may be somewhat misleading to describe each seta, whatever its size, as a similar unit, for the setae differ greatly from one another in size and form. Some are stumpy, some are feathery bearing numerous setules, whilst some are bare and extremely fine, and some are small. In order to ascertain the setation formulae with certainty it proved necessary to draw each limb in detail. In Figs. 5 and 6 these drawings are reproduced, all to the same scale.

COMPARISON WITH ALLIED FORMS

Bassindale (1936) described the naupliar stages of *Balanus balanoides*, *Chthamalus stellatus* and *Verruca stroemia*, compared them with those of *Balanus perforatus* as described by Groom (1894) and gave data for several other species. Pyefinch (1948) compared larvae of *B. balanoides*, *B. crenatus* and *Verruca stroemia*, with special reference to characters which can be recognized at a glance under

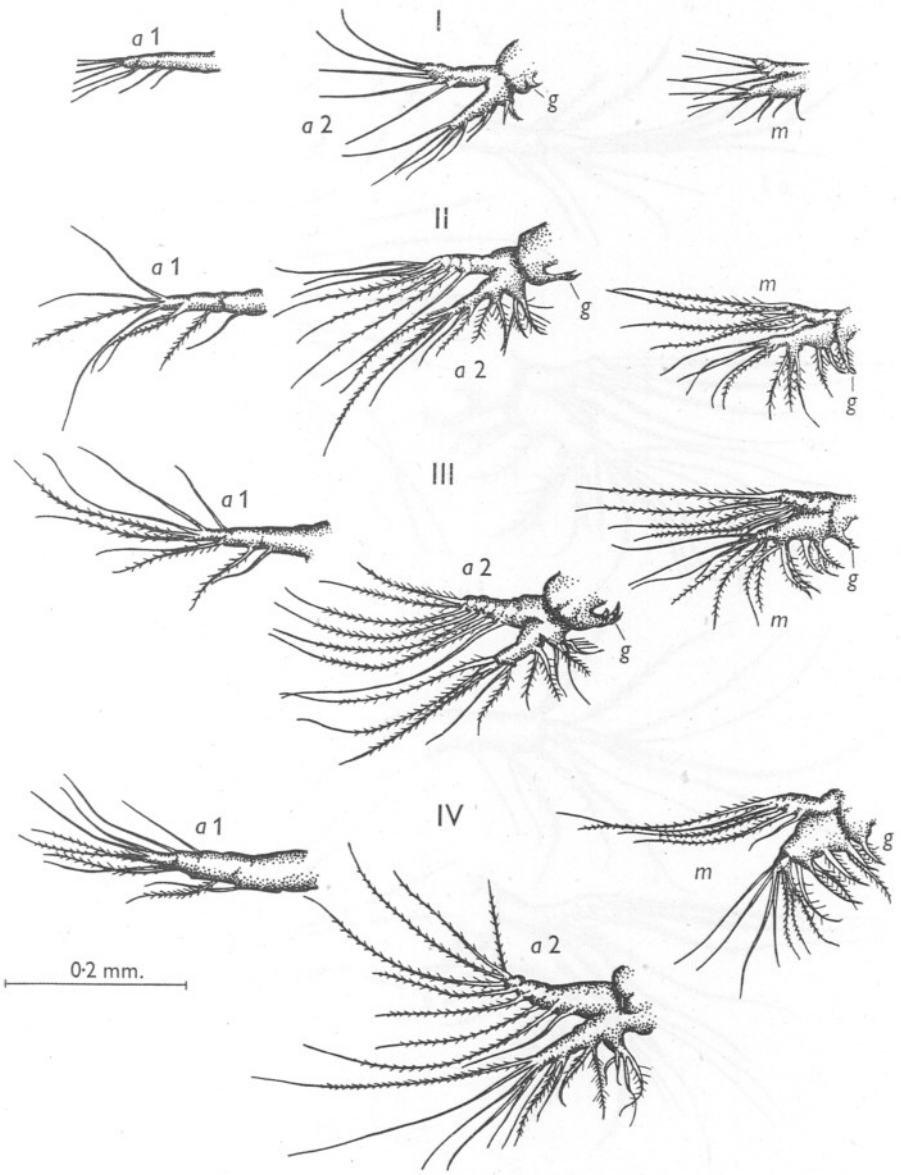


Fig. 5. *Elminius modestus*. The limbs of naupliar Stages I–IV; antenna 1 (*a* 1) on the left, antenna 2 (*a* 2) in the centre; mandible (*m*) on the right; *g*, gnathobase.

Fig. 6. *Elminius modestus*. The limbs of naupliar Stages V and VI; *a* 1, antenna 1; *a* 2, antenna 2; *m*, mandible; *g*, gnathobase.

a low-power binocular microscope. Herz (1933) had described the development of *Balanus crenatus*, but the work of Bassindale and Pyefinch suggests strongly that he was wrong in ascribing eight naupliar stages to these species. Pyefinch found that *B. crenatus* in the Clyde passed through only six naupliar stages, like every other species of barnacle so far described. We have not examined the larvae of these species, but it may be useful to draw attention to the points in which *Elminius* larvae differ from the published descriptions of them. The only species which was observed in our plankton samples from June onwards, besides *Elminius*, was *Balanus improvisus*. No adequate description of the larvae of this species is yet available in this country. The figures of Stages I and II given by Buchholz (Münter & Buchholz, 1870) and reproduced by Hoek (1909) are somewhat schematic and the limb setation is inaccurately reproduced. Figures of later stages by Filatowa (1902) and Tengstrand (1931) are too small to be of value, and we were not able to consult the account of Lucks (1940), referred to by Thorson (1946) as figuring Stages IV and VI and the cyprid.

We have obtained Stage I nauplii from adult *B. improvisus*. They moulted overnight to give Stage II nauplii and we also observed this stage in the plankton of the River Crouch and the River Conway (North Wales). We examined one larger larva from the plankton which was not *Elminius modestus* and did not agree with the description of any other form. It had abdominal appendages clearly visible within the cuticle of the swollen abdomen, and it was probably the stage of *Balanus improvisus* immediately preceding the metanauplius, i.e. probably a Stage V nauplius.

The following appear to be the main points of comparison between the larvae of *Elminius modestus* and those of native barnacles.

Size

The particularly squat nauplii of *Chthamalus* are so much shorter and the bulky nauplii of *Balanus balanoides* so much larger than those of *Elminius modestus* that it is unnecessary to go further into the differences between these species in size and shape. *Balanus crenatus* larvae from the Clyde are also markedly larger than the corresponding stages of *Elminius modestus*, whilst *Balanus perforatus* and *Verruca stroemia* are slightly larger. The larvae of *Elminius modestus* and *Balanus improvisus*, however, are very similar in size.

Shape

The later stages of *Verruca* are unlikely to be confused with those of *Elminius* because *Verruca*, like *Chthamalus*, has a short rounded carapace and no carapace spines. A Stage II *Verruca* differs from that of *Elminius* in possessing a much longer abdominal process which reaches to the end of the caudal spine. A Stage III *Verruca* is considerably longer than any *Elminius* stage younger than Stage IV, and is quite unlike a Stage IV *Elminius* in having no posterior edge to its carapace.

The larvae of *Balanus improvisus*, *B. crenatus* and *B. perforatus* resemble the corresponding stages of *Elminius modestus* fairly closely in general shape. A Stage II *E. modestus* can be distinguished, however, by its long caudal spine and short abdominal process (Fig. 3). In *E. modestus* of this stage the caudal spine is longer than the abdominal process by 0·06–0·10 mm. In *Balanus improvisus* the caudal spine is longer by only 0·01–0·05 mm., and in *B. crenatus* the difference in length appears to be smaller still. Although the total length of the abdominal process in Stage II of *Elminius modestus* is comparatively small the prongs of the forked terminal portion (included in the total length) are of great relative length and comparatively great absolute length (0·05–0·06 mm.). In *Balanus improvisus* they are only 0·03–0·04 mm., and in all other British species of barnacle so far described they appear to be shorter still.

In *B. perforatus*, Stages II and III, the outline is unlike that of *Elminius* and of other native species of *Balanus* so far described, in that there is a distinct notch in the lateral margin on each side. This is shown in Groom's figures (1894) of Stages II and III, and Lochhead's figure (1936) of Stage II, all seen in ventral view. It appears to correspond to the posterior margin of the carapace.

In *Elminius modestus* the great length of the caudal spine in Stage II is foreshadowed by a slight elongation of this region in Stage I. Nauplii of the corresponding stages of *Balanus improvisus*, though similar in width to *Elminius modestus*, are shorter. Measurements of a few larvae of *Balanus improvisus* from the River Crouch and from the estuary of the River Conway, North Wales, were as follows:

	Greatest width (mm.)	Total length (mm.)
Stage I	0·13	0·20–0·21
Stage II	0·15–0·16	0·33–0·36

Limb setation

Bassindale, after giving the setation formulae for Stages I and II of *B. crenatus* and *B. perforatus*, remarked that 'a close comparison of these formulae with those for *B. balanoides* indicates the close similarity of the nauplii which are also similar in general shape and size'. This seems to imply that the similarity between the setation formulae of the early stages of these three species confirms that their taxonomic relationship is close. Such an interpretation is misleading, for the formulae which he gave for the same stages of *Chthamalus* and *Verruca* are also very similar to each other and to those given for *Balanus*.

It now appears that there is remarkable resemblance between the setation formulae of the earlier stages of all barnacles which have so far been studied. This is shown in Table IV. The formulae for *Elminius modestus* and *Balanus improvisus* were derived from specimens from the River Crouch, the remainder are taken from Bassindale (1936). It will be seen that the formula for Stage I nauplii of *Elminius modestus* is identical with that of *Balanus improvisus*, and

with that given by Bassindale for *B. crenatus*. Otherwise there are small differences at both stages between *Elminius modestus* and the various species of *Balanus*, although these barnacles are all closely related, being included in the same family (Balanidae). On the other hand, the formulae for Stage II nauplii of *Elminius modestus* (Balanidae), *Chthamalus stellatus* (Chthamalidae) and *Verruca stroemia* (Verrucidae) are identical. Evidently the small differences and resemblances between the setation formulae of the early larvae of different species are of no systematic importance within these three families.

The formulae for the later stages of *Elminius modestus* (and of barnacles generally) are more distinctive, although that of Stage III nauplii of *Elminius* is identical, and that of Stage IV nauplii almost identical, with those given for the corresponding stages of *Chthamalus stellatus* (another point of resemblance which extends across an accepted taxonomic division).

TABLE IV. THE SETATION FORMULAE FOR THE FIRST TWO NAUPLIAR STAGES OF SEVEN COMMON SPECIES OF BARNACLE

Species	Stage	Antennule	Antenna	Mandible
Balanus balanoides	I	0.4.2.1.1;	0.1.4–0.3.2.2.2.G;	0.1.3–0.3.2.3.2.G
	II	0.4.2.1.1;	0.1.6–0.3.2.2.2.G;	0.1.3–0.3.3.3.2.G
B. perforatus	I	0.4.1.1.1;	0.1.4–0.3.2.2.2.G;	0.1.3–0.2.1.2.2.G
	II	0.4.2.1.1;	0.2.5–0.3.2.2.3.G;	0.1.3–0.3.2.3.2.G
B. crenatus	I	0.4.2.1.1;	0.1.4–0.3.2.2.2.G;	0.1.3–0.3.2.2.2.G
	II	0.4.2.1.1;	0.1.6–0.3.2.2.2.G;	0.1.3–0.3.2.3.3.G
B. improvisus	I	0.4.2.1.1;	0.1.4–0.3.2.2.2.G;	0.1.3–0.3.2.2.2.G
	II	0.4.2.1.1;	0.1.6–0.3.2.2.3.G;	0.1.4–0.3.2.3.2.G
Elminius modestus	I	0.4.2.1.1;	0.1.4–0.3.2.2.2.G;	0.1.3–0.3.2.2.2.G
	II	0.4.2.1.1;	0.1.6–0.3.2.2.3.G;	0.1.3–0.3.2.3.2.G
Chthamalus stellatus	I	0.4.1.1.1;	0.1.4–0.3.2.2.2.G;	0.1.3–0.3.2.2.2.G
	II	0.4.2.1.1;	0.1.6–0.3.2.2.3.G;	0.1.3–0.3.2.3.2.G
Verruca stroemia	I	0.4.2.1.1;	0.1.4–0.3.2.2.3.G;	0.1.3–0.3.2.2.2.G
	II	0.4.2.1.1;	0.1.6–0.3.2.2.3.G;	0.1.3–0.3.2.3.2.G

Because of this close resemblance between species and because the study of the limb setation of barnacle nauplii is at present incomplete, Bassindale's formula can safely be used only for confirming an identification made on other grounds, and for distinguishing between the different stages of a given species.

Labrum

In *Ch. stellatus*, and in *Verruca stroemia*, the labrum is a single tongue-shaped lobe with a rounded posterior end. In *Balanus*, in all stages except the earliest, the labrum is more or less square posteriorly. The labrum figured by Bassindale for Stage II nauplii of *B. balanoides* has three lobes, but the median lobe does not extend posteriorly beyond the lateral lobes so it does not interrupt the square shape. In his figure for Stage V nauplii of this species, no median lobe is shown. Stages I and II nauplii of *B. improvisus* also have a trilobed labrum, with a median lobe which does not extend posteriorly beyond the lateral lobes.

The single large nauplius which we observed in the plankton and which was probably a Stage V of *B. improvisus* had a square labrum with no obvious median lobe. In all stages of *B. crenatus* (Herz, 1933) and in all stages, except the first, of *B. perforatus* (Groom, 1894) the labrum is trilobed, but the median lobe extends posteriorly only slightly beyond the lateral lobes.

In all naupliar stages of *Elminius modestus* the labrum is obviously trilobed with a long median lobe which extends posteriorly much farther than the lateral lobes. This character clearly marks out *E. modestus* larvae from those of all species so far described, but in using it to distinguish between *E. modestus* and *Balanus improvisus* (two species of which the nauplii are particularly liable to be confused), two pitfalls must be avoided. First, in Stages I and II of *B. improvisus*, although the median lobe of the labrum does not project posteriorly, it projects prominently in a ventral direction. It appears very prominently, therefore, in specimens of *B. improvisus* which are standing on their heads in a dish of plankton and which are being viewed posteriorly. Secondly, in many preserved specimens of *Elminius modestus*, the labrum projects from the body at an obtuse angle. The median lobe is then foreshortened in ventral view and the labrum may appear square. It follows that when using the form of the labrum to distinguish between these two species, each specimen should be viewed from the ventral direction. If the labrum is markedly trilobed, *E. modestus* is indicated. If it appears square, the specimen should be viewed under a supported cover-slip to ensure that the labrum is lying more or less flat. If it still appears square, *Balanus improvisus* is indicated.

The cyprid

The cyprid of *Elminius modestus* is colourless and of glassy transparency. Those from the River Crouch were 0·54–0·56 mm. long. This is larger than the size which Bassindale gave for the cyprid of *Chthamalus stellatus*. It resembles in size that of *Verruca stroemia*, but differs in shape (see Fig. 4*b*) from the figure given by Pyefinch for this species, which showed a straight postero-dorsal margin and a pointed posterior end. It is much smaller than that of *Balanus balanoides* and distinctly smaller than that of *B. crenatus* in British waters and of *B. perforatus*. It resembles in size that of *B. improvisus*. Tengstrand (1931) gave the length of this cyprid as 0·6 mm., in Swedish waters. A cyprid from the River Crouch, which was probably this species, was 0·53 mm. long. This specimen was quite unlike a cyprid of *Elminius modestus* in being opaque and in having a blunter posterior end.

The later nauplii of *Elminius* thus resemble those of *Balanus* and differ from those of *Chthamalus* and *Verruca* in possessing a trilobed labrum and a fairly long carapace tapering posteriorly and bearing on its posterior margin a pair of carapace spines. They do not differ from those of *Balanus* in any important

respect. Darwin (1854) suggested a close affinity between *Elminius*, *Tetraclita* and *Balanus*. He wrote that *Elminius* 'can be distinguished from *Tetraclita* only by the four compartments not being porose and by the basis being always membranous', and that *Tetraclita* 'is closely allied to *Balanus*; I can point out no difference in the animal's body, nor any constant difference in the opercular valves'.

The development of *Elminius* tends to confirm that this genus is closely related to *Balanus*.

Summary

Nauplii of the first two stages were obtained from adult *Elminius modestus* and larvae of all stages, except the smallest, were obtained from the plankton over Essex oyster beds.

Over 200 nauplii of all sizes were measured. Their size distribution, plotted graphically, showed six peaks corresponding to six naupliar stages. The later stages were much more variable in size than the earlier stages.

The size limits and characteristics of each naupliar stage are given. Briefly, Stage I has the fronto-lateral horns pointing backwards. Stage II has the caudal spine much longer than the abdominal process. Stage III has the abdominal process about as long as the caudal spine, but has no carapace fold posteriorly. Stage IV has a carapace fold but no sign of the abdominal appendages. Stage V has the rudiments of these appendages showing indistinctly within the abdomen. In Stage VI the abdominal appendages are prominent.

The limb setation of each stage is figured and described according to Bassindale's formula. The taxonomic value of this formula is limited, since there is a remarkable resemblance between the formulae for the early nauplii of all species so far studied.

The larvae are compared with those of other barnacles of which the development has been described. In general, they resemble those of *Balanus*, but they are much smaller than those of *B. balanoides* and distinctly smaller than those of the corresponding stages of *B. crenatus* in the Clyde and *B. perforatus* in the English Channel. They are most likely to be confused with those of *B. improvisus*, which they resemble in size. The shape of the labrum is the most distinctive feature of *E. modestus* nauplii. It is trilobed, with the median lobe extending posteriorly much farther than the lateral lobes.

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A STATISTICAL STUDY OF THE VARIATION IN VERTICAL PLANKTON HAULS, WITH SPECIAL REFERENCE TO THE LOSS OF THE CATCH WITH DIVIDED HAULS

By H. Barnes
The Marine Station, Millport

(Plates I, II and Text-figs. 1–6)

Introduction

Although in some branches of marine biology statistical methods have been extensively employed in considering the sampling variations so frequently encountered, little attention has yet been paid to the study of such variations arising in plankton work. Gardiner (1931), and particularly Winsor & Walford (1936), Winsor & Clarke (1940) and Silliman (1946), have given some consideration to the problem, and an account of a freshwater plankton investigation in which the techniques were carefully chosen and the results critically examined by statistical methods has been given by Baldi, Cavalli and Pirocchi (1945). Early work by Hensen (1887, 1900–12), Lohmann (1903), and Herdman (1921) indicated the order of variation to be expected in vertical hauls.

The material on which the following analysis is based was obtained by Marshall, Nicholls & Orr and some of the results of the work have already been given (1934). A further account of the material has recently been given by Marshall (1949), where all the raw data dealt with here may be found. The discrepancy observed between the total catch in divided and undivided hauls was a puzzling feature of these results, and subsequent to discussions with Dr Marshall on the origin of this discrepancy she placed at my disposal for analysis the whole of the data. Thanks are due to Dr Marshall not only for providing the data but also for giving further details of the technique and circumstances of the collections. It is also a pleasure to acknowledge the assistance of Dr R. A. Robb, who read the manuscript at several stages of its preparation and who, by his critical comments and advice, has enhanced its value.

The material was all collected by means of a net hauled vertically. Some details of the work have been given in the references already cited, but since the analysis will be of use to other workers only if the conditions under which the hauls were made are precisely defined, the salient features of the technique must be summarized.

(i) The hauls were made with a modified international net fitted with a Nansen (1915) closing mechanism. The net differed from the standard

pattern in the absence of a coarse net band above the canvas band carrying the throttling device.

(ii) Hauling was by hand winch.

(iii) The speed of hauling was controlled by timing the rate of haul (depth being followed by means of the metre wheel) with a stop-watch, instructions being shouted to the person working the winch. An attempt to maintain a hauling speed of 0·5 m./sec. was made.

(iv) The bucket used on the net was a simple metal cylinder tied on with string.

(v) After completion of the haul the catch was washed into the bottom of the net by moving the latter up and down in the water, without, of course, allowing the mouth of the net to go under the surface of the water.

(vi) The bucket was then carefully removed and the contents emptied into a breffit containing formalin. The bucket was then rinsed out several times with sea water from a pail and the washings added to the catch; the canvas portion at the base of the net was then turned back exposing the lower portion of the net and, with this held over the breffit, all obvious organisms were carefully removed and the whole washed down several times.

(vii) In taking the divided hauls an attempt was made to release the messenger so that the net would close at the selected depth without any interruption of the hauling.

(viii) The weather conditions under which the catches were made varied throughout the season; the stations worked were inside a comparatively sheltered sea loch and at no time during this particular series were the conditions very bad.

(ix) The depth of the haul was of the order of 60 m., and its duration approximately 2 min. If 5 min. for removing the catch is allowed, this gives a period of about 10 min. in which to obtain duplicate hauls.

(x) Counts of the developmental stages of the following copepods were made and have been used in the analysis: *Pseudocalanus minutus* (Krøyer), *Microcalanus pygmaeus* G. O. Sars, *Centropages hamatus* (Lilljeborg), *Temora longicornis* (Müller), *Acartia clausi* Giesbrecht, *Oithona similis* (Claus).

It should be stated that this work was not originally planned for statistical treatment, and a selection of the data will be presented to illustrate the problems involved and their possible solution.

The Undivided Hauls

Three pairs of duplicate undivided hauls will now be considered and the data are plotted as the log of the catches for the separate stages of each pair of hauls in Fig. 1. In each of the catches eight stages of the six species were counted so that, neglecting those pairs in which the total number caught (n_1+n_2) was less than 5, there are 134 pairs of observations, each stage of every species being

considered independently. The results obtained with these undivided hauls will first be compared with the data analysed by Winsor & Walford (1936) using counts of a series of catches of fish eggs (the E-S series) and the data obtained in the course of investigations of catching powers of different types of nets by Künne (1929, 1933). The problem, as pointed out by these authors,

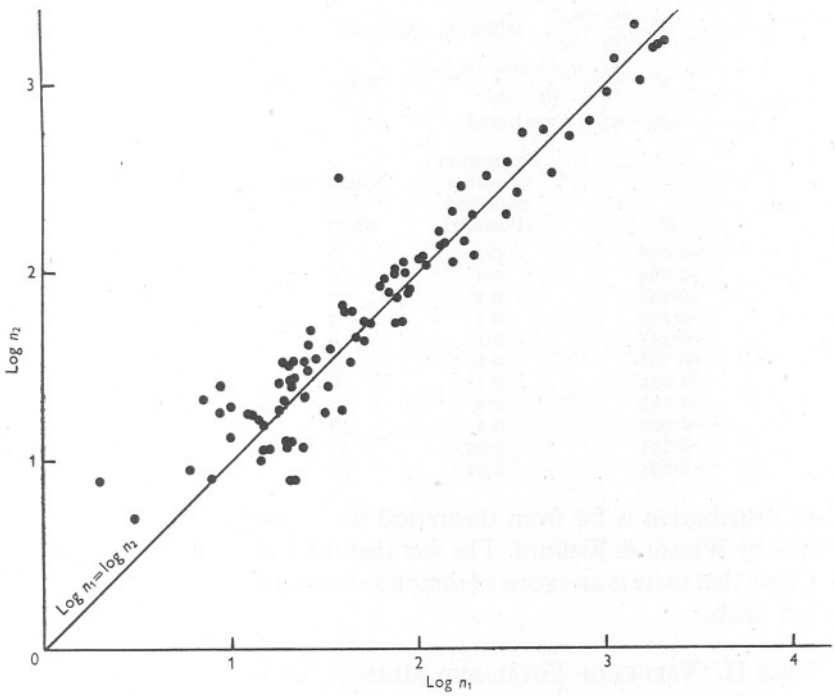

Fig. 1. The relationship between pairs of catches of all stages of six copepods for three sets of duplicate vertical hauls, plotted as logarithms of the catches.

is similar to that of the estimation of bacterial numbers, the basic distribution of which, when the experimental technique is adequately controlled, has been shown by Fisher, Thornton & MacKenzie (1922) to be Poisson. The value has therefore been calculated, for each pair of observations, of

$$\chi^2 = \frac{(n_1 - n_2)^2}{(n_1 + n_2)}, \tag{1}$$

where n_1 and n_2 are the numbers of each stage in a pair of duplicate hauls and when $(n_1 + n_2) > 10$. When $5 < (n_1 + n_2) < 10$ an adjusted value of χ^2 has been used,

$$\chi^2 = \frac{(n_1 - n_2)^2 - 2(n_1 - n_2) + 1}{(n_1 + n_2)}. \tag{2}$$

Pairs in which $(n_1 + n_2) < 5$ have been neglected.

If the basic distribution were truly Poisson this χ^2 should, in a number of random samples, have a mean value of 1 and should be distributed in a known manner. For comparison with the data of Winsor & Walford similar classes of χ^2 have been selected and the distribution of this quantity is shown in Table I.

TABLE I. DISTRIBUTION OF VALUES OF χ^2 (134 PAIRS).

$$\chi^2=\frac{(n_1-n_2)^2}{(n_1+n_2)}, \quad \text{when } (n_1+n_2)>10;$$

$$\chi^2=\frac{(n_1-n_2)^2-2(n_1-n_2)+1}{(n_1+n_2)}, \quad \text{when } 5<(n_1+n_2)<10;$$

$(n_1+n_2)<5$ neglected.

χ^2	Proportion of values expected (Poisson)	Number of values observed	Proportion of values observed
0–0·016	0·1	6	0·045
–0·064	0·1	6	0·045
–0·148	0·1	7	0·052
–0·275	0·1	3	0·022
–0·455	0·1	9	0·067
–0·708	0·1	8	0·059
–1·074	0·1	9	0·067
–1·642	0·1	12	0·089
–2·706	0·1	16	0·119
–6·635	0·09	30	0·223
> 6·635	0·01	28	0·209

This distribution is far from theoretical for Poisson, and is similar to that obtained by Winsor & Walford. The fact that there is an excess of large values of χ^2 shows that there is an excess of samples showing relatively large differences between hauls.

TABLE II. VALUES OF TOTAL AND MEAN χ^2 FOR VARYING SAMPLE SIZE

(n_1+n_2)	Number of samples	$S\chi^2$	$\bar{\chi}^2$
5–10	18	44·57	2·48
–20	8	15·68	1·96
–40	24	68·69	2·86
–60	18	43·73	2·43
–80	10	21·26	2·13
–170	16	35·53	2·22
–400	19	69·08	3·64
–1000	9	161·51	17·83
> 1000	12	1726·15	143·85

In Table II the mean values of χ^2 have been tabulated by size groups and the results are again similar to those of Winsor & Walford. Thus, the large hauls furnish a larger proportion than expected of the high values of χ^2 as shown by the increase in the mean χ^2 with increasing size of sample. It seems clear that other factors than the sampling variations of a random population are affecting the hauls.

Assuming that the most important factor contributing to these variations is the volume of water filtered (or at least affecting the sample by its effect on the volume filtered) Winsor & Walford derive the following expression for χ^2:

$$\chi^2 = 1 + n\frac{\sigma_v^2}{\bar{v}^2} = 1 + K^2\bar{n}, \tag{3}$$

where $\bar{n} = \frac{1}{2}(n_1 + n_2)$, σ_v = standard deviation of volume, $\bar{v}$ = mean volume filtered.

There is little change in the value of χ^2 up to $(n_1 + n_2) = 170$, with the present data, and beyond this point the size of these groups has to be greatly increased to obtain a reasonable number of samples. Grouping together gives Table III.

TABLE III

(n_1+n_2)	Number of samples	$S\chi^2$	$\bar{\chi}^2$
0–170	94	229·44	2·44
170–400	19	69·08	3·64
400–1000	9	161·51	17·83
>1000	12	1726·15	143·85

These values are plotted in Fig. 2, and although the number of points is inadequate they can be considered as lying on a straight line passing through the point $\bar{\chi}^2 = 1$, when $\bar{n} = 0$. The equation of this line gives a value for the constant K^2 of 0·05. The value suggested by Winsor & Walford for K^2 is 0·04–0·06 and they emphasize the fact that K is not a universal constant. The agreement of the value calculated from the present data with their value is very satisfactory.

Since the coefficient of variation of a single observation is

$$\frac{\sigma}{n} = 100\sqrt{\left(\frac{1}{n} + K^2\right)},$$

then putting $K^2 = 0{\cdot}05$, and for a total catch of 100 ($n = 100$),

$$\frac{\sigma}{n} = 25\%.$$

The above agreement appears to suggest that the basic assumption, namely a random distribution of the population, holds for the present series, and that the variations between the hauls are largely due to differences in the volumes of water filtered. It follows that since different stages of a number of species were counted, all are randomly distributed, that is, there is no association between any of the animals or their various stages. This does not mean that changes in density do not take place in a vertical direction but only that at any point in the vertical section there is a random distribution of the species and their separate stages.

An alternative method of analysing the results of such replicate hauls is possible and has been employed by Winsor & Clarke (1940). Both new data

and that previously considered by Winsor & Walford were used, and submitted to an analysis of variance; this technique will now be applied to the present data.

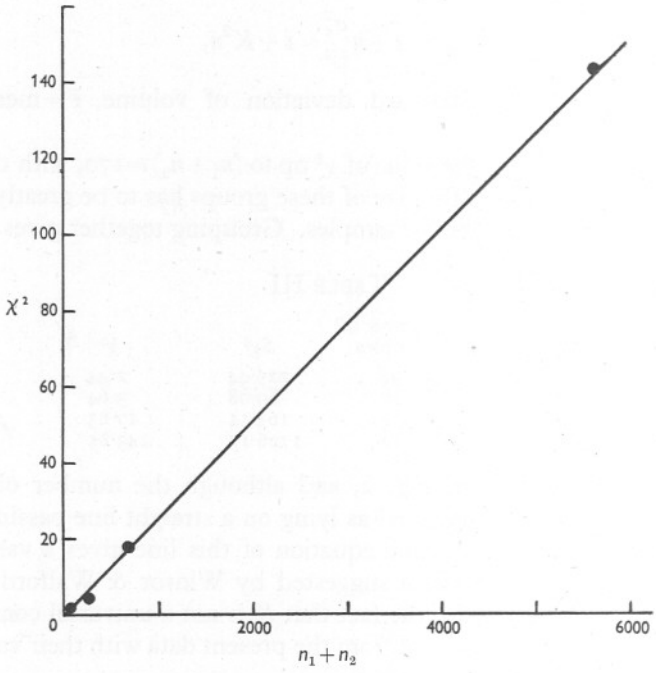

Fig. 2. The relationship between the mean value of χ^2 (grouped values) and the mean catch in paired hauls.

Four of the above six undivided hauls, which have been treated as three pairs, were taken consecutively and these four will be analysed. For the four replicate hauls with eight separate stages of each of the four species counted there are in all 128 observations. (Six results have been neglected because of small numbers.) The results of the analysis can be conveniently tabulated as follows. (Logarithmic values of the catches are used throughout; for details of the theory underlying the method, the paper by Winsor & Clarke (1940) should be consulted.)

The analysis of variance gives the following:

Source of variation	Degrees of freedom	Sum of squares	Mean square
Main effects:			
Hauls (H)	3	0·2255	0·0752
Stages (S)	31	57·3872	1·8512
Interaction:			
H × S	93	1·2251	0·0132
Totals	127	58·8378	—

The various estimates obtained from the mean squares can be conveniently summarized thus:

(i) The mean square for the interaction is an estimate of σ^2_{SH}, the 'within haul' variance. Hence $\sigma^2_{SH}=0{\cdot}0132$, standard deviation $=\sigma_{SH}=0{\cdot}1149$, and log $1{\cdot}303=0{\cdot}1149$, corresponding to a coefficient of variation of $30{\cdot}3\%$.

(ii) σ^2_H is the 'haul to haul' variance. The mean square for the hauls is an estimate of $32\,\sigma^2_H+\sigma^2_{SH}=0{\cdot}0752$. Hence $\sigma^2_H=0{\cdot}0019$, standard deviation $=\sigma_H=0{\cdot}0440$, and log $1{\cdot}1070=0{\cdot}0440$, corresponding to a coefficient of variation of $10{\cdot}7\%$.

(iii) The variance of a single observation is $\sigma^2_H+\sigma^2_{SH}=0{\cdot}0151$, standard deviation $=\sqrt{(\sigma^2_H+\sigma^2_{SH})}=0{\cdot}1228$, and log $1{\cdot}326=0{\cdot}1228$, corresponding to a coefficient of variation of $32{\cdot}6\%$.

Winsor & Clarke's results indicated a coefficient of variation of 53% for vertical hauls, and 31% for oblique hauls (n is large), and they suggest that the greater accuracy for oblique hauls is worth further consideration. However, the data now presented show an accuracy for replicate vertical hauls comparable with these authors' value for oblique hauls. It would appear that the greater accuracy of the present series may be ascribed to the more favourable working conditions, viz. a sheltered sea loch in contrast to the less favourable open sea conditions under which Winsor & Clarke's material was collected.

The Divided Hauls

Throughout the season's work four undivided hauls (bottom to surface) and one divided (bottom to 10 m., 10 m. to surface) haul were taken consecutively, the four undivided hauls being pooled and an aliquot part counted.

A preliminary inspection of the data indicated that as a first approximation the results could be divided into two classes with regard to the discrepancy between the divided and undivided hauls, depending upon whether the animals were mainly above or mainly below the point at which the hauls were broken. The results for those hauls in which the organisms were below the 10 m. level will be considered first.

Animals all below the depth at which the haul was divided.

Since the divided haul is suspect, it is first necessary to examine the assumption that it gives a reliable qualitative estimate of the distribution in relation to the 10 m. level. An inspection of the results indicated that when the organisms were above the 10 m. level the mean total catch of both divided and undivided hauls tended to be similar and under these circumstances, as shown later, they were not significantly different (p. 440). This indicates that no loss is incurred in the 10–0 m. haul. If nothing is caught in the upper 10 m. by the second part of the divided haul it can therefore be assumed that the qualitative information, namely that the animals are all below the 10 m. level, is substantially correct.

The data for *Microcalanus pygmaeus*, no stages of which (except the nauplii) were ever found in significant numbers above the 10 m. level, will first be considered. There were ten different days throughout the season when divided and undivided hauls were taken, and since seven stages were counted there are 140 observations. The results are plotted in Fig. 3 and suggest a loss in the divided haul (compare Fig. 1).

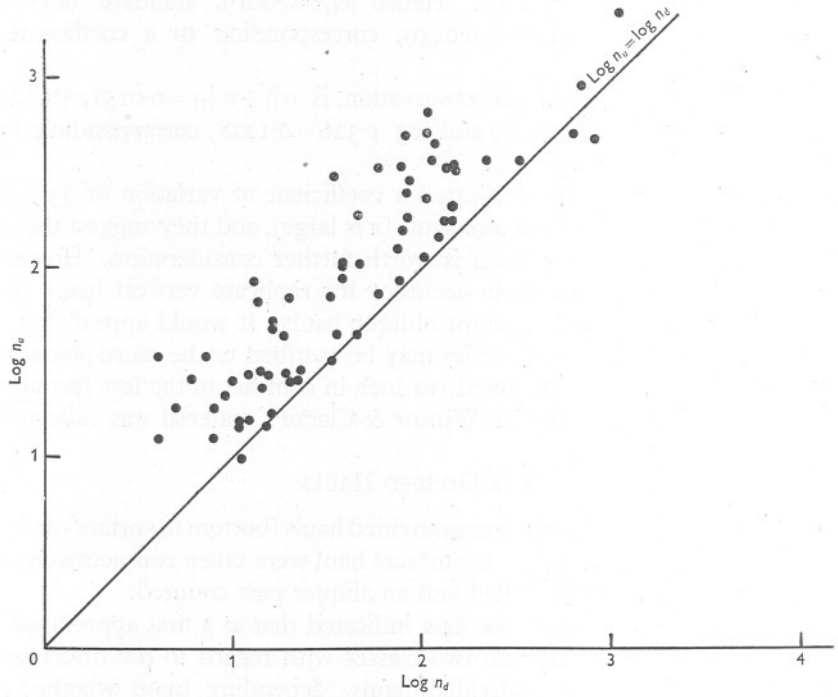

Fig. 3. The relationship (in *Microcalanus pygmaeus*) between catches (log values) for all stages in divided and undivided hauls taken over a season's work when all stages are below point of division of the haul.

The analysis of variance gives the following:

Source of variation	Degrees of freedom	Sum of squares	Mean square
Main effects:			
Stages (S)	6	20·4588	3·4098
Day (D)	9	15·6570	1·7400
Haul (H)	1	4·4500	4·4500
First-order interactions:			
S × D	54	10·0994	0·1870
S × H	6	0·3210	0·0535
D × H	9	0·9230	0·1020
Second-order nteraction:			
S × D × H	56	0·8875	0·0164
Totals	139	52·5078	—

It is difficult to assign the day-haul and stage-haul interaction to other than accidental variations, and the values obtained will therefore be added to the second-order interaction to give a residual mean square of 0·0300. The mean square for the hauls can be tested for significance against this value by the z test:

$$z = \tfrac{1}{2}(\log_e 4{\cdot}4500 - \log_e 0{\cdot}0300) \qquad n_1 = 1,\ n_2 = 71,$$
$$= 2{\cdot}15.$$

Since the 5% point for z, $n_1 = 1$, $n_2 = \infty$ is 0·6729, the difference between the hauls is significant and the loss in the divided haul indicated by Fig. 3 is significant. It should be pointed out that this is true even though replicate undivided hauls showed a significant difference, since a *set* of hauls is here under consideration. An alternative treatment, which gives the same result, is to consider the divided and undivided hauls on *each* date separately. Associating with the undivided hauls the standard error $\sigma = \sqrt{(\sigma_H^2 + \sigma_{SH}^2)}$ (p. 435) allows for the significant difference between the hauls found previously. Assuming that the divided haul has the same standard error, then the standard error of the difference $n_u - n_d$ is $\sqrt{(2\sigma)}$ and the usual test for significance can be applied.

It is desirable to consider possible reasons for the loss in the divided haul. From the bottom to the 10 m. level the divided and undivided hauls are identical, and since in the hauls under consideration no animals are present above 10 m., it is impossible to escape from the conviction that loss of animals must take place when the net is closed at the 10 m. level in the divided hauls. Two possible causes for this loss may be suggested:

(i) Any organisms still above the throttling gear in the upper part of the net when it is closed will automatically be lost.

(ii) If water is forced upwards from the bottom part of the net when it is closed a further loss of the catch may take place. Three possible mechanisms for such a passage of water upwards may be suggested:

(*a*) Probably the most important factor is the amount of slack in the throttling cord of the closing mechanism so that when the hauling line is released the net must slow down.

(*b*) Any deceleration in hauling speed immediately prior to closing the net will, if the net has been moving at a constant speed, tend to force water upwards carrying organisms with it. The person working the winch usually knows when the net is approaching the 10 m. point and may, without realizing it, tend to slow down.

(*c*) The sudden closing of the net may tend to force a small quantity of water out of the net rather than force it through the meshes.

If in a series of hauls the catch were largely obtained at the same or similar levels then, as a first approximation, all the catch would be expected to be similarly distributed throughout the net and bucket at the time of throttling. Since the loss of water due to the factors outlined above might also be expected

to be similar in a comparable series of hauls, the loss under these circumstances would be proportional to the total catch.

This relationship can be expressed in the form of the regression line of divided and undivided hauls (divided haul being considered as the dependent variable), but since it will be shown that the stages react differently during the season any such relation can only have an average value. The regression line is given by

$$\log n_d = 0{\cdot}84 \log n_u - 0{\cdot}03,$$

where n_d and n_u are the numbers in the divided and undivided hauls, respectively. This would mean that for a catch of 100 (n_u), 50% of the animals would be lost in the divided haul.

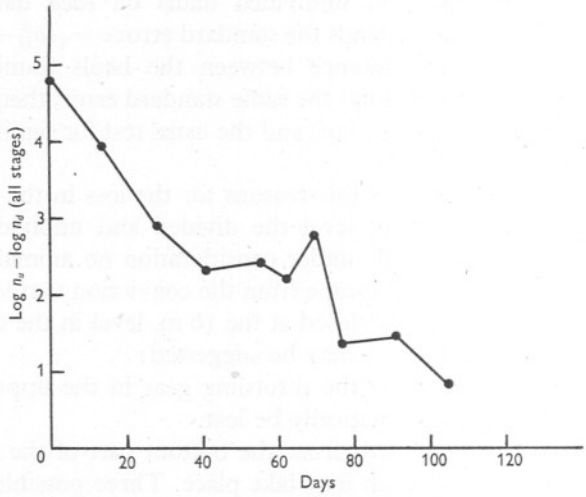

Fig. 4. The ratio of the divided and undivided hauls ($\log n_u$–$\log n_d$) for total catch, i.e. all stages, plotted against date of catch, showing change in ratio with time.

If the ratio of the catches in the two hauls is plotted against the date of the haul, the figures suggest that the loss changes (in general decreases) throughout the season (Fig. 4).

This is substantiated by analysing the values for the ratio ($\log n_u - \log n_d$) in relation to the date; the analysis of variance gives the following:

Source of variation	Degrees of freedom	Sum of squares	Mean square
Main effects:			
Days (D)	9	1·7625	0·1958
Stages (S)	6	0·0623	0·0104
Interaction:			
D × S	54	1·5008	0·0278
Totals	69	3·3256	—

The value of the mean square for days is significant, so that the difference between the catches varies significantly with the day on which the catch was taken. The difference does not vary according to the particular stage under consideration. The following is suggested as an explanation of this result. The relation between catch and loss might be expected to depend to some extent on the position in the hauls at which the catch was largely made. If the animals were caught in the same vertical range then the same amount of consolidation (if any) into the receiving vessel and the same distribution throughout the various parts of the net might be expected when the net is closed, so that under similar conditions of water loss on closure, a proportional amount of organisms would be expected to be lost. However, if on certain occasions some of the animals were caught in the deeper layers, they might be expected to be somewhat differently distributed throughout the net and receiving vessel, in general being carried farther down into the lower parts of the net during the later part of the haul. The loss on closure might then be reduced. This explanation would imply vertical migrations of the various stages during the season which is in accord with general observations. If this is true then it indicates that the stages of *M. pygmaeus*, although always below the 10 m. level, do migrate vertically throughout the season. Since the discrepancy between the divided and undivided hauls is less towards the end of the season (see Fig. 4, where $\log n_u - \log n_d$ approaches 0 later in the season), the foregoing agreement would imply a migration to the deeper level during the latter part of the year; such an implication is in agreement with the facts already ascertained for other copepods from such data on their behaviour as are available. It should be possible to relate these changes to the factors which control seasonal vertical migration, but the available information is inadequate. An inspection of the data in relation to temperature which might be expected to affect such migration gives no significant correlation. However, changes in the order of the discrepancy were most marked when there were sudden changes in temperature.

It should be pointed out that this change in the relationship between the divided and undivided haul throughout the season could conceivably be explained by some gradual change in technique; this explanation is hardly adequate.

This loss of catch with vertical divided hauls does not appear to be peculiar to the present series of observations. Thus Kemp, Hardy & Mackintosh (1929) and also Marr (1938) draw attention to the discrepancy between 'open' and 'closed' horizontal hauls using the same net, the 'closed' haul always yielding a comparatively poor catch. They suggest that the 'open' horizontal haul possibly gives a fictitious result owing to catching animals whilst hauling in the net. The loss of catch in the 'closed' haul as a result of the tendency of the net to fall backwards could have contributed materially to the discrepancy, since it would lead to losses in the 'closed' haul.

Wiborg (1948) has recently published a detailed account of a comparison of several methods of taking vertical and oblique hauls and an inspection of his Table IV indicates a loss with the vertical closing net. Some of his results are grouped together and shown in summary form in Table IV. The figures for the Clarke-Bumpus sampler (P.S.-8) are organisms per 1000 l., while those for the closing net (8/72) are the total catch. If the net is behaving in a similar manner throughout each haul it would be expected that the ratio of the

TABLE IV

	25–0		50–25		100–50		150–100	
	P.S.-8	8/72	P.S.-8	8/72	P.S.-8	8/72	P.S.-8	8/72
Calanus finmarchicus:								
Copepodites and adults	4188	21183	306	2216	117	194	46	138
Nauplii and eggs	4303	6900	4769	4609	214	60	122	25
Calanus hyperboreus:								
Copepodites and adults	109	422	54	76	26	14	1	51
Nauplii and eggs	94	500	53	—	—	—	—	—
Other organisms than copepods	598	1942	833	338	186	178	23	58

Clarke-Bumpus sampler catch to the net catch would be approximately constant, an assumption which is independent of the absolute filtration coefficient of the net. Although the species and stages do not behave in an identical way it is clear from the figures that the ratio (sampler/net) is usually much lower in the 0–25 m. haul than the deeper hauls. Since it may be presumed that the 0–25 m. hauls were made without closing the net it would appear that the lower ratio for this section of the haul is due to not closing the net and that the catches in the other divided net hauls are lower as a result of losses on closing the net.

Hauls in which all the organisms were above 10 m.

Since it has been shown that in general, in the divided haul, there is a loss of organisms caught below 10 m. it is again necessary to examine the possibility that the qualitative division is correct. In the hauls under consideration no animals were caught below 10 m. in the divided haul; a small number may have been lost but these may be neglected if there are moderate numbers above 10 m. Both the divided and undivided hauls can, therefore, be considered as catching animals only between 10 m. and the surface.

The results for *Centropages hamatus* have been used, since on three occasions six of the stages were all above the 10 m. level on three different days during the season. The analysis of variance gives the results as shown on p. 441.

The day-haul and haul-stage can again be combined with the second-order interaction to give a residual mean square of 0·074.

The difference between the hauls is not significant so that the divided and undivided hauls do not differ significantly when all the organisms are caught above the 10 m. level in the two hauls.

The coefficient of variation of a single observation can be obtained from the residual variance which is an estimate of

$$\sigma^2_R = 0{\cdot}074.$$

Hence the standard deviation $= 0{\cdot}272$, $\log 1{\cdot}871 = 0{\cdot}272$, corresponding to a coefficient of variation of 87%.

Analysis of variance

Source of variation	Degrees of freedom	Sum of squares	Mean square
Main effects:			
Days (D)	2	0·701	0·351
Hauls (H)	1	0·063	0·063
Stages (S)	5	1·221	0·244
First-order interactions:			
D × H	2	0·116	0·058
D × S	5	0·703	0·141
H × S	10	1·784	0·178
Second-order interaction:			
D × H × S	10	0·431	0·043
Totals	35	5·019	—

It is evident that the estimate of the population of these short 10 m. hauls is very much less accurate than that obtained in the long hauls previously discussed.

Several sources of error in these short hauls may be suggested. Any error in measurement of the 10 m. depth either by inaccurate adjustment of the metre wheel, or any subsequent slip in the friction drive, whilst having little effect when the animals are being caught in a 0–60 m. haul, would considerably affect the catch when it is being taken through a 10 m. haul, taking only 20 sec.; an error of $\pm 1{\cdot}0$ m. would affect the volume sampled by $\pm 10\%$. Further, the net may not begin to fish efficiently immediately winding commences; the winder may, in releasing the winch catch, drop the net a small distance, and constant speed may not be attained for some seconds.

Hauls with animals above and below 10 m.

These are subject to all the errors discussed above, and the resultant effect will be determined by the proportions of the population above and below the level at which the haul is broken. If the animals are largely above this level the estimate of the population will be a poor one with no significant difference between divided and undivided. As the animals are found in greater proportion below the dividing level the error due to losses on closing the net will become more important. It is possible to apply an overall correction factor to the lower section of the haul, but in view of the change of reaction with time of the various stages it can hardly be considered satisfactory. Further analysis of the data does not appear, therefore, to be profitable, but the above may be illustrated by plotting the ratio between the undivided and the divided hauls $(\log n_u - \log n_d)$ against the percentage in the upper 10 m. of the haul. The

results for the first part of the season's hauls on *C. hamatus* are shown in Fig. 5. If the hauls were identical the points would lie on the line $\log n_u - \log n_d = 0$, but the loss ($\log n_u - \log n_d$ positive) increases as the population of the animals below the 10 m. level increases.

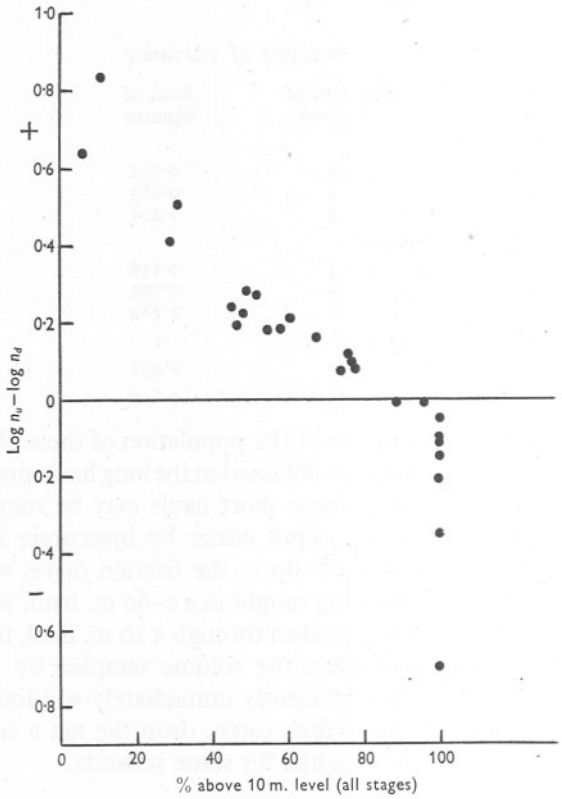

Fig. 5. Change in ratio of divided and undivided hauls (in *Centropages hamatus*) as the population is found in greater proportion below the point of division of the haul.

The Experimental Data

It has been indicated that there are losses in a divided haul when the net is closed by a throttling cord, and it has been suggested that this is largely due to deceleration with a consequent loss of water from the net and that this water carries organisms with it. The sequence of events on throttling can be illustrated by reference to the Discovery net whose dimensions are given in full detail by Kemp *et al.* (1929).

The net has 3 ft. bridles on a 50 cm. diameter mouth and between the mouth and the filtering surface is a canvas cylinder whose depth to the closing rings is 23 in., i.e. a total length of 57 in. from the release gear to the throttling band.

The total length of the throttling cord doubled is 16½ ft. The drop on closing, if the net were stationary, would be the difference between 57 in. and 99 in.—say 3½ ft. Of this drop about 1 ft. takes place before closing starts and a further 2½ ft. during closing. It should be emphasized that some slack is necessary in the throttling cord for normal working of the closing mechanism, particularly under adverse conditions, but if the throttling line were tight between the attachment to the release and throttling loops, there would be negligible fall before the closing started and the half of the circumference of the circle, 31 in., as the rope tightened.

In the case of a net which is being hauled vertically there will be a tendency for it to continue to move upwards after being released from the hauling line owing to its own momentum, and the resultant movement of the net will

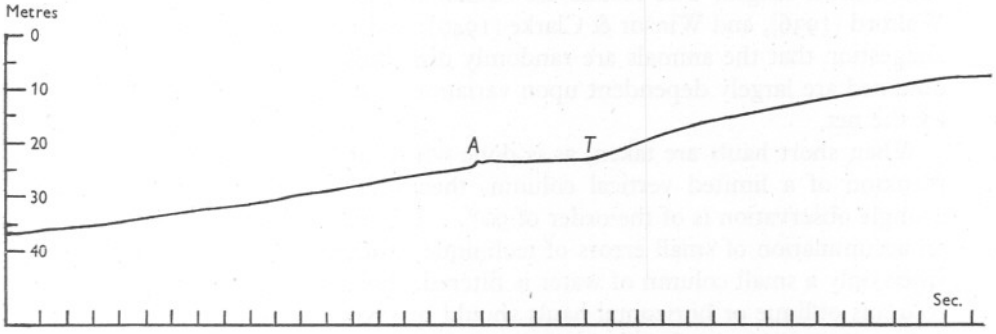

Fig. 6. Copy of the tracing of a depth record; constant speed to *A*, at which point messenger engaged, the weight coming on to throttling line at *T*. Horizontal scale in seconds; vertical scale in metres with an arbitrary zero.

depend upon the speed of hauling and the weight attached to the net. If the net remained stationary after release of the hauling rope, then at a hauling speed of 0·5 m./sec. it would be approximately 2 sec. before the weight came on the throttling line again. A record of the changes in position of a net on closing was obtained by attaching a small depth recorder to the bucket of the net. The net was handled by a mechanical winch in order to obtain a uniform hauling speed and the conditions were chosen so that there was as little movement of the ship as possible. Further, in order to exaggerate the effect about 1 ft. extra throttling rope was used. Fig. 6 is copied from a photograph of the record. No actual fall of the net is shown but after the messenger engages (at *A*), the net remains virtually at the same level until caught up again (at *T*) by the throttling rope.

That the slowing down of the net causes water to be ejected from the net was confirmed by taking a film using a model net.[1] The net was a scale model, one-

[1] This and a number of other films were taken by Mr F. M. Marshall, and his expert assistance is gratefully acknowledged.

fifth of the Discovery net, without the canvas top. In view of the difficulties of working vertically, a horizontal tow was made, using an electric motor to obtain uniform speed. Inside the opening of the net was fastened a coarse mesh bag containing finely powdered potassium permanganate. The effect of closing the net was imitated by stopping the motor and reducing the forward speed by a line attached to the tail of the net. Part of the film is shown in Pl. I. The film was taken at a speed of 64 frames/sec., and the ejection of water when the net is stopped can be clearly seen.

Discussion and Summary

The analysis of data on replicate vertical plankton hauls gives a value of the order of 35% for the coefficient of variation of a single observation for a haul of moderate length. The results are similar to those presented by Winsor & Walford (1936), and Winsor & Clarke (1940); and are not at variance with the suggestion that the animals are randomly distributed, and that the variations obtained are largely dependent upon variation in the volume of water filtered by the net.

When short hauls are taken, as is done when information is sought on the plankton of a limited vertical column, then the coefficient of variation of a single observation is of the order of 90%. It is suggested that this is due to an accumulation of small errors of technique which weight the result heavily when only a small column of water is filtered. For examination of such short columns oblique or horizontal hauls should be given consideration.

It is shown that in divided hauls in which the net is closed on the Nansen principle losses in catch take place and it would be advisable to abandon its use in quantitative plankton work. The alternative seems to be an apparatus such as the Clarke-Bumpus sampler (Clarke & Bumpus, 1940), or a Kofoid-type net for horizontal hauls (Kofoid, 1912).

Any mechanism which, as a result of its closing action, results in a tendency for the net to fall will cause a loss in the catch, although the presence of a cone and a small opening would tend to reduce this loss (Kofoid, 1911).

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EXPLANATION OF PLATES

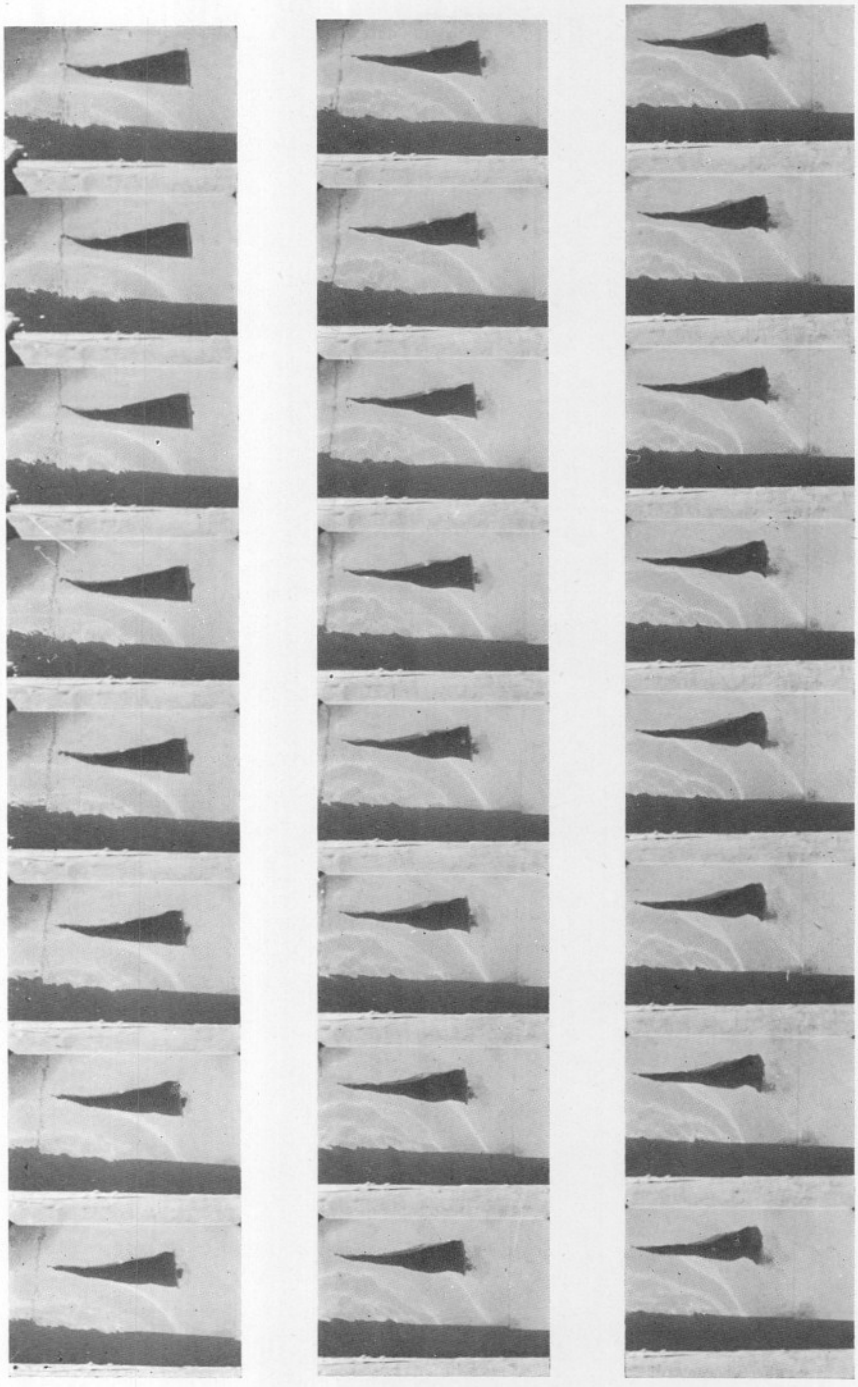
PLATE I

Photograph of escape of material from net on stopping (consecutive frames from top left to bottom right). The film was taken at 64 frames/sec. and the speed of towing was approximately 0·5 m./sec. Hauling was stopped at the 3rd frame (A).

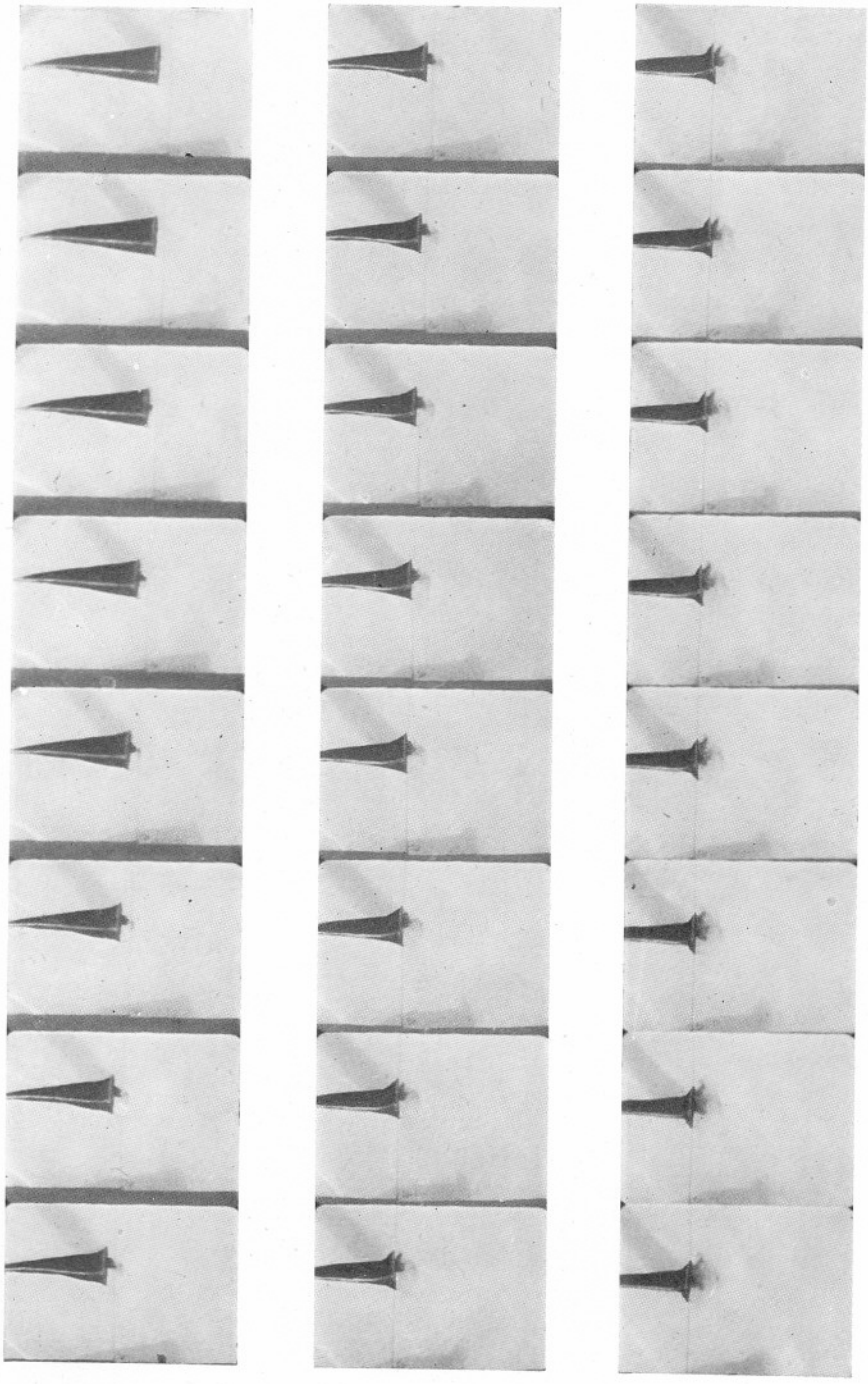
PLATE II

Another photographic record of material escaping from the net (consecutive frames from top left to bottom right). Hauling was stopped at the 3rd frame (A).

A



A



RESPIRATORY MOVEMENTS OF *ARENICOLA MARINA* L.: INTERMITTENT IRRIGATION OF THE TUBE, AND INTERMITTENT AERIAL RESPIRATION

By G. P. Wells

Department of Zoology, University College, London

(Text-figs. 1–9)

Van Dam (1937, 1938) studied the respiratory movements of lugworms (*Arenicola marina* L.) in glass tubes. He found that they propelled water through the tubes by means of wave-movements running along the body, usually from tail to head, and that 'ventilation was intermittent; ventilation pauses alternated, sometimes very regularly, with ventilation periods; in some cases the pauses lasted as long as 40 minutes'. In the following paper, the mechanism and biological significance of this intermittence are investigated. The worms were studied in glass U-tubes. It will be shown, in another paper, that very similar behaviour occurs in the burrow, in sand.

Apparatus for Studying Intermittent Irrigation

Van Dam observed the worms visually, and measured the volumes of water pumped by collecting the output in a graduated cylinder. The period of time over which a worm can be studied in this way is necessarily rather limited. With the apparatus shown in Fig. 1, the behaviour of a worm can be continuously recorded on smoked paper for 2 or 3 days, and a rough idea of the volumes pumped can be got from the records.

The worm lies in a U-tube (of internal diameter 0·75 cm.). Each limb of the U is connected with a T-piece whose lower end is constricted, to discourage the worm from creeping farther upwards. The upper end of the T-piece communicates, through a 20 c.c. pipette bulb, with a wide cylinder (internal diameter 3 cm.). The side arm of the T-piece leads through a T-tap to the same cylinder. The side arms of the taps are connected by a capillary (bore about 0·15 cm.). The whole apparatus is filled with sea water. One of the wide cylinders contains an aeration jet. The other contains a paraffin float, connected with an isotonic lever writing on a slowly moving kymograph. The time trace is provided by a clock whose minute hand is bent forward and connected to a lever with a frontal writing point. This traces an approximation to a sine curve at 1 cycle per hr.

Most of the observations were made with the taps turned as shown in the figure. When this is so, the worm can circulate water along the U, through the 20 c.c. bulbs and wide cylinders and the capillary. Thus it can get a supply of freshly aerated water. Owing to the resistance of the capillary, any such pumping results in slight variations of level in the wide cylinders and will therefore be recorded on the drum. Rather different conditions arise if the taps are turned through 180°; these will be dealt with later.

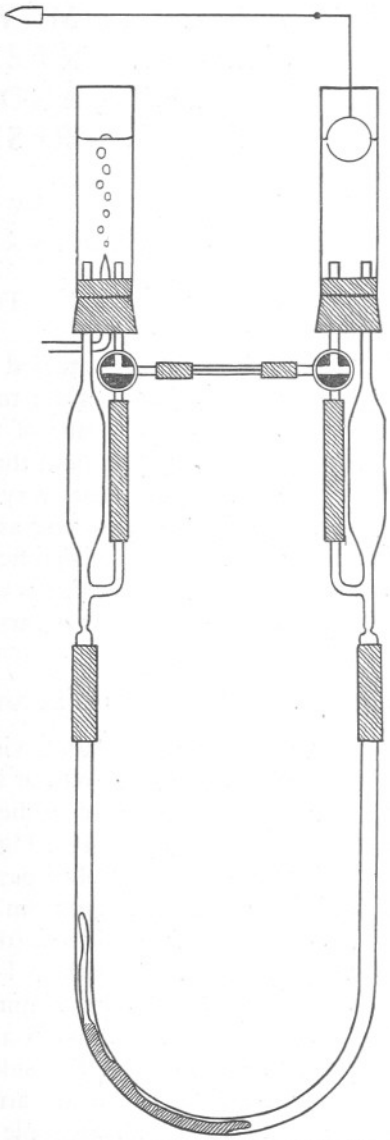


Fig. 1. Apparatus for recording the irrigation cycles (see text).

The worm's output can be estimated as follows. The lever magnification was about 12. The capillary passed 6·7 c.c./min. at a pressure of 1 cm. sea water. Hence the flow rate through the capillary is $1{\cdot}1\,d$ c.c./min., where d cm. is the displacement of the writing point from the zero position. The paper moved at 2·4 cm./hr. Hence the volume flowing through the capillary during any period is $27{\cdot}5\,a$ c.c., where a cm.^{2} is the area between the tracing and the zero line. It must be borne in mind that the flow-rate through the U-tube is not necessarily the same as that through the capillary, owing to variation in the amount of water in the wide cylinders. A 1 cm. excursion of the writing point means a transfer of 0·6 c.c. of water from one cylinder to the other; if the writing point is moving away from the zero line, the flow-rate through the U-tube exceeds that through the capillary, and if the lever is moving towards zero the opposite condition holds.

The experiments lasted for many hours, and sometimes for 2 or 3 days. They were set up in an unheated room, where the temperature varied (over the whole period of experimentation) from about 8° to 14° C.; in the course of a single experiment the variation was seldom more than 1 or 2 degrees. To avoid unnecessary stimulation of the worms, nobody but the writer, or visitors in

his company, ever entered the room; and, as it was necessary to interpret the records by watching the worms from time to time, the electric light was kept continuously on. Daylight was excluded.

Irrigation and Locomotion

The worms can displace the water in the U in several different ways, and before considering the records obtained, the characteristics of these various kinds of movement must be summarized. For further details, the works of Just (1924) and van Dam (1938) may be consulted. The movements depend on waves travelling along the whole length of the body, except the first three or four segments and the tail.

Irrigation. The worm lies in the tube, with its ventral and ventro-lateral surfaces pressed against the glass wall, but with a space (containing the gills) between the dorsal surface and the tube. Waves of swelling, which completely occlude this space, move steadily along the body and thus drive water through the tube. The waves generally run in a headward direction, but tailward waves are sometimes seen. It is of course obvious that in irrigation the direction of the water stream coincides with that of the waves.

Antikinetic locomotion. In this case the direction in which the worm creeps is opposite to that in which the waves traverse the body. The body as a whole is elongated, and at most points clear of the tube. Waves of swelling run along the body and occlude and grip the tube. The waves act as fixed points, and the worm as a whole travels, driving water before it. Headward waves result in tailward locomotion and a tailward displacement of water, while tailward waves have the opposite effects. In either case, the notopodia are so oriented as to assist the movement by preventing any backsliding. Antikinetic locomotion can be very vigorous and swift, though it is not always so.

Synkinetic locomotion. In this case, the worm creeps in the direction of wave-travel. One often sees that a worm, which is vigorously irrigating in a headward direction, creeps gently headwards at the same time. The mechanism of this movement, which is never very swift, is obscure; perhaps the orientation of the noto- and neuropodia plays a decisive part. The water in the tube is propelled headwards, because the irrigation waves move much more rapidly than the worm as a whole. Theoretically, as all the movements appear to be reversible, a worm could creep gently tailward during tailward irrigation; but this has not been noticed, either by Just (1924) or by myself.

The most fundamental point, physiologically, seems to be the direction of wave-travel along the body. Headward waves can result in headward irrigation, more or less vigorous tailward locomotion, or gentle headward locomotion, and all of these variations merge into, and can smoothly change into, each other. On the other hand, a process involving headward waves only changes into one involving tailward waves after a definite pause, as if the two performances were quite distinct and incompatible.

Description of the Irrigation Cycles

When newly put into the apparatus the worm is restless and its behaviour is unpredictable. Periods of similar restlessness may suddenly set in at other times; for instance, by narrowing itself and burrowing, so to speak, along its own ventral surface, a worm can easily reverse itself in a tube which, at other times, it seems comfortably to fill; sometimes this happens, after which, of course, the writing on the drum appears the other way up.[1] Or a worm may spoil a good record by 'running amok' and forcing itself through the

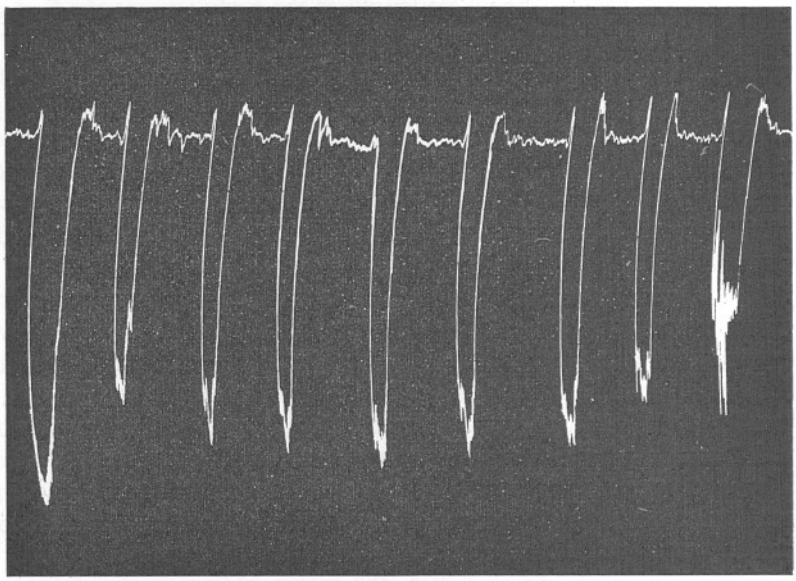


Fig. 2. Three-phase irrigation cycles, traced by a worm with its head towards the float. (Worm O 7.) Duration of printed extract 4 hr. 20 min. *In all records:* Read from left to right.

narrow constriction into one of the 20 c.c. bulbs. Generally, however, the animals settle down and show outbursts of irrigation alternating with rest periods, the cycle continuing—often for 12 hr. or so—with almost clock-like regularity.

The cycles, as traced on the record, vary somewhat in timing and in appearance from worm to worm, and, in the same worm, from day to day. Nevertheless, there is an underlying three-phase pattern, to which the outbursts always conform.

The essential features of this pattern can be seen in Fig. 2. In the relatively quiet intervals between outbursts, the worm was lying in the curved part of the

[1] To avoid confusion, the extracts in the illustrations are chosen so that the worm's head is always towards the float. This means that a headward movement of water causes a downstroke of the writing point.

U, with its head towards the float and its body rather short and thick; it showed occasional slight movements, for example of the head and proboscis. At the beginning of each outburst it lengthened and waves began to travel headwards along its body. These resulted first in tailward locomotion, causing a short rise of the lever (phase 1). But soon the locomotion passed over into headward irrigation—a change brought about by an alteration of attitude, but not of the direction of wave-travel—and as this happened, the lever plunged down (phase 2). After a period of vigorous irrigation, during which the worm crept very gently back to about its original position, the waves slowed up and stopped. There followed a 'rebound' period, when the worm irrigated in the reverse direction, i.e. with tailward waves (phase 3). This gave a second, more prolonged rise of the lever. After this the worm became quiescent.

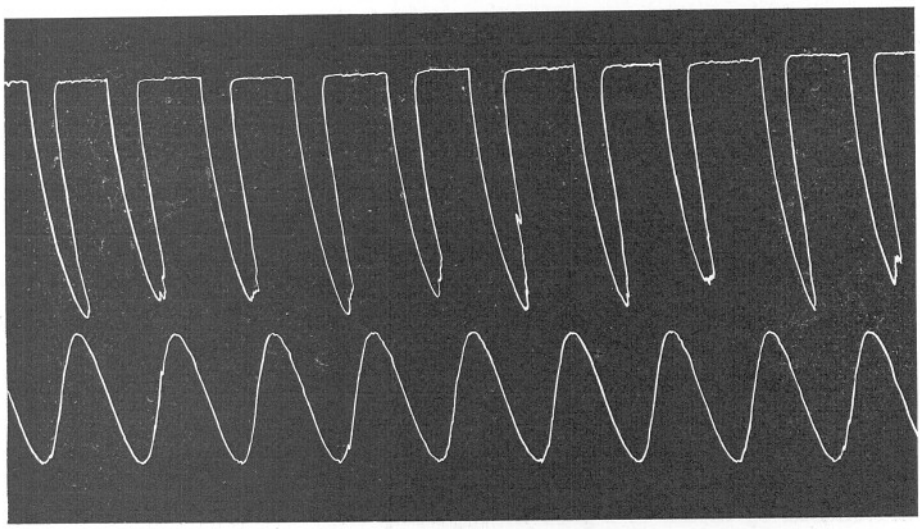


Fig. 3. Irrigation cycles in which the first and third phases are inconspicuous. Worm with head to float. (Worm O 49.) Time trace at 1 cycle per hr.

The second of the three phases—that of headward irrigation—is always the chief one, as long as the taps are turned as shown in Fig. 1. The others are more variable. The final 'rebound' phase may consist only of one or two very slow waves, taking place while the lever returns from the second phase and therefore leaving no trace on the record. Again, the backward locomotion in the first phase varies greatly in intensity. The worm of Fig. 3 gave only very slight, occasional tailward creeps, and only the faintest 'rebounds'. This is probably how the worms used by van Dam (1938) were behaving, as he makes no mention of the triphasic nature of the outbursts. The first part of Fig. 5 is particularly interesting because, as will be shown in another paper, it corresponds closely with the worm's normal behaviour on the beach. In this case, the

tailward locomotion phase is always well-marked. Starting from the bottom of the U, the worm crept up, at each outburst, until its tail had passed through the T-piece and extended for 1 cm. or so into the 20 c.c. bulb. Then, during the irrigation phase, it crept gently down again. The 'rebound' phase was vestigial, as the record shows.

In rough figures, the worm in Fig. 2 pumped about 20 c.c. of water at each burst, and the flow-rate through the capillary at the peaks was about 4·5 c.c./min. Corresponding figures for the other worms whose tracings are illustrated are: Fig. 3, 80 c.c., 6 c.c./min.; Fig. 5, 40 c.c., 7 c.c./min. The internal volume of the U-tube was 25 c.c., of which the worms occupied at least 5 c.c. It will be seen that the worms renewed all the water in the U-tube respectively once, four times and twice at each burst.

Is Intermittence Spontaneous or Reflex?

The obvious explanation of intermittent irrigation is the reflex one. As the worm lies quietly in the tube, oxygen disappears and end-products accumulate. Presently, as we may suppose, the changes stimulate rhythmic activity, which ceases again when new water has been brought and the irritating conditions are removed. One should, however, be cautious in adopting explanations of this type. Isolated strip preparations from polychaetes often show periods of rhythmic activity alternating with periods of rest, so the intermittence may be spontaneous—i.e. produced solely by processes internal to the worm (Wells, 1939).

In the present case, there is little doubt that the intermittence is truly spontaneous, as the following evidence shows.

(i) If one pins out a worm with two pins near the front end and two at the base of the tail (being careful to avoid injury to the nerve cord) and records its movements by means of a glass hook passing under the middle of the body (Fig. 4), one often gets outbursts of activity, continuing very regularly, hour after hour, with about the same period as that of the irrigation outbursts. Now, the record in Fig. 4 is part of a very regular series of outbursts, which lasted for 13 hr. It was traced by a worm pinned to a weighted sheet of cork in a wide, shallow dish of sea water; the water was aerated and stirred by an air jet. One can hardly suppose in this case that the onset of each burst of activity is due to chemical conditions arising in the neighbourhood of the worm, and its cessation to the bringing of new water by the movements. This experiment shows that there is a 'clock' of some kind in the worm, of about the right frequency to account for the irrigation outbursts.

(ii) Van Dam (1938) found that the pauses did not disappear, or even shorten, when the oxygen content of the water was reduced by bubbling nitrogen through it. There was, however, a great increase in the amount of water pumped if the worms were given well-oxygenated water after a period

of oxygen lack. These experiments tend to exclude oxygen exhaustion as a possible stimulus for the outbursts, though they do not exclude the accumulation of CO_2 or other end-products.

(iii) The aerating effect of irrigation can be greatly reduced by turning the taps through 180° from the position shown in Fig. 1. The worm can still circulate the water and any such pumping will be recorded on the drum as before—but, as the water no longer circulates through the 20 c.c. bulbs and the wide cylinders, it can no longer be aerated. There is, in fact, a slight ebb and flow between the cylinders, corresponding with the excursions of the

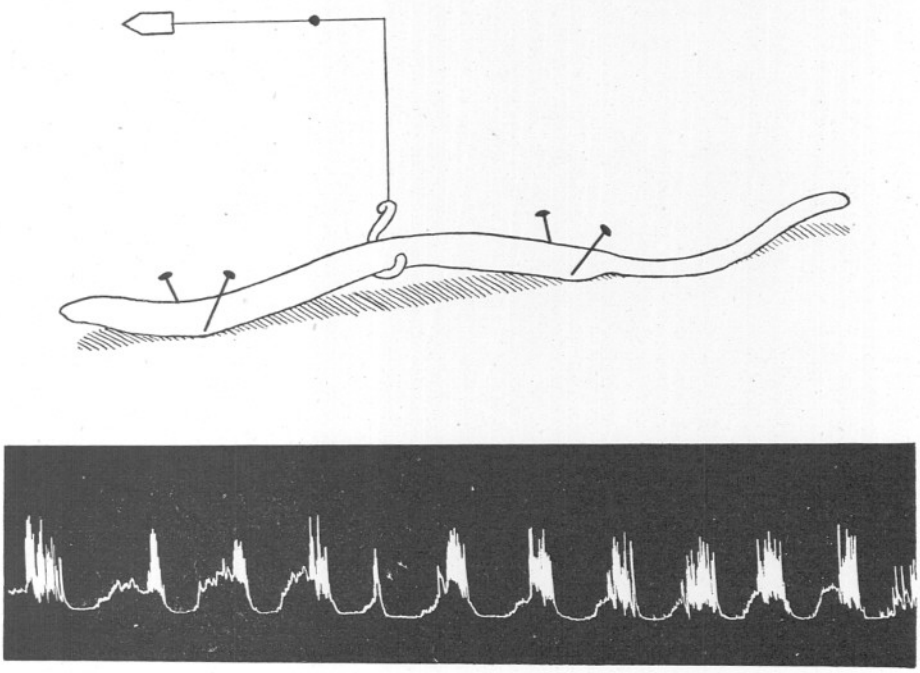


Fig. 4. *Above:* worm pinned to a cork sheet, on the bottom of a flat dish. *Below:* record traced by the same. Duration of printed extract, 7 hr.

lever; but, as this consists of 2 or 3 c.c. of water at most, moving to and fro quite slowly, its aerating effect is negligible compared with that of the circulation before reversal of the taps. The bulbs were included to reduce this effect. The worms were occasionally seen to extend about 1–2 cm. of their tails into the 20 c.c. bulbs, but it is hardly likely that they could get much oxygen, or dispose of much CO_2, by this means.

If now the outbursts are reflexly produced, they should be prolonged and intensified when the taps are reversed. But nothing of the sort occurs. Fig. 5 shows a typical result; the taps were turned at *X* (the float was lifted out of the water and dropped again, to mark this moment on the record). The

outbursts continue; their frequency is slightly raised (but in other worms it was unaltered, or even lowered); and, though the tailward excursions continue, the phase of headward irrigation is diminished and sometimes fails to appear on the record at all.

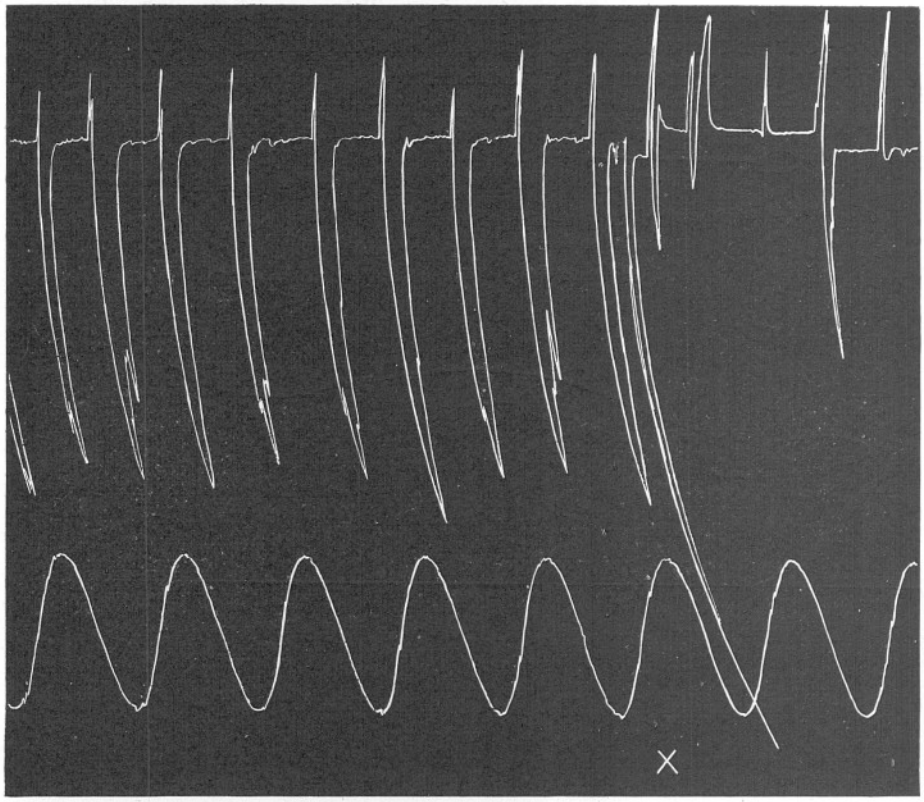


Fig. 5. Worm with its head to the float. At *X*, the taps are turned to 'no air'. (Worm O 48.) Time trace at 1 cycle per hr.

Fig. 6 shows the effect of turning the taps back to 'air' again, after a 7 hr. period of 'no air'. This worm had previously traced the record of Fig. 3. In the first part of Fig. 6, with the taps at 'no air', it was tracing outbursts at about the same frequency, but with much less voluminous irrigation. At the moment of turning the taps, there was a short spell of gentle headward, then tailward irrigation; this was probably a response to slight vibration of the apparatus caused by the handling of the taps. Then, when the next outburst fell due, the worm crept nearly to the T-piece, and began headward irrigation. It was not until this moment, that the aerated water first reached the worm. The response was very marked. Previously, the worm's movements had been

rather feeble and jerky, and its whole appearance suggested weakness and even injury by the 'no air' conditions; but now it suddenly revived and became alert and vigorous; and it began a burst of exceptionally powerful headward irrigation which lasted for 40 min. (total volume pumped 240 c.c., peak flow rate through capillary 8·25 c.c./min.). After this, the time intervals between outbursts were at first very short, and gradually lengthened out; but, even after the taps had been turned to 'air' for 10 hr., the rhythm was still quicker than at the beginning of the experiment (Fig. 3). As, however, the worm had been in the apparatus by this time for about 40 hr., an exact agreement is hardly to be expected.

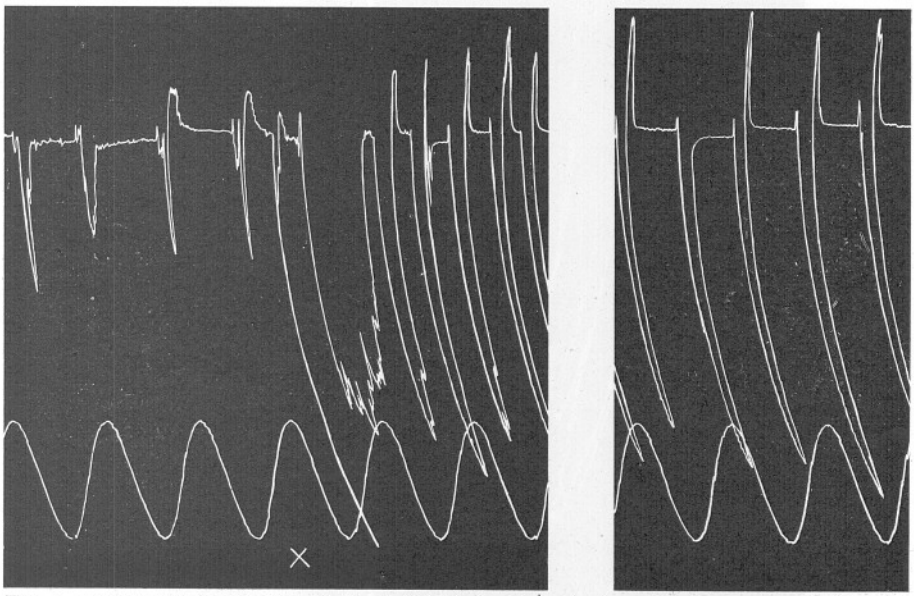


Fig. 6. Worm with its head to the float. The first extract begins with the taps in the 'no air' position. They are turned to 'air' at *X*. The second extract begins (still with the taps at 'air'), 3 hr. after the end of the first. (Worm O 49.) Time trace at 1 cycle per hr.

These results show that the cycles can be greatly modified, in amplitude, duration and frequency, by external conditions; but all the evidence tends to the conclusion that the intermittence itself is an inherent property of the worm. The case is analogous to that of the heart beat; rhythmicity is an inherent feature of the heart's organization, though the details of the rhythm can be modified by the vagus and sympathetic nerves.

Location of the Pacemaker

Wu (1939) studied the action of drugs on longitudinal body-wall strips from *Lumbricus* and *Arenicola*. He wrote: 'In contrast to the earthworm strips, those of *Arenicola* showed spontaneous activity only if the ventral cord was

present. The ventral strips were very active and often showed outbursts of rhythmic activity alternating with more quiet periods.'

To see whether the intermittent activity of isolated, innervated body-wall strips was at all comparable with the irrigation cycles, I made a series of experiments in the following way. The head, together with the first three chaetigerous segments, was removed by means of a transverse cut with a safety-razor blade. The tail, and the last two chaetigerous segments, were similarly removed. The middle part—of fourteen segments—was opened along

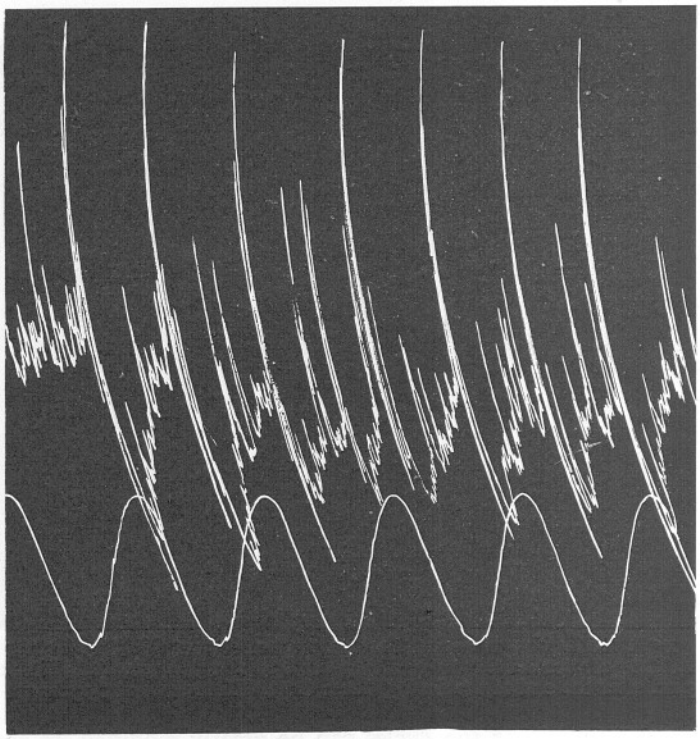


Fig. 7. Record traced by a body-wall strip, including the nerve cord, from the middle region of the body. Upstroke of lever means contraction of preparation. Time trace at 1 cycle per hr.

the mid-dorsal line, and the gut was removed. The body wall was then tied at both ends and suspended as a longitudinal preparation, in a large vessel of briskly aerated sea water, and connected to a light isotonic lever.

The resulting preparations showed continuous, rather irregular rhythmic activity, but one can generally see, on the tracings, bursts of outstanding vigour appearing at more or less regular intervals, with about the same timing as that of the irrigation cycles. Sometimes these were very evenly spaced, for several hours on end, as in Fig. 7.

In view of these results, and of Wu's observation that spontaneous activity occurs only in the presence of the ventral cord, one may reasonably place the pacemaker for the irrigation cycle, tentatively at least, in the nerve cord itself. The presence of the brain seems quite unnecessary.

Intermittent Aerial Respiration

At high tide, the lugworm can get plenty of oxygen by circulating the water in its burrow. If, however, the tide recedes, leaving the surface dry and stagnant water in the lower part of the burrow, circulation is no longer possible and serious oxygen shortage could result. During an earlier study (Wells, 1945), I placed lugworms in glass U-tubes partly filled with sea water, which they were unable to circulate, and saw on several occasions what is evidently a method of aerial respiration. The worms crept backwards to the surface of the water, and drew air between their dorsal surfaces and the tube, so that it came in contact with the gills. This process might evidently be brought about by means of an adaptation of the irrigation cycle. The phase of tailward locomotion would bring the worm to the water surface and the following headward irrigation would then draw air down to the gills. If so, aerial respiration will be intermittent; and the experiments now to be described were made to find out whether this guess is true.

The apparatus was simple (Fig. 8). The worm was placed in the same U-tube as before, but now only partly filled with sea water. One end of the U was connected with pressure tubing to a float-recording device, so that the oscillations of the level in the U were written on the kymograph. For most of the time, the worms were left to write their own stories, but occasionally they were visited to see what they were doing, and once or twice they were watched continuously for an hour or so, and their behaviour was noted minute by minute.

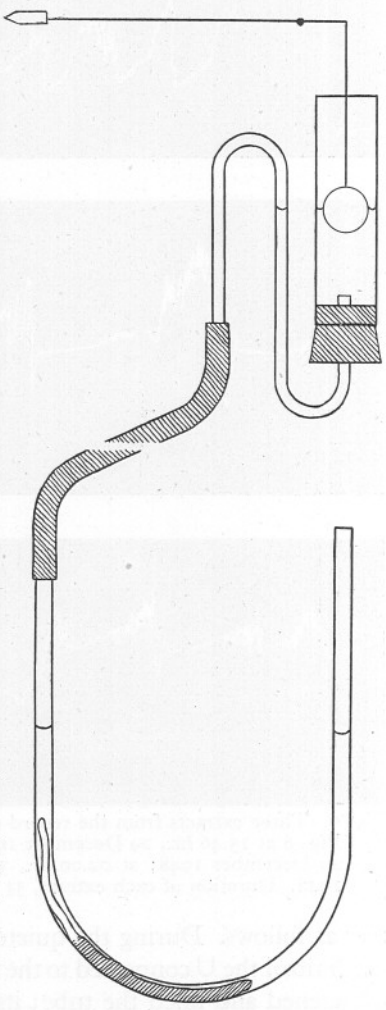


Fig. 8. Apparatus for recording aerial respiration (see text).

Parts of the tracings show confused, unanalysable activity, but usually the records are obviously periodic. The timing of the cycles varies considerably, as may be illustrated by the record of worm T 6 (Fig. 9). The worm was continuously watched during the last 2 hr. of the third extract, and its behaviour

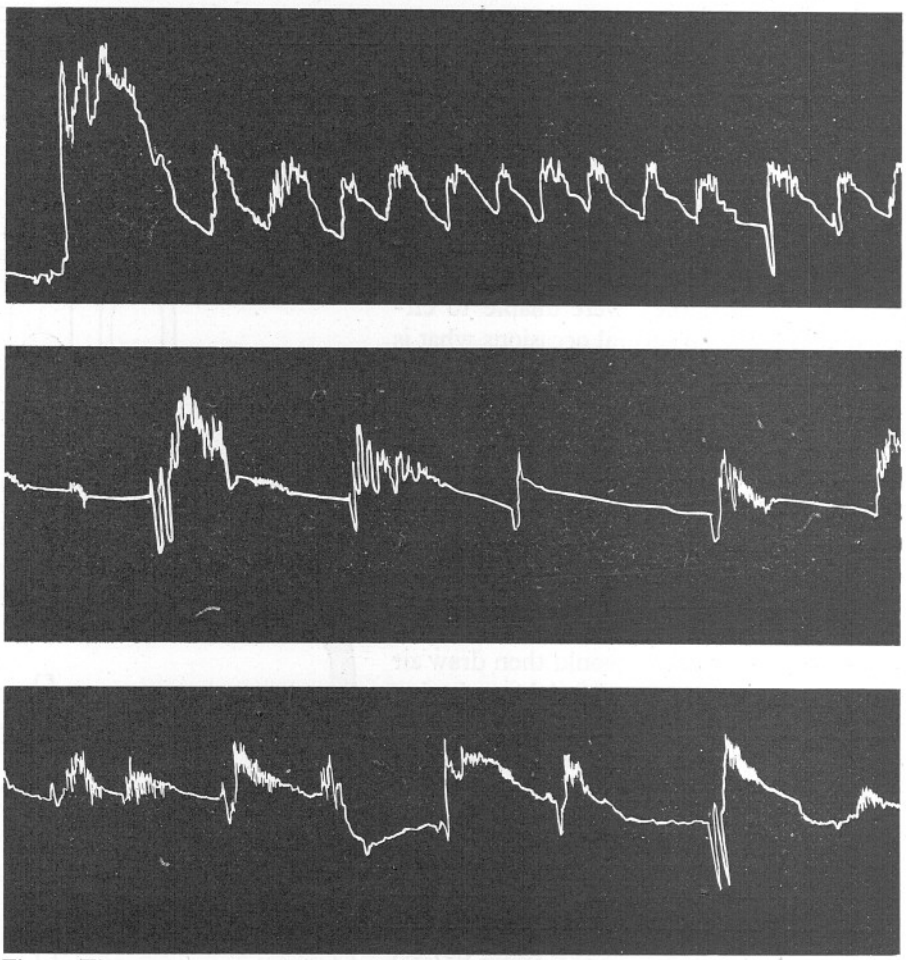


Fig. 9. Three extracts from the record of worm T 6. The worm was put in the apparatus of Fig. 8 at 15.46 hr., 29 December 1948. The three extracts start respectively at 19.00 hr., 29 December 1948; at 02.00 hr., 30 December 1948; and at 13.00 hr., 30 December 1948. Duration of each extract, 5½ hr.

was as follows. During the quieter parts of the record it was lying, tail up, in the limb of the U connected to the recording device; its body was shortened and broadened and filled the tube; its tail was short and thick, with its tip at, or near, the meniscus. As each of the bursts of rapid oscillation set in, the worm suddenly lengthened and narrowed its body. At this stage, there was usually

a drop of the writing point, presumably due to a slight upwards creeping of the worm, though this was not actually seen. Powerful headward wave-movements then began, the worm as a whole remaining in the same position. The waves began at the base of the tail, and resembled vigorous irrigation waves. Each wave drove air along the dorsal surface of the body, nearly to the most anterior gills; at this point, the bubble seemed to slip back past the wave and jerk up to the water surface again. During this phase, the water surface was mostly at the base of the tail. Each wave appears as a small oscillation of the writing point. Finally, the waves became gentler and died out, and the worm resumed its resting position.

The whole performance is clearly identical with the irrigation outbursts seen in the apparatus of Fig. 1. The variability of timing is paralleled by the irrigation records. In particular, there is an attractive resemblance between Fig. 6 and the upper extract in Fig. 9; in both cases, a prolonged outburst of great amplitude is followed by a series of bursts at short intervals. Now the worm of Fig. 9 spent the first $3\frac{1}{2}$ hr. of its time in the apparatus lying very still with its head up the open limb of the U, at about the level of the meniscus. In these circumstances it cannot have got any significant oxygen supply; its first respiratory movements are shown in Fig. 9; so the common features of the two figures may be attributed to previous oxygen shortage.

The first and second phases of the irrigation cycle are usually evident on the air-breathing tracings. The third ('rebound') is not detectable on the records; but as one watches the worm, one sometimes sees a slight, slow wave-creep in the tailward direction as the outburst passes off.

Cyclic aerial respiration of this type was seen or recorded in 13 of the 15 worms used. That it is adequate to support the worm for a considerable length of time was proved by worm no. T 5, which spent 120 hr. in the apparatus, always with the same 15 c.c. of sea water, and was in excellent condition at the end.

We may infer from these results that the worms in the field breathe air intermittently under low-tide conditions, and that they do so by adapting the irrigation cycle. Whether they continue to feed and defaecate when the tide is out will presumably depend on the mechanical properties of the drying sand.

Discussion—the Functional Significance of Intermittence

Van Dam (1937, 1938) made experiments on the respiration of animals from various phyla, several of which showed intermittent respiratory movements, and he assembled a number of other examples from the literature. The mechanism of intermittence may clearly be very different in different cases. The behaviour of *Arenicola* may profitably be contrasted with that of the larvae of the caddis fly, *Phryganea grandis*. These were studied by van Dam, after he had induced them to assume celluloid cases. They irrigate their cases by means of undulatory movements of the abdomen, and the following citations

from van Dam give the physiological picture: 'Periods of ventilating often very regularly alternated with intervals during which no movements occurred.... Crawling and struggling increased the oxygen need of the animal and so caused the intervals to be shortened.... That it was really oxygen want which brought about the respiratory movements, was proved in the following way. A tube was attached to one end of the case and a current of water was forced through it. In a current of air-saturated water no ventilation movements occurred (e.g. not for 27 min.), even if the animal moved in its case. However, if water poor in oxygen was used, the intervals were shortened and finally ventilation became uninterrupted.... Water containing from about 2 to 29% CO_2 had no marked influence on the respiratory movements.' This is a clear case of reflex response to change in oxygen tension. With *Arenicola*, on the other hand, the position is completely different. Neither in the experiments of van Dam nor in those here described were the pauses abolished or shortened by oxygen lack, and intermittence is seen in worms surrounded on all sides by air-saturated water.

Can one read any functional significance into intermittence? Wolvekamp & Vreede (1941) suggest economy of effort. If the worms are watched, one sees that their whole attitude changes as the irrigation outbursts appear. 'During the pauses the body was contracted and, except the posterior end, pressed everywhere against the tube; the gills were also contracted. The animal usually lay motionless in its tube. Before resuming ventilation the animal elongated its body' (van Dam, 1938). Perhaps this change in posture means an increase in muscle tone and in the pressure of the body fluids, for clearly the latter factor must be high if effective irrigating movements are to be performed. If this be true, it might be economical to pump the necessary amount of sea water in bursts, rather than to do it gently and continuously, for the cost of maintaining an alert posture would be saved during the intervals in the former case. Against this viewpoint, however, it may be pointed out that the worms appear to be more active between the bursts when in sand than they are in glass tubes. This will be shown in another paper. In the absence of measurements of the metabolic cost of the worm's various kinds of activity, the 'economy' argument is not wholly convincing.

The problem can perhaps be more profitably approached from another angle. If the experiment illustrated in Figs. 5 and 6 were carried out on a reflexly irrigating animal, such as a *Phryganea* larva, the result would be as follows. The animal would irrigate more and more violently and continuously —but to no purpose—when the taps were turned to 'no air'; presently it would be exhausted and would cease to show respiratory movements; after this stage has been reached, the turning back of the taps would be of no avail, since the animal must co-operate if it is to get the oxygenated water. *Arenicola*, on the other hand, behaves in a way making for long survival under the conditions of the experiment. When the taps are turned to 'no air', its irrigation

outbursts decrease in intensity; they may perhaps be interpreted as a periodic testing of the conditions; and only when the taps are turned back, and the movements bring aerated water again, is their vigour increased.

It is of course unreasonable to suppose that the worm is adapted to the special conditions of a laboratory apparatus, and one might question whether a similar situation would ever occur in the field. At high tide, the worm has a plentiful supply of oxygenated water at its disposal, and at low tide, if the sand surface dries, it can breathe air. If, however, the burrow were covered with surface water at low tide, then circumstances might arise in which behaviour of the *Phryganea* type would be injurious or even fatal, while behaviour of the *Arenicola* type would save its exhibitor.

The surface water in summer weather is often several degrees hotter than the underlying sand. Linke (1939) studied an *Arenicola* beach near Wilhelmshaven, and found the following temperatures towards the end of a long tidal exposure in July, 1935: water in surface puddles, 26·2° C.; sand at a depth of 10 cm., 21·3°; at 30 cm., 19·4° C. I have noticed similar differences, though of less extent, when collecting worms at Thorpe Bay, on the Thames estuary. This is a beach which is exposed for a couple of hours only; nevertheless, it is very noticeable in summer that worms taken away in water collected from the sea travel better than those taken in surface water from the sand flats. When experimenting on dissected worms, or keeping stocks in the laboratory, I regard 20° as about the upper limit for good results. Thamdrup (1935, p. 66) found that the O_2 consumption of *Arenicola* rose from 2° to 10° C., and from 10° to 20° C., but fell from 20° to 28° C.

It seems clear that the surface water may become hot enough to be dangerous to the animals, and we may guess that a worm, whose burrow was left at low tide under a pool of hot water, would behave rather like the animal of Fig. 6. It would refrain, for obvious reasons from irrigating its burrow; under the influence of its internal 'clock', it would make occasional testing excursions towards the surface; and, after the returning tide had brought a supply of cooler water, it would begin vigorous irrigation at the next testing excursion. A hard frost, or a heavy rain, might perhaps make the surface water dangerous at low tide, and here again behaviour of the *Arenicola* type would be useful.

The fact that the cycles typically begin with tailwards creeping adapts them to the purpose of testing the surface water, since the worm is thereby brought nearer to the surface. The intensity of the second phase, of headward irrigation, can vary, as we have seen, with the conditions. The third, or 'rebound' phase, may also have its uses; it could expel any harmful water drawn down during testing irrigation, and (since irrigation and antikinetic locomotion are closely related), it might conceivably serve to bring the worm away from the surface if the second phase has been cut out.

These suggestions imply, of course, that the worm can survive long periods of oxygen lack. The animal of Fig. 6 responded promptly to the renewal of the

oxygen supply after 7 hr., during which it can have had little external oxygen except that dissolved in the water in the U-tube, the capillary and the short connecting tubes.[1] No analyses of oxygen tension were made, but the conditions were at any rate stringent enough to induce a marked change in behaviour soon after turning the taps to 'no air' (Fig. 5).

On the question of the possible value of haemoglobin as an oxygen store, the available data are meagre. Estimates of the oxygen consumption of the worms (when shaken in a little sea water in a manometric apparatus) and of the oxygen capacity of the worms' blood were made by Barcroft & Barcroft (1924), who deduced that the oxygen in the blood, at saturation, would be 'enough to suffice the worm for an hour or thereabouts'. Similar measurements and calculations were made by Borden (1931), who concluded that the oxygen in the blood would last 71 min.—a result in good agreement with that of Barcroft & Barcroft, although the figures on which it is based are considerably higher.[2] Thamdrup (1935) made measurements of the oxygen consumption at various temperatures with the Winkler technique; his figures fall between those of Barcroft & Barcroft and those of Borden.[3] Two further points should be borne in mind. The first is that the calculations just cited assume that the worms will continue, in the absence of an external oxygen supply, to consume oxygen at the same rate as when it is abundantly available. This has not been shown to be true, and the behaviour of the worms in Figs. 5 and 6 suggests that, on the contrary, the energy usage is reduced when the oxygen supply falls. The second is that *Arenicola* has recently been found to have haemoglobin in its muscles, besides that in its blood (Fox, 1949). Both of these factors will tend to prolong the period over which the stored oxygen will last. Van Dam (1938) accepts the earlier values (about 1 hr.'s supply) and suggests that the function of the haemoglobin is to supply the worm in the intervals between consecutive irrigation outbursts. According to the hypothesis here put forward, unfavourable surface conditions may force the worm to do with little or no external oxygen during the whole of the low-tide exposure period.

Summary

The worms were housed in glass U-tubes, and were able to get a supply of aerated water from above by making pumping movements. The water movements were recorded kymographically. The experiments generally lasted for 24 hr. or longer.

The worms generally settled down to give outbursts of irrigation separated

[1] Total volume of water about 35 c.c.; the total O_2 content of this would be, at the start, about 0·2 c.c.; the worm weighed 4·8 g.

[2] The oxygen consumptions, in c.c. O_2/g./hr., are 0·01 (Barcroft & Barcroft) and 0·02–0·04 (Borden). The oxygen capacities of the blood, in c.c. O_2/g. of worm, are 0·008–0·013 (Barcroft & Barcroft) and 0·030–0·049 (Borden).

[3] Oxygen consumption, in c.c. O_2/g./hr., 0·0064 at 2°, 0·015 at 10°, 0·034 at 20°, 0·018 at 28° C.

by periods of rest, the alternation continuing with great regularity for many hours at a stretch.

An irrigation outburst consists of three phases: (*a*) tailward locomotion, (*b*) headward irrigation and slow headward creeping, (*c*) tailward irrigation. These three phases always follow each other in that order, but their relative prominence is variable. The second phase is the most conspicuous, whenever a plentiful supply of oxygenated water is available.

The following facts show that the intermittence is spontaneous, i.e. produced solely by conditions internal to the worm:

(i) If worms are pinned down in large vessels of well-aerated and stirred sea water, they often show outbursts of rhythmic activity corresponding in timing to the irrigation cycles.

(ii) Van Dam (1938) found that the pauses between outbursts are neither shortened nor abolished by lowering the oxygen tension in the water.

(iii) If the experimental conditions are so arranged that the worm can circulate the water in its U-tube without thereby getting an oxygen supply, the irrigation cycles continue with their previous timing, but with the vigour of the outbursts greatly reduced. If, after some hours under these conditions, aerated water is again admitted, irrigation is very greatly increased.

Observations on the rhythmic activity of body-wall strips indicate that the pacemaker for the irrigation cycles is in the ventral nerve cord.

If worms are placed in U-tubes partly filled with water, so that circulation is impossible, they creep tailwards to the water surface and draw air down into contact with their gills. Aerial respiration is intermittent, and is brought about by an adaptation of the irrigation cycle.

Intermittence, determined by an internal pacemaker, might have survival value if, at low tide, the burrow was covered by surface water which got too hot, or otherwise dangerous, for the worm.

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THE BEHAVIOUR OF *ARENICOLA MARINA* L. IN SAND, AND THE ROLE OF SPONTANEOUS ACTIVITY CYCLES

By G. P. Wells

Department of Zoology, University College, London

(Text-figs. 1–7)

In the laboratory, the lugworm shows two distinct types of spontaneous activity cycle. The question which the following paper sets out to answer is, have these laboratory results any bearing on the worm's normal life in the field?

The first type of cycle has tentatively been named the feeding cycle. The isolated oesophagus, suspended in sea water or the worm's body fluid, shows outbursts of rhythmic activity alternating with periods of rest. The intact worm, watched in a glass tube, generally shows periodic outbursts of proboscis extrusion and withdrawal, or of gulping and swaying of the head. These cycles, like those of the oesophagus, have an average period of about 7 min. By means of a series of dissected preparations of ascending complexity, one can show that the two rhythms are the same; the 'feeding rhythm' of the whole worm is the oesophageal rhythm, transmitted to the muscles of the proboscis and the anterior body wall (Wells, 1937).

The second type of cycle is of much longer period. The worms, in glass tubes, generally pump water through the tubes in a headward direction in rhythmically recurring bursts. Closer inspection shows that this headward irrigation is the second, and most prominent, phase of a 3-phase outburst; the first is tailwards locomotion, and the third is tailwards irrigation. The outbursts are not, as one might expect, reflexly elicited by oxygen exhaustion or CO_2 accumulation in the tube, but result from the activity of a second pacemaker, probably situated in the ventral nerve cord (van Dam 1937, 1938; Wells, 1949).

Now the intact worms, in all of these experiments, were watched under abnormal conditions. A glass tube differs, mechanically and chemically, from the sand in which the species normally lives; in order that their activities should be visible, the worms were illuminated; and they had mostly been fasting in the laboratory for days or even weeks. One might therefore suspect that the very regular periodicity, which so often characterizes their behaviour, is due to the artificial conditions and would not occur, or would be masked by reflex responses, in the more variable surroundings in the field.

To settle this point, one would have to watch or record the behaviour pattern of the worms in their natural habitat. This would be difficult. I have therefore

done the next best thing, and allowed worms to make burrows in sand in the laboratory, in which their behaviour could be recorded. The results are described below. The main conclusion is that the cycles appear with great regularity, and especially clearly when the worms are making funnels and faecal accumulations like those which signalize their presence on the beach.

The Form of the Burrow in the Field

The animal's mode of life has been described elsewhere (Wells, 1945).[1] The details of the burrow vary according to the nature of the beach, but there is

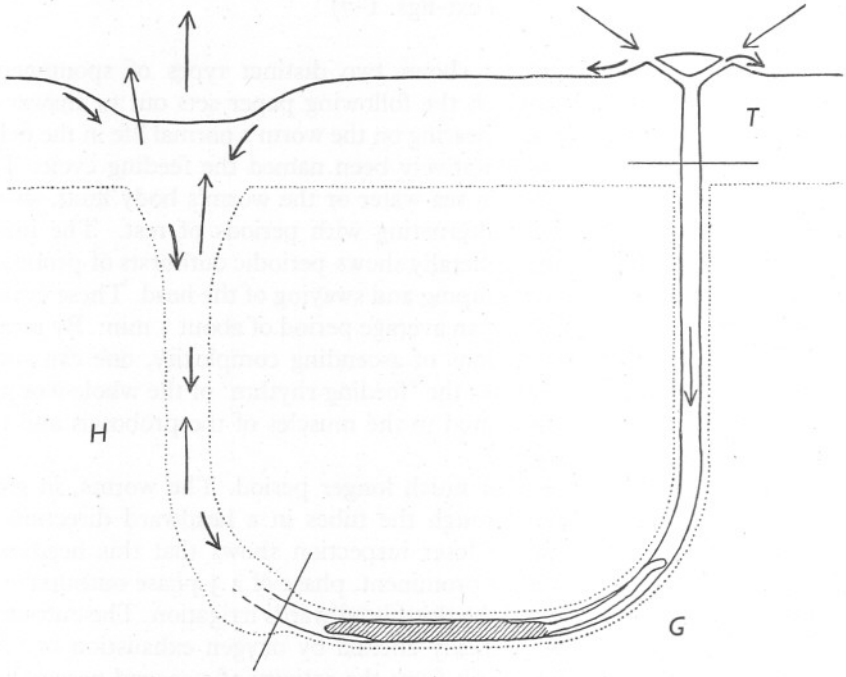

Fig. 1. Generalized diagram of a lugworm burrow, with the worm lying quietly in the gallery. The cross lines are drawn at the boundaries between head shaft (*H*), gallery (*G*) and tail shaft (*T*). The dotted line is the boundary between yellow and black sand. The long, thin arrows show the movement of water, and the short, thick ones that of sand.

a general pattern to which all of the variations conform (Fig. 1). Immediately below the well-known heap of castings, a 'tail shaft' descends vertically for several cm.; this houses the tail at the moment of defaecation. At its lower end,

[1] When I wrote that paper, I was unaware of two important works on the form of the lugworm's burrow. Häntzschel (1938) described burrows in sand. Linke (1939) described burrows in sand and mud, and gave much interesting information about the environment. Both accounts are illustrated by photographs and both stress the fact that the form of the burrow varies with the nature of the bottom.

the tail shaft widens into the 'gallery', a tube in which the worm moves to and fro, but always with its tail towards the tail shaft. The walls of the gallery are firm, due to impregnation with the worm's secretions (Osler, 1826; Häntzschel, 1938; Linke, 1939). The gallery descends more or less vertically, then swings round to become horizontal. Its lower ending communicates with the surface by the 'head shaft', a part of the burrow whose detailed structure varies greatly with the nature of the beach. Typically, the head shaft consists of a column of yellowish sand, without any lumen running through it, and its upper end is marked by a saucer-shaped depression of the surface. The chief forces by which the head shaft is set up and maintained are: (i) feeding from its lower end, causing its substance to slowly descend; (ii) upstreaming of the irrigation water, which helps to keep it soft; and (iii) occasional upward 'working' excursions of the worm.[1] If the conditions are favourable, a worm may live in the same burrow—irrigating, feeding and periodically defaecating—for months on end (Thamdrup, 1935; Linke, 1939).

Apparatus for Studying Behaviour in the Burrow

To watch the activities of a worm in sand is impossible. Even if one allows it to burrow between glass plates, so close that there is only just room for the worm, sand makes its way between worm and glass, and one gets only occasional glimpses of parts of the animal. The method used in this work was to record the water currents set up by the worms in their burrows, and to compare the resulting records with those produced by worms in glass tubes (Wells, 1949). The apparatus was as follows.

ABCD (Fig. 2) represents two squares of plate glass, about 38 cm. square. They are held apart by a U-shaped strip of rubber (shaded), which is of square section and about 1 cm. thick. This rubber is well greased with stopcock grease on the sides which meet the glass, and shorter pieces are put beside it at six points; at these places, the whole is held together by *G*-clamps, lightly applied through additional rubber pads external to the glass. Another greased rubber strip, in the centre, divides the upper part of the resulting vivarium into two.

When assembled, the vivarium is held upright in a wooden stand (not shown) and filled. The lower part contains, to a depth of about 20 cm., mud dug from the deeper layers of the beach (drawn black). On top of this is about 6 cm. of yellow surface sand (dotted), and 6 cm. of sea water. Aeration is through jet *E*. Finally a large, recently collected worm is added. The worm goes down into the mud at once, and one usually sees nothing more for a day or so; but the dimensions are such that it ultimately sets up a burrow with the funnel on one

[1] Chapman & Newell (1947, 1948) believe that the thixotropy of muddy sand plays an essential part in the processes by which the worm enters the sand and sets up a burrow, but the writer is unable to see the necessity for this (Wells, 1948).

side of the centre partition and the faecal pile on the other, as shown in the drawing.

Water currents are produced by the worm in various ways—by irrigation, or by creeping along the tube—and will clearly tend to displace the levels of the water in the two top compartments. The muddy sand is practically impermeable to water. The compartments are connected by capillary siphon *F*,

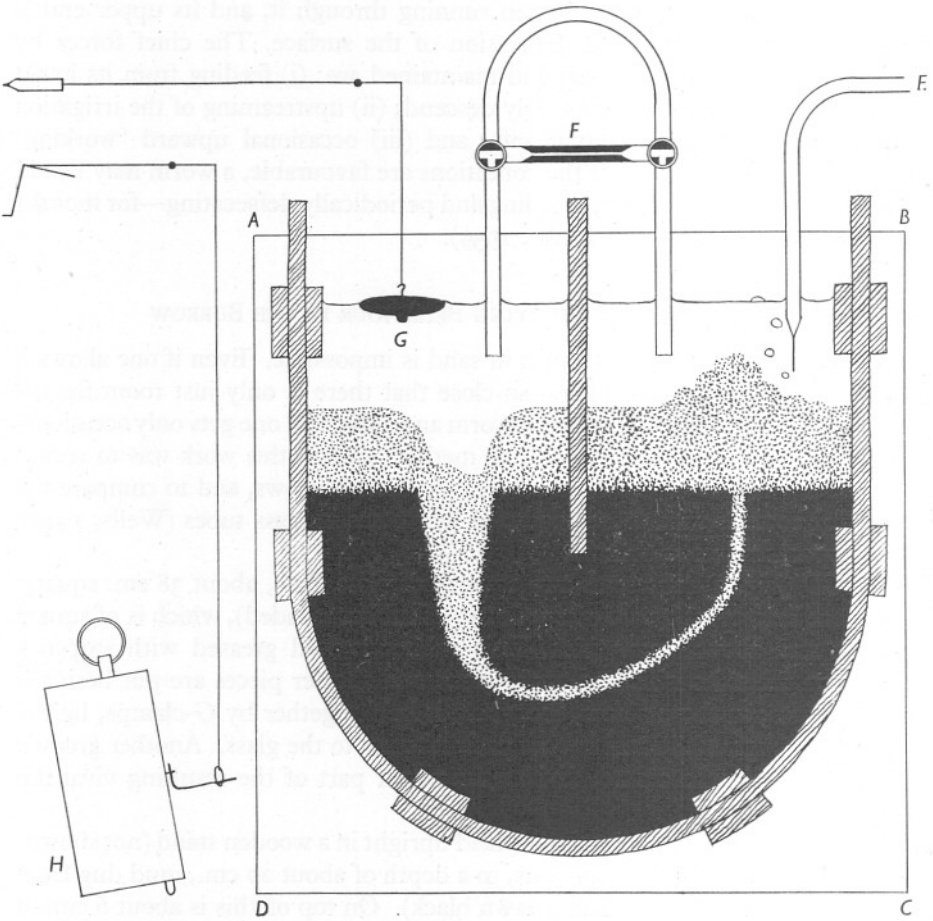

Fig. 2. Apparatus for recording the behaviour of the worm in the burrow (see text).

provided with a by-pass of wide bore to facilitate the daily routine, described below. The capillary prevents excessive piling up of water on either side, but offers enough resistance to allow the fluctuations in level to be recorded. This is done by means of float *G*, made of paraffin wax moulded on silver wire, and connected to a light isotonic lever writing on smoked paper.

The following values were found satisfactory: capillary bore about 1·5 mm.; lever magnification about 12; paper moves at about 25 mm./hr. The time trace was made by clock *H*, connected to a lever with a frontal writing point and tracing 1 cycle per hr.; it has been omitted from the illustrations to save space.

Once a day, the following routine was carried out. The smoked paper was changed, the wide by-pass siphon was opened, the sea water was topped up with distilled water to a gauge mark to compensate for evaporation; the faeces were removed and fresh sand was added to the funnel. Except for this daily operation, which took about 5 min., recording was continuous and the apparatus ran itself.

Altogether, six worms were studied, for periods ranging from 5 to 21 days; they yielded an aggregate of 72 recorded 'worm-days'. None of these worms died during the experiments and five of them were still in good condition in the sand when their records were stopped. The sixth ended its experiment by coming out on the surface of the sand on the 11th day and refusing to go down again (though apparently in good condition) for 36 hr.; this was probably due to some kind of organic decomposition in the sand. I have noticed, on other occasions, that the worms tend to leave very foul sand, and when the vivarium of this particular individual was dismantled it was unusually evil-smelling.

The Form of the Burrow in the Apparatus

The configuration of the burrows in the apparatus (as shown by a yellow stain on the black sand) resembled that found in the field. The worms fed from conical head shafts (whose upper surfaces subsided rather more rapidly than usual owing to the small sectional area of the apparatus) and piled up heaps of faecal cylinders. They appeared, however, to be rather more restless than worms kept under less cramped conditions. The head shafts often shifted a little in position from day to day, and the worms sometimes reversed their burrows, converting the old tail shaft into a head shaft, and vice versa. Both of these changes are occasionally seen in larger vivaria (and they undoubtedly occur in the field), but they were rather more frequent in the apparatus here described.

The Defaecation Cycle

Whenever the worms were feeding regularly from the head shaft, and piling up their faeces in the other compartment of the apparatus, the pattern shown in Fig. 3 was traced on the record. The obvious feature is a series of prominent diphasic excursions with a sharp, short peak followed by a broader one in the opposite direction. They occur about once every 40 min.

Now this record can very readily be interpreted by means of the experiments with worms in glass tubes. The cycles traced in Fig. 5 of my previous paper

(Wells, 1949) are evidently identical with those now under consideration.[1] We may safely conclude that the movements responsible for the tracings are the same in both cases. The sharp first peak is due to a tailward excursion of the worm, and the broad second peak is due to vigorous headward irrigation accompanied by gentle headward creeping. The third 'rebound' phase, which was sometimes very conspicuous in glass tubes, is seldom visible on the records got from actively feeding worms in sand.

If one watches the experiments with worms in sand, one sees that a faecal cylinder is suddenly shot out of the burrow at (or a moment before) the apex of each of the sharp peaks. In other words, the tailward excursion, which

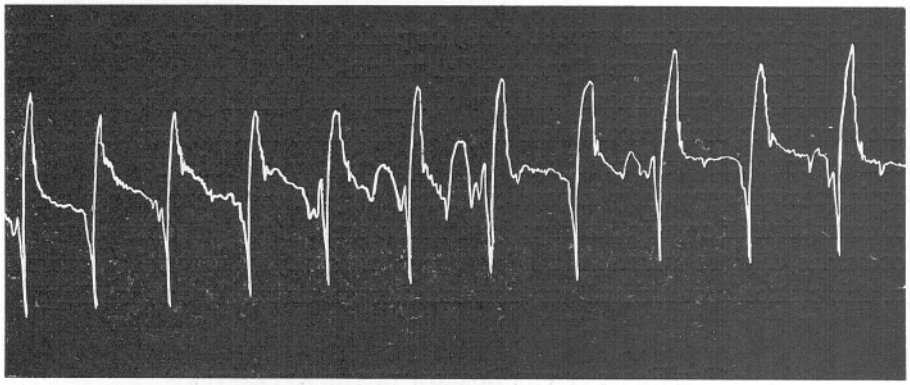

Fig. 3. Record (7 hr. long) traced by an actively feeding worm, with its tail towards the float. The worm defaecates at the tip of each of the prominent downward peaks. Read from left to right. (Worm 'Violetta'.)

begins the whole outburst, has carried the worm to the surface of the sand, and serves as a defaecatory excursion. The worm presumably creeps back to the point where it feeds, at the lower end of the head shaft, during the phase of headward irrigation.

One might have thought that the tailward excursion which brings the worm into position for defaecation is a reflex response to a full rectum, but this does not seem to be the case. Exactly similar excursions were often seen in glass tubes, in worms which had been fasting for days and whose tails were consequently empty.[2] We must therefore conclude that the tailward trip is simply an expression of one of the phases of the triphasic cycle, which is very beautifully suited to the worm's normal way of life.

[1] The worm in Fig. 3 of the present paper has its tail to the float, while that in Fig. 5 of the previous one is the other way round; so the patterns are traced the opposite way up.

[2] The worms occasionally produced faeces in the U-tubes but only if studied within 24 hr. of collection, and unfortunately never while they were being watched. The worm O 48 (in Fig. 5 of the previous paper) was collected on 11 January 1949, kept in a glass tank of clean sea water, and then put in the apparatus on 14 January 1949; its behaviour was recorded for 48 hr., during which two exposures to 'no air' were tried. The record shown in the illustration was taken in the evening of 15 January 1949.

Alternative Behaviour Patterns

The pattern just described invariably accompanied feeding and defaecation. Having once set in, it was generally written on the drum with great regularity for many hours at a stretch, while the faeces steadily piled up and the funnel subsided. During the rest of the time, records were obtained which can be classified into three groups.

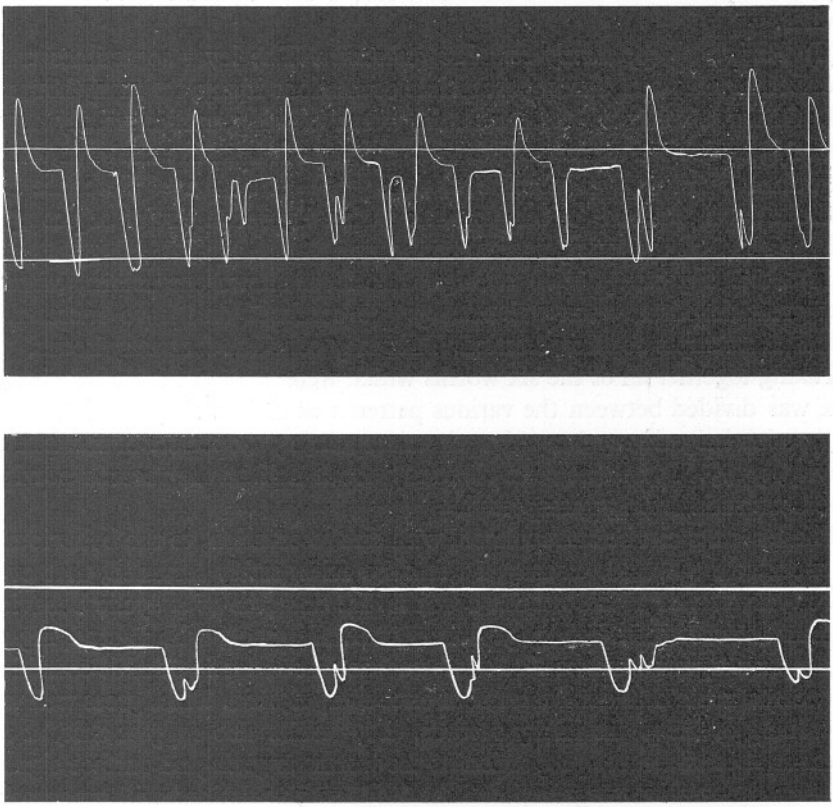

Fig. 4. Two records (each 4½ hr. long) traced by a worm which was not actively feeding and defaecating. The extracts were given on two different days. In both cases the worm's head is towards the float. The horizontal lines give the resting water levels at the beginning and end of the day. The difference is due to evaporation, which also causes the gradual upward trend of the other figures. (Worm 'Fasolt'.)

(i) *Irrigation cycles without a pronounced tailward excursion.* In sand, as in glass U-tubes, the three phases of the typical cycle can vary greatly in their relative prominence. The two records of Fig 4 were taken from the same worm, on different days, and in both cases its head was towards the float. They represent irrigation cycles in which the first phase is barely perceptible on the

tracing, while the second and usually the third are well marked (compare Wells, 1949, second part of Fig. 6). Now and again, one sees an outburst in which the third, 'rebound', phase is dropped out, and the same thing can be seen in the records got from glass tubes. With this curious exception, it may be stressed that the outbursts in any single series have an extremely constant form. The various types are modifications of an underlying triphasic pattern; having made up its mind, so to speak, which type to register, the worm sticks to that type very steadily for hour after hour. On another day, of course, it may choose another.

(ii) *Periods of apparently complete quiescence.* The lever sometimes traces a horizontal line, with barely perceptible oscillations if any, for many hours on end. One would like to know what the worm is doing, and especially how it gets oxygen, at such times. One knows only that it is inside the sand, whose untroubled surface gives no clue to what goes on below. Quiescence may continue for 24 hr. or even longer, after which vigorous activity begins again and the regular rhythmic patterns reappear.

(iii) *Periods of unexplained activity.* The lever shows excursions, often of very great amplitude, but the tracings are confused and have successfully defied all attempts at interpretation. This may continue for many hours.

Taking together all of the six worms which were studied in sand, their total time was divided between the various patterns as follows: defaecation cycles, 45%; other irrigation cycles, 5%; quiescent spells, 15%; periods of unexplained activity, 35%. It will be seen that only about half of the records obtained have been satisfactorily interpreted.

These results can be extrapolated, with due reservation, to the behaviour of the worms in the field. It may, I think, be fairly safely assumed, that every saucer and pile of faeces on the beach is the outcome of a cyclic behaviour pattern like that seen in Fig. 3. Mrs D. M. Kermack, who is studying the feeding and digestion of *Arenicola*, informs me that under favourable conditions the worms in the field defaecate about once every 45 min. This agrees well with the timing of the peaks in my records. My results also suggest that, at any moment, a considerable proportion of the worms is giving no surface signs at all—but the relative magnitude of the 'hidden population' will presumably vary with conditions. Newell (1948) assessed the density of lugworm populations by digging up areas of 1 sq.yd., and wrote 'This rather tedious method of sampling was found to be essential, since counting the number of casts per square yard is a most unreliable index of the number of worms, varying as it does with, among other conditions, the state of the tide'. There was, of course, no tide in my experiments. The time spent in active feeding and defaecation varied in different individuals from 32·5 to 68%; so it may be that the conditions determining activity are not entirely environmental. I have already described great differences in feeding activity between worms kept individually in aquaria (Wells, 1945).

The Feeding Cycle

As stated in the opening paragraphs, two distinct types of behaviour cycle are shown by lugworms in glass tubes. There is the irrigation-defaecation cycle already dealt with, and there is a cycle of anterior end activity, of period averaging about 7 min., which has been tentatively named a feeding cycle (Wells, 1937). Now the records got from worms in sand often show a considerable amount of 'background' activity between the irrigation-defaecation outbursts, and sometimes this has an obviously cyclic pattern, with a period of the same order as that of the feeding cycle. The extract of Fig. 5, for example,

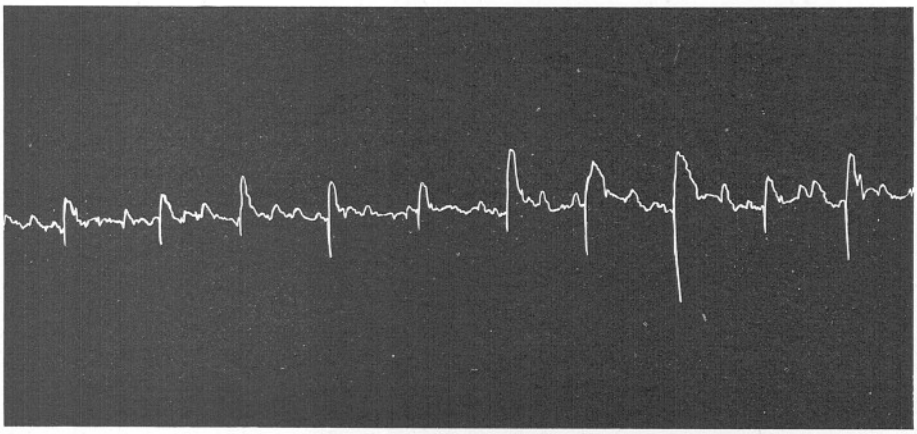

Fig. 5. Record (6 hr. long) traced by an actively feeding and defaecating worm, with its tail towards the float. The record shows a short-period cycle imposed on the main one. (Worm 'Sieglinde'.)

shows defaecatory excursions at intervals of about 35 min., and minor oscillations with a period of about 7–8 min. These may well be due to the oesophageal pacemaker, but it remains to be shown how the feeding outbursts could write themselves on the drum, with the apparatus of Fig. 1.

Just (1924) pointed out that there is a functional differentiation between the nineteen chaetigerous segments in the lugworm's body. The first three participate in the movements of the head and especially in proboscis activity, while the wave movements, which run along the body in irrigation or creeping, are the concern of the remaining sixteen. I showed in an earlier work that the excitations responsible for the feeding outbursts spread from the oesophagus to the body-wall muscles of the more anterior segments, which play a direct part in proboscis activity (Wells, 1937). The experiments now to be described were made to find out whether any influence of the oesophageal rhythm could be traced in the wave-carrying segments farther back.

The worm was pinned on a cork sheet under sea water, ventral side down

(Fig. 6). The first few segments were laid open and the extrovert was dissected as described in my earlier paper (Wells, 1937). The oesophagus was cut across and its oral end was connected to a light isotonic lever. The movements of this lever are mainly due to the proboscis muscles acting under the influence of the oesophageal pacemaker, though the muscles of the surrounding body wall also contribute to some extent. One or two of the branchiate segments were

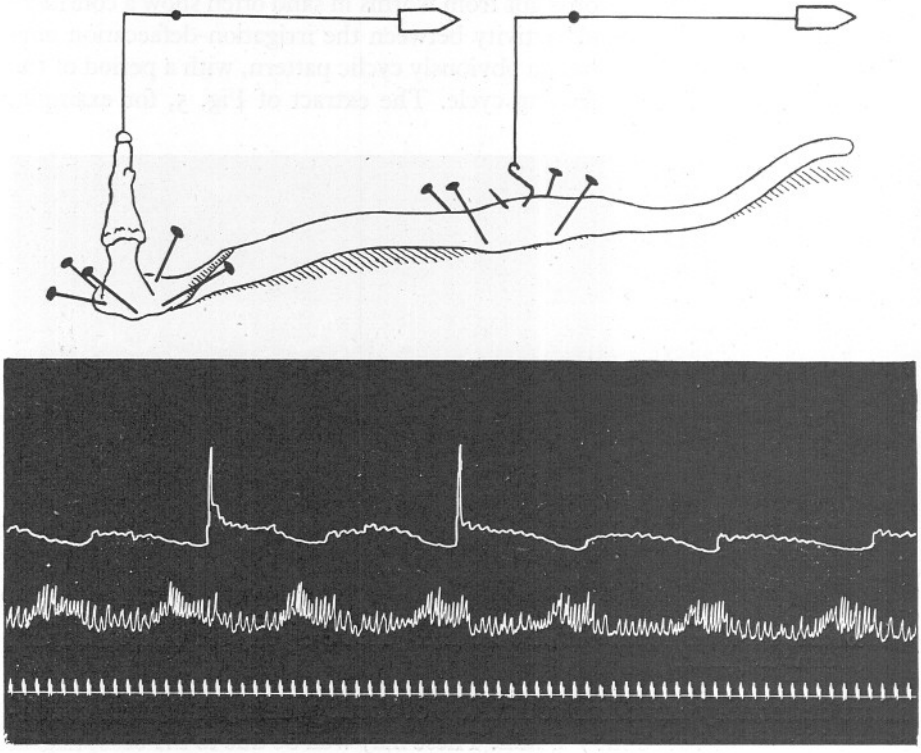

Fig. 6. Method for studying the influence of the oesophageal outbursts on the branchiate segments (above), and a record obtained in this way (below). The lower line of the tracing was made by the extrovert, and the upper by the body wall. Read from left to right; time scale in minutes. (Worm E/I 8.)

immobilized by pins inserted latero-ventrally (but avoiding the nerve cord), and a hook inserted mid-dorsally in the same region was connected to a second lever.

The results were rather capricious. In most of the worms so treated, an inhibitory influence of the oesophageal outbursts on the branchiate region could be detected. Fig. 6 gives a typical tracing; the lower line (from the oesophagus) shows the outbursts of extrovert activity, following each other in this case at intervals of 12 min., and the upper trace (from the body wall) shows very clearly how the body wall relaxes and suspends its slight spontaneous movements at each of the oesophageal outbursts. In two of the cycles, there

is an upstroke of the body-wall lever as the oesophageal outburst passes off; and this effect was seen from time to time in several of the worms.

Fig. 7 shows an experiment in which the body wall was unusually active; one can see very clearly that the inhibitory effect of the extrovert is on the amplitude, not the frequency, of contraction in the body wall.

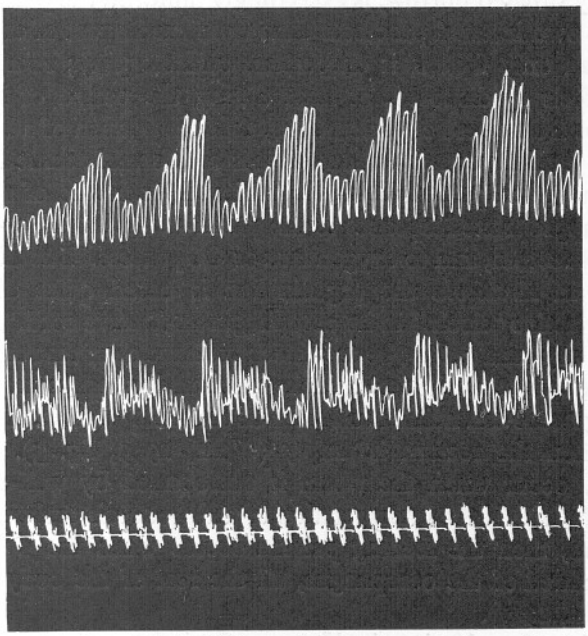

Fig. 7. Record, got by the method of Fig. 5, showing decrease in amplitude of the body-wall contractions (above) at each outburst of the extrovert (below). Time scale in minutes. (Worm E/I 4.)

These results show that the oesophageal pacemaker influences the hinder segments, though the acts of proboscis extrusion and withdrawal concern only the more anterior ones (and can be carried out by these segments after the rest of the worm has been removed). By doing so, it could influence the water-movement tracings, since the latter are produced by the activity of the wave-carrying segments. I have not as yet been able to devise means of pursuing this question into further detail. As far as they go, the results are at least not inconsistent with the view that the oesophageal pacemaker determines periodic feeding when the worm is in sand.

Discussion

To a large extent, the various activities of which a lugworm's behaviour cycles are made up are 'whole worm' activities, i.e. it cannot do more than one of them at any given moment. Vigorous tailward locomotion and vigorous head-

ward irrigation both depend on headward waves, but the attitude of the worm is different in the two cases. The facts described in the last section suggest that feeding, too, concerns more than the first few segments. Since the worm must do all of these things, and cannot do them all at once, its life must have a pattern; and because the worm's environment, once it has established itself in a favourably situated burrow, is exceedingly uniform, the pattern will result more from its own internal processes than from the impact of external events. A predator can only feed if it encounters suitable prey; *Arenicola* can eat whenever it feels so disposed, at least during the period of high tide. It already follows from these considerations, that the pattern of a lugworm's life will be pretty regularly cyclic, as long as it is comfortably settled in a burrow.

Such an integrated pattern could be achieved by means of a hierarchy of reflexes with appropriate responses to the worm's various needs—to an empty gullet, to a full rectum, and to oxygen lack or CO_2 excess. But all the evidence suggests that in *Arenicola* the organization is based quite differently, on spontaneously active 'clocks' in its oesophagus and nerve cord. This does not mean that the rhythms cannot be modified: we have seen that they can; but it means that the various activities can take place under conditions in which the corresponding needs can neither arise nor be satisfied. Defaecatory excursions may occur when the rectum is empty (Wells, 1949, fig. 5). Intermittent irrigation may occur when the worm is surrounded by well-aerated water (Wells, 1949, fig. 4). If the interpretation of the proboscis outbursts as feeding cycles is sound, then the feeding pattern occurs when the worm has been reduced to a shred of the oesophagus, all the rest of the body having been removed (Wells, 1937).

With regard to the adaptive significance of this type of organization, it has already been pointed out that under conditions which may arise from time to time in the field, intermittent irrigation cycles based on a 'clock' would have a greater survival value than those based on reflex responses to respiratory needs (Wells, 1949). The function of the presumed feeding cycle is not clear; perhaps it will come to light when the physiology of digestion in *Arenicola* is better understood.

With regard to the intimate mechanism of the cycles, it may be pointed out that both the feeding cycle and the irrigation-defaecation cycle consist of the periodic evocation—or perhaps the periodic suppression—of processes which are in themselves rhythmic. Proboscis activity, irrigation, creeping—in each of these there is a fairly rapid alternation of phases, as in a beating heart or a swimming dogfish. Such an alternation could be due to a spontaneous pace-maker, as in the heart, or to a reflex system in which each phase is the stimulus for the next, as in the dogfish (Lissmann, 1946). But the activity cycles of *Arenicola* involve bursts of rhythm separated by periods of rest; the latter, in the case of the irrigation cycles, may be of half an hour's duration; one can hardly suppose that a reflex chain is the determining factor. The same

argument holds for the oesophageal pacemaker, particularly when slowed up by magnesium excess (Wells & Ledingham, 1940). Here again, the outbursts may succeed each other very regularly, though separated by half an hour or so of complete quiescence. There must be a 'clock' mechanism, presumably of the nature of a relaxation oscillator. Occasionally, under abnormal conditions, an isolated vertebrate or crustacean heart shows grouped beats which greatly resemble the intermittent pattern of an isolated *Arenicola* extrovert (Wells, 1937); it may be that the behaviour of the lugworm's pacemakers represents a normalization of this condition.

Summary

Worms were allowed to burrow in sand in the laboratory. The general form of their burrows resembled that found in the field. Their behaviour was studied by continuously recording the water movements through the burrows for periods up to 3 weeks.

Whenever the worms were feeding from a gradually subsiding cone and piling up castings, as they do in the field, a characteristic cyclical pattern was traced. This was marked by conspicuous diphasic excursions at intervals of about 40 min. Defaecation occurs at the summit of the first phase. By comparison with records got from worms in glass tubes (Wells, 1949), it is inferred that the first phase consists of tailward locomotion to the sand surface, and the second to headward irrigation accompanied by gentle creeping back to the feeding point. The whole cycle is identical with the intermittent irrigation cycle shown in glass tubes.

In the intervals between the defaecation-irrigation outbursts, the tracing often shows a periodicity of smaller amplitude and period. This is probably due to intermittent feeding, under the influence of the oesophageal pacemaker (Wells, 1937). Experiments with dissected worms showed that an inhibitory influence of the oesophageal pacemaker can be detected in the segments responsible for creeping and irrigation.

The behaviour described above occupies about 45 % of the records (covering altogether 72 'worm-days'). Once having begun, it usually continues very regularly for many hours. For the rest of the time, other patterns were seen, which are described in the text.

The application of these results to the worm's life in the field, and the dependance of feeding, irrigation and defaecation on spontaneously rhythmic pacemakers, are discussed.

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ON THE HYDROID OF *EUTIMA GRACILIS* (FORBES AND GOODSIR)

By F. S. Russell, F.R.S.

Director of the Plymouth Laboratory

(Text-fig. 1)

In July 1938 I succeeded in rearing the hydroid of *Eutima gracilis* (Forbes and Goodsir) (also known as *Saphenia gracilis*) from adult medusae which liberated their eggs and sperm in finger-bowls of sea water. These hydroids were only in the primary polyp stage, and I withheld publication hoping to repeat the work

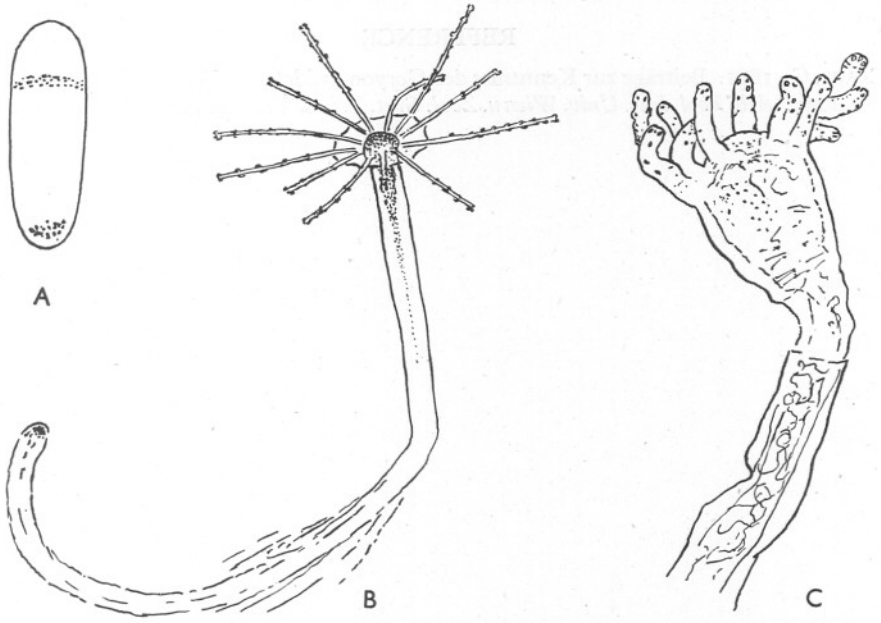

Fig. 1. *Eutima gracilis* (Forbes and Goodsir), Plymouth, 22–23 July, 1938. A, planula, showing position of blue pigment granules; B, primary polyp, showing blue pigment granules at end of stolon and on hydranth at base of tentacles (alive); C, primary polyp, fully contracted (preserved).

later and perhaps rear the hydroid to a more advanced stage. As it is unlikely that I may now have the opportunity of doing this it seems worth while to publish a short account with figures of the polyp.

I have been unable to find any notes I may have made at the time, but the original drawings are available. The planula (Fig. 1A), which is otherwise

colourless, is characterized by a girdle of blue pigment granules near its anterior end and a mass of similar granules situated posteriorly. Fig. 1B shows the primary polyp. The hydranth has a single whorl of twelve filiform tentacles whose bases are united by a membranous web. The hydrocaulus is simple and there is no hydrotheca; the hydranth is thus naked and unable to retract within the perisarc walls which at this stage are very delicate and transparent (see Fig. 1C). At the original point of attachment of the stolon to the substratum the blue pigment granules are still present, and the hydranth itself has blue pigment just below the whorl of tentacles. Unfortunately, I am unable to give measurements.

In its two chief characteristics, namely the presence of a membranous web uniting the bases of the tentacles and the absence of a hydrotheca, this hydroid resembles *Campanopsis* which was described by Claus (1881) as the hydroid of *Octorchis gegenbauri* Haeckel.

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A NOTE ON THE THEORY OF A DWARF RACE OF LOBSTERS ON THE NORFOLK COAST

By Michael Graham

Fisheries Laboratory, Lowestoft

(Text-fig. 1)

At the Annual Conference of Sea Fisheries Committees held in 1947, some members expressed the view that the lobsters being fished at Sheringham belonged to a dwarf race, distinct from the lobsters found at other ports. Such a view, acceptable as it might be to those who have always thought of lobster populations as local, presented certain difficulties to those familiar with Meek's conception of lobsters migrating long distances. Meek (1925) refers to his theory, but has not described evidence to substantiate it.

In this situation, the theory of a dwarf race seemed worth inquiry, and, fortunately, data are available.

The Interdepartmental Committee on Crabs and Lobsters (see its Report on lobsters issued in 1936) instituted investigations of the sizes of the lobsters in various districts in 1938–39, noting separately the sizes of mature females. It was evident that these data would provide the crucial test of the theory of dwarfness, namely an estimate of the size at first maturity in various districts, including that of the supposed dwarfs at Sheringham. English data obtained from these investigations have now been examined.

The data were collected at twelve stations on the English coast. At each station, one fisherman was selected to supply information of the length, sex, and condition of all lobsters in his catches. A copy of the instructions issued to the fishermen, and of the details they were asked to supply, is given in the Appendix (p. 487). (Measuring boards were supplied by the Fisheries Department.) At the same time, Collectors of Fishery Statistics were obtaining statistics of the total landings of shellfish, number of boats used, etc., at the same stations. All English records were returned to the Fisheries Department in London.

These records have now been summarized, port by port, for the period of the investigations—early summer 1938 to autumn 1939—to give distribution by length and sex of marketable and non-marketable lobsters.

Table I shows that, undoubtedly, smaller lobsters were being caught at Sheringham, where, for example, cocks and non-berried hens of less than 8 in. represent 30% of the catch, a higher figure than at any other port. This was doubtless the basis for the belief in a dwarf race of lobsters in this locality, and were this the only statistical guide available, the theory of a dwarf race would not be unacceptable. However, the size-distribution of the mature females

TABLE I. SUMMARY OF RESULTS OF LOBSTER MEASURING (TESTS MADE DURING MAY 1938 TO SEPTEMBER 1939)

District	Local restrictions	Port	Total no. of lobsters examined	Non-marketable (except where in heavy type): Berried hens		Under 8 in. (including soft)		8–9 in. (including soft)		Soft over 9 in.		Marketable over 9 in. (excluding berried hens)	
				No.	%	No.	%	No.	%	No.	%	No.	%
Northumberland Sea Fisheries	9 in. minimum, berried prohibited	Seahouses	5,495	628	11·4	278	5·1	426	7·8	365	6·6	3,798	69·1
		Beadnell	4,740	777	16·4	53	1·1	457	9·6	—	—	3,453	72·9
		Newbiggin	6,367	415	6·5	259	4·1	176	2·7	43	0·7	5,474	86·0
North-Eastern Sea Fisheries	9 in. minimum, berried prohibited	Whitby	5,466	254	4·6	293	5·4	206	3·8	259	4·7	4,454	81·5
Eastern Sea Fisheries	8 in. minimum, berried prohibited	Sheringham	10,856	299	2·8	3,259	30·0	**3,855**	35·5	67	0·6	3,376	31·1
Sussex Sea Fisheries	8 in. minimum, berried allowed	Eastbourne	7,410	**190**	2·6	519	7·0	**1,375**	18·6	3	0·0	5,323	71·8
Devon Sea Fisheries	9 in. minimum, berried allowed	Beer	2,865	**556**	19·4	383	13·4	144	5·0	181	6·3	1,601	55·9
Cornwall Sea Fisheries	8 in. minimum, berried allowed	Polperro	2,401	**193**	8·0	3	0·1	**165**	6·9	13	0·6	2,027	84·4
		Looe	4,603	**106**	2·3	758	16·5	**1,291**	28·0	—	—	2,448	53·2
		Port Isaac	3,370	**539**	16·0	43	1·3	**5**	0·1	—	—	2,783	82·6
Scilly Isles	—		1,227	177	14·4	—	—	—	—	—	—	1,050	85·6
Isle of Man	—	Port Erin	3,265	258	7·9	187	5·7	732	22·4	3	0·1	2,085	63·9

gives the correct solution on this point. In Table II and Fig. 1, which include only mature female lobsters, the figures give the number of berried hens that were taken in each 1 in. group, and show which was the most popular length-group at each port.

It will be observed, in Fig. 1, that at Sheringham, as at all other stations, few berried hens are found of less than 10 in. Furthermore, at six of the ports, including Sheringham, the 10–11 in. group is the largest represented and it shows up conspicuously at still another. The berried hens at Sheringham, then, do not show any marked difference in size from those at other ports. Since these hens are of normal size, it is most unlikely that the lobsters caught off Norfolk belong to a dwarf race.

It may be noted in passing that the same observations make it also unlikely, though not impossible, that the small size is due to stunted growth through local conditions.

The smaller size at Sheringham is most simply expressed as consisting of a higher proportion of young lobsters. This is shown by the following figures, which give the percentage of berried hens in the total catch, extracted from Table I.

North Sea		English Channel		Irish Sea	
	%		%		%
Sheringham	2·8	Eastbourne	2·6	Port Erin	7·9
Whitby	4·6	Beer	19·4	Port Isaac	16·0
Newbiggin	6·5	Looe	2·3		
Beadnell	16·4	Polperro	8·0		
Seahouses	11·4	Scilly Isles	14·4		

It will be observed that only 2·8% of the lobster population caught at Sheringham consisted of berried hens. There are some other interesting points about these figures. The ports are arranged geographically, and the percentage rises from south to north in the North Sea. In the Channel and Irish Sea, there are also some indications of an order in the figures, but with discrepancies, such as the surprising difference between Polperro and Looe, and the high figure at Beer.

From the nature of the data, it is doubtful if much weight can be given at present to these and other points of interest. Only local investigations, properly designed, could give satisfactory information. Points for such investigations are: the apparent absence of any small lobsters at the Scilly Isles; the high percentage of large lobsters shown at Polperro and Port Isaac, in spite of less protection than at some other ports; the high proportion of mature lobsters shown at Beer; and the apparent evidence of difference in the populations fished from the adjoining ports of Polperro and Looe.

The small proportion of fully grown lobsters at Sheringham might be susceptible to either of the following explanations: (i) the stocks at Sheringham may be more severely fished, or (ii) the other North Sea ports, being upstream,

Table II. Length of Berried Lobsters

(The Number Caught, and Percentage, is Shown for each 1 in. Group)

Station		Length (in.) 7–	8–	9–	10–	11–	12–	13–	14–	15–	16–	17–	18–	Total
Seahouses	No.	—	—	15	157	60	215	68	53	40	13	6	1	628
	%	—	—	2·4	25·0	9·5	34·2	10·8	8·4	6·4	2·1	1·0	0·2	100·0
Beadnell	No.	—	—	2	33	102	168	173	175	73	23	2	—	777*
	%	—	—	0·3	4·4	13·6	22·4	23·0	23·3	9·7	3·0	0·3	—	100·0
Newbiggin	No.	1	7	14	64	91	126	81	25	6	—	—	—	415
	%	0·2	1·7	3·4	15·4	21·9	30·4	19·6	6·0	1·4	—	—	—	100·0
Whitby	No.	—	—	17	95	70	63	6	2	1	—	—	—	254
	%	—	—	6·7	37·4	27·5	24·8	2·4	0·8	0·4	—	—	—	100·0
Sheringham	No.	—	1	37	148	74	32	5	—	—	—	—	—	299†
	%	—	0·3	12·5	49·8	24·9	10·8	1·7	—	—	—	—	—	100·0
Eastbourne	No.	—	—	15	81	57	21	12	3	1	—	—	—	190
	%	—	—	7·9	42·6	30·0	11·1	6·3	1·6	0·5	—	—	—	100·0
Beer	No.	—	—	67	237	189	61	2	—	—	—	—	—	556
	%	—	—	12·0	42·6	34·0	11·0	0·4	—	—	—	—	—	100·0
Looe	No.	—	—	13	57	25	10	1	—	—	—	—	—	106
	%	—	—	12·3	53·8	23·6	9·4	0·9	—	—	—	—	—	100·0
Polperro	No.	—	—	8	46	64	29	20	20	6	—	—	—	193
	%	—	—	4·1	23·8	33·2	15·0	10·4	10·4	3·1	—	—	—	100·0
Scilly Isles	No.	—	—	—	8	107	50	8	2	2	—	—	—	177
	%	—	—	—	4·5	60·5	28·3	4·5	1·1	1·1	—	—	—	100·0
Port Isaac	No.	1	—	19	148	280	70	19	2	—	—	—	—	539
	%	0·2	—	3·5	27·5	51·9	13·0	3·5	0·4	—	—	—	—	100·0
Port Erin	No.	—	3	45	106	61	28	9	6	—	—	—	—	258
	%	—	1·2	17·4	41·1	23·6	10·9	3·5	2·3	—	—	—	—	100·0

* Includes 26– size not stated.

† Includes 2– size not stated.

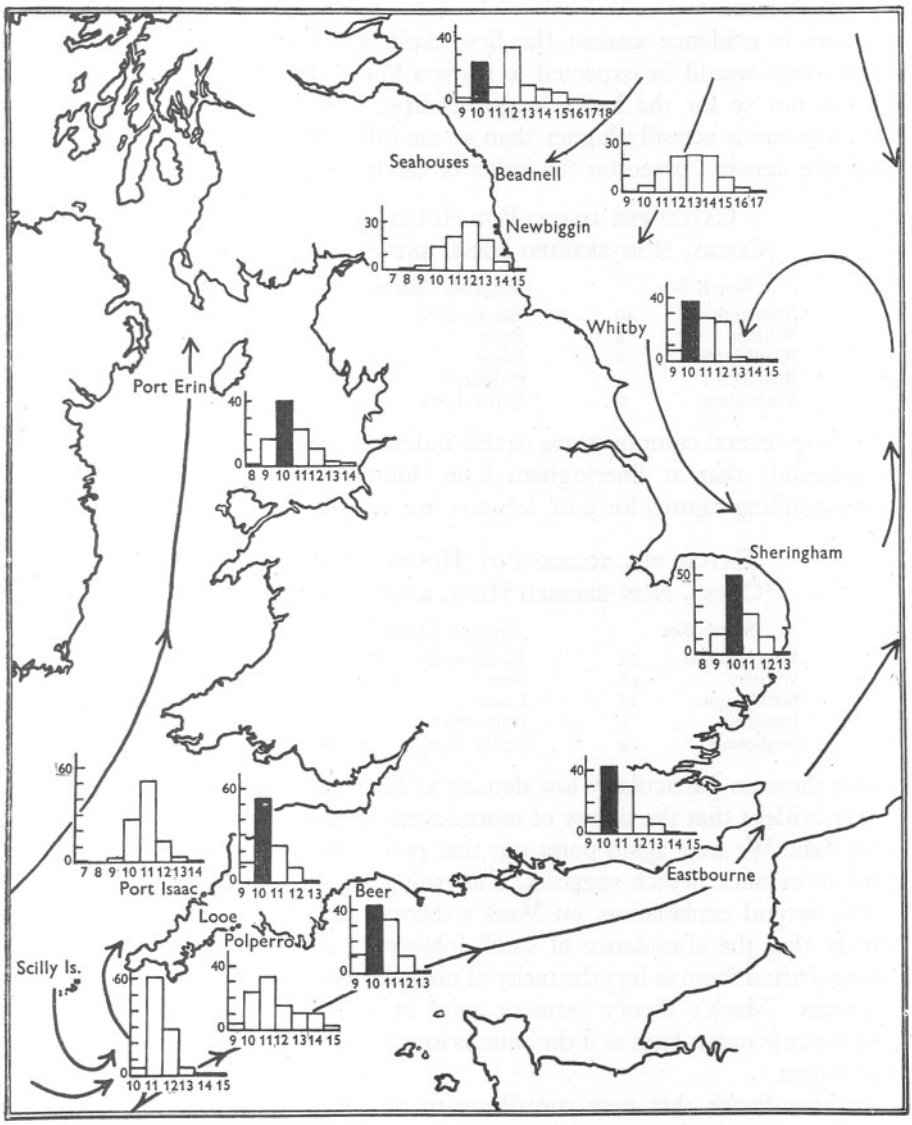

Fig. 1. Lengths of mature female lobsters. The percentage at each length, by inches, reached or passed, of one fisherman's catch of berried hens in 1938 and 1939 is shown for each of twelve ports. At seven of the ports the length group of 10–11 in. shows up conspicuously. The general current system is shown by arrows.

might receive contranatant mature lobsters from the Sheringham district, which is downstream.

There is evidence against the first explanation, because a more severely fished stock would be expected to show a lower absolute density of lobsters. This is not so for the lower length-groups. The density at Sheringham of 8 in. lobsters is actually higher than at the other ports. The following figures show the density, based on the index of catch per pot hour.

CATCH PER 10,000 POT HOURS OF 8 IN. LOBSTERS
(COCKS, NON-BERRIED HENS, AND SOFT OR UNDERSIZED)

North Sea		English Channel		Irish Sea	
Sheringham	40	Eastbourne	69	Port Erin	37
Whitby	2	Beer	6	Port Isaac	0
Newbiggin	2	Looe	18		
Beadnell	3	Polperro	2		
Seahouses	6	Scilly Isles	—		

There are several complications to this index, but its main showing can hardly be gainsaid: that at Sheringham 8 in. lobsters are remarkably abundant. Corresponding figures for 9 in. lobsters are as follows:

CATCH PER 10,000 POT HOURS OF 9 IN. LOBSTERS
(COCKS, NON-BERRIED HENS, AND SOFT OR UNDERSIZED)

North Sea		English Channel		Irish Sea	
Sheringham	21	Eastbourne	124	Port Erin	49
Whitby	26	Beer	15	Port Isaac	4
Newbiggin	18	Looe	20		
Beadnell	9	Polperro	8		
Seahouses	19	Scilly Isles	0		

These show no particularly low density at Sheringham.

It is evident that the theory of more severe fishing receives no support from these data. We may again point out that poor nurture would not explain this great abundance, which suggests, if anything, the opposite.

The second explanation, on Meek's theory, satisfies the data much better: namely that the abundance of small lobsters at Sheringham is due to their having drifted there as fry; the rarity of mature lobsters to their having migrated upstream. Meek's theory seems a good fit to these data, but the order of confidence is not as high as if the conclusions were based on a sufficient marking experiment.

Another factor that may contribute to the proportion of berried hens at various ports, and to the sizes of lobsters generally, is the fact that at the Northumberland ports the return of berried hens to the sea has been encouraged for longer than in other districts, perhaps causing more, and larger, hens to be found there.

I wish to acknowledge the assistance of Administrative and Statistical Officers of the Fisheries Department, in the preparation of this paper.

SUMMARY

The evidence points strongly to the effect that Sheringham fishes the same race of lobsters as ports farther north. The most likely explanation of the smaller average size of the lobsters at Sheringham, which is shown to be due to abundance of small and rarity of large, is that it is in some way natural, and not due to fishing. A neat theory to fit the facts is Meek's, based on the position of Sheringham downstream in the main current system.

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APPENDIX

The following instructions were issued on the front of the log book in which fisherman were to enter details of their catches:

1. Measure the whole catch.
2. Each lobster is to be measured from the tip of the beak to the end of the tail-plate.
3. All measurements are to be made in quarter inches and recorded by the last quarter inch reached or covered: thus, if the division at 10¼ inches is covered but that at 10½ inches is not reached, the measurement is to be recorded as 10¼.
4. Each length is to be recorded in a separate square.
5. The total number of each sort of lobster taken must be entered on the back of the form, including those rejected.
6. The forms, when completed, should be removed from the pads and handed to the Collector of Fishery Statistics on Monday of each week.

The details requested (Form no. **B 438/F.G.**) were as follows:

On the front of the form were columns for entering lengths under the headings of:

Landed: Cocks; hens, not berried; hens, berried. Returned to the sea: berried hens; undersized or soft.

On the back of the form entries had to be made against:

Date... Ground... Depth... Number of pots lifted... Number of hours since pots were set... How many undersized returned to the sea?... How many soft returned to the sea?... How many berried hens returned to the sea?... How many berried hens landed?... How many non-berried hens landed?... How many cocks landed?... Other shellfish taken in pots and landed: crabs... crawfish....

THE OCCURRENCE OF UNUSUAL SPECIES OF CHAETOGNATHA IN SCOTTISH PLANKTON COLLECTIONS

By J. H. Fraser

From the Marine Laboratory, Aberdeen

There are six species of Chaetognatha that are usually taken in Scottish plankton samples from the appropriate localities. These are

Sagitta setosa J. Müller, from lower salinity water such as that found in the southern and central North Sea and the Irish Sea.

S. elegans elegans Verrill, from mixed oceanic and coastal water.

S. serratodentata Krohn, from surface and subsurface warm oceanic water of fairly high salinity.

S. maxima (Conant), from cold deep water.

Eukrohnia hamata (Möbius), from cold deep water.

Sagitta lyra Krohn, from warm deep water.

All are valuable indicator species (Meek, 1928; Russell, 1935, 1939; Fraser, 1937, 1939). Of these, the first five have occurred in somewhat varying numbers and distribution according to hydrographic conditions every year since at least 1935, except possibly during the period 1940–45 when no investigations were made. *S. lyra* has been taken in most of these years, but was not found in 1935, 1936 or 1937. It was, perhaps, most abundant in 1948, and one specimen was taken in that year from the Moray Firth, though its presence there must be regarded as distinctly unusual.

Spadella cephaloptera (Busch) is widely distributed throughout the Scottish area as a bottom-living form and is therefore not included here as planktonic.

There are several other species which occur only occasionally in the Scottish plankton either as individual specimens or in small numbers in specialized localities: for convenience these may be termed unusual species. They are as follows.

Sagitta elegans arctica Aurivillius, which has occurred in several years in the Faroe-Shetland Channel associated with the community characterized by *Eukrohnia hamata* and *Calanus hyperboreus*.

Sagitta hexaptera d'Orbigny, a warm deep water species, which was found in the Faroe-Shetland Channel in 1935, 1939 and 1948 in conditions usually associated with *S. lyra*.

S. planctonis Steinhaus. This species was not recorded until 1948 when several specimens were taken in areas over deep water off the edge of the continental shelf west of the Hebrides. As this area has not yet been extensively sampled by the Scottish research vessels, it may be more common there than the number of records to date would indicate.

S. bipunctata Quoy & Gaimard, which was found off Cape Wrath in March 1949. There has been a good deal of controversy about this species, until the past decade or two *S. elegans* and also *S. setosa* were frequently recorded as '*bipunctata*'. *S. bipunctata* is normally a warm water species and the occurrence of three specimens off Cape Wrath—58° 50′ N. 6° 26′ W.—on 2 March 1949 is of considerable interest. Apart from misnomers, these are believed to be the first records of this species in Scottish plankton samples. Although generally recognized as of widespread distribution in the warmer seas, it has previously been recorded only as far north as the Azores (Burfield, 1930).

The Cape Wrath specimens, which are 9, 10 and 13 mm. in length, are all immature and the *vesiculae seminales* are only slightly developed so that their mature shape and position cannot be ascertained with certainty. They appear to be nearer the posterior fin than described by Ritter-Zahony (1911) and Burfield (1930), but agree with the description by Michael (1911), and they might well extend to the tail fin when fully mature.

Like Michael (1911) and Burfield (1930), I find no trace of a local epidermal thickening between the *vesiculae seminales* and the posterior fin such as that described by Tokioka (1939) from Japanese specimens and by Thomson (1947) from Australia. The present specimens, except for maturity, resemble some from Bermuda and South Africa that I had the opportunity of seeing, through the courtesy of Mr F. S. Russell, and Dr S. G. Gibbons.

Krohnitta (*Eukrohnia*) *subtilis* (Grassi). A single specimen of *K. subtilis* was taken in a subsurface net (50 m. depth) from 56° 50′ N. 90° 50′ W. some 80 miles west of the Hebrides, where the depth exceeded 1800 m. This record is also believed to be the first from the Scottish area. Many bathypelagic copepoda, together with *Sagitta planctonis*, *S. lyra* and *S. maxima*, and other deep-water species, were also found at this station.

There are several other species that might be expected to occur occasionally off the west coast of Scotland and in the Faroe-Shetland Channel, but which have not so far been identified from plankton samples taken by Scottish research vessels. They are *S. macrocephala*, *S. decipiens* and *Eukrohnia fowleri* (see Russell, 1938, and the literature referred to therein).[1]

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[1] Since writing this, both *Sagitta macrocephala* and *Eukrohnia fowleri* have been taken in oblique hauls from 1000 m. and 1500 m. to the surface in positions west of the Hebrides in June 1949.

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THE STRUCTURE AND MODE OF LIFE OF THE PYRAMIDELLIDAE, PARASITIC OPISTHOBRANCHS

By V. Fretter, Ph.D. and A. Graham, D.Sc.

From the Department of Zoology, Birkbeck College, University of London

(Text-figs. 1–12)

CONTENTS

Introduction

The family Pyramidellidae makes a brave show in fauna lists and similar publications: Winckworth (1932) includes at least forty-one species in his list of British marine molluscs, and Ankel (1936) mentions twenty-seven in the fauna of the North and Baltic Seas. Of the thirty-nine different species, however, of which descriptions are given by Jeffreys (1867), one-third are identified only in respect of their shell characters and nothing at all is said of the appearance of the soft parts of the mollusc; while many volumes, such as the fauna list of the Marine Biological Association (1931), enter their records of species of *Odostomia* as 'dead shells only'. It is thus largely true that the pyramidellids are a conchologist's group and that a marine naturalist of considerable experience may not have set eyes upon a member of that family. This is to some extent explained by the fact that all the Pyramidellidae are small, not to say minute, and are not conspicuously coloured, and by the fact that many of them are not particularly common. But one other factor which contributes largely to the general obscurity surrounding this group of gastropods is that each species appears to have its own extremely specialized habitat, and in ignorance of this collecting will not produce any specimens of that particular sort. It has long been known that one species, *Odostomia eulimoides* Hanley, is to be found 'chiefly (if not only) on the ears of *Chlamys opercularis* and *Pecten maximus*', in Jeffreys's words, and this habit of restricting its occurrence to

one special location appears to be a characteristic of every species of the family. Each one lives in definite relationship to another animal, usually a sedentary polychaete or mollusc, and, presumably, were one to know the particular animal in relation to which each species lives, one could then search for the pyramidellids with fair measure of success. This habit has long been known for a few species—since Jeffreys's time (1867) for *Odostomia eulimoides*, and since 1914 for *O. scalaris* Macgillivray (=*rissoides* Hanley), when Pelseneer (1914) described this species as living in the neighbourhood of, or actually on, the shell of *Mytilus edulis*. It was also known as a result of work by Pelseneer (1914), Ankel (1938), and Rasmussen (1944) that these molluscs probably fed on the animals on which, or in the neighbourhood of which, they dwelt, but the details of the feeding process and of the alimentary system were not known. All that appeared certain was that the Pyramidellidae possessed no radula, for which reason Thiele (1929) classified them in the stirps Aglossa of his order Mesogastropoda.

That this classification might not be accurate was first indicated by Thorson (1946), commenting on Lebour's description (1932) of the larvae of *Odostomia*, which she claimed were unmistakably recognizable by reason of their sinistral shell, which in many species persists throughout life on top of the dextral adult shell. This sinistral larval shell, according to Thorson (1946), is regularly found in the larvae of opisthobranchs, and on this basis he suggests, reviving the much older ideas of Mørch (1865), that the Pyramidellidae are, if not actually opisthobranchs, very closely allied to them. This, however, has been denied by Pelseneer (1899).

The work described in the following pages, carried out at the marine laboratories at Plymouth and Cullercoats as well as in London, shows how the gut of *Odostomia* species is built and functions, describes the habitat and feeding of a number of different species, the main plan of the mantle cavity, nervous and reproductive systems, the breeding habits and veligers, and concludes, on the basis of this, that the Pyramidellidae should in fact be classified along with the opisthobranchs.

We wish to record our thanks to Mr F. S. Russell, F.R.S., and to Dr H. O. Bull for the facilities provided at Plymouth and Cullercoats respectively, to Mr R. Winckworth for checking identifications, and to Birkbeck College for a grant.

The following description, unless otherwise stated, applies to the genus *Odostomia* and to the genus *Chrysallida*.

External Features

The Pyramidellidae are all small animals and, so far as external appearances are concerned, they look like any typical monotocardian prosobranch in that the visceral hump is large, wound in a dextral spiral, and enclosed in a stout,

calcareous shell into which head and foot may be completely withdrawn when the animal is disturbed. The mantle cavity is like that of any prosobranch, too, facing anteriorly and opening to the exterior over the head and almost equally to left and right. There is no clear tendency for the mantle to extend beyond the mouth of the shell except at one point on the right, where it is produced into a short spoon-shaped process.

The foot is short, with a creeping sole, broad anteriorly and tapering posteriorly where, dorsally, it carries a lightly coloured operculum, which sends several tooth-like processes some distance into the flesh of the foot as if to provide greater anchorage for the columellar muscle. Along the mid-ventral line of the sole posteriorly there is a deep longitudinal groove and at the anterior end, which is drawn out laterally into slight points, lies the mouth of the pedal mucous gland, which is well developed, not only filling the central part of the foot with mucous cells but thrusting further lobes into the head, where they lie around the front end of the alimentary canal and the nerve ring. The lateral surfaces of the foot show no outgrowths of any kind.

The foot is covered with a columnar epithelium, strongly ciliated over the entire sole, but with only scattered ciliated cells over the remainder of the surface. Under the epithelium lie large numbers of gland cells, the secretion of which is not mucous. These are spherical in shape, 20μ in diameter, and they lie in the connective tissue of the foot. Their contents are finely granular and they are discharged by ducts passing between the epithelial cells. In two special areas a second type of gland cell occurs, packed together so as to produce a lateral glandular streak on either side of the foot parallel to the edge of the sole, but placed a little more dorsally, in the same position as described by Yonge (1947) for *Patella*. The cells (Fig. 2, GC) here are also spherical and lie in the subepithelial connective tissue, opening to the exterior by ducts running between the epithelial cells, but their contents consist of large numbers of spherules which stain strongly with basic stains when ready to be discharged. Frequently smaller granulations (G) lie at the centre of the spherules. A basket-work of muscles (MS) lies around each cell, the fibres running from under the epithelium to end in vertical bundles of muscle (DMF) deeper in the foot, and it seems probable that the contents of the gland cells are squeezed out through the ducts by contraction of this muscular network. In the epithelium through which the cells of the lateral glandular streak open lie scattered cells (CC) bearing bundles of long cilia (30μ). These are perhaps sensory in nature as similar ones appear regularly in the epithelium which covers the surface of the cephalic tentacles (see below), and their presence would suggest that the lateral glandular streak is some kind of sensory organ.

From the opening of the pedal mucous gland the anterior dorsal surface of the foot curves upwards and backwards on to the head, but before that part of the body is reached the foot projects outwards into a thin fold running transversely from one side of the body to the other and slightly indented in the

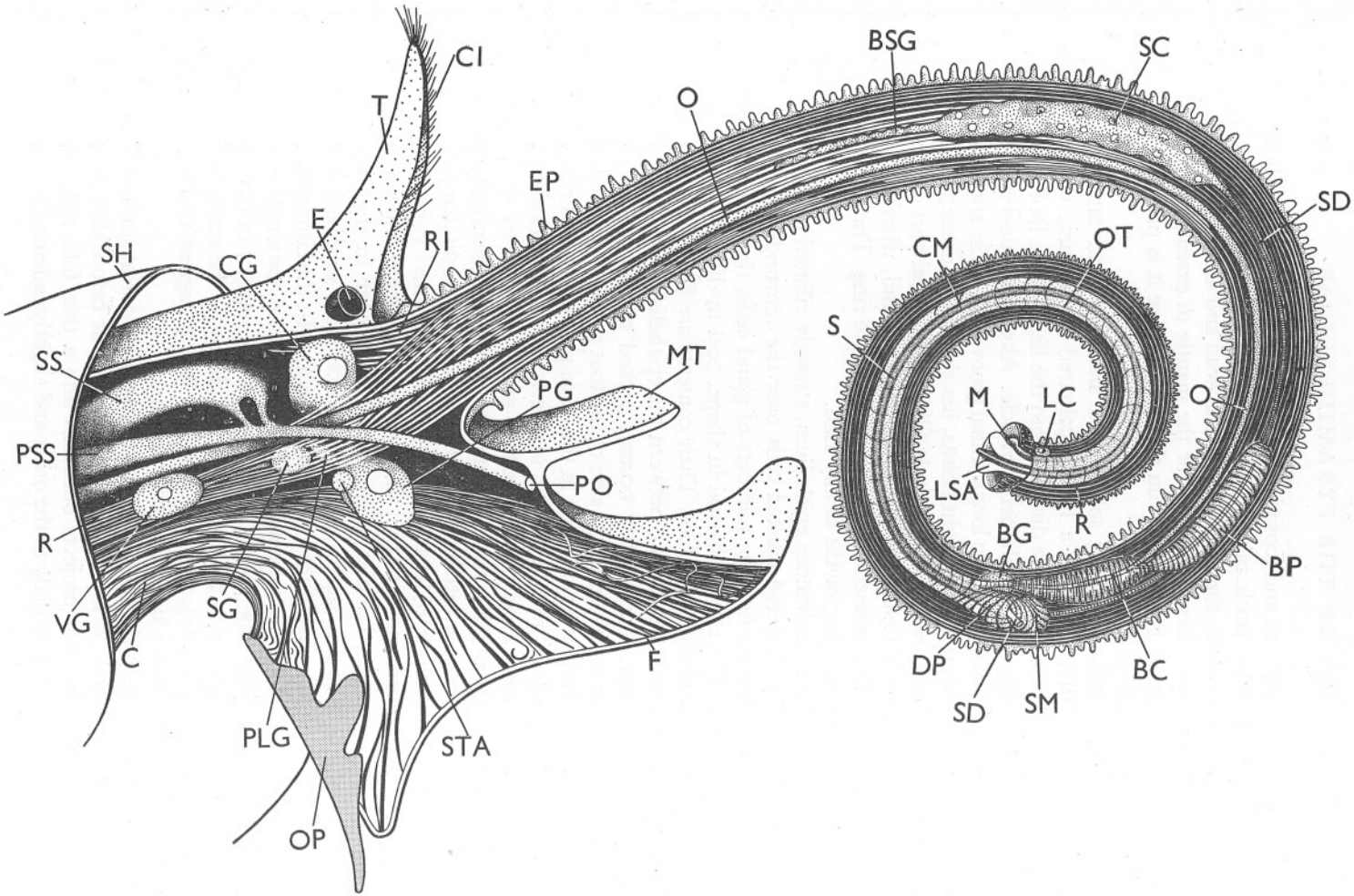

Fig. 1. *Odostomia unidentata*. Sagittal half of the anterior end of a specimen protruding head and foot from the shell, and with the proboscis everted. The position of this is diagrammatic. The haemocoel is black. × *c.* 96. BC, buccal cavity; BG, buccal ganglion; BP, buccal pump; BSG, bladder of salivary gland; C, columellar muscle; CG, cerebral ganglion; CI, sensory cirri; CM, circular muscles; DP, dorsal pouch of buccal cavity; E, eye; EP, epithelial papilla; F, foot; LC, labial commissure; LSA, lip of stylet aperture; M, mouth; MT, mentum; O, oesophagus; OP, operculum; OT, oral tube; PG, pedal ganglion; PLG, pleural ganglion; PO, opening of penial sheath; PSS, penial sheath; R, retractor muscle of introvert; RI, protractor muscles of introvert; S, stylet; SC, cell of salivary gland; SD, salivary duct; SG, suboesophageal ganglion; SH, shell: SM, muscles moving stylet; SS, sperm sac; STA, statocyst; T, tentacle; VG, visceral ganglion.

mid-line: this is the mentum (Fig. 1, MT), a structure also to be found in the family Eulimidae (Kœhler & Vaney, 1908). At first sight it looks as if it were a snout, with the mouth at its tip, and the habit which *Odostomia* has of carrying it in front of the tip of the sole of the foot, in contact with the substratum, lends support to that view. Nevertheless, this structure is pedal, carries no openings at its apex and has no special histological characteristics, resembling in all respects other unspecialized parts of the foot. Ventral to this mentum, slightly to the right of the mid-line, is an opening (Fig. 1, PO), that of the penial sheath.

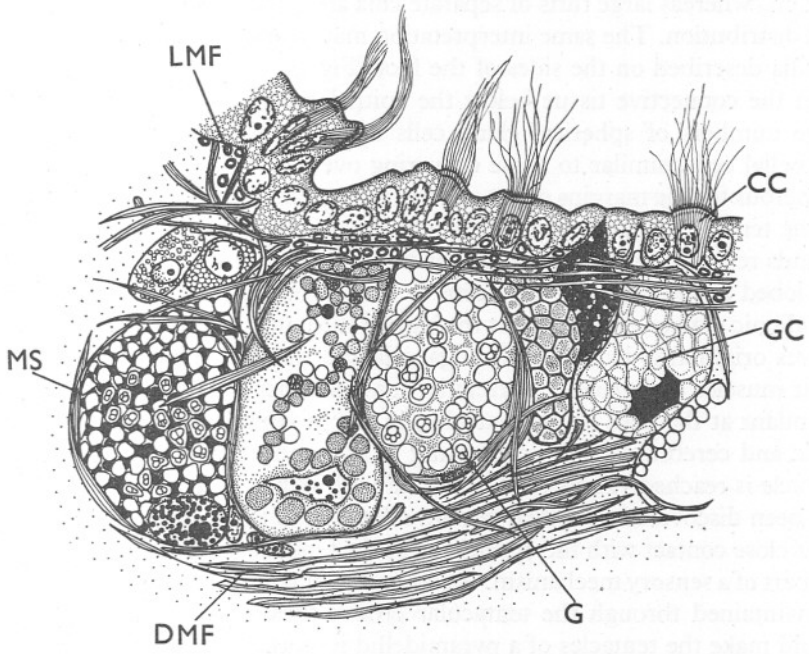

Fig. 2. *Odostomia unidentata*. Transverse section through lateral glandular streak. × 600. CC, ciliated cell; DMF, dorsoventral muscles of foot; G, granulation; GC, gland cell; LMF, longitudinal muscles of foot; MS, muscles discharging secretion.

The head carries a pair of tentacles (T), a pair of eyes (E) and a pair of apertures—and there is something unusual about each of these structures. The tentacles are shaped like the ears of a donkey or rabbit, with a concave outer surface and, like the ears of these animals, they may be moved so that the concavity may face in a variety of directions. The cavity is lined by an epithelium, reminiscent of that covering the lateral parts of the foot: the cells are mainly covered with short, strong cilia which create a current of water that swirls into the concavity of the tentacle from the outer side and passes towards the mid-line as noted by Alder (Jeffreys, 1867). When *Odostomia* is examined alive and feeding these tentacles are seen to project forwards from the head,

diverging slightly, with the concavities facing forwards, downwards and slightly outwards. The movement of particles in the water shows that the cilia on the grooves draw a strong current in from over a considerable volume of water. Examination of living molluscs will also show the presence of long spike-like cilia projecting motionless from the surface and edges of the groove, most abundantly near the summit of the tentacle, which often appears fringed as a result. These, too, were noted by Alder. They seem to be sensory in nature and are probably compound structures, made by the functional fusion of many cilia, since in sections of fixed material no comparable cilia may be seen in these regions, whereas large tufts of separate cilia are to be found with similar length and distribution. The same interpretation may probably be applied to the tufts of cilia described on the sides of the foot (Fig. 2).

In the connective tissue below the epithelium of the tentacles there occur large numbers of spherical gland cells opening by ducts lying between the epithelial cells, similar to those occurring over the foot. They are sufficiently numerous for the margins of the spheres to be practically in contact. The centre of the tentacle is filled with a padding of connective tissue round the muscle strands responsible for the tentacular movements, but in addition to this there are lobed groups of cells that seem to be nervous and of the nature of small ganglionic masses. They arise at the base of the tentacle from a number of small nerves originating in the cerebral ganglia and they lie, mixed with the tentacular muscles and glands, in irregular masses under the epithelium, especially abundant at the base of the tentacles, in the proximity of the eyes and of the optic and cerebral ganglia, decreasing in size and number as the apex of the tentacle is reached. Their connexions (if any) with cells in the epithelium have not been discovered, but their certain relationship to the rich innervation, and their close contact with the epithelium of the tentacle suggest forcibly that they are part of a sensory mechanism. In conjunction with the stream of water which is maintained through the tentacular groove these cells and nervous masses would make the tentacles of a pyramidellid important organs for the sampling of the water in the neighbourhood of the animal.

The eyes of *Odostomia* and other pyramidellids lie close together under the skin of the head on the *median* side of the tentacles, instead of on stalks at the outer side as is usual in prosobranchs.

On the under side of the head lies the inconspicuous mouth. The opening of the penial sheath (Fig. 1, PO) is present in every individual, as all these pyramidellids are hermaphrodite. From it a ciliated tract runs backwards along the right side of the head, ventral to the base of the tentacle, on to the floor of the mantle cavity to end at the single genital opening. Occasionally this tract is elevated above the general surface of the foot and head, over which it runs, so as to form a slight ridge. This is variable and is due to local muscular contractions.

Although the mantle cavity is narrow in a dorsoventral direction it is, never-

theless, capacious, because of its width and the length to which it extends along the front of the visceral hump. To it discharge (i) the genital duct, in *Odostomia* about one-third of its total depth inwards from the mouth, lying at the bottom of a deep groove on the floor to the right near the mid-line; (ii) the kidney, by a minute pore projecting downwards from the roof, at the apex of a small papilla still deeper in the cavity; and (iii) the anus, a very small opening at the innermost end of the mantle cavity, on the floor, at the extreme left side (Fig. 11, A).

The inner half of the mantle, which forms the roof of the inner part of the mantle cavity, is more or less equally occupied by two structures—the kidney, which, as in the small gastropods described by Fretter (1948), lies entirely in this position and not in the visceral mass at all, and which is placed immediately anterior and dorsal to the anus, lying on the left side; and, secondly, a vast glandular field, which extends on the right side to the innermost end of the mantle cavity. A narrow line of epithelium without glandular cells runs between the left edge of this area and the kidney, and a similar strip occupies the extreme right hand of the mantle cavity, so that the glandular region is clearly separated from neighbouring structures. Along its right-hand edge there runs a narrow strip—only about a dozen cells in breadth—of strongly ciliated epithelium, and this runs forward from the anterior end of the main glandular region to the mouth of the mantle cavity, which it reaches dorsal to and to the right of the head.

The inner half of the floor of the mantle cavity is less complex in its arrangement than the roof. The anus and genital opening lie on it and from the lips of the anus a glandular streak stretches at first across the mantle cavity from left to right and then forwards along the floor, passing to the right of the genital opening, and keeping more or less directly under the glandular area which lies on the roof of the mantle cavity, but clearly separated from it by the non-glandular strip of cells along the extreme right-hand margin of the mantle cavity. As in the dorsal area a strip of ciliated cells runs along the right-hand edge of the ventral glandular region, the two lying more or less one above the other, and this ciliated strip, too, continues to the mouth of the mantle cavity. Occasionally the two strips appear to be connected one to the other at the innermost end of the mantle cavity, but in other individuals they are clearly separate. The general arrangement is similar to what was described by Fretter (1948) in *Omalogyra* and *Rissoella*.

The outer half of the mantle is simpler than the inner and contains no special organ apart from the extensions of the ciliated strips already referred to. At no other place is the epithelium which covers it ciliated, and except at the mantle edge there are no gland cells; the epithelium is low, cubical or even squamous in character and permits ready exchange of respiratory gases between the water in the mantle cavity and the very rich bed of blood vessels which the mantle itself contains. This region would also appear to be a site of excretion, as numbers of amoeboid cells, the cytoplasm of which is loaded with spherules,

may be seen in the blood spaces and in the act of passing out into the mantle cavity. These seem to be a source of great attraction to ciliates which regularly occur in large numbers in the mantle cavity of *Odostomia*, since wherever one of these cells is found in a pallial blood space or making its way through the epithelium of the mantle, there will always be found at least one ciliate hovering directly over it, presumably for the sake of ingesting the material which the cells are about to empty into the mantle cavity.

At the mantle edge a greater degree of histological differentiation has occurred: the cells of the epithelium are columnar and there are considerable numbers of gland cells lying in the pallial thickness. Some of these are simple mucous cells, but there are others the nature of the secretion of which is unknown. The greatest degree of histological complexity, however, occurs in the two glandular areas, dorsal and ventral. The former is composed of two types of gland cell: one is a mucous cell (60 μ), tall and wedge-shaped; whilst the second secretes spherules of a material which stains very darkly with iron haematoxylin when the secretion is being elaborated, but much less intensely at the time of liberation. These cells are of the same height as the mucous cells but are columnar in shape. In some parts of the field the two types occur in equal abundance and more or less alternately, but there are other regions, where mucous cells are most abundant, or even the sole type found; whereas along the edge of the glandular area that abuts upon the kidney mucous cells are practically never to be seen and the cells are all of the other type. This is also the kind of gland cell which predominates in the ventral fold, though here, too, mucous cells are mingled with them and, in the neighbourhood of the lateral tract, are more frequent. In the neighbourhood of the genital opening there occurs a grouping of a third variety, the cytoplasm of which is crammed with vacuoles, each filled with a mass of brown-coloured material. These are packed so tightly together that they are compressed into irregular, polygonal shapes staining erratically with iron haematoxylin. Whether they are ever shed, or whether they accumulate in the cells is not known, but they make a conspicuous linear mark, usually brown-orange or pink in colour, on the body of the mollusc—the anal gland of Lebour (1932), or larval kidney of Rasmussen (1944)—which is often visible by transparency through the shell, as in *Rissoella* Fretter (1948).

The Alimentary Canal

The aperture which lies on the under side of the head is not the true mouth, but merely the opening of an introvert at the base of which the true mouth is placed, so that the animal is provided with a proboscis of the acrembolic type. When retracted, the introvert is flung into an S-shaped loop, the anterior end passing through the nerve ring, and the bulk of the loop coiled posteriorly in the haemocoel. At its innermost end lies the mouth, which is placed in all pyramidellids on a circular sucker. The sucker is shaped rather like a candle-

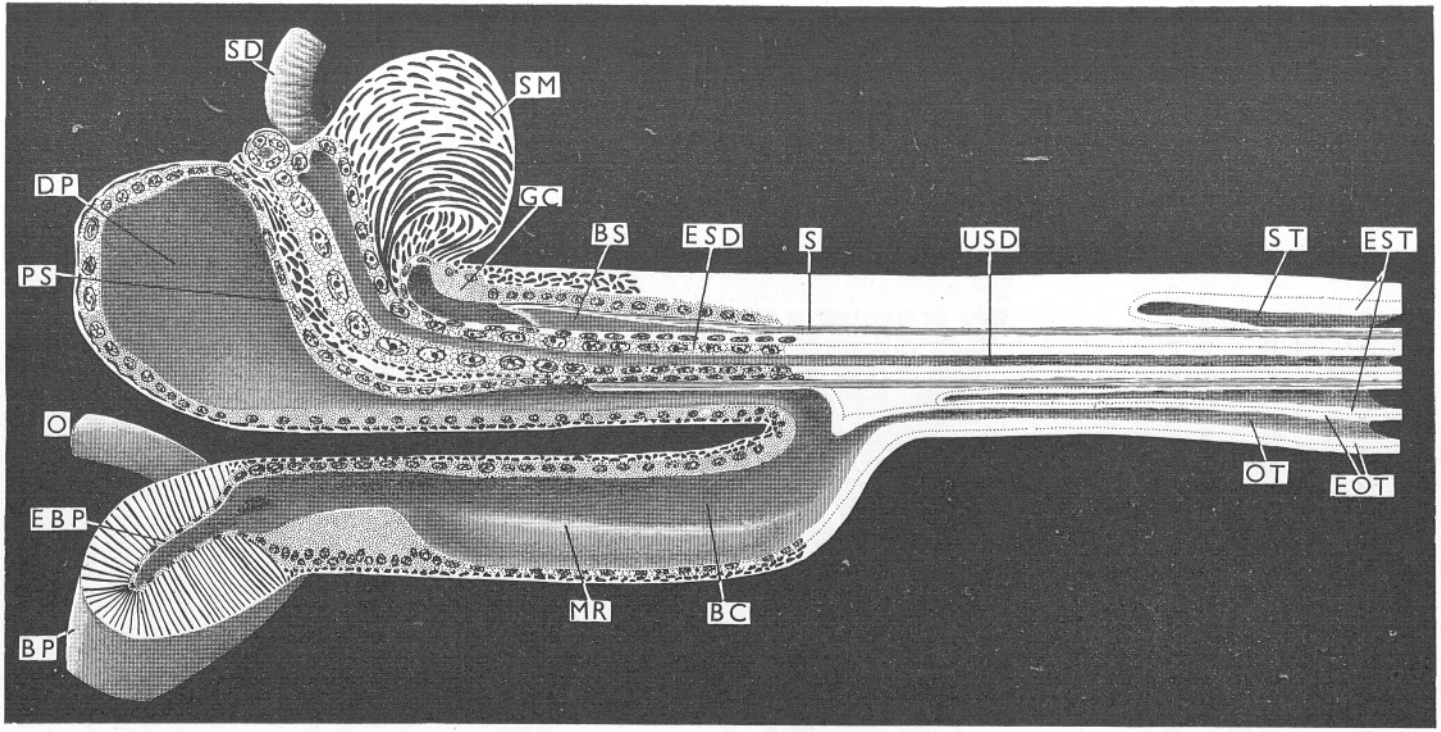

Fig. 3. *Odostomia*. Stereogram of a sagittal half of the base of the stylet and associated structures. ×600. BS, base of stylet; EBP, epithelium of buccal pump; EOT, epithelium of oral tube; ESD, epithelium of salivary duct; EST, epithelium of stylet tube; GC, gland cell; MR, mucous ridge; PS, projection containing salivary ducts; ST, stylet tube; USD, united salivary ducts. Other letters as in Fig. 1.

stick, with an elevated central region as well as raised edges. In *Odostomia* spp. the mouth (Figs. 1 and 4, M) lies about half way between the centre and the edge of the sucker on the ventral side and is a narrow slit-like opening crescentic in shape. In addition to this opening there is a second lying in the centre of the sucker, with raised lips, and corresponding to the part of the candlestick into which the candle would be placed: this (Fig. 4, SA), as will be shown later, is merely a separated portion of the mouth, through which the animal can thrust a sharp spike-like stylet.

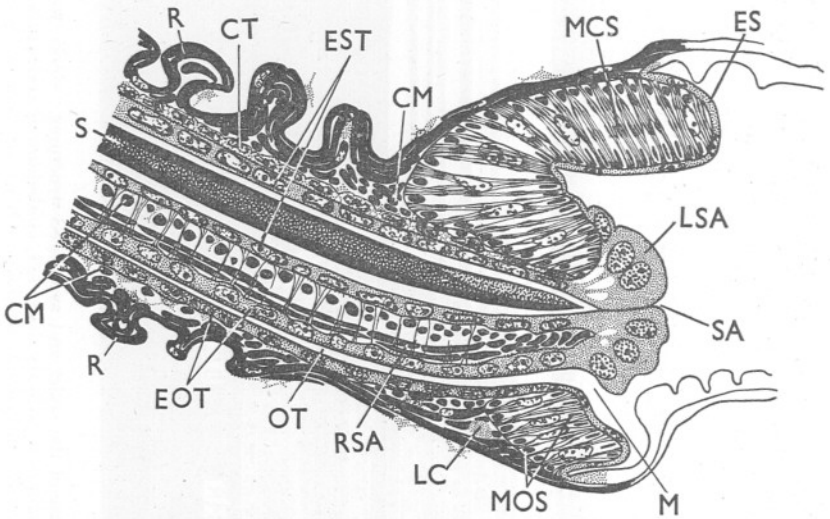

Fig. 4. *Odostomia plicata*. Longitudinal section through the mouth and initial part of the alimentary canal. ×600. CT, connective tissue; EOT, epithelium of oral tube; ES, epithelium over sucker; EST, epithelium of stylet tube; MCS, muscles arching sucker; MOS, muscles flattening sucker; RSA, retractor muscle of lips of stylet aperture; SA, stylet aperture. Other letters as in Fig. 1.

From the sucker there extends inwards an elongated initial section of the alimentary canal which will be shown later to be the oral tube. The main channel in this is the space (Figs. 1, 3 and 4, OT), exceptionally narrow in a dorsoventral direction, which runs backwards from the mouth. Near its inner end the oral tube gives off a large, dorsally placed, blind pouch (Figs. 1 and 3, DP), which is part of the buccal cavity, and then its main channel turns towards the remainder of the buccal cavity and the oesophagus (Figs. 1 and 3, O). From its mid-dorsal point there projects into the pouch a long finger-like process (Fig. 3, PS), along the centre of which runs a single duct (Fig. 3, USD) formed by the fusion of the two ducts (SD) from the pair of salivary glands. The wall of the pouch into which this structure projects is, at the innermost end, a naked epithelium of rather flattened cells which is reflected on to the surface of the projection carrying the ducts of the salivary glands. Over a considerable area

of the ventral wall of the pouch and, to a lesser extent dorsally, the cells are frequently mucus-secreting, whilst in the neighbourhood of the connexion to the rest of the buccal cavity, the epithelium is cuticularized, this production

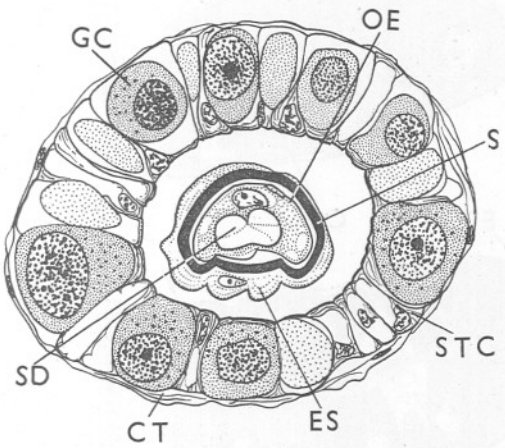

Fig. 5. *Turbonilla jeffreysii*. Transverse section through the stylet and oral tube. ×600. CT, connective tissue; ES, epithelium around stylet; GC, gland cell; OE, outer epithelium; S, stylet; SD, salivary duct; STC, supporting cell.

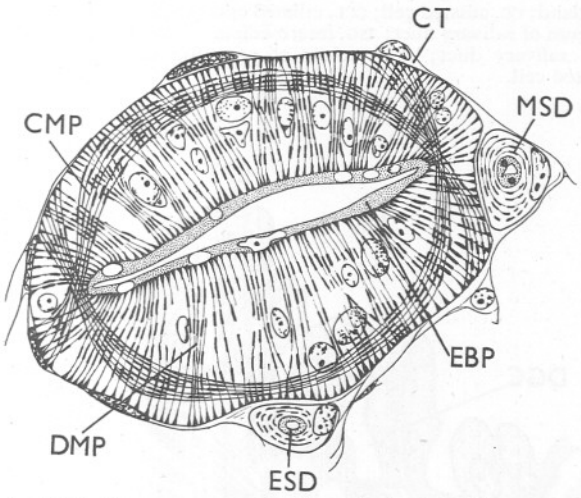

Fig. 6. *Odostomia lukisii*. Transverse section through the buccal pump and salivary ducts. ×600. CMP, constrictor muscles of buccal pump; CT, connective tissue; DMP, dilator muscles of buccal pump; EBP, epithelium of buccal pump; ESD, epithelium of salivary duct; MSD, circular muscles of salivary duct.

of cuticle spreading along the dorsal wall of the pouch to the region of the narrow belt of mucous cells near the origin of the salivary process, but affecting the lateral walls to a lesser extent. The cuticle remains attached to the underlying epithelium dorsally and dorsolaterally, where the histological picture

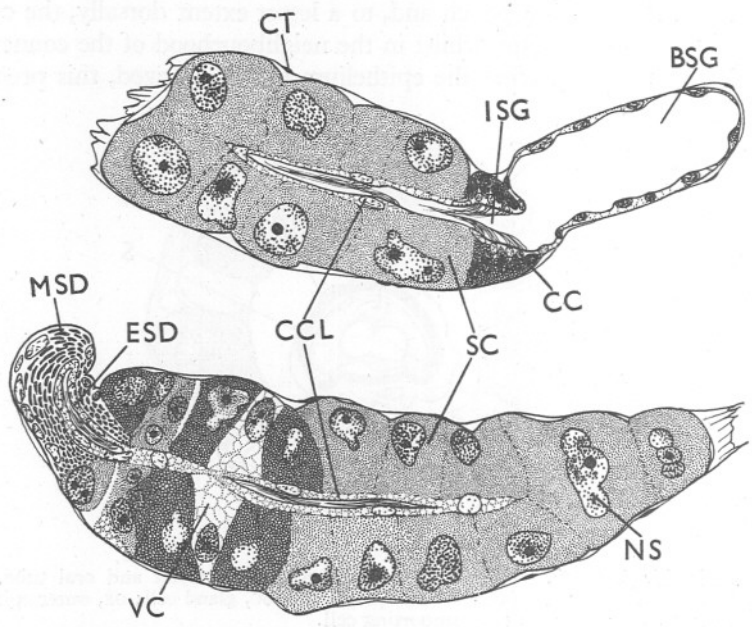

Fig. 7. *Odostomia lukisii*. Longitudinal section through the salivary gland. × 600. BSG, bladder of salivary gland; CC, ciliated cell; CCL, ciliated epithelium of lumen; CT, connective tissue; ESD, epithelium of salivary duct; ISG, intermediate section of salivary gland; MSD, circular muscles of salivary duct; NS, nucleus of secreting cell; SC, cell of salivary gland; VC, vacuolated cell.

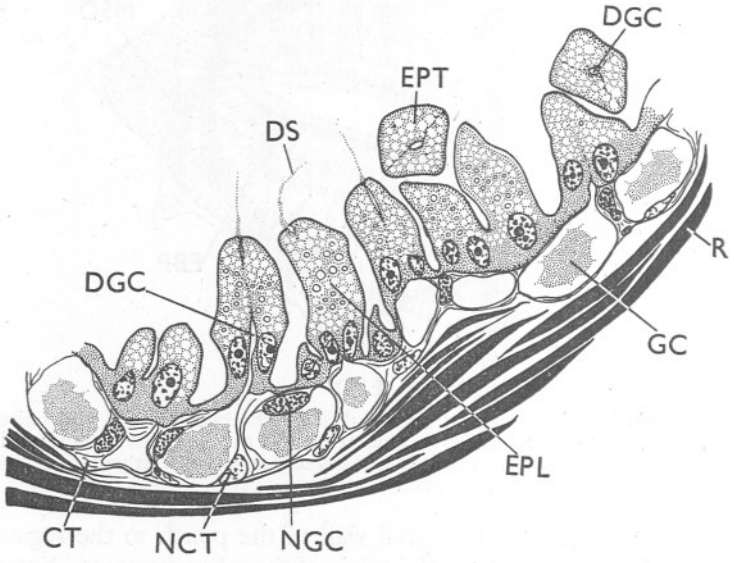

Fig. 8. *Odostomia unidentata*. Longitudinal section through a portion of the wall of the introvert. × 600. CT, connective tissue; DGC, duct of gland cell; DS, secretion discharged to lumen; EPL, epithelial papilla in longitudinal section; EPT, epithelial papilla in transverse section; GC, gland cell; NCT, nucleus of connective tissue cell; NGC, nucleus of gland cell; R, retractor muscles of introvert.

shows obviously that it is being secreted, but more ventrally it grows freely into the cavity of the pouch, losing contact with the epithelium, and embracing, as it does so, the long projection in which the salivary ducts are running. The two edges of the cuticle actually grow around this until they meet mid-ventrally in the cavity of the pouch near its mouth. In this way the common salivary duct, lying in the long process which grows out from the innermost part of the wall of the pouch, comes to be enclosed in a tubular cuticular sheath which is being continually added to at its base dorsally and dorsolaterally. On reaching the anterior end of the pouch, in *Odostomia*, this tubular cuticular structure plunges into the dorsal wall and runs for a short distance through the muscles and connective tissue of that wall. Soon, however, it emerges into a second space and runs along this to the sucker, where its anterior tip has already been described as projecting from the more dorsal of the two apertures which are placed thereon. At the base of this outer cavity the epithelium which lines it is reflected over the surface of the stylet, but this layer of cells is soon lost, and the stylet then lies naked in the cavity.

The epithelium which lines the oral tube (Figs. 3 and 4, EOT) is not remarkable in most places: it is a low cubical, almost squamous, epithelium with gland cells restricted to the dorsal wall of the space in which the stylet lies. These are mainly mucous, though a few secreting chromophile granules also occur. Sometimes these cells and the connective tissue cells around them lie under the dorsal epithelium of this cavity in such a regular way as to suggest the presence of a second epithelium in that position (Fig. 4, CT). At the lips of the mouth, and at the opening dorsal to that, through which the stylet is projected, this epithelium turns outwards over the concavity of the sucker, where it forms a very low and featureless layer of cells (ES), continued at the margin into the epithelium that lines the introvert. Only around the edge of the stylet aperture in the centre of the sucker is there any change in the character of the cells: here they are greatly enlarged (LSA), with vacuoles at their base, and large nuclei placed centrally in a mass of dense cytoplasm, so as to form a thick and rather fleshy looking rim to the opening.

The cells which line the innermost part of the introvert are shown in Fig. 8. They are raised in groups at regular intervals to form papillae, so that when the proboscis is thrust out and the lining of the introvert becomes the outer epithelium of the proboscis, it has a furry appearance (Fig. 1). Each papilla, in *Odostomia*, consists of three or four cells lying side by side; they are crushed together in the centre of the papilla where they abut against each other, but smoothly curved towards the exterior, so that each papilla rises from a narrow base, swells to a greater breadth and then tapers to a blunt apex. Up the centre of each papilla, through a long tube that seems to be formed along the line of meeting of the cells, runs a duct (Fig. 8, DGC) from a subepithelial gland placed in the connective tissue of the wall of the introvert (GC); and this opens by a minute apical opening to the lumen of the introvert when the

proboscis is withdrawn, or directly to the exterior if the proboscis be extended. The glands are spherical in shape and their contents are finely granular, reminiscent of those that lie in the outer surface of the head and on the sides of the foot—and as the introvert has presumably arisen by the in-pulling of a greatly extended snout the glands are in fact probably the same: it is their special way of opening in relation to the other cells of the epithelium which is of interest. The cytoplasmic organization of these cells, too, is in some ways specialized: the nuclei are always large and placed basally side by side in the narrow neck of the papilla. The cytoplasm is dense and contains a number of small spherules lying in irregular vacuolations which do not stain differently from the other parts of the cytoplasm, but the most superficial layer is distinctly denser than any other part and after staining with mucicarmine it has frequently a pinkish tint. On some occasions, too, it has appeared as if the cortical region were striated. In the parts of the introvert lying nearer the external opening the characteristic arrangement of papillae is gradually replaced by an ordinary columnar epithelium, the height of which does indeed vary somewhat from spot to spot, but not in the regular way which has just been described. The cells are all of similar height, their cytoplasm not specially organized and the number of gland cells reduced and without any noteworthy relationship to the others.

Underneath the epithelium of the buccal region lies a complex array of muscle fibres, many of which are part of the mechanism for the retraction of the extended proboscis. The fibres which are responsible for the greater part of the retraction (Figs. 1 and 4, R) are set on the edge of the sucker, curve round its inner face and then travel as a muscular sleeve around the stylet and oral tubes towards the inner end of the latter. The fibres of the sleeve are not, however, all parallel to one another, but gradually converge to form a closely knit bundle of muscle, lying to the ventral side of the gut. This then runs up the visceral hump alongside the columellar muscle, and is inserted like that on the columella of the shell, high up the spiral of the visceral hump. When the proboscis is extended the retractor muscle is of course relaxed and stretched taut, running alongside the gut along the whole length of the proboscis, through the nerve ring and thence on to the columellar muscle; when it is contracted it is flung into a large S-bend, one of the angles of the S being in the neighbourhood of the buccal ganglia, the other, the more distal, near the origin of the stylet. The fibres during their course from the columellar muscle to the ganglia, and then on to the second bend, are straight when contracted; those from the second bend to the sucker, however, are flung into great loops when in the same state. Subsidiary bundles of muscles run from the wall of the introvert directly to the body wall (Fig. 1, R1). All these bundles run through the nerve ring when the proboscis is retracted, and they will therefore help in its extension. This, however, is presumably brought about mainly by the pressure on the blood in the haemocoel exerted by the musculature of the body wall.

In addition to the retractor muscles there are other, intrinsic, muscles of the gut wall which help in the movement of the stylet and presumably in the feeding movements as well. The latter are mainly due to circular fibres which constitute a muscular coat of considerable dimensions lying directly within the longitudinal sheet formed by the retractors. The thickness of the coat is less at the outer end, in the neighbourhood of the sucker, than at the inner end, near the dorsal pouch of the buccal cavity, where the fibres are elaborated into a muscular mass of great complexity around the base of the stylet and the point of entry of the salivary ducts. Here they are responsible for the movements of the stylet (Figs. 1 and 3, SM). Further bundles of circular muscle fibres lie around the oral tube (Figs. 1 and 4, CM) and are presumably involved in peristaltic movements affecting that region, whilst a bundle of longitudinal fibres which runs up to the lips of the stylet aperture (Fig. 4, RSA) would apparently pull these back, and help in this way to expose the tip of the stylet.

All the muscles so far described are unstriated.

The sucker, by which animals of this genus obtain a grip on the body of the creatures upon which they feed, is provided with musculature arranged in the same plan as in platyhelminths. There are three sets of intrinsic muscles involved. A series of cells runs through the depth of the sucker between its inner and outer surfaces (MCS), attached to the under side of the epithelial cells which cover the sucker in the latter position, and ending on a sheet of connective tissue in the former. When they contract, the degree of concavity of the sucker is increased and its grip augmented. Antagonizing these is a double set of circular muscles (MOS) which lie between the ends of the cells of the first set, one group just under the outer epithelium, the other just within the inner layer of connective tissue. All these muscle cells contain groups of fibrillae and these are all striated, though the striation appears to be less complex than in vertebrate muscle cells.

The main part of the buccal cavity continues behind the point at which the dorsal pouch (Figs. 1 and 3, DP) is given off. This section is histologically similar to that pouch, with part of the wall, dorsally, near the origin of the pouch, cuticularized, and the rest rich in mucous cells. These are especially abundant ventrally, where they form two longitudinal ridges, one on either side of the mid-ventral line. Anteriorly the space between these ridges is a narrow groove lined by cells which are not glandular, but at the innermost end of the cavity the ridges converge so as to obliterate the groove, though the type of cell which lies at this spot does not alter. A thin coat of circular muscle surrounds this.

The character of the gut changes abruptly at the hinder end of this section where an extremely muscular organ, the buccal pump (Figs. 1 and 3, BP), is developed. This is a short length of the gut divisible into two halves, with the oesophagus (Fig. 1, O) coming out ventrally near the middle, its point of attachment coinciding with a constriction separating the two halves. The

second half of the pump is therefore a caecum. Both parts, however, are identical in general plan (Fig. 6); they are flattened in a dorsoventral direction with a narrow central cavity. Their walls are very thick, by far the greatest part of this being due to the development of muscle fibres, and in general, they are very reminiscent of the structure of the sucker. The epithelium (EBP) which lines the pump is extremely low (2 μ in height) and rests directly on the muscle of the wall. The bulk of this is formed of radial cells (DMP) fastened to the under side of the epithelium externally and to a sheet of connective tissue internally. Each cell, as in the sucker, has bundles of contractile fibrillae differentiated in its cytoplasm and these are all striated. Clearly, when these contract, they will give a strong and probably sudden pull on the epithelium, which will increase the dorsoventral diameter of the lumen of this part of the gut and so increase the volume. Antagonists (CMP) to this set of radial fibres are provided by transverse sheets of fibrillae, also striated, which run rather more than half way across each side of the cavity; their contraction will restore the cavity to its original volume.

Both these and the preceding section of the gut are closely linked with the salivary glands (Fig. 1, SC, SD), of which one pair is present. They lie freely in the haemocoel, though they may be attached to the body wall at their tip by fine strands of connective tissue or muscle. Each gland is connected to the gut by a long duct (Fig. 1, SD), and in the gland itself three distinct sections may be distinguished. The section lying next to the duct (Fig. 7) is composed of a series of large cells more or less quadrilateral in section. Their outer ends bulge slightly outwards against the layer of fine connective tissue (CT) that separates them from the haemocoel and it is noticeable, both in sections and in the intact gland, that the cells along one side alternate with those of the other. Almost all the cells have the same appearance—dense, even and darkly staining (iron haematoxylin) cytoplasm containing a large and irregularly lobed nucleus with a prominent nucleolus and many small granulations, the shape of the nucleus probably being an indication of intense metabolic activity (NS). In the few cells nearest to the ducts the cytoplasm is sometimes denser than in those farther away and the cells seem smaller and less well fitted together into an epithelium. An occasional cell (VC) will sometimes be distinct from all its neighbours and have a palely staining cytoplasm. Strictly speaking these are all subepithelial gland cells, because the lining of the central lumen is a layer of squamous epithelium bearing tufts of long cilia (CCL); these may be seen beating actively when a living gland is examined. The second section of the gland is brief and lies at the inner end of the secretory region: it is a short length where the same relationship of alternating ciliated and glandular cells occurs, but here the gland cells are small (ISG); they lie in the epithelium and stain even more intensely, whilst the ciliated cells (CC) are wedge-shaped with a long stalk connecting them to the basement membrane, and with their nuclei near the cilia. The lumen of the gland is broader and the cilia seem to beat with greater

vigour—though that may be merely an illusion occasioned by the fact that they have more space in which to beat. The innermost part of the gland is a thin-walled bladder (Figs. 1 and 7, BSG), lined by a squamous epithelium without cilia and without any obvious glandular appearance. The ducts are lined by an extension of the epithelium which lines the gland, but the greater part of the thickness of their wall is due to a great development of muscle cells containing circularly running fibrillae underneath the epithelium (Figs. 6 and 7, MSD). Like the fibrillae of the sucker and the pump these are striated. The two ducts run to the wall of the distal half of the pump, course along the lateral walls of that until the neighbourhood of the buccal cavity is reached, when they pass dorsally to enter the prolongation (Fig. 3, PS) which has already been described. There they unite, lose their muscular coat, and the single duct runs down the centre of the stylet to discharge saliva at the tip. When the proboscis is retracted the ducts coil irregularly in the haemocoel: when that is everted they are straight.

There are several points in the appearance of the salivary glands that suggest that there is a holocrine secretion occurring there without a restitution phase. The appearance of the cells at the two ends of the secretory part is unlike, though all the cells in a given region resemble one another. The cells are invariably larger at the inner part of the proximal region and invariably small and the epithelium less well compacted at the outer end of the same stretch, whilst if there were secretion going on from the entire gland, either in a rhythmic or arhythmic fashion, now and again a section would show cells of the latter variety in other parts of the gland. Although we have no direct evidence on this point the appearance of the gland would suggest that there is a continual (or rhythmic or post-prandial) production of new cells from the middle region of the gland, and that the cells mature their secretion as they move towards the ducts along the outermost section of the gland, discharging it, and being destroyed in the process, when they reach the outer end of this, at the beginning of the duct.

The oesophagus (Fig. 1, O) originates from the inner end of the first half of the buccal pump (BP). It is a tube of capillary dimensions (6–8 μ) at its origin, but its diameter increases slowly and steadily as it runs up the visceral hump till it ends by opening into the stomach. It behaves like the ducts of the salivary glands, with which it is, in fact, closely associated: when the introvert is withdrawn into the body it coils in a close tangle with the salivary ducts; when the proboscis is thrust out it is stretched straight. The oesophageal walls are similar from one end to the other; the lining is a columnar epithelium, most of the cells having a very fibrillar cytoplasm. Occasional cells are probably glandular because they have numerous uniform, refringent spherules enclosed within them which are not dissolved in any fixative and are darkly staining. In *Turbonilla jeffreysii*, which feeds on coelenterates, a short terminal region of the oesophagus, of slightly larger diameter than the rest, has every cell filled

with nematocysts. It would appear that a certain amount of phagocytosis of food particles goes on here, and it may also be true of *Odostomia*, although the fluid nature of the food does not allow it to be made readily visible.

The stomach into which the oesophagus leads barely merits the name, as it cannot be distinguished from the digestive gland, a condition reminiscent of *Omalogyra* (Fretter, 1948). Except for the immediate neighbourhood of the oesophageal opening the entire epithelium is occupied by digestive cells and these are invariably packed full of brown spherules, which are darkly staining. A few cells in the digestive epithelium are of a different type: their nuclei are large and are, in fact, the only nuclei easily visible in sections, for they differ from the digestive cell in that the spherules in the cytoplasm are dissolved in acid fixatives. The gland occupies the greater part of the visceral hump, lying on the outer, convex, side of the spiral.

The intestine arises close to the oesophageal aperture and runs almost directly to the upper end of the mantle cavity, passing close to the vas deferens as it does so. The epithelium is ciliated. The anus lies on a small papilla.

The Vascular System

The vascular system of *Odostomia* is built upon the usual gastropod plan, but is modified in certain respects which may be of functional significance.

The heart lies in a pericardial cavity placed within the visceral hump, at the attachment of the mantle skirt on the left side, immediately proximal to the kidney, which opens to it in the usual way. The single auricle lies anterior to the ventricle, from which only one aorta emerges, at the inner end of the pericardial cavity. This vessel climbs up the visceral hump, on the concave side of the spiral, resting on the surface of the gonad which, in turn, is enwrapped by the digestive gland, so that it is plain that it corresponds to the posterior aorta of other molluscs. Longitudinal muscle fibres lie in the aortic wall. Near the apex of the visceral hump the posterior aorta opens into a haemocoelic space interpenetrating the lobules of the digestive gland and gonad. This drains into a second vascular channel which passes down the visceral hump on the outer, convex side so that it is wrapped around (save where it is pressed against the mantle) by digestive gland. At the level of the heart this expands into a vast haemocoelic space in which the pericardial cavity itself and the bulk of the structures in connexion with the reproductive system are placed, and through which the intestine and the upper end of the oesophagus also pass. From this chamber two vessels run forwards. Of these one passes into the head and then forwards and ventrally into the foot and it would therefore seem to correspond to the anterior aorta of other molluscs, although its central connexions are different. As it runs forwards, it lies immediately under the floor of the mantle cavity, raising that up so that it projects into the mantle cavity as a long ridge. In this part of its course it lies alongside the genital duct; on reaching the head

it dives deeply into the body, curving behind the nerve ring down the right side, so as to pass ventral to the pedal ganglia in the middle line of the anterior portion of the foot, and it ends here by opening into the main haemocoelic space of the body, occupying head and foot, in which are placed all the viscera of the animal except such as are situated in the visceral hump. The second vessel which leaves the upper haemocoelic space (the afferent pallial) runs into the roof of the mantle cavity and discharges blood into the numerous sinuses with which that part of the body is filled. The main pedal and cephalic haemocoelic cavities also drain into this region. Blood collects from the mantle into another vessel (the efferent pallial) which finally enters the auricle at the upper end of the mantle cavity. Before reaching that organ, however, the blood has to pass through a capillary bed on the wall of the kidney: in sections it may be seen that the outer wall of the kidney, especially where it is contiguous with the lining of the mantle cavity, is corrugated, and that the blood from the pallial sinuses must trickle along the tiny channels made by these corrugations in order to reach the main efferent vessel by which the auricle is gained.

The main course of the circulation is obvious. Blood is pumped by the heart up the posterior aorta to the organs placed in the visceral hump, and in minute, shelled gastropods like *Odostomia* it is clear that these are the only organs which will require a direct blood supply of this nature, since they are the only parts of the body continuously enclosed within a shell and so liable to suffer from oxygen lack. Under normal circumstances, with the body of the animal not shut inside the shell, head, foot and mantle will all act as respiratory surfaces, and it is unlikely that the blood will ever be significantly short of oxygen. Movements of the blood in the principal haemocoels are more likely to be produced by the movements of the head and foot and proboscis than by the beating of the heart, and, in particular, every time that the proboscis is everted—a process largely brought about by the hydraulic action of the blood in the cephalic haemocoel—and again when it is withdrawn, there must be produced powerful currents and disturbances in the vascular system. The special arrangement of the anterior aorta seems likely to be connected with this: its origin from a blood space instead of directly from the ventricle will ensure that this vessel can pour blood into the haemocoelic spaces of the head and foot as the proboscis is everted and, on the other hand, when the reverse process is taking place, the upper haemocoel will provide a storage place for the blood and will prevent damage to the heart that might have been difficult to avoid had that structure been connected directly to the haemocoel by the aorta.

Two other points in the vascular system deserve comment. One of these is the frequency of blood cells: these may be found in many of the vessels, but are most common in the spaces in the roof of the mantle cavity, in the anterior aorta and caught against strands of muscle in the chambers of the heart (Fig. 9). They are spherical in shape, with a round nucleus placed to one pole; the cytoplasm is not prominent apart from irregularly placed, scattered, or clumped

spherules which are invariably present, staining darkly with iron haematoxylin. These granulations are presumably excretory in nature, and one of the main activities of these cells would seem to be the transport of such particles to places where they may be cast out of the mollusc. This probably explains their abundance in the sinuses of the pallial region as it is mainly there, as recorded above (p. 500), that the cells have been seen in the process of discharging their contents to the mantle cavity. It is not certain whether they do not pass out themselves at the same time.

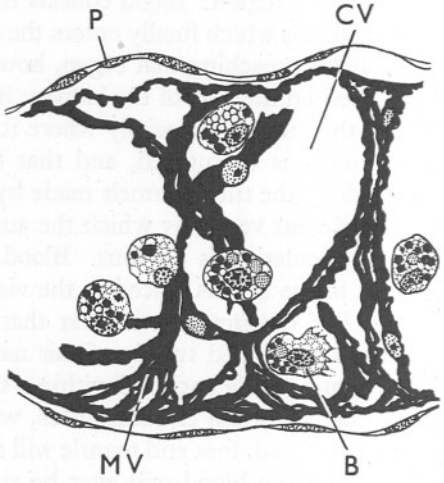

Fig. 9. *Odostomia unidentata*. Section through ventricle of heart to show blood cells. × 600. B, blood cell; CV, cavity of ventricle; MV, muscles of ventricle; P, pericardium.

The second feature connected with the vascular system of *Odostomia* which should be noted is a differentiation of the wall of the anterior aorta where it runs forwards towards the head, alongside the terminal part of the genital duct. Here the cells which line the aortic wall abutting against the genital tract are specialized to form a thick pad of tissue. They are quadrilateral when seen in section, each with a large, darkly staining and granular nucleus; the cytoplasm is also granular. The nature of this group of cells is unknown.

The Nervous System

The ganglia of the nervous system of *Odostomia* are mainly concentrated into a ring which envelopes the proboscis, and also, quite unexpectedly, the penial sheath, and in which nine ganglia may be distinguished. In addition to the constituents of this ring two other paired ganglia may be observed in relation to the introvert, and a single unpaired one lies in the mantle on the animal's left side. A diagram of the nervous system is given in Fig. 10. Dorsal to the introvert lie the two cerebral ganglia (Figs. 1 and 10, CG): they are large, oval

in cross-section and the commissure between them so short that they are practically joined across the middle line. Anteriorly and ventrally they are drawn out into lobes (Fig. 10, LO, SL) which project considerable distances towards the eyes, the tentacles, and, to a lesser degree, the sides of the body between head and mentum. These merge into the ganglionic masses already described in these situations, and the main nerves for these regions arise out of these swellings.

Ventrally the cerebral ganglia are connected to the pedal ganglia (Figs. 1 and 10, PG), which are about equal to them in size, and, like them, are closely approximated, so that the commissure is hardly a separate structure. The cerebro-pedal connective is likewise rather short. On the postero-dorsal faces of the pedal ganglia lie the statocysts (Fig. 1, STA) in each of which is placed, as already noticed by Pelseneer (1899), a single calcareous statolith. At least four nerves leave each pedal ganglion and pass into the musculature of the foot. From each cerebral ganglion there also leaves a second connective, arising so close to the point of origin of the cerebro-pedal connective that it requires close observation to be sure that there are indeed two. A strip of muscle running from body wall to introvert, however, is regularly found separating the two structures, so that there is no real doubt that these are two independent nerves. The posterior of the two connectives runs to a small ganglion lying between the cerebral above and the pedal below, to which it is also linked by a further connective, and placed slightly posterior to both (Fig. 10, PLG). This is clearly the pleural ganglion on each side.

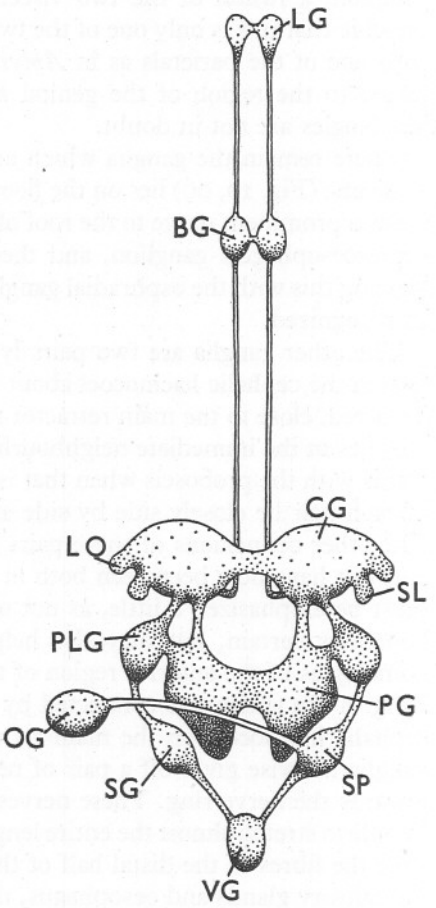

Fig. 10. *Odostomia*. Diagram of nervous system in dorsal view; the proboscis is supposed to be everted. LG, labial ganglion; OG, osphradial ganglion; LO, optic lobe; SL, sensory lobe; SP, supraoesophageal ganglion. Other letters as in Fig. 1.

From the pleural ganglia there may be traced a visceral loop lying ventral to the introvert and not exhibiting any torsion. It is much abbreviated and does not extend far behind the rest of the nerve ring. On this loop three ganglia may

be distinguished, and the most likely interpretation of these is that the one attached to the right pleural (Fig. 10, SP), is the supra-oesophageal ganglion, the one attached to the left pleural (Figs. 1 and 10, SG) is the suboesophageal ganglion, whilst the remaining ganglion would then represent the abdominal ganglion, a fusion of the two visceral ganglia (VG). It is, however, always possible that this is only one of the two visceral ganglia, the other having fused with one of the parietals as in *Aplysia*. Nerves arise from these that can be traced to the region of the genital aperture, kidney and heart so that their homologies are not in doubt.

There remain the ganglia which are not closely tied to the nerve ring. Of these one (Fig. 10, OG) lies on the floor of the mantle cavity on the left side and sends a prominent nerve to the roof of the mantle cavity. It is connected to the supra-oesophageal ganglion, and there is therefore little difficulty in homologizing this with the osphradial ganglion, although no specific osphradium can be recognized.

The other ganglia are two pairs lying in relation to the introvert, one pair (BG) in the cephalic haemocoel about half way along the introvert when that is retracted, close to the main retractor muscle of the proboscis. The second pair (LG) lies in the immediate neighbourhood of the sucker. Both pairs move outwards with the proboscis when that is extended (Fig. 1, BG, LC). The members of each pair lie closely side by side and are connected by short commissures. The other connexions of these pairs of ganglia have proved difficult to make out, but have now been seen both in dissections and in sections, a fact which must be emphasized a little, as not only do their connexions make their own homology certain, but they also help in establishing beyond any doubt the homologies of the anterior region of the alimentary canal. The pair of ganglia lying in the sucker are connected by a pair of nerves to the pair lying in the cephalic haemocoel on the main retractor muscle of the sucker. This pair of ganglia likewise gives off a pair of nerves which runs through the haemocoel towards the nerve ring. These nerves are particularly long because they must be able to stretch almost the entire length of the proboscis when that is extended. Like the fibres of the distal half of the retractor muscle, and like the ducts of the salivary glands and oesophagus, they are, for this reason, sinuously looped when the proboscis is retracted and straightened on the extension of that part of the body. On reaching the nerve ring the nerves pass dorsally and approach the cerebral ganglia, each nerve entering into a little lobe placed in a postero-ventral position on the cerebral ganglion. When one compares the plan of this part of the nervous system in a pyramidellid with the general plan of the gastropod nervous system, it is plain that only one interpretation of the homologies of these ganglia is possible: the pair which is connected to the cerebral ganglia must be the buccal ganglia, whilst those that lie in the sucker, that is in the lips of the mouth, must be the labial ganglia. The whole stomatogastric system must lie ventral to the main channel of the gut, though the

buccal commissure would be dorsal to a radular sac, from which it must be concluded that the side of the mouth on which the ganglia are placed is ventral.

Reproduction

The pyramidellids are simultaneous hermaphrodites: ripe sperm and ova lie side by side in the same tubules of the gonad. The simpler requirements of the male reproductive system enable young individuals to function as males until the ova and the relatively enormous glands associated with egg laying are mature. Both types of gamete use the same ducts and are liberated into the mantle cavity through the same genital aperture. The path of the spermatozoa is, however, extended from here by the ciliated seminal tract which leads along the floor of the mantle cavity and around the base of the right tentacle to the penis.

Fig. 11 shows the disposition of the reproductive organs of a mature individual. From the gonad (H), on the columellar side of the visceral mass, a narrow though very distensible genital duct (GD), lined by a columnar ciliated epithelium, takes a somewhat sinuous course through the haemocoel towards the posterior end of the mantle cavity. Immediately after leaving the gonad it is distended with sperm (V), acting in this region as a vesicula seminalis; sperm are stored here even during a period of spawning, when the ova make their way, one by one, through the mass of ripe spermatozoa. From the vesicula seminalis the duct loops under the intestine (I) and describes a U-shaped bend around the posterior aorta before passing forwards to open into the pallial hermaphrodite duct (GO). Along the final part of its course it receives the openings of three glands which are concerned with the production of the egg masses. Two of these, the albumen gland (AG, DA) and the mucous gland (MGU, DU), open close to one another; the third opens near the entrance to the pallial duct and is a second mucous gland attaining a greater size than the first (MGL, OL). The white, flocculent lobes of the albumen gland tend to embrace those of the upper mucous gland. In both, as elsewhere in the genital system, the secreting cells in the epithelium alternate with small ciliated cells wedged between their distal ends (GC, CC). The secretion within the cells of the albumen gland is in the form of spherules which stain lightly with Heidenhain's haematoxylin and are embedded in a more deeply staining cytoplasm; in sections the secretion can usually be found in the form of a plug blocking the narrow duct which leads towards the genital aperture. The two mucous glands can not only be distinguished by a difference in size, but also by a difference in the staining properties of the component cells: those of the lower one respond to stains which are specific for mucus more readily than those of the upper. This distal gland is the last to appear in the development of the female system, but its growth is rapid and its lobes soon come to envelope the proximal end of the pallial duct, often extending halfway down its length.

The pallial genital duct is divisible into two regions: a proximal glandular part (GO) occupying about half of the length and expanding posteriorly as a commodious pouch, and a distal ciliated, conducting region which is more muscular. Running along the median wall of the former, and as a less conspicuous tract distally, is a ciliated gutter which is confluent with the narrow

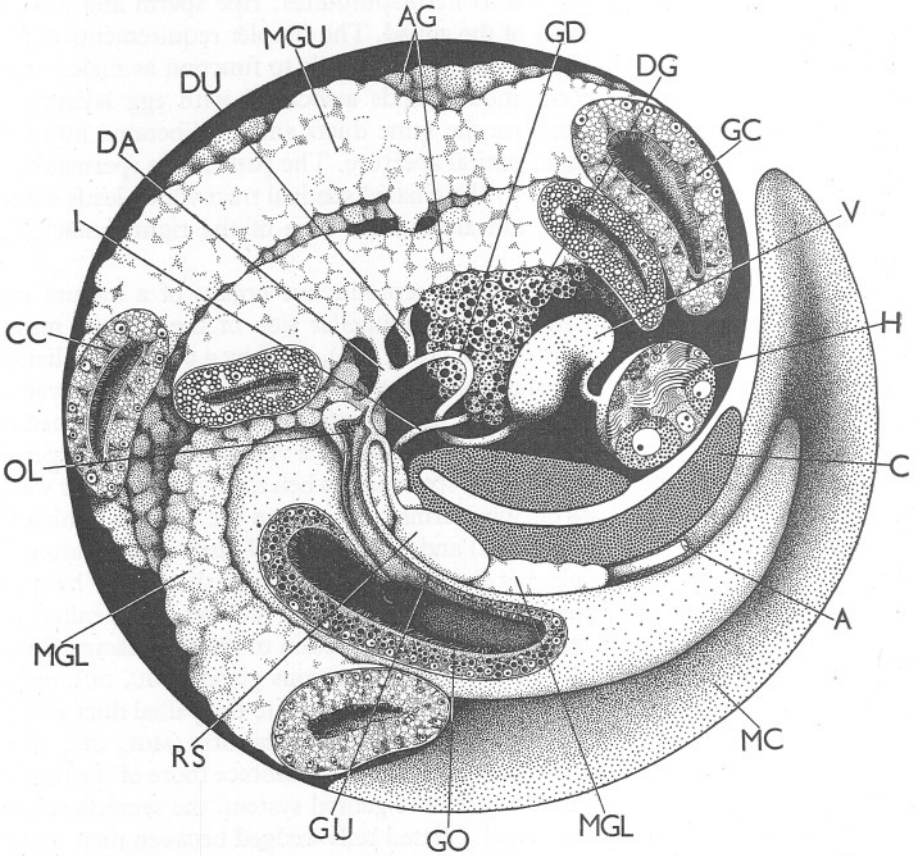

Fig. 11. *Odostomia lukisii*. Stereogram to show the disposition of the reproductive organs. The visceral hump has been cut across at the level of the reproductive ducts and the cut surface is viewed from above; the haemocoel is black. × 104. A, anus; AG, albumen gland; C, columellar muscle; CC, ciliated cell; DA, duct of albumen gland; DG, digestive gland; DU, duct of upper mucous gland; GC, gland cell; GD, gonadial duct; GO, glandular part of pallial hermaphrodite duct; GU, gutter along GO; H, hermaphrodite gland; I, intestine; MC, mantle cavity; MGL, lower mucous gland; MGU, upper mucous gland; OL, opening of lower mucous gland into pallial hermaphrodite duct; RS, receptaculum seminis; V, seminal vesicle.

hermaphrodite duct (GU). Initially this channel communicates with a globular receptaculum seminis (RS) in which unorientated sperm are always to be found. An excess of spermatozoa may surround the entrance to the duct of the receptaculum and extend in all directions from there. The gland cells of the

pallial duct are the first to differentiate and to become functional: during early sexual activity, when only the male system is mature, the cells are distended with large secretory spherules of a protein nature. Later, during a period of egg laying, the appearance of the cells suggests that they are inert—reduced in size, with less abundant and smaller spherules which stain not uniformly, but in varying degrees of intensity, with both iron haematoxylin and azan. This gland is, therefore, assumed to be a prostate, and it is uncertain whether it has any function during the female phase.

The outstanding characteristic of the reproductive system of the pyramidellids is the position of the penis: in no other family does any structure except the digestive tube and its intrinsic glands and muscles pass through the nerve ring. In the pyramidellids, however, this position is also occupied by the penis (Fig. 1). The penis is invaginable and completely concealed except during copulation, when, as a long whip-like structure, turgid with blood and tapering to a fine point, it is passed into the mantle cavity and through the genital aperture of the partner. The penis retracts into a tubular sheath (PSS), within which it lies freely, like a partly invaginated finger of a glove, with its tip at some distance from the external aperture (PO). The sheath lies in the haemocoel dorsal to the gut and may be flung into one or two broad loops when the animal is withdrawn into its shell. The walls of the penis and its sheath are continuous and retraction is brought about by their intrinsic muscles (Fig. 12, CM, LM) and the consequent expulsion of blood into the general haemocoel. These muscles resemble those of the buccal pump in that the fibrillae are striated. Opening into the dorsal wall of the penial sheath in front of the tip of the retracted penis is the short, wide duct of a large, muscular sac which lies immediately within the body wall (Fig. 1, SS). The sac and its duct are ciliated, the cilia exceeding five times the height of the cells in length. An epithelium with long, closely set cilia also lines the anterior part of the sheath to the external opening (PO). Elsewhere the epithelium of the sheath, and also that of the penis, are cuticularized. A second duct, the vas deferens, arises from the muscular sac closely behind the first and runs in the thickness of the dorsal wall of the sheath (Fig. 12, VD) towards the base of the penis into which it passes (VD 1), to open at the tip. It is not ciliated, but its walls are muscular. The path of the spermatozoa from the common genital aperture can thus be followed along the seminal groove through the anterior ciliated part of the penial sheath into the sperm sac and thence to the tip of the penis along the vas deferens.

During copulation the individual which acts as male creeps on to the dorsal surface of the shell of its partner, everts the penis and bends it ventrally to reach the mantle cavity of the female. Animals which have been separated during copulation, fixed and sectioned, show, at least as far as that acting as female is concerned, spermatozoa filling the receptaculum, surrounding the opening of its duct into the pallial oviduct and concentrated along the ciliated gutter which connects the opening with the genital aperture. Perhaps the penis

discharges the spermatozoa into the ventral gutter and then they make their own way to the receptaculum. In the animal acting as male only a few sperm are found in the sperm sac, which is probably merely a temporary storage place for them before they enter the penis. As in *Omalogyra* (Fretter, 1948), the sperm must have been transferred to this sac prior to copulation, for it is difficult to see how they could get there after the penis has been everted.

The egg masses of *Odostomia* spp. are laid in irregularly shaped heaps in the vicinity of the animals upon which they feed. The spawn of *O. rissoides* is described by Pelseneer (1914) and a later account is given by Rasmussen

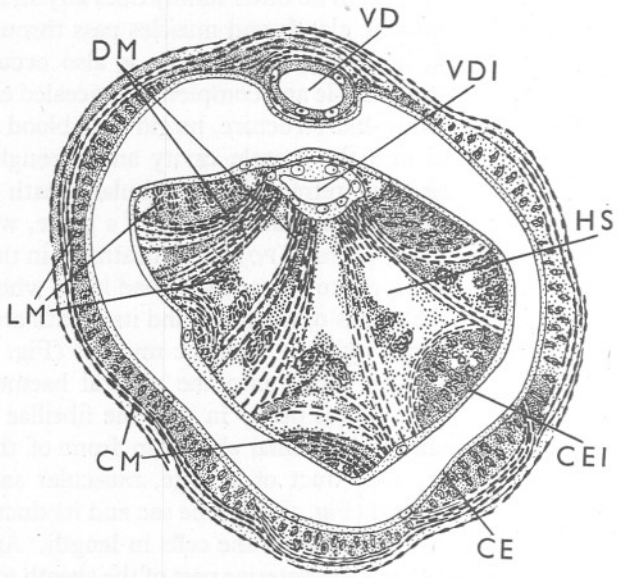

Fig. 12. *Odostomia*. Transverse section of penis in sheath. ×600. CE, epithelium of penial sheath; CEI, epithelium of penis; CM, circular muscles; DM, dilator muscles; HS, blood spaces; LM, longitudinal muscles; VD, vas deferens in penial sheath; VD I, vas deferens in penis.

(1944), who shows that each egg is surrounded by a layer of granular albumen which is, in turn, encased in a mucous envelope or capsule. Between one egg and the next the mucous layer narrows to a fine strand. In this way all the eggs in a mass, which, according to Rasmussen (1944), may amount to five hundred, are linked into a continuous chain and then are still further surrounded and cemented together by a second and more plentiful layer of mucus, the outermost covering of the spawn, by means of which it is fixed to the substratum. An examination of the egg masses of *O. plicata* and *O. eulimoides* shows that they have a similar construction; thus they agree in general plan with those of the opisthobranch *Onchidella celtica* (Fretter, 1943). The staining reactions of the secretions which surround the eggs suggest the origin of these from the three glands attached to the hermaphrodite duct—the albumen gland and the

upper and lower mucous glands—and the relative size of these is indicative of the volume of secretion produced by each in a single egg mass. The lower and larger mucous gland supplies the ample outer jelly and the upper one the capsule wall which encloses each egg with its supply of albumen and separates it from its neighbours.

The eggs are presumably fertilized in the upper part of the genital duct where sperm abound after an egg mass has been deposited, many of these superfluous spermatozoa becoming entangled in the egg coverings. The developing veliger gradually uses up the albumen as food, and in *Odostomia eulimoides* its development to a free larval stage, when kept at a temperature of about 18° C., may be completed within 10–12 days.

Lebour (1932) describes the free veliger of this species with its mobile, bilobed velum, eyes far apart, the transparency of the tissues displaying the relatively large stomach, long intestine and bilobed digestive gland. The general arrangement conforms with that of a typical gastropod veliger, for as yet no adult specialization is apparent; these first appear in the buccal and oesophageal regions of the late veliger. Lebour (1932) suggests that the larval life is short; this suggestion is supported by Thorson (1946) and has now been confirmed by actual observation: the free-swimming larval life lasts from 3 to 4 days, the larvae then becoming benthic and the metamorphosis of the gut rapidly achieved. In the metamorphosing larva the long introvert with its papillated surface, the stylet, the buccal pump and the large salivary glands may all be distinguished, and during further growth the intestine becomes relatively shorter, whilst the stomach is incorporated into the digestive gland. The eyes are now close together as in the adult. The penis, however, is not yet developed, so that the gut is the only tube passing through the nerve ring.

The eggs of *O. plicata* can be distinguished from those of *O. eulimoides* by their yellow pigmentation. They are laid in crevices of stones or rocks where the adults live. The veliger is freed from the capsule in about a fortnight and its structure agrees with that of *O. eulimoides* and *O. rissoides* (Rasmussen, 1944). Thorson (1946) suggests that according to the appearance of the larval shell the free veliger life of this species is longer than that of *O. eulimoides*, but the exact time has not been estimated.

The process of Feeding

The process of feeding has been watched in several species of *Odostomia*—*O. lukisii*, *O. unidentata*, *O. scalaris*—as well as in *Chrysallida spiralis*, and as the structure of the gut appears to show very little variation throughout the family Pyramidellidae it is probable that the process is similar in all species.

Chrysallida spiralis may be found sitting on the sandy tubes which are inhabited by the polychaete worm *Sabellaria*. When not feeding the mollusc will lurk in any little hollows in the irregular sandy mass which colonies of this

worm manufacture, but when they desire to feed they perch themselves close to the opening through which the head of the worm will protrude. For long periods of time they may be seen sitting in this position, the head and foot out of the shell, the tentacles held upwards and forwards, facing the opening of the worm's tube. Currents produced by the cilia on these bring water streaming to the head of the mollusc from the region of the opening in the tube and it is probable that the mollusc is in this way made aware not only of the presence of a tube, but of the extension or otherwise of the worm that dwells within. When the polychaete cautiously emerges from its tube, however, and starts spreading its tentacles over the surroundings in order to pick up food particles then the mollusc may also start to feed: the proboscis is everted, gradually rolling outwards from the mouth till it forms a long narrow cylinder tapering gently to the sucker at its tip. The basal covering, near the tentacles, tends to be smooth, whereas nearer the sucker the peculiar papillae that lie in the epithelium give it a villous appearance. The whole proboscis can be gently waved about in the water, and the mollusc moves it slowly and delicately up to the neighbourhood of the tentacles of the worm, until actual contact is achieved. This is obviously made as quietly as may be, but the first time that it occurs the worm will usually jerk slightly, though it will not withdraw completely into its tube. The proboscis insinuates itself gently between the tentacles until it lies on their median face; there, still elongating, it slides down the ciliated groove that runs along a tentacle towards the mouth, into which its tip disappears. At this stage the proboscis is enormously elongated and as it is almost transparent the whole of the anterior end of the alimentary canal may be seen lying within. The oral tube, buccal pump and salivary glands occupy the distal half or thereabouts and from them the oesophagus runs as a narrow tube through the basal part of the proboscis until it disappears out of sight into the denser tissue of the main part of the body of the mollusc. As the buccal pump can be seen working and waves of peristalsis passing along the gut it is clear that the mollusc is sucking food into the alimentary canal, but as the tip of the proboscis is invisible, hidden inside the gut of the polychaete, it still remains uncertain what the source of the food may be and, of more interest, what exactly the stylet is doing during the process.

This, however, may be made out with certainty if other pyramidellids, like *Odostomia lukisii* or *O. unidentata* be examined. Both of these species are to be found on stones on which the tubicolous polychaete worm *Pomatoceros* is living, and they may be found lurking at the mouth of the tubes of these just as *Chrysallida spiralis* does near the mouth of *Sabellaria* tubes. When a *Pomatoceros* has expanded its crown of branchial filaments it may be observed that a nearby *Odostomia* will then project its proboscis towards the worm. As the proboscis moves nearer the worm it often rotates in a spiral as if it were carrying out exploratory movements, and, as before, the final approach to the filament of the worm is made apparently with as great delicacy as possible

so as to disturb the prey as little as may be. When it is recalled that these delicate movements are carried out by a proboscis that extends to a length many times that of the rest of the animal the efficiency of the muscular control will be realized. On first contact the polychaete may jerk its crown of filaments away from the proboscis, or even withdraw into its tube altogether, and if this movement on its part is at all sudden a corresponding partial or total withdrawal of the proboscis of the mollusc will take place. Sooner or later, however, the proboscis will be extended once more, and it has been noted on several occasions with what remarkable accuracy the proboscis will reach out to the exact spot with which contact with the filament was previously made, as if the mollusc had some exact kind of kinaesthetic 'memory'. When contact is finally permitted by the worm the sucker at the tip of the proboscis of the mollusc is slid gently along the tentacle until, presumably, a suitable spot is found, usually on the outer side of the filament. Then suddenly the sucker grips the epithelium of the filament, and the stylet may be seen to drive outwards so that it is clearly being used to perforate the body of the worm. Vigorous pumping movements of the buccal apparatus may then be seen and it is obvious that fluid, blood and, perhaps, cells loosened from the worm are being sucked into the gut of the pyramidellid. The polychaete clearly feels the movements of the proboscis and the stabbing of the stylet in most cases, but worms have been observed which allowed the proboscis to move amongst the branchial crown and to slide up and down the filaments and feed in this way without any very pronounced reaction, though it must be remembered that the mollusc always appears to perform these movements with the very greatest caution.

The grip which the pyramidellid obtains on its prey is fairly secure; at least moderate movements of the branchial crown of the polychaete do not dislodge the sucker: it requires a sudden withdrawal to effect this, though we have not been able to avoid the conclusion that the mollusc then lets go, as if to avoid any danger of the proboscis being pulled into the tube and trapped or damaged in any way.

As the differences which have been found to exist between the alimentary canals of the various pyramidellids are confined to apparently unimportant details it would seem that all these animals feed in the same general sort of way.

Discussion

Apart from a few instances the Pyramidellidae are a group of gastropods little mentioned in the literature of malacology, though what has been said has tantalizingly indicated that the group would be of extreme interest were more known about its ways of life. Thus the work of Jeffreys (1867), Pelseneer (1914) and Rasmussen (1944) had suggested that the animals are epizoic in their habit, without making it completely clear whether their association with other animals was confined to using their shell as a home, or to picking up, using their proboscis as a pipette, mucus and other secretions from the body of the animal on

which they lived, or whether they were indeed true ectoparasites and fed on the body of a host. That some such idea was in the minds of most malacologists is probable, since the Pyramidellidae were associated by Thiele (1929) with the families Melanellidae (=Eulimidae), Stiliferidae and Entoconchidae in the stirps Aglossa, all these families containing animals known to be parasitic in their mode of life. Winckworth (1932), too, places these families side by side, although he refrains from uniting them more closely by avoiding all grouping within the order Mesogastropoda.

The description which has been given above, however, makes it quite plain that the pyramidellids are ectoparasites, and that they live on the blood and perhaps tissue débris of other animals on which, or in the neighbourhood of which, the mollusc passes the greater part of its life. Each species of pyramidellid appears to be associated with one definite host, and as might be expected these are, so far as is known, sessile organisms which are easily found, and which must, if they are to survive at all, from time to time protrude some part of their body for the collection of food, and so make it available simultaneously to the gastropod. The list of hosts which has so far been gathered definitely is:

Chrysallida spiralis	...	*Sabellaria* spp.
Odostomia unidentata	...	*Pomatoceros triqueter*
O. lukisii	...	*Pomatoceros triqueter*
O. scalaris	...	*Mytilus edulis* (small only)
O. eulimoides	...	*Pecten maximus* and *Chlamys opercularis*
O. trifida	...	*Mya arenaria*
Turbonilla jeffreysii	...	some coelenterate, probably *Halecium* sp.

These species of pyramidellid will be found, with surprising abundance, as they are not really uncommon animals, in the vicinity of the particular host upon which they feed. They will be found to feed on no other animal. At Plymouth, *Turbonilla jeffreysii* may be dredged from the localities where the hydroid *Halecium* abounds, and that the mollusc is in fact feeding upon it is suggested by the occurrence of masses of nematocysts in the cells of the innermost part of the oesophageal epithelium, which are similar in size to those in the cells of the hydroid. Actual feeding has not, however, been observed in this species. Another species of *Odostomia*, *O. plicata*, is to be found in association with *Pomatoceros*, occurring, in the Plymouth district, at a lower level on the beach than *Odostomia unidentata* and *O. lukisii*. It feeds less willingly when kept in captivity and thrusts its proboscis out at a variety of creatures—even on to the antennae of living amphipods. On two occasions sponge spicules have been found in its gut, suggesting that this species may suck the tissues of a sponge. Although the nature of the mode of life of pyramidellids has been verified for a mere handful of the forty-odd species listed by Winckworth (1932), the gut is of such homogenous structure in all the species that have been investigated, that there is little doubt that they all live in the same general

fashion and that further work will lead to the discovery of the correct host for each species. Until this is known no search for a given kind of pyramidellid can be productive, and the old records of habitat given by Jeffreys (1867) or Forbes & Hanley (1853), such as 'under stones', 'on corallines in rock pools', etc., are valueless as indications as to where the animals really live. When the host is known success in collecting can usually be relied upon.

There are a few clues in the literature regarding hosts of some of the species for which they are not yet known: Marshall (1900) notes the occurrence of *Turbonilla rufescens* on 'the leathery tube of a sessile annelid' and of 'dwarf specimens of *Odostomia albella* with littorinae'. Gardiner (1934) mentions the occurrence of *O. perezi* Dautzenberg and Fischer with *Phascolion strombi*.

The alimentary canal of the various pyramidellids which have been examined varies from species to species only in the very slightest way: the stylet is short in some (*Odostomia eulimoides*), longer in others; there is a separate stylet tube and oral tube in *Chrysallida* and *Odostomia*, whereas in *Turbonilla* there is but the one tube along the centre of which the stylet runs; the papillation of the introvert is pronounced in *Odostomia unidentata* and *O. plicata*, less so in *O. lukisii* and *Chrysallida spiralis*, and is hardly indicated in *Turbonilla*; the salivary glands are better developed in *T. jeffreysii* than in the other genera—perhaps in connexion with the habit of that species of feeding on coelenterates, where a copious salivary secretion might have a special significance in desensitizing the nematocysts (Pantin, 1942). Apart from these relatively unimportant details the gut is very similar throughout the family, and the interest in it lies, not in the variation from species to species, but in trying to homologize the very specialized arrangement found here with the more typical gastropod plan. Practically all the specialization lies in the anterior end of the gut. From the region of the buccal pump onwards the general plan of the gut does not depart significantly from what might be expected—an oesophagus runs back to a stomach and from there an intestine passes to the mantle cavity. The stomach is extremely simple, and is clearly just a place where oesophagus, digestive gland and intestine join, but that is no more than might be expected in animals of such small size feeding on a simple diet (see Fretter, 1948).

The main interest centres in the homologies of the anterior region and two structures may be used as guides to the correct interpretation of these: the salivary ducts and the labial ganglia. In the typical gastropod mollusc the mouth opens by a short oral tube into the buccal cavity. On the floor of the buccal cavity is placed the odontophore and along its roof runs the anterior end of the dorsal food channel, separated from the more lateral portions of the cavity by extensions of the dorsal folds. External to the roof of the cavity lie the salivary glands. Their ducts run in connective tissue, one at the base of each dorsal fold, and open into the buccal cavity dorsolaterally, near its anterior end, about the level at which the dorsal folds end. Anterior to this part the roof of the buccal cavity slopes ventrally into the dorsal wall of the oral tube and it is

in this region that a jaw, or jaws, will be developed, should the animal possess such structures. These arise as cuticular growths from the epithelium covering the dorsolateral wall of the buccal cavity and oral tube. Often the lateral parts, and, always, the anterior end of the jaws are lifted off the epithelium upon which they have been produced so that they project freely into the buccal cavity anterior to the apertures of the salivary ducts. Now, were the two salivary ducts to run together so as to open into the roof of the buccal cavity on a median papilla and were this then to elongate and grow forwards, it would rapidly reach the level of the jaws, and if the free edges of these structures were further supposed to grow ventrally around the salivary duct in its new position a chitinous tube would have been produced, attached dorsolaterally to the epithelium of the buccal cavity at its inner end, but free anteriorly, and this would surround a tube formed from the fusion of the two ducts of the salivary glands. In other words, the condition exhibited by the pyramidellids would have been attained. That the cuticular stylet is, indeed, dorsal, is further shown by the position of the labial ganglia, which lie on the opposite side of the oral tube at the level of the mouth, and by the buccal ganglia which are likewise placed ventral to the apparatus. These relations by themselves would indicate that nothing in the present arrangement could correspond to a radula, a structure which normally lies ventral to the buccal commissure. The glands lying in the oral tube and buccal cavity in the pyramidellids would correspond to the mucous glands which lie scattered over the buccal cavity of other gastropods, more especially in its dorsal part. Nothing comparable to dorsal folds or dorsal food channel seems to occur in the pyramidellids, however: the innermost part of the buccal cavity seems to have become specialized along completely different lines to produce the buccal bulb, whilst the oesophagus is a simple, elongated crop-like structure without any of the characteristic glandular areas of the typical prosobranch.

In *Turbonilla* a single aperture on the sucker leads into a simple oral tube in which the stylet lies (Fig. 5); in *Chrysallida* and *Odostomia* (Figs. 1, 3 and 4) the sucker has a ventral mouth and a dorsal stylet aperture, and two tubes lie parallel to one another in this portion of the gut. How may these have arisen? The probable explanation is to be seen in the occurrence, in a gastropod like *Patella*, of a pair of inner lips (Graham, 1932, Fig. 1). These are attached to the lateral walls of the oral tube, ventral to the jaws, and they may be moved across the oral tube from side to mid-line so as to act like a curtain, dividing the tube into a dorsal half into which the jaw projects, and a ventral half which would be separated from the part in which the jaws lay. Were this contiguity to become a fusion, and were the base of the jaws to abut on, or fuse to, the base of the fold, then precisely the situation which is exhibited in *Chrysallida* and *Odostomia* would have arisen. In this way stylet aperture and apparent mouth may be shown to be merely parts of the original mouth, and the stylet tube a separated portion of the original oral tube.

The evolution of a long proboscis is clearly a necessary feature in the particular feeding habits that the pyramidellids have adopted, and this has apparently involved the penis as well, so as to give rise to the peculiar arrangement by which the sheath of that organ lies within the nerve ring ventral to the oesophagus. In the typical gastropod the mouth lies ventral to the tentacles and the penis is placed on the right-hand side of the head behind and below the right tentacle. An acrembolic proboscis is produced by an elongation of the tip of the snout, anterior to the tentacles, so that the mouth comes to be placed at the summit of a long pretentacular extension, which is everted and appears as such only when the creature is feeding. At other times it is withdrawn and a 'mouth'—though not the true mouth—lies in the usual position. Now suppose that the elongation occurs behind the penis: that will then lie near the tip of the proboscis when elongated and would be carried into the introvert when the proboscis was withdrawn, and the ciliated groove running along the right side of the head from the genital opening to the penis would appear to end at the mouth of the introvert. This consequence of the production in this particular way of a long proboscis produces unnecessary complexities in the functioning of the reproductive apparatus, and it would be needful to suppose that the penis, now brought far inside the body by its association with the introvert, has gradually separated itself from the introvert, and that its external opening has migrated forwards along the ventral wall of the introvert until it finally reached the surface of the body once again. This migration forwards of the opening of the penis gives rise to a long tube, the penial sheath, which, as it has been formed by separation from the introvert, must penetrate the nerve ring, and which will open to the exterior near the mouth. The mentum must have arisen after this migration has taken place, since it separates mouth and penial opening, and it is, therefore, a novel structure without any deeper significance, perhaps, than a barrier between these two apertures. It is tempting to think that the original cephalic tentacles of the ancestral pyramidellid were also involved in the formation of the introvert and have been lost and replaced by new structures, which would explain the peculiar shape of these and the fact that the eyes lie on their inner instead of their outer sides. But this position may merely be the result of a direct migration such as occurs during development (Lebour, 1932).

The bulk of the digestive processes appear to go on inside the digestive gland, the oesophagus acting primarily as a crop. Whether the peculiar lining of the introvert has any digestive significance or not we are unable to say, but it is interesting to note that various particles of detritus, diatoms and such like, are sometimes to be found inside the retracted introvert: this is probably merely accidental contamination in view of the fact that its surface is probably sticky from the secretion of the numerous glands placed there. The precise function of these remains obscure. As they are most abundant in the neighbourhood of the sucker and least near the base of the proboscis it would seem likely that

they are concerned with the process of feeding, as it is precisely the part of the proboscis which comes most into contact with the body of the prey which carries the greatest number of glands. They therefore most probably lubricate the movement of the proboscis so as to make it less likely of notice by the prey.

The second main point to which attention must be directed is the systematic position of the family Pyramidellidae. Although from the time of Mørch (1865) suggestions have been put forward that the family, if not actually opisthobranch, may be the group of prosobranchs from which the opisthobranchs originated, they have always in fact been classified as prosobranchs, usually associated with other groups of known or suspected similar feeding habits—explicitly or implicitly in an aglossan grouping. It is true that the pyramidellids resemble, for example, the Eulimidae and Stiliferidae in having lost the radula, but the most cursory examination of a eulimid (our own unpublished observations) or stiliferid (Kœhler & Vaney, 1908) shows that otherwise there are few points of agreement between the two families. The Eulimidae and the Stiliferidae are certainly extremely specialized in connexion with their ectoparasitic habit, but this has taken place along completely different lines from the Pyramidellidae.

The question as to the true systematic position of this family has lately been raised again by Thorson (1946), who points out that the characteristically heterostrophic larval shell of the pyramidellids is a feature which they share with a large number of opisthobranchs. On the basis of the work described in the preceding pages a comparison of pyramidellids and other gastropods may now be extended to other systems and the classification of the family reviewed in the light of the results of this.

In so far as the pyramidellids have a spirally coiled calcareous shell into which the entire body is retractible, a foot bearing an operculum, and a large anteriorly directed mantle cavity they resemble the prosobranchs. The same holds for the occurrence of a long proboscis. But when these things have been pointed out then almost all the specifically prosobranch characteristics of the animals have been mentioned. The various other ways in which the body of a pyramidellid differs from that of a typical prosobranch may be due (*a*) to specialization in connexion with its ectoparasitic life, or (*b*) to the fact that it is small and may therefore be secondarily simplified, or (*c*) to the fact that it is really an opisthobranch. In relation to the third possibility it is well to recollect that opisthobranchs like *Actaeon* may have spirally wound calcareous shells into which the body may be withdrawn and which can be closed by an operculum, and that they may have an anteriorly directed mantle cavity and be streptoneurous, so that the fact that the pyramidellids have the characteristically prosobranch features enumerated above does not debar them from being opisthobranchs.

So far as external features are concerned the contents of the mantle cavity first call for attention. Here no ctenidium is developed: this may be due to

small size, as in *Omalogyra* (Fretter, 1948), but it is noteworthy that in the family Actaeonidae the gill is reduced to a single triangular leaflet, whilst the main current of water is maintained within the mantle cavity by strips of ciliated epithelium as in *Odostomia*. As Fretter (1948) has suggested, in connexion with another group of gastropods, the forward projection of the kidney into the mantle may be valuable for the sake of the capillary bed which migrates with it: this feature also occurs in pyramidellids and in *Actaeon*. In another family of opisthobranchs, too, the Diaphanidae, the mantle resembles that of the Pyramidellidae in containing a dark brown-red gland of unknown significance. The mantle edge on the right side has a small lobe-like projection in pyramidellids: the actaeonids and hydatinids amongst the opisthobranchs have a similar process, although it is there larger and glandular. The tentacles carried on the head of a pyramidellid are ear-shaped: those on the head of the opisthobranchiate Hydatinidae are similar; the eyes are placed on their median sides on both groups, and in many other opisthobranchs that is also the position in which they are found, although there they are often sunk below the surface, a tendency not noticeable in the pyramidellids, unless convergence towards the mid-line is the first stage towards such a position.

In the construction of the alimentary canal there are several points in which pyramidellids and opisthobranchs agree: the complete suppression of the oesophageal glands and dorsal food channel (Graham, 1939); the tendency for the oesophagus to form a crop-like expansion and for the stomach to be merely a space into which the ducts of the digestive gland discharge (Graham, 1949); the shortness of the intestine; the tendency for the digestive cells of the digestive gland to become laden with spherules (Fretter, 1939)—all these are characteristics of opisthobranchs in general. There are one or two points in which the pyramidellids show similarity to special groups of the opisthobranchs and these groups are, as observed in the discussion of the external features, the most primitive families. In the hydatinids, for example, Thiele (1931) notes that the oral tube is very long, and it is well known that in the Actaeonidae the radula carries only extremely small and weak teeth, a characteristic also encountered in other groups of primitive tectibranchs. In other points the anatomy of the pyramidellid alimentary canal is much specialized, as is only to be expected in view of the parasitic mode of life which the group has adopted, but even here it may be noted that the buccal pump may be paralleled in the ascoglossans (Fretter, 1940).

It is rather difficult to use the nervous system of the Pyramidellidae as a clue to the relationship of the family, as it is possible for prosobranchs to be euthyneurous and for opisthobranchs to be streptoneurous. Of greater importance, perhaps, is the degree of concentration of the ganglia towards the formation of a nerve ring, and in this connexion the pyramidellids show a clear trend towards the opisthobranchiate condition. Pelseneer (1899) attempted to refute Mørch's original suggestion that the Pyramidellidae were opistho-

branchs on the grounds that the cerebral ganglia, like the pedal, were so close together that they were practically fused with one another, that the nerve ring was not anterior to the salivary glands and that the statocyst contained only one statolith—all points on which they differed from the 'Bulléens'. The first of these characteristics, however, is by no means unknown in the Opisthobranchia, while the second may very well have arisen in relation to the extreme specialization which the anterior end of the gut has undergone.

Further evidence bearing on the relationships of the family is provided by the reproductive system, and in this, as in the alimentary system, there are several points in respect of which pyramidellids resemble opisthobranchs rather than prosobranchs: the gonad is hermaphrodite, not unisexual; the ova receive their albuminous covering as they pass along the sperm-oviduct and do not enter the albumen gland (Fretter, 1946); large mucous glands provide a jelly which forms the outer, protective covering of the egg mass and there is neither capsule wall nor pedal gland to mould it; an open seminal grove leads from the common genital aperture to the penis, which is invaginable; a sperm sac is attached to the penial sheath and is filled with spermatozoa before each copulation; the veliger has a sinistral shell. The closest agreement is with the more primitive families of the tectibranchs, in which the genital duct is monaulic and male and female apertures lie at some distance from each other. Except for minor variations in proportion the penis and its sheath agree in general plan and in histology with those of *Philine aperta* (Pruvot-Fol, 1930): when the penis is extended a flow of sperm into it is rendered impossible by the arrangement of the ducts and a reservoir or sperm sac is therefore required.

Finally, it is to be noted from the conchological side, that the tooth on the columella—from the presence of which the genus *Odostomia* acquires its name —so characteristic of the Pyramidellidae, is also to be met with in the Actaeonidae, Ringiculidae and Diaphanidae amongst the tectibranchs.

If all these points be taken into consideration there is such a large number of characters in which the resemblance between the family Pyramidellidae and the Opisthobranchia is marked that it seems logical to remove the family from the subclass Prosobranchia to the subclass Opisthobranchia.[1] As to the precise position within the Opisthobranchia that the Pyramidellidae should occupy there is some doubt, because of our lack of knowledge of the soft parts of such opisthobranchs as *Actaeon*, *Hydatina*, *Diaphana* and *Haminea*, and, until such animals have been properly investigated, any assignation of the Pyramidellidae to a definite position must be tentative. In view of their stout, spiral shell and operculum, however, they are more primitive than all the opisthobranchiate families other than the Actaeonidae; because of their euthyneurous nervous system and loss of ctenidium they are more advanced than

[1] Owing to a misprint we appear (Fretter & Graham, 1949) to have said precisely the reverse of this in a letter to *Nature*.

that family but less than the Diaphanidae. Until more is known of the anatomy of these two families of the opisthobranchs the family Pyramidellidae may be placed between them.

The Pyramidellidae is not the only family of gastropods superficially prosobranch in appearance but probably opisthobranch in reality. The Omalogyridae, in which *Omalogyra* has been recently described (Fretter, 1948)—and from a preliminary study *Ammonicera* would seem to agree—have also an imposing assemblage of characters in common with the opisthobranchs: the animals are hermaphrodite; the penis is a long, whip-like muscular tube into which, during copulation, sperm are passed from a sac; there are no oesophageal glands; the stomach is simplified and is merely a space within the digestive gland; the intestine is short; large and histologically complex glands open into the mantle cavity, which is without a ctenidium but has strips of ciliated epithelium running forwards from the anus to maintain an exhalant flow of water. Unlike the opisthobranchs, but like most prosobranchs, the Omalogyridae produce egg capsules. It is uncertain to which group of the opisthobranchs these minute gastropods should be allied, for our present knowledge of the opisthobranchs is particularly poor so far as the most primitive members of the subclass are concerned—and these are the very ones involved.

Summary

The family Pyramidellidae contains a number of species of gastropod molluscs of similar structure and mode of life.

The shell is calcareous and spirally wound and may be closed by an operculum. The foot bears a transverse fold anteriorly, the mentum (Fig. 1, MT), separating the opening of the penial sheath (PO) below from the mouth (M) above. It has a lateral glandular streak on each side (Fig. 2), presumably sensory.

The head has ear-shaped tentacles (Fig. 1, T), richly innervated and with cilia setting up a strong water current, so that they constitute a powerful sensory mechanism. The eyes (E) lie between the tentacles.

The mantle cavity faces anteriorly, is wide and deep. To it open the anus, at its inner end; the kidney, on its roof; and the single genital aperture, on its floor. There is neither ctenidium nor osphradium, but well-developed hypobranchial and other glandular fields. A circulation of water is maintained by strips of ciliated epithelium in relation to these. A special pigmented structure, perhaps glandular, lies by the genital aperture and a ciliated tract leads from there to the opening of the penial sheath.

The 'mouth' leads to a long introvert with a specially glandular papillated epithelium (Fig. 1, EP; Fig. 8, EPL, EPT). At the inner end of this the true mouth (Figs. 1 and 4, M) lies on a sucker (Fig. 4, MCS, MOS) and an elongated oral tube (OT) leads to the buccal cavity. From a dorsal pouch of this (Figs. 1 and 3, DP)

a long stylet projects forwards (S), in a separate tube in *Chrysallida* and *Odostomia* but in the main oral tube in *Turbonilla*, and may be thrust outwards from the sucker. The stylet encloses the common duct of a pair of salivary glands (Fig. 3, USD). The posterior part of the buccal cavity is differentiated into a double muscular sac, the buccal pump (Fig. 1, BP), and the walls of this, the salivary ducts and sucker contain striped muscle fibres. From the buccal pump the oesophagus (O) runs to the stomach and digestive gland and thence a short intestine passes to the anus. There is no radula.

In the vascular system only a posterior aorta leaves the heart. The anterior aorta arises from the visceral haemocoel. Blood cells, active as excretory amoebocytes, are common.

The nervous system (Fig. 10) is mainly concentrated into a ring round the oesophagus and penial sheath and is euthyneurous. An osphradial ganglion (OG) lies in the mantle on the left and two pairs of ganglia lie ventrally in relation to the anterior end of the gut: these are the buccal ganglia (Fig. 1, BG), close to the buccal pump, and the labial ganglia (LC) in relation to the sucker.

The gonad is hermaphrodite (Fig. 11, H) and from it a narrow duct passes towards the mantle cavity (GD), receiving on its way ducts from the albumen gland (AG, DA) and proximal (MGU, DU) and distal (MGL, OL) mucous glands. Opposite the opening of the latter arises the duct of the receptaculum seminis (RS). The initial part of the broad pallial duct is glandular (GO) and is probably a prostate. From the common genital aperture in the mantle cavity an open seminal groove leads to the invaginable penis (Fig. 1, PO). A sperm sac is attached to the penial sheath (SS) and is filled before each copulation.

The eggs, each surrounded by albumen and enclosed in a mucous sheath which is continuous from one egg to the next, are embedded in secretion from the distal mucous gland and deposited in irregularly shaped clumps near the feeding grounds of the adult. The veliger is characterized by the sinistral shell and the pigmented gland on the right side of the mantle. Its oesophagus, intestine and commodious stomach, into which opens the bilobed digestive gland, are greatly modified during metamorphosis at the end of pelagic larval life.

Pyramidellids are ectoparasites. Each species feeds on a particular species of host, usually a tubicolous polychaete or a lamellibranch mollusc, obtaining attachment to the body by means of the oral sucker, piercing the body wall with the buccal stylet and sucking blood, and perhaps tissue débris, by means of the buccal pump.

A consideration of the structure and reproductive habits of the group leads to the conclusion that they are opisthobranchiate gastropods.

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MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM

Report of the Council for 1948–49

The Council has to record with deep regret the deaths of Professor Sir D'Arcy Wentworth Thompson, F.R.S., one of the first members of the Association and for many years a member of the Council; of Prof. Johan Hjort, For.Mem.R.S., an Honorary Member of the Association; of Mr R. Elmhirst, Director of the Millport Marine Station of the Scottish Marine Biological Association; and of Prof. Walter Garstang, a former member of the scientific staff and later Vice-President and an Honorary member of the Association.

The following have been elected Vice-Presidents of the Association during the year: G. P. Bidder, Sc.D.; W. T. Calman, C.B., D.Sc., F.R.S.; Vice-Admiral Sir John A. Edgell, K.B.E., C.B., F.R.S.; Prof. A. V. Hill, C.H., O.B.E., Sc.D., F.R.S.; H. G. Maurice, C.B.; E. S. Russell, O.B.E., D.Sc.; Sir Edward J. Salisbury, Kt., C.B.E., D.Sc., Sec.R.S.; Admiral Sir Aubrey C. H. Smith, K.B.E., C.B., M.V.O.

The Council and Officers

Four ordinary meetings of the Council were held during the year, two in the rooms of the Royal Society, one in the rooms of the Linnean Society, and one at the Plymouth laboratory. At these the average attendance was 16. The Association is indebted to the Councils of the Royal Society and of the Linnean Society for the use of their rooms.

Mr Alfred R. Wagg has been appointed an Annual Governor representing the Fishmongers' Company in place of Mr Benjamin Travers, A.F.C.

In July 1948 Dr G. P. Bidder attended a Royal Garden Party at Buckingham Palace as a representative of the Association.

The Council wish to record their thanks to Dr G. P. Bidder for his generous gift of a portrait of himself painted by the late Mr R. G. Eves, R.A. Dr Bidder made this presentation on the occasion of his fiftieth consecutive year as a member of the Council, and all members of the Association will wish to congratulate him and record their appreciation of his great services over so long a period.

The Plymouth Laboratory

The rebuilding of the east wing of the main building as laboratory accommodation has been completed.

The stainless steel piping in the tank room of the first floor of the main building, which was badly corroded, has been replaced by ebonite piping.

The workshop-store, near the main entrance gates, the limestone walls of which were not weatherproof, has been greatly improved by the construction of cavity walls and has now been rendered completely watertight. At the same time the opportunity has been taken to enlarge the workshop on the upper floor by extending it by 12 ft. to the north. This extension has a concrete floor suitable for carrying heavy machine tools. The cost of the whole of this work has been met from the remaining investments in the Building Fund of the Browne Bequest Fund.

One of the rooms on the ground floor of the north building has been fitted out as a workshop for the physiological laboratory. It has been fully equipped with tools, including a Myford $3\frac{1}{2}$ in. lathe.

The Aquarium

The aquarium has continued to arouse much interest and to attract large numbers of visitors in addition to the frequent attendance of parties of school children under the supervision of their teachers. The health of the fishes and of many invertebrates has been very good, while deaths among the fully established inhabitants of the tanks have been rare. During the year additions have been made to the fishes shown, notably mackerel, red mullet, sea-bream, whiting and John Dory.

Research Ships

The research vessel *Sabella* has worked throughout the year. In November certain alterations and additions were made to her; part of the forward hold was converted into living accommodation for research workers and the bridge was enlarged to accommodate the echo-sounding gear.

The new $61\frac{1}{2}$ ft. motor fishing vessel *Sula* arrived at Plymouth on 21 June 1948. Mr G. A. Steven accompanied her on the trip from Sittingbourne. She was quickly in commission and has proved most efficient and capable of doing all the work required of her in home waters, including hydrographical cruises to mid-Channel.

The *Gammarus* has as usual worked continuously throughout the year.

The Staff

The Council desire to congratulate the Assistant Director, Mr E. Ford, on his appointment as Director of the Millport Marine Biological Laboratory. Mr Ford has been a distinguished member of the laboratory staff since 1913, and he will be much missed at Plymouth. He will be taking up his appointment at Millport on 1 April 1949.

The Council have to report that Mrs E. W. Sexton retired from active work at the Plymouth laboratory on 31 March 1948. Mrs Sexton has been

associated with the laboratory since 1901, for many years as a voluntary worker, and her researches on amphipod crustaceans are of international repute. All will wish her a happy retirement.

Mr D. K. Hill has been appointed to the Staff as Physiologist, in the grade of Senior Scientific Officer; he took up his duties at Plymouth in June 1948.

Mr F. S. Russell attended the eighth General Assembly of the International Union of Geodesy and Geophysics in Oslo in August 1948, as a representative of the International Council for the Exploration of the Sea.

Mr D. P. Wilson and Dr L. H. N. Cooper attended the thirty-sixth meeting of the International Council for the Exploration of the Sea in Copenhagen in October 1948.

Occupation of Tables

The following ninety workers have occupied tables at the Plymouth laboratory during the year:

B. C. ABBOTT, London (Physiology of dogfish muscle).
A. A. ALEEM, London (Littoral diatoms).
FR. AUGSBURGER, Switzerland (Library).
Dr G. BACCI, Naples (Sex differentiation in *Asterina*).
Dr E. J. BATHAM, Cambridge (Nerve net of *Metridium*).
Dr ANNA M. BIDDER, Cambridge (*Sthenoteuthis*, and digestion in *Sepia*).
Prof. A. A. BOYDEN, New Jersey, U.S.A. (Systematic serology).
Miss E. M. BROWN, London (Protozoa).
C. BURDON JONES, Bangor (*Glossobalanus*).
Dr M. BURTON, British Museum (Nat. Hist.) (Sponges).
Dr R. W. BUTCHER, Fisheries Laboratory, Nottingham (Marine Flagellates).
H. W. CHANG, Academia Sinica, Shanghai (Biology of *Callionymus lyra*).
G. CHAPMAN, London (Mesogloea of *Calliactis*).
Dr R. I. B. COOPER, Cambridge (Seismic prospecting of sea-bed).
J. B. COWEY, Cambridge (Basement membrane in Nemertines).
Dr J. F. DANIELLI, London (Nucleus transplantation in *Echinus* eggs).
Miss S. DAVIES, British Museum (Nat. Hist.) (Polychaetes).
Miss E. DRESEL, Cambridge (Excretion in Isopods and Amphipods).
B. H. DUSSART, Geneva (General).
P. S. B. DIGBY (Planktonic copepods).
E. B. EDNEY, Birmingham (Water relations in *Ligia*).
P. FATT, California (Nerve action potentials in *Sepia* and Selachians).
J. E. FORREST, London (Nudibranchs).
H. C. FOUNTAIN, Torpoint (Marine Acarines).
Dr VERA FRETTER, London (*Proneomenia*).
M. H. W. GALL, Cambridge (Light penetration in the sea).
Miss E. GONZALEZ, Manchester (Red Algae).
A. T. GOODMAN, Plymouth (Library).
Miss U. M. GRIGG (Biology of Trochids).
R. E. HALL, Southampton (Marine Chironomids).
Miss J. HANSON, London (Serpulids and Sabellids).
Prof. J. E. HARRIS, Bristol (Neurophysiology of dogfish embryos).
Dr T. J. HART, Discovery Investigations (Ice Diatoms; hake).
N. I. HENDEY, Admiralty (Hydrogen-ion concentration).

M. N. HILL, Cambridge (Seismic prospecting of sea bed; and bottom sampling).
A. R. HOCKLEY, Southampton (Occurrence of *Mytilicola* in *Mytilus*).
A. L. HODGKIN, Cambridge (Neurophysiology).
N. A. HOLME (Bottom fauna).
Dr W. HOLMES, Oxford (Nervous system of *Amphioxus*).
Prof. SVEN HÖRSTADIUS, Uppsala (Nucleus transplantation in *Echinus* eggs).
O. D. HUNT, Newton Ferrers (Fouling organisms).
A. F. HUXLEY, Cambridge (Neurophysiology).
Dr V. G. JHINGRAM, India (Fisheries).
Dr B. KATZ, Cambridge (Neurophysiology).
G. KERKUT, Cambridge (Movement in starfishes).
R. D. KEYNES, Cambridge (Neurophysiology).
Prof. W. B. R. KING, Cambridge (Bottom sampling).
Prof. H. KIRBY, California (Protozoology).
Dr P. L. KRAMP, Copenhagen (Hydromedusae).
Dr MARIE V. LEBOUR, Cawsand (Larval Decapods from Bermuda).
Miss KARIN LINDBLAD, Sweden (Algae).
Dr I. JOAN LORCH, London (Nucleus transplantation in *Echinus* eggs).
Dr O. LOWENSTEIN, Glasgow (Electrophysiology of the labyrinth in *Raia*).
Dr A. G. LOWNDES (Density of aquatic organisms).
M. D. MENON, Madras (Biology of *Gadus luscus* and *G. minutus*).
Prof. LILY NEWTON, Aberystwyth (Library).
W. G. O'DRISCOLL, Admiralty (Hydrogen-ion concentration).
Dr L. O. OHMAN, Sweden (Physiology of *Echinus* and *Pomatoceros* eggs).
Dr A. P. ORR, Millport (Research ships).
Prof. J. H. ORTON, Liverpool (Biology of *Patella*).
Dr C. F. A. PANTIN, Cambridge (Nerve net of *Metridium*).
Dr H. E. QUICK, Swansea (Marine Pulmonates).
Miss M. RIDALL (General biology).
J. M. RITCHIE, London (Physiology of dogfish muscles).
T. D. M. ROBERTS, Glasgow (Electrophysiology of the labyrinth in *Raia*).
Dr D. M. ROSS, London (Facilitation in sea anemones).
Miss H. G. Q. ROWETT, Plymouth (Library).
Dr E. S. RUSSELL, Hastings (Decapods).
G. SESHAPPA, Cullercoats (*Littorina saxatilis*).
E. W. SIMON, Oxford (Toxicity studies in *Echinus* eggs).
Miss J. SINGER, Cambridge (*Cordylophora*).
B. W. SPARROW, Newton Ferrers (Fouling organisms).
Miss F. A. STANBURY, Plymouth (Library).
U. STEFANSSON, Reykjavik (Chemistry of sea water).
Mrs O. TATTERSALL, Cardiff (Mysids).
J. A. THOMPSON, Cullercoats (Research ships and gear).
Dr M. A. THYNNE, Plymouth (Microtomy).
D. W. TUCKER, Liverpool (Ecology of *Patella*).
Miss VIDYA VATI, Lucknow (Embryology of fishes).
D. J. VAUX, Lowestoft (Physical oceanography).
Capt. R. CH. VEEN, Netherlands Indies Government (Research Ships and Hydrography).
Miss L. E. WAGGE, London (Calcium metabolism in marine animals).
P. R. WALNE, Conway (Chemistry of sea water).
Dr C. C. WANG, Academia Sinica, Shanghai (Protozoology).

Dr R. J. WEISS, Luxembourg (General biology).
G. P. WELLS, London (Physiology of *Arenicola*).
Miss E. WHITEHEAD, London (Library).
Miss E. WHITTINGTON, Exeter (Library).
E. J. FERGUSON WOOD, C.S.I.R. Australia (Algae and anti-fouling).
Dr W. H. YUDKIN, Cambridge (Phosphagens in Polychaetes).

A large number of visitors have taken the opportunity of spending a few days in Plymouth to see the work of the laboratory or discuss problems with members of the scientific staff. Among these the following have come from overseas:

Prof. Marcel Avel, Bordeaux; J. J. Baal, Jersey; T. W. Burdon, Fisheries Officer, Malaya; A. B. Cashmore, C.S.I.R., Canberra; Lt.-Cdr. A. P. Cumming, Vice-Consul, Tromsø; Prof. Jan Dembowski, Poland; Dr R. H. Fleming, U.S. Hydrographic Department; J. D. Kelsall, Fisheries Officer, Lake Victoria; Oo King, Burma; Ole Matthiesen, Oslo; Prof. D. Merriman, Director, Bingham Oceanographic Laboratory; R. J. Midwinter, Fisheries Officer, Gambia; R. T. M. Pescott, Director, National Museum of Victoria, Melbourne; H. Postma, Zoological Station, Den Helder, Holland; Dr R. R. Prasad, India; Prof. E. B. Rao, Madras; Prof. J. Runnström, Stockholm; Dr R. Dana Russell, U.S.N. Electronics Laboratory; Prof. Bradley T. Scheer, University of California; Dr Sun Yia-Chu, Director, Geographical Department, Peking University; Cdr. R. H. Thornton, C.S.I.R., Australia; Dr R. Wojtusiak, Poland.

The Easter Vacation Courses were conducted by Mr D. P. Wilson and Mr G. A. Steven, and were attended by forty-four students from the following Universities and University Colleges: Oxford, Cambridge, London, Edinburgh, Glasgow, Liverpool, Birmingham, Bristol, Sheffield, Bangor, Cardiff, Newcastle, Southampton, and from Chelsea Polytechnic and SW. Essex Technical College.

Also during the Easter Vacation Mr A. H. Lewis brought two boys from Wellington College, and Mr A. A. M. Gardiner six from Radley.

At the end of August a course for biology teachers was conducted by Dr J. E. Smith, Dr G. E. Newell and Miss G. C. Evans, at which the attendance, which included some students, was twenty.

Scientific Work of the Plymouth Laboratory Staff

Physics and Chemistry of Sea Water

Dr W. R. G. Atkins continued the recording of daylight during 1947 and 1948 with Miss P. G. Jenkins. The period from 1930 covers thirteen years.

With Dr H. H. Poole and Mr F. J. Warren seasonal changes in the penetration of daylight into the sea were further studied. The cube photometer, with

new rectifier cells, measures the vertical component, downwards and upwards. The visibility of objects viewed against deep water is related to the latter. The horizontal component is measured in four azimuths, and the average angle of obliquity is thus determined. The vertical component was also measured with vacuum cells and colour filters. For some of this work a d.c. amplifier of R.C.A. design was assembled by Mr Warren. In addition to measurements with Dr Poole's original apparatus, some were made with a Tinsley galvanometer on gimbals. Prof. J. H. J. Poole's neon tube photometer, used successfully at sea previously, was combined with an amplifier and counter. Though excellent ashore there is some leakage trouble at sea. A faster rate of flashing—up to 10–12 per sec.—can be measured with the counter than is possible by eye. A simple method has been introduced for determining the extinction coefficient of sea water at moderate depths. Two rectifier photocells, mounted as usual, are connected to a small microammeter so as to oppose each other and their sensitivities are equalized. For the small currents generated when the cells are under opals and green filters the current-illumination relation is rectilinear. The deck cell is then covered by an additional opal which reduces the light to about 65 %, and the sea cell is lowered to balance. A denser opal being substituted, the cell is lowered further and the depth noted again. Finally, both opals are used together, so that the deck cell gives about 6 % of its original current. As always, accuracy depends upon the height of the waves. The microammeter can be held in the hand and is inexpensive. Mr Maurice Gall used an apparatus embodying the same principle on a coastal cruise. It may be termed 'the photoelectric balance by depth method'.

For comparison, extinction coefficients were measured by photoelectric cells and Pulfrich photometer, using the method introduced by Dr Cooper for the latter; though the conditions are fundamentally different it was not expected that the Pulfrich values would be three times as great. The Pulfrich readings altered on standing. It was surprising to see that water from 20 miles out had suspended matter which settled so quickly. The optical examination of sea water was begun to study the effects of light, but is now used to follow the movement and variation of suspended matter and because non-motile organisms suffer vertical movements which alter the light they get. Though the layering, found by Prof. Pettersson in Scandinavian Fjords, is unlikely to be as well marked here, it may be considerably better developed than we thought. Thus for physical and biological reasons it became desirable to study the scattering of a beam of light. Accordingly, a photo-cell was mounted in a tube capable of rotation around a flask and the brilliance of the Tyndall effect was measured at a series of angles, throughout the year, mostly with a selenium cell, but later with a caesium antimony cell and amplifier. For very small currents the Winfield electrometer triode null method is good and was also used to restandardize old photocells and to test new ones.

Dr Atkins and Mr J. M. Ritchie continued the measurement of very low

illuminations using the R.C.A. electron multiplier cell. The use of over 1000 V. in a marine atmosphere entails special precautions. The light of the night sky is detectable over the area covered by a theodolite telescope, and gives a few scale divisions, at the end of nautical twilight (about 80 min. after sunset). This is about 10^{-5} lux, and full sunlight as much as 10^{5} lux, so the range of natural illumination measured is of the order of 10^{10}.

During the war Dr Atkins worked on visual range and lamp penetration range for the Air Ministry. He and Dr Poole are trying to apply similar conceptions to under-water visual range. For horizontal visibility a periscope, converted from the drift indicator of a bomber, is used.

Dr Atkins had suggested that autotrophic flagellates might be the major constituent of the phytoplankton, since silicon consumption was inadequate to account for phosphorus taken up were diatoms alone responsible and diatom tests are extremely insoluble. To follow this relation, and gear it to the optical work, he determined the seasonal changes in the phosphate and silicate throughout the water column at E1. The copper cycle was also studied, but for the surface only, since the water-bottles give off copper. To ascertain whether clay in suspension is a source of silicate, with the help of Mr F. A. J. Armstrong, who was appointed an Experimental Officer last spring, a carboy, about 20 l., of water was filtered monthly and the residue analysed after ignition. Inorganic matter—clay and diatom tests—was 12–190 mg. Mr Armstrong's analyses showed that the solids in suspension contained a far greater weight of silica and of iron than was in solution. The aluminium content of the residue decreased greatly in summer, suggesting that an alumino-silicate had gone into solution. It would be well to supplement analyses of nutrients in solution by analyses of suspended matter; for 10 mg. from 20 l. means 0·5 mg./l., or 0·5 g./m.^{3}, or one part in two million, whereas phosphorus, for example, is reckoned in parts per thousand million.

To follow seasonal production of the phytoplankton the deposit on the filter-paper was extracted with acetone. The April extract was a deep yellowish green, but that for August was almost colourless. If the filtration were carried out immediately after collection of the water such extracts could give quantitative results. The extracts now in hand show the general trend well.

Dr H. W. Harvey has continued investigations on the total phosphorus and phosphate in the sea off Plymouth.

The data so far obtained are indicating that the total quantity of phosphorus in the whole water column undergoes no significant seasonal change, although there is some redistribution in depth, the quantity in the upper 20 m. layer becoming somewhat less in summer, with a slight increase in the 20–40 m. layer. Thus, evidence is accruing that the total phosphorus in the water is a distinctive index of different water masses. The quantity in the water off Plymouth fluctuates from month to month, as the water occupying the area moves away to be replaced with water from other areas.

Water masses in the English Channel have been encountered during the course of our ships' cruises, having very different contents of total phosphorus —water columns averaging 11 mg. and others averaging 20 mg. phosphorus per cubic metre.

The increase in dissolved organic phosphorus compounds, which takes place from winter to summer, is presumably an index of the population density of living organisms in the water during this interval; the magnitude of this increase is very different in different water masses. In those with a greater content of total phosphorus more dissolved organic phosphorus had been set free during the first six months of the year, and also, at the time of sampling, there is frequently more plankton present in the water column. With the object of obtaining more data concerning the relation between the momentary plankton population and the total phosphorus content of the water, Dr Harvey has been engaged in developing a meter which registers the water filtered by plankton nets. It is of interest that the eddies or negative pressure set up in the wake of a conical net aid the passage of an unexpectedly large volume of water through the pores of fine-meshed nets.

A method of estimating manganese in solution has been developed and has shown that the sea off Plymouth contains less than 1 mg. soluble Mn per cubic metre, a result in agreement with previous biological estimations. This small quantity is mostly adsorbed on organisms and detritus. In the sea off the Isle of Man more than twice this quantity was found. This is an area where flagellate algae are usually very numerous in summer; these plants have been shown to be particularly sensitive to low concentration of manganese in solution. Various river and lake waters were found to contain 1–40 mg. soluble Mn per cubic metre—considerably more than in the adjacent sea. The results are being published in Vol. XXVIII, No. 1 of the *Journal*. Experiments designed to show what happens to dissolved manganese which enters the sea have led to tentative conclusions which it is hoped to develop by the use of radio-active manganese.

During more than half a century a very large mass of physical, chemical and biological records has accumulated from the western English Channel and neighbouring waters. With our present knowledge, particularly of the distribution of nutrient salts and of biological indicators, much of the earlier work now reveals meaning which could not have been seen at the time it was done. Since 1945, Dr L. H. N. Cooper has spent much of his time in an attempt to reassess and correlate the earlier work in the area. At the same time he has been attempting to apply recent developments in the theory of physical oceanography to problems of shelf hydrology. Papers are almost complete on the following: the distribution in the Atlantic in relation to hydrology of the siphonophores, *Muggiaea atlantica* and *M. kochi*, which show much promise as biological indicators, not so much of local water movements as of changes in oceanic circulation; a theoretical method of computing wind-drift of

water with especial reference to an observed change in distribution of *M. atlantica*; the relation of tidal energy to the distribution of plankton species; and some hydrological themes. Four papers have appeared in Vol. XXVII, No. 2 of the *Journal* on the distribution and physical chemistry of iron in the sea, on the possibility of the existence of particulate ammonia in the sea and on some reflexions of phosphate distribution shown by fishery statistics. A review on the nutrient balance in the sea has been published elsewhere.

Mr F. A. J. Armstrong now undertakes the monthly hydrological cruises and the subsequent determinations of inorganic and total phosphorus. He is also adapting and improving other methods, such as that for nitrate, for use with Dr Harvey's photoelectric absorptiometer.

The echo-sounder has revealed a submarine declivity parallel with, and about two miles outside, Plymouth Breakwater. A study by Dr Cooper has shown that its height lies at a mean depth of 39 m. below L.W.S. and its height from foot to brow is about 10 m. It appears to represent a cliff cut during a period when the level of the sea stood at least 40 m. lower than to-day. The submerged banks of the estuarine channel of the combined Tamar and Plym are clearly evident for several hundred metres inshore of the coastal declivity.

Plankton

Mr F. S. Russell has continued the preparation for publication of his monograph on British Medusae. During the year Dr P. L. Kramp of the University Zoological Museum at Copenhagen spent a short time at Plymouth and kindly read through much of the manuscript and gave helpful advice.

Examination of the year's series of half-hour oblique hauls with the 2 m. stramin ring-trawl has not yet been completed by Mr P. G. Corbin. It is, however, evident that the numbers of young fish have again remained low, and *Sagitta* species have been generally scarce. Both *Muggiaea atlantica* and *M. kochi* occurred during the summer, and in the autumn small numbers of salps and doliolids were taken, as well as considerable numbers of the medusa, *Liriope*, an *elegans* water indicator. Other *elegans* water indicator species were, however, not numerous.

A paper on the post-larval *Ammodytes* species of the Celtic Sea and Plymouth area by Mr Corbin and Miss Vati will be published in Vol. XXVIII, No 1 of the *Journal*. Four species of *Ammodytes* post-larvae occur. These belong to *A. lanceolatus*, *A. tobianus*, *A. marinus* and a fourth species of *Ammodytes*, the adult of which, it is concluded, is not yet known. With *A. cicerellus*, of which further adult specimens have been taken during the year, this makes a total of five *Ammodytes* species for the area.

A study has also been made by Mr Corbin of the distribution pattern of the scales on adult *Ammodytes* species. It has been found that the pattern in *A. tobianus* is quite distinct from that in *A. marinus*. This character, which

applies over the wide variation in the number of vertebrae occurring within the geographical range of *tobianus* and *marinus*, provides grounds for concluding that both are good species. There previously existed considerable divergence of opinion as to whether they were species, subspecies or races. The different patterns are recognizable in individual specimens. The two species may thus be identified without counting the number of vertebrae in a large sample, which was formerly necessary for their satisfactory separation.

Mr P. S. B. Digby, with a grant from the Development Fund, continued the work on the collections of smaller planktonic copepods made in the Plymouth area during 1947 and until June in 1948. On the basis of the relative numbers of the different stages of the various species and their size graphs, provisional conclusions can be drawn regarding the breeding and number of generations passed through in the course of the year. The observations have been made at the hydrographical station L 4, close to Plymouth, and the validity of the conclusions rests on proof that the changes observed at Plymouth occur in similar fashion over a large area, and are not unduly affected by movements of the water masses. Subject to these limitations we may say that for the species investigated—*Paracalanus*, *Pseudocalanus*, *Oithona*, *Temora* and *Acartia*—breeding is continuous in that nauplii are found throughout the year. The adults which live through the winter die out in February or March, having given rise to nauplii which produce a sparse population of adults of large size in March and April. The individuals of the following brood of adults are of smaller size and occur in May, June and July, and the next are of smaller size still and occur in August and September.

Thus it would appear that in the sea off Plymouth these copepods all pass through four generations in the year in a closely similar manner. It may well be that factors influencing survival of the nauplii and young stages of all the species together may serve to keep the breeding times of the population in step, when each species might have a different time if reared individually under laboratory conditions.

During the summer Mr Digby went to Spitsbergen, where he was based, mainly in Advent Bay, from 11 July to 10 September. A large number of plankton collections were made with vertical tow-nets and a modified Clarke-Bumpus Sampler to study the vertical distribution of plankton under conditions of continuous daylight.

Cultures of marine planktonic diatoms and flagellates have been maintained throughout the year and subcultures have been sent to other countries and other institutions in Britain for research purposes. A study, started at the Port Erin Marine Biological Station, of six of these marine flagellates has been completed by Dr Mary Parke and will be published in Vol. XXVIII, No. 1 of the *Journal*. A form of reproduction in a palmelloid-phase, not previously described, is recorded for those species belonging to the Chrysophyceae. All six are new and four of them have been placed in three new genera.

Fauna and Flora of the Sea Floor

Mr D. P. Wilson has published in Vol. XXVII, No. 3 of the *Journal* a description of the development of the polychaete *Ophelia bicornis* Sav. and an account of his experiments in 1946 and 1947 on the settling reactions of the larvae of this species. These experiments were continued in 1948 with the object of obtaining further data from which the factor or factors responsible for initiating metamorphosis could more certainly be deduced. The earlier experiments had shown fairly conclusively that size and shape of the interstices among the sand grains, a purely physical environmental character, was the main factor responsible, but it was felt that further evidence was desirable in view of the important bearings these findings have on the ecology of larval settlement generally. The 1948 experiments, therefore, while on similar lines to the earlier ones, included tests with various non-marine sands, with artificial glass spheres (Chance's 'Ballotini') and with sand from the *Ophelia* grounds at Exmouth graded and recombined with an unnaturally large proportion of the smallest grains. The results obtained fully confirmed previous conclusions that physical size and shape of the sand grains is all important, while there was no indication whatever that anything in the nature of a soluble substance present in the natural sand plays a part in stimulating *Ophelia* larvae to metamorphose.

Difficulties in obtaining healthy fertilizations were experienced during the early part of the breeding season. After discussions with Dr Cooper it was decided to compare larvae reared in Channel water from the immediate vicinity of Plymouth with larvae from the same batches of eggs reared in western water from a region well to the west of the Isles of Scilly. In a few trial comparisons it was found that *Ophelia* larvae were healthier and lived longer in the western water than in the Channel water. This difference could not be due to food as both kinds of water had been passed through a Berkefeld filter and the larvae at the time were not feeding. However, the experiments were too few for definite conclusions to be drawn; it is proposed to continue them next year.

In the course of preparation of Part II of 'the distribution of *Gammarus* species in estuaries', Mr G. M. Spooner has examined some new collections from the Rivers Avon and Yealm to fill in gaps in the data previously obtained. A clearer picture is now available of the sporadic distribution of *G. chevreuxi* which, though plentiful in suitable points in all branches of the big watershed which includes the Plym, Tavy, Tamar and Lynher, appears to be completely missing from the Yealm and its branches, as well as from the Avon, and apparently from other South Devon rivers, for which records to date are all negative. Though it is a south-western species (with its range extending eastward to Hampshire and northward to north-east Ireland and Anglesey),

such an abrupt break in its distribution as occurs between the Plym and Yealm estuaries is difficult to explain.

Some further samples of *G. zaddachi oceanicus* from the west coast of Scotland, kindly sent by the late Mr R. Elmhirst, have been seen, indicating that this is a prevalent form in sea lochs at least as far south as Loch Duich opposite Skye. Examination of additional material of *G. locusta* from pure marine habitats suggests that a distinct form is separable in which the male antenna 2 has dense hair tufts in which many hairs are curled, and the female a shorter gnathopod 2 hand; but decision whether this is a habitat form or possibly a valid species awaits more information.

Some attention has been given to the distribution of *Corophium volutator* as an estuarine species, with the immediate result that a new species, hitherto confused with *volutator*, has come to light. The new species occurs at the top end of estuaries in low salinities, in a variety of situations, such as amongst clumps of *Cordylophora*, in the debris of reed beds, and in brackish ditches; but apparently not often in bare flat ground or open saltings pools as does *Corophium volutator*. So far it has been found in the Rivers Plym and Tamar. Immatures can be recognized from those of *C. volutator*.

Samples of *Corophium arenarium*, collected by Mr N. A. Holme on the Exe estuary, have been examined and additional characters distinguishing this species from *C. volutator* have been noted. The two species are confirmed as distinct, and all individuals can be separated, a point which the existing description leaves open to doubt.

Dr Mary Parke has published in Vol. XXVII, No. 3, her first paper on the British Laminariaceae, dealing with *Laminaria saccharina* (L). Lamour.

The occurrence in Plymouth Sound of a species of *Laminaria* new to Britain, *L. ochroleuca* De La Pylaie, has been recorded by Dr Parke. Its distribution in the Sound has been ascertained but so far it has not been found on any other part of the South Devon coast. A record has been kept of the colour change in the frond throughout the year and the times of rapid and slow growth have also been observed for comparison with the other species. Growth in this species is very similar to the growth in *L. digitata*. The gametophytes have been grown in culture from the zoospores and the young sporophyte stages obtained from them. The gametophytes and young sporophytes show little variation from those of the other British *Laminaria* species.

At the same time the opportunity was taken of testing whether certain algae secrete antibiotic substances which can inhibit the development of competitive algae and other cultures of *L. ochroleuca* were set up. To these were added pieces of living tissue of different brown algae. All cultures produced healthy gametophytes on which numerous sporophytes developed, as did those cultures without the addition of other algae; none of the gametophytes was decolorized by the addition of any one of the other species. These experiments

need to be repeated, however, using the zoospores of other *Laminaria* species and the fertilized oogonia of the Fucaceae.

Additions have been made to the collection of preserved specimens of marine algae being built up at the laboratory; the most interesting of these are *Desmarestia dudresnayi* Lamour. and *Carpomitra costata* Batt., since neither has been recorded since 1896. Further information has also been accumulated on the distribution and periodicity of reproduction of the marine algae of the Plymouth area.

Mr H. G. Vevers has now carried his investigation of the growth and reproduction of *Asterias rubens* over two breeding seasons and some of the results will be published in Vol. XXVIII, No. 1 of the *Journal*. In addition to the populations studied in 1947 a new population of starfishes was found in the spring of 1948 in Plymouth Sound. Although living in an area subject to a low winter temperature and to pollution by fresh water this population showed a very high percentage of large ripe gonads. As in the other populations it is considered that the high percentage of ovarian maturity in this population and the large absolute size of the ripe gonads is primarily correlated with the richness of the available food supply, which in this area consisted of a large bed of mussels. In general, the investigation has shown that the productivity of a starfish population is not related to age. Poorly-fed starfish survive and show little or no gonad maturing while well-fed starfish grow fast and reach breeding condition in their first year. The production of a large homogeneous population of starfishes depends upon the availability of a food animal which must not only be present in large numbers but whose mean size must be at an optimum to suit the size of the starfishes.

Preliminary work has been done on the development of an underwater camera for work at 70–100 m. This is designed to take a series of 40–45 photographs of the sea bottom at a single lowering, and it is hoped that by this means information may be obtained on the horizontal distribution of starfishes and other bottom-living animals.

An investigation has also been started on the breeding biology of *Amphioxus lanceolatus* in the Plymouth area.

Mr N. A. Holme, on a D.S.I.R. grant, has spent much of the year working on material collected from the Exe estuary in the summer of 1947. As a result of peculiar conditions arising from erosion of Dawlish Warren it has been possible to study the fauna of soils ranging from sand to mud, differences other than those directly due to the type of soil being eliminated. A paper giving the results of the survey is being published in Vol. XXVIII, No. 1 of the *Journal*.

In addition, preliminary attempts have been made at an evaluation of the quantity of animal life on the sea bottom. A new grab has been designed and built which takes rather better samples than those obtained with the Petersen Grab. During a cruise in Great West Bay in August 1948 the grab was worked on a variety of soils with success. The material collected is being

identified, and it is hoped that a note on the fauna of this area will be published shortly. The fauna of Great West Bay is rather poorer than that of the Plymouth area, but a number of interesting species have been recorded, including a specimen of *Lepidasthenia argus* Hodgson previously recorded only from Salcombe and from one locality near Plymouth.

Miss U. M. Grigg, also on a D.S.I.R. grant, has been working on the four species of Trochid molluscs common near Plymouth, *Monodonta lineata* (da Costa), *Gibbula cineraria* (L.), *G. umbicalis* (da Costa) and *Calliostoma zizyphinum* (L.): all are shore animals.

It appears that the change in shell shape from a flat cone to a tall tumid one occurs with size and is not conditioned by environment. The length of life is probably not more than two years. Males and females appear to be present in about equal numbers. The breeding season of the *Gibbula* species is in the early spring, *Calliostoma* breeds in May and June, and *Monodonta* in July and August. Attempts to rear the young, and to find where they metamorphose, have so far failed. The members of this family avoid a shifting substratum, turbid water, strong currents and low salinity. *Monodonta*, which has the most restricted habitat, is more common in the area than the accounts of its distribution would suggest.

Specimens of the deep-water *Gibbula magus* (L.), *Calliostoma papillosum* (da Costa) and the dwarf albino variety of *C. zizyphinum*, mentioned by S. Pace, have been obtained from localized collecting grounds where they do not appear to be common. No examples of *Gibbula tumida* (Montagu) or any of the three species of *Cantharus* recorded for the district have been observed.

Physiology of Marine Animals

Mr D. K. Hill has been continuing on a line of work which was started at Cambridge in the spring of 1948 concerning the nature of a change in optical opacity of non-myelinated nerve fibres resulting from stimulation. A first step in the attempt to discover the cause of this phenomenon has necessitated the construction of an apparatus with the aid of which the effect of electrical stimulation can be compared with any change in opacity that can be induced by chemical agencies, such as drugs known to affect the metabolism of nervous tissues (e.g. veratrine), or by changes in the ionic content of the fluid surrounding the isolated nerve. The evidence obtained in this way made it seem probable that the phenomenon could largely be accounted for by the swelling or shrinking of individual fibres in response to osmotic pressure or volume changes across the membrane. To test this hypothesis a direct measurement has been made of the alteration in diameter of a single giant fibre from *Sepia*. The change is very small, but it has proved possible to measure it: there is an increase in diameter of about 0·16 micron as the

result of 10,000 impulses passed down the fibre. It seems likely that the effect is largely due to the difference in volume between the hydrated sodium and potassium ions which are known to exchange across the membrane during activity. The next step will be to record the alteration in opacity of a nerve with a much higher speed than has been possible so far, and in this way to determine what happens during the interval while the action potential is passing.

Some preliminary experiments have been made by Mr G. M. Spooner to examine possible effects on organisms of radioactive elements present in solution in the water in which they are living. Certain isotopes emitting β-rays are being used. *Gammarus chevreuxi* kept in 25% strength sea water is a convenient invertebrate animal for investigating lethal and sterilizing doses. An approximate lethal dose for adults has been found. For the young the dose is rather less, especially if treatment starts two to three days before they are extruded from the mother's pouch. A much lower dose, however, is effective in causing sterilization of breeding adults.

Tests with a marine green flagellate (*Chlamydomonas* sp.) show a high resistance to treatment. Cultures persist with the activity of the medium of 100 μcurie per ml.

Further experiments testing the absorption of certain isotopes by different types of marine algae are in progress, using simple 'tracer' technique.

Fish and Fisheries

During the year, Mr E. Ford has continued his study of the anatomy and spatial form of the neurocranium in gadiform fishes. The growth centres of the supraoccipital, frontal plate, mesethmoid, prevomer, parasphenoid and basi-occipital lie in the longitudinal vertical plane about which the neurocranium is bilaterally symmetrical. By sawing skulls in half along this plane, and then marking the position of these bone centres, the form of the polygon between them can be accurately determined in both linear and angular dimensions. This polygon is not only highly diagnostic of species, but is a very practical and informative means for drawing comparisons between species, according to a natural and strictly comparable set of coordinates. It is hoped that a first report on the work will soon be ready for publication.

Mr G. A. Steven has continued to work up the results of his investigations into the life-history and biology of the mackerel and a paper on 'Mackerel Migrations in the English Channel and Celtic Sea' was published in Vol. XXVII, No. 3 of the *Journal*.

Following upon these studies of the migrations a relevant study of the Newlyn deep-sea fishery has now been made. This reveals that, in general, the best catches are to be expected near the periphery of the areas of greatest

spawning intensity especially on the landward side. The reason why fishing is not successful actually in those areas of high spawning activity has not been established, but there is some evidence to suggest that mackerel in full spawning are at too great depths to be taken in the drift nets. Now that the Association's larger vessel is equipped with echo-sounding gear it is hoped that a survey of the spawning grounds at spawning time with the echo-sounder may yield useful data on this point.

It has also been found that by far and away the best catches are taken in what east-coast fishermen call 'yellow' water and Cornishmen call 'cow-dung' water. This is water of a yellowish green colour that is not very common and in some years may not be found at all. When present it is rich in calanoid copepods. These, when preserved, often release into the preserving liquid certain pigments, possibly carotenoids, that cause the fluid to assume nearly the same hue as the 'yellow' water from which they were taken. But this, of course, also applies to calanoid copepods taken in waters of other colours. The problem of 'yellow' water is, therefore, being further investigated. At present the explanation seems to be that the presence of extra large numbers of calanoid copepods attracts mackerel to the spot, and that the colours of the fish and those of copepod pigments (either in the living animals or in faecal products) combine to produce the characteristic 'yellow' colour.

It has been established that the shoreward migration of the mackerel in this area is not a spawning migration; but neither is it a feeding migration, as has also been suggested. There is nothing to support the belief that the fish come inshore *in order to* feed because they pass through and leave behind them an abundance of food on the way. There is merely a change of diet from predominantly planktonic crustacea in offshore waters to a diet consisting largely of small fish in inshore localities. A detailed study of the distribution of mackerel food on the fishing grounds, and of the feeding habits of the fish, is nearing completion and is now being written up.

The Library

The thanks of the Association are again due to numerous foreign Government Departments, and to Universities and other Institutions at home and abroad for copies of books and current numbers of periodicals presented to the Library, or received in exchange for the *Journal*. Thanks are also due to those who have sent reprints of their papers, which are much appreciated.

The Association is also very grateful to Sir Sidney Harmer, F.R.S., for his gift of a collection of scientific papers, including a long run of Monographs of the Siboga Expedition, and to the late Prof. W. Garstang, especially for a copy of Jonathan Couch's *Cornish Fauna*, annotated and illustrated by Couch himself.

Published Memoirs

Vol. XXVII, No. 2, of the *Journal*, was published in April 1948, Vol. XXVII, No. 3, appeared in December, and Vol. XXVIII, No. 1, is nearing completion.

The following papers, the outcome of work done at the laboratory, have been published elsewhere than in the *Journal* of the Association:

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ATKINS, W. R. G., 1948. Note on the spectroscopic and biological detection of potassium in sea water and 'potassium-free' artificial sea water. *Journ. du Conseil*, Vol. XV, pp. 169–72.

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BURTON, MAURICE, 1948. The synonymies of *Haliclona angulata* (Bowerbank) and *H. arcoferus* Vosmaer. *Ann. & Mag. Nat. Hist.* (12), Vol. 1, pp. 273–84.

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COOPER, L. H. N. & STEVEN, G. A., 1948. An experiment in marine fish cultivation. *Nature*, Vol. 161, p. 631.

DAS, S. M., 1948. British Folliculinidae (Ciliata, Heterotricha). *Nature*, Vol. 162, p. 534.

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HODGKIN, A. L. & KATZ, B., 1949. The effect of sodium ions on the electrical activity of the giant axon of the squid. *Journ. Physiol.*, Vol. 108, pp. 37–77.

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Membership of the Association

The total number of members on 31 March 1949 was 505, being 47 more than on 31 March 1948; of these the number of life members was 72 and of annual members 433. The number of Associate members is now six, Dr W. T. Calman, C.B., F.R.S., Mrs S. W. Kemp, Mr J. L. Parkinson and Mr R. A. Todd having been elected during the year and Mr G. H. Wailes having died.

It is gratifying to record that since March 1945 the total membership of the Association has been increased by 139.

Finance

General Fund. The thanks of the Council are again due to the Development Commissioners for their continued support of the general work of the laboratory.

Capital Grants. The Council wish to record their thanks to the Development Commissioners for generous capital grants from the Development Fund towards the cost of rebuilding the East Wing, the completion of the research vessel *Sula*, and the modification of the *Sabella*.

Private Income. The Council gratefully acknowledge the following generous grants for the year:

From the Fishmongers' Company (£500), the Royal Society (£50), British Association (£50), Physiological Society (£30), The Ray Lankester Fund (£20), the Cornwall Sea Fisheries Committee (£10), the Universities of London (£210), Cambridge (£125), Oxford (£100), Bristol (£50), Birmingham (£31. 10*s*.), Leeds (£20), Durham (£10. 10*s*.), Manchester (£10. 10*s*.), Nottingham (£10. 10*s*.), Exeter (£10. 10*s*.), Leicester (£10. 10*s*.), Southampton (£10. 10*s*.), Sheffield (£5), and the Imperial College of Science and Technology (£10).

President, Vice-Presidents, Officers and Council

The following is the list of those proposed by the Council for election for the year 1949–50:

President

Prof. JAMES GRAY, C.B.E., M.C., Sc.D., LL.D., F.R.S.

Vice-Presidents

The Earl of IVEAGH, C.B., C.M.G.
Viscount ASTOR
Sir NICHOLAS E. WATERHOUSE, K.B.E.
Sir SIDNEY F. HARMER, K.B.E., Sc.D., F.R.S.
Col. Sir EDWARD T. PEEL, K.B.E., D.S.O., M.C.
The Rt. Hon. TOM WILLIAMS, M.P.
G. P. BIDDER, Sc.D.
W. T. CALMAN, C.B., D.Sc., F.R.S.
Vice-Admiral Sir JOHN A. EDGELL, K.B.E., C.B., F.R.S.
Prof. A. V. HILL, C.H., O.B.E., Sc.D., F.R.S.
H. G. MAURICE, C.B.
E. S. RUSSELL, O.B.E., D.Sc.
Sir EDWARD J. SALISBURY, Kt., C.B.E., D.Sc., Sec.R.S.
Admiral Sir AUBREY C. H. SMITH, K.B.E., C.B., M.V.O.

COUNCIL

To retire in 1950

H. CARY GILSON
C. F. HICKLING, Sc.D.
MORLEY H. NEALE
Prof. LILY NEWTON, Ph.D.
Prof. J. Z. YOUNG, F.R.S.

To retire in 1951

Miss ANNA M. BIDDER, Ph.D.
Prof. F. W. ROGERS BRAMBELL, D.Sc. F.R.S.
J. N. CARRUTHERS, D.Sc.
O. D. HUNT
J. E. SMITH, Ph.D.

To retire in 1952

MICHAEL GRAHAM, O.B.E.
C. E. LUCAS, D.Sc.
L. HARRISON MATTHEWS, Sc.D.
J. D. H. WISEMAN, Ph.D.
Prof. V. C. WYNNE-EDWARDS

Hon. Treasurer

Major E. G. CHRISTIE-MILLER, 38 Hyde Park Street, London, W. 2

Secretary

F. S. RUSSELL, D.S.C., D.F.C., F.R.S., The Laboratory, Citadel Hill, Plymouth

The following Governors are also members of the Council:

G. P. BIDDER, Sc.D.
P. D. H. DUNN, C.M.G., O.B.E. (Ministry of Agriculture and Fisheries)
The Worshipful Company of Fishmongers:
The Prime Warden
Major E. G. CHRISTIE-MILLER
ALFRED R. WAGG
Prof. A. C. HARDY, D.Sc., F.R.S. (Oxford University)
C. F. A. PANTIN, Sc.D., F.R.S. (Cambridge University)
Prof. H. GORDON JACKSON, D.Sc. (British Association)
H. G. MAURICE, C.B. (Zoological Society)
Prof. A. V. HILL, C.H., O.B.E., Sc.D., F.R.S. (Royal Society)

THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM

BALANCE SHEET 31ST MARCH 1949

	£ s. d.	£ s. d.
CAPITAL RESERVE ACCOUNT:		
As at 31st March 1948	21688 8 2	
Add: Amount arising on valuation placed on R.V. 'Sula'	11000 0 0	
		32688 8 2
SURPLUS ACCOUNT:		
As at 31st March 1948	1882 9 3	
Add: Excess of Income over Expenditure for the year ...	240 6 8	
		2122 15 11
		34811 4 1
AQUARIUM SINKING FUND:		
As at 31st March 1948	133 17 1	
Add: Donations for rebuilding Aquarium Tanks	36 0 0	
		169 17 1
E. T. BROWNE—BEQUEST FUNDS:		
Building Fund, as at 31st March 1948 ...	1317 3 0	
Add: Interest on Investment	20 2 4	
Profit on sale of Investment	17 3 0	
	1354 8 4	
Less: Expenditure during the year on extension of Workshops	1304 1 3	
	50 7 1	
Library Fund, as at 31st March 1948 ...	1168 17 4	
Add: Interest on Investment	35 14 2	
	1204 11 6	
Special Apparatus Fund, as at 31st March 1948	2643 10 6	
Add: Interest on Investment	80 15 2	
	2724 5 8	
Less: Expenditure during the year	73 7 0	
	2650 18 8	
Scientific Publications Fund, as at 31st March 1948	1982 15 8	
Add: Interest on Investment	60 11 6	
	2043 7 2	
		5949 4 5
'GAMMARUS' REPLACEMENT FUND:		
As at 31st March 1948	570 0 6	
Less: Balance transferred to Vessels Hire and Capital Expenditure Fund	570 0 6	
		— — —

	£ s. d.	£ s. d.
FIXED ASSETS, at valuations as estimated by the Director at 31st March 1949:		
Boats and Equipment:		
R.V. 'Sula'	11000 0 0	
Motor Boat 'Gammarus'	200 0 0	
Nets, Gear and General Equipment	100 0 0	
	11300 0 0	
Laboratory Apparatus, Engines and Pumps	5860 0 0	
		17160 0 0
LIBRARY, at valuation by Mr Ridgill Trout in January 1941, plus additions at cost		16600 0 0
		33760 0 0
STOCKS ON HAND, as valued by the Director:		
Specimens	600 0 0	
Chemicals	250 0 0	
Journals	400 0 0	
		1250 0 0
GENERAL FUND INVESTMENT at Book Value £352. 2s. 3d. 2½ % Treasury Stock ... ... (Market value £281. 13s. 10d.)		232 7 10
E. T. BROWNE—BEQUEST FUNDS INVESTMENT, at cost: £5901. 8s. 7d. 3 % British Transport Stock ... ... (Market value £5989. 19s. 0d.)		5795 3 6
VESSELS HIRE AND CAPITAL EXPENDITURE FUND INVESTMENT, at cost: £580. 9s. 6d. 3 % British Transport Stock ... ... (Market value £589. 3s. 8d.)		570 0 6
COMPOSITION FEES FUND INVESTMENTS, at cost:		
£18. 8s. 6d. 2½ % Treasury Stock	15 15 0	
£660. 14s. 8d. 3 % British Transport Stock	652 3 2	
(Market value £685. 7s. 8d.)		667 18 2
SUNDRY DEBTORS:		
Sales of Specimens, etc.	584 3 1	
Admiralty—R.V. 'Sula' Engine Repairs	233 7 8	
		817 10 9
PREPAYMENTS		69 10 3
RECOVERABLE EXPENDITURE:		
Research Fund—P. S. B. Digby:		
Balance at 31st March 1948	39 15 10	
Expenditure during the year	433 15 7	
	473 11 5	
Less: Grant received	473 11 5	
		— — —

Composition Fees Fund:			
As at 31st March 1948	573 8 2		
Add: Fees received	94 10 0		
		667 18 2	
Biological Investigations on Algae Fund:			
As at 31st March 1948	8 1 3		
Less: Transfer to Income and Expenditure Account ...	8 1 3		
		— — —	
Special Squid Tank Fund:			
As at 31st March 1948	70 0 0		
Less: Expenditure during the year	70 0 0		
		— — —	
Buildings Reconstruction Fund:			
Compensation received during year from War Damage Commission	6860 0 0		
Grant received	2668 5 0		
	9528 5 0		
Less: Balance at 31st March 1948 ... ... 457 19 8			
Expenditure during year:			
Rebuilding East Wing 7698 4 0			
Reconstruction of Main Building ... 609 0 0			
	8765 3 8		
(Dr)		763 1 4	
Sundry Creditors:			
Accrued Expenses	2484 13 3		
Subscriptions and Grant received in advance	184 6 0		
		2668 19 3	
Bank Overdraft:			
Coutts & Co.	2907 5 10		
Less: Cash at Bank and in Hand:			
Lloyds Bank Limited 214 19 5			
Cash in Hand 27 2 11			
	242 2 4		
(Dr)		2665 3 6	
		£47,695 7 10	

Vessels Hire and Capital Expenditure Fund:			
Hire of R.V. 'Sabella' for year to date	1380 0 0		
Modifications to R.V. 'Sabella'	17 13 6		
Purchase and Modifications to R.V. 'Sula'	10600 7 5		
Loss on Sale of Investment	711 2 5		
	12709 3 4		
Less: Balance at 31st March 1948 ... ... 7467 14 2			
Balance on 'Gammarus' Replacement Fund transferred 570 0 6			
Interest on Investments 138 11 10			
	8176 6 6		
(Cr)		4532 16	
		£47,695 7 10	

JOHN E. HARRIS
O. D. HUNT
Members of the Council.

REPORT OF THE AUDITORS TO THE MEMBERS OF THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM:

We have obtained all the information and explanations which to the best of our knowledge and belief were necessary for the purposes of our audit. In our opinion proper books of account have been kept by the Association so far as appears from our examination of those books. We have examined the above balance sheet and annexed income and expenditure account which are in agreement with the books of account. Capital expenditure on erection of buildings on land held on lease from the War Department is excluded. Subject to this remark, in our opinion and to the best of our information and according to the explanations given us the balance sheet gives a true and fair view of the state of the Association's affairs as at 31st March 1949 and the income and expenditure account gives a true and fair view of the excess of income over expenditure for the year ended on that date.

Prudential Buildings, George Street, Plymouth.
2nd May 1949.

PRICE, WATERHOUSE & CO.

INCOME AND EXPENDITURE ACCOUNT FOR THE YEAR ENDED 31ST MARCH 1949

	£ s. d.	£ s. d.
To SALARIES, including Association's contributions to Superannuation Scheme and National Insurance ...		15685 12 9
,, LABORATORY AND BOATS' CREWS' WAGES, including National Insurance, contributions to Superannuation Scheme, War Bonus and Employer's Liability Insurance		12406 5 4
,, UPKEEP OF LIBRARY		273 8 11
,, SCIENTIFIC PUBLICATIONS, LESS SALES		1199 7 3
,, UPKEEP OF LABORATORIES AND AQUARIUM:		
Buildings and Machinery	547 5 0	
Electricity, Oil, Gas, Coal and Water	441 4 6	
Chemicals and Apparatus	821 9 3	
Fire Insurance, Tithe, Ground Rent and Rent of Store	130 0 11	
Travelling Expenses	528 6 1	
Audit Fee	10 10 0	
Stationery, Postages, Telephone, Carriage and Sundries	737 9 7	
Specimens	214 10 9	
		3430 16 1
,, MAINTENANCE AND HIRE OF BOATS:		
Petrol, Oil, Paraffin, etc.	364 8 4	
Maintenance and Repairs to Nets, Gear and Apparatus	1752 12 5	
Purchase of Materials for Nets, etc. for Re-sale ...	769 19 4	
Boat Hire, Collecting Expenses and Upkeep of Truck	177 6 9	
Insurances	645 6 11	
		3709 13 9
,, ENTERTAINMENT EXPENSES		39 11 3
,, BANK CHARGES		16 18 8
,, TRANSFER TO MACKEREL RESEARCH FUND		— — —
,, TRANSFER TO VESSELS HIRE AND CAPITAL EXPENDITURE FUND		— — —
,, BALANCE, BEING EXCESS OF INCOME OVER EXPENDITURE (Cr) FOR THE YEAR		240 6 8
		£37,002 0 8

Note: No provision is made for replacement of Fixed Assets.

	£ s. d.	£ s. d.
By GRANTS AND TABLE RENTS:		
Ministry of Agriculture and Fisheries Grant from Development Fund	30000 0 0	
Fishmongers' Company	500 0 0	
Miscellaneous (including British Association £50, Royal Society £50, Physiological Society £30, Cornwall Sea Fisheries Committee £10, Universities of London £210, Cambridge £125, Oxford £100, Bristol £50, Birmingham £31. 10s. od., Leeds £20, Durham £10. 10s. od., Exeter £10. 10s. od., Leicester £10. 10s. od., Manchester £10. 10s. od., Nottingham £10. 10s. od., Southampton £10. 10s. od. and Sheffield £5; Imperial College £10, Ministry of Works £104, and Ray Lankester Fund £20) ...	1206 14 7	
		31706 14 7
,, SUBSCRIPTIONS (excluding Subscriptions received in advance)		430 1 1
,, FEES FOR TESTS OF MATERIALS		30 0 0
,, SALES:		
Specimens	2216 8 11	
Photographs	— — —	
Fish	366 12 2	
Nets, Gear and Hydrographical Apparatus	933 15 3	
		3516 16 4
,, INTEREST ON INVESTMENTS		26 5 10
,, SALE OF DR M. V. LEBOUR'S BOOK		6 17 6
,, SALE OF 'PLYMOUTH MARINE FAUNA'		12 5 0
,, AQUARIUM:		
Admission Fees	1463 14 3	
Sale of Guides and Postcards	108 16 2	
	1572 10 5	
Less: Maintenance of Buildings ...	53 16 0	
Printing Guides and Tickets ...	79 9 4	
Food	90 12 0	
Wages	83 14 0	
	307 11 4	
		1264 19 1
,, TRANSFER FROM BIOLOGICAL INVESTIGATIONS ON ALGAE FUND		8 1 3
		£37,002 0 8

THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM

THE ASSOCIATION was founded in 1884 to promote accurate researches leading to the advancement of zoological and botanical science and to an increase in our knowledge of the food, life, conditions and habits of British fishes. The work of the Association is controlled by a Council elected annually by its subscribing members.

Professor T. H. Huxley took the chair at the initial meeting held in the rooms of the Royal Society and was elected the first President. Among those present were Sir John Lubbock (afterwards Lord Avebury), Sir Joseph Hooker, Professor H. N. Moseley, Mr G. J. Romanes, and Sir E. Ray Lankester who, after Professor Huxley, was for many years president of the Association. It was decided that a laboratory should be established at Plymouth where a rich and varied fauna is to be found.

The Plymouth Laboratory was opened in June 1888. The cost of the building and its equipment was £12,000 and, since that date, a new library and further laboratory accommodation have been added at an expenditure of over £23,000.

The Association is maintained by subscriptions and donations from private members, scientific societies and public bodies, and from universities and other educational institutions; a generous annual grant has been made by the Fishmongers' Company since the Association began. Practical investigations upon matters connected with sea-fishing are carried on under the direction of the Council, and from the beginning a Government Grant in aid of the maintenance of the Laboratory has been made; in recent years this grant has been greatly increased in view of the assistance which the Association has been able to render in fishery problems and in fundamental work on the environment of marine organisms. An account of the Laboratory and the scope of the work undertaken there will be found in Vol. XV (p. 735) and Vol. XXVII (p. 761) of this *Journal*.

The Laboratory is open throughout the year and its work is carried out under the supervision of a Director and with a fully qualified research staff. The names of the members of the staff will be found at the beginning of this number. Accommodation is available for British and foreign scientific workers who wish to carry out independent research in marine biology and physiology. Arrangements are made for courses for advanced students to be held at Easter, and marine animals and plants are supplied to educational institutions.

Work at sea is undertaken by two research vessels and by a motor boat and these also collect the specimens required in the Laboratory.

TERMS OF MEMBERSHIP

		£	s.	d.
Annual Members	per annum	1	1	0
Life Members	Composition fee	15	15	0
Founders		100	0	0
Governors		500	0	0

Members of the Association have the following rights and privileges: they elect annually the Officers and Council; they receive the Journal of the Association free by post; they are admitted to view the Laboratory at Plymouth, and may introduce friends with them; they have the first claim to rent a place in the Laboratory for research, with use of tanks, boats, etc.; they have the privilege of occupying a table for one week in each year free of charge; and they have access to the books in the Library at Plymouth.

All correspondence should be addressed to the Director, The Laboratory, Citadel Hill, Plymouth.

CONTENTS

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