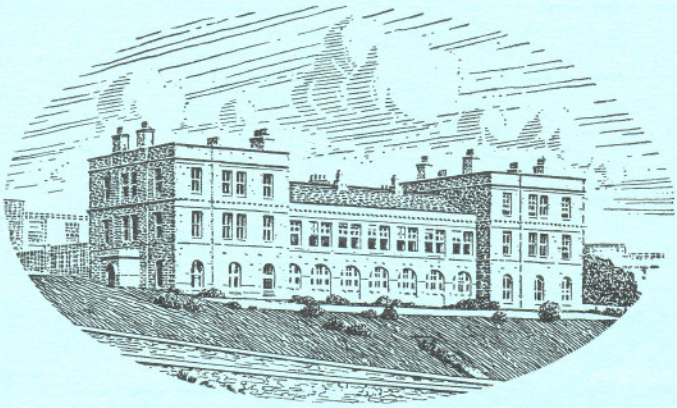
JOURNAL OF THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM



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ON SOME COPEPODA FROM PLYMOUTH, MAINLY ASSOCIATED WITH INVERTEBRATES, INCLUDING THREE NEW SPECIES

By R. U. GOODING

From the Plymouth Laboratory[1]

(Text-figs. 1–6)

Work on copepods at the Plymouth Marine Laboratory in 1954–55 revealed some new species and some which have been described but whose occurrence in that region had not previously been reported. Specimens from both these categories are discussed in the present paper.

The names of copepods associated with the fish of the region are comparatively well known through the work of Bassett-Smith, Leigh-Sharpe and others (although the present record for *Peniculus fistula* suggests that the list is still incomplete; and others might bear re-investigation); but little attention has been paid to invertebrates as hosts. Norman & Scott (1906) and Leigh-Sharpe's paper on the Herpyllobiids (1926) together formed the basis of the 1931 Plymouth Fauna list for records of species associated with these animals; and additions have later been made in the following papers: Gray (1933), Gurney (1933), Atkins (1934), and Leigh-Sharpe (1933). These references, in conjunction with the present publication, indicate that the invertebrate fauna of Plymouth is probably as prolific a source of associated copepods as any.

My sincere thanks are due to Dr J. P. Harding, under whom this work was done, and to Dr Paul Illg in particular for reading this paper and for giving me the benefit of so detailed and constructive a criticism; to the Director for facilities at the Marine Laboratory, Plymouth, and for constant encouragement; to the members of the Staffs of that Laboratory and this Department for help, host specimens and advice at the times I needed them most; and, finally, to the Government of Barbados, B.W.I., for allowing me to apply funds from a 1950 Scholarship to this study.

DEFINITIONS

The word 'associated' has been used in the title and throughout this paper because it is felt that terms like 'parasitic', 'semi-parasitic', 'commensal',

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etc., should be restricted to cases where there is some definite evidence about the nature of the association, and little work to this end has been done on the Copepoda (cf. especially Baer, 1951; Gotto, 1954). Symbiosis, in its widest sense (Allee, Emerson, Park, Park & Schmidt, 1949; Davenport, 1955; etc.), is perhaps broad enough for use in this context, but the term adopted has the advantage of simplicity and is unlikely to cause confusion through previous usage in a stricter sense. There seems no need for formal definition except to say that, in the Copepoda, it is intended to include the range from forms firmly attached to a single host, usually of a particular species, to those with as free-and-easy a host requirement as some lichomolgids; and may be applied equally to the earlier instars, if they are found in contact with the host, as to adults. But it still seems necessary to distinguish between the partners in the association: I suggest that the concept of 'host' is already wide enough, and that 'associate' should here refer to the copepod.

Several terms have from time to time been used to differentiate the regions of the copepod body, some purely descriptive, others borrowed to express opinions on comparative crustacean morphology. I am adopting, for descriptive work, those introduced by Sars (1901), but, in addition, have added 'cephalothorax'—for use in a restricted sense—and proposed 'prosome'—as antithetic to 'urosome'—to include both 'cephalosome' and 'metasome'. (There seem definite advantages in retaining Sars's original meanings for these terms in preference to Wilson's, 1932, p. 9, interpretation.) These regions may now be defined:

Prosome: the anterior region of the body, commonly limited posteriorly by a major articulation;

Cephalosome: the head region when this includes only the somite of the maxillipedes;

Cephalothorax: the head region including, in addition to the maxillipedal somite, pedigerous segments in a fused complex;

Metasome: those free thoracic segments in front of the major articulation;

Urosome: that part of the body behind the major articulation.

This terminology is applicable to all divisions of the Copepoda despite the fact that, for instance, in the Calanoida, the urosome may include only the genital and succeeding segments, while in some Caligoida it contains all segments behind the third pedigerous; but it is hoped that the division of the body into two main parts will facilitate description especially in the Cyclopoida, where the anterior region is usually sharply defined from the posterior by a considerable difference in width.

The homology of the poecilostome mouthparts has also been a source of some discussion: whether the same number as is present in other groups may here be distinguished or, if not, which is lacking. Lang (1946*a*) has discussed the arguments but, despite his conclusion—partly modified in 1948

(p. 24)—I shall presume that a mandible, maxillule, maxilla, and maxilliped can be identified in the two new poecilostomes described here. Also, although it now seems generally agreed that the somite bearing the maxillipedes is the first thoracic segment (permanently included in the head region), I have tried to avoid confusion by using the terms 'pedigerous' instead of 'thoracic', when discussing the somites bearing the thoracic legs as a whole, or that of the fifth leg by itself, and 'prosomal' to refer to those bearing legs one to four. In the descriptions of many appendages, 'articulated process' denotes both setae and spines (for a summary of the differences between these see Gurney, 1931, p. 38), 'process' being restricted to the usual carcinological connotation of an unarticulated projection.

The following is a list of abbreviations which have been used in referring to the swimming legs:

P1, P2, etc.—first, second, etc., pairs;
basp.—basipodal segments;
(basp. 1—coxa; basp. 2—basipodite);
end.—inner ramus (endopodite);
exp.—outer ramus (exopodite);
Si—inner border of segments;
St—terminal border of segments;
Se—outer border of segments.

I have followed Sewell (1949) in differentiating the spines by Roman, the setae by Arabic numerals.

METHODS

Collection methods are dealt with under the individual records.

Much of the examination, and all measurements and drawings (for which a camera lucida was used) were made from preparations cleared and mounted temporarily, in lactic acid. (I am very grateful to Dr Harding for suggesting this method.) Whole specimens were mounted in a 'hanging drop' to avoid compression by the cover-slip. For measuring, the specimens were oriented dorsal surface uppermost; and the length taken from the rostrum to the end of the caudal rami (not including the caudal setae).

CYCLOPOIDA: SIPHONOSTOMA

Family MICROPONTIIDAE nov.

Only one genus, *Micropontius*, is at present known.

MICROPONTIUS gen.nov.

The characters of the type and only species will serve to define this genus.

Micropontius ovoides sp.nov.

Specimens examined. (1) Numerous adult females, several with ovisacs, and males in magnesium chloride washings (cf. pp. 203–4) from *Spatangus purpureus*, O. F. Müller, trawled or dredged on the Looe–Eddystone and Eddystone Shell Gravel Grounds near Plymouth, March–June 1955. (2) Rather fewer of these from *Echinocardium cordatum* (Pennant), *E. pennatifidum* Norman and *E. flavescens* (O. F. Müller), similarly collected, mainly obtained from the Bigbury Bay and Looe–Eddystone Grounds during the above period. (3) One female from a *Brissopsis lyrifera* (Forbes), dredged 15 miles south of Penmarche Lighthouse (off Concarneau, east coast of France), depth about 53 fathoms; 23 May 1955.

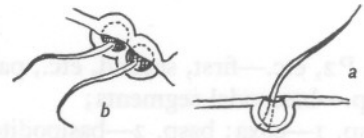


Fig. 1. Detail of the setae on the prosome of *Micropontius ovoides* (semi-diagrammatic). *a*, a view from the side showing the integumental cup, with its narrow opening, and the seta extending to the bottom; *b*, surface view: the ventro-lateral ridge of the segment can be seen to extend as a hood over the outer part of the pit.

Type specimens. The holotype, an adult female, and paratypes, including males and ovigerous females, all selected from the first category above, have been deposited at the British Museum (Natural History). The generic name refers both to size and affinities, the specific to shape.

Description of the female

The ovigerous female is nearly elliptical in outline; a specimen without ovisacs appears somewhat spade-shaped in dorsal view; both nearly twice as long as wide (Fig. 2*a*).

The prosome occupies much the greater part of the body area. The cephalothorax includes the first pedigerous segment, whose anterior limit is indicated only by a thickened strip dorsally and, in part, laterally. There are three metasomal segments, the dorsal articulations of which are also thickened. The postero-lateral corners of all the prosomal segments are produced backward for a short distance into a sharp point; and the posterior border of the third pedigerous is extended to form an 'apron', with a thickened distal edge, which covers the urosome in dorsal view as far as the insertion of the caudal rami. The tergites of the segments bearing the second and third pairs of

Legend to Fig. 2

Fig. 2. *Micropontius ovoides*, gen. et sp.nov., adult female. *a*, dorsal view (an ovisac and parts of the body, which would otherwise have been obscured, are represented by broken lines in this and other figures); *b*, side view; *c*, antennule; *d*, antenna; *e*, maxilla; *f*, maxilliped; *g*, first swimming leg; *h*, abnormal third endopod segment of first leg; *i*, second swimming leg; *j*, third swimming leg; *k*, fourth swimming leg; *l*, fifth leg; *m*, urosome (detail is shown on one side only).

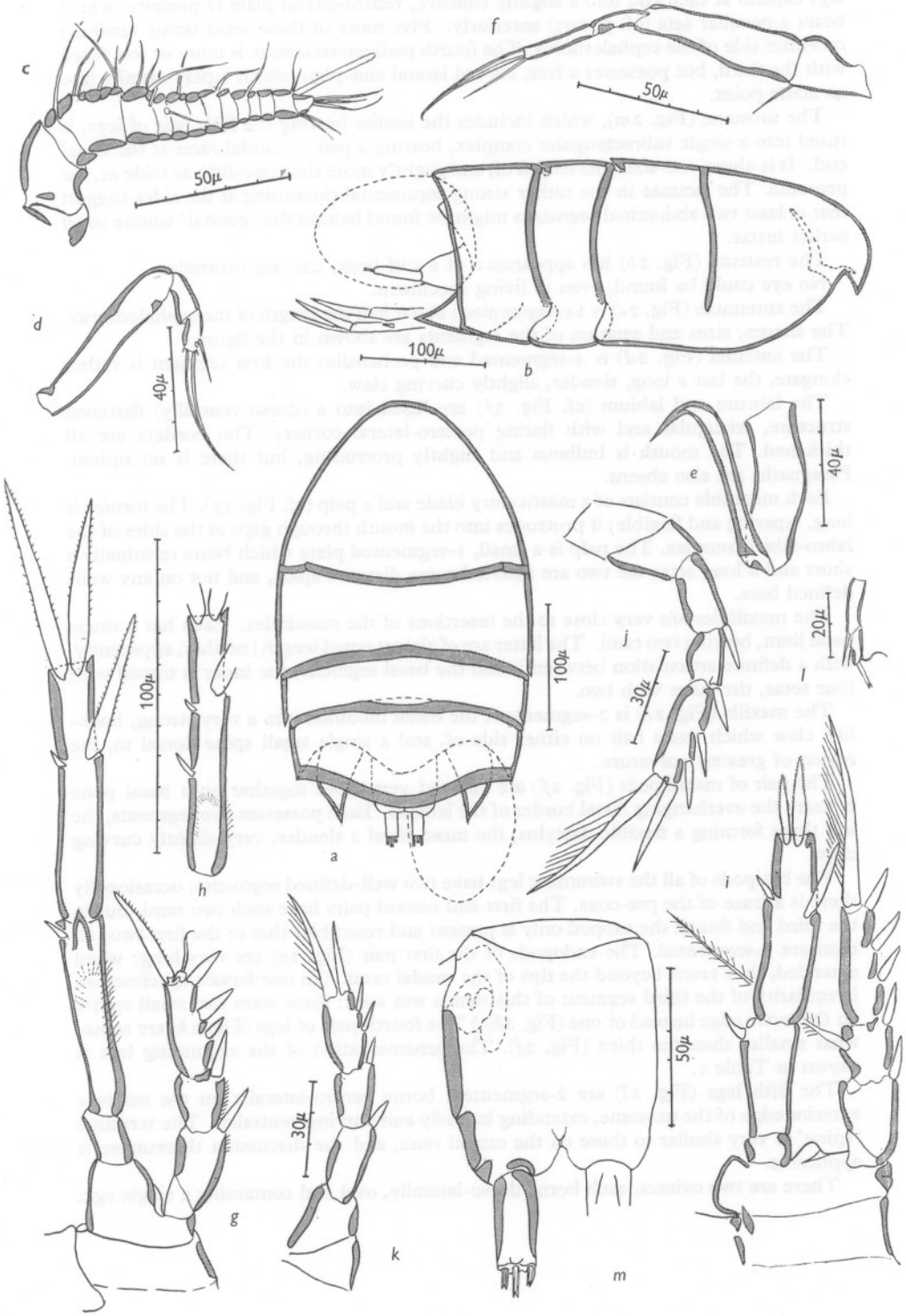


Fig. 2

legs expand at each end into a slightly concave, ventro-lateral plate (? pleurite) which bears a peculiar seta (cf. p. 203) anteriorly. Five more of these setae occur ventrally on either side of the cephalothorax. The fourth pedigerous somite is more or less fused with the third, but possesses a free, curved lateral end-plate which tapers distally into an acute point.

The urosome (Fig. 2*m*), which includes the somite bearing the fifth pair of legs, is fused into a single subrectangular complex, bearing a pair of caudal rami at the distal end. It is about one-sixth the length of, and slightly more than one-fifth as wide as, the prosome. The lacunae in the rather strong tegumental thickening at the sides suggest that at least two abdominal segments might be found behind the 'genital' somite in an earlier instar.

The rostrum (Fig. 2*b*) has appearance of a stiff beak, curving ventrally.

No eye could be found, even in living specimens.

The antennule (Fig. 2*c*) is 14-segmented; about half the length of the cephalothorax. The shapes, sizes and setation of the segments are shown in the figure.

The antenna (Fig. 2*d*) is 4-segmented and prehensile; the first segment is rather elongate, the last a long, slender, slightly curving claw.

The labrum and labium (cf. Fig. 3*f*) are fused into a (dorso-ventrally) flattened structure, triangular and with flaring postero-lateral corners. The borders are all thickened. The mouth is bulbous and slightly protruding, but there is no siphon. Paragnaths are also absent.

Each mandible consists of a masticatory blade and a palp (cf. Fig. 3*g*). The former is long, tapering and flexible; it protrudes into the mouth through gaps at the sides of the labro-labial complex. The palp is a small, 1-segmented plate which bears terminally a short and a long seta; the two are inserted some distance apart, and not on any well-defined base.

The maxillules are very close to the insertions of the mandibles. Each has a single basal joint, bearing two rami. The latter are of almost equal length; neither, apparently, with a definite articulation between it and the basal segment; the inner is tipped with four setae, the outer with two.

The maxilla (Fig. 2*e*) is 2-segmented; the distal modified into a very strong, hook-like claw which has a hair on either side of, and a single small spine dorsal to, the region of greatest curvature.

The pair of maxillipeds (Fig. 2*f*) are inserted very close together on a basal plate beneath the overhanging distal border of the labium. Each possesses five segments, the last three forming a flexible dactylus, the most distal a slender, very slightly curving claw.

The basipods of all the swimming legs have two well-defined segments; occasionally there is a trace of the pre-coxa. The first and second pairs have each two rami, but in the third and fourth the exopod only is present and resembles that of the first two; all rami are 3-segmented. The endopods of the first pair (Fig. 2*g*) are very long: when extended, they reach beyond the tips of the caudal rami. (In one female specimen an irregularity of the third segment of this ramus was seen: there were two small spines on the outer edge instead of one (Fig. 2*h*).) The fourth pair of legs (Fig. 2*k*) are somewhat smaller than the third (Fig. 2*j*). The ornamentation of the swimming legs is shown in Table 1.

The fifth legs (Fig. 2*l*) are 2-segmented, borne ventro-laterally on the extreme anterior edge of the urosome, extending laterally and curving ventrally. The terminal 'spine' is very similar to those on the caudal rami, and the discussion thereunder is applicable.

There are two ovisacs, each borne dorso-laterally, oval and containing a single egg.

The caudal rami (Fig. 2*m*) are cylindrical, nearly three times as long as wide, and armed terminally—at least in preserved specimens—with three (or occasionally four) short, stout 'spines'. In some specimens which were examined alive and immediately after capture, however, these appeared to be very fine setae about half as long as the urosome; and, if this is the case, they must break during fixing and manipulation.

TABLE 1. ORNAMENTATION OF THE SWIMMING LEGS OF *MICROPONTIUS OVOIDES* SP.NOV.

	Basp.				End.							Exp.						
	1		2		1		2		3			1		2		3		
	Si	Se	Si	Se	Si	Se	Si	Se	Si	St	Se	Si	Se	Si	Se	Si	St	Se
P1	Very small, thread-like				0	0	I	0	I	II	I	0	I	0	I	0	I	III
P2	setae are irregularly				0	0	I	0	I	II	I	0	I	I	I	0	I	III
P3	present in some of these				.	.	.	.	.	.	.	0	I	0	I	0	I	III
P4	positions				.	.	.	.	.	.	.	0	I	0	I	0	I	III

Description of the male

As for the female, except that the body (Fig. 3*a–c*) is an almost perfect ellipse in outline. There is no major articulation, the urosome being firmly fused to the prosome.

The second metasomal segment has no 'apron' projection on its distal edge; the lateral end-plates of the third are fused, near the base to the framework strengthening the insertion of the urosome and more posteriorly to the urosome itself; the two are joined dorsally by a chitinous membrane whose posterior edge is thickened and also fused to the urosome.

The urosome (Fig. 3*a*, *b*) is much wider and more rounded, with a strongly thickened framework. There is no hint of segmentation.

The antennule (Fig. 3*d*) is 13-segmented and doubly geniculate (between the fourth and fifth, and eleventh–twelfth segments). The aesthetasc, on the last segment, is unusually stout.

All the swimming legs (Fig. 3*j–m*) are a little smaller in proportion.

The fifth legs (Fig. 3*n*) are borne ventrally near the middle of the extreme anterior edge, and thus very difficult to distinguish except in a carefully dissected specimen.

A pair of sixth legs are occasionally represented, in well-preserved specimens, by a single small seta at each distal corner of the spermatophoral apparatus.

The caudal rami are inserted rather more ventrally than those of the female (but still visible in dorsal view), and are much shorter.

Dimensions

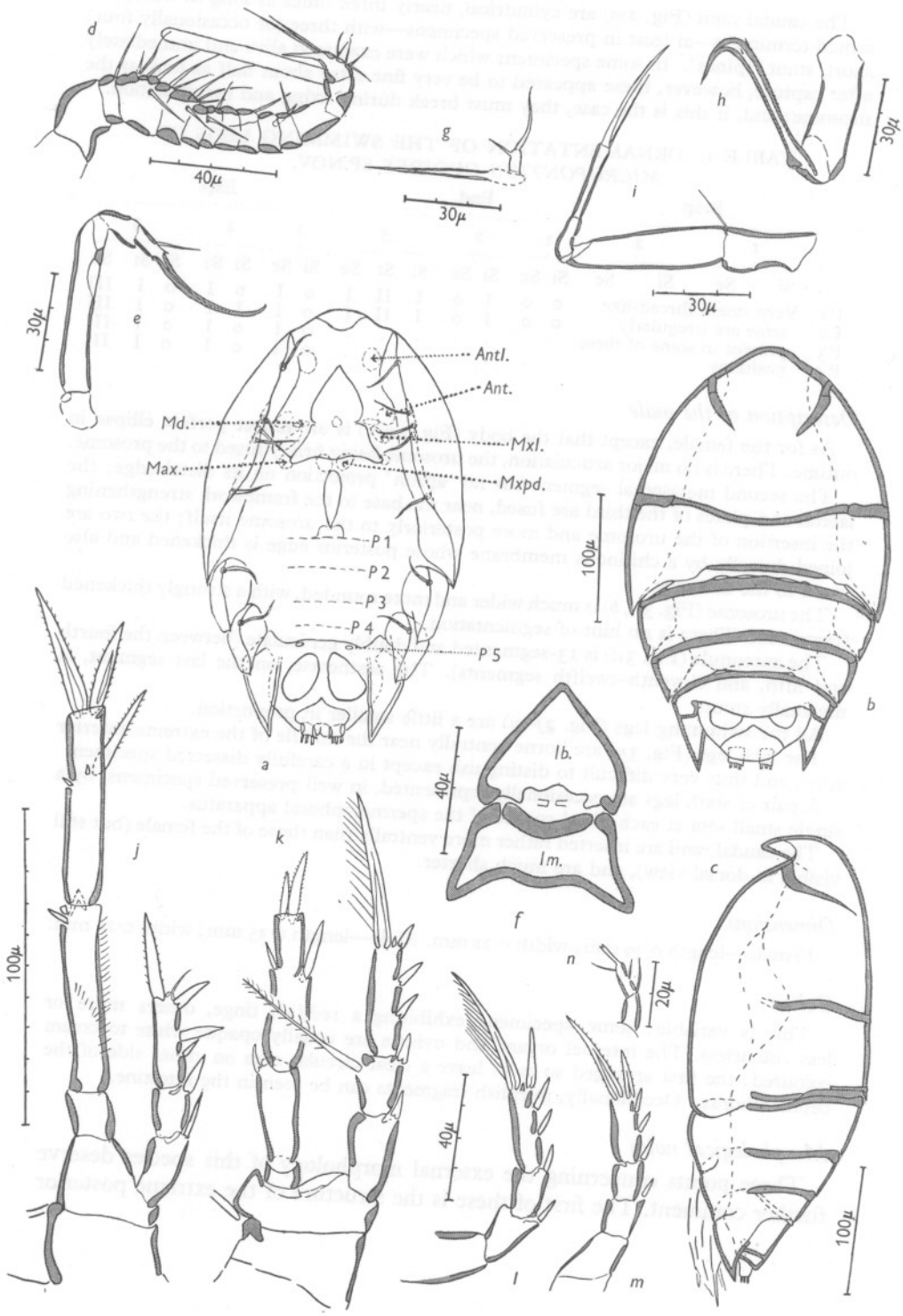
Female—length 0·39 mm; width 0·22 mm. Male—length 0·35 mm; width 0·21 mm.

Colour

This is variable: some specimens exhibiting a reddish tinge, others more or less colourless. The internal organs and ovisacs are usually opaque white to cream coloured; the first arranged so as to leave a clear circular area on either side of the cephalothorax. Occasionally, purplish fragments can be seen in the intestine.

Morphological notes

Three points concerning the external morphology of this species deserve further comment. The first of these is the structure of the extreme posterior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P 5
a
100μ
b
lb.
40μ
lm.
f
c
100μ
j
k
100μ
n
20μ
40μ
l
m

Fig. 3

part of the body in the female. That this forms a very efficient means of providing support and some degree of protection for the ovisacs may be seen by a comparison of Fig. 2*a* and *b*. The first pair of legs are normally carried fully extended, so that their endopods reach backwards as far as do the ovisacs and support these. The latter are separated dorsally by a prominence just under the distal margin of the 'apron' (cf. Fig. 2*b*), and rather more ventrally by the urosome itself; while the 'apron', both dorsally and laterally, helps to keep them in place.

The second concerns the arrangement of the setae on the ventro-lateral margins of the prosome (Fig. 3*a*). The base of each seta is enclosed in a pit with thick chitinous walls. These pits may often be rather less regular than depicted in both shape and construction—especially in the male, and are situated on the inner side of the ventro-lateral ridge of the segment which continues as a hood over the outer part of the pit, restricting movement of the base of the seta to the shaded portion in Fig. 1*b*. The setae themselves are very long and flexible, and are not plumose. It seems very probable that they have a sensory function though no movement of them could be detected in specimens examined alive. In any case they appear to be unique in structure and position in the Copepoda.

The final note is also related to structures which are probably sensory in function. These have the appearance, in the living specimen, of long, thread-like hairs, but usually form papilla-like projections when preserved. Like the spines on the caudal rami and fifth legs, this may be due to the hardening and subsequent breaking. They are scattered over the exterior of the body, including the rostrum, but are much more frequent on the dorsal and lateral surfaces. Similar structures have been noted while examining specimens of other species, and they are probably present on the majority of, if not all, copepods, being easily overlooked unless the body is minutely examined.

Micropontius ovoides can easily be recognized by a combination of the following characters: body shape and size; arrangement of the pro- and urosomes; lack of the endopods to the third and fourth pairs of swimming legs, and the ornamentation of all the latter; the peculiar setae on the ventral surface; and the mouth shield (labro-labial complex).

Biology

This species (and the other echinoid associates) was obtained by a slight modification of Bocquet's (1952) method; the host was left in a dry dish for

Legend to Fig. 3

Fig. 3. *Micropontius ovoides*, gen. et sp.nov., adult male. *a*, ventral view, to show where the appendages are inserted (*Antl.*, antennule; *Ant.*, antenna; *Max.*, maxilla; *Md.*, mandible; *Mxl.*, maxillule; *Mxpd.*, maxilliped; *P*1, first, *P*2, second, etc., pairs of legs); *b*, dorsal view; *c*, side view; *d*, antennule; *e*, antenna; *f*, mouth complex (*lb.*, labrum; *lm.*, labium); *g*, the mandible, the basal part is shown by broken line since its extent is not easy to see; *h*, maxilla; *i*, maxilliped; *j*, first swimming leg; *k*, second swimming leg; *l*, third swimming leg; *m*, fourth swimming leg; *n*, fifth swimming leg.

about half an hour, and then sufficient magnesium chloride solution added to cover it completely. (This was the usual $7\frac{1}{2}\%$ solution in fresh water, diluted approximately by half with filtered sea-water; application for a short time seems to anaesthetize most copepods, with the exception of certain harpacticoids). After a period of some 15 min, the liquid was filtered off through fine netting—tied over the nozzle of a large funnel—and the residue washed into a small dish with Plymouth filtered 'outside' sea-water (to avoid introducing extraneous species). The copepods were picked out from this under a binocular dissecting microscope (several were always found trapped in the surface film from which they could be dislodged only with difficulty) and transferred to a dish of clean water, where they recovered rapidly and could be kept alive for some time.

These copepods were found only on the spatangids listed above (p. 198), but no experiments were done on host specificity. That *Spatangus purpureus* is the definitive host at Plymouth is suggested not only by the fact that every one examined over a period of 3 months yielded at least ten, and usually forty or more, *Micropontius ovoides* while specimens of the species of *Echinocardium* never had more than four and were often free from these copepods; but, more particularly, by the following instance: six *Spatangus purpureus*, trawled inside the Eddystone Shell Gravel on 19 May 1955, yielded 289 specimens; an *Echinocardium pennatifidum*, from the same haul and brought in in the same jar, had only two. The water in the jar in this case was also filtered, since it had not proved possible to obtain bottom samples from the *Spatangus* ground for testing to see whether the copepods were confined to the echinoids or generally distributed throughout the substratum, and sixteen specimens were found: most of these proved either dead or moribund.

It is possible, however, that this 'host specificity' may have a correlation with some physical factor, such as particle size of the substrate, *Spatangus*—at Plymouth—preferring a coarse sand and *Echinocardium* spp. a rather more muddy bottom. In this connexion, a *Spatangus raschi* Loven (dredged about 150 miles west of Ushant—48° 05′ N., 08° 11′ W.—in 220 fathoms, 10 April 1955, and kindly identified by Mr George Nicholls, Museum of Zoology and Comparative Anatomy, Oxford) is interesting since, though it was in excellent condition, no copepods were obtained from it; the bottom in this case was a very fine, thick, black mud, with numerous stones. The specimen from *Brissopsis* (bottom marked on chart as 'soft sand, grey mud') is valuable in extending the known distribution of *Micropontius ovoides*, but it cannot be considered an accurate estimate of abundance since the echinoderms were all dead when examined.

To give some idea of the relative abundance of the sexes, a sample from *Spatangus*, obtained on 19 May 1955, was analysed: the 289 specimens included 188 females, of which 46 were ovigerous, and 101 males. No other complete

analysis was done, but it is the author's impression that this proportion is about average. The fact that adults are relatively numerous, while only one egg, rather large in proportion to its parents, is ever found in each ovisac, suggests an efficient means of infection and/or a short larval life. Although it was not possible to obtain a satisfactory figure or description of the form which hatches from the egg, it can be stated that this is a perfectly normal siphonostome first naupliar stage, suggesting that if development is abbreviated it must be in the later stages. At no time was anything resembling a late instar found, despite a particularly careful search (since this might have done much to clear up the systematic position of the species).

Careful observations, under magnification ($\times$ 24 to 100) made on more than one occasion on hosts which were later proved to be infected, also failed to show any *Micropontius in situ*; but with creatures so small and inconspicuous, in addition to the difficulties of observing a spatangid under such magnification, this cannot be taken as definite proof that the body surface is not their natural habitat. No satisfactory method was devised to test the other hypothesis: that they live in the alimentary or body cavities and move out when the host is dried and immersed in magnesium chloride.

Behaviour in laboratory

Micropontius ovoides usually remains relatively immobile on the bottom of the dish, occasionally working its mouthparts or making quick jerks with its swimming legs. It always comes to rest on its back, and seems unable to swim off from this position.

When a spatangid spine is introduced, however, and the creature manoeuvred until it has grasped this, it becomes rather more active. The antennae and maxillipeds are used both to grip the spine and to keep the body clear of it; the swimming legs are held close to the body surface; the antennules usually at right angles to the body and above the substrate. Occasionally, when at rest, the aesthetasc is used, apparently to palpate the spine. When 'walking', the antennae and maxillipeds move in a typically quadripedal succession, and the creature may scurry up and down the spine quite rapidly.

Attempts to dislodge a specimen from a spine, for example by gentle nudges with a needle, may produce any of four responses: scuttling away to another part of the spine; 'freezing', in which the body is pressed close to the spine, the maxillae probably (this could not be observed) being used to provide greater gripping power; transference to the needle point; or an 'annoyance' reaction, when the animal swims up and away from the spine with rapid jerks of its swimming legs and then sinks motionless until it lies on the bottom, ventral surface uppermost. Since the creature seems unable to swim off except from some support, it is possible that the long endopods of the first legs, with or without assistance from the antennae or maxillipeds, are used to give a 'shove off'.

Specimens pipetted on to a living *Spatangus* and observed under a binocular dissecting microscope did not behave in any way differently from that described above. Most remained holding on where they fell—occasionally, if they were on a spine, moving up or down it—and exhibiting the usual reactions when touched with a needle. None ever left the host, or swam to a different spine, or, when near the mouth, attempted to enter this.

Systematics

The systematic position of the new genus *Micropontius* is doubtful. It is certainly siphonostome, and, as the Siphonostoma stand at present, it possesses many characters which suggest relationship with the Dyspontiidae and Asterocheridae. As Nicholls (1944, pp. 15–16) points out, the former is not a very well-defined family; and there are several anomalous genera, such as *Stephopontius* Thompson & Scott (referred by Sewell, 1949, p. 167, to ? Cancerillidae), which he does not include in it but which exhibit certain resemblances both to the Dyspontiidae and to this new genus. My opinion is that *Micropontius* is sufficiently distinct to be separated, for the present, as the type of a new family, the Micropontiidae, but, since a future (and much needed) revision of the Siphonostoma may uncover possible evolutionary lines into which it will fit, I have decided not to expand this idea further in the present paper.

Family ASTEROCHERIDAE Giesbrecht, 1899 (*sens. strict.*)

Asterocheres violaceus (Claus, 1889)

Occurrence. Numerous adult males and females were found in magnesium chloride washings of *Echinus esculentus* L., obtained from various localities in the region, throughout the year. Specimens averaged about fifty per host; with a sex ratio of nearly two females to every male. Instars from 'Copepodid II' (i.e. an immature specimen with three pairs of legs and the rudiments of a fourth) to adult occurred rather rarely in March and April 1955.

Distribution. North Sea to Mediterranean; adults (? and stages) typically associated with camarodont echinoids, but occasionally with asteroids or free from a host.

Notes. I have followed Giesbrecht (1899) in regarding the genus *Echinocheres* Claus as a synonym of *Asterocheres* Boeck, since the distinction between them seems too slight to justify retention of the former. In support of this view, it may be mentioned that in my specimens, as in those of A. Scott (in Herdman & Scott, 1896)—which both Giesbrecht (1899) and Sars (1913–18) agree in referring to this species—the mandibular palp was distinctly 2-jointed and the fifth pair of legs in the female ciliated on both sides; this appears to leave only the lengths of the siphon and maxillular setae—surely characters of specific rather than generic importance?

Family DYSPONTIIDAE Sars, 1915

Scottomyzon gibberum (T. & A. Scott, 1894)

Occurrence. One male was found in a jar containing *Spatangus purpureus* Müll., dredged inside the Eddystone Shell Gravel Grounds, 19 April 1955.

Distribution. Norway to English Channel; adults typically found associated with *Asterias rubens* L.

Notes. Several *A. rubens* were searched at various times throughout the year, but the 'loges irrégulières' mentioned by Bocquet (1952) were not found, nor did washings from the surface yield any of these copepods.

CYCLOPOIDA: POECILOSTOMA

Family LICHOMOLGIDAE Kossmann, 1877

Lichomolgus leptodermatus sp.nov.

Specimens examined. Several males and females (most of the latter ovigerous) from the gills of a single *Laevicardium crassum* (Gmelin) trawled on the Looe–Eddystone—'Two-in-one' Grounds, 8 March 1955.

Type specimens. The holotype (an adult female) and several paratypes (both males and females), all cleared in lactic acid have been deposited at the British Museum (Natural History).

Description of the female

The body shape (Fig. 4*a*) is cyclopoid, nearly three times as long as wide; urosome about equal in length to the prosome, one-third its width.

The prosome is oval in dorsal outline, nearly one and a half times as long as broad; slightly inflated. The dorsal plates of the prosomal segments are separated laterally, and rounded at the corners. The cephalothorax includes the first pedigerous segment, the line of fusion being indicated by a groove dorsally and laterally.

The urosome is 5-segmented, though there is a flexible intersegmental region between the genital and fifth pedigerous segments. The genital is the widest segment in the urosome, and is divided dorsally (but not ventrally) by a distinct line; it is spindle-shaped. The succeeding abdominal segments are all alike in size.

A spoon-shaped rostrum (Fig. 4*b*) is present, which extends forward and down, and is not prehensile.

There is also an eye.

In the 7-segmented antennule (Fig. 4*c*), the articulation between the third and fourth segments is indistinct. There are not very many setae, and the representation of these in the figure is approximate only, since, even when stained, they are very difficult to make out. No aesthetasc could be seen.

The antenna (Fig. 4*d*) is 4-segmented, the third being small and indistinctly defined. The appendage is weakly prehensile, the terminal segment tipped with a curved and jointed claw and two weaker but unjointed ones, the inner the longest.

The labium is inflated and cone-shaped (in lateral, anterior and ventral views). The posterior edge has a deep, even groove down the mid-line.

No paragnaths could be found.

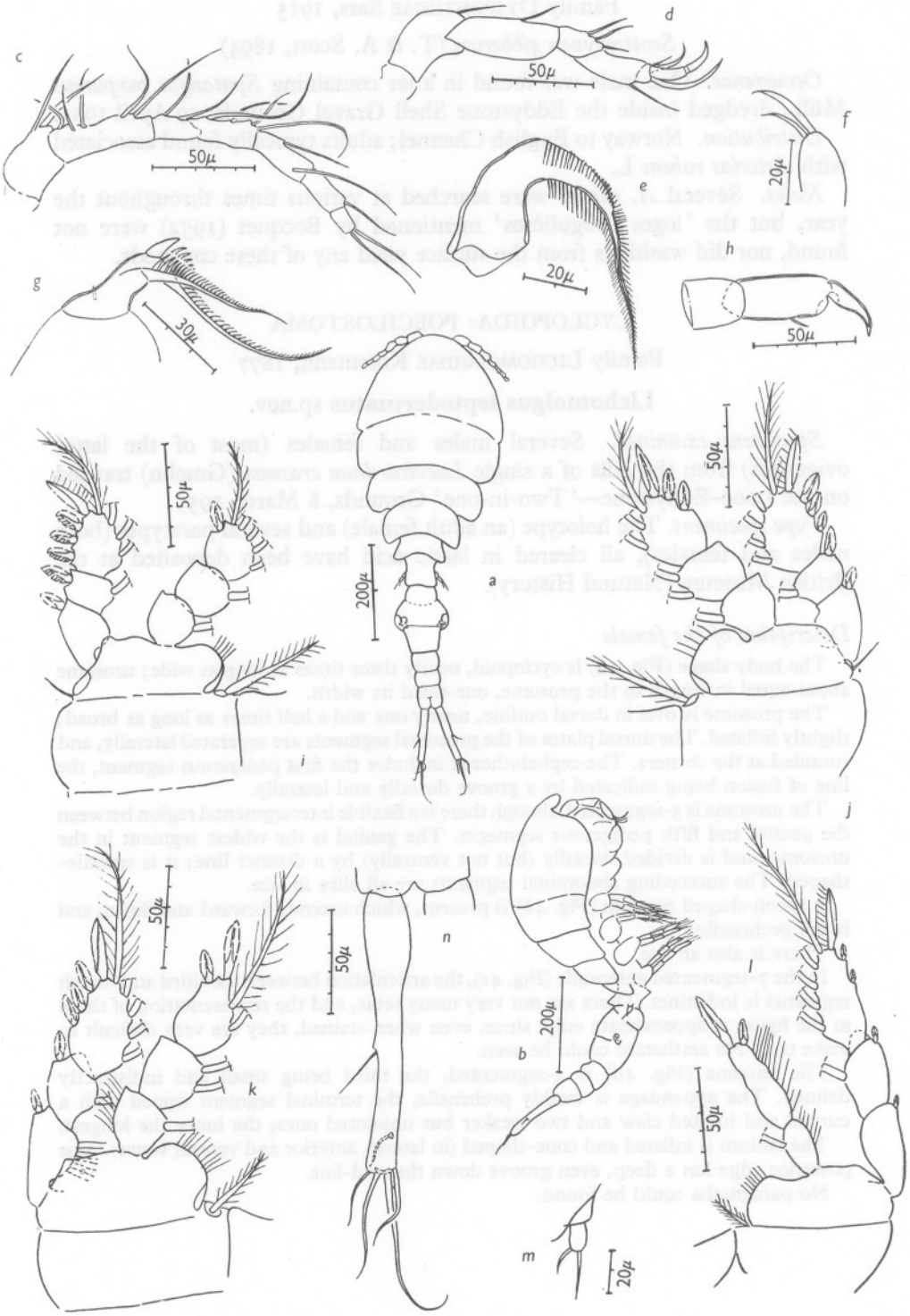
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Fig. 4

The labium is so indistinctly defined that no details of size, shape or texture could be made out.

The mandible (Fig. 4*e*) is of the usual lichomolgid type, with a single long, tapering lappet which is finely spinose on either edge; none of these spinules is enlarged.

There is a small, palp-like maxillule (Fig. 4*f*) with two rather stout terminal setae of differing lengths.

The basal segments of the 2-segmented maxilla (Fig. 4*g*) is rather short and inflated. The distal has a terminal, seta-like blade which is spinose—the spinules becoming longer and stronger towards the base, the proximal one very stout—on the inner edge only; and a shorter, but otherwise very similar, accessory blade borne a short distance towards the 'outside' (considering the part *in situ*). There is a small spine near the base of the segment.

The maxilliped (Fig. 4*h*) is also 2-segmented, with a strong complex attachment to the framework of the head. The first segment is rather long, with a small seta on the inner side; the last modified into a stout, but not very strong, claw.

The swimming legs (Fig. 4*i–l*) have each a basipod of two segments, and two rami, all 3-segmented except the endopod of the fourth legs which has two only. Their ornamentation is illustrated in the figures mentioned above, and summarized in Table 2.

TABLE 2. ORNAMENTATION OF THE SWIMMING LEGS OF *LICHOMOLGUS LEPTODERMATUS* SP.NOV.

	Basp.				End.							Exp.						
	1		2		1		2		3			1		2		3		
	Si	Se	Si	Se	Si	Se	Si	Se	Si	St	Se	Si	Se	Si	Se	Si	St	Se
P1	I	0	0	1*	1	0	1	0	5	0	I	0	I	1	I	4	I	III
P2	I	0	0	1*	1	0	2	0	3	I	II	0	I	1	I	5	I	III
P3	I	0	0	0	1	0	2	0	2	I	I	0	I	1	I	5	I	III
P4	I	0	0	0	1	0	0	0	.	.	.	0	I	1	I	5	I	II
							II	(St)										

* This may occasionally be absent.

The fifth pair of legs (Fig. 4*m*) are very small; 2-segmented, the basal fused with but sharply defined from, the thoracic somite, and borne midway along this. There is no seta on the basal segment, but two terminally on the distal, the inner shorter and thicker.

A small seta and a curving spine laterally near the middle of the genital segment represent all that could be seen of the sixth legs.

The caudal rami (Fig. 4*n*) are very elongate, about as long as the post-genital segments together, and eight or nine times as long as wide. There is an outer-edge seta just in the distal half, and four terminal ones—the longest only five-eighths the length of the ramus, none setose—and a small dorsal seta near the distal border.

Legend to Fig. 4

Fig. 4. *Lichomolgus leptodermatus*, sp.nov., adult female. *a*, dorsal view; *b*, side view; *c*, antennule; *d*, antenna; *e*, mandible; *f*, maxillule; *g*, maxilla; *h*, maxilliped; *i*, first swimming leg; *j*, second swimming leg; *k*, third swimming leg; *l*, fourth swimming leg; *m*, fifth leg; *n*, dorsal view of the left caudal ramus.

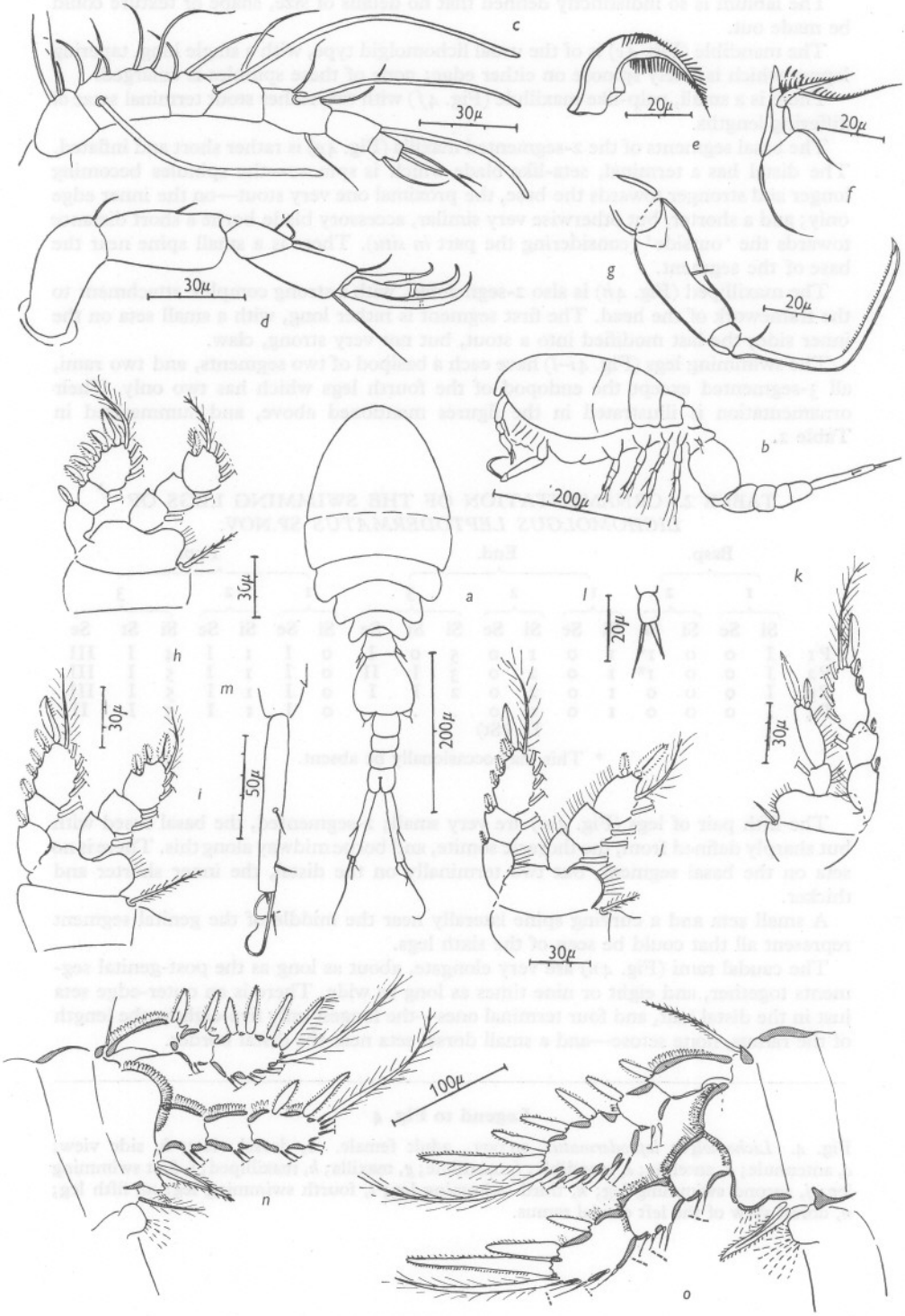
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Fig. 5

Description of the male

As for the female, except the body shape (Fig. 5*a*) is slightly more elongate—more than three times as long as wide. This is due, in great measure, to a lengthening of the prosome, so that the urosome attains more than one-third the width of this. The junction of the first pedigerous segment with the rest of the cephalothorax is not very well-defined.

The urosome is 6-segmented, with no intersegmental region; it is four times as long as wide. The genital segment broadens from front to rear, and is undivided.

The antennule (Fig. 5*c*) has an aesthetasc on each of the second, fourth, fifth and sixth segments.

All three terminal claws of the antenna (Fig. 5*d*) are jointed, but this is less clear in the outer and inner ones.

The mouthparts (Fig. 5*e–f*) have a slightly stronger integument.

Of the three free segments of the maxilliped (Fig. 5*g*), the last is a very long, narrow claw, bent in the centre almost into a right-angle, the distal half with a row of very fine hairs on the inner side; there is a short seta near the base of this segment.

The setae on the outer side of the second basipod segment, present in the first and second pairs of swimming legs in the female, may be lacking.

The sixth pair of legs are represented by a single small seta on each postero-lateral corner of the genital segment; these appear in dorsal view to be borne on a small mammiform projection.

Dimensions

Female, length 0·90 mm, greatest width 0·33 mm. Male, length 0·59 mm, width 0·19 mm.

Colour

Colourless and transparent except for the ovary, ovisacs and testes which were opaque by transmitted, and white (in the case of the first two) or pale rose by reflected light; and the ruby-red, shining eye.

Morphological notes

A most noticeable feature of the living animal was the posture of the body. Even when swimming freely, this was bent sharply between the fourth and fifth pedigerous segments (the major articulation) and again between the genital and succeeding abdominal segments—roughly like a 'Z' which had been pulled out at either end until the angles between the parts were obtuse. (An attempt to show this has been made in Fig. 5*b* but the original drawing was made on a lactic acid-cleared specimen, in which the exoskeleton was too flexible to hold its original shape, and this necessitated some alterations to obtain the desired effect.)

Legend to Fig. 5

Fig. 5. *a–m. Lichomolgus leptodermatus*, sp.nov., adult male. *a*, dorsal view; *b*, side view; *c*, antennule; *d*, antenna; *e*, mandible; *f*, maxilla; *g*, maxilliped; *h*, first swimming leg; *i*, second swimming leg; *j*, third swimming leg; *k*, fourth swimming leg; *l*, fifth leg; *m*, side view of caudal ramus. *n–o. Conchyliurus cardii*, sp.nov., adult female. *n*, first swimming leg; *o*, second swimming leg.

Systematics

The nearest attempt at a key to the genus *Lichomolgus* Thorell is to be found in Sewell's (1949, pp. 93-94) analysis of the setal formulae in the various species. *L. leptodermatus* represents a variation of that author's 'final stage of reduction', since the suppression of spines has extended to the third pair of swimming legs where one has been lost on the terminal segment, not of the exopod, but of the endopod.

In addition, the following characters appear to be distinctive, either separately or in conjunction: the very large proximal spine on the main lappet of the maxilla; the proportions of the caudal rami and their setae; the terminal armature of the antenna; the dactylus of the male maxilliped; and the very thin exoskeleton. It will be seen that the species does show a resemblance to *L. albens* Thorell.

Biology

The specimens were all found in small swellings of the gill tissues of the host. Each of these 'cysts' contained usually one male and one female, but as many as two females and three males did occur together. Both the large and small gills were infected, and these on either side (the swellings showing up clearly as whitish spots against the pink of the gill tissue); but neither the mantle nor the labial palps yielded any; nor were any seen swimming in water taken from the mantle cavity.

No movement could be detected in specimens lying in these swellings but, when they were released, there was a brief initial period of intense activity, usually terminating when the creature came to rest on surface of the gill. The males were, as usual, more active than the females. In a dish, this alternation of periods of activity with long quiescent phases—provided no sudden external stimulus was applied—persisted; under these conditions, too, ovigerous females soon shed their ovisacs.

Some of the specimens collected must have been in the last copepodid stage since cast skins were found in a culture which had been kept overnight; but these moult stages proved too delicate for manipulation and no immature specimens were found on subsequent re-examination. Infection of *Laevicardium* may take place in one of the later copepodid stages, as a careful search of the gills failed to discover any early instars.

Pseudanthessius liber (Brady & Robertson, 1875)

Occurrence. This species was found several times, but only in small numbers (one or two per host), together with *Asterocheres violaceus* in washings from the surface of *Echinus esculentus*, January and February 1955.

Distribution. Coasts of Norway, British Isles and Channel, Indian Ocean; adults typically associated with camarodont echinoids, but occasionally taken from other invertebrates or not associated.

Family CLAUSIDIIDAE Embleton, 1901

Conchyliurus cardii sp.nov.

Specimens examined. Eight females—two samples of three and five respectively—all ovigerous, were found in jars containing *Cardium* (*Acanthocardia*) *echinatum* Linn. dredged in Bigbury Bay, near Plymouth; 23 May 1955 and 6 July 1955.

Type specimens. Holo- and paratypes have been deposited in the British Museum (Natural History). The specific name refers to the host.

Description of the female

The body (Fig. 6*a*) is rather more elongate than the typical cyclopoid form; and strongly built. The prosome is little expanded, its dorsal outline forming an ellipse (truncated posteriorly), whose long axis would be (if not truncated) about twice the short. The greatest width is in the region of the first pedigerous segment; this somite is included in the cephalothorax; and there is no trace of a line of fusion between it and the rest of the 'head' region. The cephalothorax occupies about half the prosomal area. There is a band of very fine spinules just outside its ventro-lateral border. The lengths of the three metasomal segments are about equal; the postero-lateral corners of the first two and the cephalothorax appear slightly produced and pointed in dorsal (or ventral) view.

The urosome is 5-segmented, with a flexible intersegmental region between the fifth pedigerous and the genital segments. (This has the appearance of another somite, and is marked off with equal distinctness from both the foregoing. It is probably, however, part of the fifth pedigerous segment: the integument is not thickened as it is in the other urosomal segments, and in dead specimens the body is usually bent sharply at this point, cf. Fig. 6*b*). The segment bearing the fifth pair of legs is rather narrower than that preceding it, and not very long. The genital segment is the widest in the urosome, but slightly longer than wide. It is structurally very complex, and more material will be necessary before all the details can be satisfactorily elucidated. The anal segment is equal in length to the two preceding abdominal somites, and has a row of very fine teeth ventrally near the proximal end and similarly on the distal border. The widths of these three abdominal segments decrease evenly from front to rear.

The rostrum (Fig. 6*c*) is rather well-developed; it is visible in dorsal or ventral view rather than lateral (where it tends to be concealed by the antennules), and apparently non-mobile.

There is a double kidney-shaped eye, which can be seen in the living animal to have a shining spot (? lens) on the anterior end of either side.

The antennule (Fig. 6*d*) extends only about half the length of the cephalothorax. It is 6-segmented; the relative lengths, widths and armature of the segments are shown in the figure, and there are aesthetascs on the fifth and seventh segments.

The antenna (Fig. 6*e*) is a strongly prehensile, 4-segmented structure, with a large claw on the penultimate segment and seven articulated processes terminally. The surfaces of the segments are covered with patches of denticles, some small and spine-like, others—especially on the second and third segments—larger and more robust. In addition to the claw on the distal corner of the third segment, there is a small toothed projection near whose base a short seta is borne. The terminal segment is, as usual in the Clausidiids, somewhat offset.

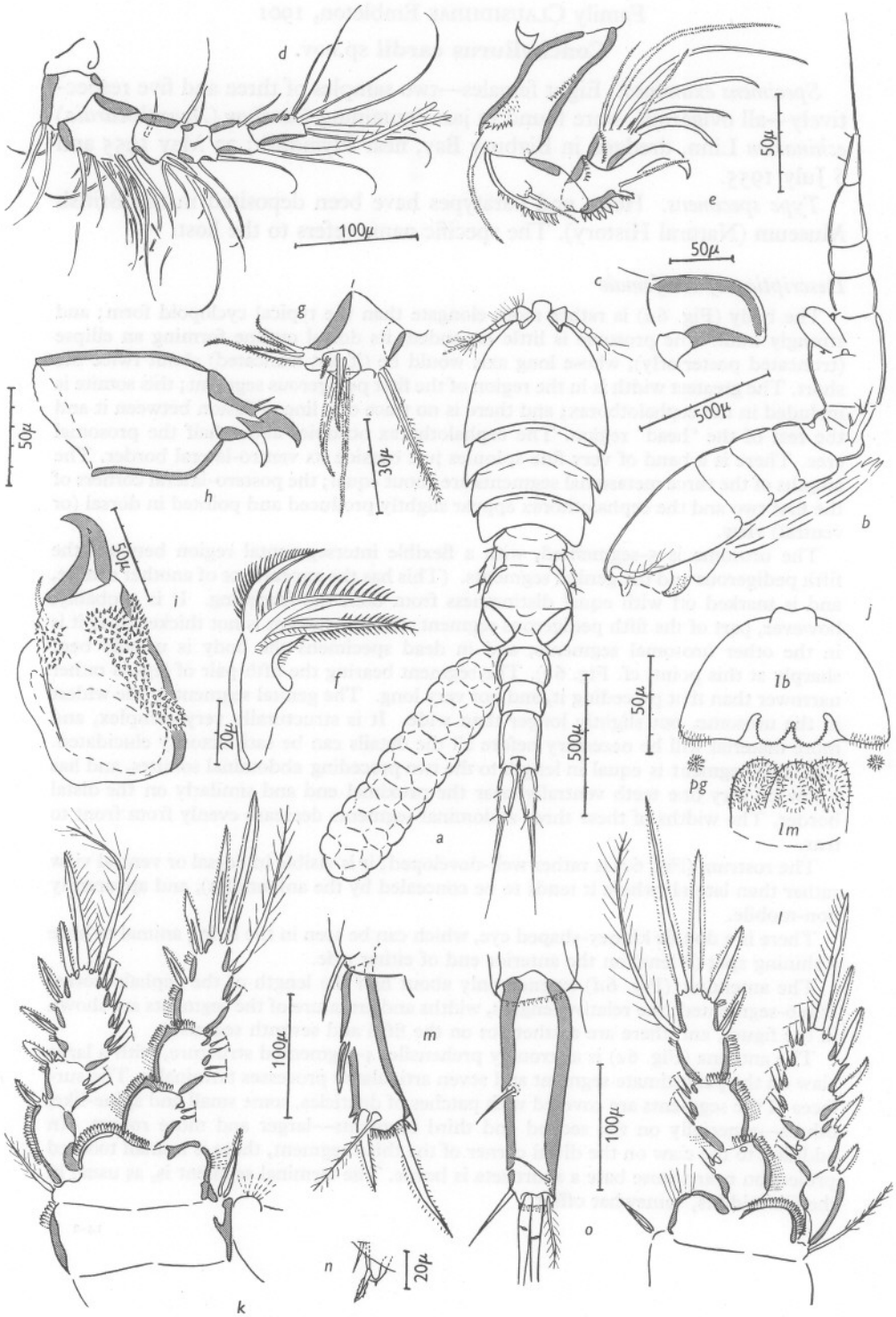
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Fig. 6

The mouthparts are all very closely appressed to each other. The labrum (Fig. 6*j*) has a sinuate posterior margin, beneath which are two small serrate lobes, one on either side of the mid-line. The paragnaths are rudimentary, being represented by small ciliated projections between the mandibles and maxillae. A small, indistinct, spinose structure, with two grooves dividing it into three aproximately equal lobes represented all that could be identified as the labium.

The mandible (Fig. 6*f*) has three lappets, almost equally elongate although the fact that the two upper ones are usually curved makes the lowest seem longer; these are all borne on a thickened base, the innermost partly joined to a prominence. The middle lappet is coarsely setose, the others more finely.

The maxillule (Fig. 6*g*) consists of a single free segment, partly bi-lobed. Its shape and ornamentation are as illustrated.

The maxilla (Fig. 6*h*) is 2-segmented; the first large and easily seen in ventral view: the second is modified into a very strong, stout, curved claw which bears two smaller claws, one on the concave surface and the other to one side, usually projecting above the large claw. The first segment has no ornamentation.

TABLE 3. ORNAMENTATION OF THE SWIMMING LEGS OF *CONCHYLIURUS CARDII* SP.NOV.

	Basp.				End.							Exp.						
	1		2		1		2		3			1		2		3		
	Si	Se	Si	Se	Si	Se	Si	Se	Si	St	Se	Si	Se	Si	Se	Si	St	Se
P1	1	0	1	1	1	0	1	0	2	2	II	0	I	1	I	4	I	III
P2	I	0	0	1	1	0	2	0	2	I	II	0	I	1	I	5	I	III
P3	I	0	0	1	1	0	2	0	2	II	II	0	I	1	I	5	I	III
P4	I	0	0	1	1	0	2	0	1	II	II	0	I	1	I	5	I	III

The maxilliped (Fig. 6*i*) is very similar to the maxilla. The first free segment, however, has patches of small spinules on the posterior (considering the appendage *in situ*) surface, and a short seta near the distal edge. The other segment is, like that of the maxilla, modified into a strong uncinate claw which lacks secondary claws but has, on either side in the region of greatest curvature, a small, stout denticle.

The last three pairs of mouthparts project ventrally more or less at right angles to this surface of the cephalosome, the maxilla and maxilliped curving distally in towards one another.

A 'postoral protuberance' (Humes, 1953, p. 101), similar to that present in many copepods, can clearly be seen in lateral view (Fig. 6*b*). It is an inflated region, with thin integument and an almost square base, located between the maxillipeds and first swimming legs.

The swimming legs (Figs. 5*n*, *o*, 6*k*, *l*) have all 2-segmented basipods and two rami, each of three segments. The ornamentation is shown in Table 3 and figures. It is interesting to note that the seta on the proximal basipod segment of the first legs is replaced in this position on the other swimming legs by a spine. The outer and distal edges of several of the segments have a row of very small cross-set teeth and/or hairs. The basal

Legend to Fig. 6

Fig. 6. *Conchyliurus cardii*, sp.nov., adult female. *a*, dorsal view; *b*, side view; *c*, rostrum; *d*, antennule; *e*, antenna; *f*, mandible; *g*, maxillule; *h*, maxilla; *i*, maxilliped; *j*, mouth complex (abbreviations as for Fig. 3*f*, plus *pg*, position of paragnath); *k*, third swimming leg; *l*, fourth swimming leg; *m*, fifth leg; *n*, sixth leg; *o*, dorsal view of caudal ramus. In *a* and *b* spermatophores can be seen.

plates (lamellae joining the basipods of each pair of legs) possess a rounded lobe, with a tuft of hairs, distally at either end; and the second basipod segment of the first swimming legs has a pointed prominence on the inner side.

The fifth pair of legs (Fig. 6*m*) is 2-segmented, the basal being completely fused with the thoracic segment and represented only by a widening of this and a seta. The latter is borne on a small papilla, rather more dorsal to the insertion of the free segment than is usually the case (cf. Fig. 6*b*). The distal segment is more or less triangular with almost straight sides; about four times as long as wide; with three spines—two more or less terminal, a plumose seta between them, the inner the longer—and one on the outer edge. The terminal margin has a row of close-set spinules, the inner- and outermost rather larger and longer.

The sixth pair of legs (Fig. 6*n*) are represented by a pair of projections on the dorsal surface of the genital segment: they are concealed for most of their length by the attached spermatophores. Each has a long feathered spine terminally and another (unornamented) near the base.

The ovisacs (Fig. 6*a*) are rather longer than the urosome, and relatively stout; borne laterally from the middle of the genital segment. Each contains about a hundred eggs.

The caudal rami (Fig. 6*o*) are nearly five-sixths the length of the anal segment and, like the latter, each has a row of very fine teeth ventrally on the distal border. The setae are as illustrated: the two longest with no other ornamentation than a very finely dentate border and a narrow wing for the distal three-quarters of their length.

Dimensions

Length 1·83 mm; greatest width 0·48 mm.

Colour

Colourless, with opaque whitish spots; the ovaries, oviducts and egg-sacs showing rose-pink, and the alimentary canal and region of the fused spermatophores brown.

Male. Unknown.

Biology. The external morphology suggests that this species is an associate, but specimens were never found actually in contact with a *Cardium*, always in the water surrounding it. A careful search of gills and mantle cavity in both samples of specimens (and one from the Looe–Eddystone Grounds in which no copepods occurred) being negative, it is suggested that future examination of the digestive system might be valuable. In any event, it is unlikely that the

TABLE 4. DIFFERENCES BETWEEN ADULT FEMALES OF *CONCHYLIURUS SOLENIS* AND *C. CARDII*

C. solenis Bocquet & Stock	*C. cardii*, sp.nov.
1. Accessory hooks on maxilla poorly developed	Accessory hooks on maxilla well developed
2. Knob on inner side of basipod P1 rounded	Knob on inner side of basipod P1 pointed
3. No process on outer distal edge of P5	Large spinule on outer distal edge P5
4. No spines on anal segment	A line of fine spines on ventral surface of anal segment both near the proximal and on the distal border
5. Spermatophores not retained on genital segment	Spermatophores retained and fused to genital segment in a complex fashion
6. Specimens found on gills of host	Specimens probably in digestive tract of host

specimens were associated with any other host, since the jars in which they were found contained only this species of *Cardium* and were covered, immediately after the molluscs were introduced, with fine netting.

Remarks. Bocquet & Stock (1957) erected the genus *Conchyliurus* for a species (*solenis*) which was found on the gills of *Solen marginatus* near Roscoff. Thanks to the kindness of the latter author, I was able to compare paratypes of this with my specimens. The two are very similar; indeed, it is open to question whether they might be considered host or geographic variations of a single species. However, I have decided to separate mine as a new species by the differences shown in the table, since these seemed both consistent over the range of specimens and of more than phenotypic character. It is hoped that a future comparison of material of both species from a particular locality will determine whether this is the best statement of their relationship.

Family BOMOLOCHIDAE Wilson, 1911

Bomolochus confusus Stock (1953)

B. soleae auct., non Claus

Occurrence. Adult females and males occurred in the nostrils of the Cod (*Gadus callarias* Linn.), Pout (*G. luscus* Linn.), and Whiting (*G. merlangus* Linn.), all trawled in the Plymouth region. Incidence figures are not given: they vary markedly, depending on whether the hosts are examined immediately on capture or after being brought into the laboratory. However, at sea, nearly every *G. luscus* of moderate size had at least one female—with a maximum of five—in each nostril; in the laboratory, an average figure for *G. merlangus* was one female to every eight hosts; while only one of several *G. callarias* examined had this associate. Males were very rare.

Distribution. British coasts; adults in nostrils of gadoid fishes.

Notes. This species was distinguished by Stock (1953) from *Bomolochus soleae* Claus mainly on differences in structure of the antennae, maxillipeds and swimming legs—especially the second pair. The specimens I have examined (from the three hosts mentioned) support his distinction, but seem to show minor differences from one another; this suggests that it might be possible to distinguish host-specific forms on morphological grounds.

CYCLOPOIDA: GNATHOSTOMA

Family CYCLOPIDAE Sars, 1913

Euryte longicauda Philippi (1843) var. *minor* T. Scott (1905)

Occurrence. One ovigerous female was found in washings from clinkers and pieces of bored limestone dredged on Asia Shoal, Plymouth Sound, 14 March 1955.

Distribution. Var. *minor* occurs in the North Sea and English Channel, adults not associated with animals. Typical *E. longicauda* has been recorded from the Arctic Ocean, Atlantic coasts of Europe, British Isles, Mediterranean, Black Sea and Suez Canal; adults littoral.

Notes. Kiefer (1929) includes this form in *E. longicauda*, but Lang (1946*b*, pp. 1, 2) distinguishes it as a separate species by the relatively longer abdomen and divergent caudal rami. I think Scott's intermediate course is the best until some experimental work has been done on the relationship between these two forms.

CALIGOIDA

Family LERNAEOCERIDAE Gurney (1933)

Peniculus fistula Nordmann (1832) f. *pagelli* Delamare Deboutteville & Nunes (1951)

Occurrence. (1) One female on the caudal fin of the Common Sea Bream (*Pagellus centrodontus* de la Roche), hand-lined near the Eddystone Lighthouse *ca.* 15 fm; June, 1954. (2) One female on the pelvic fin, one ovigerous female on the caudal fin of a Spanish Sea Bream (*P. erythrinus* Linn.) removed from the Plymouth Aquarium; October 1954. (This fish had been trawled on the Mewstone Grounds and kept in the Aquarium for some time. It is probable that it was infected before capture.) (3) One female on the caudal fin of *P. centrodontus*, trawled on the Looe–Eddystone Grounds; July 1955.

Distribution. The species is known from the English Channel to the Mediterranean, the adult female on a variety of hosts (Candeias, 1955). Forma *pagelli* occurs through this range, the adult female on the fins of *Pagellus* sp.

Notes. There seems some difference of opinion about the authorship of the name *Peniculus fistula*. Nordmann (1832), who described the species, mentions (p. 107) that his specimens had been found by Rudolphi in 1817. The latter (he says) had sent these, together with unpublished notes and a suggested name (*Dirhynchus fistula*), to him; he changed the generic name, since it was already in use, but retained the specific for the purpose of his description. According to the Rules of Nomenclature, therefore, Nordmann should be credited with this name.

My specimens agreed closely with the description and figures of f. *pagelli* given by its authors except that the lengths, even of the ovigerous female, were slightly less. Also, each exhibited a slight curvature of the 'neck' so that the main part of the body was in life held parallel to, and slightly above the surface of the fin to which the head was attached.

This appears to be the first record of the genus in Britain; and of *Pagellus centrodontus* as host for this form.

HARPACTICOIDA: OLIGOARTHRA

Family TISBIIDAE Stebbing (1910) *sensu* Lang (1948)

Tisbe elongata (A. Scott, 1896)

Occurrence. All stages from the 'Nauplius V' (that is, a stage corresponding to the one described as Nauplius V for *T. furcata* by Johnson & Olson, 1948) to adults were found among the gills of the common lobster (*Homarus vulgaris* M. Edwards) at Plymouth. The copepods were very abundant, averaging nearly fifty per host; and each lobster examined over a period of about a year was infected. In August 1953, also, while working for the Scottish Home Department's Fisheries Laboratory in Aberdeen, I found this species to be very common on lobsters in the Orkneys.

Distribution. British Coasts; adults and stages typically found on gills of *H. vulgaris*.

Notes. This record is included, although the species has already been noted from Plymouth, both to extend the distribution (by the Orkneys record) and, by emphasizing their abundance and the extent to which developmental stages occur on lobster gills, to support Gurney's (1933, p. 299) suggestion that the species is definitely associated with *H. vulgaris* rather than 'usually free-living' (Humes, 1954).

SUMMARY

The adults of three new cyclopoid copepods are described and figured, namely *Micropontius ovoides*, gen. et sp.nov., occurring on spatangid echinoids; *Lichomolgus leptodermatus*, sp.nov., and *Conchyliurus cardii*, sp.nov., both associated with pelecypod molluscs. *Micropontius* is made the type of a new family, the Micropontiidae.

Some other copepods, *Asterocheres violaceus* (Claus), *Scottomyzon gibberum* (T. & A. Scott), *Pseudanthessius liber* (Brady & Robertson), *Bomolochus confusus* Stock, *Euryte longicauda* Philippi var. *minor* T. Scott and *Peniculus fistula* Nordmann, are recorded for the first time from the Plymouth region; and mention is also made of *Tisbe elongata* (A. Scott).

Points of interest in the biology, morphology, systematics and distribution of all these are discussed.

REFERENCES

ALLEE, W. C., EMERSON, A. E., PARK, O., PARK, T. & SCHMIDT, K., 1949. *Principles of Animal Ecology*. 837 pp. Philadelphia: Saunders.

ATKINS, D., 1934. Two parasites of the Common Cockle *Cardium edule*; a rhabdocoele, *Paravortex cardii* Hallez and a copepod *Paranthessius rostratus* (Canu). *J. mar. biol. Ass. U.K.*, Vol. 19, pp. 669–76.

BAER, J. G., 1951. *Ecology of Animal Parasites*. 224 pp. University of Illinois Press.

BOCQUET, C., 1952. Copépodes semi-parasites et parasites des Echinoderms de la Région de Roscoff. Description de *Lichomolgus asterinae* n.sp. *Bull. Soc. zool. Fr.*, T. 47, pp. 495–504.

BOCQUET, C. & STOCK, J. H., 1957. Copépodes parasites d'Invertébrés des côtes de France. I. Sur deux genres de la famille de Clausidiidae commensaux de Mollusques: *Hersiliodes* Canu et *Conchyliurus* nov.gen. *Proc. Kon. nederl. Akad. Wetensch.*, Ser. C, Vol. 60, pp. 212–23. (Not seen.)

CANDEIAS, A., 1955. *Peniculus fistula* Nordm. on two new hosts *Trachurus trachurus* (L.) and *Trachurus picturatus* (Bowd.). *Notas Inst. Biol. marit.*, No. 8.

DAVENPORT, D., 1955. Specificity and behaviour in symbioses. *Quart. Rev. Biol.*, Vol. 30, pp. 29–46.

DELAMARE DEBOUTTEVILLE, C. & NUNES, L. P., 1951. Existence de 'formes biologiques' chez *Peniculus fistula* (Rudolphi) (Copepoda). *Vie et Milieu*, T. 2, pp. 448–58.

GIESBRECHT, W., 1899. Die Asterocheriden des Golfe von Neapel und des angrenzenden Meeres-Abschnitte. *Faun. u. Flor. Neapel*, Monogr. 25, 218 pp.

GOTTO, R. V., 1954. *Lichomolgides cuanensis* n.g., n.sp., an ascidicolous copepod occurring in *Tridemnum tenerum* (Verrill). *Parasitology*, Vol. 44, pp. 379–86.

GRAY, P., 1933. *Mycophilus rosovula* n.sp., a notodelphyoid copepod parasitic within *B.* (*Botrylloides*) *leachii* Sav. with a description of the nauplius and notes on the habits. *J. mar. biol. Ass. U.K.*, Vol. 18, pp. 523–8.

GURNEY, R., 1931. *British Fresh-water Copepoda. General Part and Calanoida*, Vol. 1, 238 pp. London: Ray Society.

—— 1933. Notes on some copepods from Plymouth. *J. mar. biol. Ass. U.K.*, Vol. 19, pp. 299–304.

HERDMAN, W. A. & SCOTT, A., 1896. Report on the investigations carried out in 1895 in connection with the Lancashire Sea-Fisheries Laboratory at University College, Liverpool. Section IV: Description of new and rare Copepoda (by A. SCOTT). *Proc. Lpool. biol. Soc.*, Vol. 10, pp. 103–77 (134–58).

HUMES, A. G., 1953. *Ostrincola gracilis* C. B. Wilson, a parasite of marine pelycopods in Louisiana (Copepoda Cyclopoida). *Tulane Stud. Zool.*, Vol. 1, pp. 99–107.

—— 1954. *Tisbe celata* n.sp., a Harpacticoid copepod from the mantle cavity of the Edible Mussel in New Brunswick. *J. Fish. Res. Bd Can.*, Vol. 11, pp. 816–26.

JOHNSON, M. W. & OLSON, J. B., 1948. The life history and biology of a marine Harpacticoid copepod, *Tisbe furcata* (Baird). *Biol. Bull., Woods Hole*, Vol. 95, pp. 320–32.

KIEFER, F., 1929. Crustacea Copepoda: II. Cyclopoida Gnathostoma. *Das Tierreich*, Bd. 53, 102 pp.

LANG, K., 1946*a*. A contribution to the question of the mouthparts of the Copepoda. *Ark. Zool.*, Bd. 38A, No. 5.

—— 1946*b*. Einige für die schwedische Fauna neue marine Cyclopoida Gnathostoma, nebst Bemerkungen über die Systematik der Unterfamilie Cyclopininae. *Ark. Zool.*, Bd. 38A, No. 6.

—— 1948. Copepoda 'Notodelphyoida' from the Swedish West Coast with an outline on the systematics of the Copepoda. *Ark. Zool.*, Bd. 40A, No. 14.

LEIGH-SHARPE, W. H., 1926. The Herpyllobiidae, a family of Copepoda parasitic on polynoid worms. *Parasitology*, Vol. 18, pp. 269–76.

—— 1933. Second list of parasitic Copepoda of Plymouth with a description of three new species. *Parasitology*, Vol. 25, pp. 113–18.

NICHOLLS, A. G., 1944. Littoral Copepoda from South Australia (II): Calanoida, Notodelphyoida, Monstrilloida and Caligoida. *Rec. S. Aust. Mus.*, Vol. 8, pp. 1–62.

NORDMANN, A., 1832. *Micrographische Beiträge zur Naturgeschichte der wirbellosen Thiere*, Heft 2, 150 pp. Berlin: Reimer.

NORMAN, A. M. & SCOTT, T., 1906. *Crustacea of Devon and Cornwall.* 232 pp. London: W. Wesley.

SARS, G. O., 1901. *An Account of the Crustacea of Norway.* Vol. 4, Copepoda, Calanoida. Parts 1 and 2. 28 pp. Bergen Museum.

—— 1913–18. *An Account of the Crustacea of Norway,* Vol. 6, Copepoda, Cyclopoida. 225 pp. Bergen.

SEWELL, R. B., 1949. The littoral and semi-parasitic Cyclopoida, the Monstrilloida and Notodelphyoida. *Sci. Rep. Murray Exped.*, Vol. 9, No. 2.

STOCK, J. H., 1953. *Bomolochus soleae* Claus, 1864 and *B. confusus* n.sp., two hitherto confounded parasitic copepods, with remarks on some other *Bomolochus* species. *Beaufortia*, No. 24.

WILSON, C. B., 1932. The Copepods of the Woods Hole Region Massachussetts. *Bull. U.S. nat. Mus.*, No. 158. 635 pp.

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ON THE ATTENUATION OF LIGHT IN THE SEA

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(Text-figs. 1 and 2)

Recently Jones & Wills (1956) have related the attenuation of light in the sea and in estuarine waters to the concentration of suspended solid matter. The attenuation was measured with an *in situ* hydrophotometer with a beam acceptance angle of approximately 3·20°. The concentration of suspended materials was determined by filtering in the case of natural samples or by adding known weights of kaolin or mud to tap water. In the discussion of their data and methods they have made application of the diffraction theory for opaque particles relatively large compared to the wave-length of light.

It seems worthwhile to extend the discussion in terms of electromagnetic theory for scattering of light by small relatively transparent spheres of the order in size of the wave-length of light. From an analysis of this type it may be possible to roughly estimate the predominant size of the material present in the water which was examined.

Fig. 1 (adapted from Burt, 1954) shows the theoretical extinction due to scattering as a function of particle size for uniform suspensions of small spherical particles. Extinction was computed for green light (550 mμ, approximately the centre of the visual response curve and thus corresponding to the centre of response curve of the hydrophotometer used by Jones & Wills) for 1 mg per litre suspensions of mineral material with a relative refractive index of 1·15 and a density of 2·65. The latest computations of Mie scattering for a refractive index of 1·15 were used (Pendorf, 1956). The solid lines are for light scattered in all directions, while the dashed line shows the theoretical extinction corrected to exclude light scattered into a cone of half angle 3° centred about the forward direction. The latter approximates the field of acceptance of the hydrophotometer.

Fig. 2, showing the experimental measurements of extinction v. concentration, is taken from Jones & Wills. Lines have been added which represent the theoretical relationship between extinction and concentration from the dashed line in Fig. 1. In making a rough comparison between the data and the theoretical results it should be kept in mind that a size range is present in each sample with particles of different density, shape and refractive index.

For the natural water samples taken from the Thames and the sea near Plymouth the predominant size range lies between 2·5 and 10 μ with a wide scatter between individual samples. There is a trend toward increase in particle size in the more turbid samples. The Thames Estuary samples tend to have larger particle sizes than those taken near Plymouth. The suspensions which

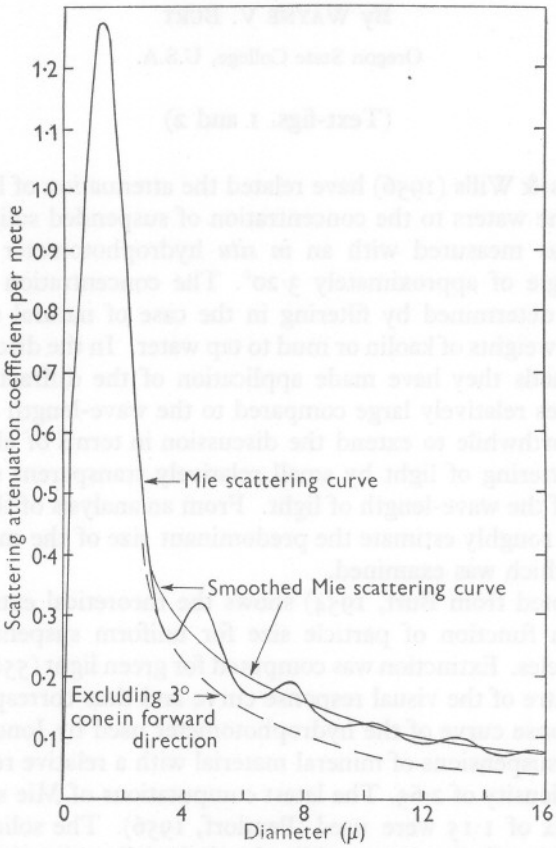

Fig. 1. Theoretical specific scattering for concentrations of suspended material of 1 mg per litre. Calculations are for green light (550 mμ) for material with a relative refractive index to water of 1·15.

were made up of Thames mud and tap water have predominate particle sizes near 3 μ, while the Kaolin suspensions probably have much smaller particles around 0·2 μ in diameter.

The anomalous change in slope near the origin in the data for Kaolin and Thames mud suspensions may be due to fine material around 1·2 μ in diameter in suspension in the tap water which would displace the Kaolin and Thames mud suspension lines upward. Another possibility is that the dispersion may vary with the concentration at very low concentrations.

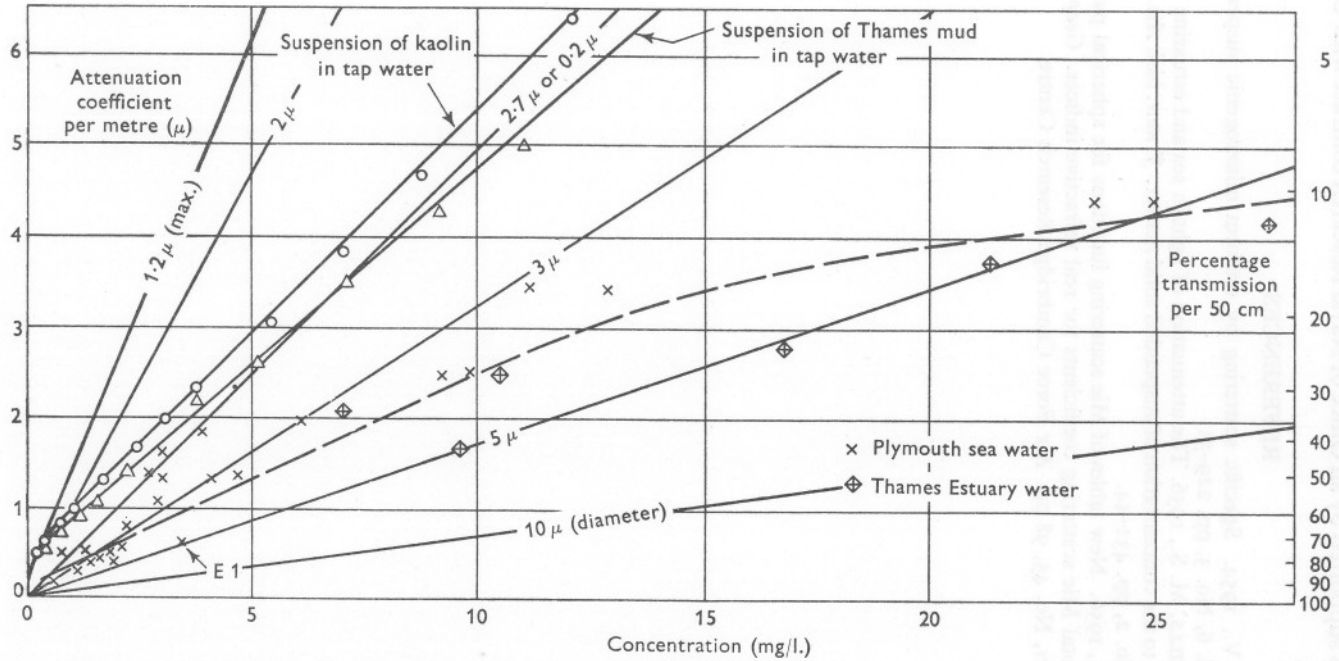

Fig. 2. Relation between attenuation coefficient per metre and concentration of suspended solid matter (from Jones & Wills, 1956). The solid lines have been added to show theoretical attenuation due to scattering by small particles with diameters of 0·2, 1·2, 2, 2·7, 3, 5 and 10 μ. E1 refers to a hydrographic station south of the Eddystone.

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REFERENCES

BURT, WAYNE V., 1954. Specific scattering by uniform minerogenic suspensions. *Tellus*, Vol. 6, No. 3, pp. 229–31.

JONES, D. & WILLS, M. S., 1956. The attenuation of light in sea and estuarine waters in relation to the concentration of suspended solid matter. *J. mar. biol. Ass. U.K.*, Vol. 35, No. 2, pp. 431–44.

PENDORF, R. B., 1956. New tables of Mie scattering functions for spherical particles. Part 6. Total Mie scattering coefficients for real refractive indices. *Geophysical Res. Papers*, No. 45, 98 pp. Air Force Cambridge Research Centre.

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NOTES ON OXYGEN SAMPLING ON THE FLADEN GROUND

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(Text-fig. 1)

For the years 1951–53 sampling of phosphate concentration has been used to describe the plant production on the Fladen Ground (Steele, 1956). Further studies in 1955–56 have compared the phosphate sampling with the ^{14}C technique (Steele, 1957). On most occasions samples were also taken for dissolved oxygen concentration and these notes discuss some attempts made to interpret those data. A set of oxygen profiles for Fladen are shown in the earlier paper.

There are four main causes of change in oxygen concentration; two physical, water mixing and surface exchange; and two biological, increase due to photosynthesis and decrease due to the breakdown of organic matter and to respiration. Except for surface exchange, these effects should have concomitant changes in the phosphate concentration and the main problems arise through the attempts to compare them.

When studying the phosphate data, the amount of vertical mixing was estimated from temperature profiles and its effect subtracted from the observed phosphate changes between two dates to leave what was called the 'biological change'. The same procedure can be carried out for the oxygen data except for the 0–20 m layer where an estimate of surface exchange is required before the biological change can be found. A fairly successful attempt to estimate exchange was made by Redfield (1948), using a formula which states in effect that the rate of exchange is proportional to the difference between the surface concentration and the equilibrium concentration. For Fladen, the best available oxygen data are those for 1953, when two stations were worked at fairly regular intervals and the computations of 'biological change' and surface exchange were made for these data. The values for oxygen solubility used in Redfield's formula were taken from the nomogram given by Richards & Corwin (1956), which is based on the data of Truesdale, Downing & Lowden (1955).

To compare these calculations with the similar ones for phosphate, a conversion factor is necessary, and one is given by Sverdrup, Johnson & Fleming (1942, p. 237). This depends on the phosphorus/carbon ratio found by chemical analysis of plankton and on an association of carbon and oxygen in the form CO_2. The numerical value in the usual units is

1 μg atom phosphorus $\equiv$ 2·36 ml. oxygen.

However, when this factor was used it was found that in the region below 40 m, where the 'biological changes' showed an increase for phosphate and a decrease for oxygen, the phosphate gain was equivalent to approximately two-thirds of the oxygen loss.

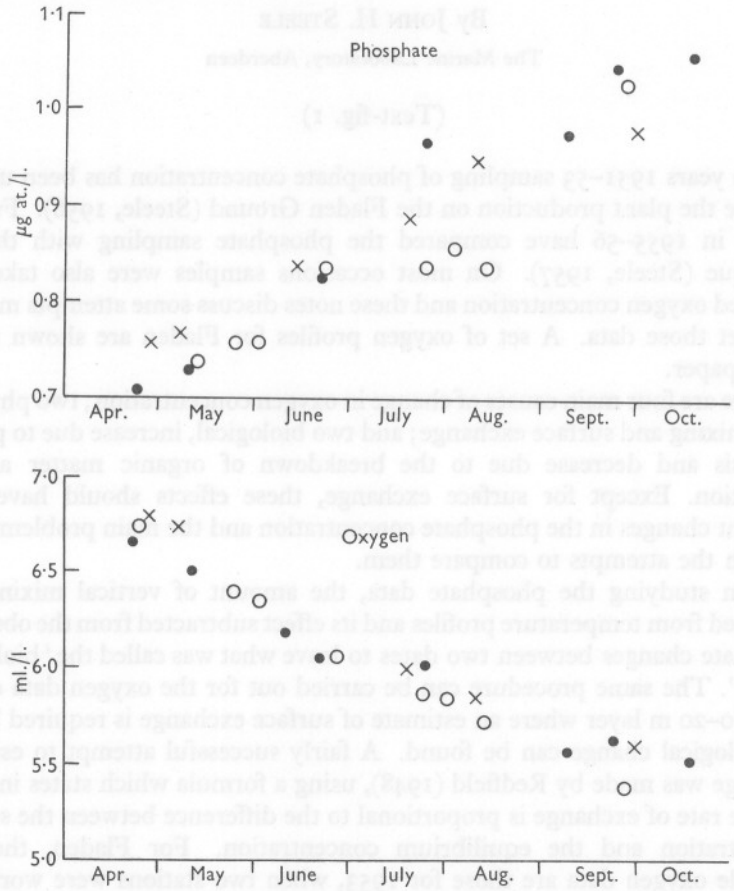

Fig. 1. The near-bottom concentrations of phosphate and oxygen for the years 1953 (●), 1955 (○) and 1956 (×).

To check this feature independently of the calculation, the oxygen and phosphate changes can be compared directly for the water below the thermocline which remains unmixed from April to October. In Fig. 1, the near-bottom concentrations are plotted for the years 1953, 1955 and 1956. There is considerable variability in the values, especially the phosphate, but the general rates of change seem to be consistent from year to year. These rates give a conversion factor of

$$1\ \mu\text{g atom phosphorus} \equiv 3{\cdot}87\ \text{ml. oxygen.}$$

The increase confirms the results of the calculations and the explanation probably lies in the fact that the basis of the oxygen/carbon comparison was a carbohydrate metabolism.

It has been shown that *Calanus finmarchicus* probably have a protein content of about 50% (Marshall, Nicholls & Orr, 1934) which would lead to a higher oxygen/phosphate ratio. In a full discussion of this problem Riley (1951) deduced that with a protein content of 68%, the metabolism of zooplankton and their bacterial oxidation would give a ratio approximately double the value given by Sverdrup *et al.* (1942). For phytoplankton it has usually been found that the photosynthetic quotient is nearly unity, which would entail a carbohydrate metabolism and so require the earlier conversion factor. However, Cramer & Myers (1948) have obtained a quotient of 1·47, and they believe that the previous values are due to a temporary shift to carbohydrate synthesis caused by the high light intensities required in the experiments (see also Ryther, 1956). Their results would lead to a conversion factor of 3·5 which is near the value given by the Fladen data. For these reasons, a conversion factor of about 3·87 may be applicable not only in the lower waters but also in the euphotic zone, and this value is used in the following comparison.

The biological changes in phosphate and oxygen are compared by converting the phosphate changes to oxygen units and then adding these to the calculated oxygen changes. What is left over will be termed the 'residual' thus:

$$\text{residual} = \text{oxygen change} + 3{\cdot}87 \text{ phosphate change}.$$

If the phosphate changes always corresponded to oxygen changes then the residuals would be zero except for the 0–20 m layer where they would be balanced by the surface exchange. Such agreement is not found and the values for the various factors are given in Table 1.

The first point to be noted is that the estimates of surface exchange are greater than the residuals for 0–20 m by a factor which varies from 1·05 to 8·8. Thus the formula does not appear to be successful in this case. Below 20 m the residuals are very variable, and all that can be said is that in general they are less than the oxygen changes; the few cases in which the oxygen changes have been accentuated, are printed in bold type.

Another problem concerning oxygen:phosphate ratios arises from results given by Riley (1956). By similar methods to those used for the Fladen data, he estimated the biological changes of oxygen and phosphate in Long Island Sound. He found that the over-all ratios for production were normal but the phosphate was absorbed at a lower level than the oxygen was produced. On Fladen, in the 20–30 m layer, this occurs to some extent in the spring but not in the summer (Table 1). However, it is the summer that is of most interest since at this time the phosphates show maximum production in the 20–30 m layer. Direct observations of this feature are available for one particular time interval, 21 June–24 July 1953, when there was very little mixing at or below

30 m. During this period the average changes at 30 m for four stations were: temperature, +0·25° C; phosphate, −0·19 μg at./l.; oxygen, +0·98 ml./l. In fact the oxygen increase is greater than that required by the phosphate decrease, so it would seem that the rate of production was at least that indicated by the phosphate data. This case may be peculiar due to the lack of vertical mixing, and later data using ^{14}C (Steele, 1957) do not support the phosphate results.

TABLE 1. ESTIMATES OF SURFACE EXCHANGE, 'BIOLOGICAL CHANGE' OF OXYGEN AND RESIDUALS FOR FLADEN IN 1953

	21. iv.–11. v.		11. v.–11. vi.		11–21. vi.		21. vi.–24. vii.	
Exchange...	—	3·36	—	6·36	—	1·52	—	3·64
(m)	Ox.	Res.	Ox.	Res.	Ox.	Res.	Ox.	Res.
0– 20	1·62	−0·38	0·48	−1·37	−0·77	−1·02	−0·58	−1·40
20– 30	−0·46	**−0·64**	−1·26	**−2·15**	−0·05	**−0·41**	0·96	0·11
30– 40	−0·14	**−0·50**	−0·60	0·72	−0·32	−0·22	0·44	0·01
40– 50	−0·38	0·01	−0·31	−0·23	−0·36	−0·03	0·04	**0·53**
50– 60	−0·28	−0·05	−0·24	−0·13	−0·26	0·04	0	**0·39**
60–140	−0·86	−0·17	−1·74	0·46	−1·74	0·49	−0.04	**1·80**

	24. vii.–8. ix.		8–25. ix.		25. ix.–19. x.	
Exchange...	—	3·87	—	0·98	—	0·70
(m)	Ox.	Res.	Ox.	Res.	Ox.	Res.
0– 20	−2·05	−2·30	−0·91	−0·93	0·49	−0·30
20– 30	0·82	−0·26	0·71	0		
30– 40	1·33	−1·31	−0·04	0·19	0·35	−0·44
40– 50	−1·16	−0·08	−0·35	0·06	0·10	−0·24
50– 60	−0·58	−0·35	−0·20	0·32	−0·02	0·06
60–140	−4·35	−2·86	0·28	**1·80**	−0·64	0·74

SUMMARY

A comparison is made of oxygen and phosphate data from the Fladen Ground. It is found that the conversion factor for oxygen:phosphorus given by Sverdrup *et al.* (1942) does not agree with the changes below the euphotic zone and an alternative factor is calculated. Problems concerning surface exchange and production are also discussed.

REFERENCES

CRAMER, M. & MYERS, J., 1948. Nitrate reduction and assimilation in *Chlorella*. *J. gen. Physiol.*, Vol. 32, pp. 93–102.

MARSHALL, S. M., NICHOLLS, A. G. & ORR, A. P., 1934. On the biology of *Calanus finmarchicus*. V. Seasonal distribution, size, weight and chemical composition in Loch Striven in 1933 and their relation to the phytoplankton. *J. mar. biol. Ass. U.K.*, Vol. 19, pp. 793–827.

REDFIELD, A. C., 1948. The exchange of oxygen across the sea surface. *J. mar. Res.*, Vol. 7, pp. 347–61.

RICHARDS, F. A. & CORWIN, N., 1956. Some oceanographic application of recent determinations of the solubility of oxygen in sea water. *Limnol. Oceanogr.*, Vol. 1, pp. 263–7.

RILEY, G. A., 1951. Oxygen, phosphate and nitrate in the Atlantic Ocean. *Bull. Bingham oceanogr. Coll.*, Vol. 13, Art. 1, 126 pp.

—— 1956. Oceanography of Long Island Sound, 1952–1954. IX. Production and utilization of organic matter. *Bull. Bingham oceanogr. Coll.*, Vol. 15, pp. 324–44.

RYTHER, J. H., 1956. The measurement of primary production. *Limnol. Oceanogr.*, Vol. 1, pp. 72–84.

STEELE, J. H., 1956. Plant production on the Fladen Ground. *J. mar. biol. Ass. U.K.*, Vol. 35, pp. 1–33.

—— 1957. A comparison of plant production estimates using ^{14}C and phosphate data. *J. mar. biol. Ass. U.K.*, Vol. 36, pp. 233–41.

SVERDRUP, H. U., JOHNSON, M. W. & FLEMING, R. H., 1942. *The Oceans; their Physics, Chemistry and General Biology*. 1087 pp. New York: Prentice-Hall.

TRUESDALE, G. A., DOWNING, A. L. & LOWDEN, G. F., 1955. The solubility of oxygen in pure water and sea water. *J. appl. Chem.*, Vol. 5, pp. 53–62.

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A COMPARISON OF PLANT PRODUCTION ESTIMATES USING ^{14}C AND PHOSPHATE DATA

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(Text-figs. 1–6)

In an earlier paper (Steele, 1956) estimates of the yearly cycle of plant production were given for a part of the northern North Sea known as the Fladen Ground. These estimates were made from a study of the changes in inorganic phosphate in relation to the effects of vertical mixing.

The method is indirect since several hypotheses have to be made relating phosphorus and carbon uptake by phytoplankton. The problems which these raise are most acute during the summer when the results show a low rate of production. Either of two factors, a high rate of regeneration of phosphorus to inorganic form in the euphotic zone, or the ability of plants to use organic phosphorus compounds, could make the production rate much greater.

For these reasons a check on the method was desirable and this has been done using the ^{14}C technique devised by Steeman Nielsen (1952) which gives directly a measure of the carbon uptake during a short period of time.

The main purpose of this paper is to show from data collected in 1955 and 1956 that there is general agreement between the two methods. This purpose is attained in so far as the mean daily production calculated from phosphates was 0·20 g C/m^2 between 1 June and 13 August 1955, while the three values found from the ^{14}C experiments during this period were 0·20, 0·21 and 0·15. The results are also used to continue the study of the changing vertical distribution of plants in terms of the effects of sinking and grazing.

It is a pleasure to thank Dr H. W. Harvey for his advice and Mr R. I. Currie of the National Institute of Oceanography for instruction in the details of the ^{14}C technique and for working up the samples collected in 1955.

METHODS

The technique for estimating ^{14}C uptake was essentially that described by Steeman Nielsen (1952). The only variation that was made in the method concerns the estimation of the activity of the ^{14}C solution from the self-absorption curve. It was found difficult to obtain satisfactory precipitates of

very small quantities of barium carbonate, and the need for this was avoided by using the known form for the equation of the curve. This gives the activity at thickness T as

$$G(T) = G(O)\,\frac{1-e^{-\mu T}}{\mu T},$$

where μ is a constant and $G(O)$ is the value required (Calvin *et al.*, 1949, p. 30). A curve is fitted to the mean values at three thicknesses; the goodness of the fit acting as a check. Fig. 1 gives the curve for the ampoules used in 1956.

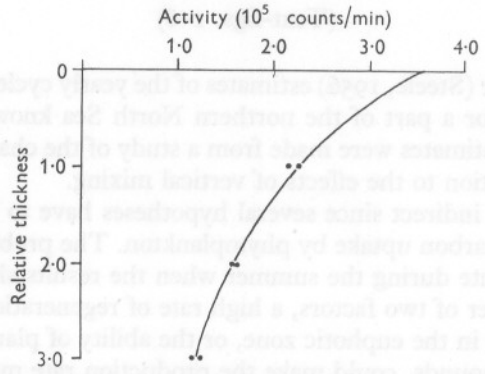

Fig. 1. Self-absorption curve for the ampoules used in 1956.

The bottles used in the experiments were of approximately 170 c.c. capacity. They were filled in pairs from the following depths: 1, 10, 20, 30, 40 and 50 m. The bottles were lowered to the depths from which the water came and left there for the whole (1955) or half (1956) of the period of daylight.

The methods of estimating production from the phosphate data, chlorophyll concentration and zooplankton dry weight have already been described (Steele, 1956).

ESTIMATION OF CARBON ASSIMILATION

In his experiments, Steeman Nielsen collected water samples from different depths and exposed them in a water bath to the same light intensity for 4 h. In converting the measures of ^{14}C uptake to values of carbon assimilation he allowed 6% for isotope factor and 4% for loss due to respiration giving a total addition of 10%.

When samples are exposed at different depths the effect of respiration will be proportionally greater in the deeper water where there is a low rate of photosynthesis. The importance of this effect will depend on the extent to which the ^{14}C is available for respiration during the period of the experiment. Since there is not yet sufficient evidence to estimate this effect, the values for carbon assimilation were calculated by Steeman Nielsen's method. These

values are shown in Figs. 2 and 3, together with the profiles of population, estimated from the chlorophyll concentrations.

It is generally thought that photosynthesis varies directly with the light intensity except near the surface where there is some inhibition (Jenkins, 1937; Steeman Nielsen, 1952). To study the present data from this point of view, Secchi disc readings (Table 2) were used to estimate the extinction coefficient, K, defined by the rough conversion factor of Poole & Atkins (1929) as

$$K = \frac{1{\cdot}7}{\text{S.D. reading}}.$$

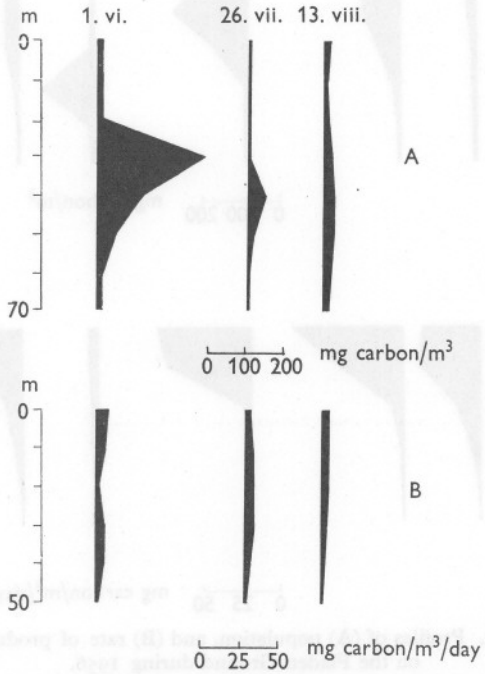

Fig. 2. Profiles of (A) population and (B) rate of production on the Fladen Ground during 1955.

Assuming that the light which is effective for photosynthesis decreases as $\exp(-KZ)$, where Z is the depth in metres, then the light intensity relative to the surface can be found. Since no measurements were made of the absolute light intensity at the surface, the values for each date are not directly comparable. On this basis the values for C shown in Table 1 were calculated where

$$C = \frac{\text{carbon assimilation/day}}{\text{population} \times \text{rel. light intensity}}.$$

Thus C provides an index for the increase in cellular carbon in terms of the quantity of chlorophyll present multiplied by a rough measure of the relative light energy at each depth.

There is considerable variation in the values of C, but this is not large in terms of the range of values of both assimilation and light intensity which can vary by a factor of several hundreds between surface and 50 m. The expected

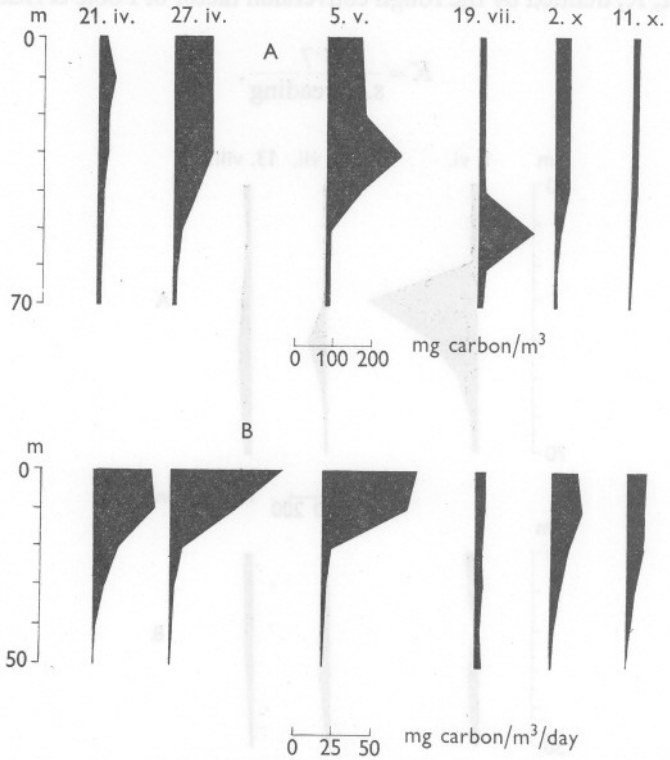

Fig. 3. Profiles of (A) population, and (B) rate of production on the Fladen Ground during 1956.

TABLE 1. VALUES OF C DURING 1955 AND 1956 (SEE TEXT)

Date	Depth (m) 1	10	20	30	40	50
1. vi. 55	0·5	1·3	1·0	0·5	3·0	1·5
26. vii. 55	0·5	2·1	3·8	12·0	3·2	5·0
13. viii. 55	0·2	0·8	1·6	1·0	0·8	0·5
21. iv. 56	1·8	2·8	5·8	8·6	6·6	20·0
27. iv. 56	0·8	2·4	2·4	2·0	16·0	22·0
5. v. 56	0·8	3·4	1·8	1·4	2·0	—
19. vii. 56	—	1·4	2·8	8·8	10·0	5·2
2. x. 56	0·5	1·4	2·0	2·8	2·4	3·1
11. x. 56	0·7	2·0	5·8	7·6	11·2	16·4

decrease in C near the surface is found and it occurs also to some extent at 10 m. At 40 and 50 m the values are more variable, but in general they tend to be larger. It is at these depths, however, that lower values of C would be expected if much of the ^{14}C were being lost through respiration. On this rather tenuous basis it would appear that ^{14}C estimates more nearly represent total photosynthesis rather than net assimilation.

Some idea of the magnitude of the respiration loss can be obtained from the formula given by Riley, Stommel & Bumpus (1949),

$$r_T = 0{\cdot}0175 \exp(0{\cdot}069\,T),$$

where r_T is the respiratory coefficient in g C/day/g phytoplankton carbon at temperature T. In Table 2 the ratios of respiration to production are given as the average for the layer 0–50 m. Only one value exceeds one third and the mean is about 0·22 which can be considered a reasonable general value (Steeman Nielsen, 1952). There is a considerable fluctuation in the figures, and for this reason no allowance has been made for respiration in the following discussion.

TABLE 2. OBSERVATIONS ASSOCIATED WITH ^{14}C EXPERIMENTS (SEE TEXT)

	1955			1956					
	1. vi.	26. vii.	13. viii.	21. iv.	27. iv.	5. v.	19. vii.	2. x.	11. x.
Secchi disc reading (m)	15·5	19·0	21·0	15·0	10·0	10·0	17·0	18·0	14·5
Respiration/production	0·65	0·15	0·33	0·04	0·11	0·19	0·21	0·18	0·09
Mean dry weight of zooplankton (g C/m²)	2·2	1·4	2·3	0·7	2·1	2·7	4·0	0·6	0·4

COMPARISON OF PRODUCTION ESTIMATES

The general comparison of the estimates of production given by ^{14}C and by phosphate change is shown in Fig. 4. A detailed comparison is difficult since the ^{14}C uptake measures production rate on a given day, whereas the phosphate data give a value for production between two dates. The main point is that there is no large and systematic discrepancy between the two sets of data. The ^{14}C values are on the average slightly less than the phosphate values and the difference would be accentuated if respiration were taken into account. This is important for, on this basis, there is no evidence that the phosphate estimates are fallaciously low due to regeneration or to the use of organic phosphorus compounds by the phytoplankton. To this extent the phosphate method is validated.

Given this general agreement between phosphate and ^{14}C estimates one main difference must be noted; this is found in the depth distribution of production. The most suitable examples are the four occasions when two ^{14}C experiments were made within a short time interval. The phosphate profiles for these intervals are shown in Fig. 5, and it can be seen that they differ from the relevant ^{14}C profiles of Figs. 2 and 3.

For the final interval, 2–11 October 1956, the difference can be explained by the fact that the water column is homogeneous from 0 to 40 m. This means that, although the production rate at any moment has the depth distribution shown by the ^{14}C data, mixing spreads this production evenly through the homogeneous layer so that, effectively, production is constant in this depth range. However, this type of explanation is not sufficient to account

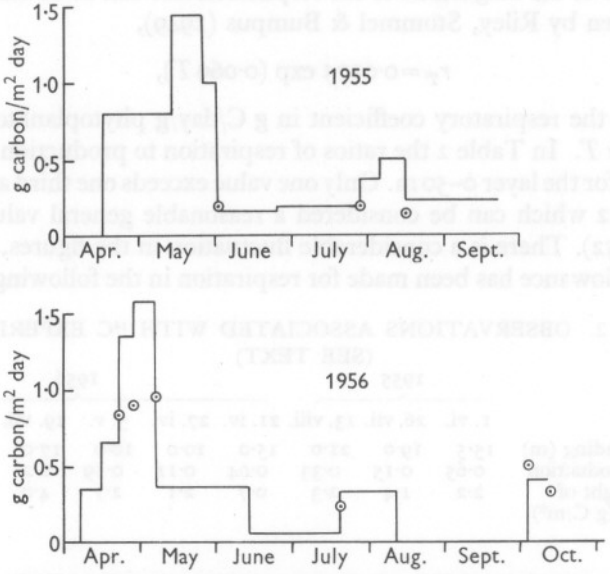

Fig. 4. Histograms of production for the years 1955 and 1956 derived from the phosphate data. The circles show the rates of production estimated by the ^{14}C method.

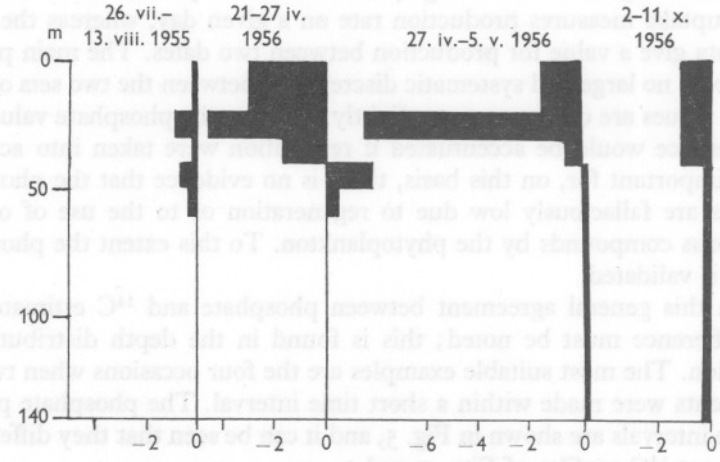

Fig. 5. Some profiles of 'biological change' of phosphate on Fladen in $10^2 \times \mu g$ at./cm² day.

for the fact that maximum phosphate consumption in the summer seems to occur between 20 and 30 m (Steele, 1956). Oxygen data appear to support the phosphate results (Steele, 1957) but, although the anomaly remains, it seems probable that the ^{14}C values are more trustworthy.

SINKING AND FILTERING RATES

In the earlier paper (Steele, 1956) an attempt was made to explain variations in plant population throughout 1953 in terms of production, sinking, grazing and vertical mixing. The first step was to calculate sinking rates of phytoplankton and filtering rates of zooplankton from the mean changes in and below the euphotic zone during the interval between two sampling dates. Using these values and the population profile at the beginning of the interval, a profile was derived for the end of the interval which could be compared with the observed profile. As a continuation of this work the four intervals discussed in the previous section were analysed in the same way using the ^{14}C estimates of production. The values for dry weight of zooplankton used in the equations are given in Table 2.

TABLE 3. SINKING AND FILTERING RATES

	1955	1956		
	26. vii.–13. viii.	21–27. iv.	27. iv.–5. v.	2–11. x.
Sinking rate (m/day)	2·2	3·3	1·9	6·0
Filtering rate (m^3/day/g carbon)	5·8	7·7	7·7	78·0

Table 3 gives the estimated sinking and filtering rates. The values for the last interval are excessively high and no satisfactory explanation can be given. The remaining values are comparable with those of 1953. In particular, the higher filtering rate in the spring agrees with the conclusions made in the earlier paper.

Fig. 6 shows the comparison of observed and calculated profiles for the first three intervals. The agreement between them is not very good; in particular the sharp increase at 30 m on 5 May 1956 cannot be explained. The use of the phosphate estimates of production does not give any appreciable improvement.

CONCLUSIONS

As so often happens in this type of work the results are not completely consistent. Hypotheses are partly supported, partly disproved, and further data alter previous conclusions. Such difficulties have arisen in these attempts to explain in detail the changing vertical distribution of production and of population.

In three out of the four cases considered, a broad division of the water column into the euphotic zone and the region below leads to estimates of sinking and filtering rates which are in good agreement with previous values.

The profiles deduced from these rates are not always satisfactory, and the question remains whether this defect is due to some combination of sampling errors, inadequacy of approximating over periods of weeks, and arithmetical artifacts; or are the hypotheses themselves insufficient to explain such detail? One obvious conclusion is that much further study is required on these basic problems.

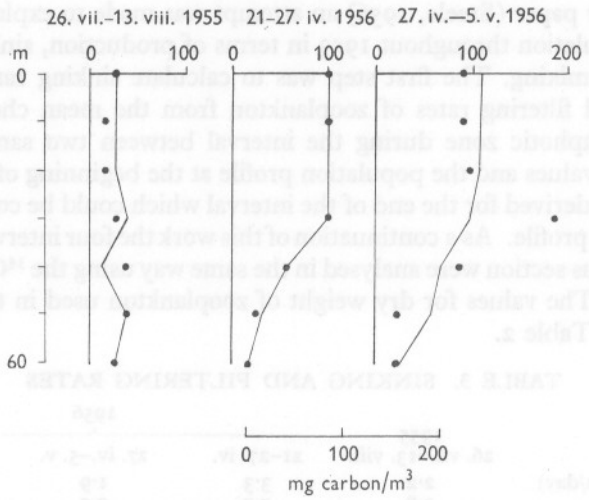

Fig. 6. Comparison of observed and calculated population profiles.

A rough analysis of the depth distributions of ^{14}C uptake gives some evidence that these agree with the accepted relations of photosynthesis and light intensity. For this reason these distributions are more acceptable than those given by the phosphate data.

There remains the fact that as measures of production below a given area of sea surface the two methods are in good agreement. Differences are to be expected since there will be day-to-day variations in carbon uptake due to changes in weather, vertical mixing, etc. From this point of view phosphate estimates are valuable since they measure production during an interval of weeks. Further, because of the way they are derived, phosphate estimates display the relations between production and such features of the environment as vertical mixing and nutrient deficiency. For these reasons the two methods may be regarded as complementary.

SUMMARY

Organic production in the sea can be measured by studying the changes in phosphate throughout the water column. Results obtained by this method are compared with estimates of carbon uptake using ^{14}C made on the Fladen

Ground during 1955 and 1956. There is good general agreement between the two methods but some differences in the vertical distribution.

The results are also used to calculate filtering rates of phytoplankton and sinking rates of zooplankton, and to compare observed and predicted vertical distributions of chlorophyll.

REFERENCES

CALVIN, M., *et al.*, 1949. *Isotopic Carbon.* 376 pp. New York: Wiley.

JENKINS, P. M., 1937. Oxygen production by the diatom *Coscinodiscus excentricus* Ehr. in relation to submarine illumination in the English Channel. *J. mar. biol. Ass. U.K.*, Vol. 22, pp. 301–43.

POOLE, H. H. & ATKINS, W. R. G., 1929. Photo-electric measurements of submarine illumination throughout the year. *J. mar. biol. Ass. U.K.*, Vol. 20, pp. 1–27.

RILEY, G. A., STOMMEL, H. & BUMPUS, D. F., 1949. Quantitative ecology of the plankton of the western North Atlantic. *Bull. Bingham oceanogr. Coll.*, Vol. 12, Art. 3, 169 pp.

STEELE, J. H., 1956. Plant production on the Fladen Ground. *J. mar. biol. Ass. U.K.*, Vol. 35, pp. 1–33.

—— 1957. Notes on oxygen sampling on the Fladen Ground. *J. mar. biol. Ass. U.K.*, Vol. 36, pp. 227–31.

STEEMAN NIELSEN, E., 1952. The use of radio-active carbon (C^{14}) for measuring organic production in the sea. *J. Cons. int. Explor. Mer.*, Vol. 18, pp. 117–40.

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THE LARVAE OF SOME MONOGENETIC TREMATODE PARASITES OF PLYMOUTH FISHES

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(Text-figs. 1–28)

The Order Monogenea of the Class Trematoda contains (Sproston, 1946) upwards of 679 species, but in only twenty-four of these species has a larval form been described. Of these larvae, fourteen belong to adults that parasitize fresh-water fishes, amphibians or reptiles, and ten to adults that parasitize marine fishes. *Udonella caligorum* is known (Sproston, 1946) not to have a larval stage in its life history. In the present study, accounts will be given of eleven hitherto undescribed larvae which belong to adults that parasitize marine fishes at Plymouth, and which represent seven of the eighteen families (Sproston, 1946) of the Monogenea.

For the most part the literature on larval monogeneans consists of isolated studies of individual species, and these have been listed by Frankland (1955), but the descriptions of four new larvae by Euzet (1955) appeared too late for inclusion in Frankland's list. More general observations on monogenean life cycles have been made by Stunkard (1937) and Baer (1951), and Alvey (1936) has speculated upon the phylogenetic significance of monogenean larvae.

Previous accounts of monogenean larvae have included but scant reference to culture techniques, presumably because the methods adopted have been simple and successful; in my hands, however, many attempts to rear larvae have been unsuccessful, and so some details of those procedures which have yielded successful cultures are included. At the same time it must be pointed out that the main object of the present study was to obtain specimens of monogenean larvae for morphological investigation, and properly designed experiments to determine factors influencing embryonic development were not attempted.

In addition to the studies made upon the eleven previously undescribed larvae, observations were made upon the larvae of *Diclidophora luscae* and *Polystoma integerrimum* in order to facilitate comparisons and to provide practice in techniques.

In past accounts of monogenean larvae it has been customary to describe the egg capsules, but the variations in the form of the capsules of the species studied here appear likely to be related more to variations in habits of oviposition than to larval characters, and so it is intended later to study the egg

capsules in relation to their respective adults. However, it seems worth while to record now that the thirteen species of monogeneans that I have studied, together with those in previous descriptions of larvae, all have operculate capsules. It is remarkable therefore that Dawes (1946, p. 13) should have stated that in Monogenea, operculate eggs are sufficiently rare to make this character of general diagnostic value in distinguishing between Monogenea (non-operculate eggs) and Digenea (operculate eggs).

MATERIAL AND TECHNIQUES

Specimens of adult trematodes were obtained from fishes at Plymouth in July and August, some in 1954 and 1955, but mainly in 1956. The gills of the fish hosts were examined in a manner described previously (Llewellyn, 1956), and in addition trematodes were obtained from the skin of the Common Sole and the Cuckoo Ray. A list of the parasites studied, named and classified according to Sproston (1946), is included in Table 1.

TABLE 1. CLASSIFIED LIST OF THE PARASITES STUDIED

		Host	
Monopisthocotylea			
Gyrodactyloidea			
Dactylogyridae	*Diplectanum aequans*	*Morone labrax*	Gills
Capsaloidea			
Capsalidae	*Entobdella soleae*	*Solea solea*	Skin
Acanthocotyloidea			
Acanthocotylidae	*Acanthocotyle lobianchi*	*Raja clavata*	Skin
Polyopisthocotylea			
Aviellloidea			
Polystomatoidea			
Polystomatidae	**Polystoma integerrimum*	*Rana temporaria*	Bladder
Hexabothriidae	*Rajonchocotyle emarginata*	*Raja clavata*	Gills
Diclidophoroidea			
Discocotylidae	*Plectanocotyle gurnardi*	*Trigla cuculus*	Gills
	Anthocotyle merluccii	*Merluccius merluccius*	Gills
Microcotylidae	*Gastrocotyle trachuri*	*Trachurus trachurus*	Gills
	Pseudaxine trachuri	*Trachurus trachurus*	Gills
	†Unidentified microcotylid species	*Trachurus trachurus*	Gills
	Microcotyle labracis	*Morone labrax*	Gills
Diclidophoridae	*Diclidophora merlangi*	*Gadus merlangus*	Gills
	**Diclidophora luscae*	*Gadus luscus*	Gills

* Described by previous authors, but studied from fresh material in the present investigation.

† This is the same trematode as referred to previously (Llewellyn, 1956, p. 117); a description of the adult will be published later.

Adult trematodes were transferred as soon as possible to dishes of fresh sea water and rinsed free of mucus with jets of sea water from a pipette. Even specimens that appeared moribund usually became active after this treatment, although it was sometimes several hours before egg-laying was resumed. The trematodes were rinsed in several changes of Berkefeld-filtered sea water and then placed at the various controlled temperatures that from time to time

became available. As stated previously, it was not possible to conduct properly designed experiments on the factors influencing the rate of egg-capsule production and the period of embryonic development, but the following general observations on about 480 adults and about 2600 capsules may be of use to future workers.

It seems likely that although adult parasites survive for at least 2 or 3 weeks, and probably longer at temperatures of 3–7° C, very few or no egg capsules are produced below about 8° C. At 13° C, which is approximately the temperature of the bottom water in the localities from which the hosts were trawled, the rate of capsule production per parasite per hour varies according to species between about 1·0 and 0·5 on the first day or two, falling to about 0·25 on the third day, and ceasing altogether on the fourth day excepting in *Entobdella*, which continues to lay at gradually decreasing rates for another 2 or 3 days. At 18° C the rate increases to about 3 or 4 capsules per hour for the first 12 h, but the parasites do not survive longer than about 24 h. At 20° C in most species there was no egg production, and the parasites died within about 12 h, but *Plectanocotyle*, *Pseudaxine*, *Gastrocotyle*, *Microcotyle* and *Diplectanum* were able to lay about 0·5 per hour before dying.

An attempt was made to collect eggs from parasites still attached to a living host by keeping isolated specimens of living *Trachurus trachurus* in small tanks, but a collection of only fifty-seven capsules in 7 h from a host subsequently found to be harbouring thirty specimens of *Gastrocotyle trachuri* was disappointing, and collecting from isolated parasites was thought to be more profitable.

Culture dishes were examined daily with a stereomicroscope, and egg capsules were transferred by means of a pipette to dishes of fresh, filtered sea water. Dishes of various shapes and sizes were tried, and eventually it was found that covered Petri dishes of 4 cm diameter and 2 cm depth provided the most acceptable compromise between the conflicting desiderata of a small volume of water to facilitate searching for and capturing larvae with a pipette, and a large volume to minimize the frequently fatal osmotic effects due to evaporation from the sea water. The use of filtered sea water, combined with incubation in darkness, helped to restrict contamination of the cultures, for while the presence of extraneous organisms appeared to have little effect upon actual embryonic development, conditions for observation were made more difficult. The chief disadvantage of contamination, however, was the damaging attack by ciliates upon larvae during the period of their actual emergence from the capsule.

Little or no embryonic development took place in any species at temperatures of 8° C and below. At 13° C the period of embryonic development in *Plectanocotyle* was found to be something between 21 and 30 days, precise determination being complicated by the habit of the adult of accumulating the capsules in the uterus for 3 or 4 days before laying, and thus the exact

age of the capsules at the commencement of incubation was not known. Embryos of *Anthocotyle*, *Gastrocotyle* and *Diclidophora merlangi* all failed to complete development at 13° C in the 28-day period available to me for observation. At 18° C *Plectanocotyle* hatched after 13–16 days' incubation, and *Anthocotyle* after 21 days. At 20° C the periods in days of embryonic development were as follows: *Diplectanum*, 5; *Plectanocotyle*, 8–11; 'microcotylid species', 10; *Acanthocotyle*, 12; *Entobdella*, *Microcotyle labracis*, *Gastrocotyle* and *Pseudaxine*, 14–16; *Rajonchocotyle*, 25; and *Diclidophora merlangi*, 27.

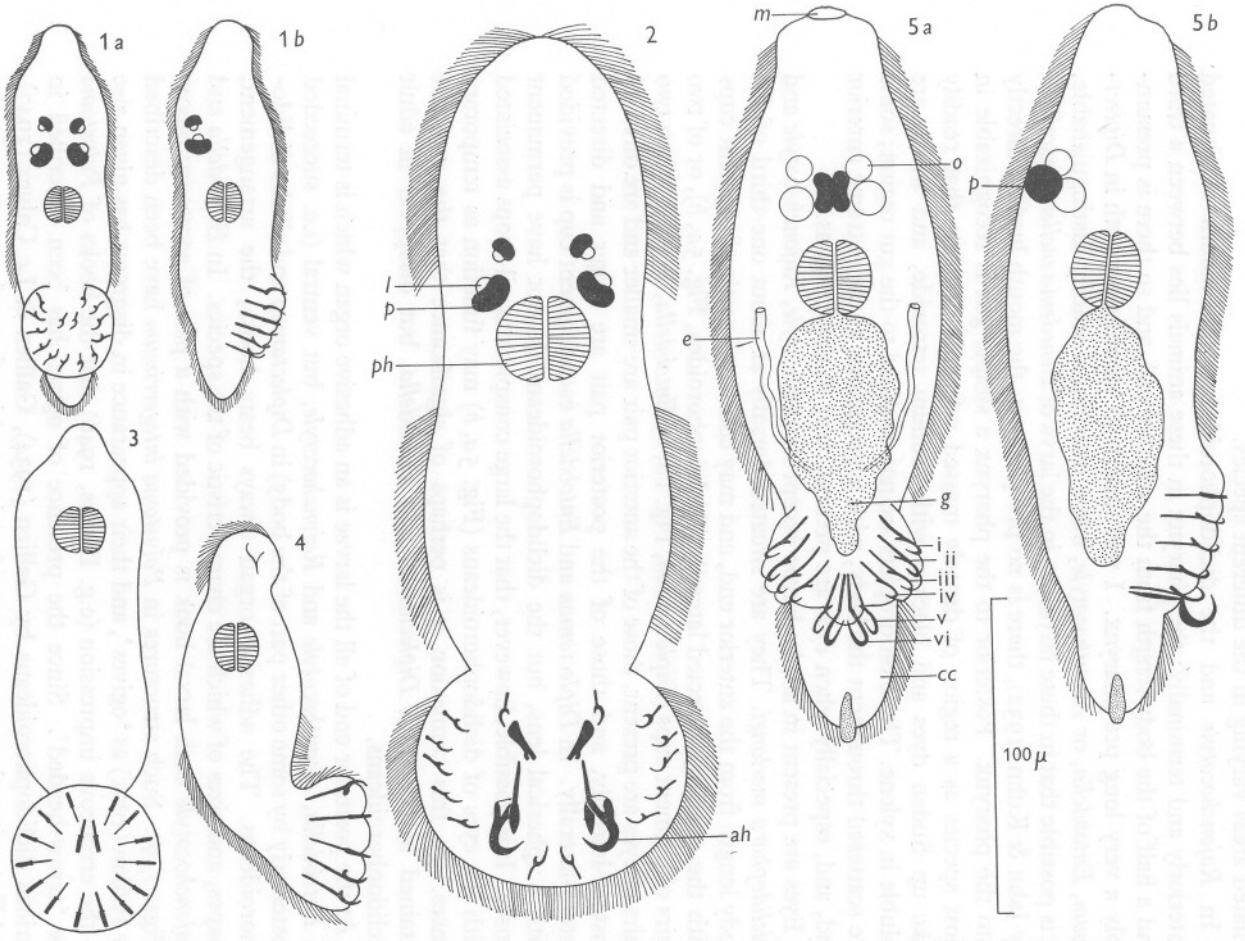
Hatching in all species appeared to be brought about entirely by repeated pressure against the operculum by muscular extension of the larvae as described by Frankland (1955) for *Diclidophora denticulata*, and in no case was there present a 'viscous cushion' mechanism as has been described in *Fasciola hepatica* by Rowan (1956).

From time to time it was found convenient to delay hatching by storing capsules containing active larvae at a temperature of about 4° C. Such specimens could subsequently be induced to hatch by returning them to a temperature of about 20° C, following which hatching usually took place in the course of some 6–12 h.

Free-living larvae and active larvae still enclosed in their capsules were examined under the microscope by mounting them on slides in sea water under cover-glasses supported by petroleum jelly in the manner generally practised for the study of digenean larvae. These fresh preparations, pressed to the required degree by the withdrawal of sea water with filter paper, were found to be much more useful than more permanent preparations, the best of which were made by mounting specimens either directly in Farrant's Medium, or, after fixation in formaldehyde and staining in borax carmine, in Canada Balsam. With temporary preparations, an apochromatic water-immersion objective was found more suitable than an oil-immersion objective since there was less tendency for the cover-glass to be moved with the objective during focusing. Extensive use of photography was made in recording the shapes of the larvae, and Figs. 1–28 were prepared from such photographs.

DESCRIPTIONS OF THE LARVAE (Figs. 1–28)

The larvae of the monogeneans studied are all cylindrical or ovoid organisms between 100 and 300 μ long, and between 30 and 100 μ in diameter. Although belonging to the 'flatworm' phylum, the degree of dorso-ventral flattening in these larvae is at most only very slight (compare Fig. 1*a* with *b*, and Fig. 5*a* with *b*). The anterior end of the body is tapered to form a conical region that may be marked off from the rest of the body by a shoulder region, and the posterior end is similarly tapered (*Diplectanum*, Fig. 1*a*, *b*, and the diclidophoroideans, Fig. 5*a*, *b*), or ends in a terminal adhesive organ (*Entobdella*, *Acanthocotyle*, *Rajonchocotyle*, Figs. 2–4 respectively).



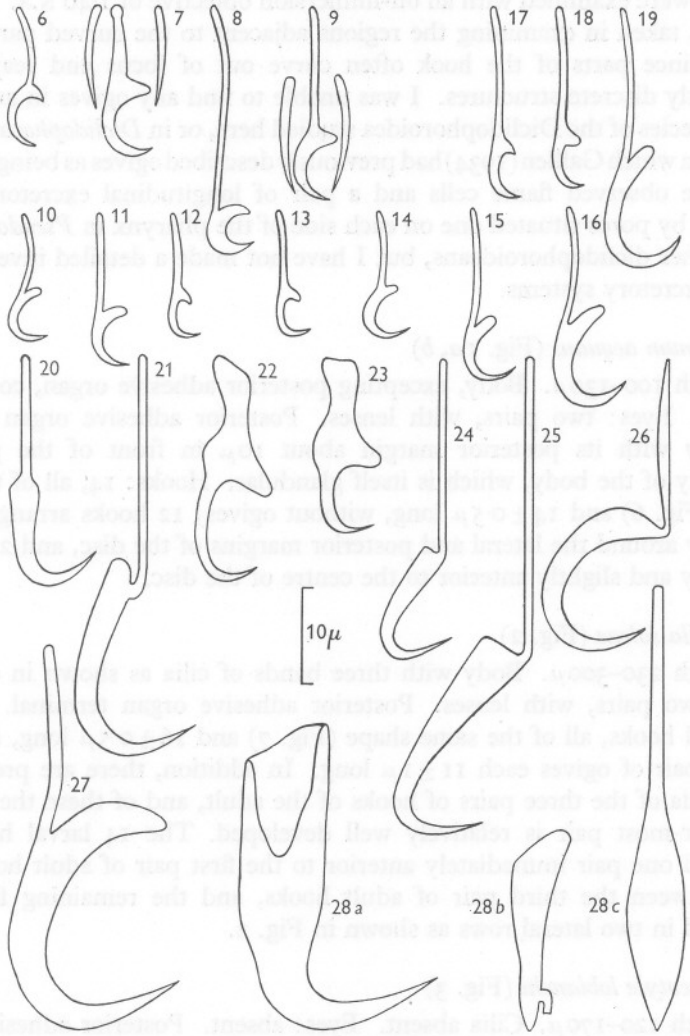
Figs. 1–5. Monogenean larvae, all drawn to same scale (ventral view unless otherwise stated). Fig. 1*a*, *Diplectanum aequans*. Fig. 1*b*, *D. aequans* (side view). Fig. 2, *Entobdella soleae*. Fig. 3, *Acanthocotyle lobianchi*. Fig. 4, *Rajonchocotyle emarginata* (side view). Fig. 5*a*, *b*, schematized larva of the superfamily Diclidophoroidea (Fig. 5*b* side view). *ah*, primordia of hooks of adult; *cc*, ciliated cone; *e*, excretory canal; *g*, gut; *l*, lens of eye; *m*, mouth; *o*, oil droplet; *p*, pigment cup of eye; *ph*, pharynx; i–iv, lateral hooks; v, postero-lateral hook; vi, posterior hook.

In all larvae except *Acanthocotyle* the body is ciliated, the extent of the ciliated areas varying in the different species.

In *Rajonchocotyle* and the diclidophoroideans, the mouth is situated anteriorly and terminally; the pharynx in these animals lies between a third and a half of the body length from the anterior end, and so there is presumably a very long pre-pharynx. I was unable to identify a mouth in *Diplectanum*, *Entobdella*, or *Acanthocotyle*, but a pharynx is readily distinguishable. It is possible that in these larvae, as in the larva of *Benedenia melleni* described by Jahn & Kuhn (1932), there is no pre-pharynx, the mouth leading directly into the pharynx. Posterior to the pharynx a simple gut is recognizable in most species as a region of densely massed refractile droplets that readily take up Sudan dyes and blacken with osmium tetroxide, and which are soluble in xylene. These oil droplets are not confined to the gut region; some are scattered throughout the body, with aggregations at the extreme anterior end, and, especially when eyes are present, near to these organs.

Eyes are present in all the larvae except *Acanthocotyle*, *Rajonchocotyle* and *Diclidophora merlangi*. They are situated dorsally at about one-third of the body length from the anterior end, and may consist of a pair of pigment cups with the openings directed laterally (Diclidophoroidea, Fig. 5*a*, *b*), or of two pairs of pigment cups (*Diplectanum*, Fig. 1*a*, *b*; *Entobdella*, Fig. 2). When two pairs of eyes are present, those of the anterior pair are smaller and are directed postero-laterally, and those of the posterior pair are larger and directed antero-laterally. In *Diplectanum* and *Entobdella* each pigment cup is provided with a spherical lens, but the diclidophoroideans do not have permanent lenses. It is possible, however, that the large conspicuous oil drops associated with the eyes of diclidophoroideans (Fig. 5*a*, *b*) may function as temporary lenses. In this connexion it is perhaps of significance that the eyes are retained in the adult *Diplectanum* and *Entobdella*, but disappear in adult diclidophoroideans.

At the posterior end of all the larvae is an adhesive organ which is terminal in *Entobdella*, *Acanthocotyle* and *Rajonchocotyle*, but ventral (i.e. succeeded posteriorly by some other part of the body) in *Diplectanum* and all the diclidophoroideans. The adhesive organ always bears hooks, the arrangement, shapes, and sizes of which are characteristic of the species. In *Entobdella* and *Rajonchocotyle* each larval hook is provided with a pair of accessory pieces (Figs. 7, 9). Such structures in *Polystoma integerrimum* have been described by Halkin (1901) as 'ogives', and their appearance in diagrams has given rise to the erroneous impression (e.g. Dawes, 1946) that the hooks of *Polystoma* are 'arrow-headed'. Since the presence of ogives has been described in various diclidophoroideans by Gallien (1934), Gallien & Le Calvez (1947), and Euzet (1955), great care was taken in searching for such structures in the diclidophoroideans studied in the present investigation. Thoroughly flattened specimens, mounted in sea water, glycerin, Farrant's Medium, or Canada



Figs. 6–28. Hooks of larval monogeneans, all drawn to same scale. Fig. 6, *Diplectanum aequans*. Fig. 7, *Entobdella soleae* (with ogives). Fig. 8, *Acanthocotyle lobianchi*. Fig. 9, *Rajonchocotyle emarginata* (with ogives). Figs. 10–16, typical lateral hooks of diclidophoroidean larvae. Fig. 10, *Plectanocotyle gurnardi*. Fig. 11, *Anthocotyle merluccii*. Fig. 12, *Gastrocotyle trachuri*. Fig. 13, *Pseudaxine trachuri*. Fig. 14, unidentified microcotylid species. Fig. 15, *Microcotyle labracis*. Fig. 16, *Diclidophora merlangi*. Figs. 17–19, postero-lateral hooks of diclidophoroideans. Fig. 17, *Gastrocotyle trachuri*. Fig. 18, *Pseudaxine trachuri*. Fig. 19, *Diclidophora merlangi*. Figs. 20–26, posterior hooks of diclidophoroideans. Fig. 20, *Plectanocotyle gurnardi*. Fig. 21, *Anthocotyle merluccii*. Fig. 22, *Gastrocotyle trachuri*. Fig. 23, *Pseudaxine trachuri*. Fig. 24, unidentified microcotylid species. Fig. 25, *Microcotyle labracis*. Fig. 26, *Diclidophora merlangi*. Figs. 27–28, primordia of adult hooks present in larva at time of hatching. Fig. 27, *Microcotyle labracis*. Fig. 28 *a*, *b*, *c*, 3rd, 1st and 2nd hooks respectively of *Entobdella soleae*.

Balsam, were examined with an oil-immersion objective of 1·40 N.A. Especial care was taken in examining the regions adjacent to the curved parts of the hooks, since parts of the hook often curve out of focus and reappear as apparently discrete structures. I was unable to find any ogives in any of the seven species of the Diclidophoroidea studied here, or in *Diclidophora luscae*, a species in which Gallien (1934) had previously described ogives as being present.

I have observed flame cells and a pair of longitudinal excretory canals opening by pores situated one on each side of the pharynx in *Pseudaxine* and some other diclidophoroideans, but I have not made a detailed investigation of the excretory systems.

Diplectanum aequans (Fig. 1 *a*, *b*)

Length 100–130 μ. Body, excepting posterior adhesive organ, completely ciliated. Eyes: two pairs, with lenses. Posterior adhesive organ situated ventrally with its posterior margin about 10 μ in front of the posterior extremity of the body, which is itself glandular. Hooks: 14, all of the same shape (Fig. 6) and $14 \pm 0{\cdot}5\,\mu$ long, without ogives; 12 hooks arranged equidistantly around the lateral and posterior margins of the disc, and 2 situated medianly and slightly anterior to the centre of the disc.

Entobdella soleae (Fig. 2)

Length 230–300 μ. Body with three bands of cilia as shown in diagram. Eyes: two pairs, with lenses. Posterior adhesive organ terminal. Hooks: 14 larval hooks, all of the same shape (Fig. 7) and $16 \pm 0{\cdot}5\,\mu$ long, and each with a pair of ogives each $11 \pm 1\,\mu$ long. In addition, there are present the primordia of the three pairs of hooks of the adult, and of these the third or posterior-most pair is relatively well developed. The 14 larval hooks are arranged one pair immediately anterior to the first pair of adult hooks, one pair between the third pair of adult hooks, and the remaining five pairs arranged in two lateral rows as shown in Fig. 2.

Acanthocotyle lobianchi (Fig. 3)

Length 120–170 μ. Cilia absent. Eyes: absent. Posterior adhesive organ terminal. Hooks: 16, all of same shape (Fig. 8) and $26 \pm 0{\cdot}5\,\mu$ long, without ogives, with 14 arranged peripherally and equidistantly and two situated more centrally. An adhesive organ exactly similar to this larval structure is found immediately posterior to the large adhesive organ of the adult, thus it seems extremely probable that the larval adhesive organ survives unaltered throughout life.

Rajonchocotyle emarginata (Fig. 4)

Length 100–140 μ. Body with two bands of cilia as shown in diagram. Eyes: absent. Posterior adhesive disc terminal. Hooks: 10, all of the same

shape (Fig. 9), $20 \pm 0{\cdot}5\,\mu$ long, each provided with a pair of ogives $12 \pm 1{\cdot}0\,\mu$ long, and arranged approximately equidistantly round the periphery of the adhesive organ. All of my preparations were slightly distorted, and I was unable to recognize the bilateral arrangement of hooks illustrated by Euzet (1955) for *Neoerpocotyle catenulata* (Hexabothriidae), but it is possible that such arrangement is present in *Rajonchocotyle*.

Diclidophoroidea (Fig. 5*a*, *b*)

Body, excepting adhesive organ, completely ciliated. Eyes: a single pair of laterally directed pigment cups without permanent lenses but with conspicuous oil droplets that probably function as lenses; paired nature of eyes easily recognizable in some, e.g. *Plectanocotyle*, but the two eyes so closely adpressed as to appear as one in others (e.g. *Pseudaxine*); eyes absent in *Diclidophora*. Body terminating posteriorly in a ciliated cone, the apex of which is glandular and from which a drop of viscous material in the course of being secreted may frequently be observed. This ciliated cone is probably a deciduous organ, since it is not recognizable after the shedding of the ciliated epidermis. Posterior adhesive organ ventral and bears a pair of lateral 'wings' on which are borne some of the larval hooks. Hooks: 12, without ogives, arranged in 6 pairs that exhibit serial differentiation into two or three kinds (Figs. 10–26). The hooks of the first four pairs (=lateral hooks) are invariably all alike in size and shape (Figs. 10–16), and are borne on the lateral wings of the adhesive organ; the hooks of the fifth pair (=postero-lateral hooks) are similar in shape to the lateral hooks, but may be larger (Figs. 17–19), and are borne more medianly than the lateral hooks; the hooks of the sixth pair (=posterior hooks, Figs. 20–26), are invariably larger than and of a different shape from the first five pairs, the particular shape and size varying with the species (Figs. 20–26).

Plectanocotyle gurnardi

Length 100–150 μ. Lateral and postero-lateral hooks all of same shape (Fig. 10) and all $13 \pm 0{\cdot}5\,\mu$ long. Posterior hooks (Fig. 20) $23 \pm 0{\cdot}5\,\mu$ long, with the shaft joined to the middle of the proximal border of the blade.

Anthocotyle merluccii

Length 160–200 μ. Lateral and postero-lateral hooks all of same shape (Fig. 11) and $16 \pm 1{\cdot}0\,\mu$ long. Posterior hooks (Fig. 21) $40 \pm 2\,\mu$ long, with a long slender shaft attached to the blade at some little distance down the inner border of the blade.

Gastrocotyle trachuri

Length 160–200 μ. Postero-lateral hooks ($21 \pm 1\,\mu$ long, Fig. 17) longer than the lateral hooks ($13 \pm 0{\cdot}5\,\mu$, Fig. 12). Posterior hooks with shaft region expanded into a stout curved base (Fig. 22).

Pseudaxine trachuri

Length 160–200 μ. Lateral hooks (Fig. 13) indistinguishable from those of *Gastrocotyle*, postero-lateral hooks ($19 \pm 1\,\mu$, Fig. 18) with shafts slightly shorter than those of *Gastrocotyle*. Posterior hooks ($19 \pm 1\,\mu$, Fig. 23) similar in shape to those of *Gastrocotyle*, but smaller.

Microcotylid species from *Trachurus*

Length 100–140 μ. Lateral hooks and postero-lateral hooks all identical with each other ($13 \pm 0{\cdot}5\,\mu$, Fig. 14). Posterior hooks ($32 \pm 1\,\mu$, Fig. 24) with long slender shaft attached at the junction of the proximal border of the blade to the inner border of the blade.

Microcotyle labracis

Length 200–240 μ. Lateral and postero-lateral hooks all identical with each other ($18 \pm 1\,\mu$, Fig. 15). Posterior hooks similar in shape to those of previous microcotylid species, but larger ($51 \pm 1\,\mu$, Fig. 25). In the newly hatched larva of *M. labracis* there are present the primordia of one of the pairs of hooks of the adult (Fig. 27).

Diclidophora merlangi

Length 210–250 μ. Postero-lateral hooks ($27 \pm 2\,\mu$, Fig. 19) similar in shape to the lateral hooks ($21 \pm 2\,\mu$, Fig. 16), but larger. Posterior hooks ($31 \pm 2\,\mu$, Fig. 26) with outer margin of the proximal region of the blade sloping to meet the shaft.

COMPARISONS WITH OTHER MONOGENEAN LARVAE

Diplectanum aequans

The larva of *Diplectanum aequans*, in possessing 2 pairs of eyes and having 14 larval hooks, resembles the following larval gyrodactyloideans: *Dactylogyrus vastator*, described by Kulwieć (1929); *D. anchoratus*, described by Kulwieć (1927); *Neodactylogyrus macracanthus*, described by Wilde (1936); and *Acolpenteron ureteroecetes*, described by Fischthal & Allison (1942). *Diplectanum* differs from another gyrodactyloidean *Ancyrocephalus vistulensis*, described by Siwak (1932), only in that the latter is reported as having only 12 hooks, although Siwak's illustration of the larva appears to show 13 hooks. *Ancyrocephalus* was illustrated as having a posterior ciliated cone such as is present in *Diplectanum* and also in *Neodactylogyrus macracanthus*.

Entobdella soleae

The larva of *Entobdella soleae* bears a very close resemblance to the larva of *Benedenia melleni*, described by Jahn & Kuhn (1932), and differs from it only

in the presence in the larval *Benedenia* of the anterior suckers which characterize the adult. The larvae of *Entobdella* and *Benedenia*, both capsaloideans, resemble the previously discussed gyrodactyloidean larvae in having 2 pairs of eyes and 14 larval hooks, but in the capsaloideans primordia of the 3 pairs of adult hooks are also present.

Acanthocotyle lobianchi

The larva of *Acanthocotyle lobianchi*, as described in the present study, resembles the embryo of *A. pugetensis*, as described by Bonham & Guberlet (1938), and thus differs slightly in the arrangement of its 16 hooks from the embryonic *A. pacifica*, which was also described by Bonham & Guberlet. Of other young forms of Monogenea, the embryos and larvae of *Acanthocotyle* with their 16 hooks and absence of eyes and cilia resemble most the embryo of *Gyrodactylus elegans*, described by Katheriner (1904). The significance of this similarity may, however, be slight when the clearly abnormal polyembryonic development of *Gyrodactylus* is considered.

Rajonchocotyle emarginata

The larva of *Rajonchocotyle emarginata*, with its absence of eyes and its 10 hooks, resembles very closely the larva of *Neoerpocotyle catenulata* described by Euzet (1955) and belonging to the same family, the Hexabothriidae.

Diclidophoroidea

Among the Diclidophoroidea the only previously known larval discocotylid is *Diplozoon paradoxum*, described by Zeller (1872*a*). This species differs from *Plectanocotyle gurnardi* and *Anthocotyle merluccii* in that the newly hatched young does not have a larval adhesive organ, the clamps of the adult being already present. One pair of hooks is present, and these persist in the adult, but insufficient is known of their development to permit comparisons with the larval hooks of other species. In common with other diclidophoroideans, the newly hatched *Diplozoon* has 2 eyes which disappear in the adult.

The larvae of *Microcotyle labracis* and of the 'unidentified microcotylid species' from *Trachurus trachurus* resemble the larvae of *Microcotyle chrysophrii* and *Axine bellones*, described by Euzet (1955), in that they are diclidophoroideans having the lateral and postero-lateral hooks all similar to each other, and in that the shapes of the posterior hooks in all four species are all very similar. In all these microcotylideans except the one from *Trachurus*, a seventh pair of hooks, which appears to be primordia of adult hooks, is present. Such hooks are also present in the larva of *Microcotyle spinicirrus*, described by Remley (1942), and very probably in *Diplasiocotyle johnstoni* also, but Sandars's (1944) description of the latter species was insufficiently

detailed to be certain about this point. *Microcotyle spinicirrus* differs from all the other known microcotylid larvae in that it has *six* pairs of lateral and postero-lateral hooks in addition to its posterior hooks and its primordial adult hooks.

The larvae of *Gastrocotyle trachuri* and *Pseudaxine trachuri* resemble each other very closely indeed, and in fact are only distinguishable from each other in the slight differences in size of their hooks (see pp. 251–2). Both species differ from the other members of the Microcotylidae, in which they are at present classified, in the differences between lateral and postero-lateral hooks, in the very different shapes of the posterior hooks, and in the absence of primordia of adult hooks.

A comparison of the larva of *Diclidophora merlangi* with those of *D. denticulata*, described by Frankland (1955), and *D. luscae*, described by Gallien (1934), reveals no differences excepting in the relative sizes of the lateral and postero-lateral hooks. Gallien (1934), without giving a separate description, stated that the structure of the adhesive organ of the larva of *D. pollachii* was identical with that of *D. luscae*.

The above comparisons have included reference to all the known larval monogeneans excepting the two diclidophoroideans *Kuhnia scombri*, described by Gallien & Le Calvez (1947), and *Hexostoma thynni*, described by Euzet (1955), and the Polystomatidae *Polystoma integerrimum*, described by Zeller (1872*b*), Halkin (1901), and Gallien (1935); *Sphyranura oligorchis*, described by Alvey (1936); *Polystoma nearcticum* and *Polystomoidea oris*, both described by Paul (1938); and *Diplorchis scaphiopodis*, described by Rodgers (1941).

Kuhnia scombri differs from other larval diclidophoroideans in that the hooks are all similar, there being no differentiation into lateral, postero-lateral and posterior hook types, and in that no eyes are present. *Hexostoma thynni* resembles the discocotylideans *Plectanocotyle* and *Anthocotyle* in its equipment of hooks, but differs from all other diclidophoroideans in that it has 2 pairs of eyes and a curious asymmetrical longitudinal band of pigment. The five larval Polystomatidae all resemble each other in having 16 larval hooks with one or 2 pairs of primordial adult hooks. Four of the species have two pairs of eyes, but in the fifth species *Sphyanura osleri*, which hatches in an advanced state of development, eyes (and cilia) are absent. The polystomatid larvae are thus quite similar to the larval gyrodactyloideans and capsaloideans from which they differ in having 16 instead of 14 larval hooks.

DISCUSSION

Monogenean larvae were in the past variously referred to as 'miracidia' or merely as 'ciliated larvae', until Gallien (1934) proposed the term 'gyrodactyloid larva' for the larvae of *Diclidophora* and *Polystoma*, on account

of their resemblance to *Gyrodactylus*. However, *Gyrodactylus* has a very abnormal embryonic development, and the adult does not have the cilia or eye-spots characteristic of most monogenean larvae. Moreover, the use of a term which is also used to refer to the members of one particular superfamily of the Monogenea could cause confusion when it is desired to refer to the larvae of species belonging to other superfamilies. Thus in place of Gallien's 'gyrodactyloid larva' as a name for monogenean larva, I propose the substitution of 'oncomiracidium' (Greek, *onkos*, hook; *meirakidion*, youth), which suggests affinity with the familiar digenean miracidium and reflects the presence of the characteristic monogenean hooks.

The contribution that studies of larvae may make to the study of the phylogeny of the Monogenea will now be considered. If the 33 oncomiracidia now known (*Diplozoon* and *Sphyranura* are omitted because of their very advanced development on hatching) are arranged according to their complements of eyes and hooks, the following groups readily emerge.

1. Gyrodactyloideans (except *Gyrodactylus*) and capsaloideans, both with 14 larval hooks and 2 pairs of eyes with lenses (9 spp.).
2. Polystomatidae with 16 larval hooks and 2 pairs of eyes with lenses (4 spp.).
3. Diclidophoroideans with 6 pairs of larval hooks exhibiting serial differentiation, and with 0, 1, or 2 pairs of eyes without permanent lenses (16 spp.).
4. Hexabothriidae with 10 larval hooks and without eyes (2 spp.).
5. *Acanthocotyle* and *Gyrodactylus*, both with 16 hooks and without eyes. On account of the abnormal development of *Gyrodactylus* and the difference in hosts (one on elasmobranchs, the other on teleosts), the resemblance of these species may be no more than superficial (2 spp.).

This grouping differs from the present classification of adults (Sproston, 1946), mainly in the divorce of the family Hexabothriidae from its place alongside the Polystomatidae in the superfamily Polystomatoidea, and in the inference of a closer affinity than is now recognized between the Polystomatidae on the one hand, and the Gyrodactyloidea and Capsaloidea on the other. A consideration of the affinities between the respective hosts yields strong support for the re-arrangement since the Hexabothriidae parasitize Chondrichthyes, the Polystomatidae parasitize Amphibia and Reptilia, and both the Gyrodactyloidea and Capsaloidea parasitize Teleostii.

It becomes pertinent therefore to examine the criteria used at present in the classification (Sproston, 1946) of the Monogenea. The main diagnostic features separating the two suborders Monopisthocotylea and Polyopisthocotylea (including the Hexabothriidae, Polystomatidae and Diclidophoroidea)

are the relationship of the adhesive organs of the adult to those of the larva, and the presence or absence of a genito-intestinal canal.

The use of the first of these characters is of extremely doubtful validity. The Polyopisthocotylea were defined as being Monogenea in which (among other characters) the functional haptor (=adhesive organs) of the adult is developed immediately anterior to the larval haptor. So far as I can discover, this conception can only be based upon what appears to be a misinterpretation of some rather confused observations by Remley on the development of *Microcotyle spinicirrus*. Remley (1942, p. 151) stated that the larval haptor of *M. spinicirrus* bore 6 pairs of hooklets (=lateral and postero-lateral hooks in my descriptions) along the lateral and posterior border, and that 2 pairs of large anchor hooks (=posterior hooks and primordial adult hooks in my descriptions) were medianly located near the posterior end. Later on p. 151, and on p. 152, Remley used the term 'larval haptor' in a different sense—to include only that part bearing the 'anchor hooks', and when he stated that by the 20 to 30-clamp stage the haptor was lost, he was referring only to the anchor-bearing part. There are no grounds then for supposing that the adhesive organs of the adult do not develop around and replace the larval hooks as they have been described to do so in *Diclidophora denticulata* by Frankland (1955) and in several polystomatids by various authors.

The use of the second character appears to be more valid: a genito-intestinal canal is invariably present in the Polyopisthocotylea, but has been reported as being present also in the Protogyrodactylidae and in some turbellarians, and so it is possible that its occurrence throughout the Polyopisthocotylea is due to convergence. However, the genito-intestinal canal in the Polyopisthocotylea may be associated with another feature that may be shown eventually to be exclusive to the group: I have shown that in eight representative species the gut epithelium consists of scattered 'pigment cells' associated with a blood-feeding habit (Llewellyn, 1954), and it is possible that there may be a connexion between an obligatory blood-feeding habit and the presence of a genito-intestinal canal. It is known (see Caullery, 1952) that there is a close correlation between strict haematophagy and the presence of intestinal symbionts, and that such blood-feeding animals are obliged to have some means of transferring the symbionts to succeeding generations. I have observed cells laden with bacteria (=mycetocytes?) in the intestine of adult specimens of *Axine bellones*, in the egg capsules of *Polystoma integerrimum*, and in the egg capsules of most of the diclidophoroideans that I have described in this paper. The genito-intestinal canal *could* be the pathway whereby such mycetocytes may be transferred from the gut to the egg capsules. If this hypothesis be shown eventually to be correct, the inference would be of a common origin for those monogeneans having a blood-feeding habit, gut pigment cells, and a genito-intestinal canal. This in turn would mean that the similarity between the larvae of the Polystomatidae and those of the

Capsaloidea is superficial unless it be due to the present-day Polystomatidae being in fact those Polyopisthocotylea which have diverged least from an ancestral stock that is common also to the Capsaloidea.

Within the present suborder Monopisthocotylea, the inference from larval studies is that there is a closer affinity between the Gyrodactyloidea (excepting the Gyrodactylidae) and the Capsaloidea than is suggested by the present classification, and this is supported by the widespread occurrence of 14 marginal hooks (=persistent larval hooks?) in many adults of both the Gyrodactyloidea and the Capsaloidea.

With regard to the Diclidophoroidea, while an insufficient number of species is known yet to permit a classification of the group on larval characters, it is possible to make the following observations: (1) In *Kuhnia scombri* (Mazocraeidae) the presence of undifferentiated hooks appears to be the survival of a primitive character, and Sproston (1945) has already regarded the clamp structure of the adult *Kuhnia* to be the basic type from which other diclidophoroidean clamps have evolved—a view which I have opposed (Llewellyn, 1957). (2) The larvae of *Gastrocotyle trachuri* and *Pseudaxine trachuri* (at present classified in the Microcotylidae) appear to have less in common with microcotylid larvae than the microcotylids have in common with the discocotylids, diclidophorids, and hexastomatids. This would support Price's (1943) proposal, on the grounds of the clamp structure of the adults, of a new family Gastrocotylidae.

It is again a pleasure to record my thanks to the Director and Staff of the Plymouth Laboratory for providing excellent working facilities. I am especially grateful to Mr G. R. Forster for supplies of *Morone labrax*, to Mr A. D. Mattacola for assistance with fish matters, and to Mr J. E. Green for help in collecting parasites.

SUMMARY

Techniques for the rearing of monogenean larvae are described.

The new term 'oncomiracidium' is proposed for the larvae of monogenetic trematodes.

Eleven new oncomiracidia of fish parasites are described, bringing the total now known to thirty-five.

These oncomiracidia are tentatively classified, and the classification is compared with the existing classification of adult monogeneans.

REFERENCES

ALVEY, C. H., 1936. The morphology and development of the monogenetic trematode, *Sphyranura oligorchis* Alvey, 1933, and the description of *Sphyranura polyorchis* n.sp. *Parasitology*, Vol. 28, pp. 229–53.

BAER, J. G., 1951. *Ecology of Animal Parasites*. 224 pp. Urbana: University of Illinois Press.

BONHAM, K. & GUBERLET, J. E., 1938. Ectoparasitic trematodes of Puget Sound fishes. *Acanthocotyle. Amer. Midl. Nat.*, Vol. 20, pp. 590–602.

CAULLERY, M., 1952. *Parasitism and Symbiosis.* 340 pp. London: Sidgwick and Jackson.

DAWES, B., 1946. *The Trematoda.* Cambridge University Press.

EUZET, L., 1955. Larves gyrodactyloïdes nageantes de quelques trématodes monogénétiques de poissons marins. *Bull. Soc. neuchâtel. Sci. nat.*, T. 78, pp. 71–9.

FISCHTHAL, J. H. & ALLISON, L. N., 1942. *Acolpenteron catastomi* n.sp. (Gyrodactyloidea: Calceostomatidae), a monogenetic trematode from the ureters of suckers, with observations on its life history and that of *A. ureteroecetes. Trans. Amer. micr. Soc.*, Vol. 61, pp. 53–6.

FRANKLAND, H. M. T., 1955. The life history and bionomics of *Diclidophora denticulata* (Trematoda: Monogenea). *Parasitology*, Vol. 45, pp. 313–51.

GALLIEN, L., 1934. Sur la larve de *Dactylocotyle luscae* v. Ben. and Hesse, trématode monogénétique marin. *Bull. Soc. zool. Fr.*, T. 59, pp. 68–73.

—— 1935. Recherches expérimentale sur le dimorphisme évolutif et la biologie de *Polystomum integerrimum* Froel. *Trav. Sta. zool. Wimereux*, T. 12, pp. 1–182.

GALLIEN, L. & LE CALVEZ, J., 1947. Description de la larve d'*Octobothrium scombri* van Beneden & Hesse, trématode monogénétique marin. *Bull. Soc. zool. Fr.*, T. 72, pp. 76–8.

HALKIN, H., 1901. Recherches sur la maturation, la fécondation et le développement du *Polystomum integerrimum. Arch. Biol. Paris*, T. 18, pp. 291–363.

JAHN, T. L. & KUHN, L. R., 1932. The life-history of *Epibdella melleni* MacCallum, 1927, a monogenetic trematode parasitic on marine fishes. *Biol. Bull., Woods Hole*, Vol. 62, pp. 89–111.

KATHERINER, L., 1904. Über die Entwicklung von *Gyrodactylus elegans* v. Ndm. (Abstract). *Zool. Jb.*, Bd. 7, suppl., pp. 519–51.

KULWIEĆ, Z., 1927. Untersuchung an Arten des Genus *Dactylogyrus* Diesing. *Bull. int. Acad. Cracovie (Acad. pol. Sci.) sci. nat.*, Ser. B (1–2), pp. 113–44.

—— 1929. Observations sur le développement de *Dactylogyrus vastator* Nyb. *Arch. Hydrobiol. Ichthiol.*, T. 4, pp. 277–86.

LLEWELLYN, J., 1954. Observations on the food and gut pigment of the Polyopisthocotylea (Trematoda: Monogenea). *Parasitology*, Vol. 44, pp. 428–37.

—— 1956. The host-specificity, micro-ecology, adhesive attitudes, and comparative morphology of some trematode gill parasites. *J. mar. biol. Ass. U.K.*, Vol. 35, pp. 113–27.

—— 1957. The mechanism of the attachment of *Kuhnia scombri* (Kuhn, 1829) (Trematoda: Monogenea) to the gills of its host *Scomber scombrus* L., including a note on the taxonomy of the parasite. *Parasitology*, Vol. 47 (in the Press).

PAUL, A. A., 1938. Life-history studies of North American fresh-water polystomes. *J. Parasit.*, Vol. 24, pp. 489–510.

PRICE, E. W., 1943. North American monogenetic trematodes: VI. The family Diclidophoridae (Diclidophoroidea). *J. Wash. Acad. Sci.*, Vol. 33, pp. 44–54.

REMLEY, L. W., 1942. Morphology and life-history studies of *Microcotyle spinicirrus* MacCallum, 1918, a monogenetic trematode parasitic on the gills of *Aplodinotus grunniens. Trans. Amer. micr. Soc.*, Vol. 61, pp. 141–55.

RODGERS, L. O., 1941. *Diplorchis scaphiopi*, a new polystomatid monogenean fluke from the Spadefoot Toad. *J. Parasit.*, Vol. 27, pp. 153–7.

ROWAN, W. B., 1956. The mode of hatching of the egg of *Fasciola hepatica. Experimental Parasitology*, Vol. 5, pp. 118–37.

SANDARS, D. F., 1944. A contribution to the knowledge of the Microcotylidae of Western Australia. *Trans. roy. Soc. S. Aust.*, Vol. 68, pp. 67–81.

SIWAK, J., 1932. *Ancyrocephalus vistulensis* n.sp., un nouveau trématode, parasite du Silure (*Silurus glanis* L.). *Bull. int. Acad. Cracovie* (*Acad. pol. Sci.*), *sci. nat.*, Ser. B II (7–10), pp. 669–79.

SPROSTON, N. G., 1945. A note on the comparative anatomy of the clamps in the superfamily Diclidophoroidea (Trematoda: Monogenea). *Parasitology*, Vol. 36, pp. 191–4.

—— 1946. A synopsis of the monogenetic trematodes. *Trans. zool. Soc. Lond.*, Vol. 25, pp. 185–600.

STUNKARD, H. W., 1937. The physiology, life cycles and phylogeny of the parasitic flatworms. *Amer. Mus. Novit.*, no. 908, 27 pp.

WILDE, J., 1936. *Dactylogyrus macracanthus* Wegener als Krankheit-serreger auf den Kiemen der Schleie (*Tinca tinca* L.). *Z. Parasit.*, Bd. 9, pp. 203–36.

ZELLER, E., 1872*a*. Untersuchungen über die Entwicklung des *Diplozoon paradoxum*. *Z. wiss. Zool.*, Bd. 22, pp. 168–80.

—— 1872*b*. Untersuchungen über die Entwicklung und Bau des *Polystomum integerrimum* Rud. *Z. wiss. Zool.*, Bd. 22, pp. 1–28.

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LUMINESCENCE IN POLYNOIDS

II. DIFFERENT MODES OF RESPONSE IN THE ELYTRA

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(Text-fig. 1)

Earlier studies (Nicol, 1953, 1954) showed that two kinds of luminescent responses are produced by electrical stimulation of isolated polynoid scales, viz. brief flashes and a long-lasting glow, the latter frequently being brighter. The brief flashes were regarded as the normal response of the photocytes to nervous excitation, whereas the long glow might be the result of direct excitation of the photocytes. A prolonged glow can usually be evoked by strong shocks (well above threshold). It is sometimes succeeded by rhythmic flashing (Nicol, 1954, fig. 1B); alternatively, a series of rhythmic flashes may be succeeded by a prolonged glow (Nicol, 1954, fig. 3A).

In the present paper I shall consider the two kinds of responses in more detail.

MATERIAL AND METHODS

The species studied were *Polynoë scolopendrina*, *Lagisca extenuata* and *Gattyana cirrosa*; most observations were made on *Polynoë*. Two kinds of preparations were used. These were isolated elytra, and short sections of worm consisting of a few segments and an elytrum. The material was prepared from worms narcotized with iso-osmotic $MgCl_2$. To induce luminescence electrical stimulation was employed, either condenser discharges or square waves, delivered from an electronic apparatus. The isolated elytrum was placed in a moist chamber over a pair of silver electrodes. To stimulate pieces of the body, silver electrodes were placed on the nerve cord. Luminescent responses were detected with photomultiplier, d.c. amplifier and cathode-ray oscilloscope. Records were made on moving paper. Temperatures were $18° \pm 1°$ C.

OBSERVATIONS

STIMULATION THROUGH THE NERVE CORD

The following observations were made on short sections of worm containing an elytrum, and stimulated via the ventral nerve cord.

Polynoë. A single shock sometimes produces one flash, or causes repetitive flashing; or several shocks may be required to elicit the first recordable response. Fast repetitive flashing occurs at frequencies up to 10/sec.

Consecutive flashes show facilitatory increment. Flashing follows pulse-rate up to about 20/sec, above which there is no longer a flash to each shock. Following several flashes at short intervals, the final flash may pass over into a glow response, having a lengthened decay period (Fig. 1A). A normal quick flash has a duration of some 120 msec, and rise time of *ca.* 25 msec; decay time is about 100 msec. The decay time of the glow response is variable and prolonged, from 0·25 to 3 sec. When a flash gives way to a prolonged glow, there may be an initial period of fast decay, followed by a secondary rise and slow decay (Fig. 1A). I would emphasize that the prolonged glow may appear long after the stimulatory shock has been delivered (0·3–0·6 sec).

Gattyana. A single shock elicits either a flash or repetitive flashing. Flashing follows stimulation up to pulse-rates of about 24/sec (Fig. 1B), above which the scale does not respond to each shock. During a high-frequency burst, repetitive flashing tends to give way to a steady glow, but prolonged glow responses are not otherwise apparent in these records. Consecutive flashes show facilitation. Flashes vary in duration from 54 to 145 msec; rise time is 8–25 msec. In a series of flashes, later ones, of no greater amplitude than the first, may have greater duration and rise time.

Stimulation of the nerve cord in narcotized pieces

Short sections of worm (*Polynoë*) containing nerve cord and one elytrum were narcotized for 4 h or longer in 0·2 % novocaine, and then stimulated via the nerve cord. Weak luminescent responses could only be obtained with very strong shocks (5 × threshold of unanaesthetized preparations). These were glow responses, rather than quick flashes. I assume there was spread of current at the very high voltages to the underlying elytrum, which was excited directly.

ELECTRICAL STIMULATION OF ISOLATED ELYTRA (NARCOSIS-FREE)

Polynoë. In an isolated elytrum a single shock produces either one flash, or a series of flashes, variable in number. Temporal characteristics are similar to those recorded in a previous section (latency, 13–21 msec; duration, *ca.* 100 msec; rise time, 26–30 msec) (Nicol, 1953). Consecutive flashes show facilitation (Nicol, 1954). With bursts of shocks, the scale gives off a train of flashes. At high frequencies (> 20/sec), the scale either follows the rate of stimulation, or flashes to every 2nd or 3rd pulse. Light pulsations at rates up to 64/sec have been observed. The responses at high rates are of low intensity, and when stimulation ceases the scale continues to flash at some lower rate (*ca.* 10/sec) and higher intensity (Fig. 1C). After a bout of repetitive flashing, induced by one or multiple shocks, there is often a prolonged glow with long decay period (up to 8 sec). Fast repetitive flashes are sometimes superposed on background glow. Strong shocks (2 × threshold) induce rapid repetitive flashing accompanied by a prolonged glow response. Decay of the latter occupies about 2 sec.

Gattyana. Isolated scales of *Gattyana* tend to give the prolonged glow response, even when stimulated at threshold. A single shock evokes responses of the following kinds: (1) initial quick flash followed by a prolonged glow; (2) rapid repetitive discharge passing over into a prolonged glow; (3) prolonged glow, with longer rise and decay time than a quick flash (Fig. 1D); (4) prolonged glow passing into repetitive flashing (Nicol, 1953, fig. 9). In some records the initial repetitive flashes return to base-line (zero intensity), whereas later responses become superposed on a rising background. Latency of the prolonged glow response varies from *ca.* 25 to 100 msec; rise time is 0·25 sec; duration is 4–8 sec.

Lagisca. A shock near threshold usually evokes a flash or a bout of repetitive flashing. When rapid, the latter may end in a prolonged glow response. The maximal rate of rhythmic flashing to a single shock is *ca.* 10/sec. Normal flashes follow repetitive stimulation up to frequencies of about 12/sec. At higher frequencies the scale responds to every 2nd, 3rd, or other stimulus with normal flashes; or closely follows the stimulus-rate with weak pulsations, which give way to bright normal flashes when stimulation ceases (Nicol, 1954, fig. 4C, D). Consecutive flashes show facilitation (Fig. 1E). Flash duration varies from 100 to 200 msec; rise time is 17–50 msec. In a series of flashes later ones tend to be more prolonged. Occasionally, a single shock evokes a glow response, with slow rise (*ca.* 0·3 sec) and long decay (>2 sec) (Nicol, 1954, fig. 1A). Following rapid flashing, there may be a glow response (Nicol, 1954, fig. 3A).

STIMULATION OF NARCOTIZED ELYTRA

Isolated elytra were placed in solutions of certain anaesthetics, and their responses to electrical stimulation were tested later. Narcotics used were: cocaine, 0·2%; novocaine, 0·2–0·5%; chloretone, 0·05–0·2%; M.S.222 (Sandoz), 0·025–0·1%; all in sea water. Also employed were iso-osmotic solutions of $MgCl_2$ plus sea water (ratios 1:3 to 1:1).

Evidence, presented elsewhere, has shown that continued rhythmic flashing, after stimulation has ceased, is dependent upon an elytral ganglion. Multiple flashes to a single shock, therefore, have been used as an index of continued nervous functioning. Multiple flashing (two or more flashes) to a single shock was observed in scales immersed for 97 min in 0·1% chloretone, and 54 min in 0·2% novocaine. Immersion times were considered insufficient, and the following observations are based on elytra immersed in narcotic solutions for 4 h or more.

Novocaine 0·2%

Polynoë. Responses of several kinds to single pulses were recorded as follows: (1) quick flash with latency *ca.* 10 msec, rise time 20 msec, duration *ca.* 0·5 sec; (2) initial quick flash followed by a long glow: rise time 20–80 msec,

duration up to 10 sec (Fig. 1F); (3) prolonged glow response having a slow rise and long decay period: rise time 0·3 sec, duration 7–8 sec (Fig. 1G). These various kinds of responses are really arbitrary, and I believe there is every gradation in narcotized *Polynoë* scales between a brief flash lasting a half second to a prolonged glow lasting many seconds. Rise time is equally variable. Some records show an initial quick flash in which the decay period is interrupted by a secondary slow rise, succeeded by prolonged plateau and slow decay (Fig. 1H). With repetitive stimulation discrete flashes have been recorded up to rates of 18/sec. In some records there is little or no facilitatory increment in consecutive responses; in other records facilitation is well marked in the first few responses (Fig. 1J).

Gattyana. Only glow responses were observed. These have a latency of *ca.* 27 msec, and duration of 5–9 sec. Rise time is sometimes long, up to 1 sec, but many responses begin with an initial quick flash (rise time some 30 msec) which passes over into a prolonged glow. Occasionally, there is a secondary slow rise after the initial quick flash has started to decay. Facilitation to consecutive pulses is sometimes marked.

Lagisca. Single shocks produced a flash, repetitive flashing, or a prolonged glow. Repetitive flashing was sometimes succeeded by a prolonged glow response. The latency of the glow response was rather long, 0·5–1 sec; rise to maximum was 0·4 sec; total response duration was 3–4 sec. Because of the repetitive flashing observed, it appears that *Lagisca* elytra are not always narcotized by novocaine at 0·2% level.

Novocaine 0·3%

Lagisca. Stimulation produced glow response. Latency *ca.* 20 msec; duration some 10 sec; rise time 0·7 sec. The first two of a series of responses show facilitatory increment.

Novocaine 0·5%

Lagisca. Nil response.

Cocaine 0·2%

Polynoë. Following treatment with cocaine, the following kinds of responses were observed.

(1) Quick initial flash followed by a long glow.

(2) Quick initial flash, with decay period interrupted by a secondary rise.

(3) A quick flash showing rapid return to base-line (Fig. 1K). Latencies are 13–14 msec; rise time is *ca.* 27 msec. Minimal flash duration is about 0·25–0·3 sec; the more prolonged glows last up to 8 sec. With repeated stimulation, the response becomes more prolonged. Facilitation is shown in consecutive flashes (Fig. 1K).

Chloretone 0·05%

Polynoë. Responses obtained after chloretone show rapid rise (*ca.* 30 msec), and slow decay (2–4 sec). Latency is *ca.* 15 msec. In some records the decay curve is regular; in others an initial decay is followed by a slow secondary rise and long period of secondary decay. There is facilitation to consecutive flashes (Fig. 1L–N).

*M.S.*222, 0·025%

Polynoë. Responses were a prolonged glow, lasting up to 3 sec, with slow rise time (0·25–0·3 sec). The glow response usually was preceded or accompanied by a few weak oscillations, almost imperceptible in the records. Latency varied in different records from 0·025 to 0·4 sec. The small pulses accompanying the prolonged glow would indicate some residual nervous excitation, and this concentration of M.S.222 can be considered near threshold.

*M.S.*222, 0·05%

Polynoë. Pulses produce a long glow (duration up to 7 sec). Rise time varies from 0·25 to 1 sec. Facilitation is shown in consecutive responses.

*M.S.*222, 0·1%

Polynoë. Nil response to electrical stimulation.

$MgCl_2$: *sea water* 1:3

Polynoë. Single shocks usually elicited multiple flashing, with responses similar to those of non-narcotized scales. Occasional scales gave the prolonged glow response. Consecutive flashes showed facilitation.

$MgCl_2$: *sea water* 1:2

Polynoë. Pulses evoked quick flashes passing into a prolonged glow, or repetitive flashing sometimes ending in a glow response. Facilitation was evident.

$MgCl_2$: *sea water* 2:3

Polynoë. Single flashes tended to be prolonged. Stimulation sometimes evoked a glow response, on which was superposed repetitive flashing.

$MgCl_2$: *sea water* 1:1

Polynoë. Nil response.

COMMENT

Treatment with each of three narcotics, viz. novocaine, chloretone, and M.S.222, abolishes repetitive flashing to a single shock. This result is taken to indicate that anaesthesia stops nervous excitation and transmission. The

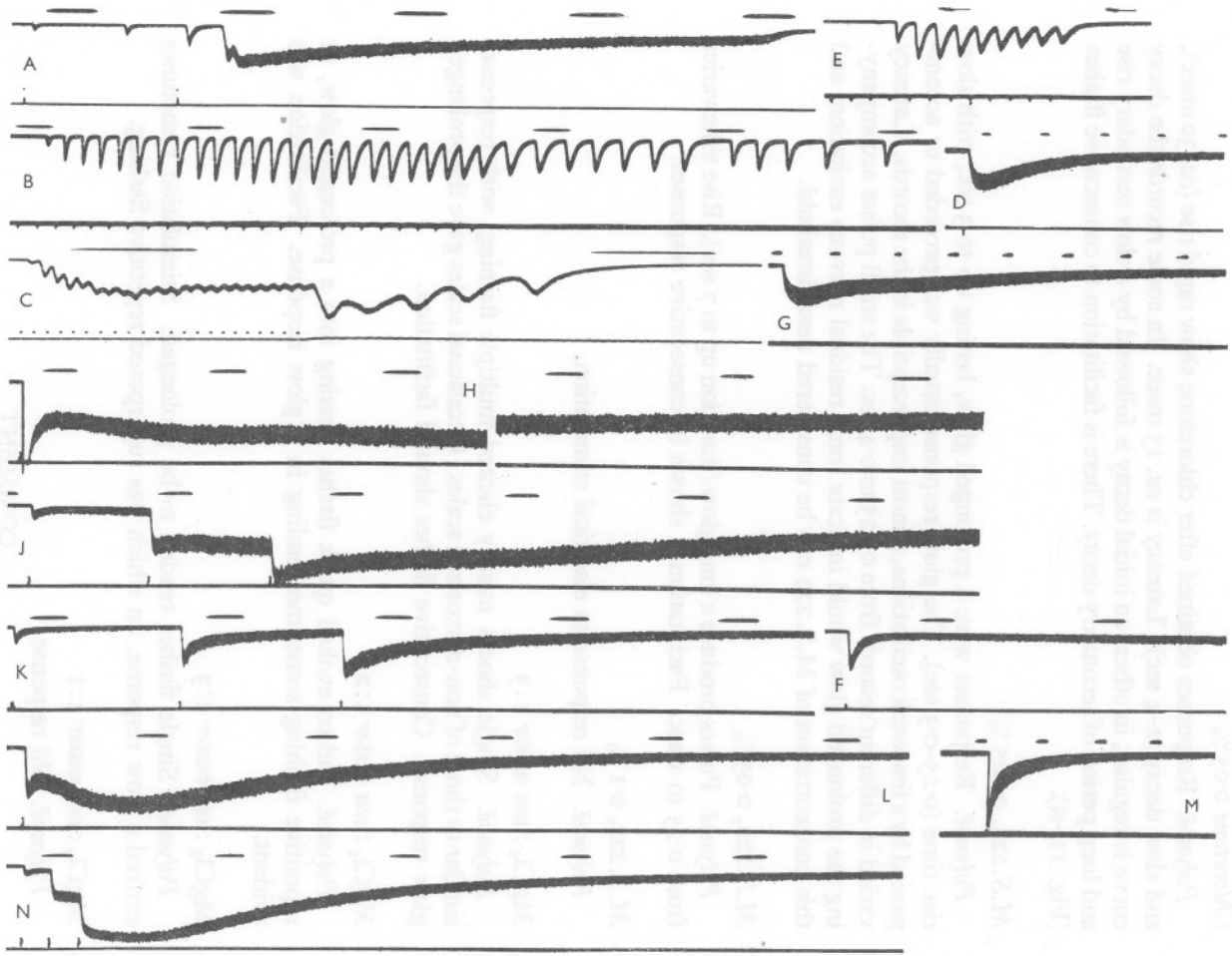

Fig. 1

luminescent responses which are still obtained by electrical stimulation after anaesthesia presumably arise from direct excitation of the photocytes.

Rhythmicity and nervous conduction are admittedly two different phenomena, although the same neurones are concerned with both. A possibility remains, therefore, that nervous conduction is still occurring, even though rhythmic discharge has disappeared. In view of the concentrations of narcotics employed, and the duration of their action, this contingency seems improbable.

Two kinds of responses have been arbitrarily selected, viz. the quick flash (duration *ca.* 100 msec), and the prolonged glow (duration 0·25 sec or longer). The former only appears after nervous stimulation (i.e. in unanaesthetized scales); the latter, following nervous stimulation or direct excitation (i.e. in unanaesthetized and in anaesthetized scales). It has not been possible to produce the quick flash by direct excitation of anaesthetized scales.

There are several reasons for believing that the glow response can be induced by nervous excitation, even under conditions when the isolated scale is stimulated. First, it is produced by stimulation of the nerve cord, when there is no current escape to the scale. Secondly, it succeeds rapid flashing some considerable time after stimulation has ceased. When evoked by indirect excitation, via the nervous system, the prolonged glow is associated with fast repetitive flashing. It seems that the conditions obtaining during fast repetitive flashing create a state favouring prolonged luminescence.

It is not known where the excitation takes place that produces the long glow response. Minimal latent periods of quick flash and glow response are about the same, and provide no help in resolving the question. Conduction time would be very brief in the short distances involved. Since quick flashes

Legend to Fig. 1

Fig. 1. Oscillograph records

A. Luminescent responses of *Polynoë scolopendrina*. The preparation consisted of a piece of the body containing 3 segments plus 1 elytrum. Electrical stimuli were applied to the nerve cord. Downward deflexions of middle trace are light flashes. Time signal above, 1 sec. Electrical stimuli on lower line.

B. *Gattyana cirrosa*. Repetitive stimulation of the nerve cord. Recording from one elytrum.

C. *Polynoë scolopendrina*. Responses of an isolated elytrum to repetitive electrical stimulation (burst at 42/sec).

D. *Gattyana cirrosa*. Prolonged glow response of an isolated elytrum.

E. *Lagisca extenuata*. Flashing of an isolated scale to repetitive stimulation.

F, G. *Polynoë scolopendrina*. Glow responses of a scale in 0·2 % novocaine, 4 h 20 min.

H. *P. scolopendrina*. Glow response of elytrum in 0·2 % novocaine, 5 h 47 min. Five-second interval between the first and second halves of this record.

J. *P. scolopendrina*. Three consecutive glow responses of an elytrum in 0·2 % novocaine, 5 h 11 min.

K. *P. scolopendrina*. Consecutive responses of a scale in 0·2 % cocaine, 4½ h.

L, M, N. *P. scolopendrina*. Glow responses of a scale in 0·05 % chloretone, 4 h 25 min.

are sometimes superposed on the prolonged glow response, it follows that the transmission of seriated impulses and repeated excitation of the photocytes are not impeded during the lengthy course of the glow response.

The glow response often has a rapid increment, with rise time equal to the quick flash. Decay time greatly exceeds that of the flash, from 0·25 to 10 sec. A secondary rise in intensity, seen in many records, must be of more than fortuitous significance.

After a bright glow response the scale fails to respond, or gives only feeble responses, to further stimuli. The prolonged glow consumes much or all of some substance essential for the luminescent reaction.

Weak stimulation of unanaesthetized scales evokes quick flashes; strong electrical stimulation induces the glow response. Weak shocks excite the nervous system; stronger shocks excite the photocytes directly. These differences need not be one of threshold; they may be due to the geometrical relations of the excitable elements with reference to the cathode.

It has been observed frequently in narcotized scales that repetitive stimulation can engender facilitatory increment (staircase). This is seen most clearly at slow rates of stimulation, when the effect is not obscured by summation. In facilitation some improving effect of a response is carried over to a later response, appearing in a brighter flash. Since the nervous system is excluded, the effect must be ascribed to processes taking place in the photocyte. The facilitatory increment seen in flashes of non-narcotized scales may also depend upon processes occurring within the photocytes, although concomitant neuro-photocyte facilitation is not excluded.

During repetitive flashing later responses may become prolonged. This lengthening of decay period may be due to conditions similar to those responsible for the glow response.

Finally, it has been noted that normal flashing ceases to maintain correspondence with stimulation at rates above *ca.* 20/sec; weak pulsations are sometimes seen at much higher rates, when the isolated scale is stimulated. This problem remains unresolved. It is possible that this very fast pulsation, above that which seems permitted by the refractory period of the nerve, depends upon irregular rotation among a large population of nerve fibres.

I conclude that the prolonged glow response is physiologically possible, and is sometimes produced by fast repetitive excitation from the nervous system. The latter creates conditions favouring a massive luminescent discharge. The duration of a glow response can be greatly exceeded by a bout of protracted iterative flashing; the light, of course, is fluctuating in the latter condition.

Since facilitation or staircase is observed in anaesthetized scales, it appears to depend upon processes taking place within the photocytes.

SUMMARY

Elytra of polynoids show two kinds of luminescent responses, viz. a quick flash (duration *ca.* 100 msec) and prolonged glow (duration 0·25–10 sec). Quick flashes are produced by nervous excitation; prolonged glow responses accompany or follow fast repetitive flashing, or are elicited by strong electrical stimuli. Anaesthetized isolated elytra still give the prolonged glow response when electrically stimulated. Facilitation is also evident in consecutive glow responses. From these various observations it is concluded that the prolonged glow response can be produced by fast repetitive nervous excitation or by direct electrical excitation of the photocytes. The occurrence of facilitation in glow responses of anaesthetized elytra raises the problem whether the same phenomenon in consecutive normal flashes may be due to intracellular changes taking place within the photocytes.

REFERENCES

NICOL, J. A. C., 1953. Luminescence in polynoid worms. *J. mar. biol. Ass. U.K.*, Vol. 32, pp. 65–84.

—— 1954. The nervous control of luminescent responses in polynoid worms. *J. mar. biol. Ass. U.K.*, Vol. 33, pp. 225–55.

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LUMINESCENCE IN POLYNOIDS

III. PROPAGATION OF EXCITATION THROUGH THE NERVE CORD

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Luminescent polynoids emit light from their elytra. These structures are arranged in two longitudinal rows covering most or all of the dorsal surface of the worm. Light emission is evoked by stimulation and appears as a single flash or series of flashes (Nicol, 1953, 1957).

When a polynoid is subjected to tactile stimulation, scales anterior and posterior to the stimulated region emit flashes. The response is a reflex, the excitatory pathways of which involve peripheral receptors, nerve cord, and a peripheral ganglion in each elytrum on the efferent side of the arc (Bonhomme, 1942; Nicol, 1954).

It has been observed that when a polynoid is transected, only the part posterior to the cut flashes, the anterior fragment remaining dark (Kutschera, 1909; Nicol, 1953). There is a seeming discrepancy between this restricted response, and the more widespread luminescence which attends tactile stimulation (Harvey, 1952). The observations could be explained if there existed some form of functional polarity in the nerve cord, and I have tested this possibility by means of electrical stimulation.

MATERIAL AND METHODS

Gattyana cirrosa was selected for study because it is large, tough, and sluggish. Specimens were anaesthetized in iso-osmotic $MgCl_2$, and heads and tails were cut off. The majority of elytra were removed, leaving a few at restricted levels, namely at the anterior end, middle of the body, and at the posterior end. The animal was slit longitudinally along the mid-dorsal surface, and the nerve cord was exposed. The preparation was then pinned out so that the residual elytra could be seen from above, and a pair of electrodes could be placed on the nerve cord.

Electrodes were platinum wire, insulated to near the tips. Electrical stimuli were condenser discharges or square wave pulses delivered from electronic apparatus. Stimulus strengths were kept near threshold.

OBSERVATIONS

When severed in two halves with a clean quick cut, *Gattyana* behaves like other polynoids, all elytra in the posterior fragment flashing, while elytra in

the anterior fragment remain dark. Tactile stimulation causes all elytra to flash.

Electrodes were placed on the nerve cord at the following levels: anterior quarter, middle, and posterior quarter.

Electrodes in the anterior region

Results of stimulation were variable. Usually flashing occurred in the elytra at the anterior end, either on the first pulse or after a series of pulses. In these instances continued stimulation led to flashing in middle elytra. In other preparations stimulation caused middle and posterior elytra to flash (first pulse), followed by flashing in anterior elytra when stimulation was continued.

Electrodes in the middle of the body

Stimulation at this level evoked light in contiguous middle elytra and in elytra at the posterior end (first pulse). Protracted stimulation was followed by flashing in anterior elytra.

Electrodes in the posterior region

A single pulse caused posterior elytra to flash. A series of pulses evoked light in anterior elytra.

Protocols of two experiments are as follows:

(1) Preparation with two pairs of elytra, at anterior and posterior ends; electrodes in middle of worm.

1 shock: flash in posterior elytra. 24 shocks at 1/sec: flickering light in posterior elytra. Long bursts at 2, 3, 4 and 5/sec: flickering light in posterior elytra.

(2) Preparation with three pairs of elytra, anterior end, middle and posterior end; electrodes in anterior region.

Burst at 1/sec: flashing in anterior elytra, beginning with eighth shock. Burst at 1/sec: flashing in anterior elytra, beginning with fourth shock. Burst at 1/sec: flashing in anterior elytra, beginning with seventh shock.

Electrodes moved to posterior region.

Burst at 2/sec: flash on first shock in posterior elytra. Burst at 2/sec: flashing in posterior elytra beginning with first shock; flashing in middle elytra beginning with ninth shock.

CONCLUSIONS

In the anterior quarter of the body, excitation for luminescence tends to show preferential conduction anteriorly. Behind this level there is a preferential tendency towards posterior conduction. A single pulse in the posterior half of the body excites elytra behind the electrodes; with continued stimulation light spreads to elytra anterior to that level. Thus, there is evidence for functional polarity in the nerve cord, such that luminescent excitation is conducted with greater facility posteriorly over a large part of its length. The evidence is more equivocal for the anterior end: in the majority of instances conduction

occurred with greater facility anteriorly. It would seem, therefore, that when a polynoid is cut in half, the brief excitation can travel only posteriorly. More protracted tactile stimulation generates longer excitation, overcoming resistance to anterior transmission.

REFERENCES

BONHOMME, C., 1942. Recherches sur l'histologie de l'appareil lumineux des Polynoinés. *Bull. Inst. océanogr., Monaco*, No. 823.

HARVEY, E. N., 1952. *Bioluminescence*. New York: Academic Press.

KUTSCHERA, F., 1909. Die Leuchtorgane von *Acholoe astericola* Clprd. *Zeit wiss. Zool.*, Bd. 92, pp. 75–102.

NICOL, J. A. C., 1953. Luminescence in polynoid worms. *J. mar. biol. Ass. U.K.*, Vol. 32, pp. 65–84.

—— 1954. The nervous control of luminescent responses in polynoid worms. *J. mar. biol. Ass. U.K.*, Vol. 33, pp. 225–55.

—— 1957. Luminescence in polynoids. II. Different modes of response in the elytra. *J. mar. biol. Ass. U.K.*, Vol. 36, pp. 261–9.

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ON A NEW SPECIES OF SCYPHOMEDUSA, *ATOLLA VANHÖFFENI* N.SP.

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(Plate I and Text-fig. 1)

It seems to be the general opinion that there are only two species of *Atolla*, *A. wyvillei* Haeckel, with smooth marginal lappets, and *A. chuni* Vanhöffen in which the marginal lappets have warts.

But Vanhöffen (1902, p. 21, pl. v, figs. 27–29) described in some specimens organs which he thought might be excretory in function. These organs appeared as eight dark spots disposed radially on the subumbrellar walls of the stomach where the gastric cavity narrows towards the ostia. In these dark spots the ectoderm and endoderm cells are higher than those in the neighbouring areas, the ectoderm cells being more darkly pigmented than the endoderm cells. Sections do not show any passage through the mesogloea so that there are in fact no pores.

Maas (1903, p. 10, and 1904, p. 52) drew attention also to these spots and reproduced an excellent photograph of a specimen with them (Maas, 1903, pl. XII, fig. 108).

They were subsequently referred to by Stiasny (1934, p. 52) who saw them in some of the specimens in the 'Discovery' collections.

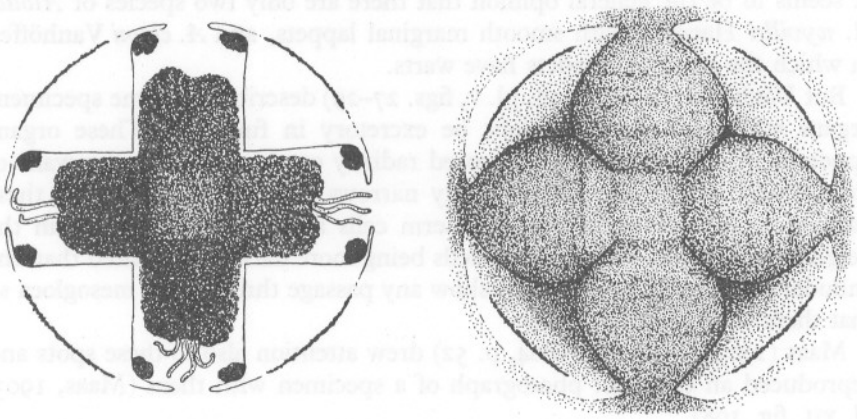
Recently I found two such specimens in a collection made on R.R.S *Discovery II* with a 2 m stramin ring trawl hauled obliquely from *ca.* 2400 m at 39° 38′ N., 11° 30′ W. on 26 February 1956 (Discovery Station 3370). The general appearance of these medusae was so different from that of all the other specimens of *Atolla* that I had seen that I suspected they might belong to a separate species. I was fortunate enough to find another such specimen in a collection made on R.V. *Sarsia* with a 2 m stramin ring trawl with 900 fathoms of wire out at 47° 03′ N., 5° 47′ W., on 3 July 1956. This specimen was in an excellent state of preservation, and with it was another well-preserved specimen of the same size without spots and with the pigmentation typical of *A. wyvillei*. It could be seen at once that they were so different that they must be specifically distinct (Pl. I).

Besides the difference of the presence or absence of the eight spots there are other quite obvious distinctions.

In the medusae with spots the basal attachment of the stomach forms a cross whose arms slope downwards towards the umbrella margin and are of approximately uniform width until they narrow suddenly to form the ostia into

the gastrovascular sinus (Text-fig. 1*a*). In the typical *A. wyvillei* the basal attachment is quite different and has rather the form of a four-leaved clover (Text-fig. 1*b*).

In the medusa with spots the umbrella is almost entirely unpigmented, except for some faint pigmentation at the bases of the marginal tentacles; some clusters of minute spots on the ring muscle; and four curved lines of pigment along the bases of the four triangular septa. The gonads are yellowish brown on the exumbrellar side, and this pigmentation curves over the side of each gonad leaving a circular patch free of pigment on the subumbrellar side; one gonad is missing in this specimen (Pl. I).



Text-fig. 1. Exumbrellar view of the base of the stomach of *a*, *Atolla vanhöffeni* n.sp., and *b*, *A. wyvillei*. For clarity the buccal portion of the stomach has been omitted.

The stomach and the eight spots are intense blackish purple. The pigment stops short before the end of each arm of the cross leaving transparent spaces in which one or two of the pigmented gastric cirri may be seen. Beneath these transparent areas are the perradial pillars of jelly running down the outside of the buccal walls of the stomach.

This pigmentation is in marked contrast to the varying range of coloration to be found on the umbrella of *A. wyvillei*, in which the pigment is more reddish brown in colour. Even those specimens of *A. wyvillei*, in which only the stomach and gonads are pigmented (group I of Broch, 1913, p. 15), are immediately distinguishable by the shape of the base of the stomach and its reddish brown colour.

Vanhöffen (1902) described the dark spots in a general account of the histology of the genus *Atolla*, ascribing the character to no single species. Maas (1903, pl. I, fig. 4; pl. XII, fig. 108) figured the spots as *A. valdiviae*, but later (Maas, 1904, pl. V, fig. 38) as *A. bairdi*. Stiasny (1934) referred to them under a general account of *A. wyvillei*.

Since, therefore, the species with spots cannot be allocated to any known specific name I propose to call it *A. vanhöffeni* n.sp. in honour of Ernst Vanhöffen who was the first to draw attention to the occurrence of the spots.

I have so far seen three specimens: these were 15, 18 and 20 mm in diameter. Two of these had twenty tentacles, but the third was cut up for sectioning before they were counted. Two were females and one male. In the female shown in Pl. I each gonad had one very large egg about 1 mm in diameter with a few smaller eggs.

Pl. I gives a photograph of *A. vanhöffeni*, and, for comparison, the specimen of *A. wyvillei* found with it in the same collection.

I hope that I may find more specimens of *A. vanhöffeni*, when it may be possible to determine other specific characters. At any rate the following characters are quite sufficient for the identification of the species.

A. vanhöffeni	*A. wyvillei*
With eight pigment spots	Without pigment spots
Umbrella almost completely unpigmented	Umbrella with characteristic pigment pattern
Base of stomach in form of a cross	Base of stomach in form of a four-leaved clover
Colour of stomach and spots blackish purple	Colour of stomach and on umbrella brownish red

The largest specimen I have is 20 mm in diameter. It seems possible that *A. vanhöffeni* may not grow to so large a size as *A. wyvillei*, since all previous authors when recording specimens with spots have remarked that they are usually young specimens.

The specimen of *A. vanhöffeni* figured in Pl. I has been deposited in the British Museum (Natural History) and has been given the registration number B.M. 1957.1.30.1.

My thanks are due to Dr J. A. C. Nicol who preserved two of the specimens for me while on a cruise on R.R.S. *Discovery II*; to Captain C. A. Hoodless and the crew of R.V. *Sarsia* who collected the fine specimen on which the above account is based; and to Mr A. C. G. Best who took the photographs reproduced in Plate I.

SUMMARY

In 1902 Ernst Vanhöffen drew attention to the occurrence of eight dark pigment spots in *Atolla* which he thought might be excretory organs.

It is shown that these spots are a specific character occurring only in some specimens, and medusae with this character have been named *Atolla vanhöffeni* n.sp. This species can now be distinguished from *A. wyvillei* by other characters.

REFERENCES

BROCH, HJALMAR, 1913. Scyphomedusae from the *Michael Sars* North Atlantic Deep-Sea Expedition 1910. *Rep. Sci. Res.* '*M. Sars*' *Exped.*, Vol. 3, Part I, 20 pp.

MAAS, OTTO, 1903. Die Scyphomedusen der Siboga Expedition. *Siboga Exped.*, Monogr. XI, pp. 1–91.

—— 1904. Méduses provenant des Campagnes des Yachts *Hirondelle* et *Princesse-Alice* (1886–1903). *Rés. Camp. sci. Monaco*, Fasc. 28, pp. 1–71.

STIASNY, G. 1934. Scyphomedusae. '*Discovery*' *Rep.*, Vol. 8, pp. 329–96.

VANHÖFFEN, ERNST. 1902. Die acraspeden Medusen der deutschen Tiefsee-Expedition 1898–1899. *Wiss. Ergebn.* '*Valdivia*', Bd. 3, pp. 3–52.

Note added in proof

I have now found two more specimens of *A. vanhöffeni*, both collected from 47° 09′ N., 7° 38′ W. on 21 July 1955. One was a small specimen 8 mm in diameter: it had 18 marginal tentacles and developing female gonads. The other, beautifully preserved, was 25 mm in diameter; it had 20 marginal tentacles and was a female with one very large egg among other eggs in some of the gonads. This specimen differed from the description given above in that the muscles at the bases of the marginal tentacles were strongly pigmented.

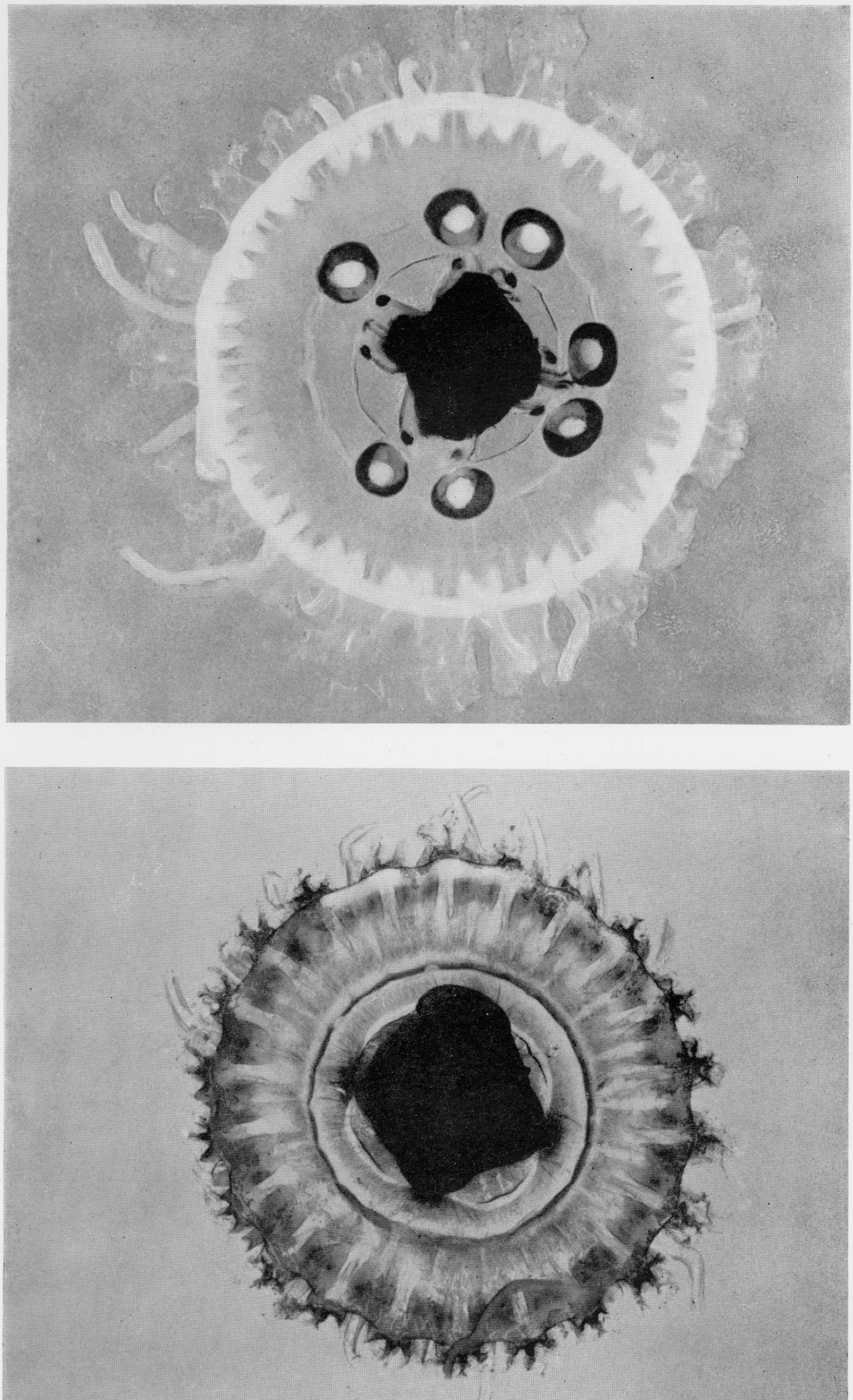
Through the kindness of Dr P. L. Kramp I have also been able to see several specimens of *A. vanhöffeni* picked out from the collections of *Atolla* from the Atlantic in the Universitetets Zoologiske Museum in Copenhagen by Dr Kay Petersen. The details are given below.

			Metres wire	Diameter (mm)	Sex	No. of tentacles
Thor						
3. ix. 1906	St. 180	48° 19′ N., 13° 53′ W.	—	12	♀	20
28. ii. 1909	St. 69	36° 13′ N., 9° 44′ W.	600	15	♀	20
4. iii. 1909	St. 71	39° 35′ N., 9° 45′ W.	600	13	♀	20
				12	♀	20
				11	♀	20
				10	? ♂	20
				8	?	Damaged
4. iii. 1909	St. 71	39° 35′ N., 9° 45′ W.	1600	29	♀	19
18. vi. 1910	St. 91	35° 53′ N., 7° 26′ W.	1600	10	♂	20
				10	No gonads	20
				9	No gonads	20
				8	♀	20
				7	? ♀	19
				6	♀	20
				9	♂	Damaged
9. ix. 1910	St. 232	36° 28′ N., 9° 06′ W.	2000	16	No gonads	20
				16	♀	20
				13	♂	20
Dana						
1. vii. 1931	St. 4206 II	53° 38′ N., 29° 41′ W.	600	25	♀	20

It will be noted that nearly all these specimens had 20 marginal tentacles, and none had more. I have now examined 21 complete specimens, 18 of which had 20 tentacles, two had 19, and one had 18. It seems probable that this is a constant character distinguishing the species from *A. wyvillei* in which the number of tentacles is typically 22.

EXPLANATION OF PLATE I

Above, *Atolla vanhöffeni* n.sp.; below *A. wyvillei*. Both specimens were collected from 47° 03′ N., 5° 47′ W. on 3 July 1956. They are photographs from the subumbrellar side and are both enlarged × *ca.* 4·5.



(*Facing p.* 280)

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THE BIOLOGY OF A COMMENSAL COPEPOD, *ASCIDICOLA ROSEA* THORELL, IN THE ASCIDIAN *CORELLA PARALLELOGRAMMA* (MÜLLER)

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(Text-figs. 1 and 2)

The considerable advantages offered by ascidians as hosts to small commensal crustaceans are clearly implied by the large number of ascidicolous copepods which have been described; and the attractions of this particular niche are further evidenced by the fact that these copepod mess-mates are of polyphyletic origin and cosmopolitan distribution.

The study of such associations, however, has been limited almost entirely to a bare note of their existence, although the papers of Canu (1892) and Chatton & Brément (1915) are partial exceptions.

That ascidians so frequently act as hosts is not in itself surprising. Their comparative immunity from predation, their maintenance of a feeding current and the capaciousness of many of their internal cavities afford protection, accessible food and a certain freedom of movement. Furthermore, the elaborate ascidian mechanism of food intake and concentration offers, in its several stages, different possibilities of utilization to copepod commensals of varying structure and mobility. Thus, in the pharynx alone, a commensal might exploit the particles entering the oral aperture; or it might seek these as, trapped in the moving sheets of mucus, they are slowly swept towards the dorsal lamina; or, yet again, the concentrated food string, *en route* to the oesophagus and stomach, might be the focus of attention. Encompassed, therefore, by this complex nutritional mechanism many variously adapted copepods find optimal living conditions.

In any attempt to shed some light on associations of this type, three conditions must be satisfied. The chosen copepod species must be of relatively large size, the ascidian concerned must possess an unusually transparent test, and observations must be made in a fairly large volume of undisturbed sea water to ensure normal behaviour on the part of the host. After a prolonged search for suitable material in Strangford Lough, Co. Down, it was found that the association between *Ascidicola rosea* Thorell and *Corella parallelogramma* (Müller) proved almost ideal. The female *Ascidicola rosea* attains a length of over 4 mm, while the glass-clear tunic of *Corella parallelogramma* is perhaps

its most striking feature. A Perspex tank, coupled with a viewing system of lenses and ground-glass screens, with adequate background lighting, solved most of the problems of observation under nearly normal conditions.

GENERAL CONSIDERATIONS

C. parallelogramma, a solitary ascidian belonging to suborder Phlebobranchiata, occurs sparingly around the British coasts, being found attached to stones, weed, shells, etc., usually in clear offshore waters down to depths of 150 m (Berrill, 1950). Abroad, its range includes a large part of the Scandinavian coast and the Mediterranean. It attains a length of some 5 cm, large specimens being easily dredged in about 12 m in Strangford Lough, where the species is abundant on suitable ground, especially during the autumn months. As well as *Ascidicola rosea*, *Corella* is known to harbour several other ascidicolous copepods—*Notodelphys agilis* Thorell, *N. caerulea* Thorell, *Doropygus porcicauda* Brady, *D. pulex* Thorell, *Pachypygus gibber* Thorell, and the cyclopoids *Ascomyzon lilljeborgi* Thorell and *Lichomolgus albens* Thorell, the last-named sometimes cohabiting with *Ascidicola*. At the beginning of October, *A. rosea* was present in about 25% of *Corella* examined; three weeks later 60% of the hosts were infected.

Ascidicola rosea is usually classified as the sole member of the family Ascidicolidae, suborder Notodelphyoida. In a recent paper, however, Lang (1948) has suggested that this very heterogeneous suborder should be split up, in which case the Ascidicolidae, along with several other notodelphyoid families, should be regarded as a special tribe of gnathostomatous cyclopoids—a taxonomic realignment which has much to recommend it. This copepod has been reported from several localities around Britain and Ireland, while abroad it is found on the Norwegian coast as well as in the Baltic and Mediterranean. In addition to *Corella* its hosts include *Halocynthia papillosa* (L.), *Ascidia mentula* (Müller), *A. obliqua* Alder, *Ascidiella aspersa* (Müller), *A. opalina* M'Gill, *Ciona intestinalis* (L) and *Phallusia* sp. I have also obtained a single female specimen from *Pyura squamulosa* (Alder).

During the winter months, the *Corella* population of Strangford undergoes a very marked diminution. Since the commensal breeds throughout the year, the copepodids must therefore seek alternative hosts during the colder months in order to complete their development. *Ascidiella aspersa*, which remains plentiful during the critical period, is a frequent choice, and it seems likely that it is this species which carries the main bulk of the overwintering *Ascidicola* population.

Until recently, the genus *Ascidicola* was thought to be monotypic and restricted to the northern hemisphere, but Lang (1949) has described a second, closely allied species, *A. aculeoretusa*, from *Pyura georgiana* Mchlsn. taken in 250 m off South Georgia.

POSITION AND FEEDING ACTIVITIES OF THE COPEPOD

Schellenberg (1921) summarized in tabular form the then available information regarding the site occupied by *Ascidicola rosea* within its various ascidian hosts, and the occasional records of the past thirty years have added to his list little of material value. In most cases, it is reported to occur in the pharynx, although a minority of observers have collected specimens from the stomach and intestine. Examination of infected living *Corella*, however, leaves little doubt that (in this host at least) *Ascidicola's* normal 'operational base' is neither pharynx nor stomach, still less the intestine, but the oesophagus. The stomach is entered only in certain circumstances, while excursions into the pharynx proper are rare indeed. On only one occasion, in fact, was *Ascidicola* observed to cross the pharyngeal wall.

The preference shown for the oesophageal region is explained by the proximity of the food string descending the dorsal lamina, for the particles entrapped on it appear to provide this copepod with its only source of nourishment. During active feeding, *Ascidicola* grasps the mucus cord with the four anterior pairs of pereiopods and climbs up it for a short distance, feeding intermittently. Although as much as two-thirds (or, exceptionally, the whole) of the body may project head first into the pharynx, the slow downward movement of the food string as it passes into the ascidian's stomach tends continually to draw the copepod back into the oesophagus. After sinking a short distance in this way, *Ascidicola* adjusts its position by another climbing movement. The initiation of a fresh ascent often appears to follow contact between the urosome of the passively descending commensal and the curving wall of the oesophagus where the latter narrows before entering the stomach. During its ascent, *Ascidicola* may climb in a straight path or adopt an irregular side to side course. Not infrequently a complete spiral is achieved, although this is probably due in part to the twisting of the cord itself. While on the food string, the copepod twitches its antennules intermittently and various unidentifiable movements of the antennae and mouthparts can be seen. Occasionally it may tug at the food string with a vigorous movement of the head, sometimes producing a noticeable kink in the mucus cord. Whether this action is designed to remove an attractive food particle or to accelerate the downward passage of the still unexplored upper portion of the string, it is difficult to say. Evidence in support of the latter interpretation may be provided by the fact that this movement generally takes place when the food string is thin and poorly developed. Feeding activities may cease for short periods, the copepod withdrawing its head and anterior segments from contact with the cord and remaining motionless in an attitude somewhat resembling that of a resting sphingid moth larva. Climbing activity appears to be greatly reduced in the presence of a very thick food string, the commensal remaining almost motionless and pressed against the oesophageal wall.

When active feeding is not taking place, *Ascidicola* lies cradled in the oesophageal bend, usually with the ventral surface uppermost. Since, in this position, the food string is passing in close proximity to the mouthparts, it is possible that some feeding still occurs. Close observation, however, indicates that this must be on a reduced scale, if in fact it takes place at all.

Feeding activity appears to be of a non-cyclical nature. Certainly no daily periodicity is involved, since copepods may still be seen on the food string several hours after darkness has fallen as well as during the day. The periods of quiescence, therefore, spent cradled in the oesophageal curve, in most cases probably follow optimal feeding on a rich food string, thus establishing an intimate link with the trophic activity of the host.

Under laboratory conditions, *A. rosea* will often adopt a third position, lying in the oesophagus with its head towards the ascidian's stomach. When in this attitude, the copepod may bend the terminal segment of the urosome upwards to an angle of 45°, in this way perhaps achieving a braking effect against the ciliary current of the oesophagus. This inverted position is very frequently associated with a poorly developed or completely interrupted food string, and suggests that the commensal turns to follow the final truly nutritive section of the cord as it passes into the digestive regions of the host's canal. Often this attitude is maintained for long periods, *Ascidicola* sometimes seeming to grasp and halt the receding portion of rich food string before it slowly vanishes into the host's stomach. In this way the stomach may be actually entered for varying periods of time, although in the natural state it is probably seldom necessary to seek food in this region. An interruption of the host's normal feeding pattern, consequent upon its capture, may well account for some of the reported instances when *Ascidicola* has been found in an ascidian's stomach. (There is, however, some slight evidence that rather more time may be spent in this region when the host concerned is *A. aspersa*.) Only twice during the present study have copepods been seen in the intestine and twice in the rectum.

Two occasions on which the commensals were observed to enter the stomach are worthy of record. Once, after several ascents, the copepod remained quiescent on the descending food string and was eventually drawn, tail first, into the stomach. Some minutes later, after several exploratory movements, it emerged head foremost and once again mounted the food string. In another instance, following the introduction of a second *Ascidicola* which became trapped on the descending cord, the rightful occupant turned completely round and crawled into the stomach, followed passively by the immobilized specimen. A similar turning reaction sometimes takes place if an abrupt stimulus is applied—for example, focusing a concentrated spot of light on the copepod.

Several hitherto puzzling features of *A. rosea's* anatomy become explicable in the light of its intimate association with the food string. Thus Sars (1921)

described the penultimate abdominal segment as 'having the ventral part of the hind edge remarkably thickened and densely clothed with small pricks'—a feature which was also noticed by Brady (1878). These 'small pricks' are in fact tiny sharply pointed spines, and since the region in which they occur is pressed closely against the mucus cord there can be little doubt that they aid in maintaining a firm grip, functioning, in fact, rather like a crampon (Fig. 1).

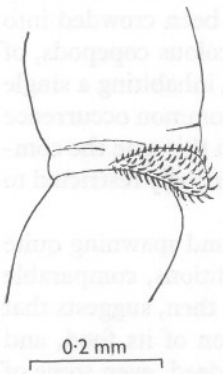

Fig. 1

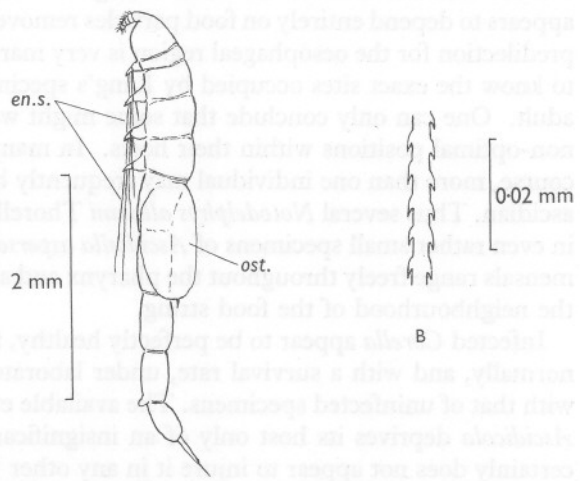

Fig. 2

Fig. 1. Distal part of penultimate segment of female *Ascidicola rosea* to show the spinous pad. The proximal part of the anal segment is also shown.

Fig. 2. A, female *Ascidicola rosea* in lateral view to show the long endopodal setae (*en.s.*) and the left oostegite (*ost.*). B, a small portion of an endopodal seta, showing the spines with which it is beset.

During a climb, it is occasionally noticeable that the anterior urosome segments will extend telescopically, carrying the body upward, while the posterior two remain temporarily motionless in close contact with the food string, thus providing a point of leverage. The above-mentioned bending of the terminal urosome segment is also apparent during some climbs, although its object in this case is clearly to bring the spinous pad on the penultimate segment into more effective play.

The extraordinarily long setae carried by the endopodites of the four anterior pereiopods are also of interest in a similar connexion. In life, their tips are directed posteriorly (Fig. 2A) and the entire length of each seta is applied to the main axis of the food string. In spite of Sars's assertion (1921) that these setae are quite smooth, examination under high power reveals them as beset with minute spines (Fig. 2B). It is possible that these spines, by engaging in the food string, likewise represent an adaptation to assist in maintaining a secure grip while in a vertical position on the cord.

RELATIONS WITH THE HOST

Although Lang (1948) records single specimens of *Corella parallelogramma* as harbouring up to five females of *Ascidicola rosea*, the rule in dredged ascidians from Strangford Lough seems to be one copepod per host. Occasionally, however, a very young female will be found with an adult, the former occupying a more anterior site on the food string. As this rather large commensal appears to depend entirely on food particles removed from the string, and as its predilection for the oesophageal region is very marked, it would be interesting to know the exact sites occupied by Lang's specimens if the latter were fully adult. One can only conclude that some might well have been crowded into non-optimal positions within their hosts. In many ascidicolous copepods, of course, more than one individual may frequently be found inhabiting a single ascidian. Thus several *Notodelphys allmani* Thorell are of common occurrence in even rather small specimens of *Ascidiella aspersa*—but in this case the commensals range freely throughout the pharynx and are not virtually restricted to the neighbourhood of the food string.

Infected *Corella* appear to be perfectly healthy, feeding and spawning quite normally, and with a survival rate, under laboratory conditions, comparable with that of uninfected specimens. The available evidence, then, suggests that *Ascidicola* deprives its host only of an insignificant fraction of its food, and certainly does not appear to injure it in any other way. Indeed, even some of the food particles filched from the string might subsequently become available to the host in the form of the copepod's faecal material, since organic debris is, of course, utilized by ascidians as well as living micro-organisms. While we are therefore faced with the usual, if artificial, difficulty of deciding on the precise ecological status of *Ascidicola*, its description as an endocommensal would seem to fit the known facts accurately enough.

REPRODUCTION

A. rosea carries its pink-coloured eggs in two thin oval masses protected by the dorsally situated lamellate oostegites (see Fig. 2A). These structures were regarded by Canu (1892) as the enlarged and modified fifth pair of pereiopods, although his interpretation was later disputed by Chatton & Brément (1915), who maintained that they could equally be akin to the alate processes of the notopterophorids. Their exact nature, therefore, may still be regarded as *sub judice*. Each egg-mass is slightly concave ventrally, being moulded to the contours of the body, and each contains approximately the same number of eggs. The actual egg number, however, may vary within rather wide limits. This variability may be governed, as Marshall & Orr (1952) have shown for *Calanus finmarchicus* (Gunnerus), by the food supply available to the parent, or alternatively may be correlated with the decreasing fertility of a female which has already, perhaps, produced several broods. Whatever the reason, an

egg-mass may contain as few as 20 or as many as 70 eggs. Individual eggs measure 0·13–0·14 mm in diameter.

The male, which attains little more than 1 mm in length, lacks the obviously specialized features of the mature female and is adapted for an active free-swimming existence. As one might expect, it is encountered much less frequently. Sars (1921) mentions having found only a single specimen, dredged in the free condition. None have been seen in ascidians from the Strangford area and it can probably be assumed that its occurrence as an adult in the host is in the nature of a fleeting visit only, during which mating takes place. The possibility, however, cannot be excluded that fertilization is performed by a male which had developed within the same host as a young female and which has subsequently left the ascidian, since Marshall & Orr (1955) have shown that in *Calanus* fertilization takes place at a relatively early stage of ovarian development. On the other hand, the fact that not one adult male has been detected within *Corella* during the Strangford investigation renders this a less likely explanation.

Perhaps the most interesting problem which arose during the study of this association concerned the mode of exit from the host of the copepod's young stages. Short of rupturing both mantle and tunic—a task manifestly beyond the powers of either eggs or nauplii—and in the absence of evidence that the peribranchial slits were utilized, the only available escape routes would be via either the oral or the atrial siphons. If the eggs hatched *in situ* on the parent copepod and the nauplii attempted to reach the outside world via the oral route, they would encounter not only the force of the inhalant current but the dangers attendant upon a journey through the mucus-lined pharynx—a structure specifically evolved for the capture of micro-organisms. To traverse the entire length of the food-laden alimentary canal, however, would involve an equally hazardous passage for these fragile forms. It seemed probable, therefore, that egress took place in the egg stage. This would, however, need very accurate timing, since to shed relatively large demersal eggs from the protection of the host long before hatching would unnecessarily present hostages to fortune in view of the ubiquity of benthic scavengers.

In the account which follows, although the initial part of the process has not been observed in detail, due largely to the opacity of the ascidian's stomach wall, it can be inferred beyond any reasonable doubt to take place as described. Some time before the eggs are due to hatch, the female leaves her position in the oesophagus and enters the stomach. Here the ripe egg-masses are detached from beneath the oostegites. (This occurs quite regularly in females extracted from the host.) Shortly after being deposited in the stomach, the inner membrane of each egg, with its contained nauplius, becomes free, leaving the cluster of adherent outer membranes to remain as a honey-combed ghost-like replica of the original egg-mass—again a noticeable occurrence with ripe isolated ovisacs. From the host's stomach, the nauplii—still sheathed in their

protective inner membranes—are carried in small or large groups through the intestine and up the rectum, in which region they can be clearly seen provided only a small quantity of food material is present in the host's gut. In one instance a cluster of some 30 eggs took 30 min to traverse the last 8 mm of the rectum. As the anus is reached, and the full strength of the exhalant current encountered, final rupture of the delicate enveloping membrane takes place and the freed nauplii are expelled with almost explosive force through the atrial siphon. In a few of the hatchings observed, a group of eggs became lodged in a small terminal 'pocket' of the host's rectum, where they remained for some hours, but whether this would occur in ascidians with a full gut is difficult to determine. Meanwhile the female copepod has re-entered the oesophagus, and a new batch of eggs has, in most cases, been squeezed into the space beneath her oostegites. Eighteen days elapsed between successive hatchings of nauplii from one female observed in the laboratory.

This method of egg dispersal via the food canal of the host has not, to my knowledge, been described in any other copepod—though it is quite possibly the usual method for many of the species living in simple ascidians. It is, in its way, quite as remarkable as the egg-depositing migration of another ascidicolous form, *Enterocolides ecaudatus* Chatton & Brément, in which the mature female burrows up from the depths of its compound ascidian host to leave its egg-masses at the surface of the colony (Chatton & Harant, 1924). It is interesting also to observe how the presence of the inner egg membrane (a common feature in many free-living copepods, as shown by Marshall & Orr, 1954) is here of vital adaptive significance, serving as it does to protect the fragile nauplius during its passage through the host's gut.

Although only a subsidiary part of the present study, the various larval stages of *Ascidicola* perhaps merit the following brief notes, though it must be emphasized that the times given are approximate only. There are four clearly defined naupliar stages. The first-stage nauplius measures between 0·191 and 0·197 mm and swims with the usual jerky movement, exhibiting a marked preference for certain light intensities. After about 21 h, at a laboratory water temperature varying between 10·9° and 16·9° C, it moults to the second nauplius, which measures 0·206 mm. Again after approximately 21 h, the third nauplius appears, measuring 0·211 mm. 24 h later, the final nauplius stage is found, which attains 0·224–0·229 mm in length. This instar persists for about 31 h before the moult takes place to the first copepodid, which measures 0·349 mm and possesses six segments in all. At this stage the three anterior pairs of swimming legs are developed, though the third pair are still somewhat rudimentary. After a further 54 h, the second copepodid appears. This shows an increase in length to 0·369 mm, and possesses seven segments as well as a fuller development of the third pair of legs. After swimming freely for some time it displays a different type of behaviour, seeking the bottom of the dish and remaining quiescent for lengthy periods. If a *Corella* is now

placed in the same vessel, on subsequent examination it will be seen to contain copepodids scrambling about on the food string in the oesophageal region. Although fuller confirmation is desirable that the second copepodid represents the infective phase, there is little doubt that the developmental pattern will prove similar to that of *Enterocola fulgens* van Beneden (see Canu, 1892), in which further moults to the adult female stage occur within the host after entry by the second copepodid. It seems highly probable that a period spent in the ascidian is obligatory for all copepodids, male as well as female, if one can judge by the universal demise of copepodids not provided with a potential host. It must be admitted that these stages have not been seen often in *Corella*, but as they are so small they could very easily be overlooked, even when specifically sought.

It is hoped at some later date to investigate the nature of the attraction which the host ascidian apparently exerts over the second-stage copepodid. It seems unlikely that intake by chance alone should exercise a controlling influence on a life cycle so perfectly attuned in all other respects to the survival requirements of this specialized commensal.

Acknowledgements are due to Professor R. A. R. Gresson for the provision of research facilities; to Dr R. H. Millar for information regarding the ascidian host, and to my wife for assistance in the collection of material and for much helpful discussion.

SUMMARY

A study has been made of the feeding activities and reproductive behaviour of the copepod *Ascidicola rosea* within one of its ascidian hosts, *Corella parallelogramma*.

Ascidicola rosea feeds on particles which it removes from the food string as the latter is passing through the oesophagus of the host. When active feeding is not taking place, the copepod remains quiescent in the oesophageal bend. An inverted position within the oesophagus is sometimes adopted; this is generally associated with a meagre development of the food string. Certain peculiar structural features—notably the spinous pad on the penultimate segment and the long endopodal setae—are considered to be adaptations which assist the copepod while clinging to the food string.

The eggs of *A. rosea* are deposited in the ascidian's stomach and the nauplii pass through the host's alimentary canal still enveloped by the inner egg membrane. On reaching the anus, hatching takes place and the nauplii are expelled from the atrial siphon. There are four naupliar and two copepodid stages. Free-swimming life lasts for about 6 days.

REFERENCES

BERRILL, N. J., 1950. *The Tunicata, with an Account of the British Species.* London: Ray Soc.

BRADY, G. S., 1878. *A Monograph of the Free and Semi-Parasitic Copepoda of the British Islands*, Vol. I. London: Ray Soc.

CANU, E., 1892. Les copépodes du Boulonnais. *Trav. Sta. zool. Wimereux*, Vol. 6, 354 pp.

CHATTON, E. & BRÉMENT, E., 1915. Les oostégites, les ptérostégites et la cavité incubatrice des Ascidicolidae (Copépodes); développement, homologies, valeur phylogénitique et taxonomique. *Bull. Soc. zool. Fr.*, Vol. 40, pp. 143–55.

CHATTON, E. & HARANT, H., 1924. *Lequerrea perezi* n.g., n.sp., enterocolien parasite d'une ascidie simple. *Bull. Soc. zool. Fr.*, Vol. 49, pp. 24–30.

LANG, K., 1948. Copepoda 'Notodelphyoida' from the Swedish west-coast with an outline on the systematics of the copepods. *Ark. Zool.*, Bd. 40A, pt. 14, 36 pp.

—— 1949. On a new copepod family related to Notodelphyidae and on two new copepod species from South-Georgia. *Ark. Zool.*, Bd. 42B, pt. 4, 7 pp.

MARSHALL, S. M. & ORR, A. P., 1952. On the biology of *Calanus finmarchicus*. VII. Factors affecting egg production. *J. mar. biol. Ass. U.K.*, Vol. 30, pp. 527–47.

—— 1954. Hatching in *Calanus finmarchicus* and some other copepods. *J. mar. biol. Ass. U.K.*, Vol. 33, pp. 393–401.

—— 1955. *The Biology of a Marine Copepod*, Calanus finmarchicus (*Gunnerus*). Edinburgh.

SARS, G. O., 1921. *An Account of the Crustacea of Norway*, Vol. 8. Copepoda Monstrilloida and Notodelphyoida.

SCHELLENBERG, A., 1921. Neue Notodelphyiden des Berliner und Hamburger Museums. II. Teil. *Mitt. zool. Mus. Berl.*, Bd. 10, pp. 277–98.

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ON THE HORMONAL INHIBITION OF MOULTING IN DECAPOD CRUSTACEA

II. THE TERMINAL ANECDYSIS IN CRABS

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(Text-figs. 1–5)

When a crab moults it usually, though not invariably, increases in volume and in linear dimensions. The interval between successive moults or ecdyses frequently varies with the temperature and becomes greater as the individual grows larger. An exception is to be found in some crabs which have a regular moulting season, moulting perhaps once or twice a year. In some species at least the cycle of growth and moulting terminates with a final terminal anecdysis, beyond which the crab never progresses. This lays an upper limit to the size which the animal may attain. Teissier (1935) was, so far as I am aware, the first to draw attention to this phenomenon, whereby a crab—in Teissier's investigations the spider crab, *Maia squinado*—never moults again once it has entered upon this final instar. The occurrence of this terminal anecdysis has been demonstrated in the grapsoid crab *Pachygrapsus crassipes* (by Hiatt, 1948), the female blue crab *Callinectes sapidus*, and the green shore crab *Carcinus maenas* (by Carlisle, unpublished); it may be inferred from the somewhat scanty population statistics for other species of crabs, e.g. *Portunus depurator*, which have a definite size limit. The terminal anecdysis is, however, unknown in prawns which may go on moulting and increasing in size until they are overtaken by death, and the same is evidently true of the lobster, *Homarus gammarus* (L.) and the edible crab, *Cancer pagurus*, which may, apparently, increase in size indefinitely; reports of 'giant' crabs and 'giant' lobsters are not infrequent in the lay press and in the fishing periodicals.

In this paper the nomenclature of the moult cycle proposed by Carlisle & Dohrn (1953) will be adopted with addition of the expression 'terminal anecdysis'. Briefly the stages are as follows.

Proecdysis: a period of preparation for the moult, often accompanied by a raised blood-calcium level.

Ecdysis: the act of casting the shell or moulting.

Metecdysis: a period of recovery from the moult, when the animal is still partially soft but is rapidly hardening the new exoskeleton.

Diecdysis: a brief period between the end of one metecdysis and the beginning of the next proecdysis.

Anecdysis: a long period between the end of a metecdysis and the beginning of the succeeding proecdysis; this period often separates groups of moults which are themselves separated by diecdyses, but in species which moult seasonally, it is the normal stage separating two ecdyses.

Diecdysis and anecdysis are often both called intermoult periods, but their endocrine basis appears to be different (see Knowles & Carlisle, 1956) so that separate names are required for them. The term 'intermoult period', moreover has often been used to indicate the total period between two moults, including metecdysis and proecdysis. 'Terminal anecdysis' is a period at the end of the life of a crab when the physiological condition resembles a normal anecdysis, but the animal is incapable of further moulting. It will be noticed that this condition is strictly an anecdysis, but it can hardly be called an intermoult, for it does not lie between two moults. Some differences between animals in non-terminal and in terminal anecdysis will become apparent during the course of this paper.

The problem which has been investigated in the work now to be described is that of the failure to undergo further moults once terminal anecdysis is reached. The approach has been endocrinological.

MATERIALS AND METHODS

THE CRABS

Two crabs have been the subject of these investigations, the oxyrhynchan *Maia squinado*, the spider crab, and the brachyrhynchan *Carcinus maenas*, the green shore crab. All crabs were collected in the Plymouth area. *Carcinus* of the Plymouth population are biometrically and physiologically distinct from two races which occur on the opposite coast of the English Channel and it is probable that other local populations are likewise distinct (see Démeusy & Veillet, 1953; Démeusy, 1953; Carlisle, 1955); numerical data and dimensions refer specifically to the Plymouth population unless some other locality is mentioned.

Maia squinado has been the subject of intensive biometrical study by Teissier (1934–55), who has shown that it never moults again after the moult of puberty. Sexual maturity is achieved at this moult; copulation takes place while the female is still soft after the moult and is not possible thereafter. No further growth takes place. The terminal anecdysis, therefore, is the anecdysis succeeding upon the attainment of sexual maturity. It follows that female *Maia* can only breed once. The earlier moults are separated by long intervals, and the intermoult period appears to be of the nature of an anecdysis, rather than a diecdysis. So far as we are aware at present *Maia* only moults during late July and early August (always excluding the very young crabs). As a seasonal moulter, therefore, its intermoult period is almost certainly an anecdysis.

Carcinus maenas on the contrary moults throughout the greater part of the year, refraining from doing so only during the coldest part of the winter, January to March. The moults are separated by diecdyses during the summer and autumn; the only anecdysis is that during these three cold months. I have shown (Carlisle, 1954, 1955, and unpublished data) that the endocrine control of these two types of intermoult period is somewhat different. A detailed biological account of a brachyrhynchan crab, *Pachygrapsus crassipes*, whose moulting cycle follows the same pattern is given by Hiatt (1948). Like *Pachygrapsus*, *Carcinus maenas* ends its life in anecdysis, a terminal anecdysis after which it never moults again. In the Plymouth population almost all *Carcinus* over 70 mm carapace breadth and all over 75 mm are in the terminal anecdysis. The largest of the males are regularly 86 mm in carapace breadth, never in my experience exceeding this figure by even 1 mm. The females are smaller than the males. Analysis of the dimensions of egg-bearing females reveals a bimodal curve of size. I take this to indicate that there are two age-groups breeding each year. In the laboratory I have reared a crab caught when egg-bearing, with a carapace breadth of 23 mm, through four moults to a second breeding and egg-bearing a year later when the carapace breadth was 51 mm. After egg-bearing it moulted once more to a carapace breadth of 63 mm when it entered terminal anecdysis. The moult of puberty takes place in *Carcinus* at about 16 mm carapace breadth (Cornubert, Démeusy & Veillet, 1952), and the animal undergoes about ten more moults before entering on the terminal anecdysis. The contrast with *Maia* is obvious. It will be shown in the course of this paper that the endocrine basis of terminal anecdysis differs profoundly in the two species of crabs.

THE ENDOCRINE ORGANS

The X-organ-sinus gland complex of the eyestalk has been described in various species of decapod Crustacea by Bliss, Durand & Welsh (1954), Passano (1953) and Carlisle (1953) among others. It has repeatedly been shown to be the source of a moult inhibiting hormone (see especially Passano, 1953), but it does not apparently secrete a moult accelerating hormone, such as is found in the natantian decapods (see discussion in Knowles & Carlisle, 1956).

The Y-organ described by Gabe (1953) has been shown by Echalier (1954, 1955) to secrete a moult-promoting hormone. It is possible that the moult-inhibiting hormone of the eyestalk acts not on the tissues, but on the Y-organ, to restrain it from producing the moult-promoting hormone.

In this study attention was directed to these two endocrine complexes.

All extracts of the endocrine organs have been made in distilled water, by grinding up the fresh organ with fine silica sand in a fused alumina mortar and pestle. The resulting suspension was then either filtered or centrifuged, before it was injected intramuscularly.

Previous studies have shown that eyestalk removal and removal of the

X-organ-sinus gland complex have identical effects on moulting (see especially Passano, 1953). As far as the moult-inhibiting hormone of this complex is concerned eyestalk removal is simply a cruder way of effecting ablation of the X-organ-sinus gland complex. Both types of operation have been performed in this investigation, and the results have been strictly equivalent. Eyestalk removal has been performed by cutting through the base of the stalk with fine pointed scissors. One eyestalk has been removed at a time, the other left to the next day in order to reduce the mortality. Removal of the X-organ-sinus gland complex was effected by the method described by Passano (1953), with the obvious modifications necessitated by the slightly different anatomy of the species used. The Y-organ was removed by the method of Echalier (1954).

ASSAY OF EXTRACTS

All assays were performed upon non-egg-bearing female *Leander serratus* of the size-range 55–70 mm overall length. Individuals were chosen which were in diecdysis at the time of injection. Intact individuals were employed and each was injected with a single dose of 0·15 ml. of extract or control saline. Each dose level was administered to twenty prawns and the death-rate during the assay was of the order of 4%. In no group was more than a single test animal lost during the course of an assay. Five days after the injection the prawns were examined under the binocular microscope to determine what proportion of each group had begun proecdysis. The moult-inhibiting hormone of the X-organ-sinus gland complex inhibits the onset of proecdysis while the moult-promoting hormone of the Y-organ promotes its onset. The statistical analysis followed the recommendations of Finney (1952). Graphical illustrations of assays (Figs. 1, 2, 4 and 5) will explain their layout. No units of activity are established: all assays are strictly comparative, devoted to comparing the titre of hormone in the glands in one stage of life with that in another.

RESULTS

Carcinus maenas

Moult-inhibiting hormone

A comparative assay of sinus glands taken from the eyestalks of male *Carcinus* in the terminal and in earlier anecdyses is illustrated in Fig. 1. It will be seen that the titre of moult-inhibiting hormone per gland is roughly four times greater in the sinus glands of crabs taken during the terminal anecdysis than during earlier anecdyses. Statistical analysis of the data gives the ratio between the effectiveness of the two as 4·25 with 1% fiducial limits at 3·44 and 5·79. It is to be noted that crabs in the terminal anecdysis are larger than younger crabs, so if the data are presented in terms of mg of glandular tissue rather than numbers of glands, the ratio is diminished. Weight for weight the sinus glands of the older crabs are 2·68 times more effective than those of the younger crabs in preventing the initiation of proecdysis in *Leander serratus*,

and the 1% fiducial limits are 1·38 and 3·64. On either basis then, the sinus gland contains more moult-inhibiting hormone during the terminal anecdysis than during earlier anecdyses.

The difference is even greater between the terminal anecdysis and diecdysis. Here the ratio of titres of moult-inhibiting hormone (on a weight for weight basis) is 7·92 with 1% fiducial limits at 6·75 and 9·37. This emphasizes once more that during diecdysis there is a lesser production of moult-inhibiting hormone by the eyestalk than during anecdysis; the endocrine status is different.

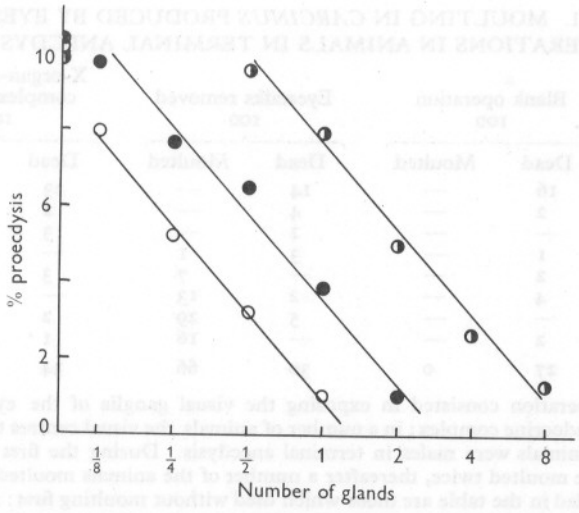

Fig. 1. Pooled results from a number of assays of the moult-inhibiting hormone of the sinus gland of *Carcinus* on *Leander*. The abscissa gives the number of glands supplying the extract which was injected into each individual; the ordinate gives the percentage of *Leander* which were found to be in proecdysis 5 days after the injections were made. All the *Leander* were in diecdysis at the beginning of the assay. Donors in terminal anecdysis—open circles; donors in non-terminal anecdysis—black circles; donors in diecdysis—half-black circles.

The high titre of moult-inhibiting hormone present in the sinus glands of *Carcinus* during the terminal anecdysis suggests that it may be part of the cause of this phenomenon. Removal, therefore, of the source of the hormone should test this hypothesis. This may be performed most simply by removing the whole eyestalk or by removing the X-organ-sinus gland complex, leaving the visual centres of the eyestalk intact. Both operations have led to the same result. All crabs in terminal anecdysis so operated have immediately entered proecdysis, as evinced by the heightened blood-calcium level and the modifications of the structure of the shell and cuticle. Eventually all which have survived long enough have moulted. The numbers are summarized in Table 1. During twelve months following the operation one crab whose eyestalks had been removed and two from which the X-organ-sinus gland complex had been

removed moulted three times, while one whose eyestalks had been removed moulted four times. This last crab at death had a carapace breadth of 132 mm, compared with the largest specimens caught wild in Plymouth which regularly have a carapace breadth of 86 mm, and one large specimen from the Scilly Islands which measured 92 mm. It is noteworthy that *Carcinus* in terminal anecdysis have never survived more than 7 months in the laboratory.

There can be little doubt that the moult-inhibiting hormone of the eyestalk in *C. maenas* is a major agent in preventing ecdysis once the crab enters

TABLE 1. MOULTING IN *CARCINUS* PRODUCED BY EYESTALK OPERATIONS IN ANIMALS IN TERMINAL ANECDYSIS

No. operated ...	Blank operation 100		Eyestalks removed 100		X-organ-sinus gland complex removed 100	
Week	Dead	Moulted	Dead	Moulted	Dead	Moulted
1	16	—	14	—	23	—
2	2	—	4	—	2	—
3	—	—	2	—	3	—
4	1	—	3	1	—	4
5	2	—	—	7	3	8
6	4	—	2	13	—	9
7	—	—	5	29	2	23
8	2	—	—	16	1	19
Total	27	0	30	66	34	63

The blank operation consisted in exposing the visual ganglia of the eyestalk, without damaging the endocrine complex; in a number of animals the visual centres themselves were damaged. All animals were males in terminal anecdysis. During the first 8 weeks of the experiment none moulted twice, thereafter a number of the animals moulted a second time. The dead recorded in the table are those which died without moulting first: a small number died after starting or completing the moult; these are counted among the animals which moulted.

upon its terminal anecdysis. To stimulate further moulting it is merely necessary to remove the gland system responsible for secreting this hormone. It has earlier been shown (Brown & Cunningham, 1939; Passano, 1953) that injection of this hormone, or implantation of the gland, is sufficient to prevent the onset of proecdysis and subsequent ecdysis in crabs which have been deprived of the X-organ-sinus gland complex or of the eyestalks.

The Y-organ

It is not known for certain whether the moult-inhibiting hormone of the eyestalk acts directly on the tissues in restraining the onset of proecdysis, or whether, as Echalier (1954, 1955) and Gabe (1953) suggest, it acts in preventing the Y-organ from secreting a moult-promoting hormone which is essential for the processes of proecdysis and ecdysis to take place. Echalier has shown that extirpation of the Y-organ in *Carcinus* leads to a cessation of all the processes of proecdysis, so that a crab lacking this organ cannot enter

proecdysis, nor continue further with it if it was part way through this stage when the operation was performed.

The Y-organs of 20 male *Carcinus* in the terminal anecdysis had a mean weight of 12·1 ± 1·1 mg, while 20 male *Carcinus* in the penultimate diecdysis had Y-organs with mean weight 13·0 ± 1·2 mg. When the weights, however, are expressed as a ratio of the body weight they become 10·9 ± 0·99 mg% and 21·1 ± 1·95 mg%. The difference appears to be significant at the 1% level. Relative to body size therefore the crabs in terminal anecdysis have smaller Y-organs than those slightly younger.

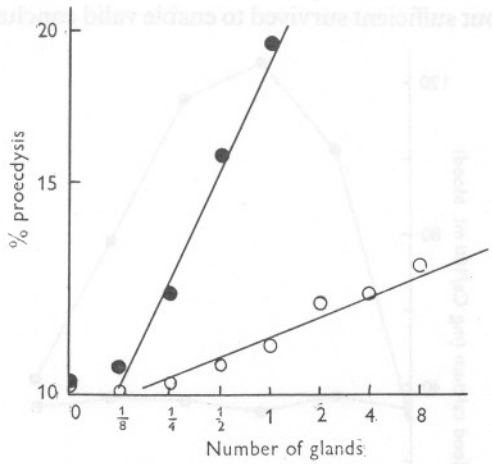

Fig. 2. Pooled results of a number of assays of the moult-promoting hormone of the Y-organ of *Carcinus* on *Leander*. The abscissa gives the number of glands supplying the extract which was injected into each individual; the ordinate gives the percentage of *Leander* which were found to be in proecdysis 5 days after the injections were made. Both scales are logarithmic. All the *Leander* were in diecdysis at the beginning of the assay. Donors in terminal anecdysis —open circles; donors in diecdysis—black circles.

An assay of the content of moult-promoting hormone in the Y-organ of *Carcinus* is illustrated graphically in Fig. 2. The Y-organs from crabs in diecdysis are significantly more potent ($P < 0{\cdot}001$) in this respect than organs from crabs in the terminal anecdysis.

A single injection of an extract of Y-organ into *Carcinus* in terminal anecdysis resulted in a fourfold rise in blood-calcium level, lasting about 5 days (see Fig. 3). This may be taken as indicative of the beginning of proecdysis, albeit temporary. Accordingly I carried out a prolonged programme of injecting such *Carcinus* twice a week with Y-organ extracts. The extracts were prepared from younger crabs which were in the period of proecdysis, when *a priori* reasoning led me to believe that the titre of the moult-promoting hormone would be highest. Each crab received at each injection the extract of two

Y-organs. After 2 weeks on this regime 20 crabs all showed a heightened blood-calcium level, about four times that in the controls injected with an extract of leg nerve. One crab moulted after 37 days, three more in the next fortnight and one more on the 58th day. On the 60th day the remaining 12 crabs (three had died) were sacrificed, together with the 16 surviving control crabs. All of the latter were still in anecdysis, while all of the former were in late proecdysis. Repeated injections of Y-organ extract had therefore induced a further moult in crabs which had entered upon the terminal anecdysis.

Bilateral removal of the Y-organ from *Carcinus* in terminal anecdysis leads to no obvious effects. Bilateral eyestalk ablation following this operation led to a high mortality but sufficient survived to enable valid conclusions to be drawn.

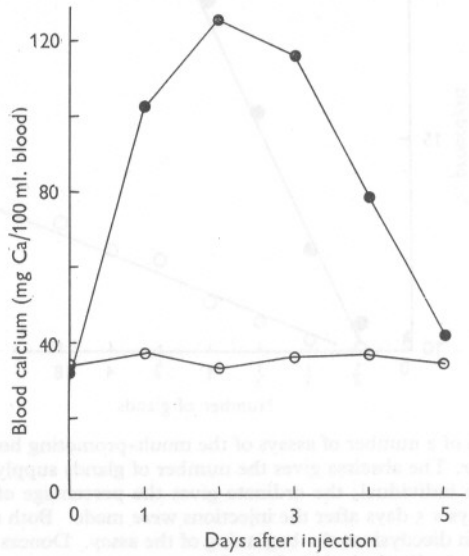

Fig. 3. The effect of injection of an extract of the Y-organ of *Carcinus* on the blood-calcium level of the same species during the terminal anecdysis. The controls (open circles) received an injection of extract of leg nerve.

Sixty days after the last stage of this double operation was completed not one of the 13 crabs which had survived so long had begun proecdysis; all were still in anecdysis. This may be contrasted with the results of simple eyestalk removal (see Table 1), when the crabs immediately began proecdysis, and had mostly moulted 60 days after the operation. We may conclude that the Y-organ is necessary for proecdysis to proceed, even in the absence of the moult inhibition afforded by the hormone of the eyestalk. It seems probable that the moult-inhibiting hormone of the X-organ-sinus gland complex of the eyestalk acts primarily in restraining the Y-organ from producing the moult-promoting hormone. It seems likely, however, that it has also a direct action on the tissues, for otherwise the slight titre of moult-promoting hormone

produced by the inhibited Y-organ of the terminal anecdysis (see Fig. 2) would surely lead to a very slowly progressing proecdysis unless the tissues are actively inhibited to counterbalance its effects.

Moult-inhibiting hormone — *Maia squinado*

A comparative assay of sinus glands taken from the eyestalks of male *Maia* in the penultimate and the terminal anecdysis is illustrated in Fig. 4. It is evident from this that the titre of moult-inhibiting hormone is much lower—about eight times lower—during terminal anecdysis than during the penultimate anecdysis, despite the larger size of the older animals. Statistical

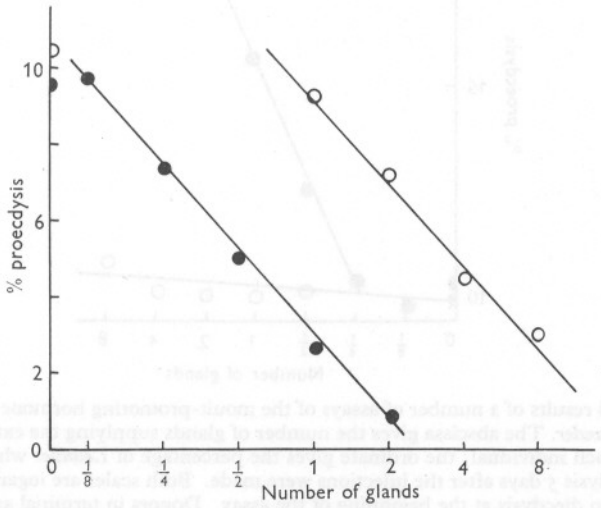

Fig. 4. Pooled results of a number of assays of the moult-inhibiting hormone of the sinus gland of *Maia* on *Leander*. The abscissa gives the number of glands supplying the extract which was injected into each individual; the ordinate gives the percentage of *Leander* which were in proecdysis 5 days after the injections were made. All the *Leander* were in diecdysis at the beginning of the assay. Donors in terminal anecdysis—open circles; donors in non-terminal anecdysis—black circles.

analysis of the data gives the ratio between the titre per gland as 7·31, with 1% fiducial limits at 6·03 and 9·22. Expressed as titre per unit weight of tissue the ratio is 16·02 with 1% fiducial limits at 14·11 and 20·05. A similar assay using female *Maia* as donors gave comparable results.

There can be little doubt that the failure to moult again once the terminal anecdysis has begun is not a result of excessive production of the moult-inhibiting hormone of the eyestalk—a situation quite contrary to that which we have found in *Carcinus*. In *M. squinado*, therefore, we must look elsewhere for the cause of the cessation of moulting.

The Y-organ of Gabe

During the penultimate anecdysis this organ is large and prominent, whereas during the terminal anecdysis it is much diminished in size so that it is often difficult to find upon dissection. During the penultimate anecdysis the Y-organs of 20 male *Maia* had a mean weight of $57{\cdot}36 \pm 7{\cdot}32$ mg, while those of 20 male *Maia* in the terminal anecdysis had a mean weight of $3{\cdot}35 \pm 0{\cdot}92$ mg. The difference is statistically very significant, with $P < 0{\cdot}001$.

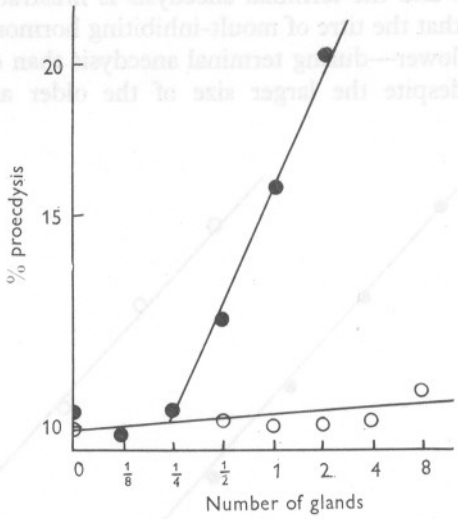

Fig. 5. Pooled results of a number of assays of the moult-promoting hormone of the Y-organ of *Maia* on *Leander*. The abscissa gives the number of glands supplying the extract which was injected into each individual; the ordinate gives the percentage of *Leander* which were found to be in proecdysis 5 days after the injections were made. Both scales are logarithmic. All the *Leander* were in diecdysis at the beginning of the assay. Donors in terminal anecdysis—open circles; donors in non-terminal anecdysis—black circles.

An assay of the moult-promoting hormone of the Y-organ of male *Maia* is illustrated graphically in Fig. 5. The regression line for the activity of the extracts prepared from the glands of crabs in the terminal anecdysis has a gradient which does not differ significantly from the horizontal, i.e. there is no noticeable effect of these extracts upon moulting. In contrast, the extracts prepared from glands of crabs in the penultimate anecdysis clearly have a pronounced effect in promoting the onset of proecdysis. The gradient of the regression line is $9{\cdot}74 \pm 1{\cdot}33$, which differs very significantly from zero ($P < 0{\cdot}01$).

A single injection of the extract prepared from ten Y-organs from *Maia* in the penultimate anecdysis, injected into each of ten crabs in the penultimate and ten in the terminal anecdysis, led in all of them to a transient threefold rise in the blood-calcium level, quite comparable to that found in *Carcinus* (Fig. 3).

This may be taken as a sign that the injection has led to a transient initiation of proecdysis in both groups of animals. A single injection of a similar extract prepared from the 25 Y-organs of *Maia* in the terminal anecdysis had no effect on the blood-calcium level in any of ten crabs.

We must conclude, then, that the absence of the moult-promoting hormone of the Y-organ during the terminal anecdysis in *Maia* is concerned in some way with the cessation of moulting. In this species the cessation of moulting is not a result of excessive production of moult-inhibiting hormone by the X-organ-sinus gland complex of the eyestalk. The cause of the functional degeneration of the Y-organ in the terminal anecdysis of *M. squinado* must be sought elsewhere than in the effects of the moult-inhibiting hormone of the eyestalk.

DISCUSSION

In *M. squinado* the last moult is that at which it attains sexual maturity, a state comparable with that found in insects. Once maturity is reached there is no further growth. Crustacea, however, suffer from one disability from which insects are free: copulation can only take place when the female has a soft integument and the male a hard one, that is, when the female is in the first stage of metecdysis and the male in some later stage of the moult cycle. In *Maia*, therefore, copulation is only possible when the female has just completed her final moult and the male has completed his some time previously. But the final moult in *Maia*, in Plymouth waters, takes place at a fixed time of year, in late July or August. It is thus impossible for the newly moulted male of that year to copulate with a newly moulted female: copulation must be between a male whose final moult took place one year or more previously and a newly moulted female. The heaps of *Maia*, which may be observed in July and August, are mixed heaps of moulting and copulating crabs (see Appendix). It is not until about 6 months after copulation that the eggs are finally fertilized, by sperm stored in the bursa copulatrix, and oviposited onto the pleiopods where they remain for about 9 months before hatching. A male, therefore, survives at least 12 months and a female at least 15 months after the final ecdysis. Nevertheless, once a *Maia* has entered upon the terminal anecdysis it may be considered as aged, for it is no longer capable of regenerating damaged tissue or limbs, or of repairing more than the most superficial injury. It is noteworthy in this respect that a *Maia* in terminal anecdysis is very much less ready than a younger crab to autotomize a damaged or captive limb. A mature *Maia* may be suspended by one leg out of water, even if the leg is damaged severely, without autotomizing the limb: it will die in this situation without casting the leg. A younger *Maia*, whose powers of regeneration are much greater, will cast the limb so treated and escape back to water with great rapidity. Echalier (1955) has reported that in the absence of the Y-organ, a crab cannot regenerate missing limbs, nor even produce the bud with which such regeneration normally begins.

The experiments reported in this paper suggest that in *Maia* the terminal anecdysis is brought about by the degeneration of the Y-organ. Correspondingly, no further ecdysis can begin, nor can regeneration of damaged parts. It seems likely that in the absence of predation, the death of a mature *Maia* is brought about by an accumulation of minor damage to the shell and tissues. It must also be remembered in this context that moulting in Crustacea often seems to serve as a mode of excretion (see Richards, 1951), since the exoskeleton stores waste material and especially nitrogen, which is discarded from the body on moulting. A crab in terminal anecdysis, therefore, is unable to use this method of excretion and may thus be constrained to accumulate toxic waste products in the tissues.

TABLE 2. INCREASE IN VOLUME OF *MAIA SQUINADO* AT MOULTING

Moult	Mean increase
Fourth before prepuberty	2·17
Third before prepuberty	2·15
Second before prepuberty	2·20
Before prepuberty	2·19
Prepuberty	2·26
First after prepuberty	2·20
Second after prepuberty	2·19
Last (puberty)	1·89

The increase in volume at each of the last eight moults is expressed as the ratio of the volume after moulting to that before it. Each ratio is the mean of at least fifteen observations and includes data of my own, supplemented by computations from the data of Teissier, 1934–55.

If the immediate controlling factor of terminal anecdysis in *Maia* is the degeneration of the Y-organ, we yet have no evidence as to the causation of this degeneration. All that can be said is that the inhibitory action of the X-organ-sinus gland complex is not the cause. The causative factor must be sought earlier in the life history. A clue to what is involved may be seen in the size increase which *Maia* undergoes at each moult. For most of the moults the relative increase in volume (in the male) is *ca.* 2·18 (see Table 2). At two moults only is the relative increase significantly different—the moult of prepuberty, when the gonads begin to increase in size and show the first signs of approaching maturity, and the moult of puberty three moults later, that is to say, the final ecdysis when the animal becomes sexually mature. At the prepuberal moult the relative increase in volume is *ca.* 2·26, greater, that is, than at other moults, while at the puberal moult the relative increase in volume is *ca.* 1·89, correspondingly less than at other moults. I have shown previously (Carlisle, 1955) that increase in volume at moulting is a function of the activity of the water balance hormone of the X-organ-sinus gland complex. It is possible that this is implicated in the control of the final ecdysis and may have some influence on the Y-organ, though such a concept must remain a mere speculation for the moment.

In *Carcinus maenas* we meet with rather a different situation. Here there can be little doubt that the main restraining influence preventing further moulting during the terminal anecdysis is over-production of the moult-inhibiting hormone of the X-organ-sinus gland complex. It seems likely that its prime action lies in restraining the Y-organ from producing the moult-promoting hormone, but nevertheless I believe that it must have some direct action on the tissues also; for otherwise the tissues would respond sooner or later, however slowly, to the small amounts of moult-promoting hormone which are produced by the incompletely inhibited Y-organ. What factor it is which leads the X-organ to produce the excess amounts of the moult-inhibiting hormone we have as yet no idea. But in *Carcinus* the terminal anecdysis only differs from earlier anecdyses as far as I have yet discovered in the higher titre of moult-inhibiting hormone. The control of the terminal anecdysis in this species seems to be merely an accentuation of the control of the earlier anecdyses and may well be gradually approached in these successive earlier anecdyses. *Carcinus* undergoes at least ten moults, eight diecdyses and two or three anecdyses between the moult of puberty and the terminal anecdysis (in the male, and probably also in the female). As I have repeatedly pointed out in previous papers (see Knowles & Carlisle, 1956) the control of anecdysis is different from that of diecdysis, and it is to this difference that we must look for origin of the terminal anecdysis in *Carcinus*.

One such difference between *Carcinus* in diecdysis and in anecdysis is in the level of secretion of the moult-inhibiting hormone of the X-organ-sinus gland complex. It will be obvious from a perusal of Fig. 1 that this difference is accentuated when we compare terminal anecdysis. During terminal anecdysis the eyestalk appears to be producing the moult-inhibiting factor faster than at any previous time in the life of the crab. There is thus in *Carcinus*, in contrast with *Maia*, a positive inhibition of the initiation of a further proecdysis once the animal has entered upon the terminal anecdysis. It is obvious, furthermore, that the Y-organ of *Carcinus* is not degenerate like that of *Maia* during the terminal anecdysis, and correspondingly a *Carcinus* in this stage is more capable of repairing minor damage to the shell. Once the inhibition to moulting is removed by surgical interference *Carcinus* enters upon a new proecdysis, stimulated to this, no doubt, by the moult-promoting hormone of the Y-organ. *Maia*, in contrast, lacks both the inhibiting factor and also the factor which might provoke renewed moulting.

It is evident that the type of control of the terminal anecdysis which is exemplified by *Carcinus* is more flexible than that found in *Maia*. Among the Portunidae, to which *Carcinus* belongs, there is great variation in the moulting cycle. At one extreme are to be found crabs like *Carcinus* and *Portunus depurator*, which have ten or a dozen moults after the moult of puberty, so that the terminal anecdysis does not coincide with sexual maturity, but rather begins several years later. At the opposite extreme are crabs such as *Callinectes*

sapidus in which in the female the moult of puberty is the final moult, after which the animal is sexually mature and enters upon the terminal anecdysis, while in the male the moult of puberty appears to be several moults earlier—the copulatory appendages are present throughout the last few intermoult periods. Such variation between closely related species is hardly conceivable with the type of control of the terminal anecdysis found in *Maia*.

This investigation has served to reveal the existence of two distinct mechanisms whereby the terminal anecdysis, which is characteristic of the end of the life-span of most species of crabs, may be regulated. A mental review of the biology of crabs suggests that the mechanism found in *Maia* may well be characteristic of all the oxyrhynchan Brachyura, while that found in *Carcinus* may be characteristic of the brachyrhynchan Brachyura, or at least of the Portunidae. The mechanism found in *Maia* is reminiscent of the control of the final instar of insects and the organs concerned may be homologous (see Gabe, 1953). The dynamic equilibrium which seems to exist in *Carcinus*, on the other hand, appears to be unrelated to anything found in insects and to be a mechanism developed in the one group of crabs.

It must be emphasized that the hormonal influences which this investigation has shown to be effective in regulating the terminal anecdysis are only the immediate causes of this phenomenon. The mediate causes must be sought elsewhere as must the reason for the existence of the phenomenon. The problem of the terminal anecdysis, the ageing of crabs and the factors which cause natural senescence and death in these creatures is no more than touched, but in the hormonal factors concerned in inhibiting moulting we see an influence which is the last agent in the chain of events which brings about senescence.

SUMMARY

In many if not most species of crabs (but not quite all) there is a limit to growth, when no more moulting or ecdysis is possible in normal circumstances. This condition of permanent anecdysis is known as the terminal anecdysis. In the spider crab *Maia squinado*, the last moult is the moult of puberty, when the animal finally attains sexual maturity, and this moult has different biometrical characteristics from the others. In *Carcinus maenas*, in contrast, the moult of puberty takes place when the animal is quite small and may be succeeded by about ten further moults before the terminal anecdysis begins.

The immediate cause of the cessation of moulting in *Maia squinado* is shown to be the degeneration of the Y-organ, which secretes a moult-promoting hormone. In the absence of this gland and its secretion moulting can no longer continue. In *Carcinus* the Y-organ does not degenerate after the final ecdysis and the cause of the cessation of moulting is to be sought in the excessive production by the X-organ-sinus gland complex of the moult-inhibiting hormone. This effectively prevents moulting from proceeding.

Removal of the X-organ-sinus gland complex in *Carcinus* allows ecdysis to continue, so that giant crabs can be produced in the laboratory by this means, and at the same time the life-span may be increased. The operation has no such effect on *Maia*. In either species injection of Y-organ extracts produces transiently the first signs of an approaching moult, in the form of a heightened blood-calcium level. In *Carcinus* repeated injection led to eventual ecdysis. The presence of the Y-organ is shown to be necessary for removal of the X-organ-sinus gland complex to stimulate moulting in *Carcinus*.

Two separate methods of producing terminal anecdysis exist in crabs, both involving the hormones which normally regulate the moult cycle, but no reason is known for the existence of the phenomenon.

REFERENCES

BLISS, D. E., DURAND, J. B. & WELSH, J. H., 1954. Neurosecretory systems in decapod Crustacea. *Z. Zellforsch.*, Bd. 39, pp. 520–36.

BROWN, F. A. & CUNNINGHAM, O., 1939. Influence of the sinus-gland of crustaceans on normal viability and ecdysis. *Biol. Bull., Woods Hole*, Vol. 77, pp. 104–14.

CARLISLE, D. B., 1953. Moulting hormones in *Leander* (Crustacea Decapoda). *J. mar. biol. Ass. U.K.*, Vol. 32, pp. 289–96.

—— 1954. On the hormonal inhibition of moulting in decapod Crustacea. I. *J. mar. biol. Ass. U.K.*, Vol. 33, pp. 61–3.

—— 1955. On the hormonal control of water balance in *Carcinus*. *Pubbl. Staz. zool. Napoli*, Vol. 27, pp. 227–31.

CARLISLE, D. B. & DOHRN, P. F. R., 1953. Studies on *Lysmata seticaudata* Risso (Crustacea Decapoda). II. Experimental evidence for a growth- and moult-accelerating factor obtainable from eyestalks. *Pubbl. Staz. zool. Napoli*, Vol. 24, pp. 69–83.

CORNUBERT, G., DÉMEUSY, N. & VEILLET, A., 1952. Effets de l'ablation des pédoncules oculaires sur le développement des caractères sexuels externes des Décapodes Brachyoures *Carcinus maenas* Pennant et *Pachygrapsus marmoratus* Fabricius. *C.R. Acad. Sci., Paris*, T. 234, pp. 1405–7.

DÉMEUSY, N., 1953. Comparaison biologique de deux populations de *Carcinus maenas* Pennant: mue de puberté. *C. R. Acad. Sci., Paris*, T. 236, pp. 1203–5.

DÉMEUSY, N. & VEILLET, A., 1953. Sur l'existence de deux populations de *Carcinus maenas* Pennant et sur les caractères morphologiques qui les distinguent. *C.R. Acad. Sci., Paris*, T. 236, pp. 1088–90.

ECHALIER, G., 1954. Recherches expérimentales sur le rôle de 'l'organe Y' dans la mue de *Carcinus moenas* (L.), Crustacé décapode. *C.R. Acad. Sci., Paris*, T. 238, pp. 523–5.

—— 1955. Rôle de l'organe Y dans le déterminisme de la mue de *Carcinides* (*Carcinus*) *moenas* L. (Crustacés décapodes). Expériences d'implantation. *C.R. Acad. Sci., Paris*, T. 240, pp. 1581–3.

FINNEY, D. J., 1952. *Statistical Method in Biological Assay*. London, 661 pp.

GABE, M., 1953. Sur l'existence, chez quelques Crustacés Malacostracés, d'un organe comparable à la glande de la mue des Insectes. *C.R. Acad. Sci., Paris*, T. 237, pp. 1111–13.

HIATT, R. W., 1948. The biology of the lined shore crab, *Pachygrapsus crassipes* Randall. *Pacif. Sci.*, Vol. 2, pp. 135–213.

KNOWLES, F. G. W. & CARLISLE, D. B., 1956. Endocrine control in the Crustacea. *Biol. Rev.*, Vol. 31, pp. 396–473.

PASSANO, L. M., 1953. Neurosecretory control of moulting in crabs by the X organ-sinus gland complex. *Physiol. comp.*, Vol. 3, pp. 155–89.

RICHARDS, A. G., 1951. *The Integument of Arthropods*. Minneapolis, 411 pp.

TEISSIER, G., 1934. Différences sexuelles dans la croissance des appendices de *Maia squinado* (L.). *C. R. Soc. Biol., Paris*, T. 117, pp. 668–71.

—— 1935. Croissance des variants sexuelles chez *Maia squinado* (L.). *Trav. Sta. biol. Roscoff*, Fasc. 13, pp. 93–130.

—— 1937. Allométrie de taille et variabilité. *C.R. Soc. Biol., Paris*, T. 124, pp. 1071–3.

—— 1955*a*. Sur la détermination de l'axe d'un nuage rectiligne de points. *Biometrica*, Vol. 11, pp. 344–56.

—— 1955*b*. Allométrie de taille et variabilité chez *Maia squinado*. *Arch. Zool. exp. gén.*, T. 92, pp. 221–64.

APPENDIX

A number of reports have appeared in the lay press and in fishing journals of the occurrence of heaps of spider crabs (*Maia squinado*) at various points around the coast. One such account is given of large heaps 'about two feet high and three feet in diameter' on the coast of Jersey during the autumn of 1952, by Le Sueur (1953)[1]. He interpreted these heaps, which were observed by fishermen and by the president (an amateur zoologist) of the Société jersiaise, as a means of protection against *Octopus* which will successfully attack crabs larger than themselves. While congregation for mutual defence is certainly a major part of the explanation of such a heap it is by no means all. Some observations which I was able to make during July to September 1956, on a heap of *Maia* at Mothecombe, South Devon (50° 18·3′ N., 3° 57·9′ W.) have enabled me to supplement this explanation.

Like those in Jersey, the heap at Mothecombe was about 1 m in diameter, or rather more, and 0·5 m or more high. It consisted of about 60 *Maia*. When first observed on 12 July the top of the heap was about 1 m below low tide level, and the depth of water at that point was, therefore about 1·5 m. From the tide tables it is apparent that there was never less than 90 cm of water above the top of the heap, at any stage of the tide or phase of the moon, for the tide on 12 July was a spring tide and low water prediction was 0·5 ft (15 cm) below chart datum (the mean level of low water spring tides throughout the year). The crabs in the heap remained almost completely stationary even when sand was thrown in a cloud over them. The animals of the bottom layer of the heap were clinging to an isolated rock about 1·2 by 0·9 m, which was completely surrounded by sand. This rock stood about 20 cm above the surrounding sand and lay about 60 cm from the main reef which ran close by. A moderately heavy growth of *Laminaria*, chiefly *L. saccharina*, was attached to the rock and fronds rose through the heap of crabs, floating about above their backs, providing a partial cover. About twenty of the crabs were full-grown males, in terminal anecdysis; the rest were about equal numbers of smaller, immature males and females, of a size which indicated that they were in the penultimate instar. During the course of the next month the heap was swollen by the addition of about a further 20 crabs, making 80 in all. On 25 July a newly cast shell lay beside the heap and I located a soft male in the centre of the heap. During the next three weeks one or two crabs moulted every day, and always the soft crabs were to be found in the centre of the heap, not on the surface. As time wore on it became apparent that each female as soon as she moulted entered into copulation with one of the old, hard males. So that by mid-August six or eight pairs could be observed in copula at

[1] *Bull. Soc. jersiaise*, Vol. 16, pp. 37–8.

one time. By mid-September the heap was beginning to disperse, but had not completely done so when equinoctial gales rendered the sea too opaque to continue observations.

During the summer of 1956 *Octopus* were too rare around the Devon coasts to be a major predator of *Maia*, and so far as I am aware no other common animal of the English fauna is capable of attacking a hard *Maia*. A soft crab, however, is vulnerable to attack from a great many predators, for not only is its shell soft, but its muscular system is inefficient until the skeleton is hardened. Most brachyrhynchan crabs before and after moulting hide away in crannies amongst the rocks, or buried in the sand. *Maia* from its very shape is incapable of doing either. With most species of crabs, which are carnivorous, the predator which is most likely to attack a soft crab is another crab. *Maia*, however, is not a carnivore and, therefore, will not attack another of the species, even when soft. It is, therefore, feasible for them to congregate together for mutual protection when moulting, an unthinkable happening in a carnivorous species of crab. It seems to me reasonable to suppose that this is in fact the primary purpose of the heaps, to which is inevitably added the secondary purpose of mating. Copulation could equally well take place between pairs of crabs in isolation, as happens in other species of crabs, but if there is communal moulting then it will take place where moulting happens. It seems not improbable that the seasonal moulting of *Maia*, which only takes place in July and August and not at other times of the year, has arisen because of this method of mutual protection that this species has developed.

In support of my contention that *Maia* is not a carnivorous species of crab I will mention observations I have made at Mothecombe on the feeding of this species. In addition to the heap of crabs numerous isolated individuals were observed, mainly animals in terminal anecdysis. Many of these, when observed closely, were found to be feeding by browsing on tufted growths, both animal and plant. Such plants as *Enteromorpha*, *Corallina*, *Heterosiphonia* and *Griffithsia*, and animals such as tufted Bryozoa and hydroids appeared to be the main foods of *Maia*. The crabs were often to be seen browsing directly on the ends of the longer tufts, while the shorter organisms were detached from the substratum or broken by the chelae and thence conveyed to the mouth. It is an undoubted fact that *Maia* are often taken in crab pots, enticed there by the bait, but in the wild it seems unlikely that fresh or decaying flesh forms any major part of the diet. The enlarged chelae of the mature male seem to serve especially in fighting, or rather in warding off other males, while coupling with a female. Any fights which may be observed are slow moving affairs and I have never seen any sign of damage to an animal resulting from this cause.

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SOME QUANTITATIVE ASPECTS OF FEEDING IN SABELLID AND SERPULID FAN WORMS

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INTRODUCTION

It is apparent, from Jørgensen's recent review (1955) of quantitative aspects of filter feeding in invertebrates, that virtually nothing is known of the rate of filtering in polychaete suspension feeders, of which the sabellid and serpulid fan worms are perhaps the most important.

There seems to be little variation in the filter-feeding mechanism in different sabellid and serpulid polychaetes. The most detailed account of the feeding mechanism of these worms is that of *Sabella* published by Nicol (1930) with a résumé of earlier work on sabellids and serpulids. Some information on feeding and the anatomy of the crown in other genera may be found in the works of Soulier, 1891 (*Serpula*, *Hydroides*, *Protula*, *Branchiomma*, *Spirographis* and *Myxicola*), Johansson, 1927 (*Serpula* and *Pomatoceros*) and Thomas, 1940 (*Pomatoceros*). That the crown arises as a paired structure from the prostomium was shown by Wilson (1936) in *Branchiomma*. In adults, the crown may retain a clearly divided form, as in many serpulids such as *Pomatoceros*, or form an almost continuous single cone as in *Myxicola* or *Salmacina*. It is not, however, the purpose of the present paper to describe these variations in morphology, but to present some quantitative data on the filtering process. The species investigated were those which could be obtained in sufficient quantity at Plymouth. The results of experiments on the sabellids, *Myxicola infundibulum* (Rénier) and *Sabella pavonina* Savigny, and on the serpulids, *Pomatoceros triqueter* (L.), *Hydroides norvegica* (Gunnerus), *Spirorbis borealis* Daudin, and *Salmacina dysteri* (Huxley) are presented here.

This work was done during the summer of 1956 at Plymouth, and I am grateful to the Director and Staff of the Laboratory for all the various facilities that made the work possible. I wish to thank especially Dr Dorothy Ballantine for supplying the algal cultures used, Mr R. F. H. Freeman, of Queen Mary College, for kindly lending me his absorptiometer, and Prof. G. P. Wells, F.R.S., for helpful criticism of the typescript of this paper, and discussion of the results.

METHODS

The total volume of water strained, not the actual quantity of particles ingested, has been measured. Suspensions of 'Aquadag', a colloidal graphite suspension in water supplied by Acheson Colloids Ltd., London, was used. The method depends on the assumption that all the particles in the water filtered are removed from suspension, and those remaining are evenly distributed. The removal of particles from a closed system is exponential and as the filtering rate in fan worms was found not to vary with density, the volume and initial density of suspension could be adjusted to any convenient value. Both Jørgensen (1949), working with *Mytilus*, and Ballantine & Morton (1956), working with another lamellibranch, *Lasaea*, have found graphite suspensions to give variable results. Nevertheless, all the worms investigated fed and behaved normally in 'Aquadag' suspensions, and the values for filtering rates obtained here were consistent for each species. The suspensions were made up in the following way. A knife-point of the graphite paste was shaken vigorously in a test-tube with distilled water for 1–2 min, and then poured into a small beaker. After 5 min the resulting suspension was carefully decanted into a bottle, made up to 50 ml. with distilled water and allowed to stand a further 5 min. Such freshly made-up suspensions were used for each experiment and were found to give even suspensions consisting of particles almost entirely 1–2 μ in size, with a few larger particles up to 4–5 μ. In distilled water such dilutions are stable for at least some days. For the experiments, 1–2 ml. of this stock suspension was added to about 250 ml. of sea water. After 4 h all the particles were less than 10 μ and most 1–2 μ across. After 12 h, aggregates up to 50–60 μ had appeared; 18 h afterwards, 100 μ aggregates had formed, and after 24 h the aggregates rapidly sedimented. The optical density decreases during this aggregation process, but not materially during the first 4 h after preparing the sea-water suspension. The density of the suspension and the number of animals used in each experiment was therefore adjusted to give an easily measurable value in 2–3 h. The rate of filtering was calculated from the formula used by Jørgensen (1943) from measurements of the decrease in optical density of the suspension by means of an absorptiometer. Jørgensen (1949) found a change in feeding rate during the experiments using colloidal graphite with *Mytilus*. This may have been due to the suspensions being initially uneven, rather than to more rapid aggregation of small particles. Only by following the shaking and decanting process described here was it found possible to obtain even and stable suspensions. In some test experiments with *Myxicola*, estimation of filtering rate using suspensions in sea water, 12 and 18 h old, did not give values significantly different from those obtained with freshly made suspensions. While much of the graphite was ingested by the worms in all experiments, some was rejected, probably owing to the rather dense sus-

pensions used. As all the particles caught on the pinnules become entangled in mucus, however, the fall in optical density of the suspension gives a measure of the volume strained through the crown. Probably under natural conditions, where the density of small particles in suspension is much less, the majority of suitable particles would be ingested, so that the filtering rate becomes equivalent to the feeding rate.

Animals were acclimatized for some days to the experimental vessels kept under circulation before measurement of filtering rate. Care was taken to see that the animals were filtering and behaving normally before each experiment. Most species, especially *Sabella*, were found to become much less sensitive to shock if the vessels containing the animals were handled repeatedly for a day or so before the experiment. This was done so that the supernatant water could be sampled for measurement of optical density without causing retraction of the worm and interruption of feeding. Momentary, and apparently spontaneous, retractions take place, but the recovery and resumption of filtering is more prompt than after a shock reaction. *Hydroides* was found the most sensitive to experimental conditions. The *Sabella* (in their own tubes), were arranged individually, in small specimen tubes cemented to the bottom of the vessel, so that the crowns could be expanded and twirled without obstruction. *Myxicola* was allowed to secrete new tubes in the bottom of the vessel before being used in an experiment. Vessels with a capacity of 750 ml. were used for these large sabellids, with 1–3 worms in each. For the experiments on *Pomatoceros*, animals were selected with their tubes cemented to pebbles of convenient size, and these scraped clean of other filter-feeding animals before being acclimatized to vessels of 250–300 ml. capacity. *Hydroides*, growing on *Pecten* and *Buccinum* shells, were placed in 100 ml. vessels; pieces of *Salmacina* colony, and *Spirorbis* growing on *Fucus*, were placed in 10 ml. vessels for measurement of their filtering rates.

The worms used in the experiments were dried on filter paper and weighed; the larger species individually. *Spirorbis* and *Salmacina* were weighed in batches. Ten worms were placed on a cover-slip, the crowns dissected off, and surplus moisture drained off with filter paper; the whole process being performed under a binocular microscope. After weighing, the crowns were removed, and the cover-slip weighed again; the difference was taken as the weight of the crowns. Weighing was performed on an aperiodic microchemical balance with a sensitivity of 0·01 mg. In serpulids, the operculum and its stalk were dissected off, and, while included in the total body weight, are excluded from the weight of the crown. The extreme values for the weights of *Salmacina* and *Spirorbis* (Table 1, column 4) represent the means of ten of the largest and ten of the smallest selected from those used in the experiments.

TABLE 1. RESULTS OF EXPERIMENTS ON FILTERING RATES USING COLLOIDAL GRAPHITE SUSPENSIONS

(The figures in parentheses represent the number of animals or experiments from which each calculation is derived)

	1	2	3	4	5	6	7
	Total number of animals used	Total number of experiments	Arithmetic mean of total (fresh) weight (g)	Extreme total (fresh) weights (g)	Temperature range of experiments (° C)	Arithmetic mean filtering rate/animal (l./h)	Standard deviation of mean filtering rate/animal
Myxicola infundibulum	137	45	2·695 (65)	1·410–4·360	17–20	0·28600 (120)	0·06323
Sabella pavonina	150	50	0·187 (45)	0·043–0·236	18–20	0·07300 (150)	0·04266
Pomatoceros triqueter	42	45	0·0185 (42)	0·0117–0·0273	16–17	0·02700 (42)	0·01557
Hydroides norvegica	41	44	0·0123 (41)	0·0081–0·0235	16–17	0·01116 (44)	0·04908
Spirorbis borealis	2500	99	0·00024 (75)	0·000089–0·00052	17–19	0·00023 (2475)	0·00016
Salmacina dysteri	340	50	0·00014 (56)	0·00012–0·00015	17–18	0·00029 (340)	0·00012

	8	9	10	11	12	13
	Arithmetic mean filtering rate/unit total (fresh) weight (l./h/g)	Mean crown weight (g)	Standard deviation of crown weight	Arithmetic mean filtering rate/unit crown weight (l./h/g)	Ratio of total weight to weight of crown	Standard deviation of ratio
Myxicola infundibulum	0·10 (120)	0·323 (24)	0·1118	0·842 (48)	7·99 (21)	0·905
Sabella pavonina	0·39 (150)	0·0195 (47)	0·00486	3·620 (48)	9·48 (48)	5·400
Pomatoceros triqueter	1·40 (42)	0·004 (36)	0·000415	5·400 (42)	4·62 (42)	0·832
Hydroides norvegica	0·90 (41)	0·00256 (41)	0·000806	2·300 (41)	4·81 (41)	0·976
Spirorbis borealis	0·95 (75)	0·00008 (50)	0·000003	5·320 (75)	2·99 (50)	0·279
Salmacina dysteri	2·09 (56)	0·00005 (50)	0·0000038	5·860 (56)	2·80 (50)	0·235

DISCUSSION OF THE RESULTS

The results of all the experiments using colloidal graphite suspensions are summarized in Table 1. The detailed results need not be given here; measurements and calculations of general interest are included in the table, and the consistency of the values obtained may be judged from the standard deviations given, bearing in mind the random selection of the animals and their size range. About fifty experiments were performed on each species.

It is not surprising that the largest species, *Myxicola infundibulum*, should have the highest individual filtering rate (286 ml./h), which is over 1000 times that of *Salmacina* and *Spirorbis* (0·23–0·29 ml./h). On the other hand, the size range within the group is very great; the weight of *Myxicola* is over 25,000 times that of *Salmacina*. Thus the largest species have lower filtering rates per unit of weight than the smallest. This is in accordance with the general dictum that larger animals have lower metabolic rates than smaller ones within a phylogenetic series. The respiration rates of the smaller serpulids have not been measured, but Wells (1952) found the respiration rate of *Myxicola* to be 0·035 ml. O_2/g fresh weight/h, and *Sabella* about 0·05 ml. O_2/g/h, a similar value for *Sabella* having been found also by Ewer & Fox (1940). It is of interest to note also that, as far as is known, the larger species with lower filtering rates have a longer life span than the smaller. *Spirorbis borealis* lives for a few months only, *Pomatoceros* for at least two or three years (Robertson & Pantin, 1938), and a single *Sabella* has been recorded as living in the Plymouth Aquarium for at least ten years (Wilson, 1949).

If the filtering rate is expressed as a function of the crown weight alone, it is found that the rates are not significantly different in any of the species studied. The higher filtering rates per unit total weight in the smaller species are therefore not attained by crowns which for some structural reason are more efficient—that is, capable of straining a larger quantity of water per unit weight and time—than those of larger species, but rather of having relatively larger crowns. In *Spirorbis*, the crown represents a third of the total weight, in *Hydroides* about a fifth, in *Sabella* only a ninth. Conversely, the greater apparent complexity of the crown in *Myxicola* must be related to other factors. While both *Myxicola* and *Sabella* are found at the mouths of estuaries in mud banks, *Sabella* builds a tube projecting well above the surface, so that when the crown is expanded it is held away from the bottom. The slimy tubes of *Myxicola* are completely buried, so that the expanded crown only just projects from the surface. The inter-filamentary membranes probably prevent the crown from becoming clogged, the current bearing the finer suspended particles on which the worms feed entering from the rim. As Wells (1952) noticed, the pinnules are somewhat rotated so that the ventro-lateral cilia have a stronger longitudinal, as opposed to transverse, component with

reference to the axis of the filament. The high standard deviation of the ratio of crown to total body weight (Table 1, column 13) in *Sabella* is due to some of the animals having partially regenerated crowns.

With the larger species it was not found practicable to measure the filtering rate with algal cultures owing to the very large volume which would be required. A few experiments using *Phaeodactylum tricornutum* Bohlin with *Myxicola*, and a number using cultures of *Phaeodactylum*, *Isochrysis galbana* Parke, and *Chromulina pusilla* Butcher, were made with *Spirorbis*. These three species of algae were selected, not only because of their availability at the Plymouth Laboratory, but because of their size differences: *Phaeodactylum* cells are 20–40 μ; *Isochrysis*, 5–6 μ; *Chromulina*, 1–2 μ in length. All the fan worms avoided dense suspensions of *Phaeodactylum* and *Isochrysis*, and even when much diluted the filtering rates were very small compared with those obtained with colloidal graphite. *Myxicola* and *Spirorbis* both removed *Phaeodactylum* from suspension at less than a tenth of the rate recorded with colloidal graphite. The other fan worms would not keep their crowns expanded in dense suspensions of these algae. This is certainly not merely a matter of size. *Myxicola* in 18 h old 'Aquadag' suspensions filtered at the same rate as in freshly made suspensions in which the majority of the particles were less than 2 μ, and which had a greater density than the *Phaeodactylum* suspensions used. *Chromulina* are closely similar to such fresh graphite particles in size, but dense suspensions of this alga produced repeated retractions of the crown in *Spirorbis*. The *Spirorbis* would remain with the crown expanded in more dilute cultures, but the filtering rate was negligible. One can only conclude that these algae can escape from the pinnules which are thus only capable of filtering inert particles of detritus from suspension. This is perhaps one explanation of the abundance of fan worms at the mouths of estuaries where there is much fine detritus in suspension.

During the present work a few experiments were made on *Chaetopterus*, using 'Aquadag' suspensions. Using seventeen different animals in their own tubes in groups of 1–3, allowing 1·5 l. of suspension for each group, and measuring the filtering rate over a 2 h period, it was found that at 16° C the mean filtering rate was 0·3 l./h/animal (standard deviation 0·183 l./h). The mean fresh weight of these animals was 6·0 g, giving a value of 0·05 l./h/g. Jørgensen (1955) calculated the filtering rate as 0·96 l./h from data given by Wells (Wells & Dales, 1951), but this was based on a calculation of the flow through the tube of one worm on a single occasion. The highest value obtained here over the 2 h period was 0·75 l./h, in a vessel containing a single animal. It is known from the work of MacGinitie (1939) and Wells (Wells & Dales, 1951) that *Chaetopterus* may both irrigate the burrow without feeding and feed without secreting a complete mucus bag such as might be expected to retain all the graphite particles in the water strained. It is also known that such activities are discontinuous. The value for the 'filtering rate' given here

may, therefore, bear little relation either to the feeding rate or the total volume of water passed, and is not comparable with the values for fan worms which filtered more or less continuously during the course of an experiment. It is impossible to observe the activity of the animals in their own tubes as these are opaque.

The values obtained for the fan worms (Table 1) are all low compared with known values for other invertebrates. For example, from the information given by Jørgensen (1955), derived from various sources, *Ostrea virginica* filters at the rate of about 0·5 l./h/g, *Mytilus edulis* at 1·6 l./h/g and *Ciona intestinalis* at 0·23 l./h/g, at comparable temperatures. *Ciona* has much the same fresh weight as *Myxicola*, which strains at less than half this rate (0·1 l./h/g). Clearly the fan worms are less efficient than other suspension-feeding invertebrates, both in the volume of water they are capable of straining, and in the kind of particles which can be retained. While some sorting according to size occurs in *Sabella* (Nicol, 1930) and in other fan worms, this is crude compared with sorting mechanisms in some other suspension-feeding invertebrates.

SUMMARY

The rate of filtering has been examined in a series of sabellids and serpulids of widely different size, using suspensions of colloidal graphite and algal cultures. The filtering rates have been expressed as individual rates, as the volume strained per unit fresh weight, and per unit weight of the crown. It may be concluded that the smaller fan worms filter at a relatively higher rate than the larger. This is achieved partly by the relatively larger crown. Free swimming algae escape through the crown; only inert particles down to 1–2 μ are retained, implying that fan worms depend on suspended detritus alone. The filtering rates are briefly compared with those of *Chaetopterus* and some other filter-feeding invertebrates.

REFERENCES

BALLANTINE, D. & MORTON, J. E., 1956. Filtering, feeding, and digestion in the lamellibranch *Lasaea rubra*. *J. mar. biol. Ass. U.K.*, Vol. 35, pp. 241–74.

EWER, R. F. & FOX, H. M., 1940. On the function of chlorocruorin. *Proc. roy. Soc.* B, Vol. 129, pp. 137–53.

JOHANSSON, K. E., 1927. Beiträge zur Kenntnis der Polychaeten-Familien Hermellidae, Sabellidae und Serpulidae. *Zool. Bidr. Uppsala*, Bd. 11, pp. 1–183.

JØRGENSEN, C. B., 1943. On the water transport through the gills of bivalves. *Acta physiol. scand.*, Vol. 5, pp. 297–304.

—— 1949. The rate of feeding by *Mytilus* in different kinds of suspension. *J. mar. biol. Ass. U.K.*, Vol. 28, pp. 333–44.

—— 1955. Quantitative aspects of filter feeding in invertebrates. *Biol. Rev.*, Vol. 30, pp. 391–454.

MACGINITIE, G. E., 1939. The method of feeding of *Chaetopterus*. *Biol. Bull., Woods Hole*, Vol. 77, pp. 115–18.

NICOL, E. A. T., 1930. The feeding mechanism, formation of the tube, and physiology of digestion in *Sabella pavonina*. *Trans. roy. Soc. Edinb.*, Vol. 56, pp. 537–98.

ROBERTSON, J. D. & PANTIN, C. F. A., 1938. Tube formation in *Pomatoceros triqueter* (L.). *Nature, Lond.*, Vol. 141, pp. 648–9.

SOULIER, A., 1891. Études sur quelques points de l'anatomie des Annélides tubicoles de la région de Cette. *Trav. Inst. Zool. Univ. Montpellier*, T. 2, pp. 1–310.

THOMAS, J. G., 1940. *Pomatoceros*, *Sabella* and *Amphitrite*. *L.M.B.C. Memoirs*, No. 33, 88 pp. Liverpool: University Press.

WELLS, G. P., 1952. The respiratory significance of the crown in the polychaete worms *Sabella* and *Myxicola*. *Proc. roy. Soc.* B, Vol. 140, pp. 70–82.

WELLS, G. P. & DALES, R. P., 1951. Spontaneous activity patterns in animal behaviour: the irrigation of the burrow in the polychaetes *Chaetopterus variopedatus* Renier and *Nereis diversicolor* O. F. Müller. *J. mar. biol. Ass. U.K.*, Vol. 29, pp. 661–80.

WILSON, D. P., 1936. The development of the sabellid *Branchiomma vesciculosum*. *Quart. J. micr. Sci.*, Vol. 78, pp. 543–603.

—— 1949. Notes from the Plymouth Aquarium. *J. mar. biol. Ass. U.K.*, Vol. 28, pp. 345–51.

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PHOSPHORUS AND SILICON IN SEA WATER OFF PLYMOUTH DURING 1955

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(Text-figs. 1–4)

Analyses of sea water collected during 1955 at the International Hydrographic Station E1 (lat. 50° N., long. 4° 22′ W.) are here presented in the same form as in previous reports (Armstrong, 1954, 1955). The methods of collection and analysis were substantially unchanged.

Temperature and salinity

The minimum surface temperature recorded was 7·7° C on 15 March, the maximum 18·53° C on 13 July. A quite surprising fall in surface temperature took place between 13 July and 11 August, during a spell of unusually warm weather. Temperatures and salinities on these dates are shown in Table 1. During July and August air temperatures recorded at Mount Batten meteorological station, Plymouth, were as follows:

July	Mean max. 22·0° C	Mean min. 13·1° C	Mean 17·6° C
Aug.	Mean max. 22·4° C	Mean min. 14·7° C	Mean 18·6° C

Winds were mainly light north-east and east.

The vertical distribution of temperature at E1 is shown in Fig. 1. At the beginning of the year temperatures were, as is usual, uniform from top to bottom of the water column, some surface warming becoming just apparent in April. By 9 May there was a slight temperature gradient in the column, but no marked thermocline; one was, however, well established at about 30 m on 13 June, and persisted, with some fluctuation in depth, until September. By 18 October the water column was again isothermal.

The highest salinities were recorded on 15 March (mean 35·27‰). During summer the values were low (34·89‰ on 11 August), rising in the autumn, though November (35·04‰) was significantly lower than October (35·17‰) or December (35·13‰). The change in salinity below 25 m between 13 July and 11 August, shown in Table 1, is probably significant of a change in water mass.

Phosphate

The winter maximum was notably high, the integral mean values of 0·59 and 0·58 μg atom P/l. for February and March being the highest recorded since 1929. In an attempt to determine the extent and, if possible, the source

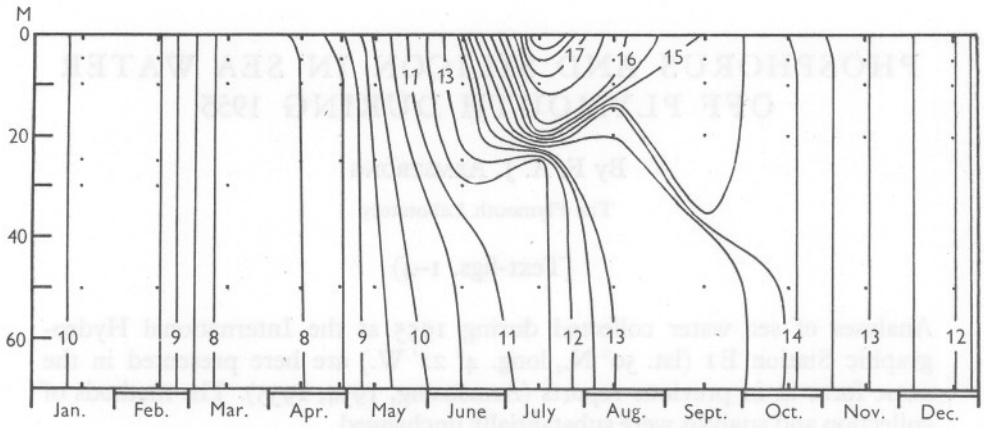

Fig. 1. Vertical temperature distribution at International Hydrographic Station E1, 1955. Contour lines at 0·5° C intervals.

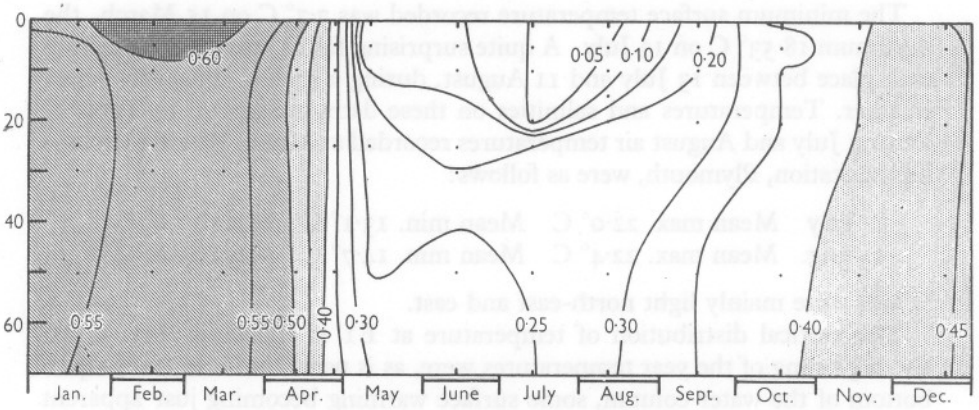

Fig. 2. Vertical distribution of phosphate at International Hydrographic Station E1, 1955. Contour lines at 0·05 μg atom P/l. intervals.

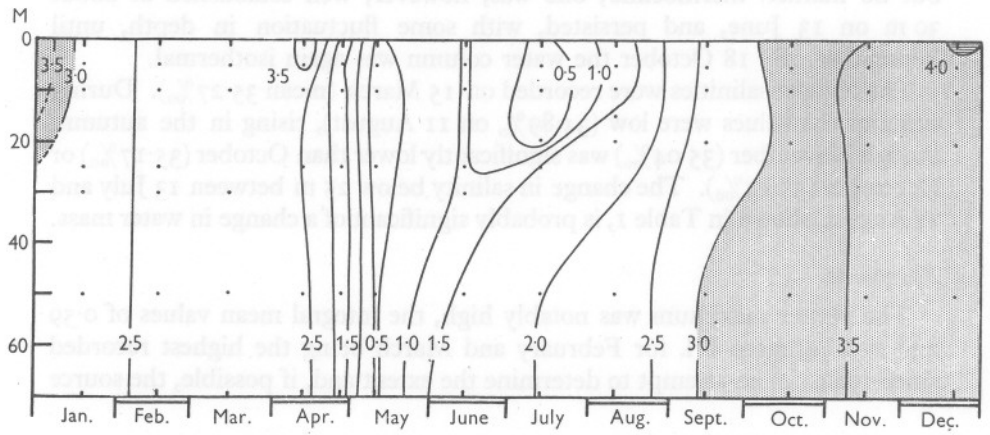

Fig. 3. Vertical distribution of silicate at International Hydrographic Station E1, 1955. Contour lines at 0·5 μg atom Si/l. intervals

TABLE 1. TEMPERATURES AND SALINITIES AT INTERNATIONAL HYDROGRAPHIC STATION E1, 13 JULY AND 13 AUGUST 1955

	Temperature (° C)		Salinity (‰)	
Depth (m)	13 July	11 Aug.	13 July	11 Aug.
0	18·53	16·20	34·97	34·98
5	17·55	16·15	34·92	34·91
10	16·77	16·04	34·93	34·90
15	—	13·75	—	34·90
20	15·27	13·49	34·93	34·91
25	11·36	—	34·93	—
50	11·30	13·07	34·96	34·85
72	11·22	13·07	34·93	34·89

TABLE 2. INTEGRAL MEAN CONCENTRATIONS IN WATER COLUMN AT STATION E1

Date	Phosphate-P (μg atom P/l.)	'Total-P' (μg atom P/l.)	Silicate (μg atom Si/l.)
18. i. 55	0·54	0·61	2·12
16. ii. 55	0·59	0·70	2·82
15. iii. 55	0·58	0·71	2·65
12. iv. 55	0·49	0·62	2·72
27. iv. 55	0·36	—	1·77
9. v. 55	0·22	0·49	0·39
13. vi. 55	0·22	0·31	1·33
13. vii. 55	0·17	0·35	1·40
11. viii. 55	0·19	0·39	1·87
15. ix. 55	0·25	0·44	2·94
18. x. 55	0·32	0·47	3·11
17. xi. 55	0·36	0·54	3·68
21. xii. 55	0·38	0·54	3·26

TABLE 3. POSITIONS OF STATIONS AND PHOSPHATE CONCENTRATIONS AT 10 m DEPTH, WESTERN APPROACHES, 14–21 MARCH 1955

Date	Station no.	N. Lat.	W. Long	Phosphate at 10 m (μg atom P/l.)
14. iii. 55	1 (E2)	49° 27′	4° 42′	0·58
	2 (E3)	48° 34′	5° 13′	0·15
15. iii. 55	3	47° 46′	6° 05′	0·58
	4	47° 20′	6° 28′	0·56
16. iii. 55	5	46° 30′	8° 00′	0·56
17. iii. 55	6	47° 14′	7° 55′	0·55
	7	47° 50′	7° 40′	0·63
18. iii. 55	8	48° 18′	7° 30′	0·60
	9	49° 00′	9° 00′	0·60
	10	49° 47′	10° 15′	0·63
19. iii. 55	11	50° 35′	11° 28′	0·72
	12	50° 34′	11° 10′	0·76
	12A	50° 32′	10° 56′	0·72
	12B	50° 32′	10° 50′	0·75
	13	50° 19′	10° 20′	0·64
20. iii. 55	14	50° 07′	8° 43′	0·63
	15	49° 50′	8° 00′	0·64
	16	49° 50′	7° 15′	0·56
	17	49° 50′	6° 00′	0·54
21. iii. 55	18	49° 53′	5° 12′	0·58

of this phosphate-rich water, Dr L. H. N. Cooper in R.V. *Sarsia* made a survey of the area at the mouth of the English Channel, working twenty stations as shown in Fig. 4 between 14 and 21 March 1955. Table 3 gives the positions of the stations and phosphate concentrations found at 10 m, and areas characterized by differing phosphate concentrations are indicated by shading in the figure.

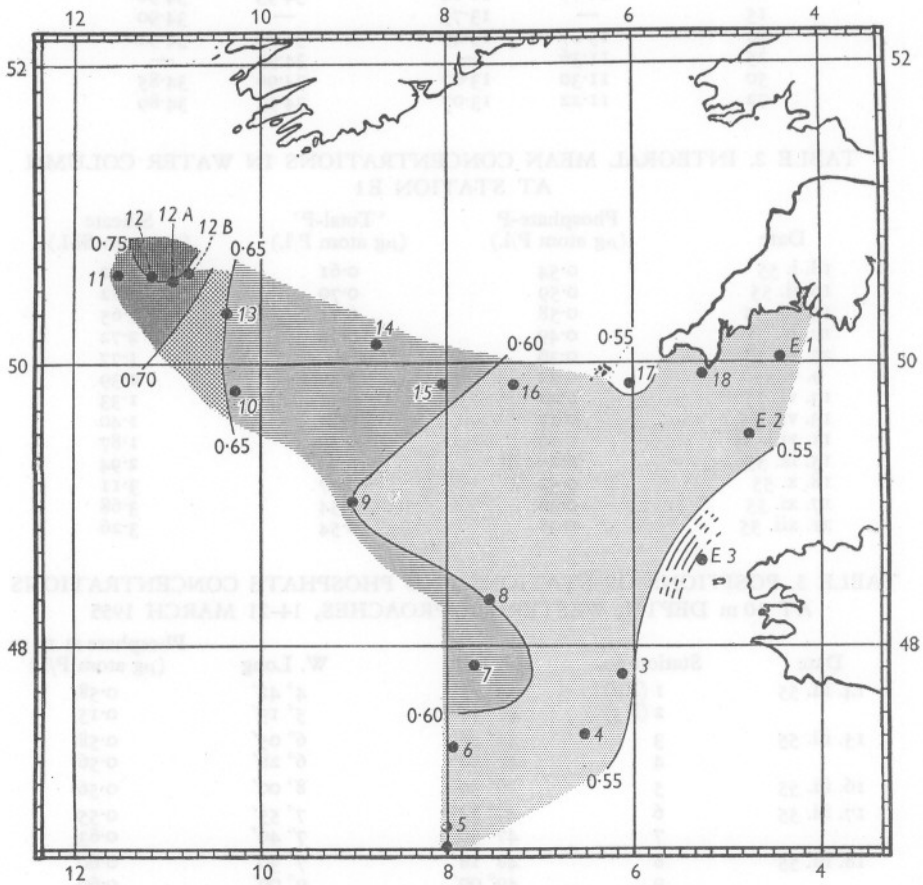

Fig. 4. Distribution of phosphate at 10 m depth in part of Western Approaches, 14–21 March 1955. Contour lines at 0·05 μg atom P/l. intervals.

Although notably high phosphate concentrations were found in surface waters over the continental slope southwest of Ireland there is no evidence that water from there has ever entered the English Channel, and no satisfactory source for the high phosphate water was found within the area surveyed. Low values of around 0·05 μg atom P/l. were found in the upper 10 m layer in July and August.

The vertical distribution of phosphate is shown in Fig. 2, and it will be seen that the water column was almost homogeneous until 9 May, by which date plant growth had removed a considerable amount of phosphate from the upper 25 m. Low concentrations of phosphate in the upper layers persisted until the breakdown of the thermocline.

Silicate

The vertical distribution of silicate is shown in Fig. 3 It is seen that the water column was homogeneous up to and including 9 May. On that date there was little variation in silicate concentration with depth, in contrast to the marked layering of phosphate. Silicate was low throughout the water column. During the summer, silicate was less in the layer above the thermocline than in the deeper water, but no very low concentrations were recorded, the smallest being around 0·2 μg atom Si/l. in the upper 20 m on 13 July.

Silicate at these depths had increased to about 1·5 μg atom Si/l. on 11 August, although the intervening period had been notable for bright warm weather (as recorded above) such as would be expected to favour growth of diatoms and consumption of silicate. It has already been observed that in the deeper water at least, a significant change in salinity occurred between these dates.

By 18 October silicate concentration was uniform throughout the water column, and was higher than at the beginning of the year. Mean values for December are lower than for November, which is unexpected.

Integral mean concentrations

The computed figures are given in Table 2. The decreases in the spring representing consumption of nutrients by the phytoplankton were: phosphate 0·42 μg atom P/l., 'total phosphorus' 0·40 μg atom P/l., silicate 2·43 μg atom Si/l.

SUMMARY

Temperatures and salinity, phosphate, total phosphorus and silicate analyses of water from the International Hydrographic Station E1 during 1955 are discussed. The seasonal variation is shown, and it appears that consumption of nutrients by plants in the spring was: phosphate 0·42 μg atom P/l., 'total phosphorus' 0·40 μg atom P/l., silicate 2·43 μg atom Si/l., these being means for the whole water column. Some irregularities are pointed out; they are probably attributable to changes in the water mass.

REFERENCES

ARMSTRONG, F. A. J. 1954. Phosphorus and silicon in sea water off Plymouth during the years 1950 to 1953. *J. mar. biol. Ass. U.K.*, Vol. 33, pp. 381–92.

—— 1955. Phosphorus and silicon in sea water off Plymouth during 1954. *J. mar. biol. Ass. U.K.*, Vol. 34, pp. 223–8.

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ON THE BEHAVIOUR OF BARNACLES

III. FURTHER OBSERVATIONS ON THE INFLUENCE OF TEMPERATURE AND AGE ON CIRRAL ACTIVITY

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(Text-figs. 1–3)

The results of investigations into the relation between temperature and cirral activity in certain barnacles were described in Part I of this series (Southward, 1955*a*). It was shown that in each of five species commonly found on the shore in Britain, the range of temperature over which the cirri were active and the temperature at which this activity was greatest could be related to the geographical distribution of the species and to the temperatures experienced in the normal habitat. In a further paper it was shown that in one of these species (*Chthamalus stellatus*) the frequency of beating was apparently lower in older individuals (Southward, 1955*b*). These results have been confirmed and extended by experiments made on a further five species of barnacles from a wider range of habitats (Table 1).

TABLE 1. SPECIES OF BARNACLES INVESTIGATED

Species	Where collected	Tide-level or depth	Speed of water current in apparatus
Lepas anatifera L.	Growing on cork lifebelt, found off Plymouth	—	Nil
Balanus improvisus Darwin	Upper reaches of Tamar estuary, near Weir Quay	L.W.N.	0·5 cm/sec, with occasional bursts of 5–10 cm/sec
B. amphitrite Darwin var. *denticulata* Broch	On piles near outflow of warm water from power station, Plym estuary	L.W.N.	As *B. improvisus*
B. balanus L.	On shells of *Modiolus* from Anglesey	*ca.* 12 fathoms	As *B. improvisus*
Hexelasma hirsutum Hoek	Continental slope in vicinity of 48° 33′ N., 10° 4′ W.	570–770 fathoms	4–16 cm/sec

All temperatures are quoted in degrees Centigrade. Climatic details have been taken from the following references: Admiralty, 1946; Air Ministry, 1949; International Council, 1933.

I am indebted to Dr D. J. Crisp, who supplied living *Balanus balanus*, for advice in this work and to Mr F. G. C. Ryder for construction of apparatus. The experiments were carried out during the tenure of a D.S.I.R. Senior Research Award.

EXPERIMENTAL CONDITIONS

The experimental conditions differed slightly from those of the earlier work. The animals were observed in a long trough of Perspex, divided by a central partition. The trough was filled with filtered offshore water, which was replenished from time to time. All water movement was set up by means of an enclosed paddle wheel, also of Perspex, placed at one end of the trough and driven by belt and pulleys from an electric motor.

The temperature of the water in the trough was raised or lowered by immersing in it small vessels containing hot water or ice. During the duration of each experiment the temperature was easily controlled to within 0·5°, the temperature limits adopted in the previous work. However, for temperatures below 4° some difficulty was experienced because of warming by the air during the long period of observation necessitated by the slow frequency of beating at low temperatures, and a smaller number of barnacles was placed in a finger bowl standing in ice water or freezing mixture. Under these circumstances water movement was set up by a jet of compressed air.

In the trough, the water currents could be controlled by means of a resistance in series with the electric motor. The current speed was measured approximately by timing the movement of small particles in the water. As previously, the frequency of beating was assessed by noting the time taken for ten complete openings and closings of the valves accompanied by partial or complete protrusion of the cirri. The values so obtained were converted to the number of beats per 10 sec. Approximately ten specimens were examined at each temperature. The temperature intervals were about 4° or 5° and the rate of heating or cooling was adjusted to 4°/h.

Except for *Balanus amphitrite* (see below) all specimens were observed while still attached to small pieces of the substratum.

Only *B. improvisus* and *B. amphitrite* were examined within 24 h of collection; *B. balanus* was sent by post and nearly 7 days elapsed between collection and examination; *Lepas* was examined after an unknown period out of water followed by nearly 24 h in the aquarium water at Plymouth; *Hexelasma* was brought back on R.V. *Sarsia* under running sea water and examined within 7 days of being dredged up. Chances of acclimatization to temperatures other than those normally experienced must therefore be allowed for in interpreting the results.

RESULTS

Lepas anatifera (Fig. 1; Table 3)

All specimens of *Lepas* at times showed a tendency to hold the cirri extended (extension response—see Part I), even in still water. The rate of water

movement had no observable effect on the proportion of individuals beating, and the actual measurements were made without a current. It was necessary to observe a large number of specimens and choose those that were showing rhythmic beating.

Some beating was noted below 1·5°, although there was almost instantaneous and complete chill coma on lowering the temperature to 0·5°. The mean frequency of beating increased almost linearly between 3·8° and 19·8°, from 0·55 to 2·85 beats per 10 sec. Above 20° the frequency slowed down, and all beating ceased at 33°. More than half the specimens succumbed to heat coma at 33·5°.

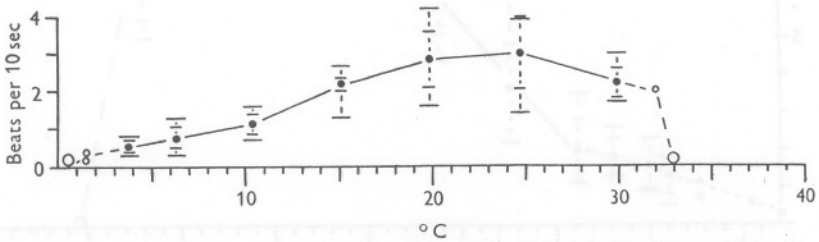

Fig. 1. *Lepas anatifera*: frequency and range of beating of the cirri. The larger circles denote absence of beating, and the smaller circles single observations; the dots indicate the mean frequency at each temperature, while the large and small cross-lines mark, respectively, the range and standard deviation of the samples on either side of the mean.

Both the optimum cirral activity and the position of maximum cirral frequency shown by these specimens occur at relatively low temperatures for a species which has been recorded from all the oceans (see Darwin, 1854). There is, therefore, a strong possibility that the species contains physiological varieties adapted to different temperature regimes. Certainly, these specimens would be ill-suited to temperature conditions prevailing in the Atlantic north of Nova Scotia and North Norway, or south of Cape Cod and Gibraltar.

Balanus improvisus (Fig. 2A; Table 4)

Specimens of *B. improvisus* showed cirral activity over a wide range of temperatures. Between 8·8° and 20° the mean frequency increased uniformly from 2 to over 8 beats/10 sec, and a maximum was reached at 30°. Above 30° the frequency of beating declined sharply, and beating was not detected above 35·5°.

The behaviour at low temperatures was most interesting. There was a change in the temperature coefficient at about 8–9°, and the mean frequency of beating declined only slowly as the temperature was lowered. Most specimens continued to beat rhythmically down to 4°, and one or two continued to do so down to −2°, the lowest temperature tested. Even after remaining at this low temperature for 10 min, less than half the specimens (4 out of 10) showed chill coma.

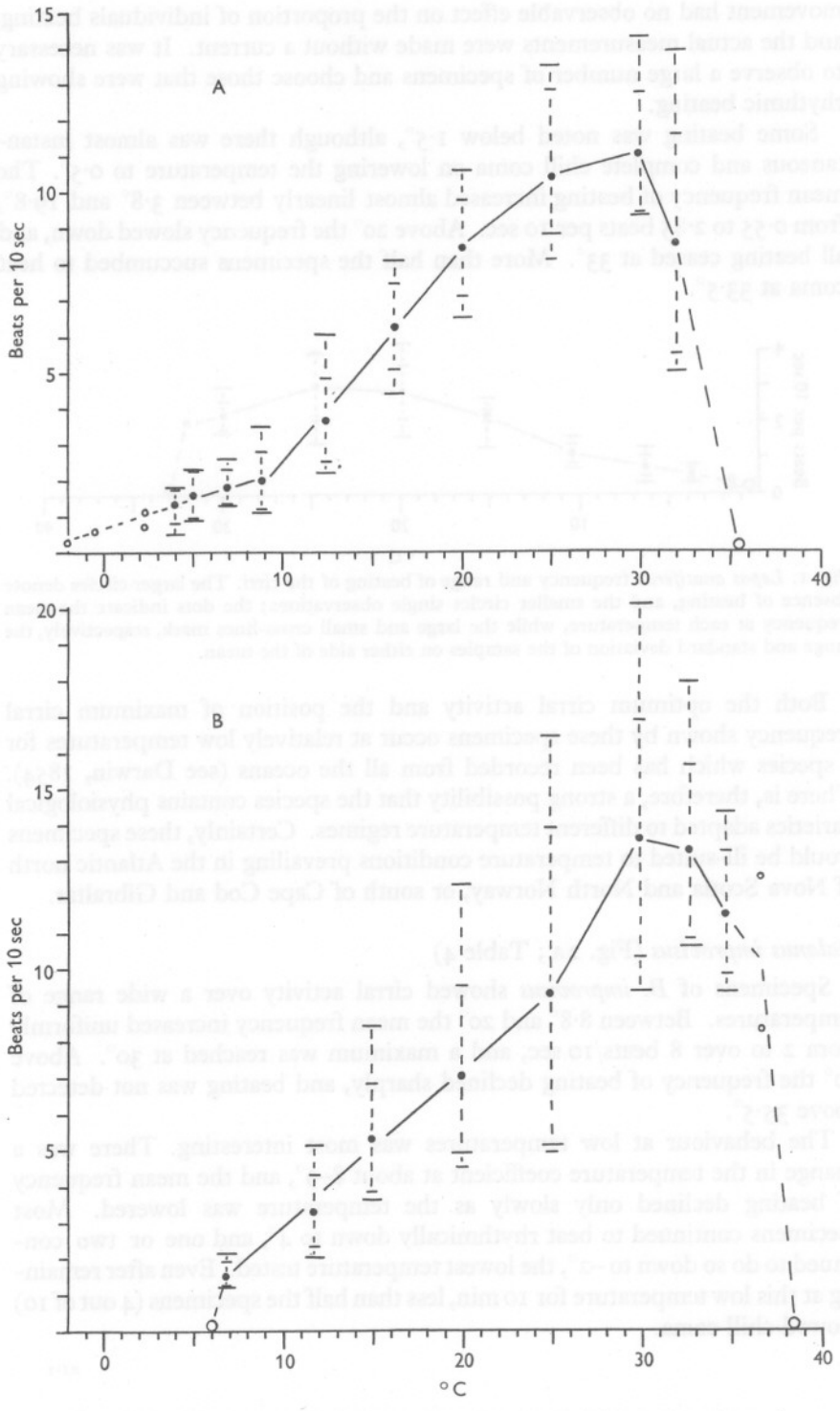

Fig. 2. The frequency and range of beating of the cirri of (A) *Balanus improvisus*, (B) *B. amphitrite*. For explanation of symbols refer to Fig. 1.

The wide range of optimum temperature in this species is in accordance with its wide geographical range; it has been recorded from Nova Scotia and the Baltic, and extends through the tropics to southern South America (Darwin, 1854; Pilsbry, 1916; Segerstråle, 1953). Nevertheless, the position of the maximum cirral frequency is more characteristic of a tropical species.

Balanus amphitrite (Fig. 2B; Table 5)

Only twelve specimens of *B. amphitrite* were collected with their calcareous bases intact; they were mounted on glass slides with SIRA wax before being placed in the trough. A few specimens showed the fast type of beat at some temperatures; they have not been included in the results. At most temperatures it was possible to measure the cirral frequency of nine specimens. Below 10° only five individuals were active, and beating was not observed below 6°. Between 6·8 and 24·9° the mean frequency of beating increased linearly from 1·5 to 9·3 beats/10 sec. The maximum frequency was reached at 29·9°, with a mean of 13·5 beats/10 sec. Beating slowed down slightly between 30° and 36°, and ceased completely at 38·4°.

The high upper limit to the temperature range, and the relative ease with which beating was carried on above 30°, agree well with the predominantly tropical and warm temperate distribution of the species. Its normal northern limit appears to be northern Spain (Fischer-Piette, 1955), and beyond this it is found only in docks, harbours or estuaries that are artificially warmed (see Bishop, 1950; Crisp & Molesworth, 1951). At Plymouth after a warm summer I have found young specimens on the shore of the Sound, as well as in the Plym estuary, but the adults survive only in the vicinity of the warm water outlet from the power station. The absence of beating below 6°, and the difficulty of obtaining beating between this temperature and 10° suggest that little, if any, acclimatization has taken place in the local population.

Balanus balanus (Fig. 3; Table 6)

The specimens of *B. balanus* sent by Dr Crisp consisted of four groups. The first three groups consisted of freshly collected specimens showing respectively one, two and three growth rings; the fourth group of specimens with two or three growth rings had been kept in the laboratory at Menai Bridge for 4 months without food. *B. balanus* is the only British barnacle that has been found to show clear growth marks, and the groups with one, two and three rings correspond to individuals in their second, third and fourth years since settlement (Crisp, 1954).

The behaviour of each group was noted separately, but as each group contained less than ten specimens and only the two- and three-ring groups were active at all temperatures, the results from these groups have been combined to show the effect of temperature on cirral activity. For this purpose specimens showing the fast type of beat have been ignored. One specimen

showed signs of beating at –2°, but none was active below this temperature. Above zero the frequency of beating increased fairly linearly, from between 1·1 and 1·3 beats/10 sec at 1·9° to a maximum of 4·8 beats at 20·2°. Above 20° the frequency of beating declined, at first slowly up to 26°, then more rapidly; beating ceased at 30°.

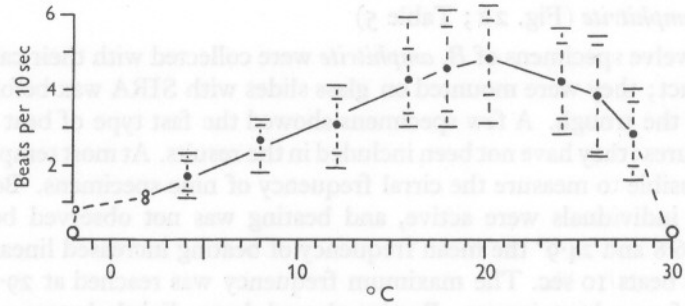

Fig. 3. *Balanus balanus*: frequency and range of beating of the cirri. For explanation of symbols refer to Fig. 1.

This species is predominantly of Arctic and Boreal distribution (Darwin, 1854; Weltner, 1900), and it seems doubtful whether it ever occurs south of the Bristol Channel and North Sea (Crisp & Southward, 1957). Thus in its normal habitat it is hardly likely to be subjected to sea temperatures above 17°; even when it occurs on the shore it is found in places well protected from the sun and the air, such as beneath *Ascophyllum* (Crisp, 1954) or in crevices and under stones (personal records). The species, therefore, is not operating at the extreme upper limit of its optimum range, unlike the other northern form *B. balanoides* (Southward, 1955*a*).

The effect of age on cirral activity in this species is shown in Table 2. The range and the mean of the cirral frequency is given for each group at four temperatures; at other temperatures one or more of the groups failed to beat the cirri. It can be seen that the younger barnacles had the highest frequency of cirral beat, and that the cirri beat progressively more slowly in the older groups. The lowest frequency of all was found in the starved specimens; except at 4° the differences between these specimens and all the others were greater than between any two age-groups of the fresh specimens.

The differences between the means are not very great for such small samples and statistically they are hardly significant. For example, in tests by the *t* distribution that the one-ring and three-ring groups belonged to the same statistical population, the value of *P* varied from 0·05 to 0·1.

However, the evidence tends to support the earlier observation that ageing in barnacles is accompanied by a slowing down of the cirral activity. It seems that starvation has a similar effect. Probably there is a depression of the metabolic rate in both old and in starved individuals.

These differences relate to the ordinary rhythmic beat. A fast type of beat was shown by a few individuals at some temperatures, but only among the youngest specimens and in the starved group. These are the groups in which the fast type of beat would be expected if it was largely a feeding reaction (cf. Southward, 1955*b*).

Further differences between the four groups of *B. balanus* were noticed at the upper limit of temperature for cirral activity. All starved specimens ceased beating at 27·9°, all three-ring and two-ring specimens at 29° and 30° respectively, while more than half the youngest group continued active to 30·5°. These differences are of the same order as those of cirral frequency.

TABLE 2. CIRRAL BEHAVIOUR IN THE DIFFERENT AGE-GROUPS OF *BALANUS BALANUS*

Temperature (° C)	Age-group	No. tested	No. showing ordinary beat	Frequency of ordinary beat			No. showing fast beat	No. not beating
				Mean	Range	S.D.		
4·0	1 ring	7	3	2·333	2·0–2·8	±0·417	0	4
	2 ring	7	4	1·950	1·6–2·3	±0·310	0	3
	3 ring	5	3	1·366	1·1–1·7	±0·307	0	2
	Starved	5	2	0·950	0·7–1·2	±0·353	1	2
8·0	1 ring	7	6	2·883	2·4–3·3	±0·338	0	1
	2 ring	7	6	2·816	2·5–3·2	±0·260	0	1
	3 ring	5	4	2·40	1·8–2·8	±0·454	0	1
	Starved	5	5	1·140	0·9–1·5	±0·251	0	0
15·9	1 ring	7	3	4·833	4·1–5·2	±0·637	0	4
	2 ring	7	6	4·583	3·4–5·9	±0·855	0	1
	3 ring	5	5	3·760	3·0–4·8	±0·695	0	0
	Starved	5	4	2·775	1·6–3·4	±0·801	1	0
20·2	1 ring	7	3	5·433	4·8–6·2	±0·711	3	1
	2 ring	7	5	4·920	3·9–5·9	±0·837	0	2
	3 ring	5	5	4·70	3·1–6·2	±1·332	0	0
	Starved	5	4	3·075	2·3–3·7	±0·684	1	0

Hexelasma hirsutum

So far, only a preliminary investigation has been made into the behaviour of *Hexelasma*. Of twenty-four specimens tested in the trough none could be induced to show rhythmic beating of the cirri under any variation of temperature, water movement or illumination. With a water current from 4 to 16 cm/sec an extension response was given by up to eight specimens simultaneously at temperatures between 2·7° and 8°. Below 2·7° and down to −2° one or two specimens showed very slight movements of the valves and reacted to touch by closing. Above 8° a few specimens showed what has been called the pumping type of beat (Southward & Crisp, 1957). The cirri were not protruded, but minor movements of the prosoma and valves caused a current of water to enter the mantle cavity near the mouth; this water passed through the mantle cavity and was ejected in puffs behind the prosoma (see Crisp & Southward, 1956). The frequency of these exhalant puffs increased from 0·05 and 0·06/10 sec at 8·5° to 0·10 and 0·18/10 sec at 19°. The temperature was not taken

higher than 19° to avoid risk of damage to the specimens, but even at this temperature there were signs of jerky movements similar to those that precede heat coma in other barnacles.

Hexelasma hirsutum has been recorded elsewhere from the Faroe-Shetland Ridge (59° 40′ N., 7° 21′ W.) at 516 fathoms (Hoek, 1883) and from the Azores (38° 31′ N., 26° 49′ W.) at 465 fathoms (Gruvel, 1920). The bottom-water temperatures at all localities at which the species has been found, or at nearby stations of similar depth, vary from 7° to 9° (Hoek, 1883; Rouch, 1948; Cooper, 1952) and the annual variation is probably less than 1° (Dr L. H. N. Cooper, personal communications). As far as cirral extension is concerned, the specimens of *Hexelasma* examined were thus living very close to the upper limit of their optimum range. Probably the species can live in colder and deeper water when other conditions allow.

The absence of rhythmic beating within the optimum range suggests that respiratory needs are satisfied by the passage of water over the branchiae caused by the twisting movements of the extended cirri, by the occasional withdrawing movements of the cirri, or by external water currents. The pumping beat at higher temperatures suggests the onset of respiratory difficulties; the low frequency of the pumping movements may indicate lack of co-ordination for rhythmic activity.

DISCUSSION

In three of the five species dealt with in this Part, namely *Balanus improvisus*, *B. amphitrite* and *B. balanus* the range of cirral activity is closely related to the geographical distribution.

The behaviour of *B. amphitrite*, and, in the upper part of its range, *B. improvisus* is similar to that of one of the two southern species discussed in Part I, *B. perforatus*. These three species belong to the same subgroup, or closely related subgroups, of the genus *Balanus* (Darwin, 1854; Pilsbry, 1916); the resemblance in behaviour is not therefore unexpected. *B. improvisus* is the only species of the group to occur in genuinely cold climates, and the form of its behaviour suggests that it is a tropical species that has been able to extend the lower end of its range of optimum temperature. This adaptation may be connected with the remarkable euryhalinity shown by the species (Darwin, 1854; Pilsbry, 1916). It seems probable that a more flexible metabolism is needed to cope with the osmoregulatory requirements of a brackish water habitat, and this may have facilitated tolerance of a wider range of temperatures.

The range of optimum temperature in *B. balanus*, and the temperature at which maximum cirral frequency was shown, differ considerably from those of the related species, *B. crenatus*, investigated previously (Part I). There is, in fact, more resemblance between *B. balanus* and *B. balanoides*. All three species are of generally northern distribution, but their exact southern limits

vary. As stated, *B. balanus* does not apparently occur as far south as the English Channel, where *B. crenatus* has its southern limit; *B. balanoides* is present in the Bay of Biscay (Southward & Crisp, 1956) and in a limited area of north-west Spain (Fischer–Piette & Prenant 1956). The order of increasing tolerance of high temperatures is *B. crenatus–B. balanus–B. balanoides*, while the position of maximum cirral frequency increases *B. balanoides–B. balanus–B. crenatus*. There is thus no exact relation between the extreme southern limits of the species and their temperature tolerances for cirral activity. No doubt other environmental factors besides temperature affect the limits of the species.

The temperature relations of *Lepas* and *Hexelasma* have already been discussed (pp. 325 and 330). The behaviour of the latter species reflects the relatively uniform temperatures experienced in deep water compared with the intertidal or shallow water habitats favoured by the species of *Balanus*.

SUMMARY

The range of temperature over which the cirri were active, and the frequency of beating of the cirri at different temperatures were measured in a further five species of barnacles from a variety of habitats. In three of the species the temperature range and frequency of cirral beat were related to the geographical distribution of the species. The tropical and warm temperate species *Balanus amphitrite* was active at higher temperatures, and showed a greater frequency of beating than the northern species *B. balanus*; conversely, the latter was active to much lower temperatures than *B. amphitrite*. The species with the widest geographical range, *B. improvisus*, showed cirral activity over the widest range of temperatures, although its behaviour at high temperatures was similar to that of the related species *B. amphitrite*. It is suggested that *B. improvisus* is a tropical species that has adapted itself to colder climates; its tolerance of a wide range of temperatures may be associated with its tolerance of low salinities.

The stalked barnacle *Lepas anatifera* showed too restricted a temperature range for its supposed world-wide distribution, and it is suggested that the species may contain physiological races adapted to different climates. The extremely restricted range of temperatures over which the cirri of the deep-sea barnacle *Hexelasma hirsutum* were active can be correlated with the almost uniform temperature conditions at great depths.

In *B. balanus* age-groups can be clearly distinguished by growth rings on the shell, and the cirral frequency was found to be slower in the older specimens. Even slower cirral beating was found in some starved specimens.

REFERENCES

ADMIRALTY, LONDON, 1946. *World Climatic Charts*, Sheets I and II.

AIR MINISTRY, LONDON, 1949. *Monthly Sea Surface Temperatures of North Atlantic Ocean.*

BISHOP, M. W. H., 1950. Distribution of *Balanus amphitrite* Darwin var. *denticulata* Broch. *Nature, Lond.*, Vol. 165, p. 409.

COOPER, L. H. N., 1952. The physical and chemical oceanography of the waters bathing the continental slope of the Celtic Sea. *J. mar. biol. Ass. U.K.*, Vol. 30, pp. 465–510.

CRISP, D. J., 1954. The breeding of *Balanus porcatus* (Da Costa) in the Irish Sea. *J. mar. biol. Ass. U.K.*, Vol. 33, pp. 473–96.

CRISP, D. J. & MOLESWORTH, A. H. N., 1951. Habitat of *Balanus amphitrite* var. *denticulata* in Britain. *Nature, Lond.*, Vol. 167, p. 489.

CRISP, D. J. & SOUTHWARD, A. J., 1956. Demonstration of small scale water currents by means of milk. *Nature, Lond.*, Vol. 178, p. 1076.

—— —— 1957. The distribution of some common intertidal organisms along the coasts of the English Channel. (In preparation.)

DARWIN, C., 1854. *A Monograph on the Sub-Class Cirripedia: Balanidae, Verrucidae, etc.* 684 pp. London: Ray Soc.

FISCHER-PIETTE, E., 1955. Répartition, le long des côtes septentrionales de l'Espagne, des principales espèces peuplant les rochers intercotideaux. *Ann. Inst. océanogr. Monaco*, T. 31, pp. 37–124.

FISCHER-PIETTE, E. & PRENANT, M., 1956. Distribution des cirripèdes intercotideaux d'Espagne septentrionale. *Bull. Centre Études et Recherches scientifiques Biarritz.* T. 1, pp. 7–19.

GRUVEL, A., 1920. Cirrhipèdes. *Result. Camp. sci. Monaco*, Fasc. 53, 88 pp.

HOEK, P. P. C., 1883. Cirripedia. *Challenger Reports, zool.*, Vol. 8, Pt. 25, 169 pp.

INTERNATIONAL COUNCIL, 1933. *Atlas de température et salinité de l'eau de surface de la Mer du Nord et de la Manche.* Copenhagen.

PILSBRY, H. A., 1916. The sessile barnacles (Cirripedia) contained in the collections of the U.S. National Museum. *Bull. U.S. nat. Mus.*, Vol. 93, pp. 1–366.

ROUCH, J., 1948. Stations hydrologiques. *Result. Camp. sci. Monaco*, Fasc. 108, 26 pp.

SEGERSTRÅLE, S., 1953. Further notes on the increase in salinity of the inner Baltic and its influence on the fauna. *Comment. biol., Helsingf.*, Vol. 13, No. 15, pp. 1–7.

SOUTHWARD, A. J., 1955*a*. On the behaviour of barnacles. I. The relation of cirral and other activities to temperature. *J. mar. biol. Ass. U.K.*, Vol. 34, pp. 403–22.

—— 1955*b*. On the behaviour of barnacles. II. The influence of tide-level and habitat on cirral activity. *J. mar. biol. Ass. U.K.*, Vol. 34, pp. 423–33.

SOUTHWARD, A. J. & CRISP, D. J., 1956. Fluctuations in the distribution and abundance of intertidal barnacles. *J. mar. biol. Ass. U.K.*, Vol. 35, pp. 211–29.

—— —— 1957. On the behaviour of barnacles. IV. Types of cirral activity and their relation to feeding and respiration. (In preparation.)

WELTNER, W., 1900. Die Cirripedien der Arktis. *Fauna Arctica*, Bd. I, pp. 287–312.

APPENDIX

TABLE 3. FREQUENCY OF BEATING OF THE CIRRI OF *LEPAS ANATIFERA*

From off Plymouth, 1. x. 56; examined 2. x. 56

Temperature (° C)	Frequency of beating, as beats per 10 sec		
	Mean	Range	S.D.
0·5	—	Nil	—
1·5	2 specimens only	0·2, 0·4	—
3·8	0·557	0·3–0·8	±0·161
6·3	0·770	0·3–1·3	±0·292
10·4	1·130	0·7–1·6	±0·283
15·1	2·20	1·3–2·7	±0·125
19·8	2·850	1·6–4·2	±0·760
24·7	2·50	1·4–2·9	±0·454
29·7	2·185	1·7–3·0	±0·422
32·0	1 only	2·0	—
33·0	—	Nil	—

TABLE 4. FREQUENCY OF BEATING OF THE CIRRI OF *BALANUS IMPROVISUS*

From the Tamar estuary, 13. ii. 56 and 15. ii. 56

Temperature (° C)	Frequency of beating, as beats per 10 sec		
	Mean	Range	S.D.
−2·0	1 only	0·3	—
−0·5	1 only	0·6	—
2·3	2 only	0·7, 1·1	—
4·0	1·344	0·5–1·8	±0·470
5·0	1·595	0·9–2·3	±0·703
6·9	1·833	1·3–2·6	±0·477
8·8	2·018	1·1–3·5	±0·778
12·4	3·677	2·2–6·1	±1·171
16·2	6·266	4·4–8·1	±1·180
20·0	8·440	6·5–10·6	±1·318
25·0	10·420	8·8–13·5	±2·360
30·0	11·057	9·3–14·3	±1·674
32·0	8·550	5·0–13·9	±3·078
35·5	—	Nil	—

TABLE 5. FREQUENCY OF BEATING OF THE CIRRI OF *BALANUS AMPHITRITE*

From the Plym estuary, 9–10. ii. 56

Temperature (° C)	Frequency of beating, as beats per 10 sec		
	Mean	Range	S.D.
6·0	—	Nil	—
6·8	1·520	1·2–2·1	±0·311
11·7	3·322	2·0–5·1	±0·983
14·9	5·30	3·6–8·4	±1·495
19·9	6·988	4·9–12·3	±2·467
24·9	9·337	5·1–16·4	±4·547
29·9	13·562	9·3–20·0	±3·271
32·7	13·20	10·6–17·9	±2·371
34·7	11·487	9·3–14·3	±1·739
36·7	2 only	8·3, 12·5	—
38·4	—	Nil	—

TABLE 6. FREQUENCY OF BEATING OF THE CIRRI OF *BALANUS BALANUS*

From Anglesey, examined 17–18. iii. 56: 2-ring and 3-ring

Temperature (° C)	Frequency of beating, as beats per 10 sec		
	Mean	Range	S.D.
−2·0	1 only	0·8	—
1·9	2 only	1·1, 1·3	—
4·0	1·70	1·1–2·3	±0·420
8·0	2·650	1·8–3·2	±0·389
12·1	3·044	1·9–4·1	±0·731
15·9	4·209	3·0–5·9	±0·862
18·0	4·544	3·0–6·1	±1·115
20·2	4·810	3·1–6·2	±1·009
24·1	4·211	2·8–5·6	±1·003
26·0	3·775	2·3–5·4	±1·563
27·9	2·80	1·6–4·0	±0·868
30·0	—	Nil	—

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VIABILITY AND GLYCOGEN RESERVES IN THE NEWLY LIBERATED LARVAE OF *OSTREA EDULIS* L.

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It has been suspected that broods of larvae of the European flat oyster, *Ostrea edulis* L., differ considerably in their vigour and in the ease with which they can be reared in the laboratory (Cole, 1939; Bruce, Knight & Parke, 1940; Walne, 1956). The discovery of the cause of this phenomenon would be a step forward in breeding experiments, and might possibly indicate a way in which the vigour of larvae could be improved. It was thought that a possible explanation might be differences in the glycogen reserves in the larvae at the time of liberation, and for this reason the series of analyses reported in this paper were made.

Method

Twelve broods of larvae were obtained from oysters kept in running sea water at the Conway laboratory. A sample of each brood, in most cases between 100,000 and 200,000 larvae, was washed with distilled water, dried and preserved for glycogen assay. The remainder of the brood was reared by Mr P. R. Walne at Conway by his standard technique (Walne, 1956). Briefly, this method involves placing about 1000 larvae in 1 l. of filtered sea water in a glass vessel, which is stood in a water bath at 20–22° C. The larvae are kept stirred by gentle aeration, and in these experiments were fed with cultures of the flagellate *Isochrysis galbana*, the density of which was kept at about 50 cells per mm^3. When eyed larvae were first observed collectors in the form of mussel shells or broken unglazed saucers were added. When all the larvae had either metamorphosed on collectors or were clearly moribund, the experiment was concluded and the number of metamorphosed larvae counted. The twelve broods which were tested gave a considerable range of results, the percentage of larvae metamorphosing ranging from 0 to 25.

It was desirable to be able to express the glycogen content as a percentage of organic matter, so as to eliminate differences due to the relative proportion of weight represented by the physiologically inert calcareous shell. The following procedure fulfilled this requirement, and at the same time eliminated errors due to sea-salt contamination. To each sample of larvae 1·2 N hydrochloric acid was added drop by drop until no more effervescence occurred and a slight excess of acid was present. The acid suspension was

transferred to the central compartment of a Perspex electrodialyser, the basis of which were Permutit ion-exchange membranes 'Permaplex' A-10 and C-10. This apparatus was similar to that described by Blainey & Yardley (1956), differing in that an iron cathode and a carbon anode were used; and instead of acid and alkali respectively in the electrode compartments, a continuous flow of tap water removed the products of electrolysis. The dialyser was connected to a 12 V battery overnight. Preliminary tests showed this to demineralize such a solution beyond the limits of weighing, but an 8 h period was insufficient. Leakage of solution from the compartment could be prevented by the careful use of vaseline on the Perspex surfaces gripping the membranes.

The suspension was transferred to a tared tube and dried at 105° C to constant weight, which ranged in the samples from 25 to 90 mg. Hydrolysis of glycogen was carried out in the same tube, 10 ml. of 3% (v/v) sulphuric acid being added. The tubes were immersed in a boiling-water bath for 3 h, and early in this operation the dried material was shaken into a good suspension in the acid. The samples were neutralized, filtered, and, with rinsings, made up to either 100 ml. or 25 ml. according to the weight available. Duplicate 10 ml. aliquots were taken, and reducing sugars determined according to the Hagedorn-Jensen method as modified by Hulme & Narain (1931).

TABLE 1. PARTICULARS OF OYSTER LARVAE

The date of liberation, parentage, size and glycogen content of twelve broods of oyster larvae collected at Conway in 1955. The parent stock were all brought in from the oysterage on 9 July. The 'Conway' oysters were 3-year-old oysters bred in the Conway tanks. The 'Brittany' oysters were imported from France in 1954 and relaid in the Tal-y-foel oysterage. The larval size is expressed as the percentage in each size category, the length of the shell being the dimension measured. The actual number of spat obtained in each experiment is shown and this number is also expressed as a percentage of the initial number of larvae in the experiment. The final column gives the glucose found expressed as a percentage of the dry organic matter (to convert to glycogen multiply by 0·927).

Date of liberation	Oyster	Percentage size distribution of larvae at liberation (μ)						Number of spat	Glucose (%)
		150–159	160–169	170–179	180–189	190–199	200–209		
16 July	Conway	—	—	4	52	28	16	0	15·7
20	Conway	8	28	40	24	—	—	0	15·0
25	Conway	—	8	52	40	—	—	0	16·6
26	Brittany	—	32	40	20	8	—	0	15·8
27	Brittany	—	—	28	72	—	—	134 (25%)	15·8
29	Brittany	—	32	56	12	—	—	0	16·6
30	Brittany	—	4	44	48	4	—	42 (7%)	14·9
22 Aug.	Brittany	4	4	40	52	—	—	0	14·5
23	Conway	4	72	20	4	—	—	139 (17%)	15·3
23	Conway	56	44	—	—	—	—	33 (5%)	16·0
24	Brittany	4	36	52	8	—	—	0	15·7
25	Brittany	4	44	48	4	—	—	0	15·1

Conclusion

The amounts of glucose found, expressed as a percentage of organic matter, lay in all twelve cases between 14·5 and 16·6 (equivalent to 13·4 and 15·4% glycogen). The details are shown in Table 1. In view of such very small differences in glycogen reserves, it was concluded that some other factor must be responsible for the large viability differences observed. Certainly no correlation can be observed between the glycogen reserves and either the size of the larvae at liberation or the yield of spat.

SUMMARY

Samples of twelve broods of oyster larvae were subjected to a standard laboratory rearing technique while other samples were assayed for glycogen. The glycogen reserves of the larvae at liberation lay between 13·4 and 15·4% of the dry organic matter. No correlation was observed between the glycogen reserve and either the size of the larvae at liberation or the yield of spat in the rearing experiments.

REFERENCES

BLAINEY, J. D. & YARDLEY, H. J., 1956. Electrolytic desalting with ion-exchange membranes. *Nature, Lond.*, Vol. 177, p. 83.

BRUCE, J. R., KNIGHT, M. & PARKE, M. W., 1940. The rearing of oyster larvae on an algal diet. *J. mar. biol. Ass. U.K.*, Vol. 24, pp. 337–74.

COLE, H. A., 1939. Further experiments in the breeding of oysters (*Ostrea edulis*) in tanks. *Fish. Invest., Lond.*, Ser. 2, Vol. 16, No. 4.

HULME, A. C. & NARAIN, R., 1931. The ferricyanide method for the determination of reducing sugars. A modification of the Hagedorn-Jensen-Hanes technique. *Biochem. J.*, Vol. 25, pp. 1051–61.

WALNE, P. R., 1956. Experiments on rearing the larvae of *Ostrea edulis* L. in the laboratory. *Fish. Invest., Lond.*, Ser. 2, Vol. 20, No. 9.

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THE BREEDING AND FECUNDITY OF THE LONG ROUGH DAB *HIPPOGLOSSOIDES PLATESSOIDES* (FABR.) AND THE ASSOCIATED CYCLE IN CONDITION

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(Text-figs. 1–11)

Although the Long Rough Dab, *Hippoglossoides platessoides* (Fabr.), is represented by two subspecies, *H. p. limandoides* (Bloch) round the northern European coasts and *H. p. platessoides* on the North American Atlantic seaboard (Norman, 1934) and is often very abundant, little is known about its breeding biology.

The American race has been discussed by Huntsman (1918), and Bigelow & Schroeder (1953), but they do not consider the breeding biology in any detail. For the European race Saemundsson (1908, 1925, 1927) for Icelandic, Krüger (1942) for Baltic, Essipow & Slastnikow (1932) and Milinsky (1944) for Barents Sea fish, refer briefly to the breeding habits. Notes on the occurrence of Long Rough Dab eggs are scattered through the literature (Bal, 1943; Williamson, 1899; Günther, 1888; Rass, 1936; Otterstrøm, 1906; Pertseva, 1939 and others). As to fecundity, Fulton (1891) and Mitchell (1913) have given egg counts for five and eleven fish respectively from British coasts, and Milinsky (1944) for three fish from the Barents Sea.

In this paper the breeding biology of the Clyde population of Long Rough Dabs will be described. Since many aspects of breeding phenomena are closely associated with the condition of the fish, this is also considered (see also Fulton, 1904). Lastly, the fecundity of the species will be considered in relation to the age, length and weight of the fish. Some of these subjects are treated statistically, and details of the analyses, together with discussions of their validity, are given separately in Appendices 1–4. The biological significance of the analyses are given along with the other results of the investigation in the first part of the paper. The growth rate of some of the fish has been considered in previous papers (T. B. Bagenal, 1955*a*, *b*).

My special thanks are due to Mrs Jean Morrison who counted the eggs for the fecundity estimates, Miss Sheila Morris, who did most of the calculations, my wife for advice on statistical treatments, and the officers and crews of the Marine Station's research vessels for the collection of the material.

METHODS AND MATERIALS

The material on which this paper is based was caught in approximately monthly samples taken from October 1953 to May 1955. The dates of capture are given in Table 1. The fish ranged from 5 to 33 cm in length and 0 to 7+ years of age. The samples were obtained with a small-mesh cotton V.D. trawl of the following dimensions: headline, 49 ft.; footrope, 78 ft.; bridles, 15 fathoms; lower wings and belly mesh size, $2\frac{1}{2}$ in. bar, all other meshes, 1 in. bar. It is thought that this trawl took an adequate sample of the population, though the mesh-size selection gave noticeably biased samples of the younger age-groups (see T. B. Bagenal, 1955*a*, *b*). Supplementary hauls (Table 2) were taken with other trawls of various dimensions.

The fish were mostly caught off Mountstuart House on the east side of the Isle of Bute at a depth of about 40 m. Before the final adoption of this sampling area, hauls were taken at various places round the Isle of Cumbrae, though prior to and during the spawning time samples were also obtained from the deeper water between Bute and Cumbrae. During the 1955 spawning season hauls were also taken at other places in the Clyde Sea area (see Table 2 and p. 348). As will be shown later, there is a segregation of mature and immature fish, and the more scattered sampling areas at spawning time were chosen to avoid any bias that this might produce.

The fish were examined fresh in the laboratory. For the purposes of this study the following information was obtained for each individual fish: overall length, sex, stage of maturity, weight of the gonads, and gutted weight; the otoliths were kept for age determination. The overall length was measured from the tip of the lower jaw to the end of the longest caudal fin ray to the nearest 0·5 cm. Later, however, the measurements were grouped into centimetre groups which ranged from $x-0{\cdot}25$ to $x+0{\cdot}75$ cm; these were, however, all classed as x cm rather than $x{\cdot}25$ cm for simplicity in computation. Each fish was assigned to a 'gonad stage' according to an arbitrary classification:

Stage 1. Fish with small translucent, clear or slightly pinkish gonads. It was thought that these fish would not spawn during the next season.

Stage 2. Fish with larger, opaque ovaries in which the eggs were usually visible and opaque. These were thought to be ripening fish that would spawn during the next season.

Stage 3. Fish with at least some translucent eggs in the ovary which had a 'plum-pudding' appearance. These fish were thought to be very close to the time of spawning and included those that were actually ripe and running.

Stage 4. Spent fish with large, blood-shot, empty and flaccid ovaries.

Later, two further stages were introduced, stage 4_1 to include immature fish that had apparently spawned during the previous season, and stage 4_2 for maturing fish which appeared to be recovering from the spent condition. This classification was as far as possible based on what the future breeding condition was supposed to be. It has the advantages of simplicity and of

not requiring later regrouping of stages to provide sufficient numbers for analysis.

The classification of the maturity of the males was difficult and no clear stages in gonad development could be found. In any case the numbers caught were so small that analysis of different stages was not practicable.

The gonad weight, and the gutted weight without gonads (in this paper called simply 'weight') were taken to the nearest 0·5 g.

The treatment of the otoliths in age determination has already been described (T. B. Bagenal, 1955*a*).

During the spawning period 20 min hauls were taken with a coarse plankton net at the surface to collect Long Rough Dab eggs. These hauls, taken regularly twice a week in Fairlie Channel, were supplemented by others from elsewhere. Later, hauls were taken for larval and post-larval stages and the young bottom-living fish were caught with a small beam trawl with $\frac{1}{4}$ in. bar cotton netting.

THE LENGTH–WEIGHT RELATION AND CONDITION

Before analysing the data on the breeding and fecundity of the Long Rough Dab it was necessary to consider the condition of the fish; many breeding phenomena might be associated with the well-being of the particular individuals. While there are a number of ways by which the condition of a Long Rough Dab might be measured, the obvious choice with the data available was the weight of the fish for a given length. It seems a reasonable assumption that the heavier fish of a given length are in better general health. In the process of arriving at the relative condition of the Long Rough Dabs, the length–weight relation was analysed, and since this relation is of interest in itself, it will be considered here.

THE LENGTH–WEIGHT RELATION

The details of the analyses of the relation of length to weight for the fish are given in Appendix 1. It is shown that for most groups of fish the weight increases at a rate slightly greater than the cube of the length (Fig. 1). This power was not found to differ between different age-groups or between the males, and immature, maturing and spent females. However, significant differences were found between the powers for immature females caught on different dates. The value of the power ($=b$, the coefficient of the regression of the logarithms of weight on length) is shown in Fig. 2 and appears to vary in an annual cycle. The significance of this would seem to be that if all the fish are gaining in weight and the power is increasing, the larger fish must be putting on weight faster than the small ones, whereas if the power is decreasing the smaller fish must be gaining faster. This aspect of the length–weight relation will be discussed in connexion with the condition of the Long Rough Dabs.

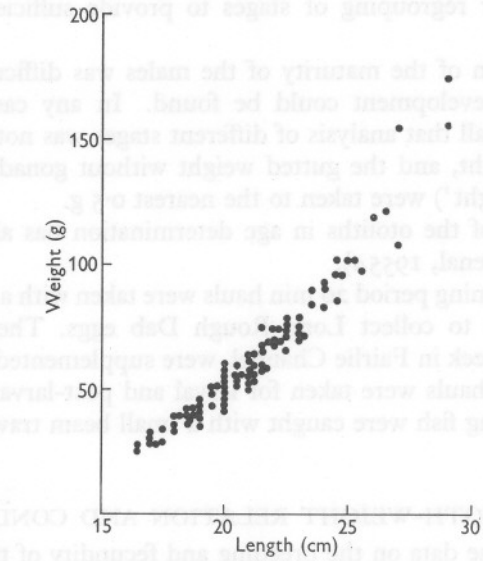

Fig. 1. Scatter diagram of length and weight of maturing (stage 2) female Long Rough Dabs caught on 2 March 1954.

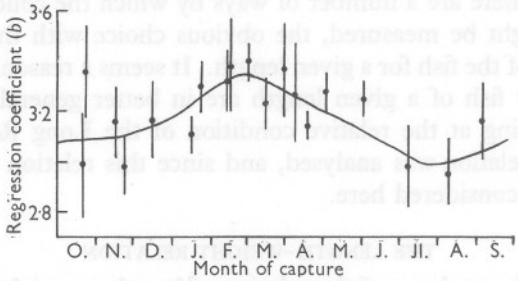

Fig. 2. The regression coefficients (b), with their 95 % fiducial limits (vertical lines), for the regressions of log weight on log length of immature female Long Rough Dabs.

THE SEASONAL CYCLE IN CONDITION

The measure of condition has been calculated as the expected weight of a 20 cm Long Rough Dab, derived from analysis of the length–weight relation. The condition of the males, immature, maturing and spent females was found to differ from month to month, and the results are illustrated diagrammatically in Fig. 3. The age-groups within these classes were pooled because on only one of the four dates tested was there a possibly significant difference in their condition.

The data are most complete for the immature female fish. It can be seen that these reach their peak of condition in November–December, and then

they lose condition until late April after which there is a recovery. In Fig. 4 are shown the cycles in condition and regression coefficients together. This figure suggests that at first the smaller fish both lose and gain condition faster than larger ones, though later this is reversed and the large fish tend to catch up.

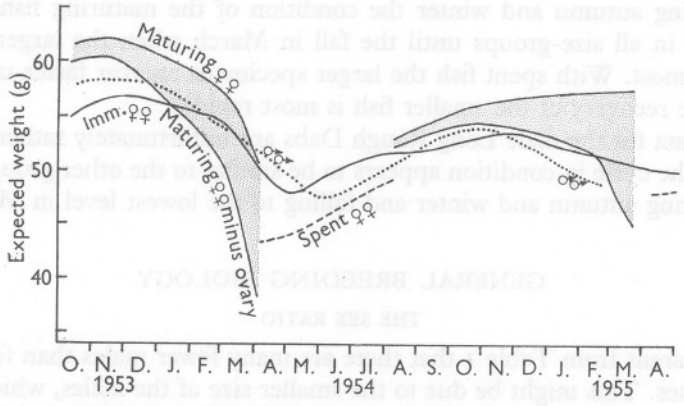

Fig. 3. Diagram of the expected weights of 20 cm male, immature, maturing and spent female Long Rough Dabs from October 1953 to April 1955. The line for spent females continues low in July and August 1954 because those fish that were obviously recovering to spawn again were classified as maturing females.

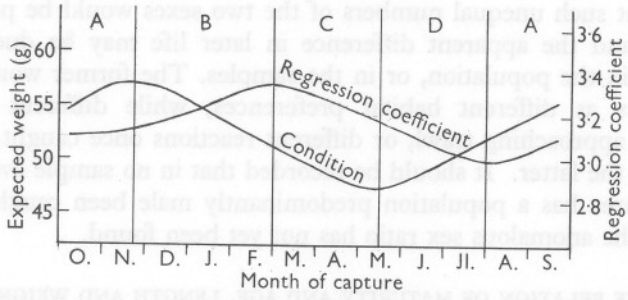

Fig. 4. Diagram of the cycles of regression coefficients (*b*) and condition of immature female Long Rough Dabs, based on Figs. 2 and 3. Period A: August–November; all fish gaining in weight, large fish gaining faster than small fish. Period B: November–February; all fish losing weight, small fish losing faster than large ones. Period C: March–May; all fish still losing, large fish now losing faster. Period D: May–July; all fish gaining in weight again; the small fish gaining faster than the large fish.

The condition of the maturing females is also shown in Fig. 3. It will be realized that any change in condition might be masked by changes in the gonads. The condition has therefore been calculated, both from the total weight including the gonads and from the weights excluding gonads. It can be seen that the total condition (based on weight including gonads) is greater than that of the immature fish, but during March those fish which spawn late

lose condition very rapidly and that even earlier the maintenance of the total condition is due to the developing gonads at the expense of the condition of the rest of the fish. The condition of the spent fish is considerably lower than any other group but recovery is rapid, and by August is at approximately the same level as the other groups. The regression coefficients (Table 17) suggest that during autumn and winter the condition of the maturing fish changes similarly in all size-groups until the fall in March when the larger fish are affected most. With spent fish the larger specimens recover faster until May when the recovery of the smaller fish is most rapid.

The data for the male Long Rough Dabs are unfortunately rather meagre, though the cycle in condition appears to be similar to the other groups, being high during autumn and winter and falling to the lowest level in May.

GENERAL BREEDING BIOLOGY

THE SEX RATIO

It is apparent from Table 1 that there are many fewer males than females in the catches. This might be due to the smaller size of the males, which would be able to escape through the net more easily (T. B. Bagenal, 1955*b*), but even for comparable size-groups the males are less numerous than the females, and as the females grow faster, one would expect to find more males in the small size-groups if equal numbers are produced and survive. It seems very unlikely that such unequal numbers of the two sexes would be produced at spawning, and the apparent difference in later life may be due either to differences in the population, or in the samples. The former would include such factors as different habitat preferences, while different behaviour towards an approaching trawl, or different reactions once caught, would be included in the latter. It should be recorded that in no sample ever taken in the Clyde area has a population predominantly male been caught, and the reason for the anomalous sex ratio has not yet been found.

THE RELATION OF MATURITY AND AGE, LENGTH AND WEIGHT

The data are given in Tables 3–7, and are based on the fish caught during the 6 months, October to March, prior to spawning (in 1954 there was no December sample). The two years 1953–54 and 1954–55 are treated separately, though the combined figures are also given, and the data are illustrated in Fig. 5 A–C.

The relation of maturity and age is given in Table 3 and Fig. 5 C. The results for the two years are quite comparable. It will be noticed that there is no definite age at which the fish become mature, for although the percentage mature increases with age, immature specimens of all but the oldest fish have been found. Data concerning the relation of maturity and length are given in Table 4 and Fig. 5 B. The agreement between the two years is again good, and,

as with age, there is no length above which all fish are mature. The single immature individual in the 32 cm size-group (6+ years of age) is probably of no significance. The data are re-arranged in Table 5 and Fig. 5A to illustrate the relation of maturity and weight. The same relationship can be seen, though in this case the agreement between the two years is not apparently so good.

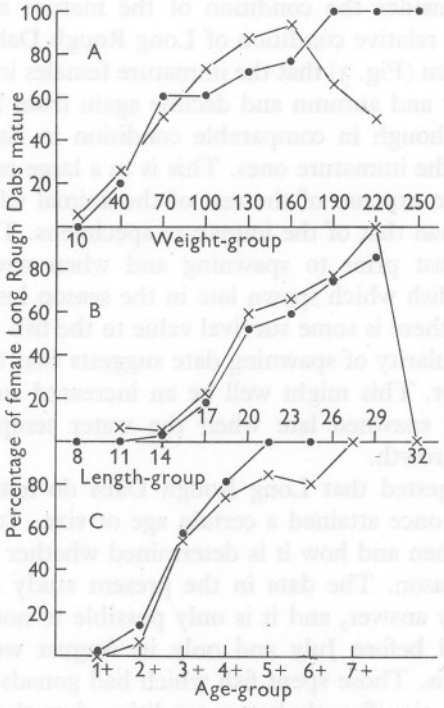

Fig. 5. The relation of percentage maturity to weight (A), length (B) and age (C) of female Long Rough Dabs, based on the 6 months prior to spawning, ●—●, 1953–54; ×—×, 1954–55.

Within a given age-group there is considerable variability in the length and weight of the fish. Tables 6 and 7 give the distribution of mature and immature fish in length- and weight-groups of Long Rough Dabs of the same age. Only in the 3+ and 4+ age-groups were there sufficient fish, well enough divided between mature and immature, to give adequate numbers in each class for comparisons to be possible. The means given in Tables 6 and 7 are based on the original data. An analysis of the percentages of mature fish in subgroups of the same age and length, and of the same age and weight are given in Appendix 2. The results of these tests show that the variability between the percentages for different ages with the same length is significantly greater than that between pairs of groups of fish of the same age and length

caught in 1954 and in 1955, though the variability between those for length-groups of the same age is not. This suggests that maturity is more closely linked with the age of the fish than its length. Thompson (1915), working on the Halibut, similarly found 'that the maturity is entirely dependent on age, not on size...'.

A further comparison of the relation of maturity, length and weight is made when we consider the condition of the mature and immature fish. A discussion of the relative condition of Long Rough Dabs has already been given, and it was seen (Fig. 3) that the immature females increase in condition during the summer and autumn and decline again from November to May. The mature fish, though in comparable condition in August, put on total weight faster than the immature ones. This is to a large extent an increase in gonad weight at the expense of the rest of the animal which is relatively in poorer condition than that of the immature specimens. The fish are in their lowest condition just prior to spawning and when newly spent. It also appears that those fish which spawn late in the season lose the most weight. This suggests that there is some survival value to the fish to spawn early, but the maintained regularity of spawning date suggests that there must be some compensating factor. This might well be an increased survival value to the offspring by being spawned late when the water temperatures are more suitable for rapid growth.

It has been suggested that Long Rough Dabs do not necessarily spawn every year, having once attained a certain age or size. It would be of great interest to know when and how it is determined whether the fish will spawn during the next season. The data in the present study are not sufficiently detailed to give any answer, and it is only possible to note that stage 2 fish were not identified before July and only in August were there sufficient numbers for analysis. Those spent fish which had gonads developing for the next season were in significantly better condition than those classed with the immature fish.

THE SEASONAL CYCLE IN GONAD WEIGHT

It was clear from a preliminary examination of the data that the weight of the gonad increased with the size of the fish, but the effect of the age on gonad weight was not apparent. The statistical analysis of the data is given in Appendix 3, where it is shown that for fish of a given length or weight there is no difference in the gonad weights of the different age-groups. After pooling the ages, the expected gonad weights for mature female Long Rough Dabs of 69·98 g were calculated for the months prior to spawning and these, shown in Fig. 6, illustrate the rate of development of the maturing ovaries.

THE SPAWNING TIME

In Table 1 can be found the dates of capture and the numbers of Long Rough Dabs of each maturity stage that were caught. The percentages of immature, ripe and spent of the total mature fish are given in Fig. 7, which also includes a graph of the numbers of Long Rough Dab eggs in 20 min tow-net hauls off Keppel Pier. From this figure it can be seen that the spawning times in 1954 and 1955 were very similar, and lasted from the beginning of March until the end of the second week in April, and half the fish had spawned by 20–22 March. It is at this time too that the fish are in the poorest condition, though the lowest level reached by the males is later than that of the mature females.

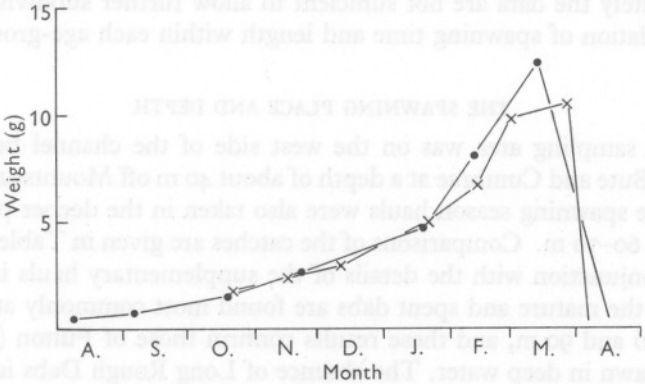

Fig. 6. The expected gonad weight of a female Long Rough Dab 69·98 g in weight, from October 1953 to March 1954 (×—×), and from August 1954 to March 1955 (●—●).

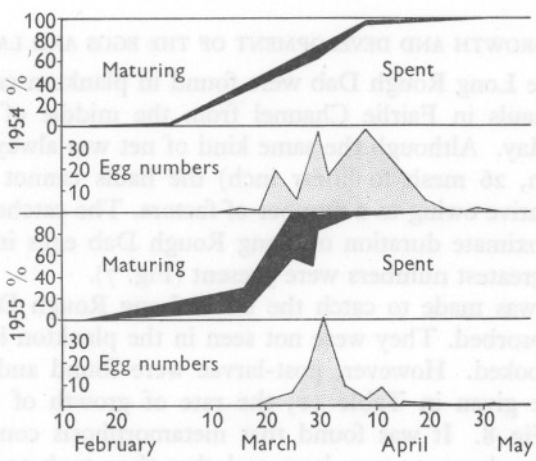

Fig. 7. The percentage of maturing, ripe (solid black) and spent female Long Rough Dabs through the 1954 and 1955 breeding seasons. The numbers of Long Rough Dab eggs in 20 min plankton hauls are also illustrated (stippled frequency diagram).

The egg collections support these conclusions very well. It appears from the small percentage of stage 3 fish caught on each occasion (never more than 50%) that this stage is of short duration for each individual fish, as was found by Fulton (1890). In this respect it is of interest that only one fish (caught on 29 March 1955) was actually fully ripe with running eggs. A comparison with previous studies in other regions, based on egg surveys or the maturity stage of the adult, is given in Table 8.

The relation of spawning time and age is shown by the data in Table 9, which suggests that the older fish spawn first. It has also been found that the larger fish spawn first; the mean length of the spent fish on 30 March 1954 was 22·7 cm compared with 19·5 cm for those that had not yet spawned. Unfortunately the data are not sufficient to allow further subdivision and to test the relation of spawning time and length within each age-group.

THE SPAWNING PLACE AND DEPTH

The main sampling area was on the west side of the channel between the islands of Bute and Cumbrae at a depth of about 40 m off Mountstuart House. During the spawning season hauls were also taken in the deeper parts of the channel in 60–70 m. Comparisons of the catches are given in Table 10. These data, in conjunction with the details of the supplementary hauls in Table 2, show that the mature and spent dabs are found most commonly at depths of between 60 and 90 m, and these results confirm those of Fulton (1890) that the fish spawn in deep water. The absence of Long Rough Dabs in the catch on 6 April 1955 in 150 m confirms the general impression, gained over a number of years, that these fish are very rare in the deepest water of the Clyde area.

THE GROWTH AND DEVELOPMENT OF THE EGGS AND LARVAE

The eggs of the Long Rough Dab were found in plankton catches obtained from 20 min hauls in Fairlie Channel from the middle of March to the beginning of May. Although the same kind of net was always used (mouth diameter 45 cm, 26 mesh to linear inch) the hauls cannot be considered strictly quantitative owing to a number of factors. The catches, however, do show the approximate duration of Long Rough Dab eggs in the plankton, and when the greatest numbers were present (Fig. 7).

No attempt was made to catch the larval Long Rough Dabs before the yolk-sac was absorbed. They were not seen in the plankton hauls, but were probably overlooked. However, post-larvae were found and the details of the catches are given in Table 11; the rate of growth of these larvae is illustrated in Fig. 8. It was found that metamorphosis commenced when the larvae were about 15 mm long and that they took to the bottom as fully metamorphosed fish at about 25 mm in length. There was considerable individual variation about these average sizes.

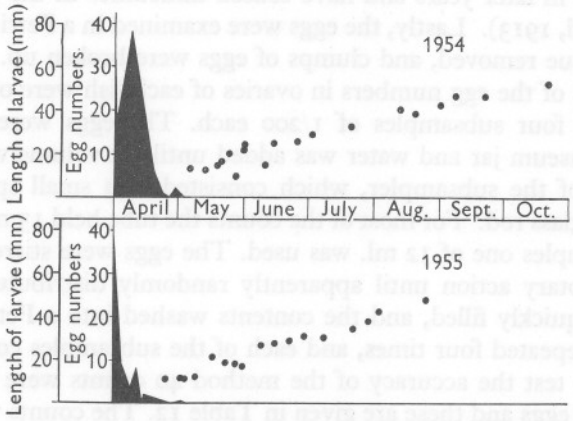

Fig. 8. The lengths of post-larval Long Rough Dabs during the summers of 1954 and 1955. The decline in egg numbers in the plankton hauls is shown in solid black for each year.

FECUNDITY

During the study of the breeding biology, fecundity estimations were made for 119 of the stage 2 Long Rough Dabs. The fish were mainly from two samples, the first consisting of the 25 fish obtained on 15 February 1954, and the second of the 91 fish on 2 March 1954 (see Table 1). On these dates all the maturing female Long Rough Dabs that were caught were examined; and they may be considered as random samples from the population; the stage 3 fish on 2 March 1954 was not included since some of its eggs may have already been shed. The remaining three fish were obtained on 15 and 30 March, and were selected because they represented the smallest size-groups of mature females and were supposed to supplement the two random samples. After the usual treatment of the fish (see p. 340), the gonads were preserved. The full details for each individual were kept separate, and these are given in Table 30.

The method of preservation and subsequent treatment of the ovaries followed that used by Simpson (1951) for plaice. The ovaries were preserved and stored in Gilson's fluid modified by doubling the amount of acetic acid. This not only preserved the eggs but also helped to liberate them by breaking down the ovarian tissue. The process was aided by repeated, though spasmodic, shaking of the bottles in which the ovaries were preserved. Before the eggs were to be counted the ovaries were teased apart and the ovarian tissue removed and any adhering eggs were returned to the bottle. Next the eggs were washed by successive shaking in Gilson's fluid and decanting the supernatant liquid, though if the eggs were to be counted immediately water was used and this was not found to affect the eggs. The decanting removed not only remaining pieces of ovarian tissue, but also those minute eggs which

would be laid in later years and have caused difficulties in the past (Fulton, 1891; Mitchell, 1913). Lastly, the eggs were examined in a Petri dish and any remaining tissue removed, and clumps of eggs were broken up.

Estimations of the egg numbers in ovaries of each fish were obtained from the means of four subsamples of 1/200 each. The eggs were placed in a cylindrical museum jar and water was added until the volume was 200 times the capacity of the subsampler, which consisted of a small specimen tube attached to a glass rod. For most of the counts the tube held 13 ml., but in the earlier subsamples one of 12 ml. was used. The eggs were stirred vigorously with a non-rotary action until apparently randomly distributed. The subsampler was quickly filled, and the contents washed into a Petri dish. This process was repeated four times, and each of the subsamples counted.

In order to test the accuracy of the method 40 counts were made on the same batch of eggs and these are given in Table 12. The counts were made in series of four and the subsamples were returned to the jar after each series. The standard deviation of forty observations was 97·308 corresponding to a coefficient of variation of 10·05%. For the means of four the standard deviation is 48·654 ($97{\cdot}308/\sqrt{4}$) corresponding to a coefficient of variation of 5·03%.

This may be compared with the method given by Simpson who used a 1 ml. stempel pipette from a 150 ml. whirling flask and got a standard deviation for forty observations of 35·393 or $C=9{\cdot}57\%$ and for means of 4 of 4·78%. The coefficient of variation based on his actual means was 3·64%, and in the present work 7·05%. This indicates that Simpson's actual means were less variable than might be expected by chance from the separate counts, while those given in Table 12 are more variable.

The analyses of the relations of fecundity to age, length, weight and gonad weight are given in Appendix 4.

RESULTS

The data given in Appendix 4 show that the fecundity of the female Long Rough Dabs varies from 25,000 eggs for a fish of *ca.* 15 cm and 20 g to 250,000 for one of *ca.* 30 cm and 200 g. The statistical analysis of the data shows that there is very great variability in the fecundity, and that while the general level can be related to the age, length, weight and gonad weight of the fish, there is still a large amount of variability after these factors have been taken into account. The analyses show that for estimating the fecundity, weight and gonad weight used together are the most accurate. However, since length is so much easier and quicker to measure, if time is limited and the fish are not, it might be more suitable to predict fecundity from a larger sample using only the length data. The variability is shown diagrammatically as scatter diagrams of fecundity and length, weight and gonad weight in Figs. 9–11. The fecundity has been found to increase at a rate slightly above

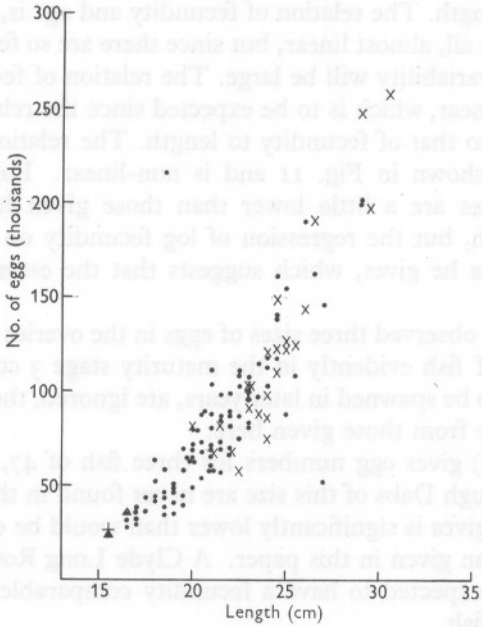

Fig. 9. Scatter diagram showing the relation of fecundity and length of female Long Rough Dabs. ×, 15 February 1954; ●, 2 March 1954; +, 15 March 1954; ▲, 30 March 1954.

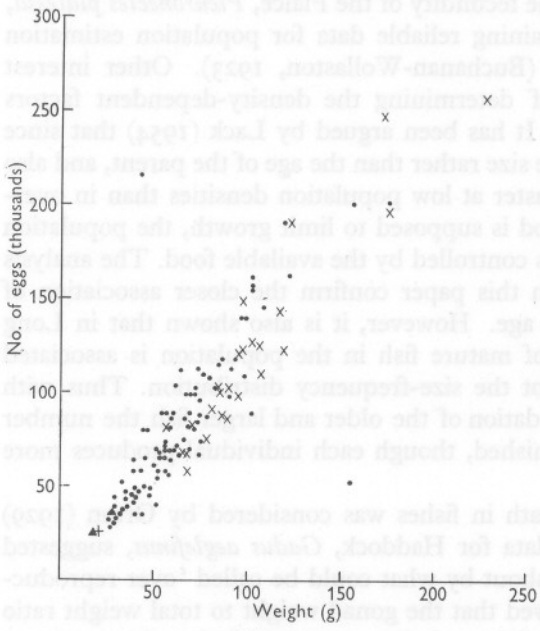

Fig. 10

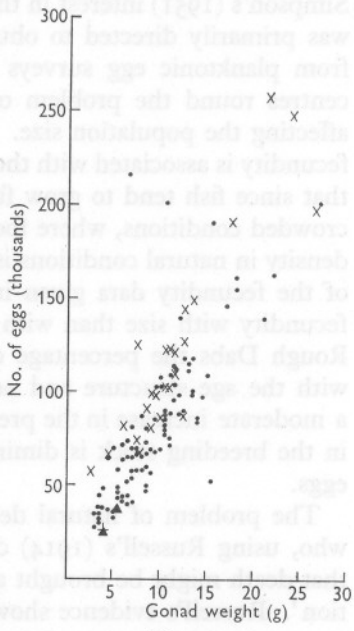

Fig. 11

Fig. 10. Scatter diagram showing the relation of fecundity and weight of female Long Rough Dabs. Symbols as in Fig. 9.

Fig. 11. Scatter diagram showing the relation of fecundity and gonad weight of female Long Rough Dabs. Symbols as in Fig. 9.

the cube of the length. The relation of fecundity and age is, in so far as there is a relationship at all, almost linear, but since there are so few age classes it is obvious that the variability will be large. The relation of fecundity to weight is also probably linear, which is to be expected since the relation of weight to length is similar to that of fecundity to length. The relation of fecundity to gonad weight is shown in Fig. 11 and is non-linear. Fulton's (1891) five fecundity estimates are a little lower than those given here for fish of a comparable length, but the regression of log fecundity on log length is not linear for the data he gives, which suggests that the estimates may not be reliable.

Mitchell (1913) observed three sizes of eggs in the ovaries she examined. If those estimates of fish evidently in the maturity stage 3 condition, and also the minute eggs to be spawned in later years, are ignored, the estimates do not differ significantly from those given here.

Milinsky (1944) gives egg numbers for three fish of 47, 48 and 49 cm in length. Long Rough Dabs of this size are never found in the Clyde area, but the fecundity he gives is significantly lower than would be expected from the regression equation given in this paper. A Clyde Long Rough Dab of about 32 cm would be expected to have a fecundity comparable to that given by Milinsky for his fish.

DISCUSSION

Simpson's (1951) interest in the fecundity of the Plaice, *Pleuronectes platessa*, was primarily directed to obtaining reliable data for population estimation from planktonic egg surveys (Buchanan-Wollaston, 1923). Other interest centres round the problem of determining the density-dependent factors affecting the population size. It has been argued by Lack (1954) that since fecundity is associated with the size rather than the age of the parent, and also that since fish tend to grow faster at low population densities than in over-crowded conditions, where food is supposed to limit growth, the population density in natural conditions is controlled by the available food. The analysis of the fecundity data given in this paper confirm the closer association of fecundity with size than with age. However, it is also shown that in Long Rough Dabs the percentage of mature fish in the population is associated with the age structure and not the size-frequency distribution. Thus with a moderate increase in the predation of the older and larger fish the number in the breeding stock is diminished, though each individual produces more eggs.

The problem of natural death in fishes was considered by Orton (1929) who, using Russell's (1914) data for Haddock, *Gadus aeglefinus*, suggested that death might be brought about by what could be called 'over reproduction'. Russell's evidence showed that the gonad weight to total weight ratio increases with the size of the fish, and Orton suggested that this tendency

would produce a size limit above which the fish could not survive. In the breeding data on the Long Rough Dab analysed in this paper it has been shown that relation of gonad weight to weight is linear and no trend was found in the relation with increasing age (p. 373). However, another aspect of the same problem is seen when we consider the fecundity. Milinsky's very large dabs did not produce the egg numbers expected from their size. Furthermore, from a consideration of the regression of log fecundity on log gonad weight (Fig. 11), it appears that the number of eggs in the gonad does not increase in proportion to the weight. This result was unexpected since the larger gonads will have a proportionally smaller surface area and so, not only should carry less surface moisture when they are weighed, but also less ovarian tissue should be found surrounding the eggs in the larger gonads. We can only suppose that the heavier gonads produce fewer eggs per gram than do the lighter ones, so the eggs are presumably larger and heavier. In future work an analysis of the eggs is needed to show how the fecundity is related to the food reserves in the eggs themselves, and so perhaps to their viability. To a large extent in fish, significance of the fecundity is obscured by the enormous numbers of eggs laid and its dependence on the size of the parent, but the significance of clutch-size in birds and litter-size in mammals have been discussed by Lack (1947, 1948*a*, *b*). It would appear that, as in these other groups, if other factors are equal the eggs from the more fecund parents would have greater chances of survival than those from the less fecund. Unless there were some compensating factor, a mutation tending to produce greater fecundity would pass through the whole population. It has, in the past (Simpson, 1951), been suggested that the factors governing the fecundity of individual fish might be: (*a*) the condition of the fish when the germinal epithelium is laid down during the first year of life; and (*b*) the condition of the fish either when the eggs to be laid each year are separated from the mass of developing ova, or when the new primary oocytes are being formed each year. The condition of the fish at these critical times is expected to be closely associated with the food supply and the temperature of the environment. These environmental factors may indeed be expected to influence the fecundity of individual fish within limits set by their hereditary characteristics. A mutation, tending to increase the general level of fecundity, would still be expected to spread through the entire population were it not for some compensating factors, which reduce the chances of survival of the entire progeny of a particularly fecund individual. Such compensating factors may act on the parent or the eggs. After spawning the female fish are in the poorest condition reached during the whole year. If fecundity and post-spawning condition were inversely correlated and the condition of the fish critical to their survival, the more fecund fish might not live to spawn again or only to spawn two seasons hence. With the data available there is no evidence of the more fecund fish being in poorer condition (Appendix 4, p. 375).

It is clear from the earlier section that some fish do not spawn every year having once reached sexual maturity. It is, however, difficult to say if this is associated with greater fecundity in the previous season.

Factors associated with the survival of the progeny would include the possibility of the eggs being smaller, and containing less food reserves.

While it is not possible at this present stage to suggest which of these factors is the most likely to control the fecundity of a given species of fish, these are the lines on which future work might profitably be directed.

SUMMARY

Details are given of the breeding biology, including the fecundity, of the Long Rough Dab deduced from samples taken in the Clyde Sea area from October 1953 to April 1955. Where possible breeding is related to the condition of the fish; the index of condition is based on the length–weight relation.

The weight of Long Rough Dabs of each sex and stage in maturity increases as a power, slightly greater than the cube, of the length. An annual cycle of fluctuations of this power is seen in the immature females, and indicates how changes in condition at different seasons affect the different size-groups. The measure of condition is taken as the expected weight of a 20 cm Long Rough Dab, and the changes in this weight are followed through the sampling period for males and for immature, maturing and spent females. All groups tend to be in best condition during November and December followed by a decline to the spawning time, in March and April, after which there is a slow recovery.

The scarcity of males in the samples cannot be satisfactorily explained. There is no definite age, length or weight above which all the female fish become mature, but the percentage of mature fish is more closely linked to the age structure than to the size-distribution. The condition of the mature and immature fish is compared; mature females are initially in better condition, and as the breeding season approaches this is maintained by the gonads developing at the expense of the flesh. The relations of the gonad weight to length and to weight appear to be similar in all age-groups, and the pre-spawning increase in gonad weight is discussed.

The spawning season was determined from the disappearance of mature fish from the samples and their replacement by spent females, and by the appearance of eggs in the plankton; it extends from the beginning of March to the middle of April. The older and larger fish have been found to spawn first; spawning takes place predominantly at depths of 60–90 m. The eggs remain in the plankton in quantity for 3–4 weeks. The larvae metamorphose at about 15 mm, take to the bottom at approximately 25 mm and for the first 6 months grow at about 10 mm per month.

The fecundity was estimated from four subsamples of 1/200 of the eggs from each of 119 fish, mostly caught on two dates. The egg numbers varied

from 25,000 for a fish of 15 cm to over 250,000 for a 30 cm fish. The data were subjected to multiple regression analyses and it is seen that the fecundity is most accurately estimated from the weight and gonad weight together, and the addition of length to these measurements does not increase the efficiency significantly. The fecundity was found to be related to weight linearly, to the length at a power greater than the cube and to the gonad weight at a power less than unity. The significance of these relations and a discussion of the wider implications of the paper is given.

REFERENCES

BAGENAL, M., 1955. A note on the relations of certain parameters following a logarithmic transformation. *J. mar. biol. Ass. U.K.*, Vol. 34, pp. 289–96.

BAGENAL, T. B., 1955*a*. The growth rate of the Long Rough Dab *Hippoglossoides platessoides* (Fabr.). *J. mar. biol. Ass. U.K.*, Vol. 34, pp. 297–311.

—— 1955*b*). The growth rate of the Long Rough Dab *Hippoglossoides platessoides* (Fabr.)—a correction. *J. mar. biol. Ass. U.K.*, Vol. 34, pp. 643–7.

BAL, D. V. 1943. A study of fish eggs and larvae from Manx waters. I. Observations on the fish eggs. *J. Univ. Bombay*, N.S. 11 B (5), pp. 54–90.

BIGELOW, H. B. & SCHROEDER, W. C., 1953. Fishes of the Gulf of Maine. *Fish. Bull., U.S.*, Vol. 53, No. 74, 577 pp.

BUCHANAN-WOLLASTON, H. J., 1923. The spawning of plaice in the southern part of the North Sea in 1913–14. *Fish. Invest., Lond.*, Ser. 2, Vol. 5, No. 2, 36 pp.

COCHRAN, W. G., 1947. Some consequences when the assumptions for the analysis of variance are not satisfied. *Biometrics*, Vol. 3, pp. 22–38.

ESSIPOW, W. J. & SLASTNIKOW, G., 1932. Zur Biologie des Kambalajorsch (*Drepanopsetta platessoides* O. Fabr.) im Barentsmeer. *Wiss. Fischereiuntersuchungen am Murman (Barents Sea)*, pp. 191–8. (In Russian: German summary.)

EWART, J. C. & FULTON, T. W., 1889. Report on the spawning of the British marine food-fishes. *Rep. Fish. Bd Scot.*, Vol. 7, pp. 186–221.

FULTON, T. W., 1890. The spawning and spawning place of marine food-fishes. *Rep. Fish. Bd Scot.*, 8 (1889), Part III, pp. 257–69.

—— 1891. On the comparative fecundity of sea fish. *Rep. Fish. Bd Scot.*, 9 (1890), Part III, pp. 243–68.

—— 1904. The rate of growth of fishes. *Rep. Fish. Bd Scot.*, 22 (1903), Part III, pp. 141–241.

GÜNTHER, A., 1888. Report on the fishes obtained by Mr J. Murray in deep water on the north-west coast of Scotland between April 1887 and March 1888. *Proc. roy. Soc. Edinb.*, Vol. 25, pp. 205–20.

HUNTSMAN, A. G., 1918. Histories of new food fishes. 1. The Canadian plaice. *Bull. biol. Bd Can.*, No. 1, 32 pp.

KRÜGER, K. VON, 1942. Erneutes Auftreten der Scharbzunge, *Drepanopsetta platessoides* Fabr. in der westlichen Ostsee. *Kieler Meeresforsch.*, Bd. 4, pp. 18–37.

LACK, D., 1947. The significance of clutch size. *Ibis*, Vol. 89, pp. 302–52.

—— 1948*a*. The significance of clutch size. *Ibis*, Vol. 90, pp. 25–45.

—— 1948*b*. The significance of litter size. *J. Anim. Ecol.*, Vol. 17, pp. 45–50.

—— 1954. *The Natural Regulation of Animal Numbers*. 343 pp. Oxford.

LECREN, E. D., 1951. The length-weight relationship and seasonal cycle in gonad weight and condition in the Perch (*Perca fluviatilis*). *J. Anim. Ecol.*, Vol. 20, pp. 201–19.

MATHER, K., 1946. *Statistical Analysis in Biology*. Second edition. London: Methuen.

MILINSKY, G. I., 1944. On the biology and fisheries of the long rough dab of the Barents Sea. *Trans. Knipovich polyar. sci. Inst.*, Vol. 8, pp. 388–415. (In Russian: English summary.)

MITCHELL, A. M., 1913. On the egg production of certain fishes. *Rep. N. Sea Fish. Invest. Comm.*, 5th Report (Northern Area), pp. 191–204.

NORMAN, J. R., 1934. *A Systematic Monograph of the Flatfishes (Heterostomata)*. Vol. I. London.

ORTON, J. H., 1929. Reproduction and death in invertebrates and fish. *Nature, Lond.*, Vol. 123, pp. 14–15.

OTTERSTRØM, A., 1906. Eggs and young of fishes in the Danish waters. *Rep. Danish biol. Sta.*, Vol. 13, 85 pp.

PEARSON, E. S. & HARTLEY, H. O., 1954. *Biometrika Tables for Statisticians*, Vol. I. Cambridge University Press.

PERTSEVA, T. A., 1939. Spawning, eggs and fry of fish in the Motovski Bay. *Trans. Inst. mar. Fish. USSR.*, Vol. 4, pp. 417–70. (In Russian: English summary and table headings.)

RASS, T. S., 1936. Spawning, eggs and fry of the food-fishes of the Barents Sea. Breeding and development of fish in the subarctic. *Int. Rev. Hydrobiol.*, Vol. 33, pp. 250–70.

RUSSELL, E. S., 1914. Report on the market measurements in relation to the English haddock fishery during the years 1909–1911. *Fish. Invest., Lond.*, Ser. 2, Vol.I, No. I, 134 pp.

SAEMUNDSSON, B., 1908. Oversigt over Islands Fiske med oplysninger om deres forekomst vigtigste biologiske forhold og okonomiske betydning. *Skr. Komm. Havunders, Kbh.*, No. 5, 140 pp.

—— 1925. Fiskirannsoknir 1923–1924. *Andvari, Reykjavik*, pp. 33–71.

—— 1927. Synopsis of the fishes of Iceland. *Rit Visind. Isl.*, Vol. 2, 66 pp.

—— 1949. Marine Pisces. *Zoology of Iceland*, Vol. 4, Pt. 72, 150 pp.

SIMPSON, A. C., 1951. The fecundity of the plaice. *Fish. Invest., Lond.*, Ser. 2, Vol. 17, No. 5, 27 pp.

SNEDECOR, G. W., 1946. *Statistical Methods*. Fourth edition. Iowa State College Press.

THOMPSON, W. F., 1915. A preliminary report on the life-history of the halibut. *Rep. Comm. Fish. B.C.*, 1914, pp. 76–120.

WILLIAMSON, H. C., 1899. On the pelagic fish-eggs and larvae of Loch Fyne. *Rep. Fish. Bd Scot.*, 17 (1898), Part III, pp. 79–131.

TABLE 1. DETAILS OF CATCHES

Date 1953	Males	Females				Total females	Grand total
		Stage 1	Stage 2	Stage 3	Stage 4		
23. x.	7	30	35	—	—	65	72
19. xi.	10	26	30	—	—	56	66
15. xii.	5	27	21	—	—	48	53
1954							
21. i. 26. i.	5	46	40	—	—	86	91
15. ii.	—	24	25	—	—	49	49
2. iii.	10	176	91	1	—	268	278
30. iii.	—	68	9	4	21	102	102
8. iv.	—	67	3	3	74	147	147
3. v.	5	74	—	—	43	117	122
2. vi.	30	111	—	1	64	176	206
8. vii.	16	57	5	—	17	79	95
9. viii.	37	46	61	—	9	116	153
7. ix.	12	31	36	—	1	68	80
21. x.	12	31	22	—	—	53	65
25. xi.	8	76	86	—	1	163	171
1955							
20. i.	3	69	41	—	—	110	113
14. ii.	5	35	36	—	—	71	76
16. iii.	2	51	12	4	1	68	70
18. iv.	2	73	—	—	36	109	111

TABLE 2. DETAILS OF CATCHES IN SUPPLEMENTARY HAULS

Date 1955	Position	Depth (m)	Males	Females				Total females	Grand total
				Stage 1	Stage 2	Stage 3	Stage 4		
14. ii.	Bute Channel	60–70	1	18	15	—	—	33	34
	Mountstuart	40–50	—	27	12	—	—	39	39
25. iii.	Skelmorlie	35–45	—	7	—	1	1	9	9
	Bute Channel	50–70	—	4	—	4	6	14	14
29. iii.	Bute Channel	60–70	—	—	—	2	1	3	3
	Bute Channel	60–70	—	1	—	—	—	1	1
	Mountstuart	40–50	—	27	—	7	6	40	40
	Mountstuart	40–50	2	35	—	4	6	45	47
30. iii.	Off Lady Isle	40–50	1	61	—	7	33	101	102
	Off Ardrossan	50–70	—	29	1	2	16	48	48
6. iv.	Off Sannox Arran 1 m	150	—	—	—	—	—	—	—
	Sannox Arran 2 m	*ca.* 90	—	54	—	1	13	68	68
	Sannox Arran 2 m	*ca.* 90	—	17	—	—	14	31	31
	S.W. Garroch Head	*ca.* 60	—	27	—	—	11	38	38

TABLE 3. THE RELATION OF MATURITY AND AGE

Age-group	1953–54			1954–55			Both years
	Immature	Mature	% mature	Immature	Mature	% mature	% mature
1+	30	1	3·2	3	—	0	2·9
2+	202	35	14·8	147	10	6·4	11·4
3+	81	109	57·4	83	97	53·9	55·7
4+	16	70	81·4	24	69	74·2	77·7
5+	—	27	100	4	22	84·6	92·5
6+	—	1	100	1	4	80·0	83·3
7+	—	—	—	—	1	100	100
Total	329	243	42·48	262	203	43·66	43·01

TABLE 4. THE RELATION OF MATURITY AND LENGTH

Length-group	1953–54 Immature	1953–54 Mature	1953–54 % mature	1954–55 Immature	1954–55 Mature	1954–55 % mature	Both years % mature
8	5	—	0	—	—	—	0
11	16	—	0	13	1	7·1	3·3
14	40	1	2·4	95	5	5·0	4·3
17	119	25	17·4	59	17	22·4	19·1
20	80	88	52·4	49	73	59·8	55·5
23	55	82	59·9	34	68	66·7	62·8
26	12	35	74·5	11	38	77·6	76·0
29	2	12	85·7	—	1	100	86·7
32	—	—	—	1	—	0	0
Total	329	243	—	262	203	—	—

TABLE 5. THE RELATION OF MATURITY AND WEIGHT

Weight-group	1953–54 Immature	1953–54 Mature	1953–54 % mature	1954–55 Immature	1954–55 Mature	1954–55 % mature	Both years % mature
10	61	—	0	101	6	5·6	3·6
40	157	41	20·7	83	29	25·9	22·6
70	58	91	61·1	46	48	51·1	57·2
100	40	63	61·2	24	67	73·6	67·0
130	10	26	72·2	5	35	87·5	80·3
160	3	10	76·9	1	15	93·8	86·2
190	—	8	100	1	2	66·6	90·9
220	—	3	100	1	1	50·0	80·0
250	—	1	100	—	—	—	100
Total	329	243		262	203		

TABLE 6. THE RELATION OF MATURITY AND LENGTH WITHIN AGES 3+ AND 4+

Age ... / Length-group	1953–54 3+ Immature	1953–54 3+ Mature	1953–54 4+ Immature	1953–54 4+ Mature	1954–55 3+ Immature	1954–55 3+ Mature	1954–55 4+ Immature	1954–55 4+ Mature
14	—	—	—	—	2	—	—	—
17	2	6	—	3	19	13	—	—
20	26	52	2	16	40	60	4	11
23	50	47	3	31	21	23	13	32
26	3	3	9	19	1	1	7	26
29	—	1	2	1	—	—	—	—
Total	81	109	16	70	83	97	24	69
Mean	22·16	21·45	24·69	22·97	19·90	20·35	23·25	23·58

TABLE 7. THE RELATION OF MATURITY AND WEIGHT WITHIN AGES 3+ AND 4+

Age ... / Weight-group	1953–54 3+ Immature	1953–54 3+ Mature	1953–54 4+ Immature	1953–54 4+ Mature	1954–55 3+ Immature	1954–55 3+ Mature	1954–55 4+ Immature	1954–55 4+ Mature
10	—	—	—	—	1	—	—	—
40	7	15	1	5	33	22	—	3
70	35	54	2	20	33	39	11	9
100	36	34	3	25	15	30	7	23
130	3	5	7	16	1	5	4	24
160	—	—	3	2	—	1	1	9
190	—	1	—	1	—	—	1	1
220	—	—	—	1	—	—	—	—
Total	81	109	16	70	83	97	24	69
Mean	82·96	80·46	115·63	99·71	56·87	66·29	89·58	98·99

TABLE 8. THE SPAWNING TIME OF THE LONG ROUGH DAB

Authority	Region	Range of spawning time	Maximum spawning
Bagenal (this paper)	Clyde	Feb.–Apr.	Mar.
Williamson (1899)	Loch Fyne	Mar.–June	Apr.
Günther (1888)	W. Scotland	Feb.–Mar.	Early Mar.
Bal (1943)	Irish Sea	Mar.–Aug.	Apr.
Ewart & Fulton (1889)	Firth of Forth	Dec.–May	Mar.
Ewart & Fulton (1889)	Moray Firth	Jan.–Feb.	—
Fulton (1890)	Moray Firth	—	Mainly Mar.
Otterstrøm (1906)	Kattegat & Baltic	—	Mar. only
Pertseva (1939)	Barents Sea	Mar.–June	End of Apr.
Rass (1936)	Barents Sea	Mar.–June	May
Saemundsson (1949)	Iceland	May–June	—
Huntsman (1918)	Bay of Fundy	Apr.–May	—
Huntsman (1918)	Gulf of St Lawrence	May–June	—
Huntsman (1918)	Newfoundland	July	—

TABLE 9. THE AGE AND MATURITY-STAGE DISTRIBUTION AT SPAWNING

		Maturity stage			
Date	Age	2	3	4	Total
30. iii. 54	3	5	1	1	7
	4	2	3	5	10
	5	1	1	12	14
	6	—	—	3	3
	Total	9	4	21	34
16. iii. 55	3	1	—	—	1
	4	8	3	—	11
	5	3	1	1	5
	Total	12	4	1	17
25. iii. 55	3	—	3	—	3
	4	—	2	5	7
	5	—	—	1	1
	6	—	—	1	1
	Total	—	5	7	12

TABLE 10. COMPARISON OF NUMBERS OF IMMATURE AND MATURE LONG ROUGH DABS IN DEEP AND SHALLOW WATER

		Depth			
		40–50 m		60–70 m	
Date		Haul III	Haul IV	Haul I	Haul II
14. ii. 55	Stage 1	31	27	15	8
	Stage 2	14	12	19	22
2. iii. 54	Stage 1	84		92	
	Stage 2	18		74	
	Stage 3	—		1	
8. iv. 54	Stage 1	55		12	
	Stage 2	—		3	
	Stage 3	1		2	
	Stage 4	11		63	
	Total non-breeding	197		127	
	Total breeding	56		184	
	Total	253		311	

TABLE 11. DETAILS OF CATCHES OF POST-LARVAL LONG ROUGH DABS

1954					1955				
Date	No.	Mean (mm)	S.D.	Gear	Date	No.	Mean (mm)	S.D.	Gear
6. v.	6	13·2	3·2	Plankton net	25. iv.	9	10·8	2·4	Plankton net
13. v.	7	12·7	2·6	Plankton net	2. v.	3	11·3	—	Plankton net
19. v.	86	15·2	3·8	Plankton net	4. v.	64	10·8	2·5	Plankton net
20. v.	16	15·9	4·4	Plankton net	9. v.	254	12·2	2·6	Plankton net
24. v.	1	20	—	Plankton net	17. v.	48	21·2	4·5	Plankton net
27. v.	1	10	—	Plankton net	23. v.	4	18·5	—	Plankton net
31. v.	1	22	—	Plankton net	28. v.	1	18	—	Plankton net
31. v.	69	23·7	1·8	Beam trawl	1. vi.	10	17·2	3·4	Plankton net
10. vi.	28	15·1	4·8	Plankton net	9. vi.	46	26·7	2·4	Beam trawl
14. vi.	26	24·8	2·7	Beam trawl	15. vi.	42	27·8	3·3	Beam trawl
25. vi.	13	26·1	2·8	Beam trawl	22. vi.	44	28·5	2·7	Beam trawl
2. vii.	22	29·0	2·8	Beam trawl	30. vi.	61	30·9	3·4	Beam trawl
20. vii.	56	33·0	3·9	Beam trawl	8. vii.	11	30·5	2·5	Beam trawl
12. viii.	26	40·8	3·5	Beam trawl	22. vii.	31	34·5	4·7	Beam trawl
19. viii.	38	38·6	4·5	Beam trawl	29. vii.	31	37·7	4·7	Beam trawl
31. viii.	33	43·1	4·1	Beam trawl	3. viii.	39	41·8	4·4	Beam trawl
7. ix.	21	47·1	4·9	Beam trawl	25. viii.	49	48·2	5·2	Beam trawl
21. ix.	37	46·8	3·6	Beam trawl					
21. x.	62	53·3	5·2	Beam trawl					

TABLE 12. DETAILS OF REPLICATE COUNTS OF LONG ROUGH DAB EGGS

Series no.	1	2	3	4	5	6	7	8	9	10
Count no. 1	1046	940	1051	917	858	1006	919	1032	1038	902
2	851	1069	1006	995	777	933	1153	1044	1009	1016
3	970	994	881	1037	844	796	931	875	1012	935
4	1114	1183	966	985	808	762	1077	960	978	1048
Mean	995·25	1046·5	976·0	983·5	821·75	874·25	1020·0	977·75	1009·25	975·25

Grand mean of 40 observations = 967·95
S.D. = 97·308
Coefficient of variation = 10·05 %

Mean of 10 means = 967·95
S.D. = 68·264
Coefficient of variation = 7·05 %

TABLE 13

Subgroup	S.S.L.	S.S.W.	S. products L.W.	Regression coefficient *b*	S.S. due to regression	Residual S.S.	Degrees of freedom
Age 1+	0·003397	0·054392	0·011935	3·513394	0·041932	0·012460	6
2+	0·223974	2·827187	0·764614	3·413852	2·610279	0·216908	124
3+	0·040840	0·535860	0·137443	3·365402	0·462551	0·063309	33
4+	0·008973	0·118283	0·032089	3·576173	0·114756	0·003527	4
					Total	0·296204	167
Total within ages	0·277184	3·535722	0·946081	3·413188	3·229152	0·306570	170
					Difference	0·010366	3
Between ages	0·964671	11·123082	3·274817	3·394750	11·117185	0·005897	2
					Sum	0·312467	172
Total	1·241855	14·658804	4·220898	3·398865	14·346264	0·312540	173
					Difference	0·000073	1

TABLE 14

Line	Source	Sums of squares	Degrees of freedom	Mean square	Variance ratio	Significance
1	Due to total regression	14·346264	1	14·346264	7939·272	**
2	Difference between 'means regression' and 'average within ages regressions'	0·000073	1	0·000073	—	—
3	Deviations of means about 'means regression'	0·005897	2	0·002948	1·635	N.S.
4	Between adjusted subgroup means	0·005970	3	0·001990	1·122	N.S.
5	Between subgroup regression coefficients	0·010366	3	0·003455	1·948	N.S.
6	Total deviations about subgroup regressions	0·296204	167	0·001774	.	.
7	Average within subgroups regression	0·306570	170	0·001803	.	.
8	Deviations about total regression	0·312540	173	0·001807	.	.
9	Total	14·658804	174	.	.	.

Line 1 is tested against line 8.
Lines 2 and 3 are tested against line 7.
Lines 4 and 5 are tested against line 6.
** indicates significance at 1 % probability level.
* indicates significance at 5 % probability level.
N.S. indicates not significant.
— indicates mean square less than that against which it is tested.

TABLE 15. SUMMARY OF THE ANALYSES OF VARIANCE TESTING THE DIFFERENCES IN LENGTH–WEIGHT RELATION BETWEEN AGE-GROUPS OF LONG ROUGH DABS IN 1954

	Females						Males	
	Immature		Maturing		Spent			
Source	2. iii.	2. vi.	2. iii.	25. xi.	8. iv.	2. vi.	2. vi.	9. ix.
Due to total regression	**	**	**	**	**	**	**	**
Difference between 'means regression' and 'average within subgroups regression'	—	—	—	N.S.	—	—	—	—
Deviations of means about 'means regression'	N.S.	**	N.S.	N.S.	—	—	—	—
Between adjusted subgroup means	N.S.	*	—	N.S.	—	—	—	—
Between subgroup regression coefficients	N.S.	—	—	—	—	—	N.S.	—

TABLE 16. SUMMARY OF THE ANALYSES OF VARIANCE TESTING THE DIFFERENCES IN LENGTH–WEIGHT RELATION OF GROUPS OF LONG ROUGH DABS IN SUBGROUPS BY DATES OF CAPTURE

	Females			
Source	Immature	Maturing	Spent	Males
Due to total regression	**	**	**	**
Difference between 'means regression' and 'average within subgroups regression'	**	**	**	N.S.
Deviations of means about 'means regression'	**	**	**	**
Between adjusted subgroup means	**	**	**	**
Between subgroup regression coefficients	**	N.S.	—	N.S.

TABLE 17. REGRESSION COEFFICIENTS (b) OF THE REGRESSIONS OF LOG WEIGHT ON LOG LENGTH TOGETHER WITH THEIR 95% FIDUCIAL LIMITS

	Females									Males		
	Immature			Maturing			Spent					
Date	Lower limit	b	Upper limit	Lower limit	b	Upper limit	Lower limit	b	Upper limit	Lower limit	b	Upper limit
1953 Oct.	3·18	3·36	3·54	2·25	2·75	3·24	—	—	—	2·75	3·16	3·57
Nov.	3·02	3·16	3·30	3·02	3·25	3·48	—	—	—	3·10	3·38	3·66
Dec.	3·01	3·17	3·32	2·91	3·19	3·46	—	—	—	2·23	3·18	4·12
1954 Jan.	3·20	3·30	3·40	3·00	3·20	3·41	—	—	—	2·92	3·55	4·18
Feb.	3·20	3·39	3·57	2·86	3·20	3·54	—	—	—	—	—	—
Mar.	3·32	3·40	3·47	2·98	3·15	3·32	—	—	—	1·96	3·01	4·06
Mar.	3·18	3·37	3·55	1·68	2·36	3·04	2·65	3·08	3·52	—	—	—
Apr.	3·08	3·28	3·47	—	—	—	3·02	3·31	3·59	—	—	—
May	3·21	3·28	3·35	—	—	—	3·17	3·34	3·51	2·39	3·97	5·56
June	3·18	3·25	3·32	—	—	—	2·97	3·11	3·25	2·75	3·00	3·25
July	2·82	2·98	3·14	—	—	—	2·70	3·33	3·95	2·82	3·11	3·40
Aug.	2·83	2·96	3·09	2·93	3·09	3·26	2·48	3·04	3·61	2·71	2·92	3·14
Sept.	3·01	3·16	3·31	2·71	3·19	3·67	—	—	—	2·65	2·99	3·32
Oct.	2·78	2·99	3·19	2·86	3·15	3·43	—	—	—	2·71	3·35	3·99
Nov.	2·87	2·99	3·10	2·87	2·98	3·10	—	—	—	2·41	2·84	3·26
1955 Jan.	3·04	3·11	3·18	2·86	3·12	3·38	—	—	—			
Feb.	3·21	3·32	3·44	2·86	3·03	3·21	—	—	—	2·25	2·89	3·54
Mar.	3·13	3·23	3·33	2·49	3·07	3·66	—	—	—			
Apr.	3·09	3·14	3·19	—	—	—	2·85	3·13	3·42	—	—	—
Total	3·14	3·17	3·20	3·04	3·11	3·18	3·04	3·14	3·23	2·95	3·07	3·18

TABLE 18. SUMMARY OF ANALYSIS OF VARIANCE TESTING DIFFERENCES OF REGRESSIONS OF LOG WEIGHT ON LOG LENGTH OF THE MAIN GROUPS (SEX AND MATURITY STAGE) OF LONG ROUGH DABS

Source	Significance
Due to total regression	**
Difference between 'means regression' and 'average within groups regression'	*
Deviations of means about 'means regression'	**
Between adjusted group means	**
Between group regression coefficients	N.S.

TABLE 19. THE EXPECTED WEIGHTS (g) FOR THE DIFFERENT MATURITY STAGES OF LONG ROUGH DABS 20·0 cm IN LENGTH FOR EACH MONTH OF CAPTURE, WITH THEIR 95% FIDUCIAL LIMITS

	Females								
	Immature			Maturing			Spent		
Date	Lower limit	$\hat{W}$	Upper limit	Lower limit	$\hat{W}$	Upper limit	Lower limit	$\hat{W}$	Upper limit
1953 Oct.	53·70	55·34	57·02	59·84	61·94	64·12	—	—	—
Nov.	55·08	57·02	59·02	60·81	62·52	64·27	—	—	—
Dec.	54·08	55·85	57·68	58·75	60·81	62·95	—	—	—
1954 Jan.	53·33	54·70	56·10	58·34	59·98	61·66	—	—	—
Feb.	51·76	53·95	56·23	56·89	59·70	62·66	—	—	—
Mar.	54·20	54·95	55·72	58·21	59·57	60·95	—	—	—
Mar.	48·53	50·23	52·00	43·85	49·77	56·49	40·09	43·25	46·67
Apr.	48·53	50·35	52·24	—	—	—	42·36	44·36	46·45
May	47·21	47·95	48·75	—	—	—	41·98	43·35	44·77
June	48·98	49·77	50·58	—	—	—	45·92	47·10	48·31
July	51·17	52·97	54·83	—	—	—	44·77	48·64	52·84
Aug.	48·75	50·23	51·76	51·76	52·97	54·20	45·50	48·08	50·82
Sept.	51·76	53·21	54·70	51·64	54·45	57·41	—	—	—
Oct.	49·09	51·29	53·58	54·33	56·10	57·94	—	—	—
Nov.	52·36	53·70	55·08	56·36	57·41	58·48	—	—	—
1955 Jan.	51·29	52·12	52·97	53·21	55·59	58·08	—	—	—
Feb.	50·47	51·64	52·84	60·53	61·80	63·10	—	—	—
Mar.	50·00	51·05	52·12	52·36	55·98	59·84	—	—	—
Apr.	49·77	50·35	50·93	—	—	—	44·16	48·19	52·60

	Males			Maturing females without gonads		
Date	Lower limit	$\hat{W}$	Upper limit	Lower limit	$\hat{W}$	Upper limit
1953 Oct.	43·05	56·75	74·82	55·59	60·39	65·61
Nov.	54·45	61·24	68·87	58·61	60·53	62·52
Dec.	35·89	56·75	89·74	56·23	58·48	60·81
1954 Jan.	45·50	59·84	78·70	53·46	55·21	57·02
Feb.	—	—	—	50·47	53·95	57·68
Mar.	36·73	52·97	76·38	50·47	51·40	52·36
Mar.	—	—	—	34·12	39·54	45·81
Apr.	—	—	—	—	—	—
May	33·73	51·76	79·43	—	—	—
June	41·11	45·19	49·66	—	—	—
July	47·42	52·60	58·34	—	—	—
Aug.	45·19	48·42	51·88	50·93	52·24	53·58
Sept.	47·42	53·21	59·70	49·55	53·46	57·68
Oct.	43·15	56·36	73·62	48·19	54·58	61·80
Nov.	43·25	51·88	62·23	49·66	52·97	56·49
1955 Jan.				49·43	52·00	54·70
Feb.	37·58	48·75	63·24	49·77	51·05	52·36
Mar.				42·85	45·92	49·20

TABLE 20. DISTRIBUTION OF PERCENTAGE MATURE FEMALE FISH IN GROUPS CLASSIFIED BY AGE AND LENGTH. ONLY PERCENTAGES BASED ON MORE THAN TEN FISH GIVEN

Age-group ...	1+		2+		3+		4+		5+	
Year	53–54	54–55	53–54	54–55	53–54	54–55	53–54	54–55	53–54	54–55
Length-group										
11	—	0	16·74	—	—	—	—	—	—	—
14	—	—	13·05	0	—	—	—	—	—	—
17	—	—	15·34	20·27	39·58	—	—	—	—	—
20	—	—	—	30·46	50·77	54·76	58·89	70·54	—	—
23	—	—	—	—	46·32	44·14	57·48	72·74	90·00	—
26	—	—	—	—	—	—	62·58	55·49	—	90·00

TABLE 21. DISTRIBUTION OF PERCENTAGE MATURE FEMALE FISH IN GROUPS CLASSIFIED BY AGE AND WEIGHT. ONLY PERCENTAGES BASED ON MORE THAN TEN FISH GIVEN

Age-group ...	1+		2+		3+		4+		5+	
Year	53–54	54–55	53–54	54–55	53–54	54–55	53–54	54–55	53–54	54–55
Weight-group										
10	0	—	0	13·94	—	—	—	—	—	—
40	—	—	20·09	15·79	55·67	39·23	—	—	—	—
70	—	—	40·22	—	51·18	47·41	72·44	42·13	—	—
100	—	—	—	—	44·20	54·76	70·91	61·14	—	73·26
130	—	—	—	—	—	—	56·54	67·78	—	—
160	—	—	—	—	—	—	—	71·56	—	—

TABLE 22. ANALYSIS OF VARIANCE OF PERCENTAGE MATURITY WITH LENGTH, WEIGHT AND AGE. ONLY PERCENTAGES BASED ON MORE THAN TEN INDIVIDUALS ANALYSED

Source	Sums of squares	Degrees of freedom	Mean square	Variance ratio	Significance
Between ages within lengths	3244·2618	7	463·466	$F=10·2$	Significant at 1 %
Between lengths within ages	570·1470	8	71·268	$F=1·6$	Not significant
Within ages and lengths	316·5692	7	45·224	—	—
Between ages within weights	1537·4635	6	256·244	$F=2·3$	Not significant
Between weights within ages	900·0838	7	128·583	$F=1·2$	Not significant
Within ages and weights	874·6500	8	109·331	—	—

TABLE 23. ANALYSIS OF REGRESSION OF GONAD WEIGHT ON LENGTH, AND OF GONAD WEIGHT ON WEIGHT FOR DIFFERENT AGES, FOR DATA OF TWO DATES

	Length (cm)		Weight (g)	
Source	15. ii.	2. iii.	15. ii.	2. iii.
Due to total regression	**	**	**	**
Difference between 'means regression' and 'average within age regression'	N.S.	N.S.	N.S.	*
Deviations of means about 'means regression'	N.S.	—	—	—
Between adjusted means	N.S.	—	N.S.	N.S.
Between regression coefficients	N.S.	**	N.S.	N.S.

TABLE 24. THE VALUES OF THE COEFFICIENTS FOR THE REGRESSIONS OF LOG GONAD WEIGHT ON LOG LENGTH AND ON LOG WEIGHT

	Length (cm)		Weight (g)	
Age	15. ii.	2. iii.	15. ii.	2. iii.
2+	—	3·408	—	0·881
3+	2·747	3·175	0·862	0·880
4+	5·845	2·339	2·082	0·650
5+	4·876	−0·797	1·092	0·076
Total regression	3·829	3·162	1·242	0·954

TABLE 25. THE EXPECTED GONAD WEIGHT OF A FEMALE LONG ROUGH DAB OF 69·98 g (THE GRAND MEAN WEIGHT)

	1953–54 (g)	1954–55 (g)
Aug.	—	0·64
Sept.	—	0·81
Oct.	1·88	1·61
Nov.	2·36	2·75
Dec.	2·99	—
Jan.	5·08	4·66
Feb.	6·70	8·13
Mar.	9·75	12·39
Mar.	10·50	—

TABLE 26. SUMMARY OF ANALYSES OF REGRESSIONS OF FECUNDITY ON LENGTH AND ON WEIGHT OF FISH IN DIFFERENT AGE-GROUPS

	Length		Weight	
Source	15. ii.	2. iii.	15. ii.	2. iii.
Due to total regression	**	**	**	**
Difference between 'means regression' and 'average within ages regressions'	—	—	—	N.S.
Deviations of means about 'means regression'	—	—	—	—
Between adjusted age means	—	—	—	N.S.
Between subgroup regression coefficients	N.S.	N.S.	N.S.	N.S.

TABLE 27. THE ABOUT REGRESSION MEAN SQUARES FROM THE ANALYSES OF THE REGRESSIONS OF LOG FECUNDITY (*F*) ON THE LOGS OF AGE (*A*) LENGTH (*L*) WEIGHT (*W*) AND GONAD WEIGHT (*G*)

F on	15. ii. 54	2. iii. 54
A	0·0949	0·1057
L	0·0233	0·0534
W	0·0161	0·0543
G	0·0272	0·0541
A and *L*	0·0240	0·0540
A and *W*	0·0168	0·0542
A and *G*	0·0195	0·0539
L and *W*	0·0166	0·0533
L and *G*	0·0128	0·0443
W and *G*	0·0103	0·0433
L, *W* and *G*	0·0108	0·0438

TABLE 28. EQUATIONS FOR ESTIMATING THE FECUNDITY (*F*) FROM LENGTH (*L*) WEIGHT (*W*) AND GONAD WEIGHT (*G*) OF LONG ROUGH DABS

Factor	Equation	Standard error of estimate (eggs)
	15. ii. 54	
L	$\hat{F}=1{\cdot}4333\ L^{3{\cdot}5533}$	±39,070
W	$\hat{F}=626{\cdot}71\ W^{1{\cdot}1388}$	±38,880
W and *G*	$\hat{F}=1674\ W^{0{\cdot}7699}\ G^{0{\cdot}2970}$	±38,750
L, *W* and *G*	$\hat{F}=3709\ L^{0{\cdot}2077}\ W^{0{\cdot}8350}\ G^{0{\cdot}2949}$	±38,750
	2. iii. 54	
L	$\hat{F}=7{\cdot}154\ L^{3{\cdot}0021}$	±26,890
W	$\hat{F}=1603\ W^{0{\cdot}9461}$	±26,910
W and *G*	$\hat{F}=3458\ W^{0{\cdot}5192}\ G^{0{\cdot}4481}$	±26,700
L, *W* and *G*	$\hat{F}=2111\ L^{0{\cdot}2556}\ W^{0{\cdot}4486}\ G^{0{\cdot}4403}$	±26,720

TABLE 29. THE 95 % FIDUCIAL LIMITS OF THE REGRESSION COEFFICIENTS (*b*) OF THE REGRESSIONS OF LOGARITHMS OF FECUNDITY ON THE LOGARITHMS OF AGE, LENGTH, WEIGHT AND GONAD WEIGHT

	15. ii. 54			2. iii. 54			
Factor	*b*	Lower limit	Upper limit	*b*	Lower limit	Upper limit	Remarks
Age	1·0033	0·6212	1·3854	1·0328	0·8894	1·1762	Linear
Length (mm)	3·5533	3·4304	3·6762	3·0621	2·8337	3·2905	>Cubic
Weight (g)	1·1388	1·1058	1·1718	0·9461	0·9235	0·9686	*ca.* linear
Gonad weight (g)	0·6907	0·6645	0·7169	0·8117	0·7806	0·8428	<Linear

TABLE 30. THE LENGTH, WEIGHT, GONAD WEIGHT, AGE AND EGG COUNTS OF FEMALE LONG ROUGH DABS

Fish no.	Total length (cm)	Flesh wt. (g)	Ovary wt. (g)	Age	Egg count 1	2	3	4	Fecundity estimate
				15 February 1954					
324	295	175·0	26·5	4+	940	1069	994	1183	209,300
325	230	84·0	10·5	3+	509	510	518	525	103,100
326	230	81·0	8·5	3+	471	430	510	408	90,950
327	245	106·5	11·5	3+	505	584	561	558	110,400
329	230	90·0	10·5	3+	515	519	520	506	103,000
330	250	101·5	12·5	3+	563	606	667	707	127,150
333	245	96·5	13·5	4+	703	730	814	731	148,900
334	240	95·0	11·5	4+	717	682	503	520	121,100
335	260	117·0	12·5	4+	767	700	693	772	146,600
337	210	65·0	4·5	3+	345	295	359	346	67,250
338	235	85·5	12·5	3+	437	406	412	508	88,150
339	255	106·0	7·5	4+	667	610	627	600	125,200
341	230	84·5	9·0	3+	538	491	513	450	99,600
342	250	118·5	10·5	3+	570	588	654	641	122,650
343	240	89·0	10·0	3+	392	383	401	553	86,450
348	215	69·5	6·0	4+	448	421	380	388	81,850
351	225	68·0	2·5	4+	268	267	342	273	57,500
354	240	95·0	9·5	4+	492	550	449	475	98,300
355	245	96·5	11·0	3+	653	573	587	646	122,950
359	290	172·0	24·0	5+	1340	1300	1245	1078	248,150
360	265	123·0	17·5	4+	967	1076	869	912	191,200
363	305	226·5	21·5	5+	1383	1256	1240	1281	258,000
365	240	78·0	7·5	5+	436	348	388	318	74,500
366	220	66·5	7·5	3+	356	310	396	307	68,450
370	200	57·0	9·0	3+	415	346	411	448	81,000
Mean	243·6	101·88	11·5	3·6		606·34			121,268
				2 March 1954					
379	190	35·0	8·5	3+	253	255	199	229	46,800
380	220	69·0	5·0	3+	354	331	366	348	69,950
381	235	83·5	13·0	4+	459	625	643	573	115,000
383	210	53·5	12·5	3+	489	399	537	347	88,600
385	245	85·5	13·5	4+	636	646	604	478	118,200
386	215	67·0	12·0	3+	558	504	447	461	98,500
387	195	50·5	6·5	3+	208	172	186	239	40,250
388	205	101·5	12·0	4+	374	464	474	458	88,500
389	220	69·0	13·5	4+	506	535	424	510	98,750
390	250	101·5	18·0	4+	873	773	780	681	155,350
391	200	47·5	5·5	3+	244	276	245	221	49,300
392	175	28·5	5·5	2+	247	242	181	202	43,600
398	290	156·0	10·5	5+	950	1025	1057	992	201,200
399	205	52·5	9·5	3+	349	345	382	286	68,100
400	215	65·5	14·0	4+	436	444	373	476	86,450
401	195	47·5	6·5	3+	250	233	216	191	44,500
402	225	65·5	11·0	4+	395	310	387	413	75,250
403	180	39·0	3·5	2+	208	219	252	213	44,600
404	200	56·0	11·0	4+	302	396	386	348	71,600
420	190	44·5	8·5	2+	266	214	285	237	50,100
421	225	73·0	13·0	3+	537	582	593	523	111,750
422	225	72·0	10·0	3+	474	537	543	506	103,000
423	190	43·5	3·0	3+	168	181	201	151	35,050
424	190	39·0	7·0	3+	189	238	172	227	41,300
425	225	77·5	11·0	3+	635	498	546	517	109,800
426	210	58·0	10·5	3+	363	435	452	360	80,500
427	210	60·5	11·5	3+	540	531	467	550	104,400
428	205	55·5	8·5	4+	416	335	363	345	72,950
429	230	73·5	11·5	3+	489	458	506	462	95,750
430	185	35·5	3·5	2+	218	190	187	177	38,600
431	200	53·5	6·5	2+	348	322	306	324	65,000
432	200	45·5	8·5	4+	401	402	428	325	77,800
433	210	64·0	11·5	3+	551	509	594	582	111,800
469	200	54·5	7·0	2+	299	370	321	312	65,100

TABLE 30 (*continued*)

Fish no.	Total length (cm)	Flesh wt. (g)	Ovary wt. (g)	Age	Egg count 1	2	3	4	Fecundity estimate
470	185	40·0	3·5	2+	161	188	174	173	34,800
471	210	55·5	10·0	3+	348	298	379	367	69,600
472	240	83·0	10·0	3+	485	520	509	546	103,000
473	200	44·0	10·5	3+	375	420	415	381	79,550
474	230	68·5	13·5	3+	517	514	503	453	99,350
475	205	52·0	7·0	4+	267	253	284	271	53,750
476	185	42·0	6·5	3+	1107	1112	1050	1057	216,300
477	175	34·0	4·5	3+	180	187	197	174	36,900
482	170	29·0	3·5	2+	166	197	210	199	38,600
483	180	32·5	6·5	2+	223	259	291	261	51,700
485	210	63·5	7·5	2+	288	336	363	347	66,700
486	215	59·0	9·5	4+	465	430	449	368	85,600
487	220	74·0	8·5	4+	368	396	369	408	77,050
488	235	90·0	14·5	3+	534	478	512	430	97,700
489	270	155·0	15·5	4+	258	270	249	273	52,500
490	200	60·0	7·5	3+	284	313	381	402	69,000
491	210	50·0	8·5	3+	280	292	351	292	60,750
492	195	42·5	7·0	3+	290	287	269	320	58,300
493	210	51·5	8·0	4+	296	266	302	305	58,450
494	180	39·0	6·0	2+	308	286	350	327	63,550
495	185	38·5	5·5	3+	271	270	346	280	58,350
496	185	40·0	6·0	3+	248	236	198	189	43,550
497	165	25·5	3·5	2+	170	191	142	141	32,200
503	245	102·0	18·0	3+	700	801	940	794	161,750
504	260	119·0	15·5	4+	1027	908	922	957	190,700
505	245	96·0	12·0	3+	700	701	701	698	140,000
506	240	93·0	12·5	4+	589	598	543	629	117,950
507	230	79·0	10·0	3+	549	510	613	492	108,200
512	220	73·5	10·5	3+	449	483	442	385	87,950
513	220	68·0	10·5	2+	377	426	380	454	81,850
514	220	68·5	11·0	3+	426	475	434	439	88,700
515	205	56·0	10·5	2+	484	421	411	454	88,500
516	215	58·0	9·0	3+	344	366	329	352	69,550
517	180	34·5	6·0	2+	236	170	229	218	42,650
518	185	41·5	5·5	2+	242	200	262	226	46,500
519	170	30·0	5·0	2+	154	172	151	175	32,600
520	170	33·0	5·0	2+	219	180	146	178	36,150
521	170	29·0	3·5	2+	150	148	130	169	29,850
522	165	27·0	3·0	2+	133	117	145	168	28,150
552	290	173·0	27·0	5+	1050	972	1055	953	201,500
553	270	107·5	17·0	5+	770	674	814	674	146,600
554	245	96·0	21·0	5+	729	662	792	610	139,650
555	255	97·5	15·0	5+	552	552	518	558	109,000
556	215	74·5	6·5	3+	347	374	360	391	73,600
557	210	62·0	6·0	3+	365	372	364	329	71,500
558	200	44·5	8·0	4+	365	316	301	326	65,400
559	195	50·5	7·0	2+	401	378	265	349	69,650
560	205	60·0	10·5	3+	476	442	387	469	88,700
561	210	55·5	7·5	3+	311	271	314	263	57,950
562	230	73·0	14·0	3+	415	403	414	445	83,850
563	225	78·0	8·0	3+	508	457	355	429	87,450
564	265	121·5	22·0	5+	872	786	752	850	163,000
565	230	70·5	7·0	3+	454	371	385	408	80,900
566	215	57·5	9·0	4+	280	288	302	268	56,900
567	240	90·5	11·5	4+	553	584	588	538	113,150
568	190	40·0	4·0	3+	272	241	199	260	48,600
569	200	59·0	4·5	2+	307	307	346	334	64,700
Mean	21·16	63·87	9·44	3·1		409·22			81,844
					15 March 1954				
669	155	21	4·0	.	102	158	136	121	25,850
					30 March 1954				
691	165	28	5·5	2+	197	202	156	191	37,300
692	150	18	4·0	2+	127	139	118	130	25,700

APPENDIX 1

THE ANALYSIS OF THE LENGTH–WEIGHT RELATION AND CONDITION

The data used in this analysis were obtained from the samples listed in Table 1. The methods of obtaining the data have been given, but it must be remembered that there is no evidence available as to the selectivity of the trawl with regard to the length–weight relation. We may suppose that the fatter and heavier fish of a given length would be more easily retained by trawl meshes of a given size.

A preliminary scatter diagram (Fig. 1) of length and weight suggested that their relationship was of the form

$$W = aL^n,$$

where W = weight, L = length, a is constant and n an exponent approximately = 3. The analysis of the data could best be accomplished by using logarithms and fitting the straight line regression of log weight on log length,

$$\log W = \log a + n \log W$$

to the data by the method of least squares.

The data were divided into four groups according to sex and maturity as follows: (1) males; (2) immature females (stage 1); (3) maturing females (stage 2); (4) spent females (stage 4). These groups were further divided into subgroups by month of capture. Although it was originally proposed to further divide the subgroups into their respective age-classes, this was not found to be practicable owing to the small numbers that would be in each division. The two largest subgroups from each main group were chosen and a preliminary analysis carried out to see if the length–weight relation differed in the different age-classes. This was carried out by an analysis of covariance in a manner similar to that used by LeCren (1951). For an account of the statistical methods see Snedecor (1946, pp. 318–29) and Mather (1946, pp. 119–28). As an example of the calculations, the data for the immature females in the sample caught on 2 March 1954 are given in Tables 13 and 14. The two most important tests (apart from line 1, Table 14) are those of lines 4 and 5 (Table 14). The first tests the significance of the differences between the expected weights in each subgroup corresponding to the grand mean length. This is therefore a test of the differences in condition between the different subgroups (see next section). The second tests the difference between the subgroup regression coefficients and is therefore a test of the difference in length–weight relation of the subgroups. The other tests are of less interest. Line 3 tests the significance of the regression of the means of the subgroups, while line 2 tests whether there is a significant difference between the average of the subgroup regressions and the regression of their means. It is obvious that if line 3 is significant, line 2 can have no meaning.

Various tests were performed on the data before the regression analyses were carried out, in order to see to what extent the assumptions made were in fact valid. Bartlett's test of homogeneity was applied to the residual variances (Pearson & Hartley, 1954); because in order that the tests of significance may be valid the data must be homogeneous. These tests showed that the data were heterogeneous. The heterogeneity was not removed by considering the age-groups separately and it was thought that Bartlett's test might have revealed non-normality in the log length and log weight frequency distributions. Tests for normality were carried out on a large number of these distributions and the majority were found to be significantly non-normal. It is clear that if the lengths are normally distributed, the weights will not be, if the length–weight relation approximates to $W = aL^3$. Although taking logarithms helps to normalize the weights, it simultaneously tends to skew the lengths. For a

critical discussion a considerably more complicated form of analysis is required, and it was not thought that such an analysis was justified with the present data. It should be borne in mind, however, first that the effects of non-normality do not invalidate the estimates of the regression; the equation found is still the 'best straight line' (by the method of least squares) for the data; it is only the tests of significance that are less reliable than would be the case with strictly normal and homogeneous data. Secondly, the effect of non-normality is usually to produce more significant results than would otherwise be found (Cochran, 1947). In this work on Long Rough Dabs it was found (for example in Tables 5 and 6) that the comparisons being tested were mostly either not significant ($P > 0{\cdot}05$) or highly significant ($P < 0{\cdot}01$), and in only a few cases would the conclusions be changed by using the 0·01 level of probability as a basis for rejection of a hypothesis rather than the more usual level of 0·05, and the more severe test may be used for these data.

THE LENGTH–WEIGHT RELATION

The analyses of the regressions of log weight on log length were first carried out on different age-groups of otherwise comparable fish (Table 15). These 'between ages' comparisons were made on the two subgroups from each main group that contained the most individuals. It can be seen that in one case there was no definite trend in the means of the different ages, and in this case too the differences in 'condition' of the fish are possibly significant. It will be noted that in no case was there a significant difference in the length–weight relation of the different ages as shown by the regression coefficients. This evidence suggests that the age-groups may be pooled and the analysis continued to test the differences on different dates of collection.

The results of these analyses are given in Table 16 and the regression coefficients for the regressions are given in Table 17 together with their 95 % fiducial limits.

These limits were calculated as

$$b \pm t[1/Sx^2 \text{ (residual s.s.}/n-2)]^{\frac{1}{2}},$$

where t = Student's 't' for $n-2$ degrees of freedom, Sx^2 = sum of squares for length, residual s.s. = residual sum of squares (e.g. from Table 13). In Table 16 it will be noted that only for the immature females are there significant differences between the coefficients for different dates.

It is usual in studies of the length–weight relation of fish to test if the regression coefficients are significantly different from 3, to see if the fish in question obey the 'cube law'. It can be seen from Table 17 that 3 is within the 95 % fiducial limits for most subgroups except those of the immature females, for which the coefficients are mostly significantly greater than 3. However, with the total regressions, based on all the points summed over dates, only with the males do the fiducial limits include 3. It is usually assumed that differences in the regression coefficients at different times are not of interest and are only estimates of the overall value. However, the fluctuations in the coefficient may be of interest since they indicate how different size-groups are behaving in their length–weight relation. For example, if all fish are putting on weight and the large fish do so relatively faster, the coefficient increases, whereas if the coefficient decreases it is indicative of relatively faster weight increase by the smaller fish. In this way the study of the regression coefficient should be closely linked with the analysis of the condition.

It has been noted that only the immature females showed significant differences in the regression coefficients of different dates. These are shown graphically in Fig. 2, where it can be seen that there appears to be a yearly cycle in the value of b. The biological significance of this cycle has already been discussed. With maturing and

spent Long Rough Dabs the differences in the coefficients are not significant, but even so they may be of interest. The values of the coefficients for the total regression (pooled over dates for each group) are also given in Table 17, and the significance of their differences are shown in Table 18. The data for the immature fish are included even though not homogeneous.

In Table 16 can be found the significance of the differences in the adjusted means for the different subgroups (dates) of the main groups of Long Rough Dabs. These adjusted means for each subgroup are the expected mean weights of fish of the grand mean length (for each main group). They are, therefore, a test of the condition between the subgroups of fish and it will be noticed that in each case the differences are significant. Within each group the adjusted weights are comparable, but in order to compare the condition of the different groups one with another it is necessary to adjust the weights not to the mean length of the group but to a length more suitable for all the groups.

An arbitrary length of 20 cm was chosen as being conveniently within the range of all the groups and sufficiently near the grand mean length. While male Long Rough Dabs as large as 20 cm are rare, this length is at the lower end of the range of mature females. The weights expected ($\hat{W}$) for fish of 20 cm calculated from the regression equations for each month are given in Table 19 together with their 95% fiducial limits, and are shown diagrammatically in Fig. 3. The differences found to be significant in Table 6 can be taken as equally applying to these variations. A discussion of the results is given earlier in the paper.

The expected weights are given by

$$\hat{W} = \overline{W} . L^b / \bar{l}^b,$$

where $L = 20$ cm, and $\overline{W}$ and $\bar{l}$ are the arithmetic means of the weights and lengths obtained from the raw data. This equation is derived from

$$\log \hat{W} = \log \overline{W} + b(\log L - \log \bar{l}),$$

but for estimating the weight from the lengths, the antilog of $\log \hat{w}$ gives a biased result since it is based on the mean of the logarithms (= geometric mean) and the arithmetic mean should be used (M. Bagenal, 1955). The 95% fiducial limits of estimated weight ($\hat{W}$) are given by

$$\text{Antilog } [\log \hat{W} \pm t[(1/n + (L - \bar{l})^2 / Sx^2) \text{ residual s.s.}/n - 2]^{\frac{1}{2}}].$$

In this case the limits may be calculated on the logarithmic values and the antilogarithm taken to give the limits in grams.

APPENDIX 2

THE ANALYSIS OF MATURITY AND AGE, LENGTH AND WEIGHT

The data for the percentage of mature fish were grouped into two tables for length and weight (Tables 20 and 21). It will be seen that in some cases the two years 1953–54 and 1954–55 provided pairs of percentages of the same age and length. The variability between these pairs provided a standard against which it was possible to test (after a transformation of percentages into angles) (Snedecor, 1946, p. 447 and table 16·8) the variability between ages within length-groups, and between length-groups within ages; and similarly for ages and weights.

The result of this test is given in Table 22, where it is seen that the variability between different ages with the same length is significantly greater than that between years, though the variability between length-groups of the same age is not.

A comparable analysis for age and weight is also given in Table 22. Here the variance between ages, although double that of the 'between weights' is not statistically significantly greater than that of the 'between pairs' variance.

APPENDIX 3

THE ANALYSES OF GONAD WEIGHT

The effect of the age of the female Long Rough Dab on gonad development was examined in preliminary regression analyses of the logarithms of the gonad weights on lengths and on weights for different ages carried out on the data of 15 February and 2 March 1954. The results of these analyses are summarized in Table 23. Full details of method and data are given in Appendix 1.

The coefficients for the regressions of gonad weight on length for the different ages were found to differ significantly for the 2 March data. To a large extent this variability was due to the inclusion of the data from the six 5-year-old fish, which were widely scattered; but even without these fish the coefficients were significantly different at the 5 % level. Since in the analysis of regression on weight the regression coefficients were not significantly different it is probably safe to ignore this anomalous result. The values for the regression coefficients are given in Table 24. There is no clear trend in the coefficients with increasing age and those for the regressions of gonad weight on weight may be taken to indicate a linear relationship; that is, the data suggest that there is no difference in the gonad weight/flesh weight ratio in the different age-groups.

The analyses summarized in Table 23 indicate that either length or weight may be used in the further analysis of the gonad weight annual cycle, and that the different ages may be pooled. The standard error of estimates of gonad weight are very comparable for the length and weight regressions, being 0·112 g for the former and 0·119 g for the latter for the March data, and 0·146 g for both length and weight for February. For further analysis the regression of log gonad weight on log weight was used. The values for the regression coefficients did not appear to change from month to month in any ordered manner, showing there was no obvious difference in the time of gonad development of fish of different sizes. The adjusted gonad weights were calculated for fish of a grand mean weight of 69·98 g and are shown in Table 25 and Fig. 6.

APPENDIX 4

THE ANALYSIS OF FECUNDITY

In Fig. 9 the fecundity and length data are given as a scatter diagram for the 119 observations, and in Fig. 10 the fecundity and weight are shown. While the latter figure suggests that the relation of fecundity and weight may be linear, Fig. 9 suggests that the relation with length would be of the form

$$F = aL^n,$$

or

$$\log F = \log a + n \log L,$$

where F = fecundity, L = length and a and n are a constant and exponent to be obtained from the data. Both these suggestions were examined by analyses of the regressions of logarithm of fecundity on the logarithm of the independent factor. First, however, analyses of covariance were carried out to determine whether the relations of fecundity and length and weight changed significantly with age. These analyses were essentially similar to those shown in Tables 3 and 4 for the length–weight relation. The results of these analyses are shown in Table 26.

The regressions analysed were those of log fecundity on log length and log weight; the values for the fecundity were the arithmetic means of the four original estimates for each fish. Since the differences between the ages were not significant, the data were pooled and the regressions of log fecundity on log age, length, flesh weight and gonad weight were analysed. Later multiple regression analyses of fecundity on combinations of these characters were also carried out. In each analysis the 'due to regression' mean square was tested against the 'about regression' variance to test the validity of the regression in question. From the four estimates of the fecundity for each fish, the 'within fish' variance could be calculated ($=\Sigma F_i^2 - 4\Sigma\overline{F}^2$, where Fi for $i=1, 2, 3$ and 4 are the logarithms of the four fecundity estimates and $\overline{F}$ their mean) and was taken as a measure of the errors inherent in the counting and subsampling method. This 'within fish' variance is the appropriate mean square for testing the 'about regression' variance, since it is hoped to reduce the variability about the regression plane (by the most suitable combination of characters for estimation) until it is no longer significantly larger than the variability of the laboratory technique. The 'within fish' variance, however, was not large (0·0019 with 273 degrees of freedom, on 2 March 1954 and with 75 degrees of freedom on 15 February 1954), and the 'about regression' variances were always significantly greater than this. The more highly statistical method outlined above for finding the most suitable factors for use in estimating fecundity seems more satisfactory than that used by Simpson (1951) for Plaice. Although Simpson also counted four subsamples of the eggs from each fish, he used these not as a measure of his experimental error, but only to arrive at a more reliable estimate of the fecundity (the standard deviation of the estimate would be reduced by $\sqrt{4}$ of that of a single count). His estimate of the errors in the laboratory method was based on his count of forty subsamples taken specially for the purpose. With the methods given here one may easily measure which factors are the most reliable for estimating fecundity, and test their significances.

After the analyses of covariance and tests of significance had been carried out, the regression equations for estimation were transformed back from logarithms to actual values, and the standard errors of estimate of the real fecundity were calculated. This (by rearrangement of equation 5, M. Bagenal, 1955) is given by the standard error of estimate

$$=\sigma_{\hat{F}}=200\overline{F}[\text{antilog}\ (\sigma_y^2/\log_{10} e)-1]^{\frac{1}{2}},$$

where σ_y^2 = the total 'about regression' residual variance in logs and $\overline{F}$ = the arithmetic mean fecundity from all the estimates. Using the above formula to obtain the 'between counts' errors for the two sets of data one obtains $\sigma_{\text{counts}}=61{\cdot}240$ for the mean count of 606·34 eggs for 15 February and $\sigma_{\text{counts}}=41{\cdot}331$ for the mean count of 409·22 eggs of the 2 March collection. These both correspond to a coefficient of variation of 0·1010 or 10·10% (since the within fish variance was the same for both dates); this closely approximates to the value obtained from the 40 replicate counts. Of the standard errors of estimate given later for each regression equation ± 12,248 eggs and ± 8266 eggs can be accounted for by the variability in laboratory method of the February and March collections respectively.

The 'about regression' mean squares, obtained from the analyses of the regressions and multiple regressions of log fecundity on the logs of age, length, weight and gonad weight are given in Table 27. In all cases these are significantly greater than the 'within fish' mean square, showing that the great variability between fish cannot be due to experimental technique alone.

Of the single factors, age alone is of little use for estimating fecundity and, indeed, for the 15 February data, the 'due to regression' mean square is only significant at the 5% level. Furthermore, the addition of age to the other factors does not produce any

significant improvement, except to gonad weight with the February data. Age is not therefore considered in any three factor analyses.

On neither date does the addition of length to the regression of fecundity on weight significantly decrease the 'about regression' sums of squares, and for the March data weight does not significantly improve length alone for prediction purposes. In all other cases the addition of a second variate significantly reduces the 'about regression' sums of squares.

From the two variate analyses it is seen that for both dates weight and gonad weight together are the best for fecundity prediction purposes, and the addition of length as a third variate does not produce a significant improvement. The most useful equations for predicting fecundity are given in Table 28, together with the standard errors of estimate. The equations were obtained, in the case of the relation with length for example, in the form

$$\hat{F}=200\bar{f}.L^{b}/\bar{l}^{b},$$

where $\hat{F}$ is the expected fecundity for a given length (L) and $\bar{f}$ and $\bar{l}$ are the arithmetic means of the egg counts and lengths obtained from the raw data. This is similar to the equation used for estimating 'condition' from the length–weight relation (p. 372).

The choice of the measurement to be used for estimating fecundity should not of course be dictated solely by a consideration of Table 27. The lengths of fish are so much easier and quicker to obtain than the corresponding weights and gonad weights that if time is limited and the fish are not, greater accuracy in estimating the mean fecundity might be obtained by measuring length alone since the standard error of estimate would be reduced by increasing the sample size.

The values of the fiducial limits at the 95 % probability level for the coefficients of the regressions of the logarithms are given in Table 29.

A further aspect of the relation of fecundity to length and weight was examined by a consideration of the correlation of fecundity and condition. The correlation ($r=0{\cdot}12$) between the log condition ($=\log W-\log \hat{W}$) and the logarithms of the deviations of the fecundities from their expected values ($=\log F-\log \hat{F}$) was not found to be significant ($\hat{W}=$ expected weight and $\hat{F}=$ expected fecundity). In other words, it was found that there was no association between the deviations of the fecundities from the line of their regression on length, and the deviations of the weights from their regression line on length.

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ANNUAL VARIATIONS IN FISH FECUNDITY

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The variation in the fecundity of a fish species from year to year has not received much attention, although the changes in the numbers of young fish in the plankton are well documented for the Plymouth area (Russell 1930–47; Corbin, 1948–51). The most important work considering fecundity fluctuations is that of Simpson (1951) who, working on Plaice, *Pleuronectes platessa* L., concluded that during 1947, 1948 and 1949 there was a steady decrease in the number of eggs laid, this being due to a decrease in the mean size of the spawning fish which he showed to be correlated with the egg numbers. Simpson's interest in the fecundity was to provide a more accurate estimate for determining the number of plaice in the total population from planktonic egg surveys similar to the work of Buchanan-Wollaston (1923). He did not consider in detail whether the fecundity for a given length might change from year to year. It is this problem which will be considered here. Estimates of fecundity of Long Rough Dabs, *Hippoglossoides platessoides* (Fabr.), will be analysed, and Simpson's Plaice data will also be considered.

MATERIAL AND METHODS

The fecundity of the fish is defined, for the purposes of this paper, as the number of eggs in the ovary before spawning.

The data for Plaice are taken from the admirably complete appendix I given by Simpson (1951), where full details are presented for Plaice caught in the North Sea Southern Bight during 1947/48 and 1948/49.

The data for Long Rough Dabs for 1954 are given in table 30, appendix 4, of Bagenal (1957) and for 1955 and 1956 in the Appendix of this paper (p. 382). The details of sampling methods and subsequent laboratory treatment of the fish, together with particulars of the storage, subsampling, counting of the eggs and statistical analysis are all given in the earlier paper (Bagenal, 1957).

I would like to thank Miss Sheila Morris who counted the eggs and did much of the computation, my wife for statistical advice and the master and crew of M.V. *Calanus* who caught the fish.

LONG ROUGH DAB FECUNDITY IN 1954, 1955 AND 1956

The mean length, weight, age and fecundity are given in Table 1 for fish caught in 1954, 1955 and 1956, together with the expected weight ($\hat{W}$) of a fish 22 cm long. $\hat{W}$ has been calculated from the log length–log weight relation

and may be taken as a measure of the condition of the fish (Le Cren, 1951; Bagenal, 1957).

The expected fecundity ($\hat{F}$) of a 22 cm Long Rough Dab is also given for each year and has been calculated from the log length–log fecundity relation (Bagenal, 1957). The results of the statistical analysis are given in Table 2 and show that the fecundities, even after allowance has been made for the length

TABLE 1. SUMMARY OF DATA GIVEN IN TABLE 5

Year	1954	1955	1956
Number of fish	116	12	23
Mean length (cm)	21·85	21·04	22·70
Mean weight (g)	72·06	55·54	79·53
Mean age (years)	3·2	4·2	3·7
Mean fecundity	90,341	68,292	98,339
$\hat{W}$ for 22 cm	73·65	64·32	71·74
$\hat{F}$ for 22 cm	92,238	78,468	89,193

TABLE 2. ANALYSIS OF COVARIANCE OF LENGTH AND FECUNDITY DATA FOR LONG ROUGH DABS IN 1954, 1955 AND 1956

Source	Sum of squares	D.F.	Mean square	F	Significance
Due to total regression	19·043581	1	19·043581	1466·1	**
Difference between 'means regression' and 'average within years regression'	0·034180	1	0·034180	2·67	N.S.
Deviations of means about 'means regression'	0·099176	1	0·099176	7·75	**
Between adjusted fecundity means	0·133356	2	0·066678	5·22	**
Between years regression coefficients	0·043802	2	0·021901	1·71	N.S.
Total deviations about years regressions	7·642091	598	0·012779	—	
Average within years regression	7·685893	600	0·012801	—	
Deviations about total regression	7·819249	602	0·012989	—	
Total	26·862830	603	—		

** indicates significance at 1 % probability level.
* indicates significance at 5 % probability level.
N.S. indicates not significant.
The degrees of freedom are based on four counts for each fecundity estimate.

differences, differ significantly at the 1 % level from year to year. The condition, as shown by expected weights, for fish of 22 cm is also significantly different over the three years, and it is of interest that the ranked order is the same for condition and fecundity.

The large mean square for the deviations of the means about their regression, when contrasted with the very large mean square due to total regression and the smaller mean square after adjustment to a common length, emphasizes the utility of an analysis of covariance based on all the data.

PLAICE FECUNDITY IN 1947/48 AND 1948/49

The fecundity data given by Simpson (1951) for Southern Bight North Sea Plaice caught in 1947/48 and 1948/49 are summarized in Table 3.

The mean weights are based on the gutted weight minus ovary weight, as with the Long Rough Dabs, and the 'condition' ($\hat{W}$) also applies to somatic tissue only. The mean age is calculated assuming the queried ages Simpson gives were correctly assessed; to ignore the doubtful otolith readings would introduce bias since older fish are the most difficult to age.

TABLE 3. SUMMARY OF SIMPSON'S DATA ON PLAICE FECUNDITY IN THE SOUTHERN BIGHT IN 1947/48 AND 1948/49

Year	1947/48	1948/49
Number of fish	169	54
Mean length (cm)	37·14	37·08
Mean weight (g)	515·21	528·37
Mean age (years)	7·28	7·17
Mean fecundity	84,030	87,740
$\hat{W}$ for 37 cm	509·34	525·20
$\hat{F}$ for 37 cm	82,996	87,152

TABLE 4. ANALYSIS OF COVARIANCE OF REGRESSION OF LOG FECUNDITY ON LOG LENGTH

Source	Sum of squares	D.F.	Mean square	F	Signi-ficance
Due to total regression	16·348027	1	16·348027	641·80	**
Difference between 'means regression' and 'average within years regression'	0·037850	1	0·037850	1·49	N.S.
Deviations of means about 'means regression'	—	—	—	—	—
Between adjusted fecundity means	0·037850	1	0·037850	1·48	N.S.
Between years regression coefficients	0·007882	1	0·007882	—	—
Total deviations about years regressions	5·583633	219	0·025496	—	—
Average within years regression	5·591515	220	0·025416	—	—
Deviations about total regression	5·629365	221	0·025472	—	—
Total	21·977392	222	—	—	—

The relation of log fecundity to log length has been re-examined by an analysis of covariance, and the results are given in Table 4. A note arising out of this analysis is given in Appendix 2.

The degrees of freedom are based on one fecundity estimate for each fish.

An examination of Tables 3 and 4 show that the decrease in length in the catches over the two years is barely reflected in the data given by Simpson. The general level of fecundity increased, but this is not statistically significant, and Simpson was justified when he pooled the results for the two years. The weights adjusted to a common length are also not significantly different.

DISCUSSION

Simpson was correct in his conclusion that the drop in the mean number of eggs laid per female Plaice in the Southern Bight in 1947, 1948 and 1949 was only due to a decrease in the mean size of the spawning fish. The fecundity adjusted to a given length actually increased, though this was not significant over the two years for which data are given. In Long Rough Dabs from the Clyde area, however, significant changes have been found in the fecundity even after allowance has been made for length differences. If population estimates based on fish egg estimates are made over several seasons one cannot necessarily assume that the fecundity–length relation remains constant. An examination of Tables 1 and 3 shows that fecundity differences cannot be explained by the different age structure of the population.

It may, however, be significant that for the Long Rough Dabs and the Plaice the ranked order of fecundity and condition for the years considered are the same. Within a year (1954) no correlation was found between the condition and fecundity of individual Long Rough Dabs (Bagenal, 1957). Comparisons between years and different localities may help to explain some of the enormous variability in fecundity of otherwise apparently similar fish, and a programme of fecundity estimates of a number of species over several years is being initiated at Millport.

REFERENCES

BAGENAL, M., 1955. A note on the relations of certain parameters following a logarithmic transformation. *J. mar. biol. Ass. U.K.*, Vol. 34, pp. 289–96.

BAGENAL, T. B., 1957. The breeding and fecundity of the Long Rough Dab *Hippoglossoides platessoides* (Fabr.) and the associated cycle in condition. *J. mar. biol. Ass. U.K.*, Vol. 36, pp. 339–75.

BUCHANAN-WOLLASTON, H. S., 1923. The spawning of Plaice in the southern part of the North Sea in 1913–14. *Fish Invest. Lond.*, Ser. 2, Vol. 5, No. 2, 36 pp.

CORBIN, P. G., 1948–51. The seasonal abundance of young fish. IX–XI. *J. mar. biol. Ass. U.K.*, Vol. 27, pp. 718–22; Vol. 28, pp. 707–12; Vol. 30, pp. 271–6.

LE CREN, E. D., 1951. The length–weight relation and seasonal cycle in gonad weight and condition in the Perch (*Perca fluviatilis*). *J. Anim. Ecol.*, Vol. 20, pp. 201–19.

RUSSELL, F. S., 1930–47. On the seasonal abundance of young fish. I–VIII. *J. mar. biol. Ass. U.K.*, Vol. 16, pp. 707–22; Vol. 20, pp. 147–79 and pp. 595–604; Vol. 21, pp. 679–86; Vol. 22, pp. 493–500; Vol. 23, pp. 381–6; Vol. 24, pp. 265–70; Vol. 26, pp. 605–8.

SIMPSON, A. C., 1951. The fecundity of the Plaice. *Fish. Invest. Lond.*, Ser. 2, Vol. 17, No. 5, 27 pp.

APPENDIX 1

TABLE 5. THE LENGTH, WEIGHT, AGE AND EGG COUNTS OF FEMALE LONG ROUGH DABS

Fish no.	Total length (cm)	Weight (g)	Age (years)	Egg count 1	2	3	4	Fecundity estimates
				16 March 1955				
2017	25·5	98·0	4	583	646	704	603	126,800
2019	20·0	52·5	4	356	330	358	384	71,400
2020	20·5	51·5	4	313	301	271	305	59,500
2021	20·5	55·0	4	396	395	405	321	75,850
2022	21·0	46·5	4	207	225	191	234	42,850
2039	24·5	86·5	5	273	288	283	277	56,050
2040	17·0	26·5	3	142	186	171	177	33,800
2075	22·0	63·5	4	604	574	605	514	114,850
2076	19·5	36·5	5	243	189	271	235	46,900
2077	19·5	36·0	4	343	326	346	332	67,350
2082	23·0	72·5	5	448	469	367	384	83,400
2083	19·5	41·5	4	190	223	199	203	40,750
				22 February 1956				
1	17·0	25·5	3	158	204	157	158	33,850
2	18·0	33·5	3	231	275	234	186	46,300
3	19·0	38·5	2	241	250	239	234	48,200
4	19·5	44·5	3	289	316	296	279	59,000
5	20·5	58·5	3	376	315	372	340	70,150
6	22·0	76·0	3	429	449	440	396	85,700
7	22·0	70·5	4	392	349	368	408	75,850
8	23·5	87·0	3	589	601	565	577	116,600
9	23·5	96·0	3	716	709	704	759	144,400
10	25·5	103·0	4	629	676	721	636	133,100
11	26·0	110·0	4	760	790	694	835	153,950
12	27·5	151·0	5	958	906	850	842	177,800
13	23·0	77·0	4	362	438	482	368	82,500
14	22·5	68·5	5	518	421	516	478	96,650
15	22·5	67·5	4	328	308	346	252	61,700
16	20·5	48·0	4	349	383	383	470	79,250
17	20·5	45·0	4	270	304	270	315	57,950
18	24·0	81·0	5	396	350	329	428	75,150
19	24·5	92·0	4	424	394	524	452	89,700
20	24·0	94·0	3	586	657	594	539	118,800
21	25·0	117·0	4	927	939	1089	922	193,850
22	25·5	113·5	3	411	427	437	545	91,000
23	26·0	131·0	4	896	762	806	943	170,350

APPENDIX 2

In the analysis of the data the values of fecundity and length were transformed to their logarithms in order to produce a linear relation and to use the standard methods of regression analysis. An interesting point which emerges from the transformation of Simpson's North Sea Southern Bight data is that the geometric mean fecundity is larger for 1947/48, whereas the arithmetic mean fecundity is greater for the 1948/49 winter. The figures are summarized in Table 6. Had the differences between the means for the two seasons been significant, it might have appeared from the analysis that this was a decrease

and not an increase. The reason for this anomaly can be seen from the relation between the arithmetic and geometric means for a normal distribution which has been given by Bagenal (1955) and may be written

$$\text{G.M.} = \text{A.M.}/(1 + \sigma^2/\text{A.M.}^2)^{\frac{1}{2}},$$

where A.M. and G.M. are the arithmetic and geometric means and σ^2 is the variance. This gives for 1947/48 calculated G.M. = 72,458; for 1948/49 calculated G.M. = 67,126. The discrepancy between the actual and calculated geometric means is probably due to the data not being normally distributed, which is shown by the difference between the range and 6σ (Table 6).

TABLE 6. SUMMARY OF FECUNDITY STATISTICS FOR SOUTHERN BIGHT PLAICE

	1947/48	1948/49
Arithmetic mean fecundity	84,030	87,740
Variance (σ^2)	2,439,500,000	6,764,600,000
Range	332,000	280,000
6σ	296,316	493,500
Mean log fecundity	4·8317	4·7916
Geometric mean	67,874	61,888

It is clear that the difference between the ranked order of the arithmetic and geometric means of the two sets of plaice fecundity data is due to the large difference between the variances.

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THE ADAPTATIONS OF *LASAEA RUBRA* (MONTAGU), A SMALL INTERTIDAL LAMELLIBRANCH

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(Text-figs. 1–8)

Lasaea rubra is very abundant at Plymouth and has a wide intertidal distribution. It is of small enough size for experiments in which large numbers of animals are needed, and it has recently been studied from several points of view by various workers. Glynne Williams & Hobart (1952) and Morton (1954) have dealt with its ecology, Oldfield (1955) has given a detailed account of its functional morphology, Ballantine & Morton (1956) have examined its feeding and filtering, and Morton (1956) has studied its digestive cycle. Much information on its distribution has been given by Fischer (1940).

Life at the level reached by the high spring tide must offer a hard challenge to a bivalve that feeds and respires by filtering. In the present work a study has been made of the ecology of *L. rubra* in different microhabitats, and experiments have been carried out which shed light on its adaptations to conditions of brief submersion on the upper shore.

INTERTIDAL DISTRIBUTION AND ECOLOGY

L. rubra is found between the levels of the mean high-water spring and low-water spring tides. After a survey had been made of the Plymouth area, the rocks in front of the Plymouth Laboratory at the south side of the municipal swimming pool, and Church Reef, Wembury, were selected as two localities giving a representative range of typical habitats. Fig. 1 shows a simplified diagram of a levelled part of the shore at both places, together with curves, adapted from Colman (1933), showing percentage of exposure at various levels. *L. rubra* typically avoids extremes of high temperature and low humidity by sheltering in shallow crevices, in empty barnacles or in tufts of the lichen *Pygmaea pumila*. In this lichen Colman (1940) found its numbers to reach 12,140 per 100 g of lichen. A dozen or so animals, minute young as well

as adults, may cluster together, attaching to the substratum or to each other by temporary byssus threads. The species shows a thigmotaxis that must enable it to avoid exposed positions. When placed in sea water the animals creep actively towards points of attachment, or, if no other substrate is available, aggregate with each other.

Table 1 shows the types of habitat occupied by *Lasaea rubra* at Wembury and at Plymouth, and indicates the composition of the 'community'. Columns 5 and 6 of the table describe the colour and the nature of the algal infection of the shells; the shells of animals from each habitat usually have such characteristic appearance that the source may be easily recognized.

The histograms in Fig. 1 illustrate that there are also characteristic size differences between populations from different habitats. The largest modal and maximum sizes were found at Wembury Low and at Wembury High Spring. As already mentioned by Ballantine & Morton (1956), the animals found at Wembury High Spring are, in fact, larger than those from Wembury High Neap, and special attention has been given to them in this study. The smallest mean size was found in animals from Wembury *Pygmaea*, and Plymouth Medium High and Plymouth Low Neap animals are only a little larger.

The habitat between and inside the empty shells of *Chthamalus stellatus* shelters a characteristic fauna both at Plymouth (see Fig. 2) and at Wembury. There is a 'marine element' consisting of four main species, in the following order of numbers at middle *Chthamalus* level: *Lasaea rubra*, the isopod *Campecopea hirsuta*, and the periwinkles *Littorina neritoides* and young *L. rudis*. Towards the upper barnacle limit *L. neritoides* progressively outstrips the others until at the highest level it alone remains. A second faunal element consists of arthropods of land derivation: the most abundant is the small blue-black collembolan *Anurida maritima*, and, much less frequent, the beetle *Micralymma marinum*. The bright red mite *Bdella interrupta* is occasionally found in large numbers and, usually as single individuals, the pseudoscorpion *Neobisium maritimum*. The primitive marine pulmonate *Otina otis*, the Wembury form of which has been described by Morton (1954), probably also belongs to this terrestrial element and is frequently found in groups of about half a dozen among *Chthamalus* bases.

Legend to Fig. 1

Fig. 1. Schematic diagrams of shore profiles at Church Reef, Wembury, and the Plymouth foreshore, showing the various habitats mentioned in Table 1 in relation to tidal levels. At the left are superposed curves from Colman (1933), showing the average percentage of exposure over a fortnightly tidal cycle. The upper curve is that for splash, and the lower one for total submersion. On the right are shown tidal curves for a single spring tide at Plymouth on 4 September 1956, the upper curve for splash, and the lower one for total submersion. At the top of the diagram are shown the histograms for size distribution (shell length in mm), of the populations of *Lasaea rubra* at the different habitats (August 1956). (1) Wembury High Spring; (3) Wembury *Pygmaea*; (4) Wembury Low Neap; (5) Plymouth High Neap; (6) Plymouth Low Neap.

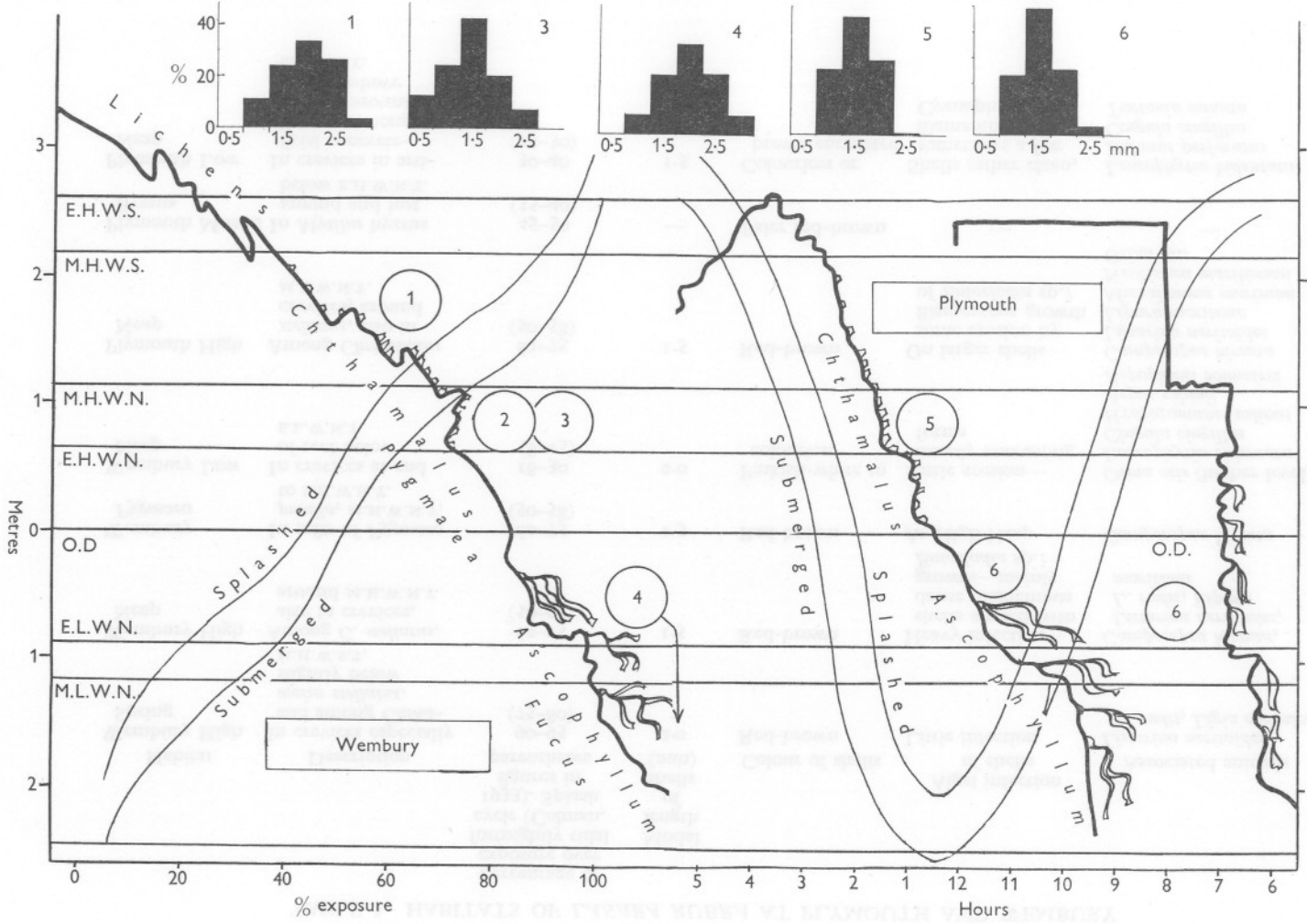
1
3
4
5
6
40
%
20
0
0·5
1·5
2·5
mm
Lichens
Chthamalus
Splashed
Submerged
pygmaea
Ascophyllum
Fucus
Wembury
Plymouth
E.H.W.S.
M.H.W.S.
M.H.W.N.
E.H.W.N.
O.D
E.L.W.N.
M.L.W.N.
O.D.
Metres
% exposure
Hours

Fig. 1

TABLE 1. HABITATS OF *LASAEA RUBRA* AT PLYMOUTH AND WEMBURY

Habitat	Description	Percentage of exposure over fortnightly tidal cycle (Colman, 1933). Splash figures in parentheses	Modal length of shells (mm)	Colour of shells	Algal infection of shells	Associated animals
Wembury High Spring	In crevices especially and among *Chthamalus stellatus*, slightly below M.H.W.S.T.	90–95 (75–80)	2·0	Red-brown	Little infection	*Littorina neritoides*, *L. rudis*, *Ligia oceanica*
Wembury High Neap	Among *C. stellatus*, also in crevices, around M.H.W.N.T.	62–75 (50–58)	1·5	Red-brown	Heavy infection—shells eroded with dense filamentous growth—mainly *Entocladia* sp.?	*Campecopea hirsuta*, *Littorina neritoides*, *L. rudis*, *Lipura maritima*
Wembury *Pygmaea*	In tufts of *Pygmaea pumila*, M.H.W.N.T. to E.H.W.N.T.	62–75 (50–58)	1·5	Red-brown	As High Neap	*Campecopea hirsuta*
Wembury Low Neap	In crevices at end of reef below E.L.W.N.T.	18–30 (8–15)	2·0	Pinkish-white to colourless	Little erosion—mainly encrusting forms	*Otina otis* (higher level) *Leucophytia bidentata* *Cingula cingillus* *Hydrogamasus salinus* *Aepus robinii* *Aepophilus bonnairei*
Plymouth High Neap	Among *Chthamalus stellatus*, also in crevices, around M.L.W.N.T.	62–75 (50–58)	1·5	Red-brown	On larger shells—some erosion by filamentous growth of *Entocladia* sp.?	*Campecopea hirsuta* *Littorina neritoides* *Lipura maritima* *Micralymma marinum* *Neobisium maritimum* *Otina otis*
Plymouth Mussel Byssus	In *Mytilus* byssus around and just below E.H.W.N.T.	45–50 (35–40)	—	Paler red-brown	—	—
Plymouth Low Neap	In crevices in artificial concrete-limestone conglomerate, around and slightly above E.L.W.N.T.	30–40 (25–30)	1·5	Colourless or brown encrusted	Shells rather clean, sometimes a few filamentous Cyanophyceae	*Leucophytia bidentata* *Balanus perforatus* *Cingula cingillus* *Turtonia minuta*

The lowest habitat of *Lasaea rubra* on the Plymouth foreshore (Table 1) is formed by chips of limestone cemented together at the base of a concrete platform. Here, *Balanus perforatus* and *Elminius modestus* are the predominant barnacles, and provide abundant cover for large numbers of pale-coloured *Lasaea rubra*. Chocolate-brown patches of the alga *Ralfsia* spread over the whole bare surface of the rock and may encrust some of the larger *Lasaea* shells.

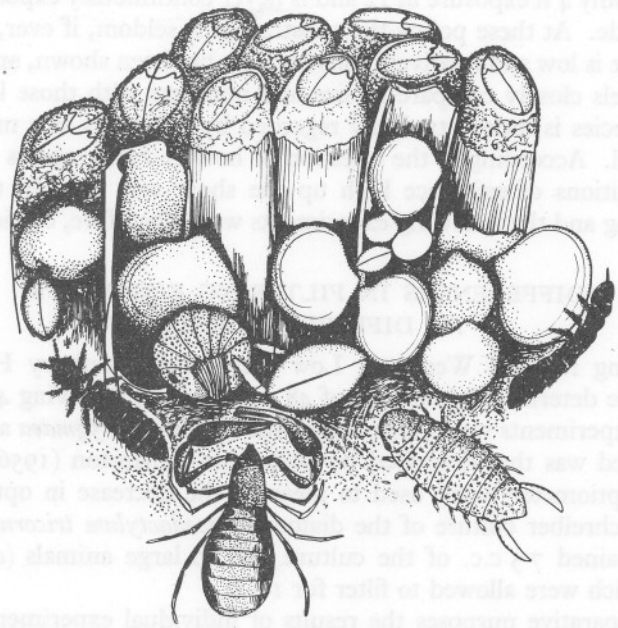

Fig. 2. A group of *Lasaea rubra* from H.W.N.T. at Plymouth, showing their typical situation between the bases of *Chthamalus stellatus*. The associated species, *Campecopea hirsuta* (isopod), *Lipura maritima* (collembolan), and *Neobisium maritimum* (pseudoscorpion) are also shown.

The small lamellibranch *Turtonia minuta* was also found in these habitats. This observation is of interest because the species has not previously been reported as a member of the Plymouth fauna. Although its habits are similar to those of the lowest occurring *Lasaea*, *Turtonia* seems to be confined to this low level and thereby differs from *Lasaea* which is also found farther up the shore. It is smaller than adult *Lasaea* and is pale yellowish white in colour, with darkened umbones. Superficially it is somewhat like *Lasaea*, but careful examination shows that it has quite a different shape, the height being only half the length, whereas it is three quarters of the length in *Lasaea*. Oldfield (1955) has presented a full account of the structure and habits of this bivalve as it occurs at Cullercoats, Northumberland.

PROBLEMS OF SHORT SUBMERSION AT HIGHER LEVELS

It has been calculated that *L. rubra* at its upper limit on Church Reef, Wembury (M.H.W.S.T.), receives an average of only 1 h submersion in 12, and at neap tides may not be totally submerged during a period of 12 consecutive days. Comparable figures for the highest *L. rubra* on Plymouth foreshore are 2·5 h and 7 days respectively. By contrast, *L. rubra* at M.L.W.N.T. receives an average of only 4 h exposure in 12 and is never continuously exposed for more than one tide. At these points the substratum is seldom, if ever, dry and its temperature is low and relatively constant. As has been shown, animals at the highest levels closely compare in size and numbers with those lower down, and the species is indeed typically regarded by collectors as a mid-to-upper tidal animal. Accordingly, the question of how *L. rubra* adapts itself to the harsh conditions of existence high up the shore was thought to be worth investigating and the following experiments were, therefore, carried out.

DIFFERENCES IN FILTERING BEHAVIOUR AT DIFFERENT LEVELS

The filtering rates of Wembury Low Neap and Wembury High Spring *Lasaea* were determined in a total of 48 experiments involving 480 animals: 6 further experiments were carried out with Wembury *Pygmaea* animals. The method used was that described by Ballantine & Morton (1956), a Harvey light absorptiometer being used to measure the decrease in optical density of an Erdschreiber culture of the diatom *Phaeodactylum tricornutum*. Each vessel contained 7·5 c.c. of the culture and 10 large animals (*ca.* 2 mm in length) which were allowed to filter for 1·5 h.

For comparative purposes the results of individual experiments are most conveniently expressed in units of optical density; conversion into volumes of culture filtered, assuming complete filtration of suspended matter, follows the relationship explained in the previous paper.

Fig. 3 shows the value of optical density at intervals of 0·5, 1·0 and 1·5 h for each experiment, and compares the results obtained from studies using Wembury High Spring and Wembury Low Neap *Lasaea*. For both series of experiments solid diagrams are also given, which express the results of experiments which gave the lowest, mean and highest values observed. These results confirm the difference first found by Ballantine & Morton (1956) in preliminary experiments on filtering rates. In general, high-tidal animals show, from the beginning of each experiment, a high and uniformly sustained rate of filtering over 1·5 h. Low-tidal animals show a very low filtering rate for the first hour, but after this time the rate gradually increases until it closely compares with that of the high-tidal animals. With Wembury High Spring animals Ballantine & Morton previously found that the filtering rate decreased after an experimental period of 3 h and became less than that of Wembury Low

Neap animals. The total volumes filtered by the two sets of animals over 6 h were thus approximately the same. Obviously, however, the quicker speed of response and initially more rapid filtering rate of high-level *Lasaea* must be a great advantage to these animals which are covered with water for little more than 1 h at any one time.

The filtering behaviour of animals from Wembury *Pygmaea* (6 experiments) and of others from Plymouth Low Neap was similar to that of the Wembury High Spring animals.

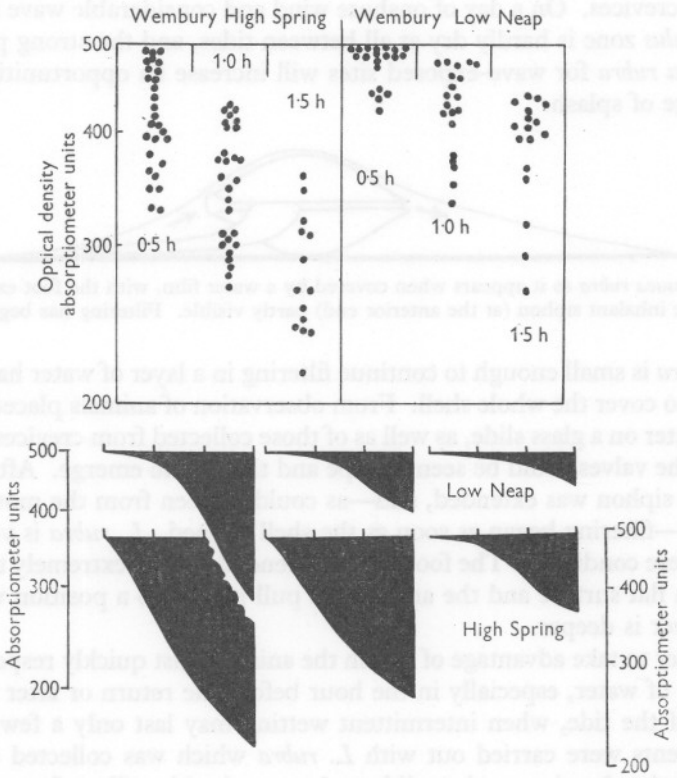

Fig. 3. Results of experiments on the filtering rate of *Lasaea rubra* from Wembury High Spring and Wembury Low Neap. In each experiment, 10 *Lasaea rubra* were placed in 3·75 c.c. of a culture of *Phaeodactylum tricornutum*, and allowed to filter for 1·5 h at room temperature (July 1956). Values are expressed in arbitrary absorptiometer units, and indicate the rate of clearing of suspended matter. *Upper half*: scatter of end values at 0·5, 1·0 and 1·5 h of all experiments (left, Wembury High Spring; right, Wembury Low Neap). *Lower half*: solid graphs from the results of experiments giving the highest, the mean and the lowest values obtained, with animals from Wembury High Spring (top row) and Wembury Low Neap (bottom row).

RESPONSE TO WAVE SPLASH

A further factor redressing the difference in filtering times is wave splash, which prolongs the effective period of submersion (Colman, 1933). The curves in Fig. 1 (right) show the results of 12 h observations of tidal level on the Plymouth foreshore on a day of slight offshore wind. The return of the tide at the *Chthamalus* level is hastened by about 1–1½ h by the action of splash and wave surge. The effective uncovering of a given spot is similarly delayed by splash and even longer by sea water lodged in the interstices of barnacles and in small crevices. On a day of onshore wind and considerable wave surge, the *Chthamalus* zone is hardly dry at all between tides, and the strong preference of *Lasaea rubra* for wave-exposed sites will increase its opportunities to take advantage of splash.

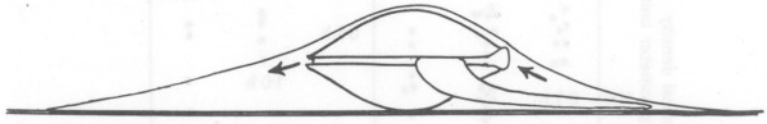

Fig. 4. *Lasaea rubra* as it appears when covered by a water film, with the foot extended and the inhalant siphon (at the anterior end) partly visible. Filtering has begun.

L. rubra is small enough to continue filtering in a layer of water hardly deep enough to cover the whole shell. From observation of animals placed in a film of sea water on a glass slide, as well as of those collected from crevices wet with splash, the valves could be seen to gape and the foot to emerge. After a short time the siphon was extended, and—as could be seen from the movement of particles—filtering began as soon as the shell opened. *L. rubra* is very active under these conditions. The foot can be extended into an extremely thin water film on a flat surface and the animal can pull itself into a position where the water layer is deeper.

In order to take advantage of splash the animal must quickly respond to the presence of water, especially in the hour before the return or after the withdrawal of the tide, when intermittent wetting may last only a few minutes. Experiments were carried out with *L. rubra* which was collected dry, then immediately placed on a glass slide and covered with a film of sea water.

Fig. 5 shows a comparison of the rates of response of Plymouth High Neap and Plymouth Low Neap animals, as estimated from the times needed for the feet to emerge from the shells and for filtering to begin. In 3–4 min each animal in a sample containing 100 was moving about freely with foot and siphon fully extended.

When treated in this way Plymouth High Neap animals were found to respond significantly faster than those from Plymouth Low Neap. Fig. 5 (below, right) indicates the scatter of values for experiments in which about 60 animals were used and in which the numbers filtering were recorded after

20, 40 80, and 120 sec. Cumulative histograms are also given which show the highest, the lowest and the mean values recorded after 2 min in experiments with animals from both levels. The results of typical experiments in which animals were totally submerged in a larger volume of sea water are included in Fig. 5 (upper row) for the purposes of comparison. Fully submerged *L. rubra* show a rate of response which is faster, but only slightly so, than that of animals covered with water on a slide. Further, the difference between High Neap and Low Neap values is greater in the experiments on slides. Although the power to respond quickly is especially well developed in *Lasaea* living at high-tidal levels, it is evidently an intrinsic feature of low-tidal animals as well.

Values for the rate of response of Plymouth High Neap *L. rubra* were plotted against the time for which the animals had previously been exposed on the shore, over the range 0·5–12 h. No obvious correlation was found. *L. rubra* is evidently able to seize any chance provided by splash or other moisture for filtering purposes, and it is probably advantageous that this power of response is highly developed at all times and independent of previous external conditions.

Relation of response rate to salinity

Fig. 5 shows percentage values for response to wetting over a period of 5 min for Plymouth High Neap *L. rubra*, in sea water of salinities ranging from 0·25 to 1·75 normal. A good tolerance, 75% or more of the normal response rate, was found at salinities between 0·75 and 1·25, within which range the animals appeared to behave normally. The ability to maintain its response to wetting in sea-water samples of widely different salinities may be of considerable importance to an animal which must make use, on the one hand of sea water diluted by rain between tides, and on the other, of sea water in which the salt content has risen by evaporation.

Comparative values are shown in Fig. 5 (lower right) for response by Plymouth High Neap and Plymouth Low Neap *L. rubra* to sea water of 0·5 normal salinity. The tolerance of half salinity appears to be significantly greater in the high-level animals. This may be partly because the animals at low-tidal levels are less likely to encounter large differences in salinity. A parallel is found in the recent report by Arnold (1957) of a higher response by high-tidal *Patella vulgata* to stimulus by water of abnormally high or low salinity. With *Lasaea rubra*, however, the difference may in part be caused by the generally slower response of low-tidal animals, as shown in the experiments described on p. 392.

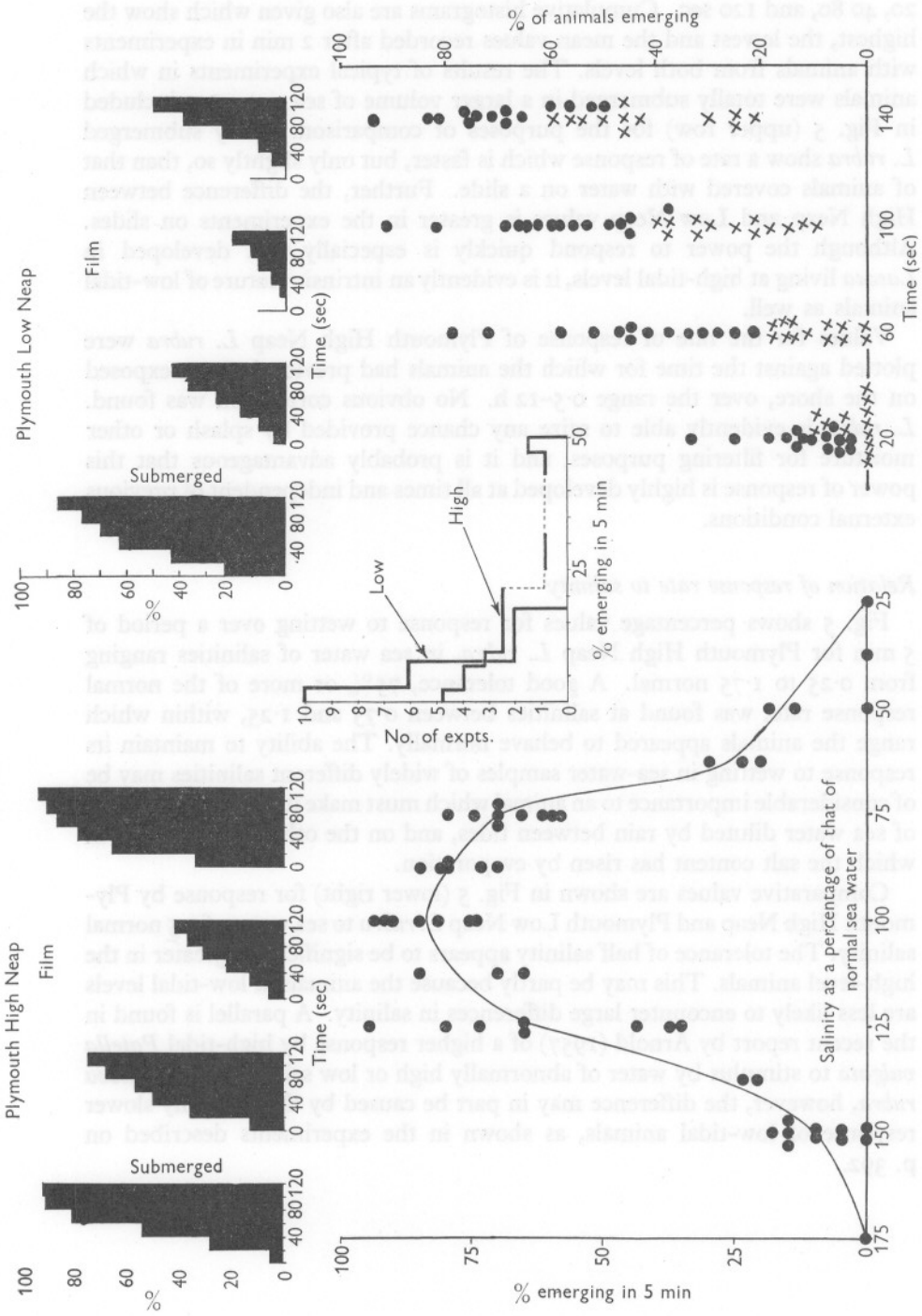
Plymouth High Neap
Film
Submerged
Plymouth Low Neap
Film
Submerged
Time (sec)
% of animals emerging
Time (sec)
No. of expts.
Low
High
% emerging in 5 min
% emerging in 5 min
Salinity as a percentage of that of normal sea water

Fig. 5

RESPIRATORY RATES OF HIGH- AND LOW-TIDAL ANIMALS

Method

Animals from Plymouth High Neap, Wembury High Spring and Wembury Low Neap levels were immersed in sea water for 6 h before measurements of respiratory rates were made. Oxygen uptakes were then followed manometrically at 25° C by the direct method of Warburg (Dixon, 1943) and the gas phase used was air. Approximately 75 animals were placed in 3 ml. of sea water in the main compartment of each flask and 0·2 ml. of 20% KOH, together with a roll of starch-free filter-paper, was placed in the centre well. Oxygen uptake was found to be independent of shaking rate in the range 50/100 oscillations/min (5 cm traverse), and there was no evidence of damage when animals were inspected at the end of each experiment. Most measurements of oxygen uptake were continued for 8 h, during which time an approximately linear rate was observed (see Fig. 6). Whitaker (1933) reports that when sea water is used as a manometric medium, the pH may increase from 8·0 to 9·5 as CO_2 is removed by the KOH in the centre well. Robbie (1946), using grasshopper eggs, concludes that the respiring material must offer a rate of CO_2-production of approximately 6μl./h in order to prevent an excessive shift in pH in an unbuffered sea-water medium. In the present work it was found that the sea water pH decreased slightly (usually from 8·0 to 7·6) during the 8 h experimental period, and this was so even when CO_2 production was considerably less than 6μl./h. Gas exchange alone would not account for this effect. Possibly the animals changed the pH of the medium by excreting substances that were slightly acidic to sea water.

After determinations of oxygen uptake had been made, the animals were left for 12 h in alcohol strongly acidified (HCl) to fix the tissues and remove the shells. They were then dried to constant weight at 100° C. The wet weight of an average sample of 100 specimens was about 120 mg, and the dry weight without the shell about 10 mg. The total nitrogen content of the

Legend to Fig. 5

Fig. 5. Results of experiments on the rate of response of *Lasaea rubra* from Plymouth High Neap and Plymouth Low Neap to splash-wetting (August and September 1956). *Above.* Cumulative histograms showing the response time, by protrusion of the foot, of *L. rubra* barely covered by a film of sea water on a glass slide. In each experiment, 100 animals were used, and observation continued for 2 min. Left: Plymouth High Neap; right: Plymouth Low Neap. In each group of histograms, the mean, lowest and highest result is represented. At the left of the group is shown, for comparison, a histogram for response time, after total submersion in sea water. *Below.* Left: a graph showing the relation between the speed of response (percentage response in 5 min) and the concentration of sea water, ranging from 0·5 to 1·5 normal. Animals from Wembury High Neap. Right: scatter of end values after 20, 60 and 100 sec, of experiments on response rate in sea-water films on slides. ●, Plymouth High Neap; ×, Plymouth Low Neap. *Centre.* Comparison of response rate in a film of sea water of 0·5 normal salinity, by animals from Plymouth High Neap and Plymouth Low Neap.

dried animals was determined by the micro-Kjeldahl method and was found to account for 3·36 and 3·30% of the shell-free dry weight of high and of low animals respectively. All oxygen uptakes were then expressed as Q_{O_2} (N), i.e. μl. O_2/h/mg tissue-N.

Preliminary experiments showed that the rate of oxygen uptake of animals at all levels varied inversely with the number of animals used in the experiment. Thus, high-level samples over the range 2·5–20 mg dry weight gave Q_{O_2} values between 2·5 and 1·2μl. O_2/h/mg dry wt. respectively: the corresponding values for low-level animals over the same range of biomass were between 1·3 and 0·45μl. O_2/h/mg dry wt. The influence of the quantity of animals on the rate of oxygen uptake was probably related to the tendency of *L. rubra* to aggregate, thereby reducing the free exchange of respiratory gases. Shaking the flasks very vigorously (*ca.* 120 oscillations/min) did not prevent aggregation, and accordingly, in order to carry out an adequate comparison of respiratory rates, it was necessary to use in all experiments the same narrow range of biomass. It was found that quantities of animals from each level yielding a dry weight of 5–10 mg gave within each group a very comparable level of results. From each tidal level studied, some 20 or more determinations were made, using approximately 1500 animals in each group of experiments.

Results

From the findings summarized in Fig. 6 it will be seen that there is a considerable difference in the rates of oxygen uptake of the medium- and low-level animals, and a smaller but significant difference between the rates of animals from medium high and high levels. Mean Q_{O_2} values are shown in Table 2 and indicate that animals from the low level possess a rate of respiration approximately 50% of that shown by those from the high level.

TABLE 2. COMPARISON OF THE FILTERING AND RESPIRATORY RATES OF *LASAEA RUBRA* WITH THOSE OF *MYTILUS EDULIS*

Mean Q_{O_2} (N) values (μl. O_2/h/mg tissue-N)		Filtering rate (ml./h/mg tissue-N)	
Lasaea rubra		*Lasaea rubra*	
Wembury High Spring	41·4	Value for 10 animals 2 mm in length deduced from data of Ballantine & Morton (1956)	53 (av.)
Plymouth High Neap	35·1		
Plymouth Low Neap	21·6		
Mytilus edulis		*Mytilus edulis*	
Value deduced from data of Jørgensen (1952) for animals 1·5 mm long	29·4	Animals 1·5 mm long	80 (av.)
		Animals 2·9–3·2 mm long (from Jørgensen, 1949)	34 (av.)

Using the results of a recent study by Jørgensen (1952) it has been possible to deduce Q_{O_2} (N) values for *Mytilus edulis* over a wide range of body size. The value corresponding to newly metamorphosed animals of the same size as the *Lasaea* used in the present work (*ca.* 1·5 mm) is included in Table 2

and shows that the respiration rates of the two species are very similar. A similar parallel between the filtering rates of larger *Mytilus edulis* (1·5–2·9 cm length) was found by Jørgensen (1949), and Ballantine & Morton's findings for *Lasaea rubra* (1956).

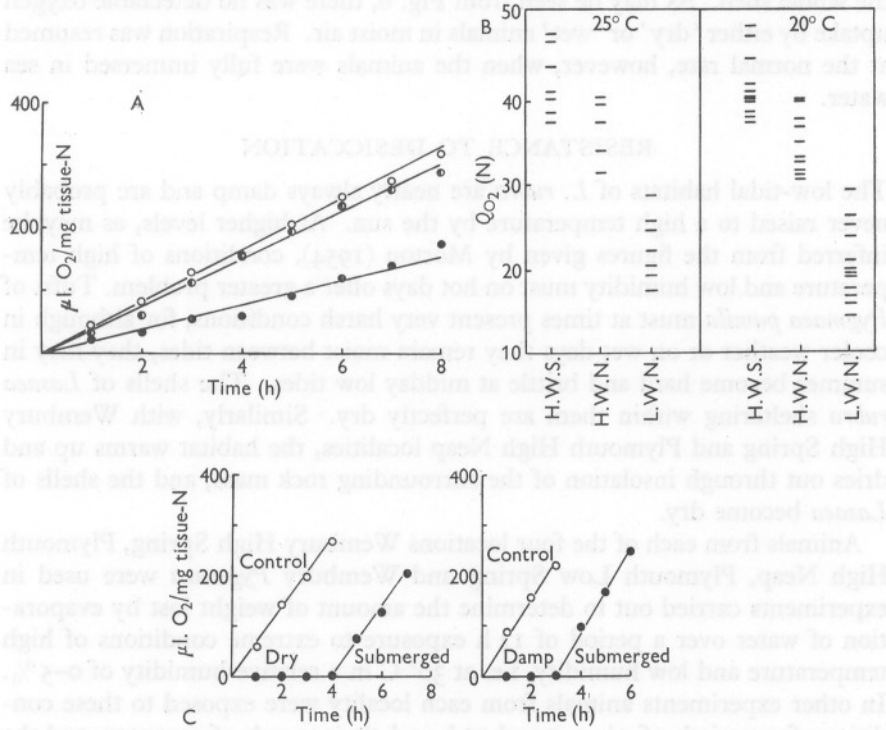

Fig. 6. (A) Respiration of High Spring (○–○), High Neap (◐–◐), and Low Neap (●–●) *Lasaea rubra*. Each point is a mean value of six determinations made at 20° C using 5–10 mg shell-less dry weight of animals. (B) Scatter of Q_{O_2} (N) values observed for *L. rubra* from three tidal levels. Left: experiments carried out at 25° C with 8–10 mg shell-less dry weight of animals for each determination. Right: experiments, conducted at 20° C, in each of which 5–10 mg shell-less dry weight of animals was used. (C) Respiration of High Spring *L. rubra* when dry (left), damp (right) and when submerged in sea water. ○–○, Animals submerged at once; ●–●, animals submerged after 4 h in a dry state (left) or 3 h in the damp state (right). Each point is the mean of four determinations carried out at 25° C with 5 mg shell-less dry weight of animals.

Respiration of 'dry' and 'wet' animals in moist air

Approximately 40 *L. rubra* from Wembury High Spring level (*ca.* 3 mg dry wt.) were placed, after careful drying of the shells, in Warburg flasks equipped with two side-arms. In each side-arm was placed 1·5 ml. of sea water. To each of three other flasks the same number of animals was added, immersed as usual in 3 ml. of sea water. Oxygen uptakes of dry and submerged animals

were then measured for 3 h, after which time the water from the side-arms was tipped upon the dry animals, and measurements of oxygen consumption continued for a further 3 h. A second experiment was made in which, instead of 'dry' *L. rubra*, the animals used lay in a water film insufficient to immerse the whole shell. As may be seen from Fig. 6, there was no detectable oxygen uptake by either 'dry' or 'wet' animals in moist air. Respiration was resumed at the normal rate, however, when the animals were fully immersed in sea water.

RESISTANCE TO DESICCATION

The low-tidal habitats of *L. rubra* are nearly always damp and are probably never raised to a high temperature by the sun. At higher levels, as may be inferred from the figures given by Morton (1954), conditions of high temperature and low humidity must on hot days offer a greater problem. Tufts of *Pygmaea pumila* must at times present very harsh conditions, for although in cooler weather or on wet days they remain moist between tides, they may in summer become hard and brittle at midday low tides. The shells of *Lasaea rubra* sheltering within them are perfectly dry. Similarly, with Wembury High Spring and Plymouth High Neap localities, the habitat warms up and dries out through insolation of the surrounding rock mass, and the shells of *Lasaea* become dry.

Animals from each of the four locations Wembury High Spring, Plymouth High Neap, Plymouth Low Spring and Wembury *Pygmaea* were used in experiments carried out to determine the amount of weight lost by evaporation of water over a period of 12 h exposure to extreme conditions of high temperature and low humidity, i.e. at 30° C in a relative humidity of 0–5%. In other experiments animals from each locality were exposed to these conditions for periods of $1\frac{1}{2}$, 4, 7 and 12 h and their speeds of recovery, and the percentages of the totals which recovered when they were replaced in sea water, were then determined. Recovery was assumed to have occurred the moment the foot or the siphon emerged.

Method

In studies of the rates of water loss, a thermogravimetric method was used in which the change of weight was measured by counterbalancing electromagnetically, as described by Gregg (1955). The balance was fixed to a wooden frame over a bath of water, the temperature of which was regulated by a Sun-Vic thermostatic control linked to an immersion heater. In the bath was placed a chamber (500 c.c.) in which the humidity was controlled by the use of appropriate concentrations of sulphuric acid. A wire gauze reaction vessel was placed in the humidity chamber, and suspended from the underside of a balance pan. In each experiment a sample of about 200 aggregated animals, drained of surplus water and with their shells only slightly wet, was placed in

the reaction vessel. The fresh weight was determined in the previously weighed reaction vessel. The humidity chamber was then closed by a divided cork, and weight loss was measured at intervals by briefly removing the cork and equilibrating the reaction vessel against the magnet of the balance.

Fig. 7 shows the curves for water loss over an experimental period of 11 h, calculated from the beginning of the second hour in the drying vessel (it was considered that most of the water loss after the first hour could be accounted for by the removal of water from the surface of the shells and the pallial

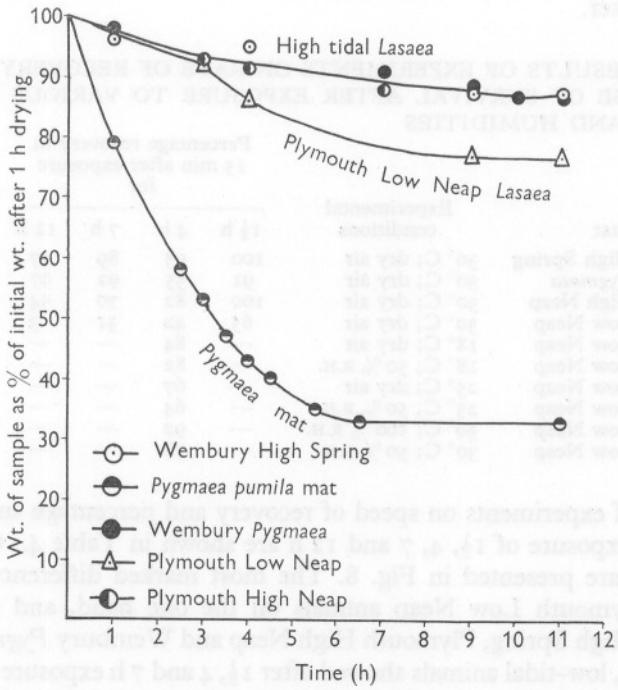

Fig. 7. Graphs showing loss of weight, by evaporation of water, of *Lasaea rubra* from various habitats. A sample of about 200 animals was exposed over a period of 12 h to a temperature of 30° C in an atmosphere of 0–5 % relative humidity. Weights are expressed as percentages of the weight of the sample after the first hour of drying, during which only surface water evaporated. The lower curve shows the values for the loss of weight by the intertidal lichen *P. pumila* under the same experimental conditions.

cavity). It is apparent that even in the high-tidal samples, the shells are unable to remain perfectly sealed against prolonged exposure to dry air, and, in fact, most of the animals replaced in water after more than 3 h drying at first floated with the umbones down. An air bubble could be seen in the pallial cavity, which was released when the animal extended its foot. Water loss from Plymouth Low Neap animals appeared to be about twice that from the

samples from the other three locations, amounting in 11 h to 23% by weight. In animals from Plymouth High Neap, Wembury High Spring and Wembury *Pygmaea*, the curves for water loss were almost identical over the 11 h experimental period. Thus, the low-tidal animals appear to be less able to keep their shells tightly closed over a long period. A behavioural difference in Plymouth Low Neap animals could sometimes be noticed which confirmed this result, namely that when these *Lasaea* were left in the dry state they did not close their shells as quickly as did those from higher levels, and occasionally their shells remained open for a considerable time after the animals were removed from sea water.

TABLE 3. RESULTS OF EXPERIMENTS ON RATE OF RECOVERY AND PERCENTAGE OF SURVIVAL AFTER EXPOSURE TO VARIOUS TEMPERATURES AND HUMIDITIES

Habitat	Experimental conditions	Percentage recovery in 15 min after exposure for				Percentage dead after	
		1½ h	4 h	7 h	12 h	7 h	12 h
Wembury High Spring	30° C; dry air	100	95	89	97	0	0
Wembury *Pygmaea*	30° C; dry air	91	55	92	97	0	0
Plymouth High Neap	30° C; dry air	100	82	70	54	0	24
Plymouth Low Neap	30° C; dry air	65	42	31	3	5	50
Plymouth Low Neap	18° C; dry air	—	84	—	—	—	—
Plymouth Low Neap	18° C; 50% R.H.	—	82	—	—	—	—
Plymouth Low Neap	25° C; dry air	—	67	—	—	—	—
Plymouth Low Neap	25° C; 50% R.H.	—	64	—	—	—	—
Plymouth Low Neap	30° C; 100% R.H.	—	92	—	—	—	—
Plymouth Low Neap	30° C; 50% R.H.	—	78	—	—	—	—

Results of experiments on speed of recovery and percentage survival after periods of exposure of 1½, 4, 7 and 12 h are shown in Table 4. Cumulative histograms are presented in Fig. 8. The most marked differences are seen between Plymouth Low Neap animals on the one hand, and those from Wembury High Spring, Plymouth High Neap and Wembury *Pygmaea* on the other. Thus, low-tidal animals showed after 1½, 4 and 7 h exposure a markedly slower rate of recovery than that of high-level animals when placed in sea water. After 7 h, 5% of the low-level animals had died, but the remainder eventually recovered. After 12 h exposure, 50% had died and although the remaining animals recovered they did so at a very slow rate. By contrast, in experiments with Wembury High Spring and Wembury *Pygmaea* animals it was found that even after prolonged exposure (12 h) there was almost complete recovery (80–90%) within 12 min of immersion in sea water. In experiments with Plymouth High Neap animals it was found that 24% of the sample were dead after exposure for 12 h and, further, the recovery of the remainder from this, and shorter, periods of exposure was slower than that observed in experiments with Wembury High Spring and Wembury *Pygmaea* animals.

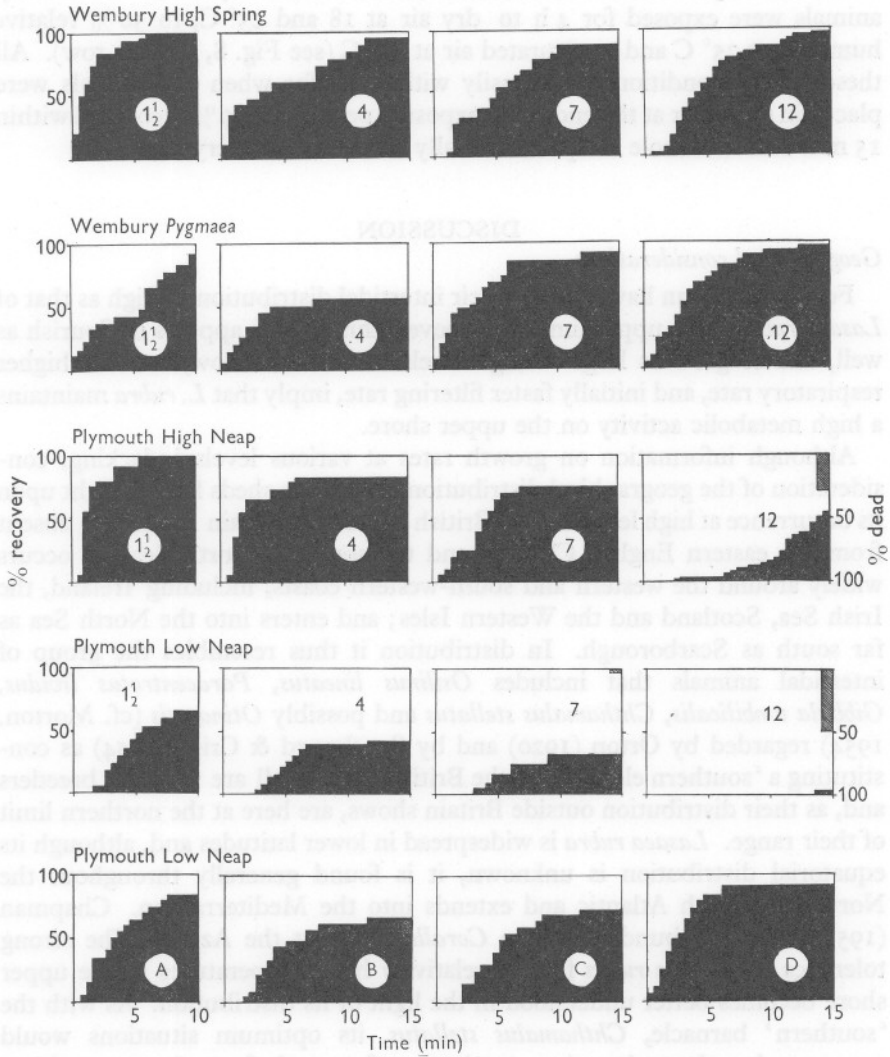

Fig. 8. Cumulative histograms showing the rate of recovery on return to sea water of *Lasaea rubra* which had been exposed to high temperatures and low humidities. Rows 1–4 describe the recovery of animals after exposure to an atmosphere of 0–5 % relative humidity at 30° C. Samples were returned to sea water after 1·5, 4, 7 and 12 h as indicated on each diagram. Row 5 describes the recovery of animals exposed for 4 h to 0–5 % relative humidity at 18° C (A); 50 % relative humidity at 25° C (B); 0–5 % relative humidity at 25° C (C) and 100 % relative humidity at 30° C (D).

Further experiments were carried out in which Plymouth Low Neap animals were exposed for 4 h to dry air at 18 and 25° C, to 50% relative humidity at 25° C and to saturated air at 30° C (see Fig. 8, bottom row). All these sets of conditions were easily withstood, for when the animals were placed in sea water at the end of the exposure period, 60–90% recovered within 15 min and the whole sample eventually recovered in every case.

DISCUSSION

Geographical considerations

Few bivalves can have pushed their intertidal distribution as high as that of *Lasaea rubra* at its upper limit. Moreover, this species appears to flourish as well, and to grow as large at high levels as it does at low, and the higher respiratory rate, and initially faster filtering rate, imply that *L. rubra* maintains a high metabolic activity on the upper shore.

Although information on growth rates at various levels is lacking, consideration of the geographical distribution of *L. rubra* sheds further light upon its occurrence at high levels on the British shore. In Britain *L. rubra* is absent from the eastern English Channel and the southern North Sea. It occurs widely around the western and south-western coasts, including Ireland, the Irish Sea, Scotland and the Western Isles; and enters into the North Sea as far south as Scarborough. In distribution it thus resembles the group of intertidal animals that includes *Osilinus lineatus*, *Paracentrotus lividus*, *Gibbula umbilicalis*, *Chthamalus stellatus* and possibly *Otina otis* (cf. Morton, 1954) regarded by Orton (1920) and by Southward & Crisp (1954) as constituting a 'southern element' in the British fauna. All are summer breeders and, as their distribution outside Britain shows, are here at the northern limit of their range. *Lasaea rubra* is widespread in lower latitudes and, although its equatorial distribution is unknown, it is found generally throughout the North and South Atlantic and extends into the Mediterranean. Chapman (1955) found it abundant in the *Corallina* turf at the Azores. The strong tolerance by *Lasaea rubra* for the relatively high temperatures of the upper shore becomes better understood in the light of its distribution. As with the 'southern' barnacle, *Chthamalus stellatus*, its optimum situations would appear to be where there is a maximum of warmth from the sun, subject always to protection from very prolonged high temperatures.

Adaptations

If, as its geographical distribution suggests, *Lasaea* has a preference for the English upper shore, considerable interest attaches to several adaptations which might help the animal to offset the adverse conditions of brief submersion and shortened filtering and respiring times. Small size is in itself an advantage which must enable the animal to filter from small volumes of water

intermittently splashed on to it between tides. In addition, there are behavioural adaptations such as rapid response to wetting—better developed at upper levels in the Plymouth population—which equip *Lasaea* as an 'opportunist' species able to take immediate advantage of splash. Southward (personal conversation) finds the same adaptation in high level *Chthamalus stellatus*. A further adaptation is that of site selection: thigmotaxis, negative phototaxis and preference for moisture all lead *Lasaea rubra* to aggregate in small crevices and in lichen tufts where splash probably collects and where desiccation is less likely. Activity in a rather wide salinity range (see p. 392) may also enable *Lasaea* to take advantage of splash diluted with rain water or to continue filtering after salinity has risen slightly by evaporation.

Our experiments suggest that animals at higher levels possess certain physiological adaptations concerned with filtering and respiration which must also protect them against the rigours of short submersion. Thus, studies of filtering rates disclose that whereas animals from high up the shore begin to filter rapidly as soon as they are wetted, low-tidal animals at first show a much lower filtering rate. After approximately 3 h, however, low-level animals build up a filtering rate approaching that of higher animals. These findings, while not implying an intrinsic difference between the filtering rates of high- and low-level *Lasaea*, do, however, draw attention to the much quicker response of high-tidal animals.

In contrast to the feeding-rate studies, investigation of the respiratory rates of *L. rubra* from Wembury High Spring, Plymouth High Neap and Plymouth Low Neap levels has shown marked intrinsic differences. Thus, animals from high up the shore respire at approximately twice the rate of Low Neap animals. Interest also attaches to the further finding that these high-level animals are unable to respire in moist air when damp or dry; evidently the price of high-tidal existence is paid not by using atmospheric oxygen, but by developing a rapid rate of aquatic respiration during brief periods of submersion.

There seems a need to explain why no respiration could be detected when animals are covered by a thin layer of water, though in this state filtering may be taking place. However, absence of measurable respiration need not imply absence of feeding, because collection of solid particles by the gill—although a ciliary process—must be relatively much faster than gaseous exchange. It is known that *L. rubra* is able to clear all particles from its own volume of water in 2 min. A few minutes' filtering of splash may thus be valuable from the point of view of feeding. The animal ingests large amounts of bottom detritus, such as may be stirred into suspension in falling splash, in addition to the rich phytoplankton found in Plymouth water samples at or near the substratum where *Lasaea* was collected (Ballantine & Morton, 1956).

Experiments on resistance to desiccation and recovery from exposure to high temperatures have shown that Wembury High Spring and Wembury *Pygmaea* animals are well able to withstand conditions of high temperature

and low humidity far more unfavourable than any which can occur in the field. In addition, it has been found that whereas Plymouth High Neap animals are only slightly less resistant than the Wembury High Spring and Wembury *Pygmaea Lasaea* to harsh experimental conditions, Plymouth Low Neap animals are much less resistant than the Wembury high-level *Lasaea* in this respect. These differences accord with tidal position (see Fig. 8), and reveal a clear physiological difference between populations at high and low levels. The shell pigmentation may be a relevant factor in temperature resistance, and it is hoped to investigate this further. Resistance to desiccation at high levels must depend upon tight closing of the shell when the animals are dry, and this evidently allows no respiratory exchange with damp air, or even when the shells are covered with a water film. Aerial respiration by a damp body surface must be paid for by restriction to 'safe' habitats of high humidity.

Comparison with other species

Other animals sharing the high-level habitat of *L. rubra* are the barnacle *Chthamalus stellatus* and the small periwinkle *Littorina* (*Melarhaphe*) *neritoides*. In some features of their ecology these bear comparison with *Lasaea rubra*. *Chthamalus stellatus* is also a filter feeder, but appears (see Monterosso, 1928) to be able to respire to some extent in a moist atmosphere. No detailed data are available for comparative respiration at various levels. Southward (1955), in a study of the influence of tidal level on cirral activity of barnacles, finds that whereas *Elminius modestus* and *Balanus balanoides* have a higher rate of cirral beat at low-tidal levels, *Chthamalus stellatus*—except at one locality—maintains an equally high rate at high levels. This feature of *C. stellatus* may offer partial compensation for short submersion time. A further advantage enjoyed by high-level *C. stellatus*—as compared with *Lasaea rubra*—must be its faster method of filtering, by means of cirri, under muscular control. A forthcoming account by Southward of filtering mechanisms of barnacles should make a comparison easier. *Littorina neritoides* depends on a film of moisture for feeding (Lysaght, 1941). It crops small algae and lichens with its radula, and does not need either submersion or heavy splash. Respiration can take place in moist air, although Fischer, Duval & Raffy (1933) have shown that it is five or six times higher in water than in air. Patané (1933) finds that *L. neritoides* regains activity after a few minutes in water, following 5 months' exposure to air.

Both the barnacle and the periwinkle reproduce by liberating free-swimming larvae. *Lasaea rubra* incubates the young between the gill lamellae. A free-swimming stage permits wide distribution and site selection, and such an opportunity for intermixture of extremes of the population and exchange of settling sites seems to be lacking in *L. rubra*. Young animals settle near the parent, and this tendency to isolation of small populations offers a method by

which physiological differences within the species—for example, in pigmentation, and in respiratory rate—might lead to ecological subspeciation.

A recent study by Segal, Rao & James (1953) of differences in water propulsion by *Mytilus californianus* at three depths, 'deep water at 30 ft.', 'low intertidal' and 'mid-intertidal', reveals higher activity as depth increases. The authors correlate this finding with temperature adaptation in a poikilothermal animal. But this situation is hardly comparable with that of intertidal *Lasaea rubra*, subjected as it is to long exposure on the upper shore. The lowest population of *L. rubra* corresponds in level to the highest ('mid-intertidal') population of *Mytilus*. The 'mid-intertidal' *Mytilus* are, moreover, smaller than the 'low-intertidal', and these in turn are smaller than the deep ones. It would appear that *M. californianus* is a species restricted as to size and probably metabolism, on entering the intertidal zone from off-shore. *Lasaea rubra*, however, with a wholly intertidal distribution, holds its own well at high water. A relevant fact is that the highest filtering rates recorded were from high-tidal animals at an experimental temperature of 22° C (Ballantine & Morton, 1956).

The mode of life, especially the reproduction and rate of growth, of *Lasaea rubra* invites further study. But from what we already know of its adaptations to life in the upper tidal zone, this bivalve seems to stand out—physiologically as well as geographically—as a member of the rather distinct 'southern component' of our intertidal fauna.

It is a pleasure to express our thanks to Mr E. R. March of Plymouth Technical College for constructing the electromagnetic sorption balance used in some of our experiments. Two of us (J.E.M.) and (A.D.B.) have been using London University Tables at the Plymouth Laboratory, and one of us (E.D.S.C.) is indebted to International Paints Ltd. for a Research Fellowship. We are most grateful to the Director and many members of the staff of the Plymouth Laboratory for the encouragement and helpful advice they have given us throughout the research.

SUMMARY

A study has been made of the ecology of the small intertidal lamellibranch *Lasaea rubra* at various tidal levels at Plymouth and Wembury. In addition, experiments have been carried out to investigate physiological and behavioural differences arising from varying amounts of submersion at different tidal levels, and the following findings have been made.

During the first hour after their submersion by sea water, *L. rubra* from high up the shore filter at a rate approximately twice that of animals which live lower down. After 2 h, however, both sets of animals filter at the same rate.

High-level animals respond significantly faster to wetting by splash and can tolerate a considerable range of salinity. They also respire at a rate

approximately twice that of low-level animals. Respiration, however, is not detectable when the animal is not immersed in sea water.

L. rubra from all levels show a good resistance to desiccation when exposed to high temperature and low humidity, but over a 12 h period low-level animals lose more water by evaporation. Moreover, when the low-level animals are subjected to these harsh experimental conditions they show a lower rate of recovery and a lower percentage of survival.

These findings are discussed with reference to the geographical distribution of *Lasaea rubra* and its status as a warmth-loving member of a southern faunal element.

REFERENCES

ARNOLD, D. C., 1957. The response of the limpet, *Patella vulgata* L., to waters of different salinities. *J. mar. biol. Ass. U.K.*, Vol. 36, pp. 121–8.

BALLANTINE, D. & MORTON, J. E., 1956. Filtering, feeding and digestion in the lamellibranch *Lasaea rubra*. *J. mar. biol. Ass. U.K.*, Vol. 35, pp. 241–74.

CHAPMAN, G., 1955. Aspects of the fauna and flora of the Azores. VI. Density of animal life in the *Corallina* alga zones. *Ann. Mag. nat. Hist.*, Vol. 8, pp. 801–5.

COLMAN, J. S., 1933. The nature of the intertidal zonation of plants and animals. *J. mar. biol. Ass. U.K.*, Vol. 18, pp. 435–76.

—— 1940. On the faunas inhabiting intertidal sea-weeds. *J. mar. biol. Ass. U.K.*, Vol. 24, pp. 129–83.

DIXON, M., 1943. *Manometric methods*. 122 pp. Cambridge University Press.

FISCHER, P. H., 1940. Sur l'habitat de *Lasaea rubra*. *Bull. Mus. Hist. nat., Paris*, Ser. 1, T. 12, pp. 433–5.

FISCHER, P. H., DUVAL, M. & RAFFY, A., 1933. Études sur les échanges respiratoires des littorines. *Arch. Zool. exp. gén.*, T. 74, pp. 627–34.

GLYNNE WILLIAMS, J. & HOBART, J., 1952. Studies on the crevice fauna of a selected shore in Anglesey. *Proc. zool. Soc. Lond.*, Vol. 122, pp. 797–824.

GREGG, S. J., 1955. An electromagnetic sorption balance. *J. chem. Soc.*, pp. 1438–9.

JØRGENSEN, C. B., 1949. The rate of feeding by *Mytilus* in different kinds of suspension. *J. mar. biol. Ass. U.K.*, Vol. 28, pp. 333–44.

—— 1952. Efficiency of growth in *Mytilus edulis* and two gastropod veligers. *Nature, Lond.*, Vol. 170, p. 714.

LYSAGHT, A. M., 1941. The biology and trematode parasites of the gastropod *Littorina neritoides* (L.) on the Plymouth foreshore. *J. mar. biol. Ass. U.K.*, Vol. 25, pp. 41–67.

MONTEROSSO, B., 1928. Studii cirripedologici III. Persistenza dei fenomeni respiratori nei Ctamalini mantenuti in ambiente subaereo. *Boll. Soc. biol. Sper.*, Vol. 3, pp. 1067–70.

MORTON, J. E., 1954. The crevice faunas of the upper intertidal zone at Wembury. *J. mar. biol. Ass. U.K.*, Vol. 33, pp. 187–224.

—— 1956. The tidal rhythm and action of the digestive system in the lamellibranch *Lasaea rubra*. *J. mar. biol. Ass. U.K.*, Vol. 35, pp. 563–86.

OLDFIELD, E., 1955. Observations on the anatomy and mode of life of *Lasaea rubra* (Montagu) and *Turtonia minuta* (Fabricius). *Proc. malacol. Soc. Lond.*, Vol. 31, pp. 226–49.

ORTON, J. H., 1920. Temperature, breeding and distribution in marine animals. *J. mar. biol. Ass. U.K.*, Vol. 12, pp. 339–66.

PATANÉ, L., 1933. Sul comportamento di *Littorina neritoides* L., mantenuta in ambiente subaereo ed in altre condizione sperimentali. *R.C. Accad. Lincei*, Ser. 6, Vol. 17, pp. 961–7.

ROBBIE, W. A., 1946. The quantitative control of cyanide in manometric experimentation. *J. cell. comp. Physiol.*, Vol. 27, pp. 181–209.

SEGAL, E., RAO, K. P. & JAMES, T. W., 1953. Rate of activity as a function of intertidal height within populations of some littoral mollusca. *Nature, Lond.*, Vol. 172, p. 1108.

SOUTHWARD, A. J., 1955. On the behaviour of barnacles. II. The influence of habitat and tidal level on cirral activity. *J. mar. biol. Ass. U.K.*, Vol. 34, pp. 423–33.

SOUTHWARD, A. J. & CRISP, D. J., 1954. The distribution of certain intertidal animals around the Irish coast. *Proc. R. Irish Acad.*, Vol. 57 B, pp. 1–29.

WHITAKER, D. M., 1933. On the rate of oxygen consumption by fertilized and unfertilized eggs. IV. *Chaetopterus* and *Arbacia punctulata*. *J. gen. Physiol.*, Vol. 16, pp. 475–95.

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STUDIES IN THE GENUS *FUCUS* L.[1]
I. *FUCUS DISTICHUS* L. EMEND. POWELL

By H. T. POWELL

The Marine Station, Millport

(Plates I and II and Text-fig. 1)

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INTRODUCTION

Apart from the alga currently known as *Fucus spiralis* L. emend. Batt., and certain hermaphrodite hybrid *Fucus* forms that will be discussed in a later paper, several other hermaphrodite forms of the genus *Fucus*[1] occur on the shores of the North Atlantic, the North Pacific and the Arctic oceans. These forms have been described under many different names by many authors; and there has been and still is much confusion, as well as real difference of opinion, concerning their delimitation and taxonomic status.

Thus, many European authors, including Rosenvinge (1893) for Greenland, Börgesen (1902) for the Faeröes, and Jónsson (1903) for Iceland, regard all such forms, occurring in the various parts of the North Atlantic studied in detail by them, as ecological forms of a single species, and have shown that, at least in some parts of this wide area, all possible intermediate forms between the more distinctive extreme forms can be found. The name *F. inflatus* L. has

[1] The full citation of author's names for this genus is *Fucus* L. (1753) pro parte, emend. Dec'ne et Thur. (1845); for most purposes, however, it is sufficient to shorten the citation to *Fucus* L. (The often used citation '*Fucus* (L.) Dec'ne et Thur.' is nomenclaturally incorrect.)

been generally used by recent European phycologists[1] for this complex of forms and several characteristic forms have been widely recognized as follows:

Rosenvinge (Greenland, 1893)	Börgesen (Faeröes, 1902)	Jónsson (Iceland, 1903)
Fucus inflatus L., M. Vahl	*Fucus inflatus* L., M. Vahl	*Fucus inflatus* L., M. Vahl
var. *edentatus* (De la Pyl.) Rosenv.	f. *edentata* (De la Pyl.) Rosenv.	f. *typica* Jónss. (=*F. edentatus* De la Pyl.)
var. *evanescens* (C. Ag.) Rosenv.	(only a few specimens found that approached f. *evanescens* (C. Ag.) Rosenv.)	f. *evanescens* (C. Ag.) Rosenv.
var. *linearis* (Oed.) Rosenv.	f. *linearis* (Oed.) Rosenv.	f. *linearis* (Huds.)
—	f. *disticha* (L.) Börg.	f. *exposita* Jónss. (=f. *disticha* (L.) Börg.)

The type form, =f. *edentatus* (De la Pyl.), and f. *evanescens* (C. Ag.), of these authors are large plants found on sheltered or semi-exposed shores; f. *linearis* is a smaller, slender plant, usually found in littoral pools; f. *disticha* (L.) Börg., =f. *exposita* Jónss., is a small, narrow, but robust form developed on coasts very exposed to swell and wave-action.

Recent North American authors, on the other hand, interpret certain essentially similar North American Atlantic and Pacific fucoids as distinct species, as follows:

(i) North-east Atlantic coast of North America (Taylor, 1937):
F. edentatus De la Pyl., *F. evanescens* C. Ag., *F. filiformis* Gmel. (in pools), *F. miclonensis* De la Pyl.; (also listed are *F. serratus*, *F. vesiculosus* and *F. spiralis*).

(ii) Pacific coast of North America (Gardner, 1922; Setchell & Gardner, 1925):
F. edentatus De la Pyl., with five forms recognized and described. (Species based upon a Newfoundland plant.)
F. evanescens C. Ag., with twenty-one forms. (Species based on North Pacific material.)
F. furcatus C. Ag., with thirteen forms. (Species based on North Pacific material.)
F. membranaceus Gardner, with six forms.
F. nitens Gardner.

These authors reject the name *F. inflatus* L. altogether, on the grounds that Linnaeus's original short description and the fragmentary specimens bearing the name '*inflatus*' in the Linnaean Herbarium are inadequate to delimit any particular species of *Fucus*.

In order to determine the correct names to apply to two forms of '*Fucus inflatus*' found in Britain it has been necessary, therefore, to consider first the following taxonomic and nomenclatural problems: (i) are the fucoids

[1] Lund (1949*a*, *b*) uses the name *Fucus edentatus* De la Pyl. in reporting the recent immigration of this fucoid into Danish waters but, in reply to an inquiry, he has informed me that he considers that the Danish plants should be named *Fucus inflatus* L., f. *edentatus* (De la Pyl.) in accordance with the views of Rosenvinge, Börgesen and others.

listed above sufficiently distinct to be regarded as separate species, or are they best regarded as forms of a single extremely variable species; (ii) if best regarded as a single species, is the use of the disputed specific epithet '*inflatus* L.' justifiable; and (iii) is the particular nomenclature adopted for formae by, for example, Rosenvinge, Börgesen and Jónsson, in best accord with modern taxonomic concepts and nomenclatural rules and procedures?

Species, subspecies, or formae?

After full consideration of all that has been published on the autecology and world distribution of these forms, I am in agreement with Börgesen (1902), Jónsson (1903), and other authors, that the numerous forms described are not sufficiently distinctive to warrant separate specific status, but are best interpreted for the present as forms of a single, extremely plastic, highly successful and widely distributed species. Chief weight is given to the fact that, at least near the centres of distribution of the species (e.g. in the Faeröe Islands and Iceland, and probably in northern Europe and on the Pacific coast of North America), whole series of forms (clines) of this fucoid intermediate in character between the extreme forms are very common. The close affinity of the various forms is further emphasized by the occurrence of caecostomata (see p. 418) in varying number in most, and probably all, of them, but not in any other species of *Fucus*.

Near the centres of distribution of the species it is possible to interpret the extreme forms as products of their ecological environment, with the intermediate forms developing under intermediate environmental conditions. Towards the southern and northern limits of distribution, however, the species is often represented by populations of only one or two of the more distinctive (best adapted) forms, confined to restricted habitats and often geographically isolated. Such isolated populations often have a very limited range of form, and several could well be regarded as genetically adapted ecotypes. For these reasons the more distinctive forms are interpreted as *subspecies* in the present paper.

THE CASE FOR REJECTION OF THE NAME *FUCUS INFLATUS* L.

The name *F. inflatus* is first used by Linnaeus (1737) in *Flora Lapponica*, Ed. 1, p. 351, No. 468, the material being collected (by Linnaeus?) at Rørstad in Nordlanden, Norway, on his Lapland journey in 1732. It is first described in this way: '*Fucus folio bifido, laciniis ovato-lanceolatis inflatis, ad apicem divisis.*' The diagnosis given by Linnaeus in *Species Plantarum* (1753, p. 1159) is '*Fucus fronde bifida: laciniis ovato-lanceolatis inflatis apice divisis. Fl. lapp.* 468, *Fl. suec.* 1004. *Habitat in Oceano Atlantico*'. Finally, in *Systema Naturae* (1766) and *Systema Vegetabilium* (1774), Linnaeus slightly enlarges the diagnosis to read as follows: '*Fronde plana, dichotoma, integerrima, punctata, ovato-*

lanceolata, inflata, apice diviso'; this may be translated as 'frond plane [flat], dichotomously branched, entire [margins], punctate [presumably this refers to the presence of cryptostomata], ovate-lanceolate [see below], inflated [probably refers to the presence of irregular inflations], divided at the apices'. These diagnoses of *F. inflatus* are certainly inadequate to define any particular species as understood to-day; Linnaeus is presumably describing sterile material and the diagnoses could fit, but could not define, forms of *F. ceranoides* L., *F. vesiculosus* L., or *F. edentatus* De la Pyl. (='*F. inflatus* L., M. Vahl' of authors), all of which may have irregular inflations in the thallus.

'*Fucus inflatus* L.' is first illustrated by Martin Vahl (1794) in *Flora Danica* (Vol. 7, fasc. 19, tab. 1127); the caption to tab. 1127 is identical with that quoted above from *Syst. Nat.*, and the reference given is 'Lin. S.V., p. 966' (i.e. it is quoted from *Syst. Veg.* of Linnaeus, 1774). However, Vahl adds the following information, presumably from his own knowledge, concerning the distribution of the species: '*Vulgaris in praefectura* Salten, Senjen *et* Tromsöen *Nordlandiae, in aliis partibus Norvegiae non mihi obvius*.'

However, throughout most of the nineteenth century (until Foslie, 1886) the name *F. inflatus* L. was not used for an independent species but, if used at all, was regarded either as a synonym or else as a form of *F. vesiculosus* L.; and, during this period, several new species of *Fucus* were first described, including *F. evanescens* and *F. furcatus* (C. Agardh, 1820), and *F. edentatus*, *F. fueci* and *F. miclonensis* (De la Pylaie, 1829).

Foslie (1886), in proposing that the name *F. inflatus* L. be revived, in particular for those Norwegian plants referred by other authors to *F. edentatus* De la Pyl., recognized that Linnaeus's description 'is no doubt incomplete' ('er vistnok ufuldstaendig'), but suggested that Vahl's illustration and further information on distribution be accepted as delimiting the species in a satisfactory manner, and proposed that the species be cited as '*F. inflatus* (L.) Fl. Dan.'. Foslie adds that certain other early authors (e.g. Lightfoot, 1777) had mistakenly used the name *F. inflatus* L. for certain forms of *F. vesiculosus* L., but suggests that it is very unlikely that Linnaeus, who correctly listed all the other true fucoids of Scandinavia in *Flora Lapponica*, would have set up two species for *F. vesiculosus*.[1] He states that it is highly probable that Linnaeus would have found the species in question at Rørstad; and adds that the epithet *inflatus* doubtless refers to the irregular swellings that are rather common, especially in sterile specimens of this species.

Foslie certainly presents as good a case as possible for retaining the name *inflatus* L. Later European authors, almost without exception, have accepted his views and so we find this species cited as '*Fucus inflatus* L., M. Vahl' by

[1] Linnaeus, however, does otherwise give two separate specific names to forms of *F. vesiculosus* as at present understood; in *Species Plantarum* (1753) in the section of *Fucus* described as '*dichotomi frondescentes*', we find the following six species: *serratus*, *vesiculosus*, *ceranoides*, *spiralis*, *inflatus* and *divaricatus*. The last-named is merely a form of *F. vesiculosus* (with single vesicles in the axils of all the branches, in the specimens in the Linnaean Herbarium).

Rosenvinge (1893), Börgesen (1902), Jónsson (1903), Kylin (1947) and others up to the present day. However, as the American authors Gardner (1922) and Taylor (1937) have decided that the type specimen of *F. inflatus* L. is a fragment that cannot be associated with any particular species, and use other specific epithets for American fucoids, it is important to resolve this nomenclatural impasse if possible.

For this reason I have been permitted to examine the specimens in the Linnaean Herbarium. The only specimens labelled *F. inflatus* L. in this herbarium are two small pieces of a fucoid mounted side by side on a single sheet (Genus 1274, *Fucus*, Sheet No. 51, in the Catalogue of Savage, 1945), and labelled near the foot of the sheet '5 inflatus' in Linnaeus's handwriting (Pl. I, fig. 1). The pieces of *Fucus* are incomplete (both lack a holdfast) and could well be parts of a single plant; both pieces are completely sterile. The left-hand specimen is 11·7 cm in length with three dichotomies; the lower part of the frond is narrow (3–4 mm) and most of the rest of the frond is less than 10 mm wide, except that midway along the two main branches the frond widens to as much as 17 mm and then becomes narrow again towards the tips. It is suggested that these wider parts are probably the reason for Linnaeus including 'ovato-lanceolata' in his description of the frond. The right-hand specimen is essentially similar, 11·6 cm long, with four dichotomies; and again the rather narrow frond broadens out half-way along its length and then becomes narrower again. The wider parts of both specimens are now pressed flat but some wrinkling of the surface, of the right-hand specimen especially, supports the view that the wider parts were once irregular inflations, such as may be supposed to have occurred in Linnaeus's *F. inflatus* (*cf.* Gardner, 1922, p. 10). It seems probable that Linnaeus, in preparing his later diagnosis in *Syst. Nat.*, had these particular specimens in mind; thus 'punctata' would seem to refer to the rather frequent cryptostomata that are present in both specimens and which appear as prominent raised white spots on the frond surface of the right-hand specimen (Pl. I, fig. 1). Microscopic examination shows that each white spot consists of an aggregation of salt crystals located round the raised orifice of a cryptostoma. Caecostomata (see p. 418) could not be detected even by sectioning a small part of the frond. The fronds are thin and have a very narrow, sharply defined midrib, strongly marked right to the tips of the branches. Near the tips of the left-hand specimen the margins of the thallus appear to be very slightly serrulate; this appearance is caused by marginal cryptostomata, and one of the Linnaean specimens of *F. vesiculosus* (Sheet 48) also shows traces of this character.

These Linnaean specimens of *F. inflatus* closely resemble forms of both *F. vesiculosus* L. and *F. ceranoides* L. as understood to-day and could be interpreted as either of these species. However, having made a critical examination and comparison of the Linnaean specimens of all three species, the author concludes that the specimens labelled '*inflatus*' on Sheet 51 are rather

closer to the specimens of *F. vesiculosus* L. than to that of *F. ceranoides* L. and are best interpreted simply as a form of *F. vesiculosus* L. lacking true vesicles.

In the Linnaean Herbarium there are four pages of notes referring to Herb. Linn. specimens, written by Dawson Turner, and it is interesting that he writes of the above specimens: 'one specimen fragment—only a var. of *vesiculosus*' (see also Turner, 1809, pp. 45–7).

The epithets *vesiculosus* L. and *inflatus* L. are both included in *Species Plantarum* (Linnaeus, 1753) and therefore have equal priority but, because *vesiculosus* L. is represented by good specimens in Herb. Linn. (with true vesicles and with unisexual conceptacles), it is desirable that the name *F. vesiculosus* L. be retained for the plant currently known by that name. Turner (1802, 1809) has already clearly united these two taxa under the name *F. vesiculosus* L. and, in accordance with Article 67 of the International Code of Botanical Nomenclature (Lanjouw *et al.* 1952), his choice of epithet must be followed.

Vahl's diagram of '*F. inflatus* L.' in *Flora Danica* (tab. 1127), on the other hand, is certainly of a plant very different from that of Linnaeus, and probably Vahl meant to illustrate the plant widely known now by the later epithet, *edentatus* De la Pyl.[1] The illustration shows a sturdy plant with a broad and prominent midrib running strongly right up to the base of the receptacles; the latter are terminal, rather elongated (4 to 5 times longer than broad), swollen-looking and distinctly pointed. The thallus has a number of irregular inflations, especially in the upper parts. This illustration, despite the much too conspicuous midrib, could be regarded as the earliest publication of the form later widely known as *F. edentatus* De la Pyl.; but the illustration alone could equally well represent a form of *F. vesiculosus* without vesicles and it is therefore recommended that it be disregarded for purposes of typification.

None of the principal defenders and users of the name *F. inflatus* L. have examined the specimens in the Linnaean Herbarium, although, in view of Linnaeus's inadequate diagnosis, the specimens must be decisive. On the other hand, Gardner (1922) obtained a description and sketch of the specimens, and Taylor (1937) examined the specimens personally, and both concluded that these fragments are not sufficiently distinctive to be associated with any particular species. However, neither of these authors mentions that there does exist in the Linnaean Herbarium a sheet of good specimens of the short, very narrow fucoid known as *F. distichus* L. and, since the epithet *inflatus* L. must now be rejected, these specimens assume great importance. If it can be shown that the taxon *F. distichus* L. is taxonomically valid, adequately defined by diagnosis and type specimens, then this name would have priority over all the

[1] See Foslie (1886); also Jónsson (1903) who states in a footnote (p. 184): 'In this connection it may be added that specimens gathered by M. Vahl in Nordland and determined as *F. inflatus* L., fully agreeing with the typical *F. inflatus* L. as it is understood now, are to be found in the Botanical Museum at Copenhagen.'

other names proposed later for the various members of this complex of forms. It will now be shown that the name *F. distichus* L. is valid, but it applies to the very narrow form usually found in littoral pools—the f. '*linearis*' of Rosenvinge, Börgesen and Jónsson—rather than to the short, but more robust, plants developed on very exposed coasts which Börgesen unfortunately and incorrectly named 'f. *disticha* (L.)'.

THE CASE FOR USING THE NAME *FUCUS DISTICHUS* L.

The name *F. distichus*[1] is first used by Linnaeus in *Systema Naturae*, Ed. 12, Tom. 2, p. 716 (1767). The diagnosis given for *F. distichus* is '*Fucus fronde plana dichotoma integerrima lineari fructificationibus tuberculatis mucronatis*'; this may be translated as: '*Fucus* with fronds plane [flat], dichotomously branched, entire [margins], linear [i.e. very narrow], with fructifications [receptacles] having small rounded humps [i.e. conceptacles probably] and sharply pointed.'

This short diagnosis could not by itself delimit any particular species of *Fucus*, and unfortunately Linnaeus does not state where the plant was found. The most significant parts of the diagnosis are the 'linear fronds' and 'pointed receptacles'; 'linear' in the sense used by Linnaeus means very narrow and elongated, and probably also implies uniform breadth.

In the Linnaean Herbarium there are two sheets of *Fucus* specimens labelled 'distichus'; the sheets are numbered '1274.56' and '1274.57', respectively, as stated in the Catalogue of Savage (1945, p. 200).

SHEET 56

Sheet 56 has five pieces of plants pasted on, and is labelled 'distichus' near the foot of the sheet in Linnaeus's hand (Pl. I, fig. 2, pieces labelled A–E by author). These pieces are the true type specimens of *F. distichus* L. and establish the validity of this taxon with certainty. All five specimens are quite short and extremely narrow; in none of them is the holdfast present; the fronds are all compressed and thin, but tough. Specimens A, B and C measure 14·7, 7·8 and 10·8 cm in length, respectively; they are extremely narrow, < 1–2 mm wide, rather cylindrical at the base (< 1 mm), becoming flat above to reach a maximum of 2 mm wide but usually slightly less; A and C have narrow, pointed, terminal receptacles up to 9 mm long and up to 1·5 mm broad, i.e. up to at least 6 times longer than broad; B is sterile.

Specimens D and E measure 7·9 and 8·6 cm in length, respectively, but appear to be only the terminal parts of plants slightly more robust than specimens A–C. The measured width of D and E is not much greater than A–C (fronds *ca.* 2·0 mm wide throughout, but up to 2·5 mm in parts), but

[1] Greek διστιχος, =*distichus*, 'consisting of two rows'; 'distichous' in modern botanical sense, implying branches disposed in two diametrically opposite ranks or rows.

the fronds appear to be rather thicker. The receptacles are very well developed, are bigger than in A–C, being up to 20 mm long × 1·5 to 2·0 mm broad, i.e. at least 10 times longer than broad, and are rather pointed at the tips.

Parts of receptacles from specimens A and E were removed and soaked, and microscopical examination of some fifteen conceptacles showed that all were hermaphrodite; there were 8 eggs per oogonium.

The midrib is rather indistinct in all five specimens, but sections of part of the narrow thallus of A showed that the midrib occupies up to about one-third of the width. Cryptostomata are few and well spaced out in A–C, but rather more frequent in D and E; in D the location of cryptostomata is again indicated by white spots on the frond surface (see p. 411). Caecostomata were quite frequent in A but could be detected only by sectioning the thallus.

Specimens A and C bore frequent calcareous tubes of the worm *Spirorbis borealis* Daudin along most of the length of the specimens; A had a few filaments of a *Ceramium* sp. entangled on the lower part of the lower left-hand branch (see Pl. I, fig. 2); and one small specimen of *Mytilus edulis* L. was found on each of specimens A and D. The delicate habit, and the associated species, of plants A–C in particular, suggest that they may well have been growing in a rock-pool.

The following items are also on Sheet 56: a small label with 'No. 25' written on it (by J. G. Koenig?); and the writing 'linearis Huds. ex syn. Gmel.' and (against the word 'distichus') 'Syst. Nat. [ed.] 12.' in pencil by Sir J. E. Smith.

A comprehensive description of *Fucus distichus* L., accompanied by a very accurate illustration of the Linnaean type specimen (Pl. I, fig. 2 A) is given in Turner (1808, pp. 7–8, and pl. 4), and this is the earliest illustration of the type form of this species that can be accepted without question. Turner describes and illustrates the receptacles and 'tubercles' (= conceptacles) in a detail that is remarkable for his time: 'Fructification situated in the apices of the frond, which are then lengthened to half an inch or more, and become receptacles, containing globular tubercles, placed immediately under their surface, perforated with a small pore, and furnished with a few oblong brown seeds surrounded with a pellucid limbus.' It is clear from his plate 4 (figs. *c*, *d*, and *e*) that the 'oblong brown seeds' are in fact undivided oogonia; his drawings of transverse section conceptacle are not sufficiently detailed to show antheridia, but it should be remembered that antheridia were not properly recognized and described in any species of the genus until much later (Decaisne & Thuret, 1845).

It is practically certain that all five specimens on Sheet 56 are of the same species, and it is quite certain that this is a plant distinct from all known forms of the *Fucus* spp. currently named *F. serratus*, *F. vesiculosus*, *F. spiralis* and *F. ceranoides*; in fact it is *F. distichus* L.

SHEET 57

Sheet 57 of the Linnaean Herbarium is labelled 'Fucus distichus' in Linnaeus's handwriting. The word 'distichus' has been crossed out later and alongside is written 'membranaceus of Stackhouse, D. Turner' in Sir J. E. Smith's handwriting (see Savage, 1945); apparently Smith is quoting Dawson Turner's opinion. Also, in the four pages of notes written by Turner in Herb. Linn., we read: '*F. linearis*,[1] 5 specimens on one paper' (i.e. Sheet 56) 'all the same and right, one on another paper' (Sheet 57) 'a very large specimen of *F. membranaceus*, it was from this latter that Linnaeus was induced to add to his descriptions "Frons nervo medio, textura herbacea".' Following this up, we read as follows in Turner (1808, p. 8, under '*Fucus distichus*')—'It appears by Linnaeus's Herbarium, that he had himself confounded it with *F. membranaceus* of Stackhouse, and this accounts for the observation in *Systema Plantarum* [1779] that the texture is herbaceous.'

'*Fucus membranaceus* of Stackhouse' is the brown alga now known as *Dictyopteris membranacea* (Stackh.) Batt. (=*Haliseris polypodioides* C. Ag.) and it can superficially resemble a plant of *Fucus*. The alga on Sheet 57 is 23 cm long, profusely branched and has thin textured, rather narrow fronds (mostly 2–4 mm broad, but swelling to *ca.* 6 mm when soaked. The author has made a critical examination of this specimen and has found that it is definitely a plant of the genus *Dictyopteris* Lamour., with abundant characteristic male sori; the species could well be *D. membranacea*, although the specimen is much more branched than is usual in this species. The existence of this plant in the Linnaean Herbarium, and the addition to the diagnosis in *Syst. Plant.* (Linnaeus, 1779), could be held to imply that Linnaeus did not have a very clear conception of the delimitation of his *Fucus distichus*. This indeed is very likely and is scarcely surprising. However, this does not alter the fact that his *F. distichus* as originally defined, and particularly as represented by the specimens on Sheet 56 in his herbarium, corresponds precisely to a narrow form of *Fucus* that is widely recognized but which passes under various names today—e.g. *F. inflatus* f. *linearis* (Oed.) Rosenv.; *F. inflatus* f. *linearis* (Huds.) Rosenv.; and *F. filiformis* Gmel. (used by Taylor, 1937). From the taxonomic point of view, it is immaterial that Linnaeus later thought that a plant we know as *Dictyopteris membranacea* should be included in *Fucus distichus* L.; we now place these algae in distinct genera, and the point is covered taxonomically simply by quoting the species as follows: *Fucus distichus* L., *Syst. Nat.*, Tom. 2, p. 716 (1767); syntypes on Sheet 56 in Herb. Linn. (*non* Sheet 57 which plant is certainly *Dictyopteris* and probably *D. membranacea* (Stackh.) Batt.).

Having thus established that the name *Fucus distichus* L. applies to a

[1] In these early (but undated) notes Turner was doubtless thinking of *F. linearis* Oeder (*excl. syn.* Hudson) which he later regarded as a synonym of *F. distichus* L. (see also p. 416).

particular and distinctive fucoid, it remains to confirm that it is either taxonomically distinct from, or else has nomenclatural priority over, several other early names for narrow forms of *Fucus* that have been revived more recently: (i) *F. linearis* Hudson (1762, *Fl. Angl.*, p. 467); (ii) *F. linearis* Oeder (1767, *Fl. Dan.*, tab. 351); and (iii) *F. filiformis* Gmelin (1768, *Hist. Fuc.*, p. 72).

Fucus linearis Hudson (1762, p. 467)

'*Fucus dichotomus planus linearis vesiculis ovatis sparsis. Anglis*, narrow-leaved Fucus, or Sea-Thongs.' (No illustration).

I fully agree with Turner (1802, p. 128; 1809, p. 45) that *F. linearis* Huds. is a narrow form of *F. vesiculosus* L., with (few or) no vesicles and with elongated receptacles, corresponding to the plant currently known in Britain as *F. vesiculosus* f. *evesiculosus* auctt. In Kew Herbarium there is a sheet of fucoids, originally part of Turner's herbarium, which includes two small pieces of a fucoid labelled '*Fucus linearis* Huds.—from himself—H.D. I divide with you an indifferent specimen'. This is material given by Hudson himself to the Rev. H. Davies who, to quote Turner (1802, p. 128), 'was kind enough to divide with me [Turner] an original specimen'. The present author has made a critical examination of this most interesting specimen and confirms that it is indeed a (male) plant of *F. vesiculosus* 'f. *evesiculosus*', without vesicles. In view of this finding, it is clear that the name 'f. *evesiculosus*' is nomenclaturally superfluous, and the narrow, reduced form of *F. vesiculosus*, with few or no vesicles, found on exposed and semi-exposed coasts, should properly be named *F. vesiculosus* L., f. *linearis* (Huds.).[1]

Fucus linearis Oeder (1767)

Tab. 351 in *Flora Danica* (Vol. 2, fasc. 6, 1767, edited by G. C. Oeder) shows a rather idealized drawing of a fucoid certainly very similar to *F. distichus* L. The caption referring to the plate (on p. 9) states:

'*Fucus marinus secundus*. Dod. Pemt. 479. *Fucus*, linearis, *dichotomus planus linearis acutus, vesiculis ovatis sparsis*. Huds. Angl. 467. Locus. *In fundo oceani Islandici*.'

Oeder is thus using Hudson's name *linearis* and quotes Hudson's diagnosis, but gives Iceland as the locality. The name *linearis* Huds. has just been shown to refer to a plant taxonomically quite distinct from *F. distichus* L., but if Oeder's sketch is indeed of a plant from Iceland then it could well be of true *F. distichus* L. I am inclined to agree with Turner (1808), Lyngbye (1819) and Hornemann (1827) that the sketch (only) of *F. linearis* in *Flora Danica* can be accepted as an illustration of *F. distichus* L. and may be cited in this respect in the following manner (='*F. linearis*' *Flor. Dan.*, tab. 351, *excl. syn.* Hudson).

[1] Batters (1902, p. 50) is therefore in error in supposing *F. linearis* Huds. to be the curious, very narrow form of *F. ceranoides* L. apparently recorded in Britain only from Loch of Stenness, Orkney Islands, where it grows in rather unusual environmental conditions (for recent information on the flora and physical conditions in Loch Stenness, Orkney, see Dunn, 1937, and Nichol, 1938). I have seen authentic specimens of this form of *F. ceranoides* from Loch Stenness in the Greville Herbarium (University of Edinburgh) and there is no doubt that it really is a form of *F. ceranoides*, with extremely thin, narrow fronds, and with the midrib very distinct and fine; the receptacles are elongated (but not markedly so) and the plants are dioecious. Lightfoot's (1777, p. 912) record of '*F. distichus* L.' from 'Loch Stennis, Orkney' also almost certainly refers to this same narrow form of *F. ceranoides*.

Fucus filiformis Gmelin (1768)

This name has been revived by Taylor (1937) for a narrow fucoid found in littoral pools in North-east America. However, again we find that Gmelin (p. 72) is merely quoting a name used for the first time by Hudson (1762, p. 472), who gives the following diagnosis for this plant: '*F. filiformis dichotomus planus. Anglis*, flat Fucus. *Habitat in littore Lancastriensi*' [Lancashire coast]. In the second edition of *Flora Anglica*, however, Hudson (1778, p. 585) gives an expanded diagnosis and additional information about '*F. filiformis*', as follows: '*Fucus fronde cartilaginea filiformis compressa dichotoma acuta. Anglis*, filiform Fucus. *Habitat in rupibus et saxis prope insula* Walney *in comitatu Lancastriensi.* Desc. *Frons semipedalis, cartilaginea, filiformis, compressa, dichotoma, diaphana, rubescens.*' This almost certainly refers to a red alga, and probably to a form of *Chondrus crispus* (L.) Stackh. Gmelin (1768) repeats Hudson's (1762) earlier diagnosis verbatim and adds some further description; for location he states '*Oceanus septentrionalis*' [northern Ocean] and he also gives a drawing of his conception of this plant (1768, tab. 1A, fig. 1). Other authors (e.g. Turner, 1808, though with some doubts) have quoted this illustration (but without the diagnosis and reference to Hudson) as a further possible illustration of *Fucus distichus* L. However, I think that the drawing is not accurate enough to be cited in this connexion; in particular, Gmelin's figure shows the midrib altogether too narrow and well defined, and clearly distinct all the way to the tips of all the branches (including running along the length of what are presumably rather flat-looking receptacles, a phenomenon that I have otherwise seen only in a few young receptacular apices of British *F. ceranoides*).

Thus the name *F. filiformis* (Hudson, 1762, 1778, Gmelin, 1768) has been used with different meanings and cannot now be associated with any particular type; it should therefore be rejected (Lanjouw *et al.*, 1952, Article 73). On the other hand, Taylor's (1937) own description and illustration of North-eastern American plants correspond precisely with the plants of *F. distichus* L. in Herb. Linn. and I have no doubt that they should be so named. (The nomenclature of North American fucoids will be discussed further on a later occasion.)

FUCUS DISTICHUS L. EMEND. POWELL

It has been shown above that the name *F. distichus* L. applies to a distinctive narrow fucoid that can be regarded as a good species. It is now proposed that the specific limits of *F. distichus* L. be amended to include the various hermaphrodite fucoids reduced to synonymy below. In the present treatment four of the many described forms are considered as subspecies. Each subspecies is fairly distinct from the others, at least in some parts of the species range. Near the centres of distribution, however, all possible intermediate forms between the four main subspecies may be found.

GENERAL CHARACTERS OF THE SPECIES AS A WHOLE

The species as a whole is extremely plastic and, in response to varying environmental conditions and in different parts of its very wide geographical range, develops into a great variety of forms, the over-all range of form being indicated in the descriptions of subspecies below. Two particular characters, however, are fundamental to the present conception of the species: (i) the

conceptacles of all forms are invariably hermaphrodite; (ii) closed cavities, termed 'caecostomata', are found in variable number in the fronds of most forms of the species, but not in any other species of the genus *Fucus*. The author cannot yet state that caecostomata are invariably present in all forms, but they have been detected (sometimes only in very small numbers) in all specimens so far examined for this character. In view of their taxonomic importance in a group (*Fucus* spp.) in which diagnostic characters are few, caecostomata are dealt with in detail.

Caecostomata

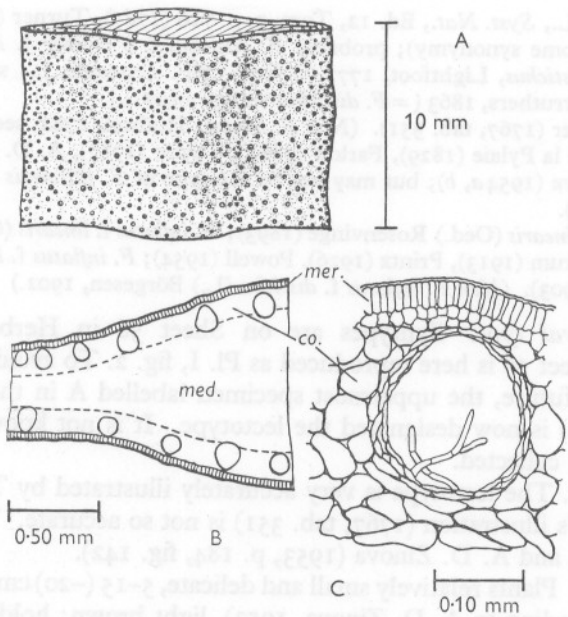
The descriptive term caecostomata was apparently first suggested by Prof. W. A. Setchell, and first used in print by Gardner (1922), for small completely closed cavities found in the fronds of certain Pacific coast fucoids referred by Gardner to the species '*F. furcatus* Ag.' (and '*F. edentatus* De la Pyl.'). Caecostomata are mentioned otherwise only by Setchell & Gardner (1925), Smith (1944), Fritsch (1945, p. 368, quoting Gardner, 1922), and Doty (1947)—all referring to Pacific coast material. However, Gardner (*loc. cit.*, p. 9) suspects that J. Agardh (1868, p. 38) may have been referring to them under '*Cryptostomata immersa saepe numerosa, plurima diu clausa*' [immersed (sunken) cryptostomata often numerous, most long since enclosed] with reference to his (J. Agardh's) conception of *F. filiformis* Gmelin, *F. linearis Flor. Dan.* and *F. miclonensis* De la Pyl.; this may be so, and J. Agardh repeats the above description (p. 40) with reference to the following fucoids: *F. edentatus* De la Pyl., *F. furcatus* C. Ag. and *F. evanescens* C. Ag. (De Toni, 1895, repeats the J. Agardh description for these same fucoids). Gardner also states (p. 18), very significantly, that he found 'a large number of caecostomata' in some of Börgesen's specimens of '*F. inflatus* f. *edentata*' from the Faeröes.

I have found caecostomata in all of the North Atlantic forms of *F. distichus* L. emend. Powell, and disagree with the taxonomic conception of Gardner (1922) that the presence of caecostomata can be used as a 'fundamental distinguishing character' of his *F. furcatus* Ag. emend.

In British material of *F. distichus* subsp. *edentatus* the presence of caecostomata may readily be detected (in both fresh and herbarium material) simply by holding a frond up to a light, when the internal cavities appear as small, lighter coloured (less dense), rounded spots in the frond, and, when the caecostomata are very numerous, the frond appears to be stippled with small light-coloured dots. Also, the meristoderm and cortex form a slight hump above each cavity, so that the frond surface appears to be covered with low, rounded, miniature pimples and has the appearance of a very fine-grained morocco-leather. The caecostomata (Text-fig. 1) are, in general, both more numerous and smaller near the thallus margins. The cavities are lined with flattened cells, are located at first mostly in the cortex (later extending a little deeper, into the outer medulla), and vary a good deal both in shape and size: the shape is most often pyriform, or rounded, or sometimes a rather flattened pear-shape; the size of the cavities is usually (50–) 100–200 (–250) μ greatest diameter. Gardner (1922) states that 'no paraphyses develop' in the caecostomata he examined, but investigation of British material has shown that reduced, colourless paraphyses may develop to a small extent in some few of the caecostomata (Text-fig. 1 C), although the paraphyses are sometimes more numerous than shown in the figure. The paraphyses may be slightly branched.

The development of caecostomata has been investigated, by sectioning and squashing thallus apices, and my observations confirm those of Gardner that caecostomata

originate in the same way as do the conceptacles and ordinary cryptostomata in *Fucus* spp. (see Fritsch, 1945, for a review of the literature relating to the origin and development of these structures; Fritsch refers to cryptostomata as 'cryptoblasts'). All three structures originate just behind the growing point from a single initial cell. This soon becomes lodged at the base of a deep and narrow cavity owing to rapid growth and division of the surrounding cells. The cavity then enlarges and becomes lined with several layers of flattened cells, which delimit these structures from the compact cortical tissue and loose medullary tissue.



Text-fig. 1. Caecostomata in *Fucus distichus* subsp. *edentatus* (plant from Lerwick harbour, Shetland Islands). (A) Surface view of part of thallus; the circles represent (internal) caecostomata. (B) Transverse section of part of thallus, showing caecostomata situated mostly in the cortex. (C) Enlarged diagram of a single caecostoma, containing two colourless paraphyses. *co.*, cortex; *med.*, medulla; *mer.*, meristoderm.

From this point onwards, the development of caecostomata differs from that of cryptostomata and conceptacles. The pores communicating with the exterior become blocked by cell-division of the meristoderm very close behind the apex (within the first few mm), and the cavities soon become completely roofed over. In the older parts of the thallus the cavities are seen to have become very much larger, and to be roofed over by slight mounds of tissue (consisting of flattened limiting cells, a few layers of cortical cells, and meristoderm), and appearing as small mounds on the surface of the frond.

It would seem best to interpret the caecostomata as small, reduced, closed cryptostomata, although cryptostomata never occur (in any species of *Fucus*) at anything like the density that caecostomata may achieve.

In British *F. distichus* subsp. *edentatus*, caecostomata are often extremely abundant (up to a maximum density of 500 per cm^2), and cryptostomata few or absent; while in

the Linnaean type of *F. distichus* subsp. *distichus*, and generally in *F. distichus* subsp. *anceps* (both with very reduced fronds), both caecostomata and cryptostomata occur only in small numbers and the caecostomata often can be detected only by sectioning the frond.

DESCRIPTION AND GENERAL DISTRIBUTION OF SUBSPECIES

Subsp. *distichus*. (Pl. I, fig. 2)

Fucus distichus L., *Syst. Nat.*, Ed. 12, Tom. 2, p. 716 (1767), Turner (1808, pp. 7–8, but excl. some synonymy); probably *F. distichus* f. *b tenuior* J. Agardh (1868). [*Non F. distichus*, Lightfoot, 1777 (=form of *F. ceranoides* L., see footnote on p. 416), Carruthers, 1863 (=*F. distichus* subsp. *anceps*).]

F. linearis, Oeder (1767, tab. 351). (*Non F. linearis* Hudson, 1762, see p. 416.)

F. filiformis, De la Pylaie (1829), Farlow (1881), Taylor (1937), A. D. Zinova (1953), E. S. Zinova (1954*a*, *b*); but may not be the type of *F. filiformis* Gmelin (1768) (see p. 417).

F. inflatus var. *linearis* (Oed.) Rosenvinge (1893); *F. inflatus* f. *linearis* (Oed.) Börgesen (1902), Norum (1913), Printz (1926), Powell (1954); *F. inflatus* f. *linearis* (Huds.) Jónsson (1903). (*Non F. inflatus* f. *disticha* (L.) Börgesen, 1902.)

Nomenclatural type. Syntypes are on Sheet 56 in Herb. Linn. (*non* Sheet 57); Sheet 56 is here reproduced as Pl. I, fig. 2. To avoid any possible ambiguity in future, the uppermost specimen labelled A in the photograph (Pl. I, fig. 2A) is now designated the lectotype. It is not known where the syntypes were collected.

Illustrations. The lectotype is very accurately illustrated by Turner (1808, pl. 4). Oeder's illustration (1767, tab. 351) is not so accurate. Taylor (1937, pl. 23, fig. 2); and A. D. Zinova (1953, p. 184, fig. 142).

Description. Plants relatively small and delicate, 5–15 (–20) cm in length (up to 40 cm according to A. D. Zinova, 1953), light brown; holdfast relatively small; stipe very thin, lax, round or oval in section; branching dichotomous and usually distichous, the axils rather acute; branches with entire margins, evesiculate, narrow, linear, 1·5–3 (–4) mm wide, thin; principal branches with a definite but not very prominent midrib and narrow lateral alae; in the lower parts of the plant the midrib becomes a little narrower but somewhat thicker, forming the thin stipe, while towards the tips of the branches the midrib usually becomes indistinct; cryptostomata and caecostomata both usually present, but few, small and obscure. Receptacles apical, narrowly cylindrical to fusiform, generally inflated, broader than the distal parts of the fronds which bear them, 0·5–3 cm long and 1–4 mm broad, unbranched or once-forked; conceptacles hermaphrodite.

Distribution. Kara Sea (A. D. Zinova, 1953); Barents Sea; White Sea; N. and W. Norway; Iceland; Faeröe Islands; Greenland; Atlantic coast of Canada and U.S.A.; Sea of Okhotsk and Gulf of Tartary (E. S. Zinova, 1954*a*, *b*). Not recorded (and probably absent) from British Isles. This plant largely occurs in rock-pools (but may occur also on open rock in some northern

parts of its range) in the upper part of the littoral zone, at both exposed and sheltered sites.

Authentic specimens examined.[1] The syntypes in Herb. Linn. (LINN) have been examined in detail; it is not known when, where, or by whom, the specimens were collected. **N.W. Russia**. 'Terra parva Samojedorum: Cap Barmin, August, *Dr* [F.] *Ruprecht'* [as '*F. vesiculosus* L. (f. *nana*)'] (K, ex Herb. Hooker). WHITE SEA: *F. Ruprecht* (K, same sheet). (Also on this sheet in Herb. Kew are some authentic specimens of subsp. *distichus* labelled '*Fucus distichus* ex herb. Linn.; Mr. Stackhouse from M. Der Fontaine 1802'.) **Norway**. FINMARK: Vardöhus (TCD); (also in Herb. Harvey, TCD, is another sheet of authentic material labelled '*F. distichus* L., ex Herb. Agardh' —presumably these are the 'authentic specimens' sent to W. H. Harvey by J. Agardh—see Carruthers, 1864); Gjesvaer, 1880, *M. Foslie* (BM, ex Herb. Holmes); 'Norv. arct., Mehavn,' May 1882, *F. R. Kjellman* (BM, ex Herb. Batters); 'West Finmarken, Maaróe' (?), July 1867, *Th. M. Fries* (BM, ex Herb. Batters). LOFOTEN: Reine, May 1952, *E. Baardseth* (MILL). NORDMÖRE: Bud, July 1955, in pools, *E. Conway* (GL). **Iceland**. Sept. 1897, *H. Jónsson* (K, *Plantae islandicae*). **Faeröe Islands**. SYDERÖ: Famien, May 1896, *F. Börgesen* (BM, *Algae marinae Faeroenses*, Nr 501 a, two sheets—one ex Herb. Batters, the other ex Herb. Holmes). **Canada**. NOVA SCOTIA: Peggy Cove (near Halifax), Aug.–Sept. 1948, *T. A. & A. Stephenson* (Herb. M.S. Doty, No. NSP. 14, two sheets).

Subsp. *anceps* (Harv. et Ward ex Carruthers) Powell, *n.comb.*
(Pl. II, fig. 1)

Fucus anceps Harv. & Ward, Carruthers (1864), Gray (1867), Batters (1902), Newton (1931); *F. anceps* Ward & Harv., Harvey (1864); *F. anceps* 'Wood & Harv.', J. Agardh (1868); *F. anceps* 'Harv. et Wood', Areschoug (1868).

F. distichus, Carruthers (1863, excl. synonymy and distribution), Du Rietz (1947), A. D. Zinova (1953); probably *F. distichus* f. *a robustior* J. Agardh (1868).

F. inflatus, Arwidsson (1937), Parke (1953); *F. inflatus* f. *disticha* (L.) Börgesen (1902, but excluding some of his synonyms), Norum (1913), Printz (1926), Hygen & Jorde (1935), Levring (1937); *F. inflatus* f. *distichus* (L.) Börg., Powell & Lewis (1952), Gauld *et al.* (1953), Burrows *et al.* (1954), Lewis (1954); *F. inflatus* f. *exposita* Jónsson (1903), Powell (1954).

The name *Fucus anceps* Harv. & Ward ex Carruthers refers to a small form of *Fucus* found growing on the very exposed face of Duggerna Rock, Kilkee, West Ireland, by Prof. W. H. Harvey and Mr N. B. Ward on 19 July 1863. The plant was first briefly reported as '*F. furcatus* Ag.' (Anon., 1863), then as '*F. distichus* L.' (Carruthers, 1863, who described and illustrated the plant

[1] The abbreviations used for herbaria are as follows: (BM) British Museum; (E) Royal Botanic Garden, Edinburgh; (GL) University of Glasgow; (K) Royal Botanic Gardens, Kew; (LINN) Linnaean Society of London; (MILL) Scottish Marine Biological Association, Millport; (TCD) Trinity College, Dublin.

in detail). However, after examining authentic specimens of *F. distichus* L. sent to him by J. Agardh, Harvey finally decided that the Irish plant was 'a distinct and hitherto undescribed species' for which (in a letter to Carruthers) he proposed the name *F. anceps* Harv. & Ward (see Carruthers, 1864)[1]; the Latin word *anceps*, means 'two-headed', or 'two-fold' and was considered appropriate by Harvey (1864) because 'this Fucus seems to combine the characters of the ribbed and ribless species'. Additional details relating to the original discovery of *F. anceps* at Kilkee are given in notes and correspondence published in *Trans. bot. Soc. Edinb.*, Vol. 8, 1866 (pp. 52, 53, 111). I propose to revive the name *anceps* for this plant of very exposed coasts because the good description and figures of *F. anceps* quoted above are the earliest really certain account of this very distinctive subspecies.

Nomenclatural type. The description of this plant given in Carruthers (1863) is based on a series of syntypes from Kilkee, now lodged in the Herbarium of the British Museum. One specimen is closely similar to the principal illustration in Carruthers (1863, tab. 12, fig. 1) and I select this specimen as the lectotype, even though it is sterile.

Illustrations. Carruthers (1863, tab. 12, figs. 1–9); Börgesen (1902, p. 471, fig. 93, this illustration is reproduced by A. D. Zinova, 1953, p. 191, fig. 146); Printz (1926, p. 210, fig. 25); present work, Pl. II, fig. 1.

Description. Plants relatively small but very sturdy, usually (4–) 6–10 (–15) cm in length; yellowish brown to dark brown; holdfast well developed, up to 2 cm diam., giving very firm attachment; stipe short, relatively very thick, almost terete and stands erect, while the more lax distal branches arch over very characteristically; branching distichous, and usually dichotomous but may be unilateral in part; the angle between older branches is often rather wide and between youngest branches very acute, so that the young terminal branches are closely crowded and run almost parallel; branches with entire margins, evesiculate, alate above but narrow, seldom more and usually less than 4 mm wide, thicker than in subsp. *distichus* and consisting mainly of a stout midrib, with very narrow lateral alae on each side; towards the tips the branches become narrower, the midrib and alae are less distinct and the frond becomes more nearly oval in section; on older branches the alae are usually absent; a small number of cryptostomata present, often as a single row on each side of midrib in the younger thalli; in older branches, the hairs of the cryptostomata are often worn down to the level of ostiole; caecostomata present in small numbers in all specimens examined, but often their presence can only be detected by sectioning. Receptacles apical, elongated, narrowly cylindrical and often slightly curved (continuation of arching of frond), generally inflated, always broader than the distal parts of the frond

[1] In another letter reporting the new name, Harvey (1864) cites the authorities in reverse order, i.e. as 'Ward & Harvey'. I propose to retain the order of authorities given in Carruthers (1864).

which bear them, usually 1·5–3 cm long and 2–3 mm wide, but occasionally up to 4 cm long and 4 mm broad, unbranched or once-forked, apices bluntly pointed and often sterile, and continued vegetative growth beyond the receptacle is often seen; conceptacles invariably hermaphrodite. Often all the apices of a frond are fertile at the same time. Occasionally irregular areas of fertile tissue (often occupying only half the width of the frond, or less) may be found some way back from the apex; this character was first noticed by Carruthers (1863, p. 354, and tab. 12, fig. 7) and described as an 'inferior lateral receptacle' (*cf.* description of subsp. *edentatus* below).

Distribution. North-west Russia (Barents Sea and White Sea) according to A. D. Zinova (1953, p. 191) who describes the plant under the name *F. distichus*; North, West and South Norway; Iceland; Faeröe Islands; British Isles (North and West Scotland and Ireland only). This plant is found only on very exposed coasts, subjected to considerable swell and wave-action, in the upper part of the littoral zone.

Authentic specimens examined. **Norway.** NORDMÖRE: Bud, July 1955, *E. Conway* (GL), *G. G. Smith* (MILL). **Faeröe Islands** (all specimens collected and distributed by F. Börgesen). MYGGENAES HOLM: July 1902 (BM, *Algae marinae Faeroenses*, ex Herb. Holmes; K, *Alg. mar. Faer.*, ex Herb. Börgesen). STORE DIMON HOLM: June 1896 [BM, *Alg. mar. Faer.*, two sheets—one (No. 895) ex Herb. Batters, the other ex Herb. Holmes]. SYDERÖ: Vaags Ejde, June (K, *Kryptogamae Exsicc.*, No. 1746); Sumbö Holm, July 1899 (BM, *Alg. mar. Faer.*, No. 1617*a*, ex Herb. Holmes; K, *Alg. mar. Faer.*). **Scotland.** SHETLAND ISLANDS: Fair Isle: (i) North Gavel, (ii) reefs S.W. of South Lighthouse, June 1952, *H. T. Powell* (MILL, GL). ORKNEY ISLANDS: Sandwick, Mainland: (i) Hole o'Rowe, Oct. 1938, and (ii) near Garson, May 1939, *J. Sinclair* (Herb. J. Sinclair, Sheets No. 445 and 511, respectively). CAITHNESS: North coast: (i) near Crosskirk, (ii) Lower Dounreay, (iii) near Sandside Head, etc., July 1951, *H. T. Powell* (MILL, BM, K). OUTER HEBRIDES: Island of Lewis: (i) 'Butt of Lewis' [?], April 1909, *W. J. Gibson* (K), (ii) Buaile na Faing (half-mile N. of Port of Ness), July 1954, *H. T. Powell* (MILL); St Kilda Islands: Glen Bay, Hirta, July 1952 and July 1956, *T. B. Bagenal* (MILL). **Ireland.** DONEGAL: Malin Head, July 1953, *J. R. Lewis* (MILL). CLARE: Duggerna Rock, Kilkee, (i) July 1863, *W. H. Harvey & N. B. Ward* [BM (syntypes and lectotype), E, K, TCD], (ii) July 1953, *H. T. Powell* (MILL); Kilkee, (i) *J. Cook* (BM, ex Herb. Holmes), (ii) Sept. 1897, *E. George* [BM, K, etc., a large collection of sterile plants widely circulated as Holmes's *Algae Britannicae Rariores Exsiccatae*, Fasc. X, No. 240]; also from (i) Donegal Point, (ii) George's Head, (iii) reefs just N. of Goleen Bay, and (iv) four sites just N. of Ross Bay, July 1953, *H. T. Powell* (MILL). KERRY: Kerry Head, June 1953, *J. R. Lewis* (MILL).

Subsp. *edentatus* (De la Pyl.) Powell, *n.comb.*
(Plate II, fig. 2)

Fucus edentatus De la Pylaie (1829, p. 84, *excl. syn.*), J. Agardh (1868), Gardner (1922), Setchell & Gardner (1925), Taylor (1937), Lund (1949*a*, *b*), A. D. Zinova (1953, 1954); *F. edentatus* f. *typica* Kjellman (1883).

F. inflatus, probably Vahl (1794, tab. 1127), Foslie (1886), Kjellman (1890), Printz (1926), Kylin (1947), Sundene (1953); *F. inflatus* f. *typica* Jónsson (1903); *F. inflatus* var. *a edentatus* (De la Pyl.) Rosenvinge (1893); *F. inflatus* f. *edentata* (De la Pyl.) Börgesen (1902, 1903); *F. inflatus* f. *edentatus*, Burrows *et al.* (1954). (*Non F. inflatus* L., see pp. 409–12.)

F. furcatus C. Agardh (1820, 1821), J. Agardh (1868), Kleen (1874), Farlow (1881), Gardner (1922, in part), Setchell & Gardner (1925, in part); (=*F. Gardneri* Silva, 1953)[1].

F. evanescens, Gardner (1922, in part), Setchell & Gardner (1925, in part).

F. nitens Gardner (1922), Setchell & Gardner (1925).

Nomenclatural type. Not seen by the present author. According to De la Pylaie (1829, p. 84) type material from Newfoundland (De la Pylaie, Herb. Terre-Neuve) was deposited in the Herbarium of the Paris Museum. Gardner (1922, p. 11) confirmed this and published a photograph (his plate 60, fig. 1) of the 'type specimen', which is presumably the holotype.

Illustrations. Kützing (1860, tab. 17 II); Börgesen (1902, pp. 467–9, figs. 90–92; 1905, p. 747, fig. 158), (1904, p. 56, fig. 7); Gardner (1922, pl. 60, fig. 1, also pls. 4, 10, 13, 18–23, 25, 54); Hylmö (1933, p. 383, fig. 4, uppermost plant); Taylor (1937, pl. 23, fig. 3); Levring (1946, fig. on p. 192); Kylin (1947, taf. 16, fig. 2); Lund (1949*a*, p. 233, fig. 1); A. D. Zinova (1953, p. 186, fig. 144); present paper, Pl. II, fig. 2. (The illustrations referred to by De la Pylaie, 1829, were unfortunately never published.)

Description. Plants typically large and sturdy, 20–45 (–60; and exceptionally –90, Taylor, 1937) cm in length; dark brown; branching regularly dichotomous and usually distichous, axils generally acute; branches with entire margins, evesiculate, leathery and more or less flaccid, alate above, but rather narrow for a fucoid of this size, (5–) 9–15 (–20) mm broad but a little broader just below the dichotomies, relatively quite thick, midrib very distinct below but may become very indistinct above (especially immediately below the receptacles); irregular inflations may occur in the lateral alae especially in distal segments; towards the base the midrib is denuded of alae and forms a firm stipe; holdfast a broad conical disk; cryptostomata typically few but can be quite numerous, usually rather small and inconspicuous in older branches; caecostomata usually present, from few to very abundant (up to 500 per cm^2). Receptacles apical, typically elongated and swollen, cylindrical

[1] Silva (1953) proposed the new name *F. Gardneri* for *F. furcatus* C. Ag., because the latter name is a homonym of *F. furcatus* Esper [1800, p. 178 (138 by error), plate 95] and is therefore nomenclaturally illegitimate; according to Silva, 'Esper's *Fucus furcatus* was based on a plant from the Adriatic Sea...most likely referable to the alga currently known as *Fauchea repens* (C. Ag.) Mont.'.

or somewhat flattened, 2–10 (–22, Gardner, 1922, p. 50) cm long, 5–15 (–25, Gardner, 1922) mm broad below, often tapering to acute (sterile) tips, usually divided 1–3 times into antler-like subdivisions, often not very sharply demarcated from sterile tissue below; vegetative growth beyond the receptacle may often occur (see Pl. II, fig. 2); conceptacles invariably hermaphrodite. Occasionally irregular areas of fertile tissue (often occupying only half the width of the frond, or less) may be found some way back from the apex (*cf.* subsp. *anceps*). When dried, the plants become very dark brown or black in colour and the receptacles of herbarium specimens are usually pressed quite flat; the midrib may appear more prominent in dried specimens than in living plants.

Distribution. North-west Russia (Barents Sea and White Sea) according to A. D. Zinova (1953, p. 185); North and West Norway, Oslofjord, West Sweden, Copenhagen; Iceland; Faeröe Islands; British Isles (only in Shetland Islands and Fair Isle); Greenland; Atlantic coast of Canada and U.S.A.; Pacific coast of Canada and U.S.A.; Kamchatka; North Japan. This plant is typically a good deal larger than the two preceding subspecies, and it grows best at sheltered or semi-exposed sites, in the sublittoral fringe and lower midlittoral zones. It may be found, however, at any level from the upper midlittoral zone down into the sublittoral zone; the plants growing at high levels or in more exposed situations are generally shorter and narrower.

Authentic specimens examined. **Norway.** TROMS: Tromsö, June 1887, *M. Foslie* (K, *Hauck et Richter Phykotheka universalis*, No. 164). LOFOTEN: Reine, May 1952, *E. Baardseth* (MILL). S. TRÖNDELAG: Trondheimsfjord, July 1955, *H. Blackler* (GL). AKERSHUS: Oslofjord, May 1953, *O. Sundene* (MILL). **Iceland.** 1897, *H. Jónsson* (K, *Plantae islandicae*). Skalaness, Aug. 1952 (GL). **Denmark.** Copenhagen harbour, May 1951, *S. Lund* (MILL). **Faeröe Islands.** STRÖMÖ: (i) Thorshavn, June 1895 (No. 224), (ii) near Kalbakfjord, June 1898, *F. Börgesen* (BM, *Algae marinae Faeroenses*, ex Herb. Batters). **Scotland.** SHETLAND ISLANDS: Mainland: Lerwick, (i) '16. 6. 1902', *F. Börgesen* (K), (ii) June 1908, *W. A. Russell* (BM, K, Holmes's *Algae Britannicae Rariores Exsiccatae*, Fasc. XII, No. 288), (iii) June–July 1952, *H. T. Powell* (MILL, GL); Scalloway harbour, July 1952, *H. T. Powell* (MILL). Fair Isle: North Haven, June–July 1952, *H. T. Powell* (MILL, GL). **Canada.** NOVA SCOTIA (all specimens collected Aug.–Sept. 1948, by *T. A. & A. Stephenson*, and now in Herb. M. S. Doty): (i) Halifax harbour (Herb. No. NSH. 13, one of three sheets labelled *F. evanescens*); (ii) Peggy Cove (Herb. No. NSP. 14, two sheets); (iii) Hall's Harbour, Minas Channel, Bay of Fundy (Herb. No. NSBF. 5, two sheets). BRITISH COLUMBIA: Vancouver Island: Beacon Hill, Victoria, June 1908, *J. Macoun* (BM, ex Herb. Geological Survey of Canada). **U.S.A.** MAINE: Eagle Island, Penobscot Bay, July 1896, *F. S. Collins* (BM, *Phycotheca Boreali-Americana*, Collins, Holden & Setchell, XIII). MASSACHUSETTS: Nahant (BM, ex Herb. F. S. Collins).

Subsp. *evanescens* (C. Ag.) Powell, *n.comb.*

Fucus evanescens C. Agardh (1820, 1821), J. Agardh (1868), Kjellman (1883), Yendo (1907), Gardner (1922, in part), Setchell & Gardner (1925, in part), Taylor (1937), E. S. Zinova (1933, 1954*a*, *b*, *c*), A. D. Zinova (1953).

F. inflatus var. *evanescens* (C. Ag.) Rosenvinge (1893); *F. inflatus* f. *evanescens* (C. Ag.) Jónsson (1903).

Nomenclatural type. Gardner (1922, p. 12) states: 'according to Setchell, the type specimen is in the herbarium of J. G. Agardh, under No. 00299, with a query.' I have not seen this (apparently doubtful) specimen and, for the present, temporarily designate as the type C. Agardh's description (1820, pp. 92–3) and illustration (1821, plate 13). C. Agardh's illustration is very well reproduced, photographically, by Gardner (1922, plate 1, fig. 2). For location, Agardh (1820) writes: 'Ad Sachalien, Tilesius; ad Kamtschatka, Chamisso; unde specimina communicaverunt' (whence specimens have been communicated); and the locality of the specimen illustrated by Agardh (1821, plate 13) is also stated to be Kamtschatka. E. S. Zinova (1933, 1954*c*) also records this alga from Kamchatka.

Illustrations. C. Agardh (1821, plate 13); Gardner (1922, plate 1, fig. 2; also plates 11, 11 a, 35, 36, 45, 46, 47, 48, 52, 56, 58, 59); Taylor (1937, plate 23, fig. 4; plate 24, fig. 2); A. D. Zinova (1953, fig. 147).

Description. This subspecies is the most variable and therefore the most difficult to define of the four subspecies recognized in the present paper. The principal features of *F. evanescens*, as originally defined and drawn by C. Agardh (1820, 1821), were: plant large, fronds broad; receptacles flattened, not markedly elongated, relatively broad; midrib indistinct in the apical parts of the plant. Some authors (e.g. Rosenvinge, 1893; Jónsson, 1903; Taylor, 1937) have applied the name to large, relatively broad, plants usually found in the lower part of the littoral zone (and in sheltered situations) in some of the more southerly parts of the over-all range of the subspecies; these large plants typically have fronds wider and receptacles shorter than subsp. *edentatus*, and correspond most nearly to the type illustration. Other authors (e.g. Kjellman, 1883; Gardner, 1922; A. D. Zinova, 1953) have applied the name to a number of relatively small and often rather narrow plants found on Arctic and other northern shores. As in subsp. *edentatus*, characters such as the midrib becoming indistinct above, and the numbers of cryptostomata and caecostomata, are in fact very variable; and, if we include the narrow Arctic forms, even the relative width of the frond varies widely. Indeed, the only characteristic morphological features of subsp. *evanescens*, throughout its geographical range, relate to the shape of the receptacles—relatively short and broad, rather flattened, and fairly distinctly delimited from the rest of the frond (*cf.* subsp. *edentatus*). From several Arctic areas, only plants with such receptacles have been reported (it is apparently the only

subspecies that is circumpolar in distribution) and such plants also are not found so far south as, for example, subsp. *edentatus*; it is therefore convenient to recognize subsp. *evanescens* as the subspecies best adapted to Arctic conditions, even though the morphological distinction from forms of subsp. *edentatus* is somewhat arbitrary, and despite the fact that the small distinctions between these two subspecies are obscured in some parts of the world by the presence of all possible intermediate forms, with receptacles intermediate in shape sometimes even on the same plant.

According to Inoh (1935), material of '*F. evanescens* Ag.' collected near Muroran, Hokkaido, Japan, has a haploid chromosome number of 32; this is the number usually reported for *Fucus* spp.

Distribution. Arctic and subarctic, circumpolar. Siberian Polar Sea, N.W. Russia, Novaya Zemlya, Svalbard, Jan Mayen, Bear Island; Greenland, Iceland; American Polar Sea, Atlantic Canada, Atlantic U.S.A.; Pacific Canada, Pacific U.S.A., Bering Sea, Aleutian Islands, Kamchatka, Sea of Okhotsk, Kurile islands, North Japan. *F. distichus* subsp. *evanescens* has not been found in Britain; the nearest locality is probably Iceland (Jónsson, 1903), although Börgesen (1902, p. 471) mentions finding a few plants possibly referable to subsp. *evanescens* at Thorshavn (Faeröes). The larger forms of this subspecies are found near or below low tide level at sheltered or semi-exposed sites. The smaller forms are found under more rigorous environmental conditions, such as, at more exposed sites, at higher tidal levels, or under Arctic conditions.

Authentic specimens examined: **West Greenland**. Godthaab, July 1886, *K. Rosenvinge* (BM, *Plantae groenlandicae*, No. 211, ex Herb. Holmes). **Canada**. NOVA SCOTIA: Halifax harbour, Aug.–Sept. 1948, *T. A. & A. Stephenson* (Herb. M. S. Doty, No. NSH. 13). BRITISH COLUMBIA: Vancouver Island: Esquimalt, Jan. 1860, probably *F. S. Collins* (BM, ex Herb. Holmes, two sheets). **U.S.A.** MASSACHUSETTS: Nahant, Aug. 1884, *F. S. Collins* (BM, ex Herb. Holmes).

OTHER DESCRIBED FORMS

Apart from the forms reduced to synonymy in the foregoing treatment, certain other described forms have been regarded as distinct species by some recent authors, as follows:

Fucus fueci De la Pyl. (A. D. Zinova, 1953).
Fucus miclonensis De la Pyl. (Taylor, 1937; A. D. Zinova, 1953).
Fucus membranaceus Gardner (1922; Setchell & Gardner, 1925).

These forms are regarded by the author as further forms of *F. distichus* L. emend. Powell, but they do not appear to be sufficiently distinctive to warrant subspecific status.

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In conclusion, the author would be grateful to receive or borrow specimens of this difficult group of plants from colleagues in any part of the world, and especially from colleagues who may not agree with the taxonomic treatment proposed above.

SUMMARY

The taxonomic status and nomenclature of the hermaphrodite forms of *Fucus* (other than the alga currently known as *F. spiralis* L. and certain hybrid forms) usually included under the name *Fucus inflatus* L. by European authors, but under several specific names by N. American and some other authors, is discussed. It is considered that the numerous forms described are best interpreted for the present as forms of a single, extremely plastic and widely distributed species.

In order to determine the correct names to apply to two forms of '*F. inflatus* L.' found in Britain, a critical study has been made of the type specimens of *Fucus* spp. in the Linnaean Herbarium. It is concluded that the two small sterile specimens labelled '*F. inflatus*' in Herb. Linn. are most probably plants of *F. vesiculosus* L.; the original diagnosis of *F. inflatus* L. is also inadequate and it is proposed that this name be regarded as a synonym of *F. vesiculosus* L.

However, the taxon *F. distichus* L. (*Syst. Nat.*, Ed. 12, 1767) is shown to be valid, based on good specimens in Herb. Linn., and this is re-established as the earliest acceptable name for the group of forms in question. The principal characters of the species as a whole are: (i) hermaphrodite conceptacles, and (ii) the frequent presence, in all forms, of closed cavities in the frond—the caecostomata. Caecostomata are described for European material (including the Linnaean type) for the first time.

Near the centres of distribution of this species whole series of forms

(clines) intermediate in character between the various extreme forms may be found; in such places the extreme forms can often be interpreted as ecological forms and it may be that in some places they have evolved into true ecotypes (genetically better adapted forms). At the limits of geographical range, on the other hand, intermediate forms are often absent and only one or two of the principal forms may persist, often as populations isolated both geographically and ecologically; it is even more likely that these isolated populations are genetically distinct ecotypes, but this could only be proved by experimentation.

The taxonomic limits of *F. distichus* L. are revised to include the following four principal subspecies: subsp. *distichus*; subsp. *anceps* (Harv. et Ward ex Carruthers) Powell, *n.comb.*; subsp. *edentatus* (De la Pyl.) Powell, *n.comb.*; and subsp. *evanescens* (C. Ag.) Powell, *n.comb.* Of these, only subspp. *anceps* and *edentatus* have been found in Britain.

For each subspecies the following information is given: important synonymy, nomenclatural type, principal illustrations, description, geographical distribution, and a list of authentic specimens examined. The illustrations include photographs of the type specimens of *F. inflatus* L. and *F. distichus* L.

It is shown, incidentally, that the plant currently known in Britain as *F. vesiculosus* f. *evesiculosus*, should more properly be named *F. vesiculosus* f. *linearis* (Huds.).

REFERENCES

AGARDH, C. A., 1820. *Species algarum...* Vol. 1, Pt. 1, 168 pp. Lund.

—— 1821. *Icones algarum ineditae.* Fasc. 2, 2 pp., pls. 11–20. Stockholm.

AGARDH, J. G., 1868. Bidrag till Kännedomen af Spetsbergens Alger. Tillägg till föregående afhandling. *K. svenska VetenskAkad. Handl.*, Bd. 7, No. 8, pp. 27–49, pl. 3.

ANON., 1863. *Fucus furcatus* Agardh, a new British seaweed. *J. Bot., Lond.*, Vol. 1, p. 283.

ARESCHOUG, J. E., 1868. Slägtena *Fucus* (L.) Decaisne & Thuret och *Pycnophycus* Kütz. jemte tillhörande arter. *Bot. Notiser, 1868*, No. 3, pp. 99–115.

ARWIDSSON, TH., 1937. Meeresalgen aus Vestagder und Rogaland. *Nyt. Mag. Naturv.*, Bd. 76, pp. 85–149.

BATTERS, E. A. L., 1902. A catalogue of the British marine algae...*J. Bot., Lond.*, Vol. 40, Suppl., 107 pp.

BÖRGESEN, F., 1902. Marine algae. *Botany of the Faeröes*, Part II, pp. 339–532, pls. XIII–XXIV. Copenhagen, 1903. (Issued separately.)

—— 1903. The marine algae of the Shetlands. *J. Bot. Lond.*, Vol. 41, pp. 300–6.

—— 1904. *Om Algevegetationen ved Faeröernes Kyster, en Plantegeografisk Undersögelse.* 122 pp., 12 pls. Copenhagen.

—— 1905. The algae-vegetation of the Faeröese coasts, with remarks on the phytogeography. *Botany of the Faeröes*, Part III, pp. 683–834. Copenhagen, 1908. (Issued separately.)

BURROWS, E. M., CONWAY, E., LODGE, S. M. & POWELL, H. T., 1954. The raising of intertidal algal zones on Fair Isle. *J. Ecol.*, Vol. 42, pp. 283–8.

CARRUTHERS, W., 1863. *Fucus distichus* Linn. as an Irish plant. *J. Bot., Lond.*, Vol. 1, pp. 353–5, pl. 12.

—— 1864. Note on the Kilkee *Fucus*. *J. Bot., Lond.*, Vol. 2, p. 54.

DECAISNE, J. & THURET, G., 1845. Recherches sur les anthéridies et les spores de quelques *Fucus*. *Ann. Sci. nat.*, Sér. 3, Bot., T. 3, pp. 5–15, pls. 1–2.

DE LA PYLAIE, A. J. M. B., 1829. *Flora de Terre-Neuve et des iles Saint Pierre et Miclon*. 128 pp. Paris. [The plates of this work were never published.]

DE TONI, J. B., 1895. *Sylloge Algarum omnium hucusque cognitarum*. Vol. III, *Fucoideae*, 638 pp. Patavia.

DOTY, M. S., 1947. The marine algae of Oregon. Part I. Chlorophyta and Phaeophyta. *Farlowia*, Vol. 3, pp. 1–65.

DUNN, M. D., 1937. Notes on the flora of Loch Harray and Loch Stenness.... *Trans. bot. Soc. Edinb.*, Vol. 32, Pt. 2, pp. 368–72.

DU RIETZ, G. E., 1947. Wellengrenzen als ökologische Äquivalente der Wasserstandslinien. *Zool. Bidr. Uppsala*, Bd. 25, pp. 534–50, 4 pls.

ESPER, E. J. C., 1800. *Icones Fucorum*... Erster Theil, Viertes Heft, pp. 167–217 [including many erroneous page numbers], pls. 88–111. [This reference not seen; obtained from Silva, 1953.]

FARLOW, W. G., 1881. *The Marine Algae of New England and Adjacent Coast*. Reprinted from *Rep. U.S. Comm. Fish.* for 1879, Appendix A–1, 210 pp., 15 pls. Washington.

'*Flora Danica*.' *Icones Plantarum sponte nascentium in regnis Daniae et Norwegiae, in ducatibus Slesvici et Holsatiae, et in comitatibus Oldenburgi et Delmenhorstiae: ad illustrandum opus de iisdem Plantis, Regio jussu exarandum, Florae Danicae nomine inscriptum*. [Usually quoted as 'Flora Danica'.] Edited at first by G. C. Oeder, later by others. 17 vols. (and 1 vol. Supplement), 3060 (and 180) pls., with descriptive letterpress. Hafniae, (1761–) 1764–1883. (See also Oeder, 1767, and Vahl, 1794.)

FOSLIE, M., 1886. Kritisk fortegnelse over Norges havsalger efter aeldre botaniske arbeider indtil aar 1850. *Tromsø Mus. Aarsh.*, Vol. 9, pp. 85–137.

FRITSCH, F. E., 1945. *The Structure and Reproduction of the Algae*. Vol. 2, 939 pp. Cambridge University Press.

GARDNER, N. L., 1922. The genus *Fucus* on the Pacific coast of North America. *Univ. Calif. Publ. Bot.*, Vol. 10, No. 1, 181 pp., incl. 60 pls.

GAULD, D. T., BAGENAL, T. B. & CONNELL, J. H., 1953. The marine fauna and flora of St Kilda, 1952. *Scot. Nat.*, Vol. 65, pp. 29–49.

GMELIN, S. G., 1768. *Historia Fucorum*. 239 pp., 34 pls. Petropoli.

GRAY, S. O., 1867. *British Sea-Weeds*, xxiii, 312 pp., 16 pls. col. London.

HARVEY, W. H., 1864. *Fucus anceps* Ward & Harvey. A letter in *Ann. Mag. nat. Hist.*, 3rd. Ser., Vol. 13, p. 184.

HORNEMANN, J. W., 1827. *Nomenclatura Florae Danicae, emendata cum indice systematico et alphabetico*. 214 pp. Hafniae.

HUDSON, W., 1762. *Flora Anglica*. xv, 506 pp. London.

—— 1778. *Flora Anglica*. Ed. 2, xxxviii, 690 pp. London.

HYGEN, G. & JORDE, I., 1935. Beitrag zur Kenntnis der Algenflora der norwegischen Westküste. *Bergens Mus. Aarb.* 1934, Nr. 9, 60 pp.

HYLMÖ, D. E., 1933. Algenimmigration nach der schwedischen Westküste. *Bot. Notiser*, 1933, pp. 377–90.

INOH, S., 1935. Embryological studies on *Pelvetia wrightii* Yendo and *Fucus evanescens* Ag. *J. Fac. Sci. Hokkaido Univ.*, Ser. V, Bot., Vol. V, No. 1, pp. 9–23, 4 pls.

JÓNSSON, H., 1903. The marine algae of Iceland. II. Phaeophyceae. *Bot. Tidsskr.*, Bd. 25, pp. 141–95.

KJELLMAN, F. R., 1883. The algae of the Arctic Sea. *K. svenska VetenskAkad. Handl.*, Bd. 20, No. 5, 350 pp., 31 pls.

KJELLMAN, F. R., 1890. *Handbok i Skandinaviens Hafsalgflora.* I. *Fucoideae.* 103 pp. Stockholm.

KLEEN, A. E., 1874. Om Nordlandens högre hafsalger. *Öfvers. VetenskAkad. Förh., Stockh.*, No. 9, pp. 3–46, pls. 9, 10.

KÜTZING, F. T., 1860. *Tabulae Phycologicae, oder Abbildungen der Tange.* Bd. 10, 39 pp., 100 pls. Nordhausen.

KYLIN, H., 1947. Die Phaeophyceen der schwedischen Westküste. *Lunds Univ. Årsskr.*, N.F., Avd. 2, Bd. 43, Nr. 4, 99 pp., 18 pls.

LANJOUW, J. (Editor) *et al.*, 1952. *International Code of Botanical Nomenclature... Adopted... Stockholm, July 1950.* 228 pp. Utrecht.

LEVRING, T., 1937. Zur Kenntnis der Algenflora der norwegischen Westküste. *Lunds Univ. Årsskr.*, N.F., Avd. 2, Bd. 33, Nr. 8, 148 pp., 4 pls.

—— 1946. Några havsalgfynd vid den svenska västkusten. *Acta Hort. gothoburg.*, 16, pp. 191–4.

LEWIS, J. R., 1954. The ecology of exposed rocky shores of Caithness. *Trans. roy. Soc. Edinb.*, Vol. 62, pp. 695–723, 4 pls.

LIGHTFOOT, J., 1777. *Flora Scotica.* 2 Vols. London.

LINNAEUS, C., 1737. *Flora Lapponica.* Ed. 1. Amstelaedami.

—— 1753. *Species Plantarum.* Ed. 1, 2 T. Holmiae.

—— 1767. *Systema Naturae.* Ed. 12, 3 T. Holmiae, 1766–68. (T. 1, 1766; T. 2, 1767; T. 3, 1768.)

—— 1774. *Systema Vegetabilium.* Gottingae and Gothae. [This is a new edition of the botanical part (T. 2) of the *Systema Naturae* and counts on from the 12th edition (1766–68) of that work.]

—— 1779. *Systema Plantarum.* Francofurti and Moenum.

LUND, S., 1949*a*. Nye Alger for de danske Farvande. (With summary in English.) *Bot. Tidsskr.*, Bd. 48, Hft. 3, pp. 231–53.

—— 1949*b*. Immigration of algae into Danish waters. *Nature, Lond.*, Vol. 164, p. 616.

LYNGBYE, H. C., 1819. *Tentamen Hydrophytologiae Danicae.* 248 pp., 70 pls. Hafniae.

NEWTON, L., 1931. *A Handbook of the British Seaweeds.* 478 pp. London.

NICHOL, E. A. T., 1938. The brackish-water lochs of Orkney. *Proc. roy. Soc., Edinb.*, Vol. 58, pp. 181–91.

NORUM, E., 1913. Brunalger fra Haugesund og Omegn. *Nyt. Mag. Naturv.*, Bd. 51, pp. 137–60, pl. 2.

OEDER, G. C. (Editor), 1767. In '*Flora Danica*' [q.v.], Vol. 2, fasc. 6, tab. 351.

PARKE, M., 1953. A preliminary check-list of British marine algae. *J. mar. biol. Ass. U.K.*, Vol. 32, pp. 497–520.

POWELL, H. T., 1954. The distribution, ecology and taxonomic status of forms of *Fucus inflatus* L. in Britain and Ireland. Summary in *Rapp. Comm., 8me Congr. Int. Bot., Paris 1954*, Section 17, pp. 135–6.

POWELL, H. T. & LEWIS, J. R., 1952. Occurrence of *Fucus inflatus* L. forma *distichus* (L.) Börgesen on the north coast of Scotland. *Nature, Lond.*, Vol. 169, p. 508.

PRINTZ, H., 1926. Die Algenvegetation des Trondhjemsfjordes. *Skr. norske Videnskd.-Akad.*, I Mat.-Naturv. Klasse, No. 5, 274 pp., 10 pls.

ROSENVINGE, L. K., 1893. Grønlands Havalger. *Medd. Grønland*, Bd. 3, pp. 763–981, 2 pls.

SAVAGE, S., 1945. *A Catalogue of the Linnaean Herbarium.* 226 pp. London.

SETCHELL, W. A. & GARDNER, N. L., 1925. The marine algae of the Pacific coast of North America. Part III, Melanophyceae. *Univ. Calif. Publ. Bot.*, Vol. 8, Part 3, pp. 383–898, incl. pls. 34–107.

SILVA, P. C., 1953. The identity of certain Fuci of Esper. *Wasmann J. Biol.*, Vol. 11, No. 2, pp. 221–32.

SMITH, G. M., 1944. *Marine Algae of the Monterey Peninsula California.* 622 pp., incl. 98 pls. Stanford University Press, California; Oxford University Press.

SUNDENE, O., 1953. The algal vegetation of Oslofjord. *Skr. norske VidenskAkad.*, I Mat.-Naturv. Klasse, No. 2, 244 pp., 1 end-map.

TAYLOR, W. R., 1937. Marine algae of the northeastern coast of North America. *Univ. Mich. Stud.*, Vol. 13, 427 pp., 59 pls.

TURNER, D., 1802. *A Synopsis of the British Fuci.* 400 pp. Yarmouth.

—— 1808. *Fuci*... Vol. 1. London.

—— 1809. *Fuci*... Vol. 2. London.

VAHL, M. (Editor), 1794. In '*Flora Danica*' [q.v.], Vol. 7, fasc. 19, tab. 1127.

YENDO, K., 1907. The Fucaceae of Japan. *J. Coll. Sci. Tokyo*, Vol. 21, No. 12, 174 pp., 18 pls.

ZINOVA, A. D., 1953. *Opredelitel' burykh vodoroslei severnykh morei SSSR.* [*Title transl. : Classification of brown algae of the northern seas of the U.S.S.R.*] 225 pp. (153 illus.) Bot. Inst., Acad. Sci., U.S.S.R. Moscow & Leningrad. [In Russian.]

—— 1954. [*Title transl.:* Notes for Flora of seaweeds found in the White Sea.] *Acta Inst. bot. Acad. Sci. URSS*, Ser. 2, Plantae Cryptogamae, Fasc. 9, pp. 245–58. [In Russian.]

ZINOVA, E. S., 1933. Vodorosli Kamchatki. [Algae of Kamchatka]. *Issledovaniia morei S.S.S.R.*, Fasc. 17, pp. 7–42. [In Russian, with short summary in French.]

—— 1954. [Seaweeds found (*a*) in Okhotsk Sea, (*b*) in the Gulf of Tartary, (*c*) round south-eastern Kamchatka (*Titles transl.*).] *Acta Inst. bot. Acad. Sci. URSS*, Ser. 2, Plantae Cryptogamae, Fasc. 9, pp. 259–310, 311–64, 365–400. [In Russian.]

EXPLANATION OF PLATES

PLATE I

Fig. 1. *Fucus inflatus* L. Photograph of the type specimens (Sheet 1274: 51 in the Linnaean Herbarium).

Fig. 2. *F. distichus* L. emend. Powell, subsp. *distichus*. Photograph of the type specimens (Sheet 1274: 56 in the Linnaean Herbarium). Specimen A is the lectotype.

PLATE II

Fig. 1. *F. distichus* L. emend. Powell, subsp. *anceps* (Harv. et Ward ex Carruthers) Powell. Photograph of a pressed specimen, 11·5 cm greatest length: Kilkee, Ireland, *J. Cook* (BM, ex Herb. Holmes, no date). ×0·55.

Fig. 2. *F. distichus* L. emend. Powell, subsp. *edentatus* (De la Pyl.) Powell. Photograph of a pressed specimen, 25 cm greatest length: Lerwick, Shetland Islands, July 1952, *H. T. Powell* (MILL). ×0·35. *r.*, elongated receptacles; *c.*, continued vegetative growth beyond the receptacles. The receptacles are not usually so much elongated as in this specimen.

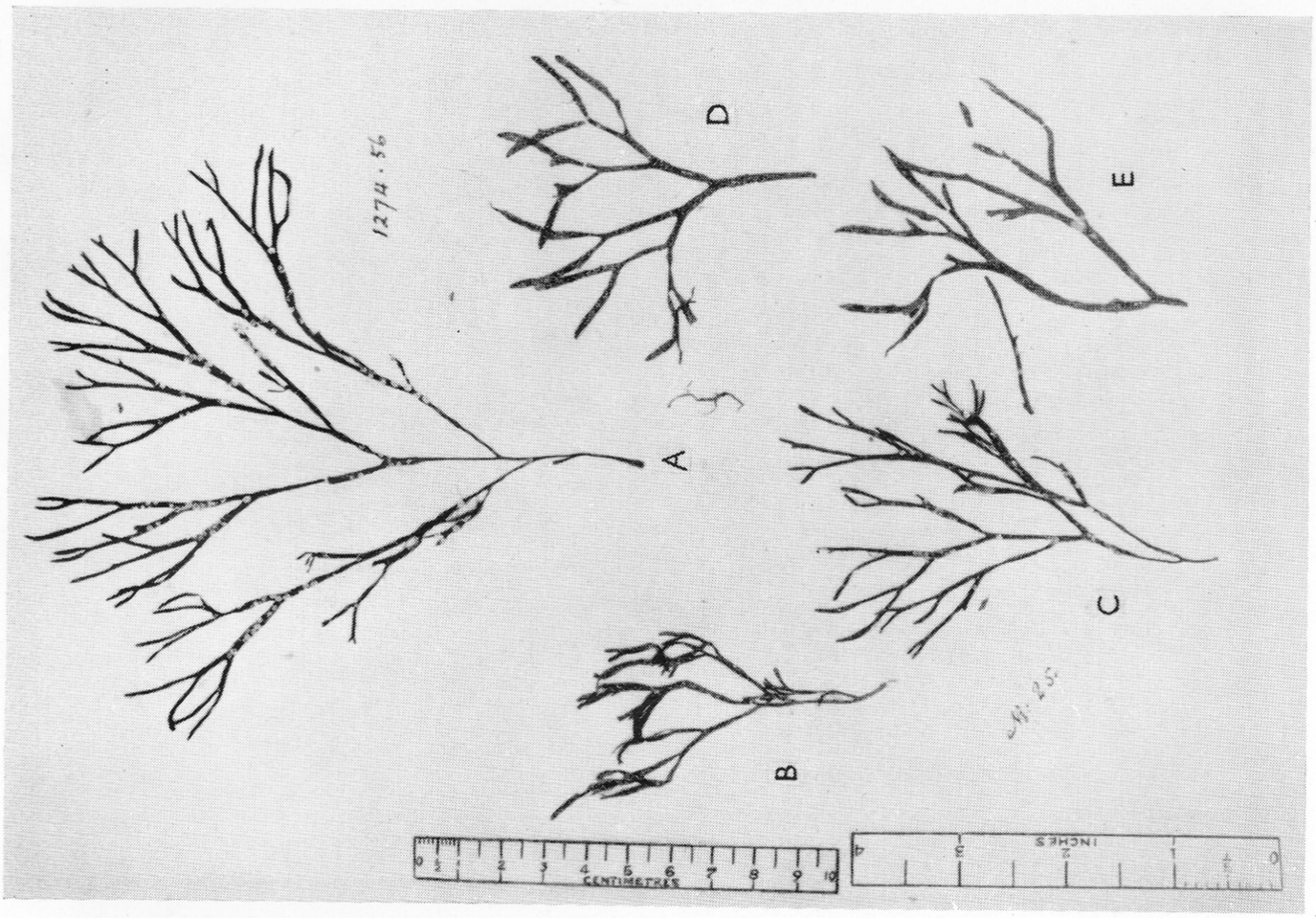

Fig. 2

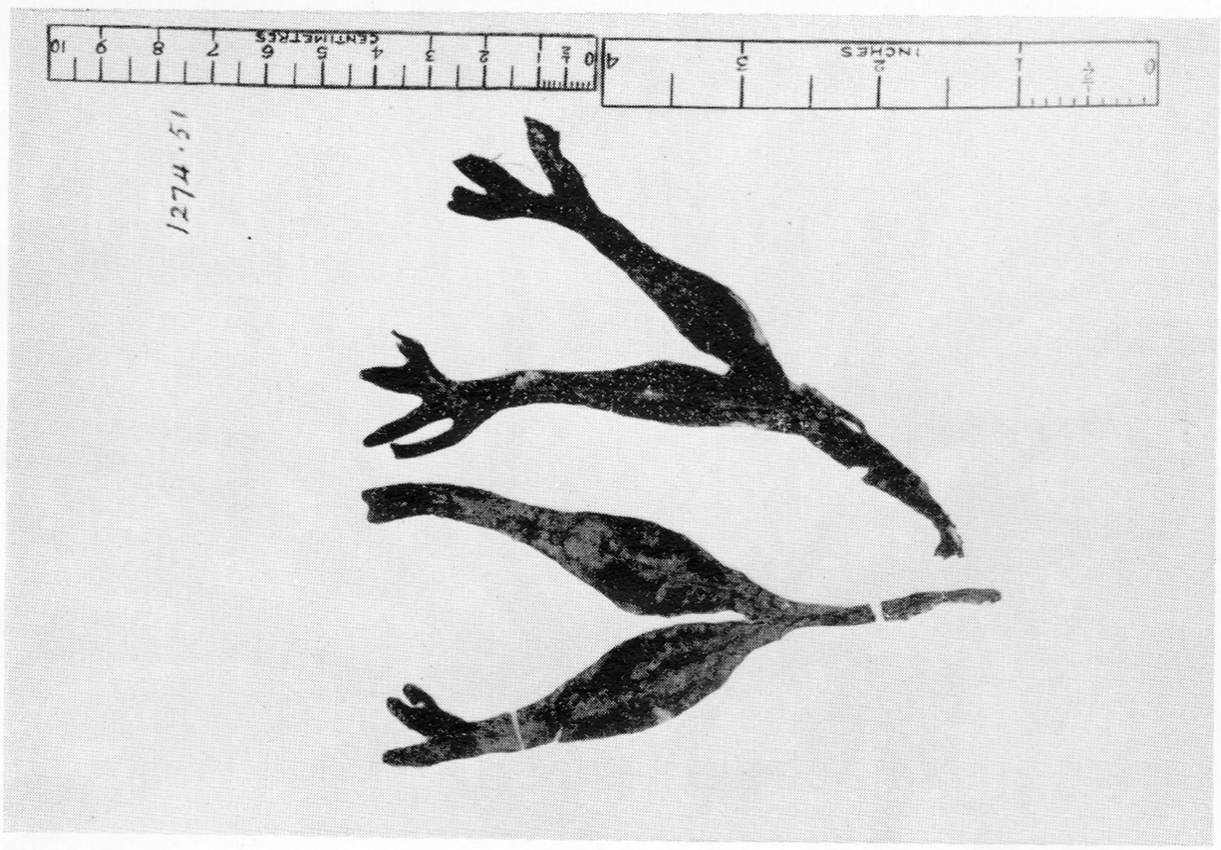

Fig. 1

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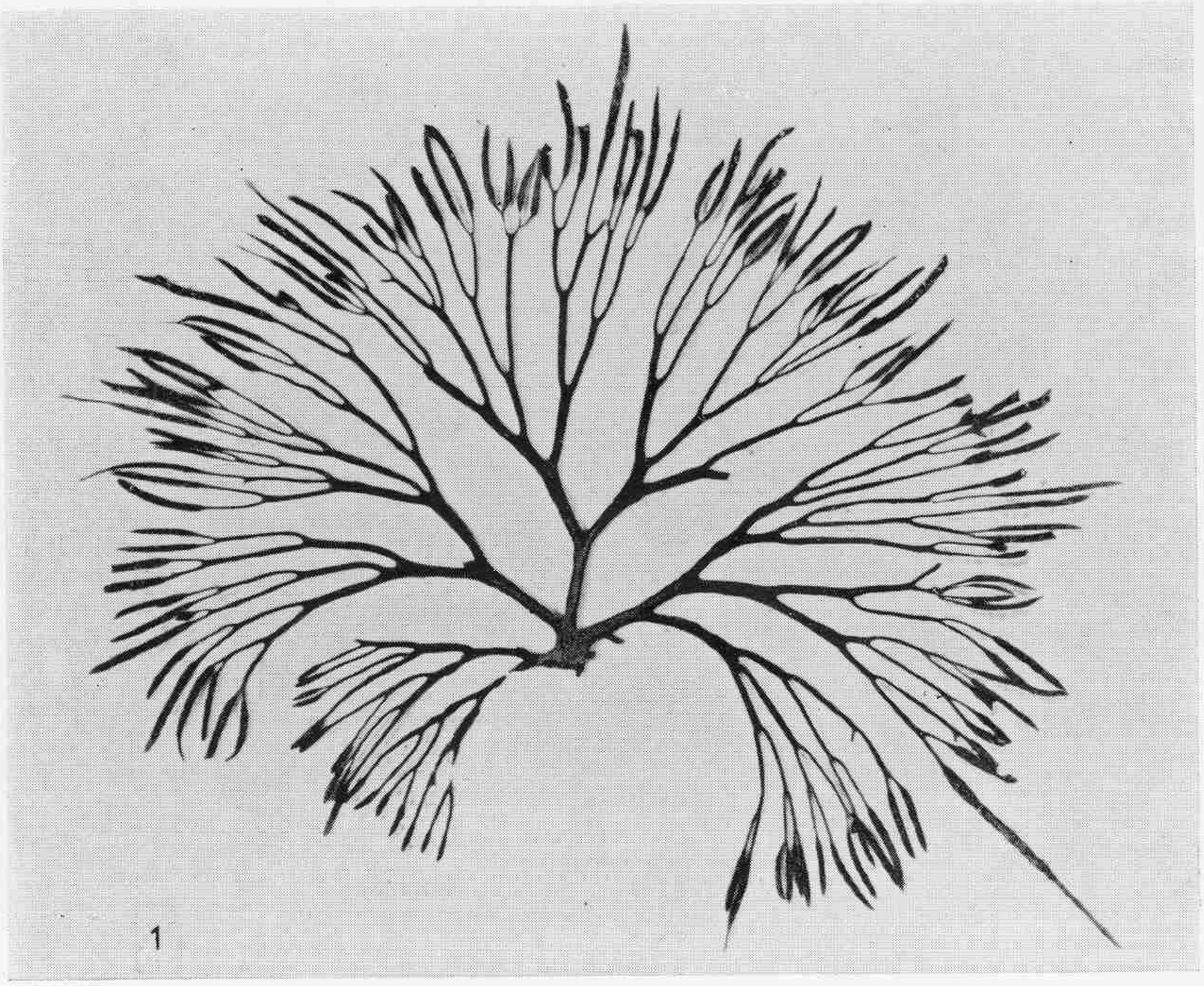

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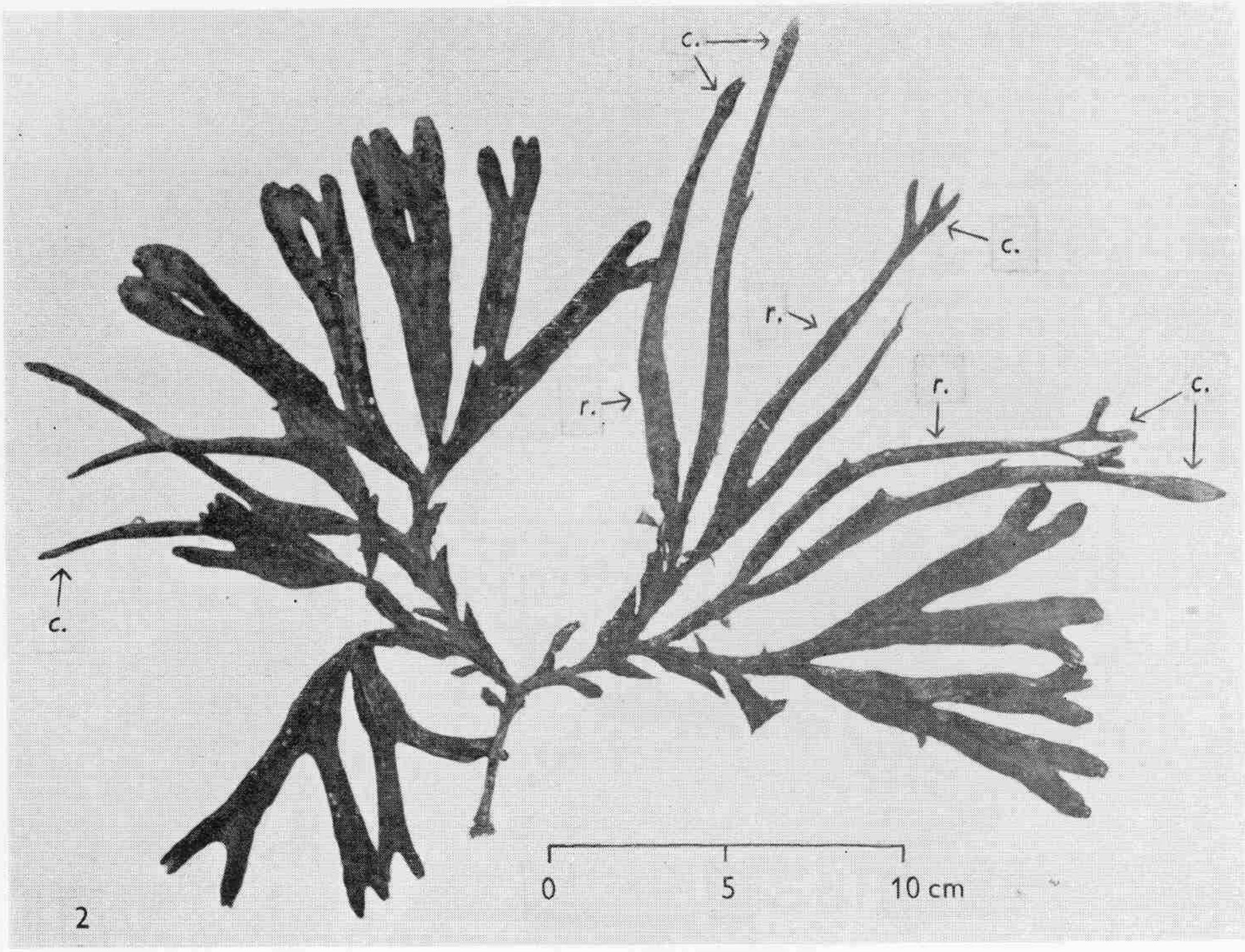

2

ABSTRACTS OF MEMOIRS

RECORDING WORK DONE AT THE PLYMOUTH LABORATORY

NOTES ON THE NERVOUS SYSTEM IN THE STOMATOPODA. IV. MUSCLE RECEPTOR ORGANS

By J. S. ALEXANDROWICZ

Pubbl. Staz. Zool. Napoli, 1954, Vol. 25, pp. 94–111

In *Squilla mantis*, muscle receptor organs have been found in the extensor muscles of the six thoracic and six abdominal segments. They are composed of thin muscles and nerve cells. In ten segments there are two muscles and two nerve cells on each side. The muscles of each pair differ in their structure. In a certain region of the muscles there is an intercalated tendon common to the two muscles. The nerve cells differ in their size and mode of ramification of their dendrites.

Differences in structure of the muscle receptor organs which might have a relation to their response at different stretch thresholds are discussed.

J.S.A.

THE EYES AND THE PHOTONEGATIVE BEHAVIOUR OF *NEPHTYS* (ANNELIDA, POLYCHAETA)

By R. B. CLARK

J. exp. Biol., 1956, Vol. 33, pp. 461–77

Three types of photoreceptor are found in the Nephtyidae: inverted, single-celled ocelli in pigment cups embedded in the brain, similar cells, though without pigment cups, anterior to the brain, and possibly epidermal photoreceptors. Morphological and experimental evidence suggests that the prostomial receptors of *Nephtys* are homologous with the eyes of *Nereis* and that they are involved in the same types of behaviour. The frequency with which *Nephtys* swims is, within limits, a linear function of the light intensity. Although the ganglionic eyes are directional receptors the worm does not orientate itself in a light beam; presumably the light reaching them is too diffuse. In the very small species *N. cornuta* the eyes are close to the surface of the brain and the worm does orientate itself in a light beam. Swimming is an essential prelude to burrowing, and the brighter the light the more frequently the worm swims and the sooner it is buried. Activity in light can be inhibited by stimulating receptors on the dorsal surface of the animal by contact.

R.B.C.

DEEP WATER MOVEMENTS IN THE NORTH ATLANTIC AS A LINK BETWEEN CLIMATIC CHANGES AROUND ICELAND AND BIOLOGICAL PRODUCTIVITY OF THE ENGLISH CHANNEL AND CELTIC SEA

J. mar. Res., 1955, Vol. 14, pp. 347–62

AND

HYPOTHESES CONNECTING FLUCTUATIONS IN ARCTIC CLIMATE WITH BIOLOGICAL PRODUCTIVITY OF THE ENGLISH CHANNEL

By L. H. N. Cooper

Deep-Sea Res., 1955, Suppl. to Vol. 3, pp. 212–23

These two papers, which need to be read together with the paper in the *Journal* on assessing the age of oceanic water with carbon-14, present a group of hypotheses to explain fluctuations in biological productivity of the English Channel, in terms of changes in Arctic climate. The first paper describes the conditions under which heavy and cold Norwegian Sea water spills over the ridges east and west of Iceland into the Atlantic to create two new water masses. The courses of these are followed down into the deep Atlantic. In each case the water is held to the right banked against the eastern side of the Reykjanes Ridge and the continental slope of East Greenland respectively. Room in the ocean for this sinking water has to be found by upward displacement of water which is already there. This upward displacement will carry the deep stock of nutrients towards the upper layers where wind-driven and thermohaline mixing processes—which are always operating—may bring them into the illuminated zone. When cold Arctic winters cause much recruitment of cold heavy water to the Norwegian Sea, a chain of events is initiated which will enrich the surface waters. Following mild Arctic winters the loss from the surface layers in temperate latitudes by sinking of detritus and defecation at depth of vertical migrants, cannot be made good by upward displacement.

This, however, is only one part of the mechanism. The second paper develops a complementary one.

The overspills into the Atlantic are believed to occur not as smooth steady streams of water but as intermittent surges. In the Atlantic these surges will behave as balls or boluses of water and may be considered to have some of the properties of an elastic solid. Whilst sinking beneath the lighter enveloping water and especially when the under-lying sea-bed or continental slope is very dissected, the boluses may initiate internal waves of considerable amplitude and energy. It is postulated that these waves may travel great distances in the ocean with little attenuation. When they strike another continental slope, particularly a dissected one, much of the energy of the internal wave system is likely to be destroyed by mixing of the waters bathing the slope. The resulting homogenization of these slope waters will tend to carry nutrients upwards

and heat downwards. This chain of events will also be favoured by cold Arctic winters and weakened by mild ones.

From the basic hypotheses it is easy to derive further ones which are capable of test by observation and experiment in the ocean. L.H.N.C.

DEMONSTRATION OF SMALL-SCALE WATER-CURRENTS BY MEANS OF MILK

By D. J. Crisp and A. J. Southward

Nature, Lond., 1956, Vol. 178, p. 1076

During work on the behaviour of barnacles it was found that ordinary cow's milk offered a better means of detecting small-scale water movements than the commonly used suspensions of carmine or graphite. The animals were observed or photographed against a black background and the milk was injected into the water above from a row of fine jets. The density of the milk could be varied by dilution with the water or by alteration of the cream content; normally it remained suspended in trails, resembling thick smoke in air. The method was used to measure the water currents set up by the cirral movements of barnacles, and to establish the presence of a through current in the mantle cavity during normal beating of the cirri. A.J.S.

LA CONTAMINATION DES POISSONS ET LE PROBLÈME DES EAUX POLLUÉES

By A. Guelin

Annales Inst. Pasteur, 1954, T. 86, pp. 303–9

It has been previously reported by the writer that the intestine of fishes caught offshore in the Mediterranean is free from enterobacteria, whereas in those caught in the littoral zone there is an intestinal flora similar to that in man or in warm-blooded animals.

The waters sampled far from any shore are as a rule free from bacteria and intestinal bacteriophages found in the littoral zone. The question arises how far the bacteriological aspect of the viscera of fishes is correlated with the sanitary state of waters in which they live.

Sixty-one specimens of *Ctenolabrus rupestris*, in which no infestation could be ascertained in preliminary examination, were contaminated with either *Enteramoeba coli* or with coliphage. In a week's time all these fish had freed themselves completely from the contaminating agent.

These results show that the investigation of the enterobacteria and enterophages in fishes could give information as to the possible pollution of the waters in which the animals live. A.G.[1]

[1] This abstract has been translated from the French.

STUDIES OF SERPULID TUBE FORMATION.
II. THE CALCIUM-SECRETING GLANDS IN THE PERISTOMIUM OF *SPIRORBIS, HYDROIDES* AND *SERPULA*

By R. H. HEDLEY

Quart. J. micr. Sci., 1956, Vol. 97, pp. 421–7

In a previous paper the author described the calcium-secreting glands in *Pomatoceros* and gave an account of the pre-secreted component of this serpulid's tube. This study has been extended to three other British serpulids and the structural variation of the calcium-secreting glands has been demonstrated.

In *Spirorbis* the gland is tubular, in which the gland cells have unusual extensions projecting into the lumen, whilst in *Hydroides* the gland is a simple tubule. *Serpula* has glands which are tubulo-racemose and similar to those found in *Pomatoceros*.

An unusual arrangement is found in *Serpula* where, in addition to the two calcium-secreting glands, there are two ventral calcium sacs in the posterior part of the peristomium. These also secrete calcareous material and contribute towards tube formation.

R.H.H.

ACTIVE TRANSPORT OF CATIONS IN GIANT AXONS FROM *SEPIA* AND *LOLIGO*

By A. L. HODGKIN and R. D. KEYNES

J. Physiol., 1955, Vol. 128, pp. 28–60

In giant axons from *Sepia* and *Loligo* the efflux of labelled sodium ions and the influx of potassium ions have been shown to be greatly reduced by metabolic inhibitors (dinitrophenol, cyanide and azide) or by cooling to a low temperature. Sodium influx and potassium efflux are relatively little changed under these conditions. Metabolic inhibitors also have little effect on the resting potential and action potential, or on the rapid sodium movements associated with the passage of impulses. Removal of potassium ions from the external medium reduces the sodium efflux to about one-third, the effect being immediate in contrast to the delayed action of inhibitors, and the absolute size of the decrease in efflux being about equal to the decrease in potassium influx caused by inhibitors.

It is concluded that in addition to a permeability system which allows ions to move down electrochemical gradients during electrical activity, there is a secretory mechanism driven by metabolism which ejects sodium and absorbs potassium against the electrochemical gradients. Conduction of impulses,

but not recovery, can take place if the secretory mechanism is put out of action with inhibitors. Sodium efflux and potassium influx are coupled, but do not seem to be linked rigidly.

R.D.K.

EXPERIMENTS ON THE INJECTION OF SUBSTANCES INTO SQUID GIANT AXONS BY MEANS OF A MICROSYRINGE

By A. L. HODGKIN and R. D. KEYNES

J. Physiol., 1956, Vol. 131, pp. 592–616

A microsyringe is described which enables precisely determined volumes of fluid to be injected into squid giant axons uniformly over distances of 3–20 mm. The volume injected is about 1/25 of the axon volume per unit length. The performance of the microsyringe was tested by injecting dye solutions. Methylene blue and eosin were observed to diffuse radially through the axoplasm, but more slowly than in free solution.

Injection of small quantities of KCl did not have any marked effect on the membrane potentials. Injection of similar quantities of NaCl reduced the reversed potential at the crest of the spike by an amount which fitted with that calculated from the change in concentration ratio. Injections of magnesium and tubocurarine chlorides had no great effect on the axons. Injections of calcium liquefied the axoplasm and tended to block conduction.

When ^{24}NaCl was injected, a steady rate of extrusion of labelled sodium was established within a minute. The diffusion coefficient of sodium in the axoplasm can have been very little less than in free solution, and the sodium pump must operate with a lag of not more than a few seconds. The sodium efflux was blocked in the usual way by inhibitors. It was established that over short periods the sodium efflux was directly proportional to the internal sodium concentration, but that the proportionality factor declined with a time constant of about 5 h.

R.D.K.

TEMPERATURE AND MACKEREL MOVEMENTS IN THE INSHORE WATERS OF TORBAY, DEVONSHIRE

By L. A. J. JACKMAN and G. A. STEVEN

J. Cons. int. Explor. Mer, 1955, Vol. 21, pp. 65–71

The arrival and departure date of mackerel in the Torquay area show a close correlation with sea surface temperature.

In the period 1945–53 inclusive mackerel made their first appearance inshore when the sea temperature was within the range 11·1–11·6° C. In six different years the temperature was exactly 11·6° C and on those occasions when it differed a reading of 11·6° C was made either one day before or one

day after the recorded appearance of the fish. Departure records for the years 1941 to 1953 show a range of 12·2°–13·9° C.

In no year did the fish arrive before a well-marked thermocline had formed at E_1. Conversely, on departure the thermocline had almost always broken down completely.

This fact will be more closely observed in future years. L.A.J.J.

SEASONAL CHANGES IN THE PHYTOPLANKTON AS INDICATED BY SPECTROPHOTOMETRIC CHLOROPHYLL ESTIMATIONS 1952–53

By PAMELA G. JENKINS

Deep-Sea Res., 1955, Suppl. to Vol. 3, pp. 58–67

Chlorophyll determinations were continued on the phytoplankton of the English Channel from September 1952 until August 1953 at depths from 0 to 70 m, the species being identified by culture. Minima 2 mg/m^3 occur in winter and June. Maxima at particular depths can occur in March, April or May. In 1952, 34·2 mg/m^3 was a maximum in the surface, whereas in 1953 cell sinking gave, in May, 78·8 mg/m^3. The autumn maximum in September 1952 was 21·1 mg/m^3.

Collodion filter disks varied from dark grey or chocolate to a light sandy colour and showed phytoplankton, fibres, copepods and other animals. Copepods were about 300,000 per square metre column down to 70 m in April.

Fifty-four species of Bacillariophyceae were recorded. As before *Skeletonema costatum*, a Navicula and *Nitzschia closterium* were the most common. Six Chlorophyceae, five Chrysophyceae, one Cyanophyceae and three Cryptophyceae were found. In the first class a *Chlorella* sp. was commonest and in the second a species of Coccolithophora grew in each sample. *Phaeocystis globosa* grew from January to May. *Hemiselmis rufescens* appeared again.

P.G.J.

COLLOIDAL PROPERTIES OF THE MESOGLOEA IN SPECIES OF *LEUCOSOLENIA*

By W. C. JONES

Quart. J. micr. Sci., 1956, Vol. 97, pp. 269–85

Isotonic potassium nitrate solution causes a rapid collapse of the oscular tubes of species of *Leucosolenia*: the cells dissociate and the mesogloea swells and disperses. Differences in the time of collapse of tubes from different specimens, or tubes derived at different times from the same specimen, suggest that the mesogloea varies in its initial degree of firmness. Replacing the collapsing tubes in sea water results in the immediate stiffening of the

mesogloea and the previously swollen cells shrink and form characteristic rod-like processes. The mesogloea seems to be secreted by the choanoderm, since just beneath this layer it may be more readily swollen by the potassium nitrate. Its dispersion can be prevented by first immersing the tubes for a time in slightly acidified sea water. Other neutral salt solutions also soften the mesogloea, but vary considerably in the time taken for the onset of plasticity. Their ions can be arranged in three lyotropic series which indicate that the mesogloea is an organic hydrophilic colloid similar to, for example, chondroitin sulphate.

The experiments show that the mesogloea has an important skeletal function.

W.C.J.

THE INTRACELLULAR CALCIUM CONTENTS OF SOME INVERTEBRATE NERVES

By R. D. KEYNES and P. R. LEWIS

J. Physiol., 1956, Vol. 134, pp. 399–407

A method is described for the determination in biological samples of 1 μg or less of calcium. Analyses of (*a*) axoplasm extruded from freshly dissected squid axons, and (*b*) whole *Carcinus* nerves which had been soaked in Ringer's solution containing various amounts of calcium, showed that in both types of invertebrate nerve the internal calcium concentration is of the order of 0·5 m-mole/kg wet weight.

R.D.K.

EVIDENCE FOR A MECHANORECEPTIVE FUNCTION OF THE AMPULLAE OF LORENZINI

By R. W. MURRAY

Nature, Lond., 1957, Vol. 179, pp. 106–7

The responses of the ampullae of Lorenzini of *Raia clavata* were investigated electrophysiologically. The spontaneous frequency of discharge of single units could be increased or decreased by stimuli which increased or decreased the pressure within the ampullae themselves relative to that outside. The responses showed partial adaptation and opposite after-effects. Possible functions of the ampullae are discussed.

R.W.M.

PHYSIOLOGICAL CONTROL OF LUMINESCENCE IN ANIMALS

By J. A. C. Nicol

Luminescence of Biological Systems, pp. 299–321. 1955. Washington: American Ass. Adv. Sci.

A review is presented of various methods known to be operative in the regulation of the luminescent responses of animals. Intensity, duration and iteration are possible variables. Control is direct (excitation acting directly on intracellular photogenic processes), or indirect, involving glandular secretion (extracellular luminescence) or movement of screening devices (symbiotic organs).

Various examples are given, and some new data presented for luminescence in ctenophores, the glow-worm and Pyrosoma.

J.A.C.N.

THE NERVOUS ANATOMY OF THE BODY SEGMENTS OF NEREID POLYCHAETES

By J. E. Smith

Phil. Trans. B, 1957, Vol. 240, pp. 135–96

An account is given of the anatomy of the giant and fine fibre systems of the nerve cord of nereid polychaetes and of the constitution of the four pairs of serially repeated segmental nerves.

The fine fibre internuncial systems are designed to transmit excitation ventro-dorsally in the cord and (by means of six longitudinal tracts) along its length. Most of the sensory and motor fibres effect their internuncial connexions within the cord in the dorsal half of the neuropilar substance. The nervous arcs which involve fine fibre internuncials are described in detail. They appear to have a more obviously direct nervous continuity than those involving giant fibres, a circumstance which is discussed in relation to previously established excitation characteristics of the two systems and their role in bringing about locomotory movements and 'escape' responses.

All the segmental nerves are 'mixed'. Their sensory fields and, in some instances, their motor distribution are described. There is, on the sensory side, anatomical evidence of the canalization of afferent excitation from a large number of widely separated sensory endings into a small number of centrally directed tracts. On the motor side the dispersal of excitation to the various muscle systems is brought about by the interpolation of relay neurons into the peripherally directed motor tracts which, at their origin from the cord, contain very few fibres. The possible significance of the small number of motor and internuncial neurons in the cord is discussed.

J.E.S.

BOOK REVIEWS

THE GALATHEA DEEP SEA EXPEDITION

Described by members of the expedition
and edited by A. F. Bruun, S. Greve, H. Mielche and R. Spärck

Translated from the Danish by R. Spink.

George Allen and Unwin, London. 296 pp. Price 40*s*. 1957.

The Galathea Expedition, which set sail from Copenhagen in 1950, was only the fourth major expedition which was equipped to explore all the great deeps of the oceans. In two years she circumnavigated the world. When she departed very few dredge hauls had been made below 6000 and only one below 7000 m. It was seriously disputed whether life existed in the abyssal depths below 10,000 m. When she returned she had fished over 100 specimens, representing six species and five phyla, from depths of over 10,000 m and thousands more embracing all the major phyla, including vertebrates, from depths greater than any previously attempted. Living bacteria were brought up from the extreme depths, in mud samples, and cultured in the laboratory, where they would only grow under pressures of 1000 atmospheres. Any account of this expedition is inevitably exciting to anyone interested in marine biology, and this account is made doubly so by the freshness imparted by description given by those who took part. A book of this nature is, of course, patchy, since the various writers have very differing styles and concepts of their readers' backgrounds, but even this adds variety. The translation is perhaps a trifle clumsy. The illustrations are more than adequate and make quite certain that this will take its place among the books of permanent value devoted to the great explorations of the world.

D.B.C.

THE AMERICAN ARBACIA AND OTHER SEA URCHINS

By Ethel Browne Harvey

Published by Princeton University Press (London: Oxford University Press). Pp. i–xiv, 1–298, with 16 plates and 12 text-figures. Price 48*s*. 1956.

Echinoid genital products are to the invertebrate experimental embryologist almost what *Drosophila* is to the geneticist; without them he would be seriously handicapped and our knowledge of fertilization and cleavage would be less advanced than it is to-day. A vast literature has grown up around these processes as they occur in *Arbacia punctulata* of the eastern coast of North America, in *A. lixula* of the Mediterranean, in *Echinus esculentus* of our own

shores and in other sea-urchins here and elsewhere. This book deals primarily with the first-named species, listing all important works about it, but including as well many works concerning other species. The book will be specially valuable to investigators at Woods Hole where the intensity of research into the embryology of *Arbacia punctulata* can be judged from the numbers of this sea-urchin used annually at the Marine Biological Laboratory there. Often several tens of thousands have been used in one year, though more recently less than ten thousand a year have sufficed. But the book will be scarcely less useful to those who work with the closely allied *Arbacia* at Naples and in other Mediterranean laboratories, and it cannot fail to be of very great value to embryologists using any species of sea-urchin. The text is delightfully written and apart from a few misprints the typography, by a Dutch firm, is good to the eye. The sequence of chapters takes us from the etymology of common and scientific names for the spiny adult urchins, their use as food for man and animals, through the classification and distribution of the different genera and species, to their embryology, normal and experimental. There are several chapters on centrifuged eggs, with which the author has herself done so much fundamental work. Most valuable of all is the compilation of notes on the experimental work of a formidable array of authors whose books and papers are listed in an extensive bibliography occupying over fifty two-columned pages. The sixteen beautifully reproduced plates, containing about 250 photomicrographs and other photographs of developing eggs, larvae and adults, merit praise. No zoological library and no worker in sea-urchin embryology and cell physiology can afford to be without this book.

D.P.W.

EELS: A BIOLOGICAL STUDY

By the late Léon Bertin

Published by the Cleaver-Hume Press Ltd., London. Pp. viii + 188 + 4.

Translated by Betty Roquerbe, under the supervision of Maurice Burton, from the second edition of *Les Anguilles* (Payot, Paris). Price 25*s*. 1956.

This curiously mixed book is the most complete and authentic account of the biology of the eel to appear in English and as such must take its place among the works of reference. All the information which the reader might require on freshwater eels (but not conger or Roman eels) is included, but often in a piecemeal and unassimilated manner. The book is evidently intended for the professional biologist or student, yet Professor Bertin occasionally felt it necessary to explain the most elementary biological principles as if he were writing for the lay reader. The bibliography has some strange omissions, notably Schmidt's paper, published in *Phil. Trans.* in

1922, in which he first announced the details of his discovery of the breeding place of eels. The half tone plates are poor, but the excellence of the line drawings compensates for this. While the factual content of the book is unimpeachable some of Professor Bertin's conclusions place too much credence on oceanographical theories of doubtful validity. His account of the larval migration of leptocephali is marred in this way and also suffers from an altogether needless attempt to convince the surely extinct sceptics of the truth of this migration. The account of the methods of statistical analysis of growth of eels is simultaneously both inadequate and unnecessary: it should have been omitted. The translation is well above average, but a few flaws have escaped revision.

D.B.C.

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, and, since that date, a new library and further laboratory accommodation have been added.

The Association is maintained by subscriptions and donations from private members, universities, scientific societies and other public bodies; 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. Accounts of the laboratory and aquarium and the scope of the researches will be found in Vol. 27 (p. 761) and Vol. 31 (p. 193) of this *Journal*.

The laboratory is open throughout the year and its work is carried out by a fully qualified research staff under the supervision of the Director. 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, physiology and other branches of science. 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

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Life Members	Composition fee	15	15	0
Founders		100	0	0
Governors		500	0	0

Members of the Association have the following rights and privileges: they elect annually the Officers and Council; they receive the Journal of the Association free by post; they are admitted to view the laboratory at Plymouth, and may introduce friends with them; they have the first claim to rent a place in the laboratory for research, with use of tanks, boats, etc.; they have the privilege of occupying a table for one week in each year free of charge; and they have access to the books in the library at Plymouth.

All correspondence should be addressed to the Director, The Laboratory, Citadel Hill, Plymouth.

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