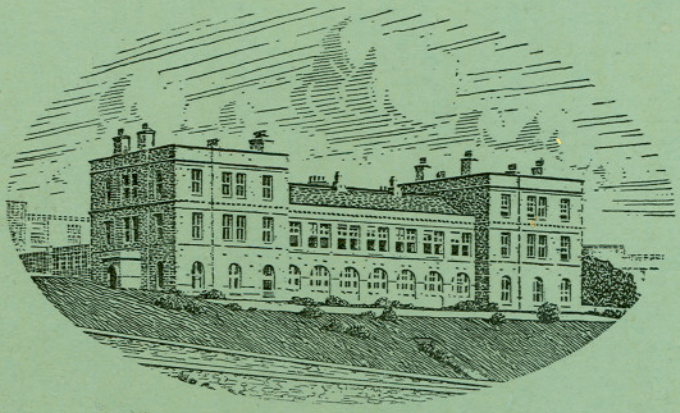
JOURNAL OF THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM



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ON THE BIOLOGY AND RELATIONSHIPS OF THE LAMELLIBRANCH *XYLOPHAGA DORSALIS* (TURTON)*

By R. Denison Purchon, Ph.D.
University of Bristol

(Text-figs. 1–16)

CONTENTS

INTRODUCTION

Xylophaga dorsalis (Turton) is a lamellibranch specialized for boring into timber in the sea. It occurs chiefly in floating timber, and probably for this reason and because of its much smaller economic importance it has never been studied in the same detail as many species of *Teredo* which do great damage to wooden ships and pier piles. The relationships of the genus *Xylophaga* are also obscure. Although it never bores into stone it has hitherto been included in the Pholadidae together with *Pholas* and other genera which are exclusively rock borers.

Specimens of *Xylophaga dorsalis* were obtained from Plymouth, and others, in two heavily-colonized pieces of driftwood, from Cullercoats and from Millport. The anatomy of the species has been studied in detail since it has never as yet been adequately described. The ciliary mechanisms in the mantle cavity were examined under the binocular microscope after the application of powdered carmine and of fine carborundum powder. Duboscq Brasil was found to be the most suitable general fixative. Sections were cut at thicknesses of from 3 to 8 μ and were stained in Delafield's haematoxylin and erythrosin.

* Owing to Dr R. D. Purchon's absence from this country on active service, this paper, which represents the greater part of the thesis he presented for the degree of Doctor of Philosophy, has been prepared for publication by Prof. C. M. Yonge.

In addition the ciliary currents and ctenidia of *Teredo megotara* Hanley and *T. norvegica* Spengler, the latter obtained from Port Erin and from Millport, were examined. This was done primarily for comparative purposes and to determine the effect of the modification of the feeding mechanisms due to the wood-boring habit upon the ciliary currents in the mantle cavity. These mechanisms have never previously been studied and new observations are recorded.

Work on *T. megotara* was carried out at the Marine Biological Station, Plymouth, in August 1937. The author wishes to express his gratitude to Dr S. Kemp, F.R.S., and members of the staff at Plymouth for the facilities provided. The remainder of the work was conducted in the Department of Zoology, University of Bristol, at the suggestion and under the direction of Prof. C. M. Yonge.

Habitat and Habits of *Xylophaga dorsalis*

Xylophaga dorsalis resembles members of the Teredinidae in its habit of boring into timber and not into stone. It is typically found in driftwood and only occasionally in fixed structures such as dock gates. It is usually, although not always, present in wood uninfected by *Teredo*. The animal which damages submarine telegraph cables and is known to cable repairers as "Teredo" is actually *Xylophaga*. Its ability to live in the gutta-percha sheath of these cables indicates that it cannot be completely dependent on wood as a source of nutriment. This matter will be discussed later.

The shell of a fully-grown *X. dorsalis* is of much the same size as that of *Teredo norvegica* the greatest antero-posterior dimension being about 10 mm. But, unlike the latter, it almost completely encloses the animal. Owing to the globular shape of the animal the borings of *Xylophaga dorsalis* are much less extensive than those of the Teredinidae. They are usually 2–3 cm. long and open to the exterior by a small pore, unless the surface wood has been broken away. Shell valves have been obtained from driftwood with an antero-posterior length of slightly over 1 in. These are probably shells of *X. praestans*. The accessory plates differ markedly in shape from those of *X. dorsalis*, and to each pair is attached a large transparent horny median plate. No such structure has been recorded in *X. dorsalis*. The excavations made by these large specimens were several inches long (Fig. 1*a*).

Xylophaga does not line its burrow with a calcareous deposition as do *Teredo* and *Bankia*, nor does it possess pallets with which to close the opening of the burrow.

Being globular in shape it might be supposed that when *Xylophaga* releases its attachment by means of the foot to the forward end of the burrow it would roll about in the cavity. But this cannot occur, nor can the animal withdraw far from the boring end of the burrow, because the posterior end of the burrow is tightly packed with faecal pellets.

As shown in Fig. 2*a*, the exhalant siphon differs from that of other lamellibranchs in that it opens at the base of the siphonal process, on its dorsal side close to the posterior margins of the shell valves (S). The opening, which is oval, entire and devoid of tentacles, lies well within the burrow (ES). The faecal

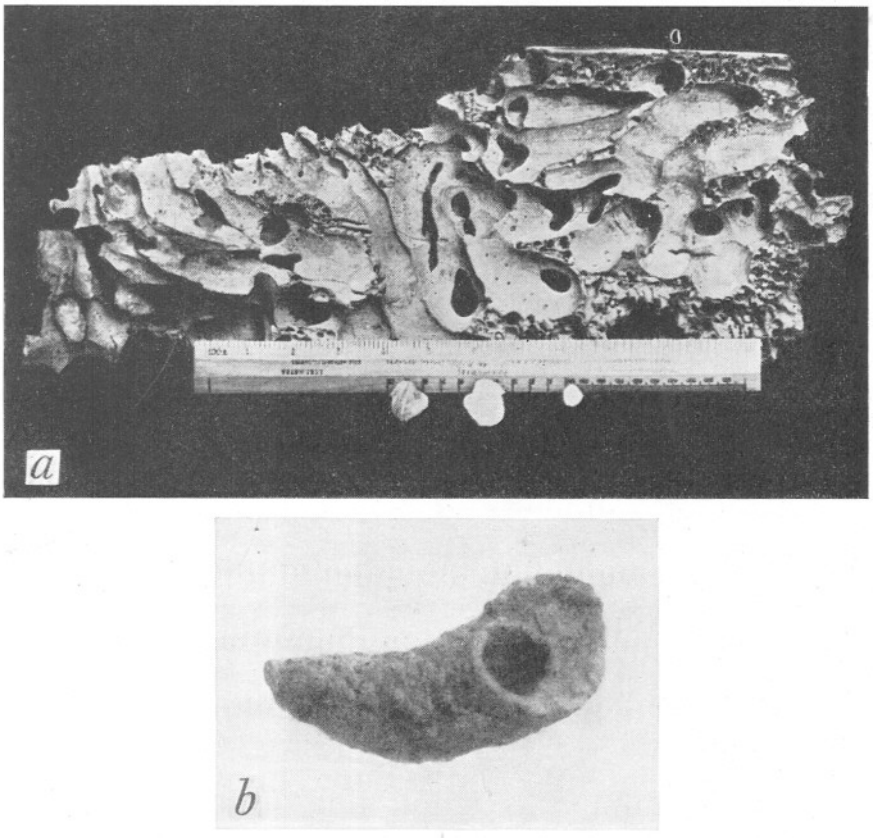

Fig. 1. *a*, Piece of wood bored by large specimens of *Xylophaga*, probably *X. praestans*. This sample was obtained by Messrs Neale and West, Trawler owners of Cardiff, and is now in an exhibition case in the Technical College, Cardiff. *b*, Faecal concretion taken from the posterior end of a burrow of one of the large specimens of *Xylophaga*.

pellets are not expelled with sufficient force to carry them out of the burrow and so accumulate at its posterior end as a compact mass, consolidated with mucus, which surrounds the siphonal process through which the exhalant water current passes. The presence of this faecal accumulation prevents any extensive movements of the animal.

The inhalant siphon (Fig. 2*a*, IS) is elongate, tubular and delicate. It may extend for as much as 1 cm. from the surface of the wood. The circular aperture is fringed with about six delicate tentacles (Figs. 2*a*, 6*b*, IS).

It is often possible to tell almost at a glance whether wood is colonized by *Teredo* or by *Xylophaga*, as in the former the siphons arise in pairs and in the latter they arise singly, being exclusively inhalant. The dorsal surface of the inhalant siphon possesses a pair of longitudinal lappets which are crenate for

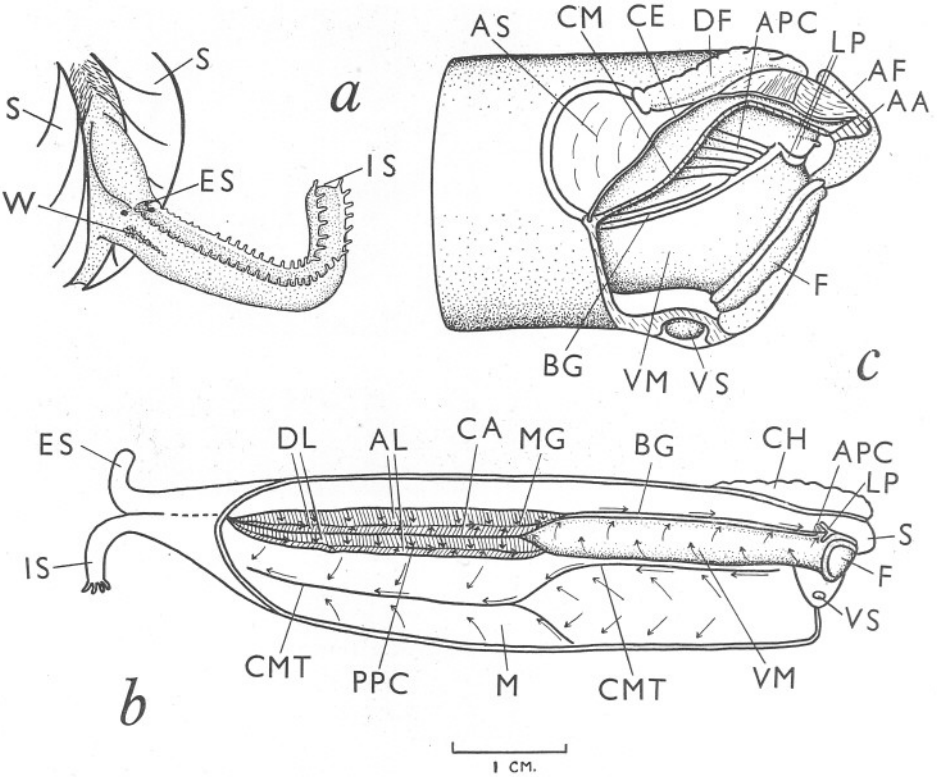

Fig. 2. *a*, *Xylophaga dorsalis*: posterior end of the shell valves and the siphonal process: ES, exhalant siphon; IS, inhalant siphon; S, shell; W, wedge-shaped mass of mucous glands. *b*, *Teredo norvegica*: mantle cavity opened laterally to show the course of the ciliary currents: AL, ascending lamella of ctenidium; APC, anterior portion of ctenidium; BG, branchial groove; CA, ctenidial axis; CH, cephalic hood; CMT, ciliated mantle tract; DL, descending lamella of ctenidium; ES, exhalant siphon; F, foot; IS, inhalant siphon; LP, labial palps; M, mantle; MG, marginal groove; PPC, posterior portion of ctenidium; VM, visceral mass; VS, ventral articulation of shell: other lettering as before. *c*, *Teredo navalis* (after Lazier): anterior portion of the mantle cavity opened to show the structure of the anterior portion of the ctenidium and the labial palps: AA, anterior adductor; AF, anterior pallial fold; AS, auricle of shell; CE, cut edge of shell; CM, cut edge of mantle; DF, dorsal pallial fold. Other lettering as before.

the proximal third of their length and then bear fine tentacles (Figs. 2*a*, 6*b*). They probably represent the original lateral walls of an elongated exhalant siphon which was attached throughout most of its length to the inhalant siphon, but the orifice of which has migrated backwards to the position which it now occupies. These fimbriated lappets support the sides of the cavity through the

faecal mass along which the exhalant water current passes. The dried remains of the siphonal process in a faecal concretion from the large specimens which were probably *X. praestans* suggest that in this species the siphonal process is similarly modified (Fig. 1*b*).

It is curious to observe that, although both Adams (1853–8) and Jeffries (1865) examined *Xylophaga* in sufficient detail to record the two longitudinal pectinated ridges which ornament the dorsal surface of the siphonal process, they erred in stating that the siphonal process was divided at its distal end into distinct inhalant and exhalant tubes. A similar error was made by Forbes & Hanley (1853) and by Pelseneer (1906), and erroneous illustrations are given by the first three of these authors. Forbes & Hanley, however, were made aware of their mistake by a Mr Cocks, as is recorded in Volume II of their work (pp. 375–6).

Near the base of the siphonal process a pair of opaque white spots can often be seen, one on each side of the opening of the exhalant siphon (Fig. 2*a*). Below each of these lies a thin but conspicuous wedge of mucous glands which have an opaque bubbly appearance (Figs. 2*a*, 6*b*, w). These may act as organs of temporary attachment (*Teredo* is weakly attached to the calcareous lining of its burrow at the base of the siphonal process), or they may exude mucus which assists in consolidating the faecal mass in the posterior end of the burrow.

Water expelled from the exhalant siphon passes slowly through the burrow and disperses at its mouth. Water is collected by the inhalant siphon about 1 cm. from the opening of the burrow and so a supply of fresh water is ensured.

It is difficult to observe the way in which *Teredo* clings to the end of its burrow, because when the burrow is opened the animal retreats from the boring end. Miller (1924), however, succeeded in observing *Teredo* making boring movements by dissecting open the burrow and covering the opening by a thin strip of glass which was stuck down at the edges by vaseline. After a short time the animal expanded and returned to the boring end of the burrow. Miller observed boring operations by means of a binocular microscope before the animal had covered the strip of glass with a deposition of calcium carbonate.

Unlike *Teredo*, however, *Xylophaga* maintains its grip on the end of the burrow while the latter is being opened, and there is no difficulty in observing the mode of attachment. Suction doubtless plays an important part in the attachment of the foot, but it was frequently observed that when a specimen of *X. dorsalis* was being removed from its burrow with the foot firmly attached, this could be prised slowly from the wood by a needle. Attachment of the foot thus continues after suction can no longer be maintained. There appears to be a sticky secretion which assists attachment. The adhesive surface of the foot is roughly circular and is bounded by a conspicuous ridge. Median to this ridge, the surface of the foot bears two lateral crescentic opaque patches one on each side; in the centre of the foot the surface is not opaque. The ridge which

surrounds the adhesive surface of the foot bears a conspicuous opaque raised disk in a median dorsal position (Fig. 6*b*, OF). Serial sections of the foot show that mucoid glands are present close to the epidermis in the regions which appear opaque externally. These glands are probably derived from the byssus apparatus, and presumably it is a sticky secretion from these glands which assists in fastening the foot to the boring end of the burrow. Sections through the foot of *Teredo* show that it also possesses mucoid glands which may assist in attachment.

Ciliary Mechanisms in the Mantle Cavities of *Teredo* and *Xylophaga*

Teredo norvegica Spengler

The ctenidia.

Sigerfoos (1908) has shown that, in the post-larval development of *Bankia* (*Xylotrya*) *gouldi* Bartsch, the ctenidium, which is composed of only one demibranch, becomes separated into two portions of unequal size due to the great broadening of the tenth or eleventh filament. The ctenidium is also divided into two portions in *Teredo*, the number of filaments in the anterior portion (Fig. 2*b*, APC) varying in different species. In *T. navalis* L. (Lazier, 1924) there are five anterior gill filaments (Fig. 2*c*, APC). In *Teredo*, as in *Bankia*, only one demibranch is present on each side of the animal. Ridewood (1903) and also Atkins (1937*b*) considered this to be the inner demibranch; but it has been shown elsewhere (Purchon, 1939) that in *Teredo* and in *Xylophaga* it is the *outer demibranch* which remains.

The ciliary mechanisms in the mantle cavity of *Teredo* have been compared with those of the closely related rock-borers in the family Pholadidae, of which American species in the genera *Pholadidea*, *Zirphaea* and *Barnea* were examined by Kellogg (1915). In the Pholadidae the ctenidia are each composed of *two complete demibranchs* (Kellogg, 1915).

Both Ridewood (1903) and Sigerfoos (1908) considered that in *Teredo* and *Bankia* the anterior portion of the gill consisted of *descending* filaments. The afferent branchial vein travels in the ctenidial axis and, bearing this in mind, consideration of the figures given by Sigerfoos (1908) for *Bankia* makes it evident that in the anterior portion of the gill the descending lamella is represented by the inner wall of the branchial groove, and that the filaments present actually form the *ascending lamella* of the gill. The same holds good for *Teredo*.

The anterior portion of the ctenidium lies close to the labial palps at the sides of the foot (Figs. 2*b*, 4, APC). The posterior part is situated for the most part posterior to the visceral mass (Fig. 2*b*, PPC). These two portions of the gill are connected by the branchial groove (Fig. 2*b*, BG), which is an extension of the marginal food groove (Fig. 2*b*, MG). In *T. norvegica*, as in *T. navalis* (see Ridewood, 1903), owing to the ventral position of the gill axis, the descending lamellae pass outwards almost horizontally (Fig. 3*g*) instead of downwards

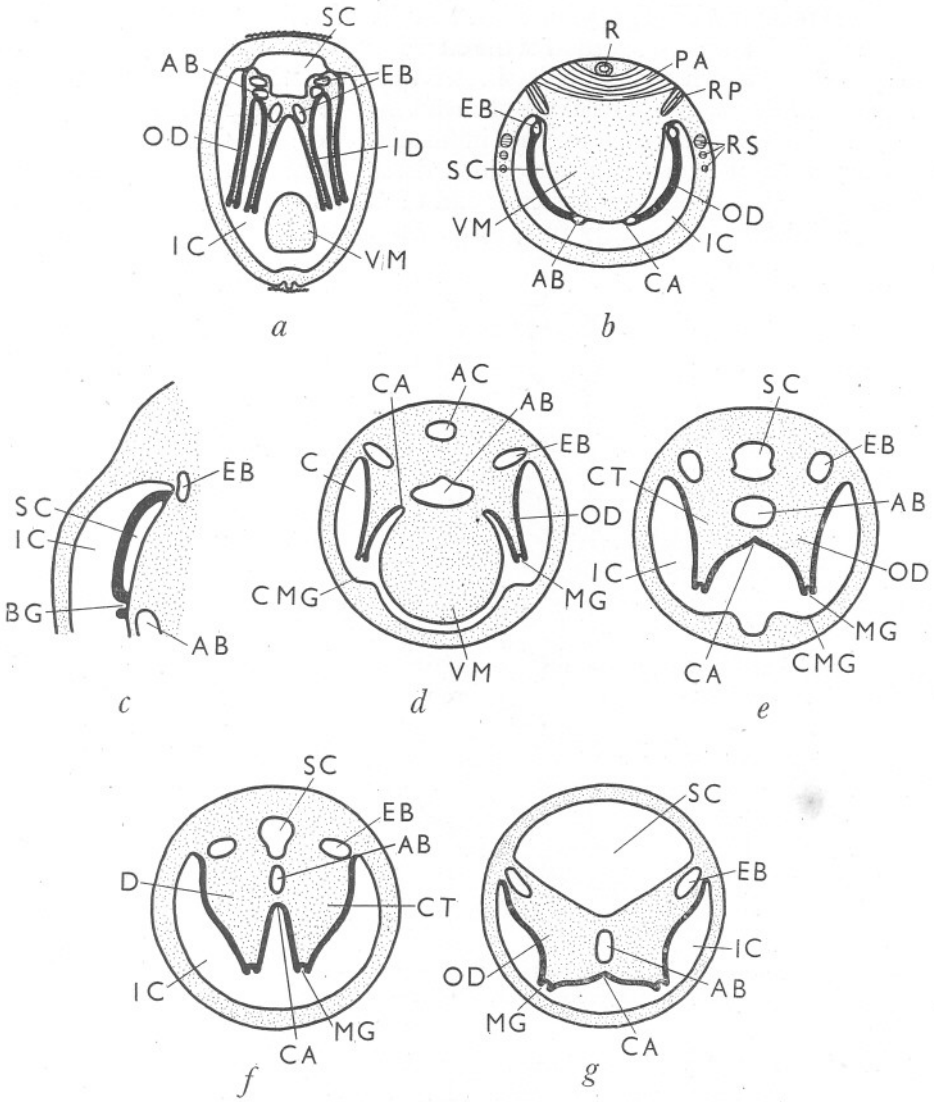

Fig. 3. Diagrammatic transverse sections through the soft parts of various rock-boring and wood-boring lamellibranchs.

a, *Barnea parva*.
b, *Xylophaga dorsalis*.
c, *Teredo norvegica*, through the anterior portion of the ctenidium.
d, *Bankia gouldi* (after Sigerfoos), through the posterior end of the visceral mass.
e, *B. gouldi* (after Sigerfoos), through the posterior portion of the ctenidium.
f, *Teredo megotara*, through the posterior portion of the ctenidium.
g, *T. navalis* (after Ridewood), through the posterior portion of the ctenidium.

AB, afferent branchial vein; AC, anal canal; CMG, ciliated mantle groove; CT, ctenidium; EB, efferent branchial vein; IC, infra-branchial cavity; ID, inner demibranch; OD, outer demibranch; PA, posterior adductor; R, rectum; RP, retractor pedis muscle; RS, retractor muscles of siphonal process; SC, supra-branchial cavity. Other lettering as before.

as in *Bankia gouldi* (Fig. 3, *d*, *e*) and in *Teredo megotara* (Fig. 3*f*). In *T. norvegica* the anterior portion of the ctenidium is composed of ten ascending filaments, of which the tenth is shorter than the others in the specimens examined. Occasionally one of the filaments may be broader near the marginal groove than elsewhere as is the case in filament two (Fig. 4).

The ctenidial axes are situated in a dorso-lateral position opposite the visceral mass, but near the posterior end of the visceral mass they approach the median line, where they fuse, as do the afferent branchial vessels. The

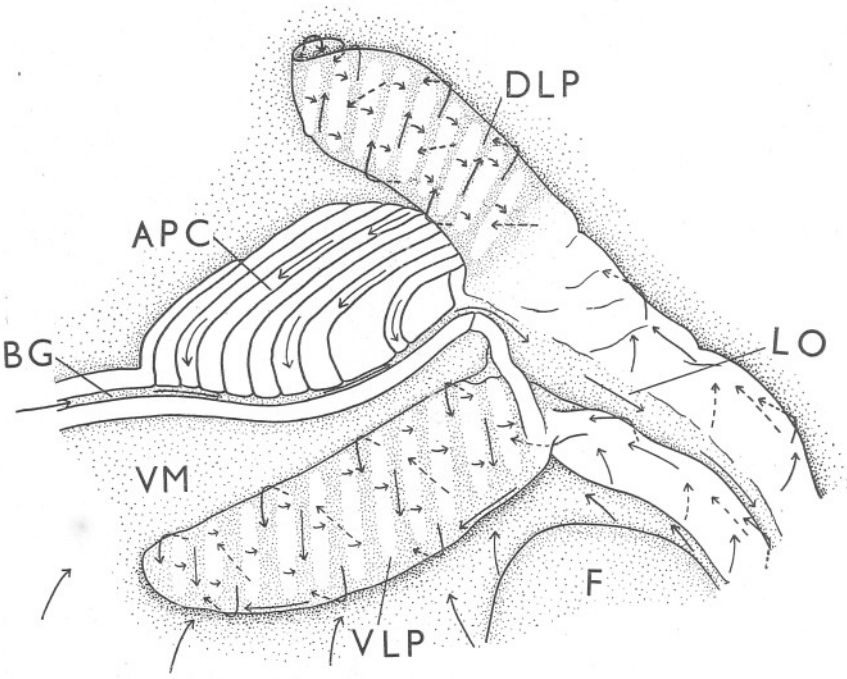

Fig. 4. *Teredo norvegica*: anterior portion of the ctenidium and the labial palps: DLP, dorsal labial palp; LO, lateral oral groove; VLP, ventral labial palp. Other lettering as before.

posterior portions of the ctenidia thus lie side by side and their descending lamellae arise from a common axis (Fig. 3 *e*, *f*, *g*, CA). The ctenidia are flat and homorhabdic; upon both portions of the ctenidium the cilia beat downwards into the marginal groove. In the marginal food grooves and in the branchial groove the cilia beat forwards, and all particles which enter them are driven towards the base of the labial palps (Figs. 2*b*, 4).

As summarized by Atkins (1936, 1937*a*) there are two main types of ctenidial sorting mechanisms in the Lamellibranchia whereby large particles are rejected and small particles are passed to the mouth. In the first of these, large particles pass down the lamellae along the crests of the plicae into the marginal

groove, whence they are eventually rejected; small particles, however, pass upwards in the grooves of the plicae and forwards along the ctenidial axes, or along the upper borders of the ascending lamellae, towards the mouth (Arcidae, Anomiidae, *Pecten*, *Ostrea*, etc.). In the second type both large and small particles pass down the ctenidium, but the small particles are allowed to pass forwards in the marginal food groove, while large particles are prevented —in some forms—by the presence of fan-like groups of large guarding cilia (*Pinna*, *Thracia*, *Musculus*, *Montacuta*, etc.).

Close examination of the ctenidia of *Teredo norvegica* showed that no such sorting mechanisms occur; all particles placed on the ctenidia passed down into the marginal food groove whence they are all passed forwards to the base of the labial palps (Fig. 2*b*, LP; Fig. 4, DLP, VLP). There is no ciliary current in the longitudinal direction either along the ctenidial axis or along the dorsal borders of the ascending lamellae.

The labial palps.

Deshayes (1845–8) and Quatrefages (1849) probably worked upon *T. norvegica*; they both figured animals with long strap-shaped labial palps, and *T. norvegica* is the only species in European waters which answers to such a description.

Of the species under consideration, the labial palps of *T. norvegica* exhibit the least reduction in size and complexity; those of *Bankia gouldi* are, according to Sigerfoos (1908), reduced to small ridges on the sides of a slight groove approaching the mouth. In *Teredo navalis* (Fig. 2*c*, LP) Lazier found "that the dorsal palps are small and inconspicuous but quite distinct, whilst the ventral palps are reduced to slightly raised ciliated patches". The labial palps of *T. megotara* are also greatly reduced; they will be described in due course.

The labial palps of *T. norvegica* are relatively large strap-shaped organs which hang freely in the mantle cavity just in front of the anterior portion of the ctenidium (Fig. 4). In comparison with the labial palps of a typical lamellibranch they are greatly reduced, although they are the largest yet recorded in the Teredinidae. Their outer surfaces are smooth, and their inner, opposed, surfaces possesses eleven indistinct transverse ridges (Fig. 4). The ciliary mechanisms on the palps are complex, and can best be understood by close reference to the figure (Fig. 4). On the inner surfaces the current in the grooves is directed towards the lower edge and over this on to the outer surface. Along the free lower edge the current is towards the tip of the palp and away from the mouth. On the transverse ridges the cilia beat across the palp towards the mouth. On the outer surface the cilia beat obliquely backwards and upwards towards the free upper edge of the palp and over this on to the inner surface as shown by broken arrows in Fig. 4.

When extremely small quantities of carmine particles are applied to the palps, the grooves between the ridges become occluded. The particles are

therefore carried by the cilia on the ridges towards the mouth. When a little more carmine is added the grooves open and the ridges become less distinct. The most prominent ciliary activity is now that in the transverse grooves. Material passed forwards from the branchial groove is picked up by the palps and passed down one of the transverse grooves on to the outer surface. Here it passes obliquely upwards and backwards on to the inner surface again. A large mass of carmine quickly forms, and this circles the palp and slowly moves backwards to the tip of the palp where it is transferred to the mantle and passed backwards in a rejection current to the base of the inhalant siphon. The labial palps therefore exercise quantitative selection, and only few and fine particles are allowed to reach the mouth.

The walls of the lateral oral groove are well defined and possess powerful rejection currents. Small quantities of carmine travel down the centre of the groove to the mouth; but if a suspension of carmine is added here, it is seen that on the walls of the lateral oral groove ciliary currents pass downwards and backwards on both surfaces. Those on the inner surfaces pass over on to the outer surfaces and thence on to the outer surface of the labial palps.

The visceral mass and the mantle.

Lazier (1924) found that in *T. navalis* the ciliation of the mantle was restricted to two narrow strips opposite the marginal and branchial grooves. In *T. norvegica* the ciliation of the mantle can be divided into two distinct types. The first consists of groups of cilia scattered over the major part of the visceral mass and the mantle. The second consists of a pair of ciliated mantle tracts (Fig. 2*b*, CMT) which in the anterior region of the mantle cavity lie close to the branchial grooves. As shown in Fig. 2*b*, they approach the mid-ventral line opposite the posterior end of the visceral mass and thence pass backwards as a single tract to the base of the inhalant siphon. Throughout these tracts the cilia beat backwards.

As shown in Fig. 2*b*, the scattered groups of cilia on the mantle beat towards the ciliated mantle tracts and assist in keeping the surface of the mantle clean. The cilia on the mantle tracts beat powerfully, and by their action skeins of mucus are drawn from the general surface of the mantle and incorporated in the stream passing backwards to the base of the inhalant siphon. This action tends to mask the activity of the scattered groups of cilia.

In the vicinity of the labial palps the scattered cilia on the visceral mass beat forwards and particles borne in these currents are collected by the palps (Fig. 4). This is probably for the collection of stray wood fragments formed during boring operations. The cilia on the remainder of the visceral mass beat towards the branchial grooves, though it is probable that under normal conditions material collected by these cilia is passed to the ciliated mantle tracts (Fig. 2*b*).

The surface of the visceral mass and of the mantle which bears the scattered groups of cilia appears to consist of a shallow syncytial epithelium. This bears

groups of long cilia which arise from distinct basal granules arranged in a plate close to the surface (Fig. 5*a*). The junction between each basal granule and its cilium can be distinguished, as also can a series of fine fibres passing inwards in the form of a spindle from the basal granules to the base of the syncytium. No lateral cell walls can be distinguished, but a certain rather regular patchiness of the cytoplasm is suggestive of cell demarcation.

Near the anterior gill filaments, this syncytium gradually becomes deeper, and lateral cell walls can be distinguished, and each cell in this region possesses a group of long cilia. This suggests that the great elongation of the visceral mass and of the mantle has been accompanied by a stretching of the epithelial layers as well as by a proliferation of the cells comprising the epithelium.

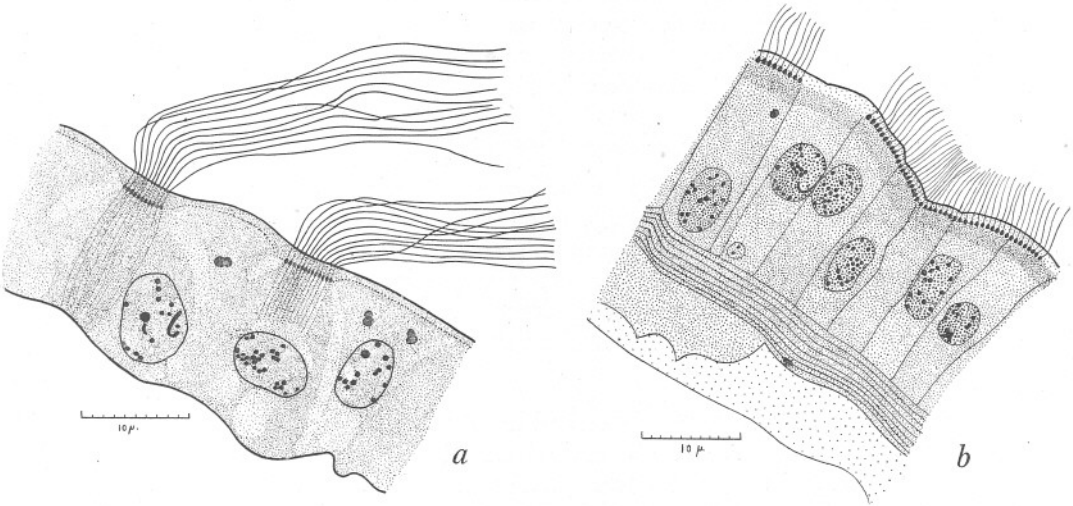

Fig. 5 *Teredo norvegica*: *a*, section through the epithelium of the visceral mass. *b*, section through the ciliated mantle tract.

There is often a slight but distinct delay before particles laid upon the visceral mass are set in motion by this scattered series of cilia, and it is possible that these cilia are under some distant control. There is a close resemblance between the spindle here described, passing from the plate of basal granules, and a spindle figured by Carter (1926), who established that certain cilia in the veliger larvae of various Nudibranchia are under nervous control.

The epithelium forming the ciliated mantle tracts differs markedly from that covering the general surface of the mantle (Fig. 5*b*). The cells are deep and columnar with distinct lateral walls. The nuclei are similar to those found in the syncytium covering the general surface of the mantle. The cytoplasm is a little more densely aggregated close to the surface, which is evenly covered with short cilia arising from a regular layer of basal granules. Very occasionally a cell is encountered which bears no cilia. There is no fibrous spindle arising

from the basal granules in these cells. Many mucous glands occur in the ciliated mantle tracts.

Similar mantle tracts have been described in *Pinna* (species not determined) by Stenta (1902), in *Pinctada vulgaris* by Herdman (1904), in *Cardium*, *Mytilus*, *Ostrea* and *Pecten* by Orton (1912), and in *Arca tetragona* and *Glycymeris glycymeris* by Atkins (1936).

In *Teredo norvegica*, as in *T. megotara* and in *T. navalis* (see Lazier, 1924), the mantle is of the same thickness throughout, but in *Bankia gouldi* (see Sigerfoos, 1908) the mantle is greatly thickened median to the ciliated mantle tracts, as shown in Fig. 3 *d*, *e*, CMG, forming well-defined "ciliated mantle grooves". Sigerfoos considered that in *B. gouldi* the mantle grooves are closely opposed to the free edges of the ctenidia and that, under the combined effect of the cilia in the marginal food grooves and in the mantle groove, food particles collected from the water are driven forwards to the mouth. But it is improbable that the cilia of the mantle groove in *B. gouldi* beat forward.

Teredo megotara Hanley

The ctenidia.

The anterior portion of the ctenidium is composed of seven ascending filaments, as shown in Fig. 6*a*, APC. The posterior portion of the ctenidium resembles that of *Teredo norvegica* in all respects save its appearance in transverse section. The ctenidial axis occupies the normal position and the ctenidium is V-shaped when seen in transverse section (Fig. 3*f*). The ciliary currents on the ctenidium are similar to those of *T. norvegica*.

The labial palps.

In *T. megotara*, which closely resembles *T. navalis* (see Lazier, 1924), reduction of the labial palps has been carried further than in *T. norvegica*. Both the upper and lower palps are triangular (Fig. 6*a*, DLP, VLP), and they differ from those of other lamellibranchs (save *T. navalis*, as described by Lazier (1924), and *Xylophaga dorsalis*, which will be described later) in that the *inner* as well as the outer surfaces are *smooth*.

The application of carmine particles and of carborundum powder revealed that no sorting takes place on the palps, all material being passed to the mouth. The ciliary currents on the outer surfaces pass material backwards and downwards and over the free edges of the palps on to the inner surface. On the opposed surfaces the currents are directed forwards and upwards to the lateral oral groove. In Fig. 6*a* the direction of the ciliary currents on the outer surfaces is indicated by broken arrows. Material passed forwards by the branchial groove enters the lateral oral groove at the base of the palps and is rapidly borne to the mouth. Particles which fall on the visceral mass close to the labial palps pass towards these and are incorporated in the food current.

The labial palps often suffer shock following dissection, as the removal of the shell valve jerks the apophysis slightly, and this is situated in an intucking of the mantle below the palps. On such occasions the mucous string arriving

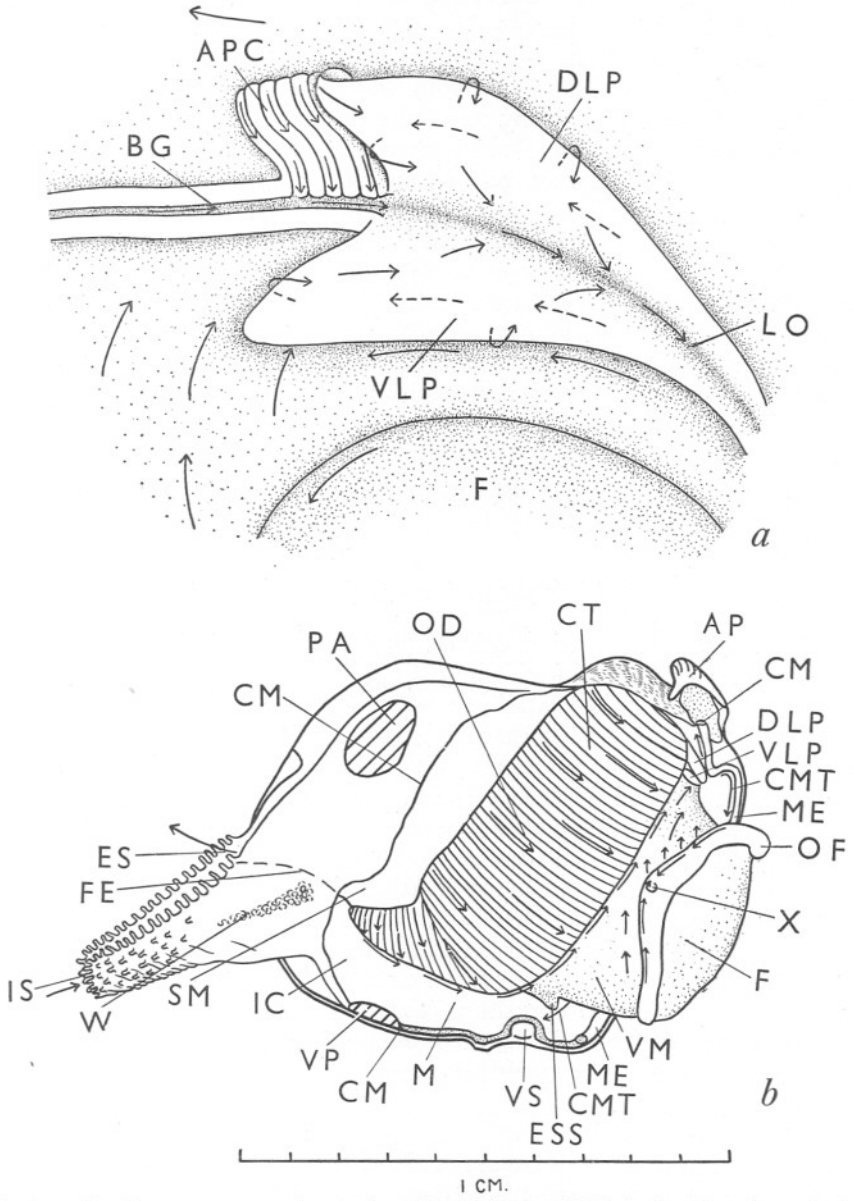

Fig. 6. *a*, *Teredo megotara*: anterior portion of ctenidium and labial palps: lettering as before. *b*, *Xylophaga dorsalis*: ciliary currents in the mantle cavity: AP, accessory plate; ESS, blind end of style sac; FE, floor of the exhalant siphon; ME, mantle edge; OF, opaque disk of foot; SM, suspensory membrane of ctenidium; VP, ventral pallial muscle; W, wedge-shaped mass of mucous glands; X, vortex in the ciliary currents on flank of the foot. Other lettering as before.

from the branchial groove is not accepted, due, it is thought, to some lack of continuity in the action of the cilia. This was not a normal rejection mechanism of the palps. When carmine is laid on the posterior portion of the ctenidia it travels up the branchial grooves on both sides of the visceral mass and, at the same time that material is being rejected by the palps on the dissected side, it can be seen, by moving the foot to one side, that the palps on the other side are accepting the food stream, passing both carmine and even carborundum powder along the lateral oral groove towards the mouth.

Thus no selective activity is displayed by the labial palps in *Teredo megotara*. There remains the selection displayed by rejection mechanisms of the mantle. If large quantities of carmine are added they become entangled as they pass along the marginal food groove, or along the branchial groove, with the mucous threads on the ciliated mantle tracts, and are then drawn away from the food stream by the superior strength of the rejection mechanisms.

The visceral mass and the mantle.

The ciliary mechanisms on the visceral mass and on the mantle are similar to those described for *T. norvegica*.

Xylophaga dorsalis (Turton)

The ctenidia.

The ctenidium is a large but delicate organ placed obliquely on the side of the visceral mass, as illustrated in Fig. 6*b*, OD. The posterior ends of the two ctenidia meet in the mid-ventral line near the origin of the inhalant siphon. The ctenidium is flat and homorhabdic and possesses no marginal groove. It is greatly reduced and consists of the direct lamellae (not divided into descending and ascending lamellae) of the *outer* demibranch (Purchon, 1939). The ctenidial axis runs along the ventral margin of the lamella (Fig. 3*b*, CA). The afferent branchial vein runs in the ctenidial axis (Fig. 3*b*, AB), and the efferent branchial vein traverses the dorsal margin of the lamella (Fig. 3*b*, EB).

The major portion of the ctenidium is broad and in life is held well away from the visceral mass by the large quantity of water that is held in the supra-branchial cavity. At the posterior end the filaments are much shorter than they are in the middle of the ctenidium (Fig. 6*b*). The ciliary currents are all directed downwards towards the ctenidial axis and forwards along it to the labial palps (Fig. 6*b*). The ctenidia possess no sorting mechanisms.

The labial palps.

The upper labial palp is a small spindle-shaped organ, the outer surface of which is fused to the visceral mass throughout its length (Fig. 7*a*, DLP). It is fleshy and tapers considerably distally. The lower palp is still smaller and is flat, and the outer surface is free from the visceral mass to a slight extent along its lower border. It forms a broad platform extending from the ctenidium to the mouth and is partially overhung by the upper palp (Fig. 7*a*, VLP).

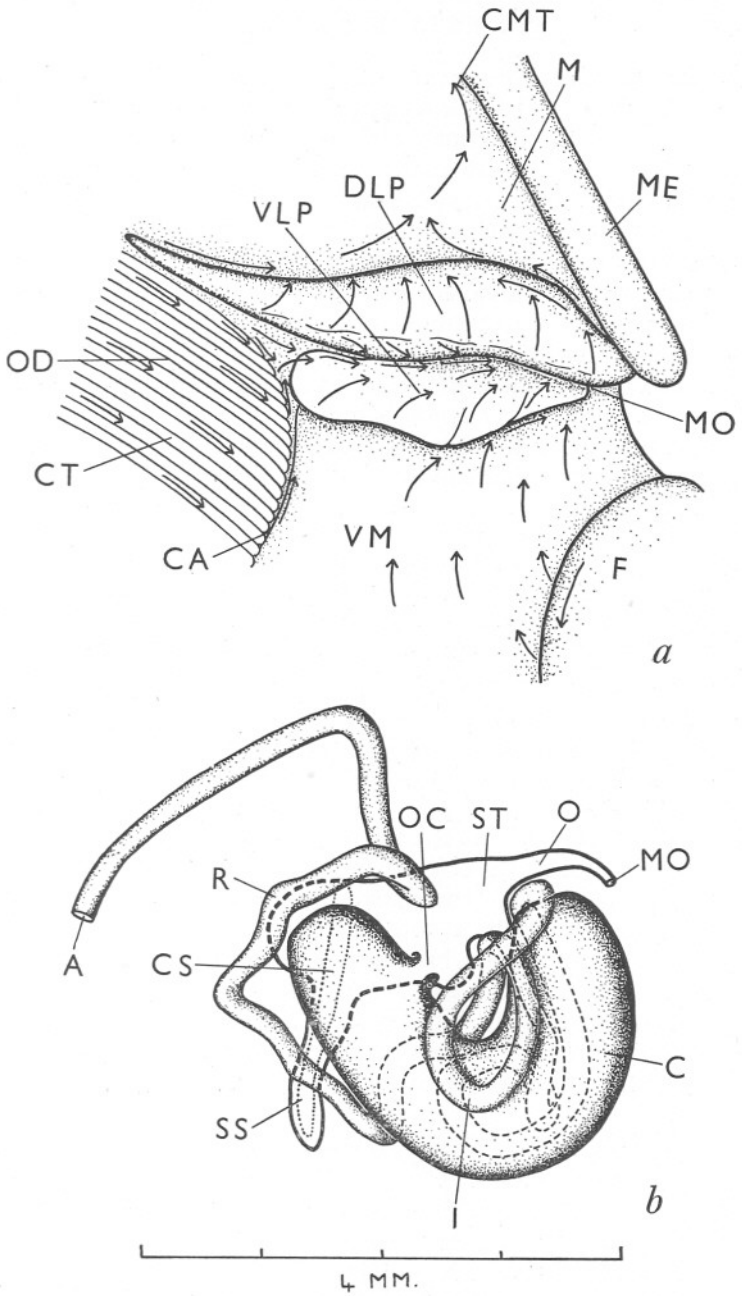

Fig. 7. *Xylophaga dorsalis*: *a*, labial palps and adjacent organs of the right side, upper palp turned slightly upwards to expose ciliary currents on the inner surface: MO, mouth. *b*, alimentary canal reconstructed from serial sections: A, anus; C, caecum; CS, crystalline style; I, intestine; O, oesophagus; OC, opening of caecum into stomach; SS, style sac; ST, stomach; R, rectum. Other lettering as before.

The sorting mechanism on the palps is greatly reduced. On the lower palp the currents, as shown in Fig. 7*a*, carry particles upwards and forwards to the mouth (MO). Along the innermost strip of the exposed, free surface of the upper palp the cilia also beat in the direction of the mouth; but over the greater extent of its surface the cilia beat outwards, away from the oral groove and on to the mantle, where rejected material is removed by the ciliated mantle tract which arises close to the upper palp (Fig. 7*a*, CMT).

Small quantities of carmine are accepted by the palps and passed to the mouth, but slightly larger quantities come under the influence of the outward-beating cilia on the upper palp. All particles are then drawn out of the lateral oral groove and transferred to the ciliated mantle tract. In Fig. 7*a* the upper palp has been turned slightly upwards in order to expose the ciliary currents on its inner surface. The labial palps in *Xylophaga* retain to a certain degree the power of quantitative selection.

The visceral mass and the mantle.

On the sides of the visceral mass the cilia beat upwards towards the labial palps as in *Teredo norvegica* and *T. megotara* (Figs. 6*b*, 7*a*). On the ventral region of the visceral mass no ciliation was observed. On the latero-dorsal flank of the foot the cilia beat upwards. At X the cilia impart a clockwise spin to material, which quickly collects there. This mass is removed from the foot by the ciliated mantle tract.

The major portion of the mantle is unciliated, particles being efficiently removed, under normal conditions, by the ctenidia. A ciliated mantle tract arises close to the upper labial palp as already described (Fig. 7*a*, CMT) and passes downwards close to the mantle edge until it is opposite the point at which particles collect on the sides of the foot (Fig. 6*b*, X). Here the mantle tract leaves the mantle edge and passes diagonally downwards to the mid-ventral line where it meets the mantle tract of the opposite side (Fig. 6*b*, CMT). A common mantle tract passes backwards from this point to the base of the inhalant siphon (as in *Teredo* and *Bankia*, the mantle lobes are completely fused in the mid-ventral line; Fig. 6*b*, CM). The ventral region of the mantle anterior to the point where the two mantle tracts unite is weakly ciliated, and particles falling here pass slowly backwards into the ciliated mantle tracts.

The Morphology of the Alimentary Canal and Digestion of Wood by *Xylophaga*

The anatomy of *Bankia gouldi* has been described by Sigerfoos (1908) and the morphology of the alimentary canal of *Teredo navalis* by Lazier (1924). The only contribution to our knowledge of *Xylophaga* was made by Potts (1923). Working upon an unidentified species of *Teredo*, he discovered that the digestive diverticula were of two types, one of which was specialized for the ingestion and intracellular digestion of wood fragments. He was unable to find any specialized area of the digestive diverticula in *Xylophaga*, and

concluded that the development of this specialized phagocytic region of the digestive diverticula in *Teredo* was associated with "the great development of the capacity for digesting wood (which was already possessed by *Xylophaga* to some extent) and a very rapid rate of growth". He concluded that *Xylophaga*, which possesses a caecal diverticulum of the stomach, has a limited capacity for digesting wood. No evidence was given in support of these views. Harington (1921) demonstrated the presence of a cellulase in the digestive diverticula of *Teredo norvegica*. Sawdust was digested, producing glucose, but not pure cellulose in the form of filter paper. The digestion of wood by *T. navalis* was demonstrated by a different technique by Dore & Miller (1923) and Boynton & Miller (1927). Chemical analyses were made of the faecal pellets of *T. navalis* and also of the wood through which the same specimens were boring. It was shown that wood loses up to 80% of its cellulose and 15–56% of its hemicellulose during its passage through the gut of the animal. Potts (1923) reared specimens of *Teredo* (species undetermined) from an early age to maturity in water freed from plankton, and concluded that the animal is more or less independent of plankton. The work of Roch (1932) supported his conclusions.

In the Lamellibranchia food normally passes through the alimentary canal in a slow steady stream so far as external conditions permit. The rhythmical production of large quantities of wood fragments in the Teredinidae and in *Xylophaga* by boring operations therefore involves corresponding modifications in the mode of digestion and the provision of a mechanical contrivance whereby the spasmodic entrance of material into the alimentary canal is converted into a slow steady stream. The functions of the caecum—a diverticulum of the stomach only possessed by wood-boring molluscs—are possibly to provide a reserve of food upon which the animal may live after it has exhausted the supply of available timber or ceased to bore, and, more probably, to release these fragments into the stomach in a slow and continuous stream.

In the rock-boring molluscs of the family Pholadidae, the products of their boring activities are not passed through the alimentary canal. The morphology of the alimentary canal of a small specimen of *Barnea parva* (Pennant) was examined so that a comparison could be drawn between the alimentary canal of *Xylophaga* and that of a typical member of the Pholadidae. The alimentary canal of *Xylophaga* was also compared with that of *Teredo navalis* as described by Lazier (1924).

In *Xylophaga* the mouth is an oval aperture situated between the labial palps just below the anterior adductor muscle (Figs. 7 *a*, *b*, MO). The oesophagus is wide but greatly flattened dorso-ventrally; it is considerably shorter than that of *Barnea parva* (Fig. 8, O). Its inner surface is smooth anteriorly but strongly ridged posteriorly; it is lined by a ciliated columnar epithelium. The oesophagus passes through the digestive diverticula and opens into the anterior end of the stomach.

The stomach (Figs. 7 *b*, 9 *a*, *b*, ST), which is situated to the left of the

median line, has an irregularly oval cavity, the surface of which is lined for the most part by the gastric shield (Fig. 9*a*, GS). The stomach of *Xylophaga* is relatively larger than that of *Barnea*. The stomach of *Teredo navalis* also is enlarged (Lazier, 1924). The stomach is lined by a ciliated columnar epithelium; the cilia are of various lengths, the longest ones being situated ventral to the gastric shield close to the point at which the crystalline style bears upon it.

The digestive diverticula consist of a number of small tubules which surround the oesophagus and lie close to the surface of the visceral mass at its anterior end. Two broad ducts open into the anterior end of the stomach (Fig. 9 *a–c*, DD). These ducts extend upwards under the umbonal beaks of

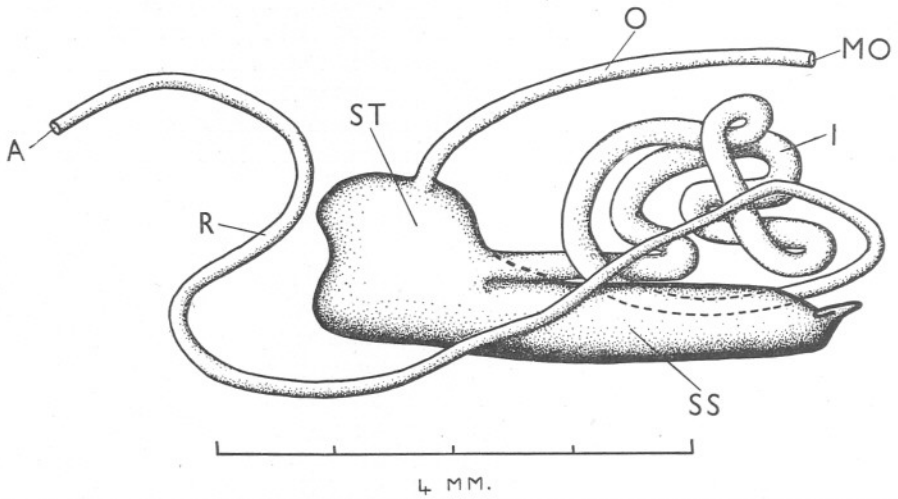

Fig. 8. *Barnea parva*: alimentary canal, reconstructed from serial sections. Lettering as before.

the shell valves, surrounding the intucking of the mantle within which the shell ligament is situated (Fig. 9 *a*, *b*, IM, L). Cilia have not been observed in sections either in the digestive diverticula (although seen in living tissue by Potts (1923) and Yonge (1926*a*)) or in their ducts, nor have phagocytes been observed in these regions. The cells forming the digestive diverticula are small and cuboid; they normally contain large numbers of very small spherical granules of a pale yellow colour. No evidence has been produced regarding the ingestion of particles, although this may be assumed in the light of previous data (Yonge, 1926*a*). Wood fragments have never been recorded either in the digestive diverticula or in their ducts, thus confirming the statement of Potts (1923) that in *Xylophaga* the digestive diverticula are not specialized for the ingestion of wood particles.

At the posterior end of the stomach the style sac enters on the right side (Fig. 7*b*, SS). This is small, and the crystalline style reduced (Figs. 7 *b*, 9 *a*, *c*, CS) when compared with that of *Barnea parva* (Fig. 8). Nelson (1918), who

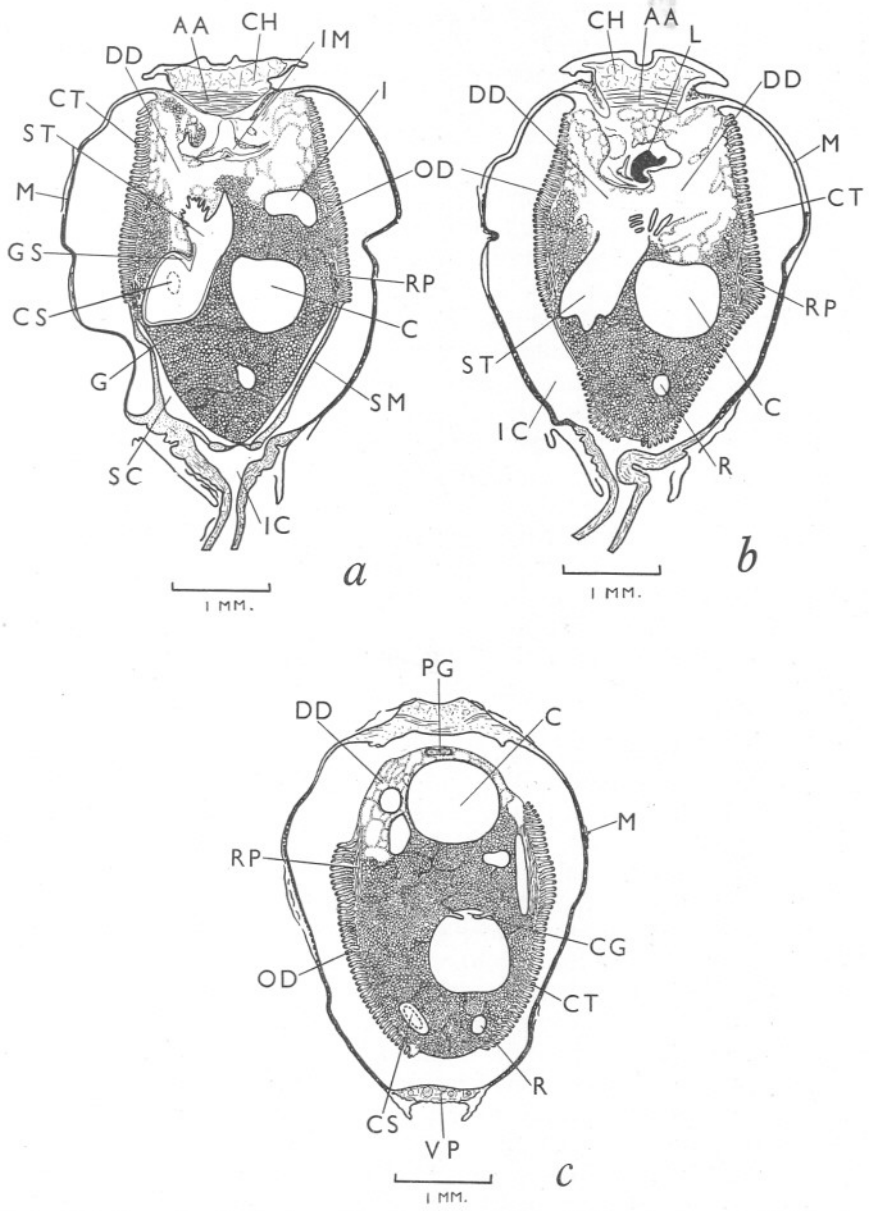

Fig. 9 *Xylophaga dorsalis*: horizontal sections through the whole animal, *a* cut slightly above *b*, and *b* above *c*: CG, ciliated groove of caecum; DD, digestive diverticula; G, gonad tubules filled with ova; GS, gastric shield; IM, intucking of mantle; L, ligament; PG, pedal ganglion. Other lettering as before.

did not personally examine *Teredo*, referred to the style, which he described as being much smaller than that of *Pholas* and of *Martesia*.

In *Xylophaga*, as in all members of the Adesmacea, e.g. *Teredo* and *Barnea*, the style sac is completely separated from the intestine. The blind end of the sac of *Xylophaga* closely approaches the surface of the visceral mass in the mid-ventral line and forms there a slight but distinct projection into the infrabranchial cavity (Fig. 6*b*, ESS). The sac is lined by the typical ciliated epithelium. The head of the crystalline style projects across the stomach diagonally (Figs. 7*b*, 9*a*, CS) and bears upon a concavity in the gastric shield on the left side of the upper border of the stomach (Fig. 9*a*, CS).

The caecum also opens into the stomach on its right side anterior to, and at the same level as, the style sac. The caecum is a U-shaped cylinder, the opening into the stomach being on the posterior limb and not quite terminal (Fig. 7*b*, OC). The distal limb of the caecum passes close under the adhesive surface of the foot and closely approaches the oesophagus (Fig. 7*b*). Sigerfoos (1908) states that in a young specimen of *Bankia gouldi* the caecum is similarly disposed, but in an adult specimen, as in *Teredo navalis* (see Lazier, 1924), the caecum is directed backwards. The inner surface of the caecum bears two conspicuous ridges seen in transverse section in Fig. 9*c*, CG. These enclose a ciliated channel which extends downwards from the opening of the caecum along its inner wall, round the bend and for a short distance up the ascending limb. Although not determined, it is probable that the cilia in this channel beat towards the stomach and that by this means a slow continuous stream of wood fragments is conveyed from the distal limb of the caecum into the stomach.

On the opposite side of the caecum to the ciliated channel the epithelium is columnar and the surface may bear cilia or may be distended into little colourless bubbles. In this region phagocytes may often be found squeezed between the epithelial cells, or at the base of the epithelium. The remainder of the epithelium lining the caecum is shallow and bears no cilia. Phagocytes have never been seen in this region. In serial sections the caecum is usually distended with wood fragments amongst which phagocytes occasionally occur. In some cases, however, phagocytes are abundant in the lumen, which is then almost entirely filled with bacteria. Phagocytes also occur occasionally in the stomach, though never in the digestive diverticula or in their ducts. Bacteria form a large percentage by volume of faeces in the rectum. When the caecum is heavily laden with wood shavings it is difficult to determine whether bacteria are present, but in some serial sections it appears as if bacteria are present as well as wood fragments.

Lazier (1924) showed that in *T. navalis* the caecum is apparently not ciliated but possesses a conspicuous two-coiled typhlosole capable of writhing movements. He thought that wood fragments were moved in and out of the caecum by muscular activity of the typhlosole and of the caecum walls. No such typhlosole occurs in *Xylophaga*.

The orifice between the stomach and the caecum in *Teredo navalis* resembles that of *Xylophaga* in possessing two lateral infoldings of the wall, this arrangement presumably providing for simultaneous ingress and egress of wood fragments. The right fold in *Teredo navalis* is continuous with the caecal typhlosole. In *Xylophaga* the two folds are continuous with the ridges which lie on the inner wall of the caecum.

The opening from the stomach into the intestine in *Xylophaga* is situated at the anterior end of the stomach on the left side of the ventral wall. The course of the intestine is complicated and can best be understood by reference to Fig. 7*b*. The intestine coils once on the left side of the stomach, rises and passes over the distal extremity of the caecum, coils once on the right side of the caecum and returns to the left side below the stomach. It then passes behind the style sac and merges into the rectum which passes forwards and upwards to the pericardium. The rectum travels upwards through the pericardium and, unlike that of *Teredo*, penetrates the ventricle.

Typically, lamellibranchs possess a typhlosole which extends throughout the intestine. Such a typhlosole is found in *Barnea parva*. Sigerfoos (1908) found that in *Bankia gouldi* the typhlosole extends throughout the intestine. According to Lazier (1924) *Teredo navalis* possesses a typhlosole only in the anterior portion of the intestine, which is greatly dilated in this region. A typhlosole has also been noted in certain portions of the intestine of *T. norvegica*, though the whole of the intestine has not been examined. In *Xylophaga dorsalis* no intestinal typhlosole is present; for this reason it is difficult to determine at which point the intestine passes into the rectum. In spite of the absence of an intestinal typhlosole, the faeces are well consolidated. They are extruded into the supra-branchial cavity and accumulate, as already described, in the posterior end of the burrow.

The absence in *Xylophaga* of a portion of the digestive diverticula specialized for the intra-cellular digestion of wood fragments (Potts, 1923) has led to a general belief that this species is incapable of digesting wood (Yonge, 1937, 1938).

Evidence is here produced which suggests that *Xylophaga* may be able to derive some nutriment from the wood through which it bores. It must be emphasized, however, that *Xylophaga* under certain circumstances is certainly independent of wood as a source of food. Specimens of *Xylophaga* living in the gutta-percha sheaths of submarine telegraph cables must subsist entirely upon plankton or other matter suspended in the water. Such specimens must penetrate metal wrappings before entering the gutta percha, unless they attack the cables only at points where the metal casings have been damaged. An outer wrapping of brass tape is now used to prevent such damage.

In order to determine whether *Xylophaga* possesses a cellulase, approximately twenty-four individuals of various sizes were extracted in sea water after grinding up with clean silver sand. The extract was diluted to 30 c.c. with clean sea water and divided into three equal parts. The substrate consisted of

fine sawdust previously treated three times with boiling water to remove any soluble sugars. The experiment and two controls were incubated at 30° C. for 14 days and the glucose present then estimated by the technique used by Boyland (1928). Full details are given in Table I.

TABLE I

Experiment	10 c.c. extract + 0·2 g. sawdust	4·725 g. glucose
Control 1	Ditto boiled	3·213 g. glucose
Control 2	Ditto without substrate	3·517 g. glucose

The glucose present in control 1 represents that originally present in the extract, that in control 2 represents this amount together with any produced by autolysis during the period of the experiment. The somewhat greater quantity of glucose present in the experiment indicates, although not with any certainty, the possibility of a cellulase. Further experiments with greater numbers of animals are necessary before this point can be settled.

If *Xylophaga* is capable of digesting wood the question arises as to where digestion takes place. In *Teredo* it was shown by Potts (1923) that wood is ingested in regions of the digestive diverticula specialized for this purpose. He also showed that these are absent in *Xylophaga*, a fact which the present investigation has confirmed. It is not impossible that the bacteria found in the caecum may feed on the wood and then be ingested by the phagocytes, which, as originally shown by Yonge (1926*a*, 1926*c*), play so great a part in the digestive processes of the Lamellibranchia. Further work is indicated on the nature of these bacteria and their presence in other wood-boring species. Final decision on the capacity of *Xylophaga* to digest wood will have to await the results of such work.

SEX CHANGE AND SEXUAL DIMORPHISM IN *XYLOPHAGA*

It is known that hermaphroditism occurs in *Bankia gouldi* (see Sigerfoos, 1908), *Teredo norvegica* (see Yonge, 1926*b*) and *T. navalis* (see Coe, 1933, 1934, 1935, 1936). To determine its possible occurrence in *Xylophaga dorsalis*, smears were made of the gonads of ninety-six specimens, while large numbers of specimens of many different sizes were sectioned to show the condition of the gonads. The greatest antero-posterior dimension of the shell of each individual examined was recorded, and the results obtained are given in Table II.

TABLE II. THE RELATION BETWEEN SIZE AND SEX IN *XYLOPHAGA DORSALIS*

Antero-posterior length of shell in mm.	Number of males	Number of hermaphrodites	Number of females
0–3	16	1	1
3–4	9	1	7
4–5	15	—	13
5–6	7	—	6
6–7	3	—	3
7–8	4	—	6
8–9	—	—	3
9–10	—	—	1

It will be seen that, of eighteen specimens not exceeding 3 mm. in length, all were males with the exception of one hermaphrodite and one female. A second hermaphrodite specimen was present in the next size group, while the remaining animals between 3 and 8 mm. long were fairly evenly divided between males and females. The four specimens which exceeded 8 mm. in length were all females.

X. dorsalis appears, therefore, to be a protandric hermaphrodite. The young specimens are male, change to the female sex occurring when they reach a length of about 3 mm.; but this change may apparently be delayed, and therefore animals of medium length are about evenly divided between the sexes.

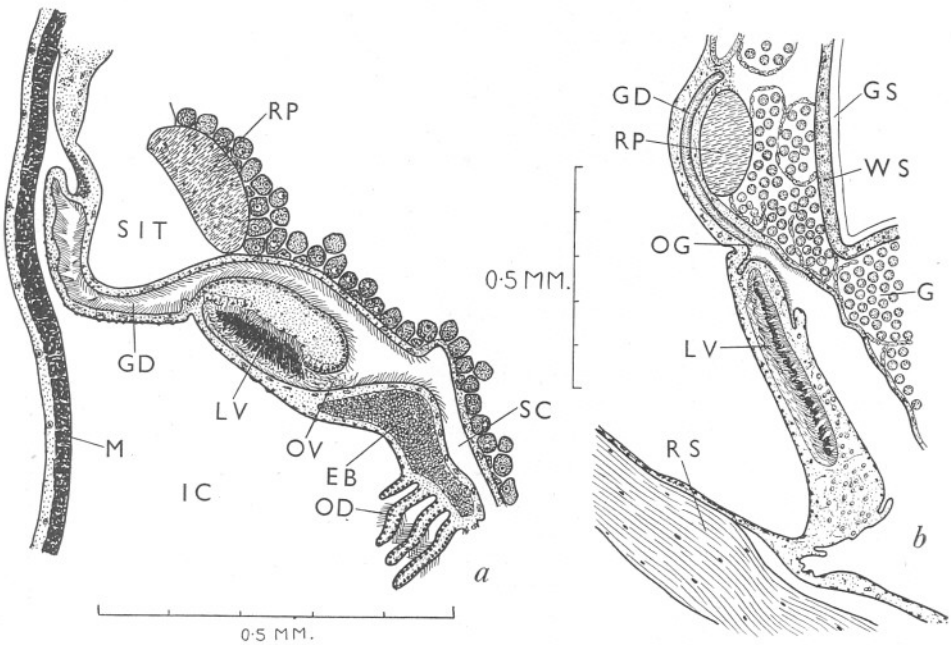

Fig. 10. *Xylophaga dorsalis*: *a*, transverse section through the vesicula seminalis: GD, genital duct; LV, lumen of vesicula seminalis; SIT, split in tissues. *b*, longitudinal section through the vesicula seminalis: OG, opening of genital duct; WS, wall of stomach. Other lettering as before.

It is possible that individuals may undergo more than one change in sex, so that the largest size groups may consist of individuals which are female for the second time. Coe (1933–6) believes that such alternation of sexes occurs in *Teredo navalis*.

Examination of serial sections of various specimens confirmed these observations. In Fig. 12*a* is shown the appearance of the gonad in a hermaphrodite individual 3 mm. long. The lumina of the gonadial tubules are filled with spermatocytes and ripe spermatozoa, whilst the walls of the tubules are lined with developing oogonia of various sizes. It is less easy to demonstrate a

change of sex from female to male because this is thought to occur relatively quickly (Coe, 1933). Evidence has been obtained, however, from serial sections of an individual 5 mm. long, of a change of the gonad from female to male. In this animal the tubules were filled with spermatocytes and spermatozoa, with no signs of oogonia. The animal, therefore, was in the male phase. In its genital ducts, however, a small number of ripe ova was found, and since there was no sign of change of sex in the gonads, it was concluded that these ova were formed in a female phase prior to the existing male phase. This may be regarded as presumptive proof that a second change of sex, from female to male, may occur. Since the largest specimens examined were all females, it is possible that a further change of sex may occur.

In *Xylophaga* the genital duct is short, passing round the retractor muscle of the foot (Fig. 10 *a*, *b*, RP) and opening at the base of the suspensory membrane of the gill into the supra-branchial cavity anterior to the opening of the kidney duct (Fig. 10*a*, GD; Fig. 10*b*, GD, OG). It is lined by a ciliated epithelium which extends for a short distance over the suspensory membrane of the gill. Situated in the suspensory membrane close to the genital opening is a cylindrical cavity with an anterior opening. The cavity is lined by a ciliated epithelium which is continuous with that extending from the genital duct over the suspensory membrane. The opening of this ciliated pocket is directed ventrally (Fig. 10*a*, OV) and is situated close to the genital opening. The lumen of this organ (Fig. 10*a*, *b*, LV) is filled with spermatozoa, which are tightly packed and orientated with their heads pointing towards the ciliated epithelium lining the cavity. Irregularly disposed spermatozoa can be seen at the orifice of the organ (Fig. 10*a*, OV), and these may have been entering or leaving the organ.

It is considered that the organ is a vesicula seminalis, and that it is loaded with spermatozoa when these are discharged at the end of the male phase of the gonad. No other records of such an organ in the Lamellibranchia have been found, and it is possible that *Xylophaga* is peculiar in the possession of a pair of vesiculae seminales. *X. dorsalis* presumably shares this distinction with other members of the genus, e.g. *X. praestans*, *X. indica*, and *X. globosa*.

The vesiculae seminales are present in specimens of all sizes, even in the smallest ones examined, in both sexes, and always contain a considerable quantity of spermatozoa. The method by which they are filled with spermatozoa will be discussed later. Whether self-fertilization occurs in *Xylophaga* to the exclusion of cross-fertilization is difficult to determine, but it appears certain that the possession of these organs renders self-fertilization possible.

Xylophaga is peculiar among the Lamellibranchia not only in the possession of vesiculae seminales, but also for the development of an unusual glandular organ in the supra-branchial cavity. This "accessory genital organ", as it will be here called, is found in a fully developed condition in the male phase only, thus making *Xylophaga* one of the few recorded cases of external sexual dimorphism in the Lamellibranchia. It lies suspended from the posterior surface of the posterior adductor muscle (Fig. 11) and when fully developed

consists of a large fleshy peduncle (Fig. 11*c*, PE) which expands distally into a broad, slightly bilobed blade or lamella (Fig. 11*c*, LA). The dorsal border of the peduncle encircles the rectum close to the anus. The blade is pressed closely against the posterior and lateral surfaces of the visceral mass. Fig. 11*c* shows the organ removed from the visceral mass, and in it the two lobes of the blade are pressed close to one another. In serial sections, the fully developed organ more or less completely occludes the supra-branchial cavity.

The posterior surface of the blade, and that of the peduncle, are sparsely ciliated, the weak ciliary currents being directed upwards towards the posterior adductor muscle. The anterior surface of the blade, which is closely pressed

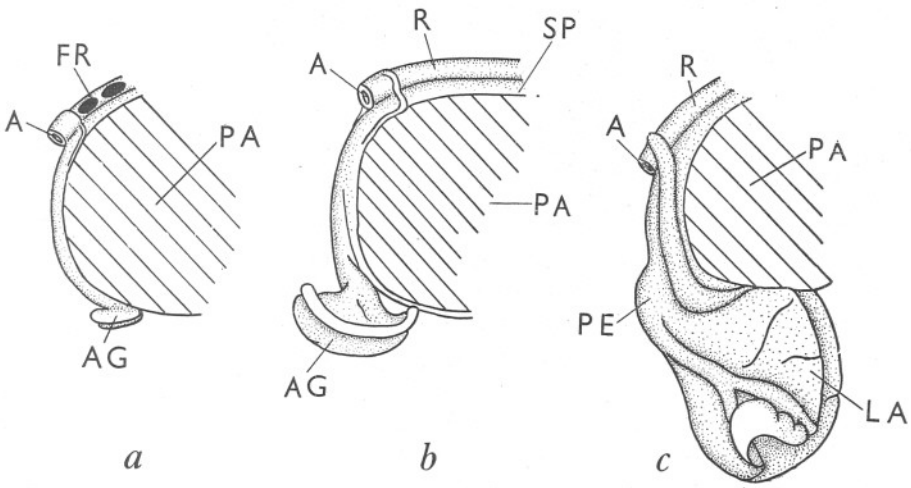

Fig. 11. *Xylophaga dorsalis*: the accessory genital organ in various stages of development, seen from the right side: *a*, small, from a female; *b*, medium, from a female, or hermaphrodite; *c*, large, from a male: AG, accessory genital organ; FR, faeces in rectum; LA, lamella, or blade, of accessory genital organ; PE, peduncle of accessory genital organ; SP, dorsal surface of posterior adductor. Other lettering as before.

against the visceral mass, is composed of a very shallow unciliated epithelium (Fig. 12 *b*, *c*). The cilia on the posterior surface of the blade, are seldom visible in sections.

The organ is of very variable size, being fully developed only in male specimens; occasionally it is of an intermediate size in female specimens—suggesting a recent change of sex—but it is always medium in size in hermaphrodite specimens. Data on this matter are summarized in Table III, which indicates the intimate relationship between the size of this accessory genital organ and the sex of the individual.

Serial sections through the accessory genital organ show that it is glandular, the posterior surface being composed of mucoid cells. This layer occupies about a third of the thickness of the blade (Fig. 12*b*). No glands open on to the anterior surface. The remainder of the lamella is composed of a glandular

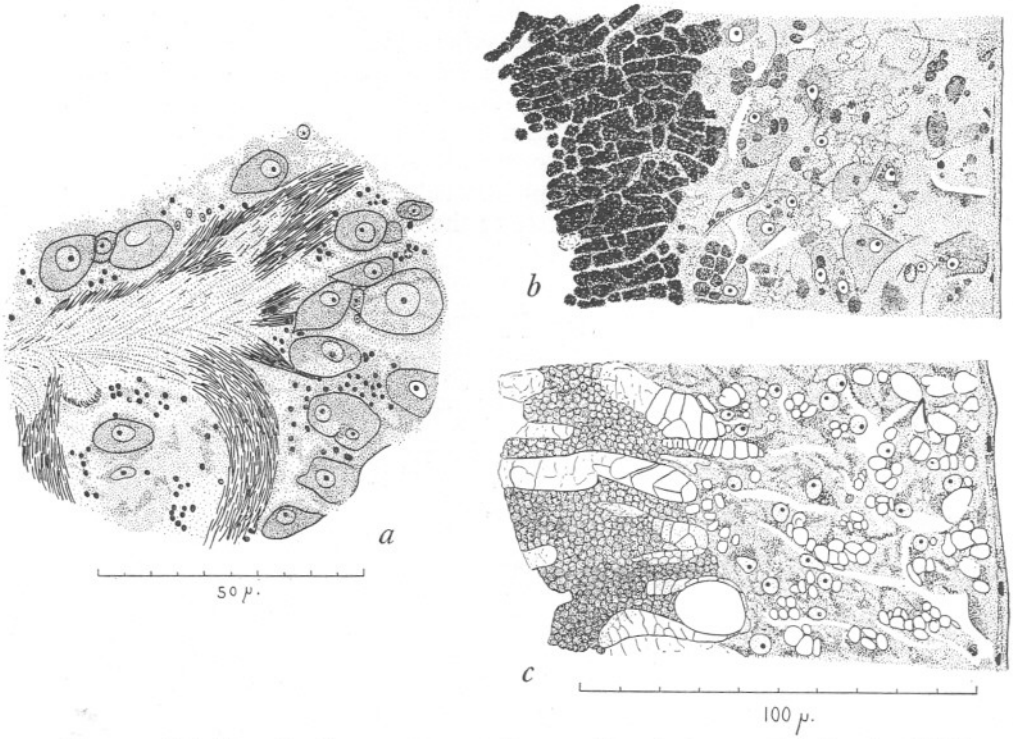

Fig. 12. *Xylophaga dorsalis*: transverse sections: *a*, through the gonad during the initial change from the male to the female phase; *b*, through the blade of the accessory genital organ, seen here in a ripe condition; *c*, through the blade of the accessory genital organ, in a spent condition.

Table III. The Relation between the Size of the Accessory Genital Organ and the Sex of the Animal

Antero-posterior length of shell in mm.	Size of accessory genital organ			
	Large	Medium	Small	Absent
0–3	16 ♂	1 ☿	—	1 ♀
3–4	7 ♂	2 ♂, 1 ☿, 3 ♀	1 ♀	3 ♀
4–5	13 ♂	2 ♂, 1 ♀	3 ♀	9 ♀
5–6	7 ♂	1 ♀	1 ♀	4 ♀
6–7	3 ♂	—	2 ♀	1 ♀
7–8	4 ♂	—	3 ♀	3 ♀
8–9	—	—	2 ♀	1 ♀
9–10	—	—	1 ♀	—
Total	50 ♂	4 ♂, 2 ☿, 5 ♀	13 ♀	22 ♀

tissue which is for the most part stained but lightly with Delafield's haematoxylin. The cells are roughly fusiform in shape, and are shown in transverse section in Fig. 12 *b*, *c*. Their nuclei are easily distinguished, for they have a distinct nuclear membrane and a large central nucleolus. The secretion arises close to the nucleus, and when first formed consists of a lightly stained packet which later acquires darkly stained walls surrounding unstained contents. The number of these packets of secretion increases until finally a reticulate mass of bubbly appearance is formed. The secretion must pass to the posterior surface of the blade, which is deeply folded close to the peduncle. In these folds strands of mucus are frequently seen. Comparison of a number of series of sections shows that the organ secretes as a whole. Either the posterior surface is loaded with secretion or all the secretion has been discharged, leaving the cells at the posterior surface empty (Fig. 12*c*). When the organ has secreted it presumably commences to degenerate.

It is probable that when spermatozoa are discharged from the gonad duct, owing to the pressure of the ripe gonads, they are forced past the openings of the vesiculae seminales, and fall upon the posterior surface of the supra-branchial organ. It is at this stage that the accumulation of mucus is discharged, and in it the spermatozoa become entangled. By the action of the cilia upon the posterior surface of the blade and peduncle the spermatozoa are driven upwards and conveyed to the openings of the vesiculae seminales. The spermatozoa are then passed into the lumina of these organs by the cilia on the suspensory membranes. Evidence has been found which supports this theory. In one series of sections both spermatozoa and spermatocytes were found entangled in mucous threads on the posterior side of the blade. The presence here of spermatocytes indicates that the spermatozoa were those produced by the animal itself, and were not foreign spermatozoa collected from the inhalant current.

When the vesiculae seminales are fully loaded the function of this accessory genital organ has been completed, and its degeneration commences. Residual sperm in the gonads may either be discharged or resorbed.

With the degeneration of the accessary genital organ the volume of the supra-branchial cavity is greatly increased and at the same time the animal changes to the female phase. It is not known whether *Xylophaga* incubates its larvae; but this occurs in some species of *Teredo* (Hatschek, 1880; Calman, 1919), and in view of the probable value of such a habit to animals inhabiting driftwood, it is probable that the same is true of *Xylophaga*. If so there is now available space for the larvae in the supra-branchial cavity. As shown in Table III, the accessary genital organ is present in all males whatever their size; thus if the animals do change sex more than once it must be redeveloped during the second male phase.

The possession of both these organs is probably of great survival value to *Xylophaga*. The animals live in isolated communities in driftwood, and the chance of fertilization might be slight were eggs and sperms discharged freely

into the sea. The retention of the sperms produced during the male phase will ensure fertilization of eggs produced during the later, female phase and so overcome this danger. Sigerfoos (1908) recorded that in male specimens of *Bankia gouldi* there is a great development of mucous glands in the roof of the supra-branchial cavity, but there is no record in any species of *Teredo* of any glandular organ. It is by no means impossible that *Bankia* and *Teredo* may also possess vesiculae seminales which have hitherto been overlooked.

The Systematic Position of *Xylophaga*

Consideration of the shell features of *Xylophaga* led systematists to the conclusion that, although these superficially resembled those of the Teredinidae, the genus was more nearly related to the Pholadidae, in which it has accordingly been included (Adams, H. & A., 1853–8; Paetel, 1890; Pelseneer, 1906; Thiele, 1926). But examination of the anatomy of *Xylophaga* gives no support to this view. Whilst showing affinities both with the Teredinidae and the Pholadidae, *Xylophaga* also possesses certain specialized characters of sufficient importance to justify the creation of a new family for its inclusion.

In the following important points *Xylophaga* has undoubted affinities with the Pholadidae.

With the exception of the siphonal process, the animal is entirely covered by the shell valves (Figs. 2*a*, 6*b*), its burrow is never lined with a calcareous deposition, nor does the animal possess pallets as do the members of the Teredinidae. *Xylophaga* possesses a pair of accessory plates (Fig. 6*b*, AP), though their absence in the Teredinidae is probably due to reduction. The rectum of *Xylophaga* passes through the ventricle (Fig. 13*a*, R), which it does not in the Teredinidae. Finally, the visceral ganglia occupy their normal position in *Xylophaga*, on the ventral surface of the posterior adductor muscle. In the Teredinidae, owing to the great elongation of the visceral mass, these ganglia are displaced backwards and lie far behind the posterior adductor.

The above are outweighed, however, by the following affinities between *Xylophaga* and the Teredinidae.

Xylophaga bores normally in wood (Fig. 1*a*), never in stone; its shell in its general appearance and fragility is not unlike that of *Teredo*. The ctenidia of *Xylophaga* (Figs. 3*b*, 6*b*) and of the Teredinidae (Figs. 2*b*, *c*, 3, 4) are composed of only one demibranch (Atkins, 1937*b*; Ridewood, 1903). This is in each the outer demibranch (Purchon, 1939). In addition there are no ctenidial sorting mechanisms in *Teredo* or in *Xylophaga*.

The labial palps in the Teredinidae have undergone various degrees of reduction (Fig. 2*c*, LP; Figs. 4, 6*a*, DLP, VLP) and may possess no ciliary sorting mechanisms; those of *Xylophaga* (Figs. 6*b*, 7, DLP, VLP) are also greatly reduced and have poor powers of selection. The ctenidia of the Pholadidae possess both inner and outer demibranchs, their labial palps are highly organized and the ciliary mechanisms on the ctenidia and the palps are highly developed (Kellogg, 1915). The alimentary canal of *Xylophaga* possesses

modifications similar to those in the Teredinidae for the acceptance of large quantities of wood fragments produced spasmodically. The oesophagus is short, the stomach is large and bears a conspicuous caecum within which wood shavings are stored. The style sac and the crystalline style are reduced in size (Fig. 7*b*, SS, CS)—contrast the large style sac of *Barnea* (Fig. 8, SS) and of

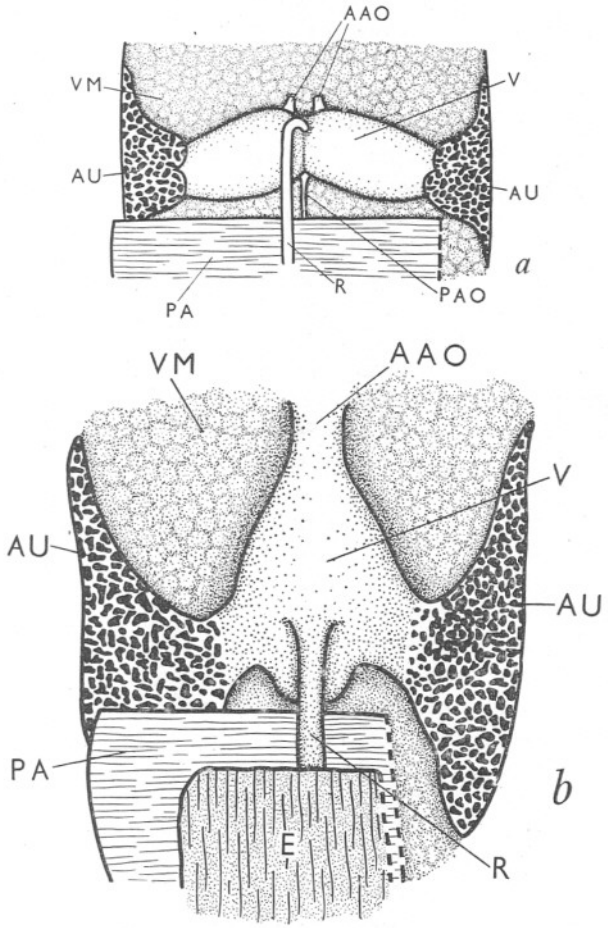

Fig. 13. Dorsal view of the organs in the pericardium. *a*, *Xylophaga dorsalis*; *b*, *Barnea parva*: AAO, anterior aorta; AU, auricle; E, epithelium of the siphonal process; PAO, posterior aorta; V, ventricle. Other lettering as before.

Martesia (see Nelson, 1918). The intestinal typhlosole has undergone various degrees of reduction in the Teredinidae (Sigerfoos, 1908; Lazier, 1924); it is absent in *Xylophaga*, but well developed in *Barnea*, a member of the Pholadidae.

It has been shown that various members of the Teredinidae are protandric hermaphrodites (Sigerfoos, 1908; Yonge, 1926*b*; Coe, 1933–6), and *Xylophaga*

also is a protandric hermaphrodite. This condition has never been demonstrated for any member of the Pholadidae. Various members of the Teredinidae incubate the larvae (Sigerfoos, 1908; Calman, 1919), and it is not improbable that *Xylophaga* also incubates its larvae, though this remains to be proved.

Finally, the structure of the ventricle of *Xylophaga* more nearly resembles that of *Bankia gouldi* (see Sigerfoos, 1908) than that of *Barnea parva*—in spite of the fact that it is traversed by the rectum. The ventricle of *Xylophaga* is short from front to back (Fig. 13*a*, V), it possesses two delicate anterior aortae which pass downwards into the visceral mass from a short median lobe which lies in front of the rectum (Fig. 13*a*, AAO), and a single posterior aorta (Fig. 13*a*, PAO) which passes under the posterior adductor muscle. The ventricle itself is short from back to front and is produced laterally into two conspicuous lobes which communicate with the auricles (Fig. 13*a*, AU). The ventricle of *Barnea parva* (Fig. 13*b*, V) is unlike that of *Xylophaga*; it possesses the typical fusiform shape, long in the antero-posterior plane, in which the rectum traverses the ventricle (Fig. 13*b*, R). The heart of *Bankia gouldi* (Sigerfoos, 1908) is deeply bilobed. In the young individual (Fig. 14*a*) the auricles are not attenuated, nor is the ventricle drawn out in the antero-posterior axis; it is more deeply lobed than that of *Xylophaga*. It is also morphologically upside down. Owing to the great length of the adult animal, the heart when fully developed (Fig. 14*b*) is quite unlike that of *Xylophaga*. The anterior and posterior aortae arise close to one another at the anterior end of the heart (Fig. 14*b*, AAO, PAO), and the auricles, which are greatly attenuated, communicate with two posterior lobes of the ventricle. In *Bankia gouldi* the ventricle of a young specimen, 2 mm. in length, is laterally bilobed, as it is in *Xylophaga*. This is doubtless a modification due to the globose shape of the two animals. In larger specimens of *Bankia gouldi* the antero-posterior elongation of the body necessitates a departure from the laterally expanded ventricle of the young animal.

There remain a number of characters in which *Xylophaga* differs both from the Teredinidae and from the Pholadidae. These characters show such a high degree of specialization that it is proposed to transfer *Xylophaga* from the Pholadidae and place it alone in a new family in the order Adesmacea, more closely related to the Teredinidae than to the Pholadidae.

Although it is typical of a member of the Adesmacea that the shell bears an apophysis upon which the retractor muscles of the foot are inserted, as in *Pholadidea penita* Conrad (Lloyd, 1897) (Fig. 14*c*, SA) and in *Teredo norvegica* (Fig. 14*e*, SA), *Xylophaga* possesses no shell apophysis (Fig. 14*d*), and the retractor muscles of the foot are inserted upon the shell in the primitive position, anterior to the insertion of the posterior adductor muscle. The siphonal process of *Xylophaga* is specialized, the exhalant siphon being reduced and opening within the burrow (Figs. 2*a*, 6*b*, ES). While there is some slight evidence that *Xylophaga* may resemble the Teredinidae in the possession

of a cellulase, it certainly possesses no regions of the digestive diverticula exclusively specialized for wood ingestion.

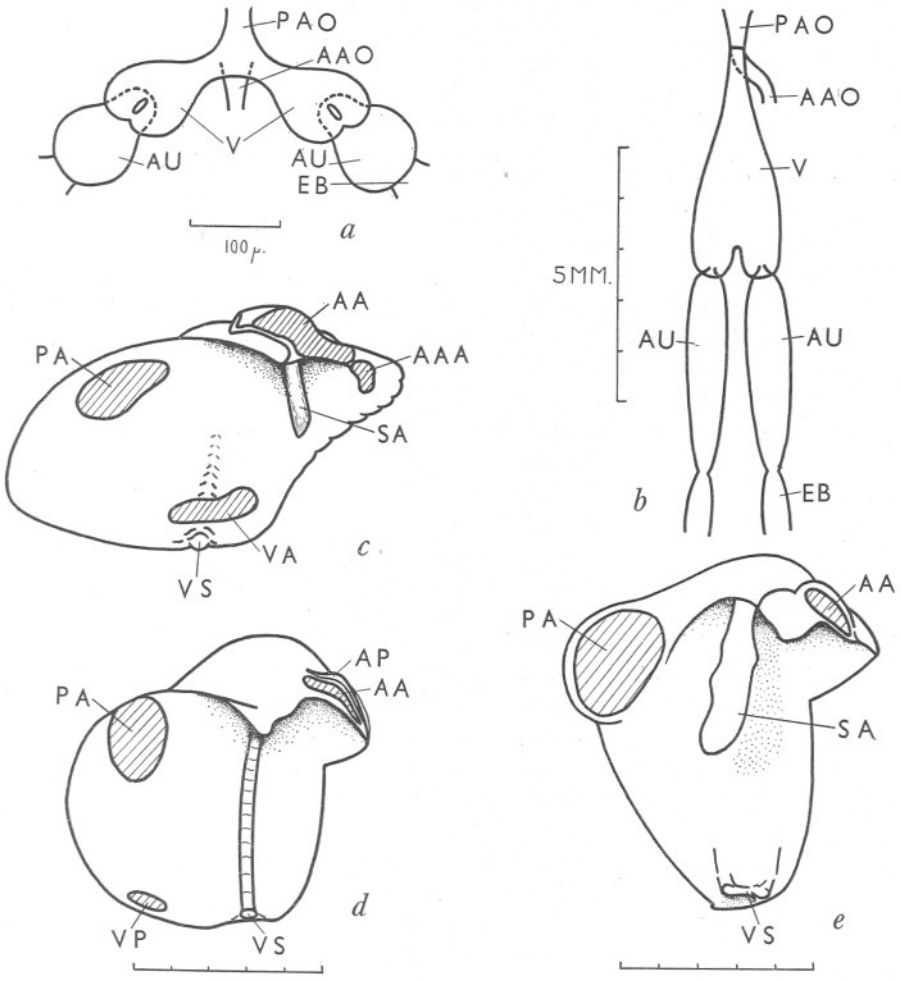

Fig. 14.

a, *Bankia gouldi* (after Sigerfoos): dorsal view of the heart of a young individual.
b, *Bankia gouldi* (after Sigerfoos): dorsal view of the heart of an adult individual.
c, *Pholadidea penita* (after Lloyd): shell and musculature.
d, *Xylophaga dorsalis*: shell and musculature.
e, *Teredo norvegica*: shell and musculature.
AAA, accessory anterior adductor; SA, shell apophysis; VA, ventral adductor. Other lettering as before.

Apart from shell characters, the most important differences between *Xylophaga* and the Teredinidae are the modifications in the reproductive system which render self-fertilization possible, namely, the vesiculae seminales

and the accessory genital organ, the presence of which appears to be correlated with the isolated life of the colonies of *Xylophaga*. Consideration of the shell and musculature of *Xylophaga* suggests possible homologies with regard to the pallets and pallet muscles of the Teredinidae. Lloyd (1897) showed that in *Pholadidea penita* (Fig. 14*c*) in addition to the anterior and posterior adductor muscles, there are auxiliary adductor muscles; of these the accessory anterior adductor (Fig. 14*c*, AAA) was probably split off the anterior adductor (Fig. 14*e*, AA). Close to the ventral articulation of the shell (Fig. 14*c*, VS) is a ventral adductor muscle (Fig. 14*c*, VA).

In *Xylophaga* no division of the anterior adductor (Fig. 14*d*, AA) has occurred. At the postero-ventral border of the shell, behind the ventral articulation of the shell is a ventral pallial muscle (Figs. 6*b*, 14*d*, VP) composed largely of longitudinal fibres, but also possessing a few transverse and dorso-ventral muscle fibres. In *Teredo norvegica* (Fig. 14*e*) the postero-ventral adductor, or ventral pallial muscle is present. In all other members of the Teredinidae the postero-ventral margin of the shell is emarginated.

It is suggested that the pallets in the Teredinidae are derived from this postero-ventral corner of the shell valves, and that the pallet muscles of the Teredinidae, the ventral pallial muscle of *Xylophaga*, and the ventral adductor of *Pholadidea* are homologous.

With regard to the accessory plates possessed by all members of the Pholadidae (not shown in Fig. 14*c*) and also by *Xylophaga* (Fig. 14*d*, AP), in the Teredinidae an anterior pallial fold, similar to that which in the Pholadidae bears the accessory plates, extends forwards over the shell valves in an antero-dorsal position (Fig. 2*c*, AF). It is therefore probable that the absence of accessory plates in the Teredinidae is secondary.

It is proposed to call the new family to which the genus *Xylophaga* is to be transferred, the Xylophaginidae. The affinities of the families in the order Adesmacea may then be summarized as follows:

Adesmacea

Common origin { Xylophaginidae, Teredinidae } Wood-boring Lamellibranchia

Common origin { Pholadidae } Rock-boring Lamellibranchia

The affinities of *Xylophaga* are shown in tabular form in Table IV.

Discussion

If it be assumed that the absence of a shell apophysis and the insertion of the pedal retractor muscles upon the shell in *Xylophaga* are primitive characters it follows that *Xylophaga* departed from the common stock of the Adesmacea before the development of the shell apophysis, as shown below in Fig. 15.

On this theory it is evident that reduction of the ctenidium to a single demibranch in the Xylophaginidae and in the Teredinidae occurred separately, which is quite possible, and that either the caecum of the stomach was also separately evolved in these two families, or that the absence of the caecum in

the Pholadidae is due to reduction. This is inherently improbable and it is therefore contended that the absence of the shell apophysis in *Xylophaga* is secondary and *not primitive*.

The implications of this second and more probable view are shown in Fig. 16. The common stock of the Adesmacea was rock-boring, and from this arose a wood-boring stock which was to evolve into the Xylophaginidae and Teredinidae. With the evolution of a wood-boring habit a stomach caecum

TABLE IV. THE AFFINITIES OF *XYLOPHAGA*

Affinities with the Teredinidae	*Specialized characters*	*Affinities with the Pholadidae*
Bores chiefly in wood, and never in stone	No shell apophysis; pedal retractor muscles inserted upon shell in primitive position	Body enclosed by shell valves
Proportions, sculpture, and fragility of shell valves	Reduction of exhalant siphon	Two accessory plates
	Faecal accumulation in burrow	No pallets
Ctenidia possess outer demibranch only and no ctenidial sorting mechanisms	Method of wood digestion: by bacteria?	No calcareous lining to burrow
		Rectum passes through ventricle
Labial palps greatly reduced	—	—
Products of boring activity passed through alimentary canal	Vesiculae seminales and accessory genital organ permit self-fertilization	Visceral ganglia in normal position
Short oesophagus; conspicuous stomach; caecum to stomach; small style sac; intestinal typhlosole absent	—	—
Possible digestion of wood?	—	—
Ventricle laterally bilobed	—	—
Alternation of sex	—	—
Possible incubation of larvae	—	—

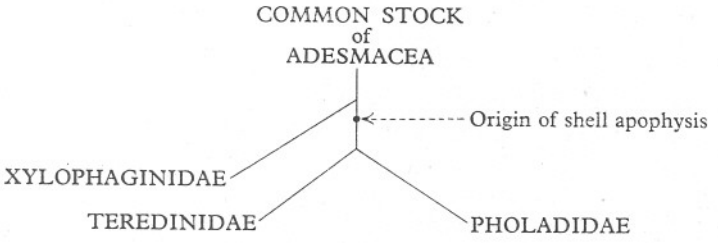

Fig. 15.

was formed as a device converting the spasmodic production of large quantities of wood fragments into a slow steady stream passing through the alimentary canal. Due to the pelagic life in driftwood, the animals seldom, if ever, encounter the heavy sedimentation and turbidity which must be endured by rock-dwelling animals. The ctenidia and labial palps were thus reduced in structure and in function.

The wood-boring stock then divided into the Xylophaginidae and the Teredinidae. In the former the shell apophysis was lost, and the insertion of the pedal retractor muscles moved back to the primitive position; the exhalant

siphon was also greatly reduced. The accessory genital organs were evolved. In the Teredinidae, elongation of the body occurred with the accompanying modifications in the anatomy set down in Fig. 16. It has not been possible to make any suggestion as to the reason for the reduction of the exhalant material in the posterior end of the burrow.

The reduction of the ctenidium in the Teredinidae and in the Xylophaginidae to a single demibranch, and the complete loss of ctenidial sorting mechanisms seem best related to the absence of turbidity in the open sea. The same explanation may be offered for the reduction of the labial palps. Where there is no danger of the mantle cavity or the alimentary canal becoming filled with sediment it is not surprising to find a corresponding reduction in the ciliary sorting and cleansing mechanisms. It is recorded that *Teredo megotara* usually

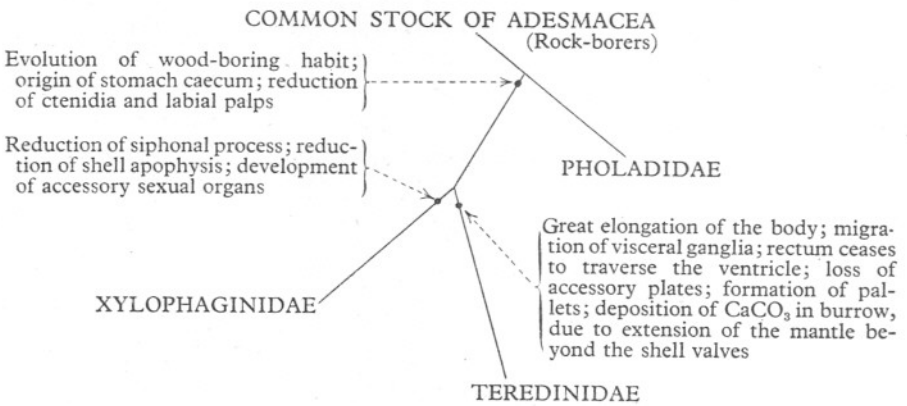

Fig. 16.

occurs in driftwood (Calman, 1919) and that *T. navalis* is intolerant of estuarine water. In these species the reduction of the labial palps has been carried to an extreme; in *Xylophaga* also, the palps are greatly reduced. *Teredo norvegica*, however, is the most common shipworm in European waters on piers or lock gates where the turbidity may be high. In this species the labial palps show least reduction.

The caecum of *Teredo* and of *Xylophaga* has been considered to be a mechanical contrivance, storing wood fragments while they are accumulating rapidly during boring operations, so that a strain is not placed upon the remainder of the alimentary canal. It is here considered that the caecum is also a contrivance to convert the spasmodic arrival of large quantities of material into a slow steady stream through the intestine. In other words, the caecum is as much a constant level reservoir as a safety valve.

The evidence obtained from the single experiment upon the digestive enzymes of *Xylophaga* suggests that this animal may be able to digest certain constituents of wood. Further evidence is required on this matter, and it must

be borne in mind that *Xylophaga* can live in the absence of wood. In the shipworms, as noted by Nelson (1918) and Lazier (1924), the style sac and crystalline style are small when compared with those of rock-boring lamellibranchs of a similar size (see Figs. 7*b*, 8, ss, cs). This is also true of *Xylophaga*. If the wood-boring lamellibranchs are all capable of digesting cellulose or hemicellulose the animal may be largely independent of digestive enzymes from the style.

If *Xylophaga* is capable of digesting wood it is important to know how this is carried out. Potts has shown that regions of the digestive diverticula, specialized for the intracellular digestion of wood fragments, do not occur in *Xylophaga*; it is possible that wood is digested by the bacteria which have occasionally been found in the alimentary canal. It would be interesting to know whether bacteria are also present in the caecum of *Teredo*. It could be postulated that wood digestion by bacteria is primitive and its intra-cellular digestion in *Teredo* a later development.

Protandric hermaphroditism has now been demonstrated in all genera of wood-boring lamellibranchs. This condition, however, has not been recorded for any member of the Pholadidae. Incubation of larvae, which is known to occur in *T. navalis* (see Calman, 1919), has not been recorded for *Xylophaga*, but owing to the exceedingly heavy colonization of driftwood by small individuals in the samples obtained, it seems highly probable that the larvae are incubated until a late stage of development. Examination of a sample collected in the summer would in all probability settle this point. Whenever the establishment of young individuals upon a suitable substrate is a question of hazard modifications may be expected in the reproductive system. Such is the case in fluviatile, or commensal lamellibranchs, where the larvae are incubated in the supra-branchial cavity. *Xylophaga* possesses certain modifications which render self-fertilization possible. These modifications are believed to be without parallel in the Lamellibranchia. A pair of vesiculae seminales store spermatozoa formed during the male phase, and an accessory genital organ in the supra-branchial cavity is thought to assist in this process by directing the sperm by ciliary activity to the openings of these organs. Grobben (1892) recorded in *Cuspidaria* a pair of internal glandular organs associated with the genital apertures in male specimens. These organs are of unknown function. With this exception, *Xylophaga* is apparently unique amongst the Lamellibranchia in the possession of accessory genital organs functional only in the male phase. These modifications and developments in the reproductive system, if, as appears probable, they render the fertilization of ova more likely, will be of the greatest survival value.

Summary

The exhalant siphon of *Xylophaga* is greatly reduced and its opening is situated within the burrow. Faeces accumulate in the posterior end of the burrow in a compact mass.

The ctenidia and labial palps of *Teredo*, *Bankia* and *Xylophaga* are modified and reduced, unlike those of the Pholadidae. The ctenidia are flat and homorhabdic and possess no ciliary sorting mechanisms; they consist of the outer demibranch only.

The ctenidia of *Xylophaga* are composed of a direct lamella; those of *Teredo* and *Bankia* are divided into anterior and posterior portions connected by a branchial groove which is an extension of the marginal food groove of the gill. The number of filaments in the anterior portion of the gill varies according to the species, and is of assistance in identification.

The labial palps of *Teredo norvegica* are least reduced; in *Xylophaga dorsalis* reduction is greater, though selection of food material is still exercised. The greatest reduction has occurred in *Teredo megotara* and in *T. navalis* where there is no selection.

The ciliated mantle tracts in *Teredo* and in *Xylophaga* play an important part in limiting the quantity of food particles passed from the ctenidia to the mouth.

The alimentary canal of *Xylophaga* is modified in a similar way to that of *Teredo* for the passage through it of large quantities of material. The stomach is enlarged and possesses a conspicuous caecum; the style sac is reduced; there is no typhlosole; the rectum passes through the ventricle.

The caecum probably serves both as a safety valve and as a mechanism to ensure a slow steady stream of wood particles through the intestine. Bacteria and phagocytes may occur in the lumen.

Xylophaga may derive some nourishment from wood, but there is no region of the digestive diverticula specialized for ingestion of wood particles.

Xylophaga is a protandric hermaphrodite; possibly more than one change in sex occurs.

A pair of vesiculae seminales lies in the suspensory membrane of the ctenidium, close to the openings of the genital ducts. They are filled with spermatozoa during the male phase. A ciliated, glandular organ is present in the supra-branchial cavity during the male phase only. This accessory genital organ probably directs spermatozoa into the vesiculae seminales.

The presence of these two structures renders self-fertilization possible and this may be of great survival value to a species which lives in isolated communities.

It was not determined whether *Xylophaga* incubates larvae in the mantle cavity, but this is regarded as probable.

The relationships of *Xylophaga* are discussed and it is concluded that the genus should be removed from the family Pholadidae and placed in a new family in the same order (Adesmacea) but more nearly related to the Teredinidae than to the Pholadidae. It is proposed to name this family the Xylophaginidae.

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LIST OF ABBREVIATIONS USED IN FIGURES

A Anus
AA Anterior adductor
AAA Accessory anterior adductor
AAO Anterior aorta
AB Afferent branchial vein
AC Anal canal
AF Anterior pallial fold
AG Accessory genital organ
AP Accessory plate
APC Anterior portion of ctenidium
AS Auricle of shell
AU Auricle (of heart)

BG Branchial groove

C Caecum
CA Ctenidial axis
CE Cut edge of shell
CH Cephalic hood
CM Cut edge of mantle
CMG Ciliated mantle groove
CMT Ciliated mantle tract
CS Crystalline style
CT Ctenidium

DD Digestive diverticula
DF Dorsal pallial fold
DL Descending lamella of ctenidium
DLP Dorsal labial palp

E Epithelium (of the siphonal process)
EB Efferent branchial vein
ES Exhalant siphon
ESS Blind end of style sac

F Foot
FE Floor of exhalant siphon
FR Faeces in rectum

G Gonad tubules
GD Genital duct
GS Gastric shield

I Intestine
IC Infra-branchial cavity
ID Inner demibranch
IM Intucking of mantle
IS Inhalant siphon

L Ligament
LA Lamella (or blade) of accessory genital organ
LO Lateral oral groove
LP Labial palps
LV Lumen of vesicula seminalis

M Mantle
ME Mantle edge
MG Marginal groove
MO Mouth

O Oesophagus
OC Opening of caecum into stomach
OD Outer demibranch
OF Opaque disk of foot
OG Opening of genital duct

PA Posterior adductor
PAO Posterior aorta
PE Peduncle of accessory genital organ
PG Pedal ganglion
PPC Posterior portion of ctenidium

R Rectum
RP Retractor pedis muscle
RS Retractor muscles of siphonal process

S Shell
SA Shell apophysis
SC Supra-branchial cavity
SIT Split in tissues
SM Suspensory membrane of ctenidium
SP Dorsal surface of posterior adductor
SS Style sac
ST Stomach

V Ventricle
VA Ventral adductor
VLP Ventral labial palp
VM Visceral mass
VP Ventral pallial muscle
VS Ventral articulation of shell

W Wedge-shaped mass of mucous glands
WS Wall of stomach

X Vortex in the ciliary currents on flank of foot

THE BIOLOGY AND TREMATODE PARASITES OF THE GASTROPOD *LITTORINA NERITOIDES* (L.) ON THE PLYMOUTH BREAKWATER

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(Text-figs. 1–11)

CONTENTS

Introduction

Crevices in rocks about high-water mark are usually regarded as the typical habitat of *Littorina neritoides* (L.). The species was thought to be viviparous until in 1935 Linke and Lebour showed that its egg capsules were pelagic, and the investigation described here was begun primarily to ascertain how these egg capsules reached the sea. The first part of the paper deals with the type of habitat occupied by the adults, and their distribution at different levels. The second part deals with spawning and comprises three sets of observations; first, the state of the gonads was determined by dissections through the year; secondly, field experiments were carried out to find whether there was any downwards migration for spawning; and thirdly, the egg capsules were collected from the plankton for a part of one winter and the following spring, and an attempt is made to show that their occurrence is related to meteorological conditions. The third part of the paper deals briefly with the distribution of size groups in the population, growth rate, and the sex ratio. The fourth part is an account of the occurrence of larval trematodes in the species. Dissections showed that the snails were heavily infected with cercariae, and records were kept of their incidence in order to find out whether they caused sterility, influenced the growth rate, or produced sex reversal.

The Plymouth Breakwater was selected as a starting-point for this investigation, as it is a long stretch where conditions are much more uniform than on the same length of shore. It was originally intended to extend the observations

to other localities, but this has been impossible save to a very limited extent; all the work described below was carried out on material collected from the Breakwater except where other places are specifically mentioned.

I am greatly indebted to Dr E. J. Allen, F.R.S., through whose kindness I was able to begin this work; to Dr Kemp, F.R.S., Director of the Plymouth Marine Laboratory, who has given me every facility and encouragement for continuing it; and to the Zoological Society for the use of its table at the Plymouth Laboratory for a month in 1939. Amongst the many people who have helped me I wish particularly to thank Dr Lebour for her constant interest, Dr H. B. Moore for much assistance with field work, Mr G. M. Spooner for his help with statistical data, and Mr G. I. Crawford for reading part of the manuscript. Mr William Searle, of the M.B. *Gammarus*, collected all the samples for me, from May 1937 to June 1938, and I am most grateful to him for much help with field work, particularly in August 1939.

The Plymouth Breakwater Habitat

The building of the Breakwater was begun in 1812 and completed in 1851; four million tons of native limestone and two and a half million tons of granite facings were used in its construction. It is approximately 1600 m. long, and consists of a central part and two arms of about 330 and 360 m. (see map in *Plymouth Marine Fauna*, 1931). The central part faces 2° west of south, the eastern arm about 15° east of south, and the western arm about 17° west of south. Levels were kindly given to me by the Civil Engineer in Chief at the Admiralty. The top is approximately 13·7 m. wide, and its mean level is 0·76 m. above high-water ordinary spring tides. The northern and southern sides are at slopes of 2 to 1 and 5 to 1, respectively. Numerous small cylindrical holes, which were probably used in hoisting the blocks into position, occur on the surface. They vary in size, but are generally 7–9 cm. across, and 8–15 cm. deep.

Very heavy seas sometimes sweep over the Breakwater during the winter. Twenty-four merchantment were wrecked in the Sound in one storm early in the nineteenth century, and about 30 years ago two 80-ton blocks of concrete lying on the southern face of the Breakwater were skidded across the top near the lighthouse at the west end. The degree of exposure is therefore very considerable and fucoids are sparse on both slopes. The factor for the wave exposure of certain localities may be calculated, according to Moore's formula (1935, p. 80; 1936, p. 66), as "the number of days per 100 days in which any wind blows into the exposed aperture of the locality in question, this opening being the seawards aperture measured at a distance of half a mile". This formula does not seem applicable to the Breakwater. If the aperture is measured at a distance of half a mile it is 180°, and the modifying effect of the land-masses to the east and west is not taken into account. It seems better then that the aperture should be taken from the angle between two lines drawn

from the middle of the Breakwater to Reny Rocks and Penlee Point, that is approximately a quadrant facing south-east to south-west. According to unpublished wind roses at the Meteorological Office at South Kensington (observations from 1893 to 1922, Fig. 1), the percentage number of winds blowing through this aperture throughout the year is 33. The mean for

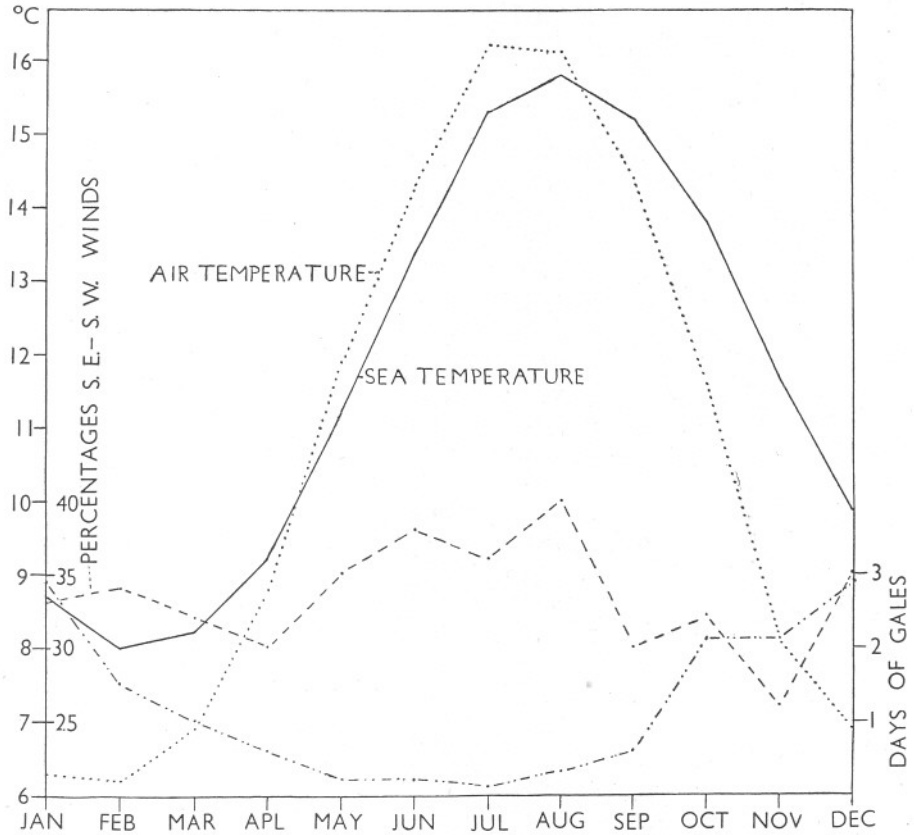

Fig. 1. Sea and air temperatures, percentages of winds blowing from the south east-south west quadrant, and the numbers of days of gales per month in Plymouth Sound.

October to March, inclusive, is 32, for the summer months 35, and the highest average for a single month 40 for August. But gales are most frequent during the winter months (Fig. 1), and, as Johnson points out (1919, p. 72), the prevailing wind may not be the dominant wind. The foreman of the repairing gang on the Breakwater tells me that the most destructive wind there comes from the south-east. The factors that affect the degree of exposure there are thus very complex and cannot be expressed by a single figure. Direct measurement of the dynamic force of the waves by some type of dynamometer

(Gaillard, 1904) will probably prove to be the most satisfactory method of comparing the exposure of different localities.

The figures for the sea temperatures were kindly supplied by the Plymouth City Meteorologists, Messrs Prigg, Lynden and Ivory. The monthly means are compiled from observations from 1897 to 1932, the temperatures being taken three times weekly at a depth of 6 ft. off the end of Promenade Pier. The air temperatures, for Plymouth Hoe, were supplied by the Meteorological Office at South Kensington. They are compiled from daily means from 1906 to 1935.

Zonation on the Breakwater

Two traverses were made across the Breakwater in August 1939, the first, A (Fig. 2), 345 m. west of the midpoint, and the second, B (Fig. 3), 184 m. east of the midpoint. Two surface samples were taken at each level at A, but, owing to limitations of time, only one at each level at B, where there were also fewer stations. Each sample consisted of the total number of snails collected in 100 sq. cm. The population in the pools on the top was estimated from two pools at each of four stations in both traverses; the first station being situated at the north edge, and the others 4·5, 9 and 13·5 m. south of it. The depth of each pool and the volume of water in it were measured and the approximate area of the sides and bottom calculated from the formula $2\pi\,(\sqrt{v/\pi H})\,H$. The results are shown in Table I and Figs. 2 and 3.

Table I

Levels of "dry" stations in relation to mean sea-level m.		Traverse A			Traverse B		
			Height of shell			Height of shell	
		No. per 100 sq. cm.	Range mm.	Mean mm.	No. per 100 sq. cm.	Range mm.	Mean mm.
North slope	0·8	0	—	—	0	—	—
	1·7	0	—	—	—	—	—
	2·2	6	2·0–3·2	2·6	—	—	—
	2·6	11·5	2·0–3·2	2·4	61	2·0–4·7	2·7
[E.H.W.S. 2·72]							
Top	3·0 *A*	6·5	2·0–5·9	3·3	27	2·0–4·4	2·6
	B	23	2·3–6·2	3·7	37	2·6–6·5	4·3
	C	83	2·0–5·9	3·0	14	2·6–7·1	5·0
	D	109	2·0–3·8	2·5	56	2·3–4·4	3·1
[E.H.W.S. 2·72]							
South slope	2·6	134	2·0–4·5	2·7	70	2·0–5·0	3·0
	2·2	59·9	2·0–3·8	2·4	—	—	—
	1·7	27	2·0–3·2	2·3	—	—	—
	1·3	6	2·0–2·6	2·3	17·5	2·0–2·9	2·4
	0·8	6	2·0–2·6	2·2	—	—	—
[M.S.L. 0]							
	−0·1	2	2·0–2·6	2·3	—	—	—
	−0·6	0	—	—	—	—	—
"Wet" stations							
Top	3·0 *A*	13·2	2·0–7·7	4·5	8·6	2·0–7·1	3·5
	B	54	2·0–6·8	4·6	19·2	2·3–8·0	5·1
	C	33·1	2·0–7·4	4·5	33·85	2·9–7·7	5·3
	D	20·8	2·0–6·8	3·8	44·2	2·3–6·8	4·1

E.H.W.S. = extreme high-water springs; M.S.L. = mean sea-level.

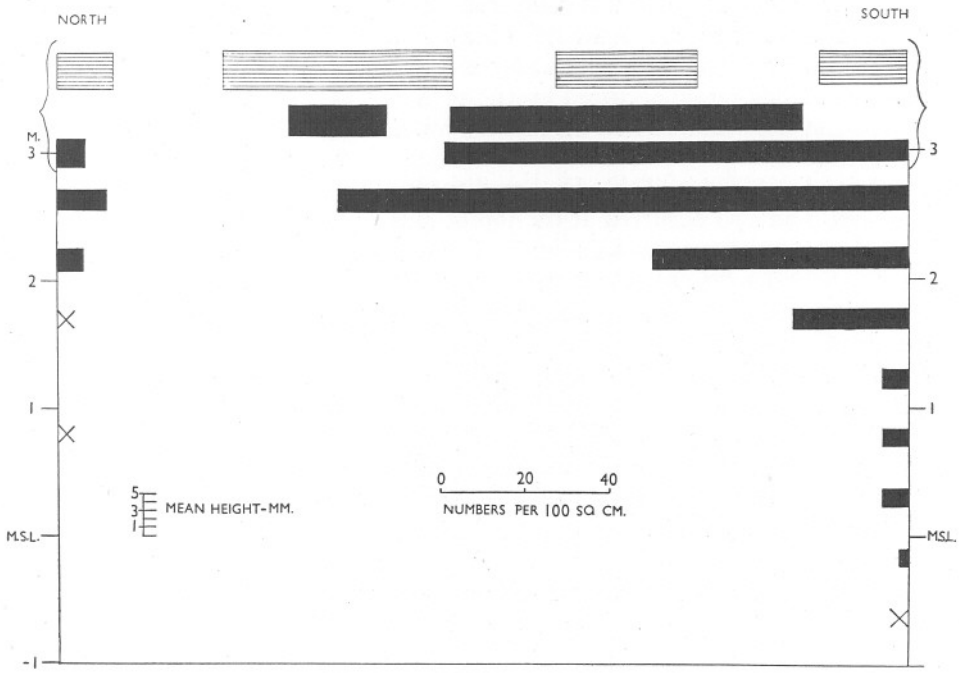

Fig. 2. Numbers of snails per 100 sq. cm. at different levels on the Breakwater in traverse A. Those collected from "dry" stations are shown in solid blocks, and those from the pools in horizontally ruled blocks. The height of the blocks shows the average height of the snails at each station. The eight bracketed samples were all taken across the top of the Breakwater, 3 m. above mean sea-level (M.S.L.).

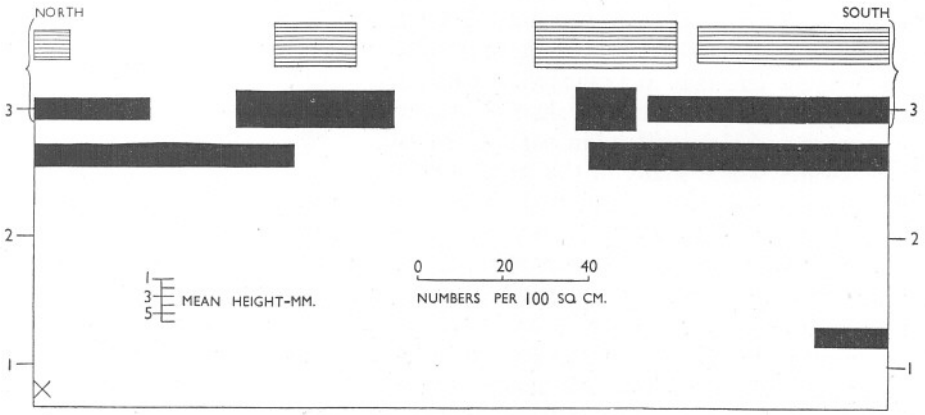

Fig. 3. Numbers of snails per 100 sq. cm. in traverse B. Explanation of blocks as in Fig. 2.

The height of the shell was measured with a pair of sliding callipers with a 0·1 mm. Vernier scale. Snails less than 2 mm. in height are included in the 2 mm. groups owing to the difficulty of measuring them with any degree of accuracy. They rarely occurred except at the lowest levels.

The traverses showed that the snails were most abundant towards the top of the southern slope just below extreme high-water springs, i.e. 2·6 m. above mean sea-level (Fig. 2, Table I). Small snails were found 0·15 m. below mean sea-level, and also occurred at the top of shelter blocks (not included in the traverses) 5 m. above mean sea-level. Colman (1933) found that at Wembury they occupied a zone of only 2·72 m., extending vertically from about 1·25 m. above extreme high-water springs down to mean high-water neaps. The zone occupied on the Breakwater is therefore of considerably greater vertical extent than at Wembury, but it is possible that the small snails at the bottom of the zone were overlooked in the latter locality as they usually shelter amongst the barnacles and are difficult to find. Owing to the high degree of exposure on the Breakwater all the snails are within the splash zone at least during the winter months, when, owing to the heavy swell, the sea washes over the top twice a day at high tide.

Relation to Ecological Factors

Light

The habitats selected are very variable with respect to light. It has already been noted that on the Breakwater the population is most dense almost at the top of the southern slope where the maximum amount of sunlight falls. During the winter the top of the Breakwater is covered with a fairly dense layer of algae, which retains moisture and gives a certain amount of shelter. During the summer, however, algal growth is negligible, and the snails have to endure prolonged exposure to the sunshine. At Tinside, Plymouth, they are common in crevices on the southern slopes, but also underneath overhanging rocks at the entrance to a cave where there is no direct sunlight. They occur in equally exposed and equally shaded situations on Drake's Island, and also at Crantock and Kelsey Head in north Cornwall. Furthermore, on the top of the Breakwater where many of the larger snails live in water in small cylindrical pits, they are equally distributed on all sides of these pits, and at all depths.

Flattely & Walton (1922), discussing the distribution of this species in Cardigan Bay, say that it occurs there in crevices just above high-water mark, which are not exposed to the midday sun, and that the same type of distribution occurs on the Devon coast. Colman (1933), however, found that at Wembury the snails "congregate not only in cracks or crannies where it is damp, but also in hollows which are quite dry and also directly face the sun". He goes on to remark that "they are always very loosely attached to the rock so that one can easily blow them off" and suggests that "the search for hollows and cracks is more an avoidance of the mechanical force of the wind than of

the desiccation caused by it". He refers to Fränkel's (1927) work on taxes in this species, which was found to be negatively geotactic, negatively phototactic when above a horizontal substratum, but positively phototactic when hanging from a horizontal ceiling. Colman concludes by saying that the resultant of these reactions would make the animals congregate round the entrance to fissures and in hollows, where, in fact, they are found in nature. Actually, Fränkel qualifies his remarks. He says (free translation): "However, this change in phototactic response occurs only in water. In air *Littorina* is negatively phototactic even when hanging from horizontal ceilings."

That these responses are highly modified under certain conditions in the field is obvious from the distribution of the snails on the Breakwater, and it seems likely that the concentration on the exposed sunlit slopes there may prove indicative of the general distribution of the species. The following observation by Fischer-Piette (1936, p. 248) is of considerable interest in this respect: "Il est curieux de voir cette espèce mieux réprésentée sur la côte anglaise que sur la côte française de la manche, étant donné que, par ailleurs, elle est particulièrement bien développée dans les régions plus méridionales telles que la Loire Inférieure, la côte basque, la Méditerranée."

Gravity

The distribution of the snails at different levels is set out in Figs. 2 and 3 and in Table I, and shows clearly that the smallest individuals are commonest at the lower levels and the larger ones at the upper levels.

The average size of the snails in the samples on the northern and southern slopes varied from 2·2 to 3·0 mm.; at the surface stations across the top from 2·5 to 5·0 mm.; and in the pools across the top (the "wet" stations) from 3·8 to 5·3 mm. The largest snail found on the slopes was 5·0 mm. high, and on the top 7·7 mm. Large snails occur in the deep crevices between the blocks where the water drains away as the tide goes down, but no estimate was made of their size or of the density of the population in such situations.

The distribution of the size groups suggests that the metamorphosing larvae settle in the *Chthamalus-Balanus* zone and that there is a gradual migration towards the higher and drier levels generally recognized as their typical habitat. Further evidence of upward migration in the field is given in the section dealing with spawning (p. 53, Table II).

In the laboratory when the snails are placed in water in a finger bowl they immediately crawl to the top; this reaction is sufficiently constant to be an efficient method of separating them from *Littorina saxatilis*, which is common in the lower part of the zone occupied by *L. neritoides*.

In the field this negatively geotactic response is sometimes reversed. Throughout most of the year the snails are evenly distributed on the vertical sides of the pits on top of the Breakwater. During the winter there is usually a swell sufficiently heavy to sweep over the top at high water, so that the water in the holes is constantly renewed. Under hot and dry conditions when tides

are low this does not happen, and evaporation causes a considerable increase in salinity. The snails then crawl up the sides and congregate in dense masses between the water level and the lip of the holes. When the water has been renewed they crawl down again. If these snails are collected and placed in water in glass finger bowls they give a negatively geotactic response and immediately crawl to the top of the bowls.

Moisture

A certain amount of moisture is essential for the survival of *L. neritoides*. First, the snails feed on minute algae that grow on the rocks, and they move about and feed only when the surface is moist; they are as active during rain as when they are submerged in sea water. Secondly, it is most unlikely that spawning occurs except when the snails are submerged; evidence supporting this is given later on.

That they live in very dry situations has long been known (Jeffreys, 1865; Forbes & Hanley, 1853). They are able to survive in situations at the top of their zone where they may not be reached by spray for months at a time. Patanè (1933) found that they were able to survive absence of moisture for at least 5 months, and that they regained their activity within a few minutes of being placed in sea water.

On the other hand, observations in recent years have shown that not only do they sometimes occur in shallow pools (Lebour, 1935), but that they are able to live in places where they are permanently submerged. When they are placed with small pieces of rock in sea water in finger bowls most of the snails remain on the projecting pieces, but a few of them crawl beneath the water and remain there. Dr H. B. Moore kindly gave me a few living specimens that he collected from old piles lying beside the pier at Plymouth, which had been submerged for at least a year, and ripe sex cells were present in both a male and a female that I dissected. Mr G. M. Spooner first drew my attention to the fact that on the Breakwater many of the snails live in water. When individuals collected from the pools there were marked with paint and replaced, 95 of 103 recovered a year later were still in the pools. The density of the population in water in the holes is very similar to that on the exposed rock surfaces (Figs. 2, 3, Table I); the most noticeable difference between the snails in the two situations is that the largest ones are more numerous in the holes. This is significant in view of the fact that no snails live in water in the holes on the slopes save just at the upper edge, so that none occurs in pools at levels where the smaller sizes predominate. Yet under laboratory conditions small snails are much less able to withstand emersion than are the large ones.

It is probable that the holes on top are inhabited mainly on account of the shelter from heavy seas that they afford and that the need for moisture plays little part in their selection. No other locality has been found in the Plymouth area where many snails live permanently in water. Fischer-Piette (1932) states

that at Cap Martin the species is abundant in holes above high-water mark. He notes particularly that there they are always to be found in the water despite great variation in the salinity.

One final point of interest with reference to moisture may be mentioned here. Fischer *et al.* (1933) have shown that the consumption of oxygen by *L. neritoides* is 5–6 times higher in water than in air.

Shelter

A suitable settling ground for the metamorphosing larvae of *L. neritoides* is afforded by populations of *Chthamalus stellatus* and *Balanus balanoides*. The presence of abundant fucoids appears to be inimical to the larvae. Hatton & Fischer-Piette (1932) state that on rocky shores the absence of these algae indicates high wave exposure, and that their abundance is proportionate to the degree of shelter available.

At the head of Crantock Bay, north Cornwall, cliffs rise from a sandy beach which is exposed for several hours at low tide. *Littorina neritoides* is not abundant there except on rocks where barnacles are present. Fucoids are absent. The mollusc is scarce on the west side of the bay where there are slopes of broken rock and these algae are fairly abundant. At the end of June 1939, a similar type of distribution was found in Northern Ireland. East of Whitepark Bay in County Antrim there is a limestone cliff at the foot of which the snails are so scarce that in 5 min. search only six were collected. A shelf of low boulders extends seawards for 20–30 yards from the foot of the cliff, and is covered with a mat of fucoids so dense that it is extremely difficult to walk across it. At the edge of the shelf there are larger limestone boulders, 2–4 ft. high, which are bare of *Fucus*, and beyond them the water deepens and *Himanthalia* and *Laminaria* are abundant. On these larger boulders there is a dense population of the snails, and *Balanus balanoides* (kindly identified by Dr H. B. Moore) is fairly common. *Littorina neritoides* was also abundant and very conspicuous on finely pitted white limestone boulders in a very wave-beaten bay, Larry Ban, west of Carrick-a-rede, where there was no appreciable algal growth above the *Laminaria* zone. It was, however, scarce on smooth-surfaced limestone rocks in a very exposed position east of Ballintoy Harbour. Barnacles are common and fucoids very sparse on the Plymouth Breakwater where the snails are very abundant.

Dr H. B. Moore has very kindly supplied me with notes (Appendix) on some localities in Scotland where he has searched for *Littorina neritoides*; these notes support my conclusions that the presence of the species is positively correlated with a high wave exposure and the presence of barnacles, and negatively correlated with abundant fucoids.

Kitching (1935) says "the absence of *Balanus balanoides* from the immediate neighbourhood of fucoids is almost certainly due to the rubbing of the fronds, which might either prevent the larvae from settling, or damage the

young barnacles", and Moore & Kitching (1939, p. 525) consider that the distribution of *Chthamalus* is affected in the same way.

It has already been observed that the small snails are able to survive emersion for a much shorter period than are the large ones. They are negatively geotactic and gradually migrate towards the top of the zone, apparently in their search for shelter. The large snails are able to withstand very dry conditions. Where, on the Breakwater, the highest and driest level available does not afford the maximum amount of protection some snails have become positively geotactic, and live permanently in water.

Spawning

The Spawning Season and its Duration

Samples of *Littorina nerotoides* were dissected at different times of the year and the state of the gonads determined. Males are defined as *unripe* when the spermatozoa were present only in bundles, *ripe* when active spermatozoa were present either alone or with bundles, and *spent* when no spermatozoa, either alone or in bundles, could be distinguished. Females are defined as *unripe* when oocytes alone or with all stages of developing eggs except ripe ones were present, as *ripe* when ripe eggs were present perhaps in addition to large numbers of unripe ones and oocytes, and as *spent* when there were no eggs, or very few, either ripe or unripe. It appears that infection with some trematode parasites produces sterility, so that individuals in which unencysted cercariae occurred are not considered here although they formed a considerable part of some samples. The snails examined were all collected from the top of the Breakwater, and most of them were taken from the pools or their immediate vicinity.

In samples containing 39, 74 and 62 normal males, collected on April 30, June 10 and July 30 1937, respectively, 85, 100 and 79 % were spent, but by mid-September active spermatozoa were present in 90 % of those examined (Fig. 4). Nearly 100 % were ripe in samples examined in October, December and January. In early March a few spent males were found, and by May and June their numbers had risen to 67 and 93 %, respectively.

Egg production is at a minimum during June, July and August (Fig. 5). In mid-September 1937, more than half the females examined contained oocytes or unripe eggs. Ripe eggs were found in 60 % of those examined in December, and in 50–60 % in January, March and May 1938. Although the percentage of ripe females did not exceed 63 in any sample examined in 1937–8, it rose to 73 and 76 in February and March 1936.

The spawning period thus lasts altogether for about 8 months, that is, from September to April. The sea temperature (Fig. 1) drops from 15·2 to 8·0° C. and rises again to 9·2° C. during this period; the corresponding figures for the air being 14·4, 6·2 and 8·8° C.

Linke (1935), working on material from Rovigno and Majorca, says that the maximum development of the whole genital apparatus in this species is

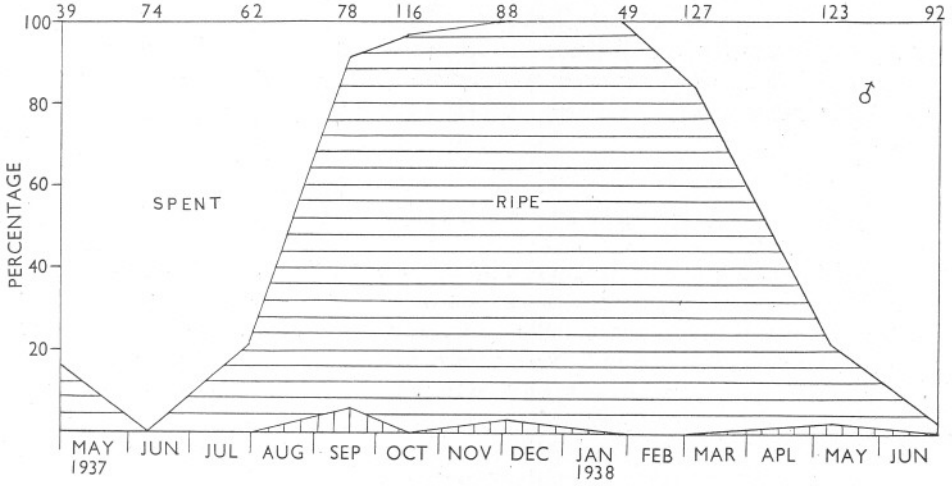

Fig. 4. Percentages of unripe, ripe, and spent males in samples examined every 4–8 weeks from May 1937 to June 1938. The upper figures show the numbers of snails in each sample.

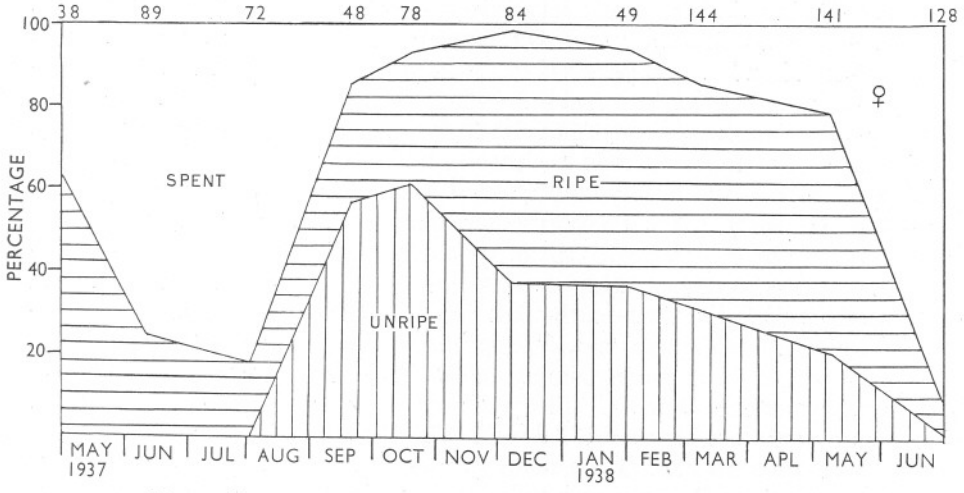

Fig. 5. Percentages of unripe, ripe, and spent females as in Fig. 4.

attained in the spring, but he does not give the size of the samples with which he worked.

An interesting point that emerged from the above dissections is the difference of more than two months in the maximum production of ripe sperms

and ova. Moore (1937, p. 733) found that in *L. littorea* the males were ripe about a month earlier than the females, and that the breeding season of this species in the Plymouth area lasted from November to June. *L. saxatilis* breeds all the year round (Lebour, 1937, p. 127). In other localities *L. littoralis* usually breeds from the spring to the autumn (Pelseneer, 1935, p. 452; Linke, 1933), but there is a considerable fluctuation, depending on the temperature, in the breeding period of this species.

Experiments on possible Spawning Migration

Field experiments on migration were carried out by marking the snails with a cellulose paint. If conditions permit the paint should be renewed after 6 months, but this was not actually done. Although a certain amount of wear occurred, some marked snails were conspicuous even after 12 months on the Breakwater: on other snails so little paint was left that they were very difficult to find. This applies particularly to the smaller sizes. Sometimes the snails were painted in situ; at other times they were brought into the laboratory, painted and replaced on the rocks the following day, or sometimes later.

On December 13 1935, two lots of 50 and 200 snails on the rocks at Tinside, Plymouth, were marked in situ with red paint. They occupied zones the lower limits of which were (A) 0·14 and (B) 0·16 m. below M.H.W.S. A month later 44 and 192 individuals respectively were recovered, and only one of these was found below the original zone. On January 24, 222 of these marked snails were placed in a horizontal cleft about 1 m. below the levels A and B. A fortnight later none could be found below these levels. The snails had crawled at least a metre up the rock face, and although they were not counted the marked population was approximately as dense as previously.

On Drake's Island, in Plymouth Sound, in an exposed position above some rocks on the shore, there is a rectangular concrete block approximately 77 cm. high, and 45 by 46 cm. broad; the top of the block is 2·74 m. above mean sea-level. The aspect is roughly south-south-east by north-north-west. On February 4 1936 the west-south-west face was divided into four equal horizontal zones. In the top one, A, 100 snails were painted red, and in the bottom one, D, 100 were painted yellow. No snails were painted in the intermediate zones, B and C. The positions of the snails recovered after 1, 2 and 12 months are shown in Table II. These recoveries show that there is a pronounced tendency for the snails to move upwards, and that only a very small proportion of them move more than a few centimetres in the opposite direction.

In a more sheltered area on Drake's Island where, on January 27 1936, 100 snails were marked with red paint, 67, 48, 49, 47 and 22, respectively, were recovered at their original level when recounts were made on February 4, March 5, April 27 and August 5 1936, and in February 1937. Whenever

recounts were made the surrounding rock surfaces were carefully examined, but although the red paint made the snails very conspicuous they were found only once or twice at more than a few centimetres from their original situation.

TABLE II. RECOVERIES OF MARKED SNAILS ON CONCRETE BLOCK, DRAKE'S ISLAND

Date	Colour	No. recovered	Percentage in zones		
			A	B and C	D
4. ii. 36	Red	—	100	0	0
5. iii. 36	,,	77	92·2	7·8	0
5. iv. 36	,,	51	78·5	19·6	1·9
– ii. 37	,,	5	100	0	0
4. ii. 36	Yellow	—	0	0	100
5. iii. 36	,,	69	0	79·8	20·2
5. iv. 36	,,	44	25·0	52·3	22·7
– ii. 37	,,	13	100	0	0

The results of these experiments make it unlikely that there is any downwards migration for spawning as suggested by Lebour (1935, p. 375); and Jeffreys (1863, p. 354) says of the snails, "they have never been observed to go to the sea when the tide comes in".

Occurrence of Egg Capsules

In order to determine when the egg capsules were present in the plankton tow-nettings were examined daily, as far as possible, from November 29 1935 to May 1 1936. The capsules were fairly common at times during the winter and spring in tow-nettings taken by the M.B. *Gammarus* in the Sound, but occurred so rarely in those taken by the S.S. *Salpa* beyond the Sound that the latter were not examined after February 4 1936. The internal diameter of the hoop supporting the mouth of the tow-nets was 45 cm. The capsules, which vary at the height of the breeding season from 0·162 to 0·225 mm. in diameter with an average of 0·205 mm., were not taken in the coarse tow-nets, with a mesh of 26 strands of silk to the inch (25·4 mm.), and very rarely in the medium, 50 strands to the inch, but were commonest in the fine and very fine nets with 100 and 180 strands to the inch, respectively. At first the "*Gammarus*" nets were arranged so that the very fine net was at the surface, the fine at a depth of 2 fathoms, and the medium at 6–8 fathoms. Most of the capsules were then taken at 2 fathoms. The medium net was replaced in March by the very fine net, and capsules were then taken at 6–8 as well as at 2 fathoms. It is obvious that the numbers of capsules collected from the tow-nettings, which were taken in several different places in the Sound and independently of the state of the tide, are not strictly comparable amongst themselves and have no direct relation with samples which were collected from the Breakwater. (In the latter situation water was pipetted from the bottom of seventy holes and about two breffits were filled at each sampling.)

The capsules were found to sink at the rate of 150 mm. in 109–203 and 271–514 sec. at temperatures of 15·5 and 10·0° C. Linke (1935) observed that they sink in still water but tend to remain suspended when it is agitated. This property was useful in separating them from the tow-nettings, which were strained through coarse muslin into a cylinder and left to settle for about half an hour. Most of the water was then gently siphoned off, and the capsules collected from the residue.

The total number of capsules collected, together with some of the factors that may influence spawning, are shown in Fig. 6. If no downwards migration takes place the possible immersion of the snails living above extreme high-water springs would depend on the phase of the moon and the corresponding tides, the direction and force of the wind, and the state of the sea. In Fig. 6 full and new moons are shown by white and black circles, respectively; the predicted tidal heights are given, and those more than 15 ft. above Admiralty Datum are blacked in; the state of the sea is scaled according to the meteorological charts issued by the Air Ministry; onshore and offshore winds tending to raise and depress the predicted tidal levels are shown by arrows pointing upwards and downwards respectively, and where the force of the wind exceeded 3 on the Beaufort scale double barbs have been used. The solid columns show the numbers of egg capsules collected from the tow-nettings in the Sound, and those which are cross-hatched the numbers from the Breakwater samples. The blanks in the base-line show the days when no samples were taken.

Notes on the stage of development of the capsules in some of the samples are given in Table III.

TABLE III. NOTES ON THE STAGES OF DEVELOPMENT OF SOME OF THE EGGS COLLECTED FROM THE TOW-NETTINGS AND BREAKWATER SAMPLES

Date	Locality	No. capsules	Remarks
9. iii. 36	Jennycliff Bay	62	All were undergoing the first or second cleavage
10. iii. 36	Breakwater	75	Most of these had not completed the first cleavage
19. iii. 36	,,	5	All were in different stages of development
23. iii. 36	Jennycliff Bay	52	Embryos with 2–32 cells were present
24. iv. 36	Breakwater	800	Many had not begun to segment and none had passed the first cleavage
31. iv. 36	Jennycliff Bay	46	At a depth of 6–8 fathoms there were 31 embryos of 32–64 cells, and at 2 fathoms 15 with 2–4 cells. Some of the eggs were abnormally small, 0·126–0·144 mm. in diameter, and were segmenting irregularly
1. v. 36	Breakwater	38	There were 2 embryos with 4 cells, 23 with 2 cells, and 14 in which segmentation had not begun

In the five months during which samples were taken there were five periods when more than 50 egg capsules per set of samples were obtained, and four of these coincided with sets of high tides. The apparently exceptional sample,

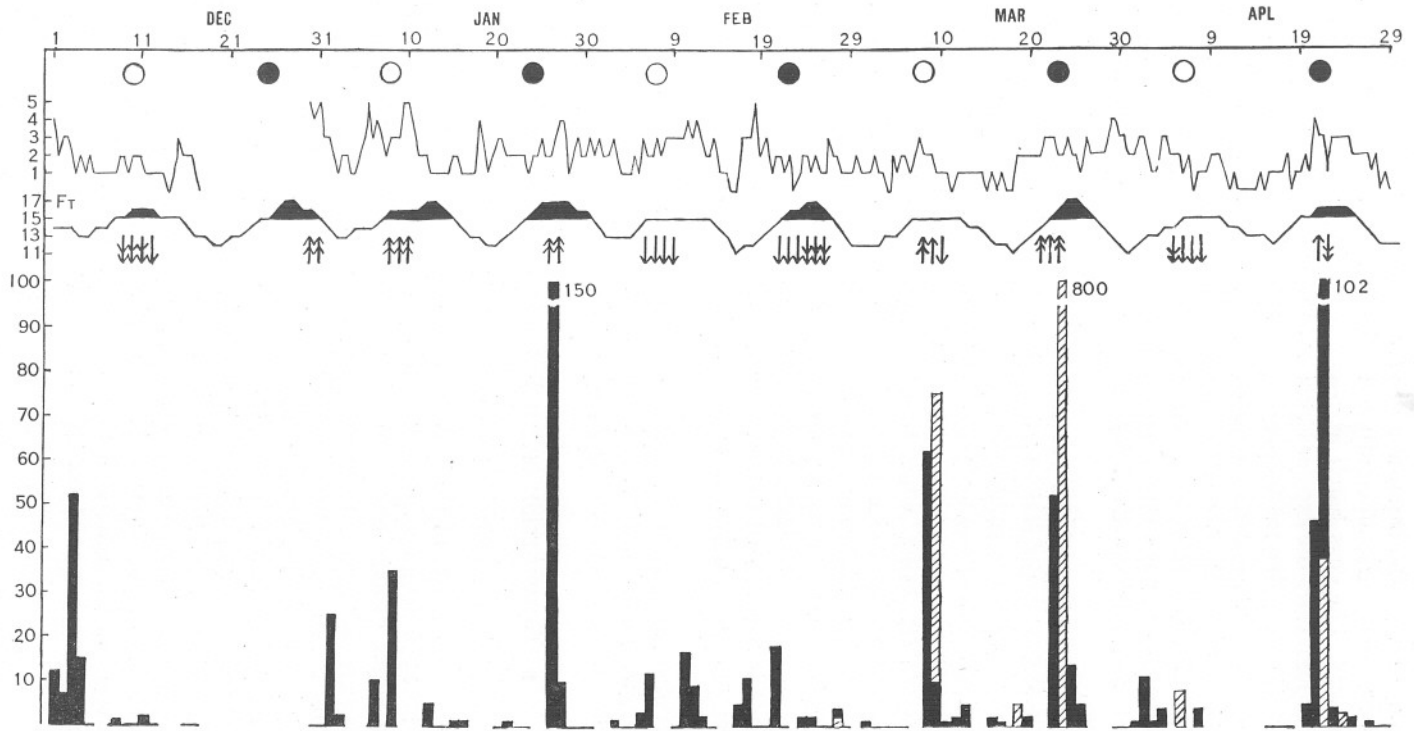

Fig. 6. Abundance of egg capsules of *Littorina neritoides* together with factors affecting the height of the tides and the moisture of the splash zone. The state of the moon is indicated by open and black circles. The upper continuous line shows the state of the sea. The lower continuous line shows the predicted height above Admiralty Datum of high tide, the highest for each day being plotted; heights above 15 ft. are blocked in. The arrows indicate onshore (upwards) and offshore (downwards) winds. For details see text, p. 54. The solid columns show the numbers of egg capsules collected from tow-nettings in the Sound; the cross-hatched columns show numbers collected from Plymouth Breakwater. Blanks in the base line indicate days when no observations were made.

taken in Cawsand Bay at the beginning of December, contained a large proportion of capsules that were sufficiently old to have been spawned during the previous high tides. The eggs hatch in 7–8 days in the laboratory. During five other sets of high tides the capsules were not found in any quantity, but it is probable that the prevailing meteorological conditions lowered the predicted tidal levels, and prevented spawning except in those adults living in the lower part of their zone. When the water in the Sound is calm, as often happens when there is a light wind from the north, even if the tide were sufficiently high to submerge those in the upper part of the zone it is probable that the capsules are not readily dispersed and are therefore less likely to be collected in the tow-nettings.

The strongest indication of the presence of a fortnightly rhythm in the spawning habits of this species is shown by the Breakwater samples. Although many of the snails there live permanently in water, egg capsules were abundant in only three out of seven sets of samples that were examined, and these three were taken when the moon was new or full. This is of particular interest, as during the winter and spring, when breeding takes place, the sea usually sweeps over the Breakwater twice a day. In these samples, as well as in the tow-nettings, when the capsules were plentiful they were usually at the same stage of development. Full notes on the incidence of these stages were not kept, but a few are given in Table III. They suggest that the onset of major spawning periods is determined by some stimulus in addition to immersion. Lunar periodicity has been shown to occur in many other species of Molluscs (Pelseneer, 1935).

Linke (1935) observes that in the spring the egg capsules of *Littorina neritoides* were fairly abundant in the neritic plankton in the Mediterranean, but he does not refer to the presence of any spawning rhythm there.

Composition of the Population

Incidence of the Size Groups

The material for this part of the investigation was all collected from the Breakwater. The 1936 samples included snails from the southern slope, so that there is a larger proportion of small snails in these than in the 1938 samples, which were all taken from the top and mostly from the pools or their immediate vicinity. The snails were measured with sliding callipers with a 0·1 mm. Vernier scale, and are grouped in 0·3 mm. series (Fig. 7).

The largest sample, measured in July 1938, consisted of 7796 snails; those averaging 4·1, 5·0 and 5·9 mm. in height occurred with the greatest frequency. Snails of 5·0 and 5·9 mm. also predominated in smaller samples collected in March and May 1938, and were conspicuous in the 1936 samples. The 5·9 mm. group is less obvious in the June 1938 sample, where the sizes were more evenly distributed, but predominated in the October sample. Snails in the 4·1 mm. group, so conspicuous in the July sample, are noticeable in only one

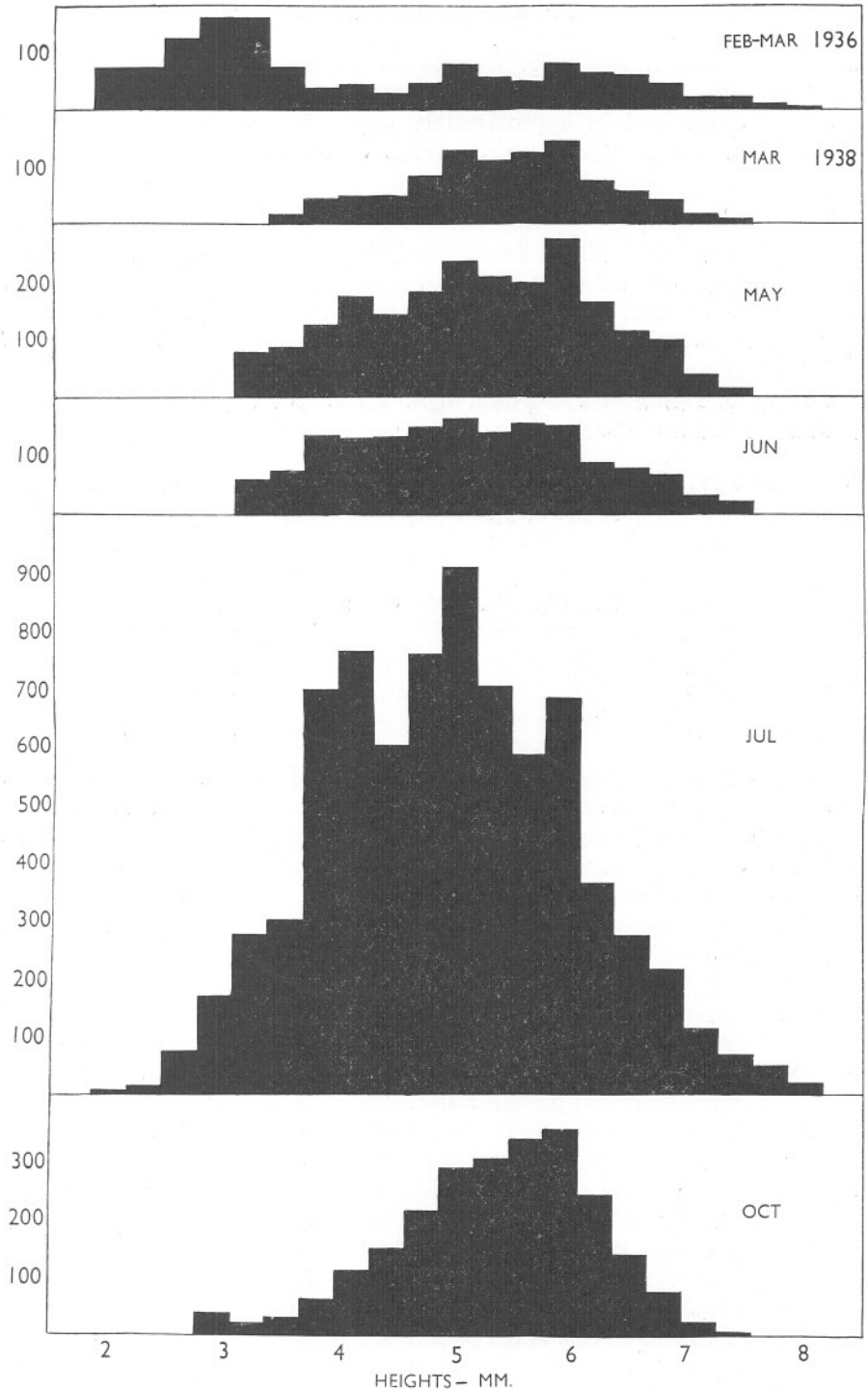

Fig. 7. Numbers of snails in 0·3 mm. size groups in random samples collected from the Breakwater in February–March 1936, and from March to October 1938.

other sample, that of May 1938. In spite of these variations in the incidence of the size groups there appears to be a tendency for the larger snails to fall into size groups separated by approximately 1 mm., but whether these actually represent successive annual broods remains uncertain.

Growth Rate and Sex Ratio

Of 2107 measured snails in five selected size groups, marked with red and yellow paint and replaced on the Breakwater in July 1938, only 102 were recovered a year later. The results of this experiment are shown in Table IV. It will be seen that the growth-rate decreases with age, and is very slow in snails of 6·0 mm. or more. It is probable that those of 8–10 mm. are many years old. The largest one found was 10·4 mm. high. It has been deposited in the British Museum of Natural History.

TABLE IV. GROWTH-RATE AND PARASITES IN MARKED MATERIAL, JULY 1938 TO AUGUST 1939

Height mm.	No. snails marked	No. snails recovered	No. males	Average increase in height mm.	No. infected with Cercaria B and C
3·9–4·0	545	1	0	0·6	0
4·9–5·0	732	38	7	0·48	22
5·8–5·9	448	26	5	0·26	17
6·0	238	9	2	0·14	8
6·8–6·9	144	28	2	0·06	26

The proportion of males is significantly higher in the smaller size groups than in the larger ones (Fig. 8), and the ratio is similar even when only unparasitized ones are considered. This may be due to a differential growth-rate such as Moore (1937) found in *L. littorea*, where the growth-rate is greater in females than in males.

Moore found that on Drake's Island *L. littorea* reached a height of about 14 mm. in the winter of its first year, and 17·4, 22·4, 25·4, and 27·3 mm., respectively, in the second, third, fourth and fifth years. It may grow to a height of 36 mm., that is, about two and a half times the height reached in the first year. In *L. neritoides* the results obtained indicate a comparable steady decrease in the growth-rate. It can also be said that the values of annual increments were such that growth must normally extend over several years.

It has to be noted that many of the snails in this experiment were found to harbour cercarial infections of trematode parasites (dealt with on pp. 59–64). Since Rothschild (1936, 1938*b*) has found that such infections stimulate growth in *Peringia ulvae*, their presence cannot be ignored when the question of growth-rate is being considered. The number of snails infected is therefore included amongst the data in Table IV. The proportion of infected specimens increases with the size of the snail, until in the largest group only two out of the 28 were found to be free of the parasites. The data as they stand do not, on

first inspection, suggest that the parasites stimulate growth; but no conclusion can be drawn, since the real information required, namely comparison of growth-rates of infected and *uninfected specimens of the same initial size*, is not available.

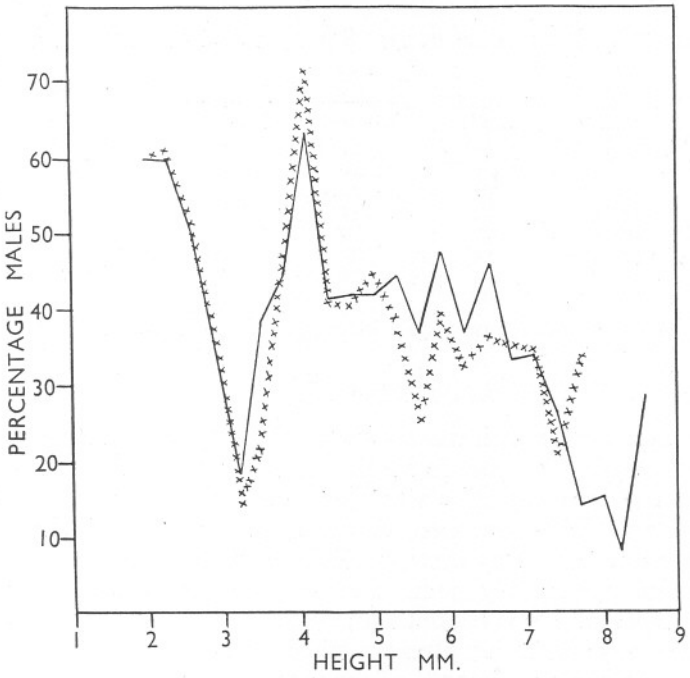

Fig. 8. Percentages of males in 0·3 mm. size groups. The continuous line shows the percentage in parasitized and unparasitized snails, and the crossed line the percentage in unparasitized snails only.

Trematode Parasites

Total Percentage Parasitism

The incidence of trematode parasites was recorded in the snails used for determining the state of the gonads at different times of the year (p. 50), comprising a total of 1270 males and 1779 females. A few samples from localities other than the Breakwater were also examined (Table VI, p. 64).

Three larval trematodes occur fairly frequently in *L. neritoides* on the Breakwater. Their systematics have not been investigated, and throughout this paper they are referred to by letters.

Infections with Metacercaria A, and Cercaria B and C occurred throughout the year, but were significantly higher in the sample examined in July 1937 (Table V) than in any other examined between April 1937 and June 1938.

The percentage of parasitism with all species rose steadily from 3·3 in snails averaging 2·0 mm. in height, to 99·8 in those of 8·8 mm. and over. The relative numbers of cercariae, both free and encysted, in the different size groups are shown in Fig. 9.

TABLE V. PARASITISM IN THE SAMPLE EXAMINED IN JULY 1938

Height mm.	No. of snails	No. parasitized		
		Observed	Expected*	Difference
5·0	20	11	10	1
5·3	24	20	13	7
5·6	30	22	18	4
5·9	42	31	26	5
6·2	22	20	15	5
6·5	32	26	23	3
6·8	37	32	28	4
7·1	20	15	16	−1

* From the mean incidence of parasitized specimens in the material as a whole.

Incidence and Effect of Metacercaria A

This metacercaria, which was always found encysted, occurred in 3·3 % of the snails averaging 2·0 mm. in height, and in 87 % of those of 8·3 mm. or more. The degree of infection with this species also increased in the larger snails (Fig. 10). Infections were classed as light, medium or heavy, when 1–6, 6–25, or more than 25 cysts, respectively, were found in any one snail. These criteria were slightly modified in the largest and smallest sizes. Sometimes the whole spire was packed with cysts.

The males were more heavily parasitized than the females by this species (Fig. 11), and altogether 60·35 % of the former and 52·7 % of the latter were infected. Snails containing no other larval trematodes account for 47·6 and 28·7 % of the total, respectively, and the remaining 12·75 % of the males and 24·0 % of the females were infected with Cercaria B (Fig. 9, and p. 61). There is a thus a reversal of the ratio of infection in the sexes, which may be due to some physiological disturbance caused by Cercaria B. This trematode usually causes sterility, and the sterile males are apparently less attractive to metacercariae about to encyst.

The mere presence of these metacercariae does not affect the seasonal development of the gonads; both males and females containing cysts produced ripe sex cells at the same time as uninfected snails. From September to April, inclusive, that is, during the breeding season, the percentages of snails with unripe, ripe and spent gonads were, respectively, 12·3, 60·0, and 27·7 in 65 snails with heavy infections, and 13·8, 77·8 and 8·2 in 152 with medium infections. The higher percentage of spent snails in those with heavy infections may include a number that were sterile, and it is quite probable that the normal development of the gonads may be inhibited through the resulting pressure when the spire is packed with cysts.

Incidence and Effect of Cercaria B

Cercaria B belongs to the *Ubiquita* Group. It was less common in the smaller size groups than Metacercaria A (Fig. 9). Infections with this species

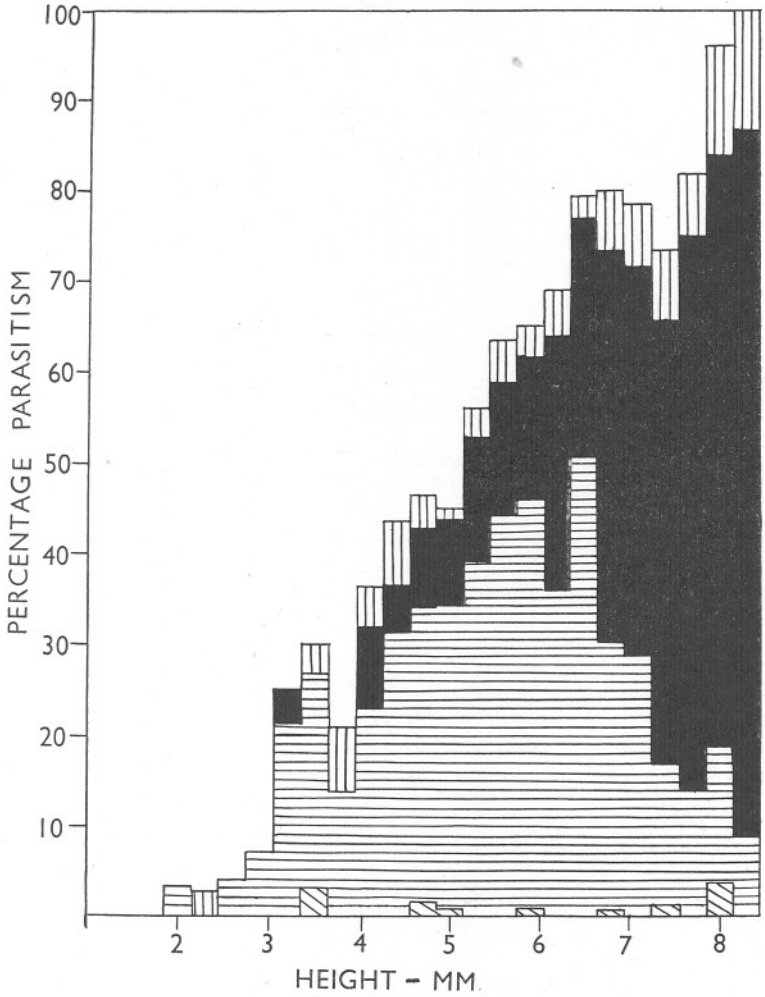

Fig. 9. Percentage parasitism in 0·3 mm. size groups (both sexes). The species of trematode larvae are indicated as follows: Metacercaria A, horizontal shading; Cercaria B, vertical shading; A plus B, solid blocking, C, diagonal shading.

were nearly always heavy, and large numbers of both sporocysts and active cercariae were usually present. Infections with this species occurred in 14·65% males, and 29·7% females, the relative difference between the sexes being much greater than in infections with Metacercaria A when total

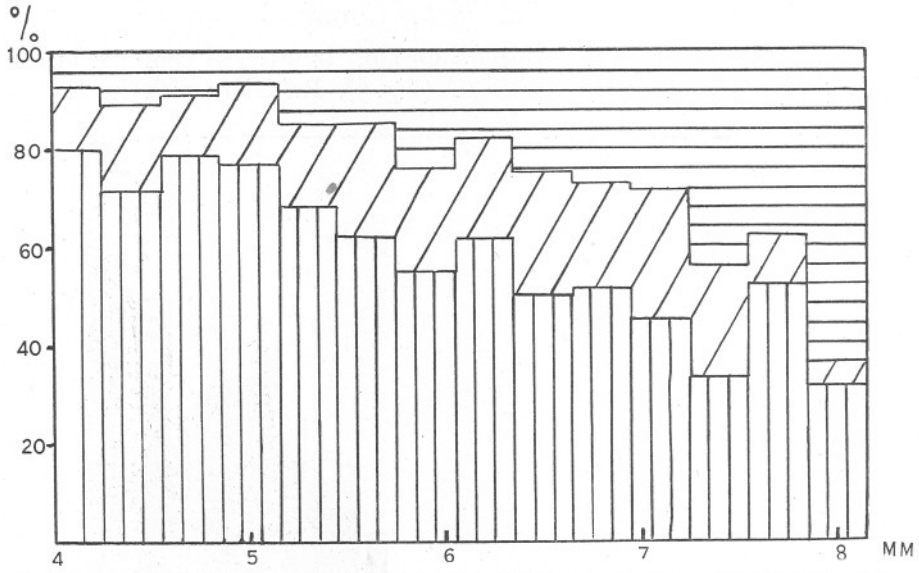

Fig. 10. Grades of infection with Metacercaria A in 0·3 mm. size groups. Vertical shading = light, diagonal = medium, and horizontal = heavy infections.

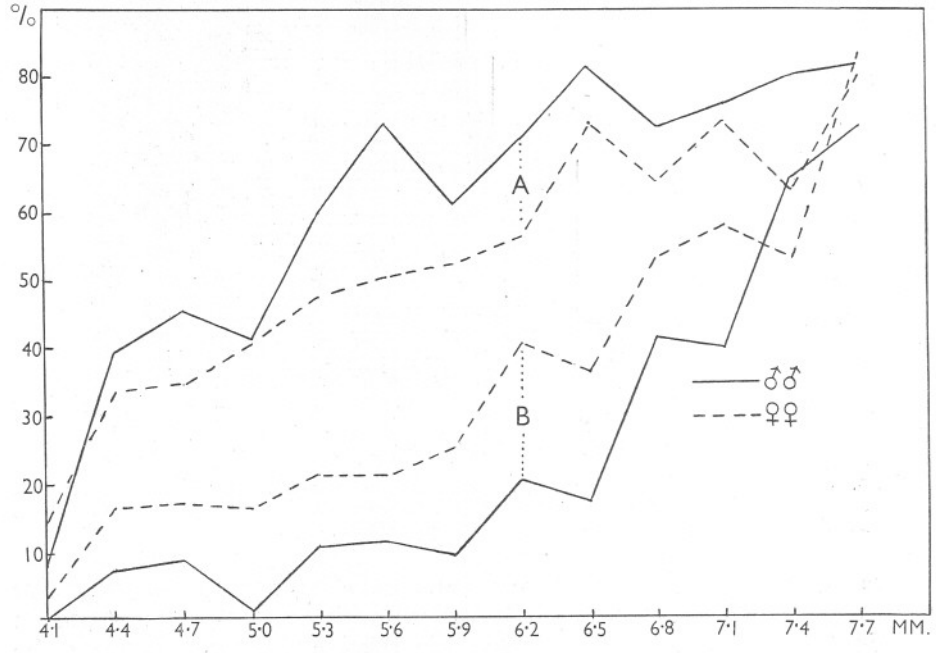

Fig. 11. Differential infections of males and females with Metacercaria A and Cercaria B.

infections are considered. The presence of Metacercaria A together with Cercaria B scarcely alters the ratio of the infections with the latter species in male and female snails, lowering it by only 1·8 % in the males and 5·7 % in the females.

During the breeding season sex cells were found in only 1 out of 86 males, and 8 out of 292 females infected with Cercaria B, so that without doubt this species usually causes sterility.

The differences in the infections of the sexes with Metacercaria A and Cercaria B are of particular interest, as male Gastropoda are usually more heavily infected than females (Pelseneer, 1928). Rothschild (1938*b*), who discusses the question in some detail, found that this was so in *Peringia ulvae*, which is a heavily infected species. Total infections have generally been considered, and it is possible that, when the incidence of separate species of trematodes has been worked out, differences such as occur in *Littorina neritoides* will prove to be common.

Incidence and Effect of Cercaria C

Cercaria C, which is closely allied to *Cercaria emasculans*, was comparatively rare and was found in only 2·23 and 2·81 % respectively of the male and female snails examined. During the breeding season 3 out of 10 infected males and 8 out of 15 infected females were sterile; these numbers are obviously too small to give any indication of the effect of this trematode on the host. Cercariae and sporocysts were both abundant in the infected snails.

Double Infections. The total number of snails infected with Cercaria C was 78; 13 of these contained Cercaria C alone, 45 Cercaria C together with Metacercaria A, and 20 Cercaria C together with Cercaria B. These last 20 infected snails were all sterile. I have followed Cort *et al.* (1937) in considering these last-mentioned as true double infections and distinct from examples in which encysted metacercariae occur with active larval forms. In these double infections both types of cercaria, B and C, appeared equally active. As the total percentage infections with these trematodes were 23·3 and 2·5, respectively, the expected mean number of double infections in the 3019 snails examined is $17{\cdot}5 \pm 4{\cdot}2$. As 20 double infections were observed there does not seem to be any mutual antagonism between these trematodes, such as Sewell (1922) has postulated for some species.

Cercaria D

This larval trematode, which belongs to the *Yenchingensis* Group (Rothschild, 1938*a*) was found only once. Active cercariae and rediae, together with a fair number of cysts of Metacercaria A, were present in a female snail 5·8 mm. high, collected at the beginning of May 1938. No eggs or oocytes were present.

Sex Reversal

There is no evidence that sex reversal occurs in *Littorina neritoides*. The penis diminishes greatly in size in males infected with Cercaria B, but this reduction is no greater than the reduction in non-breeding males during the summer months, and is certainly not comparable with that found by Rothschild (1938*b*) in *Peringia ulvae*.

Incidence of Trematode Parasites in other Localities

Metacercaria A was found in snails from Kelsey Head (north Cornwall), Drake's Island, and in two localities in County Antrim, Sheep Island and the Giants' Causeway. Cercaria B was found in those from Kelsey Head and Sheep Island; and Cercaria C in those from the Giants' Causeway. Notes on the samples from these places and from others where no parasites were found are summarized in Table VI.

TABLE VI

Locality	Date	No. of snails examined	Range of heights mm.	No. of snails infected with cercariae		
				A	B	C
Crantock	30. xii. 35	7	4·3–6·0	0	0	0
,,	14. iv. 36	90	4·6–6·0	0	0	0
Kelsey Head	26. xii. 37	25	4·9–7·2	8	5	0
Rum Bay	10. xii. 35	26	1·9–5·4	0	0	0
Drake's Island	4–20. ii. 36	55	2·8–7·2	11	0	0
Tinside, Plymouth	23. i. 36	100	2·5–6·0	0	0	0
Sheep Island	26. vi. 39	60	5·5–6·9	11	2	0
Giants' Causeway	28. vi. 39	56	4·3–6·6	6	0	2
Gwbert (Cardigan)	8. viii. 39	19	3·4–5·7	0	0	0

All the snails in which parasites occurred were collected from rocks rising steeply from the sea with a high degree of exposure.

Presence of possible Alternate Hosts

Kelsey Head is opposite a small island, the Chick, frequented by gulls, shags and cormorants. Sheep Island is a breeding ground for a large colony of puffins, and numerous razorbills, guillemots and gulls. The rocks there were so bespattered with droppings that a high degree of parasitism might have been expected, but trematodes were quite scarce in the small sample of snails that was examined.

The Breakwater is a resting place for large numbers of several species of gulls (*Larus* spp.) and, less regularly, of flocks of curlew (*Numenius a. arquata*). A flock of about 30 purple sandpiper (*Calidris m. maritima*) overwinters there, and oyster catchers (*Haematopus ostralegus*) occur regularly except in the nesting season. The only invertebrate that is comparable in abundance with *Littorina neritoides* is a small harpacticid copepod which is very plentiful in the pools along the top.

Conclusions

The observations described show that in the Plymouth area *Littorina neritoides* only spawns when it is submerged. The population is concentrated about the level of extreme high water springs, and the snails do not migrate downwards, so that except in severe storms spawning can only take place at the fortnightly spring tides. Furthermore, spawning is confined to the winter months when tidal levels are likely to be raised by stormy conditions.

The choice of the very dry habitat usually regarded as typical seems to be of doubtful value for a species with pelagic egg capsules. It is probable that it is primarily the need for shelter from the force of the waves that brings about the steady migration to the dry rocks at the top of the zone, and that except for the requirements of spawning the presence or absence of water is only of secondary importance for the adults.

Evidence is given which suggests that the larvae are only able to settle in the barnacle zone on exposed rock faces devoid of fucoids. The snails have very slight powers of adhesion, so that the degree of exposure that eliminates fucoids and is thus favourable to the metamorphosing larvae is unfavourable to the adults. The presence of a fortnightly spawning rhythm seems to be a secondary adaptation which is, perhaps, very deeply impressed. Thus, on the Plymouth Breakwater, where many of the snails find the maximum amount of shelter by living permanently submerged, spawning appears to be as rhythmical as when the snails are living in an excessively dry habitat.

Summary

An account is given of the distribution, life history and trematode parasites of *Littorina neritoides* on the Plymouth Breakwater; a few observations from other localities are included.

The smaller snails are most abundant on the exposed southern slopes of the Breakwater. Many of the larger ones live more or less permanently in water in small cylindrical pits on the top of the Breakwater. This habitat is apparently very similar to that described by Fischer-Piette (1932) as occupied permanently by this species at Cap Martin; Lebour (1935) has sometimes found it in water in other places in the Plymouth area.

The conditions necessary for metamorphosis of the larvae, the need of the adults for shelter from the force of the waves, and the requirements for spawning appear to be of more importance in determining the choice of habitat than the negatively geotactic and varying phototactic responses found in this species by Fränkel (1927).

The breeding season lasts from September to April. The males are ripe about two months before most of the females. Experimental evidence is given which makes it most improbable that there is any downward migration for spawning. From the examination of plankton samples it appears that there is a fortnightly spawning rhythm coincident with high tides, and that even the snails living in water discharge their eggs only at these periods.

The distribution of the size groups is discussed. The proportion of males decreases significantly in the larger size groups and it is probable that there is a difference in the growth-rate of the sexes.

Three species of cercariae and one metacercaria parasitize the snails. The total percentage parasitism increases with the size of the snail, and no kind of immunity appears to develop. Males were more heavily infected with the cysts of the metacercaria than were females, but the latter were more heavily infected with the sporocysts and cercariae of a species that caused sterility.

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APPENDIX

Notes by Dr H. B. Moore on the occurrence of Littorina neritoides *in some localities in Scotland*

9. vi. 36. Head of Loch Fyne. Very weedy shores. No *Chthamalus stellatus* or *Littorina neritoides*. Little *Balanus balanoides*.

11. vi. 36. Caolas Scalpay, Skye. Weedy shore. *Balanus balanoides* abundant in patches. No *Chthamalus stellatus* or *Littorina neritoides*.

18. vi. 36. Port na Cullaidh, Elgol, Skye. Western aspect, sheltered by Soay to the west, but otherwise 180 degrees exposure. All three species abundant on a reef of rock. Very few algae above the *Laminaria* zone.

15. vi. 36. Sgoir Beag, Vaternish, Skye. Aspect, west-north-west. Wave-beaten shore, few algae above the *Laminaria* zone. *Chthamalus stellatus* occupying a zone 50 to 100 cm. above *Balanus balanoides*. *Littorina neritoides* very abundant.

22. vi. 36. Bay of Stoer, Sutherland. Aspect, south west. Wave-beaten rocks. Little weed above the *Laminaria* zone. *Balanus balanoides* abundant. Small zone of *Chthamalus stellatus*. *Littorina neritoides* present.

24. vi. 36. Geodha chobhair, Sutherland. Aspect, west-north-west. Very wave-beaten coast. No algae except in pools and in the *Laminaria* zone. *Balanus balanoides* abundant. Few *Chthamalus stellatus*. *Littorina neritoides* present.

4. vii. 36. Bass Rock. Wave-exposed shore. Very little weed. *Balanus balanoides* abundant. No *Chthamalus stellatus*. *Littorina neritoides* very rare and scattered.

THE EFFECT OF TREMATODE PARASITES ON THE GROWTH OF *LITTORINA NERITOIDES* (L.)

By Miriam Rothschild

(Text-figs. 1–3)

Introduction

Observations and measurements made on the Gastropod mollusc *Peringia ulvae* (Pennant) 1777 in the wild, suggested that infection with trematode larvae (parthenitae and cercariae) produced gigantism in the host. Experiments in the laboratory (A. & M. Rothschild, 1939) showed that infected snails not only attained ultimately greater size, but also grew faster than uninfected specimens.

Unfortunately, it is difficult if not impossible to compare the growth-rate of an uninfected population with an infected one in nature, as very slight changes in environment (Rothschild, 1938) produce relatively enormous differences in size. Thus, for example, *P. ulvae* collected a few feet apart, on an apparently uniform and identical stretch of mud-flat give different growth curves. In the laboratory simple experiments have confirmed this. Young *P. ulvae* of under 2 mm. in length, were kept for three weeks in water contaminated with gull faeces and subsequently changed to clean water. Their mean size at the end of six months was approximately half that of the controls which were kept in clean water throughout the experiment.

It was hoped to obtain a suitable standard of comparison for gauging the effect of trematodes on the growth of *P. ulvae* by discovering some common parasite which itself exerted no such effect, and to study its distribution throughout a population. A trematode using this snail as second intermediate host only, seemed the most obvious object of study. Unfortunately all the plentiful metacercariae found in *P. ulvae*, either use it as both first and second intermediate host, or else encyst on the outside of the shell. At first it was thought the latter might be utilized, as the chance of finding these cysts on the shell increased proportionately with the age of the snail. Experiments, however, showed that the cysts tend to be knocked off the shells without leaving traces of their presence, and it was therefore found impossible to utilize these species.

During Dr Averil Lysaght's study of *Littorina neritoides* (1941, this volume, pp. 41–67) it was discovered that this mollusc was commonly infected with a Ubiquita cercaria using the snail as first intermediate host, and a metacercaria using it as second intermediate host only. Dr Lysaght very kindly sent me her manuscript and invited me to publish a comment on this portion

of her paper, thus giving me the opportunity of making the desired comparison. I would like to express my appreciation and gratitude for this exceedingly generous suggestion.

I would further like to thank Mr G. M. Spooner for his invaluable assistance, Miss Nora Sproston for her help in dissecting experimental gulls and chickens, and Mr W. Searle for collecting *L. neritoides* although exposed to shrapnel and gunfire.

Trematode Infections of *Littorina neritoides*

Dr Lysaght records four species of trematode larvae from this mollusc, but both Cercaria C, a species allied to *Cercaria emasculans* Pelseneer, and Cercaria D, a Notocotylid cercaria, occur too infrequently for inclusion in this study.

The commonest species met with, Metacercaria A,* using *Littorina neritoides* as second intermediate host only, is of uncertain systematic position, possibly allied to *Cercaria tuberculata* Fil. It forms a thick double-walled spherical cyst, slightly flattened dorsoventrally, and is found encapsuled in the liver and gonads of the host. Dr Lysaght states that it occurred in 3·3 % of the snails with a mean height of 2 mm., and in 87 % of those measuring 8·3 mm. The number of cysts per snail increases in the large specimens, but their presence does not affect the seasonal development of the gonad. This metacercaria was found in snails infected with Cercaria B as well as in uninfected specimens. In fact, there appeared to be definitely more of these double combinations than should be expected by chance distribution alone.

The second common species, Cercaria B, is a typical Ubiquita cercaria using *Littorina neritoides* as first intermediate host only. Dr Lysaght found the percentage of infection very high for a marine mollusc, 14·65 for males and 29·7 for females. As already stated many of these infections also harboured Metacercaria A and there were a certain small number of true double infections when Cercaria B was found in conjunction with Cercaria C which also uses this snail as first intermediate host. The presence of these cercariae caused sterility in both sexes.

The distribution of both Metacercaria A and Cercaria B in the population of *L. neritoides* is shown in Fig. 1, where the percentage of infection is plotted against size. Dr Lysaght draws attention to the fact that Cercaria B is less common in the smaller size groups than Metacercaria A. In addition to this it will be seen that the two curves are different. The one shown for Cercaria B is fundamentally the same as that demonstrated for *Peringia ulvae* infected with larval trematodes (see Fig. 2). Both display the comparatively low rate of infection in the small size groups and the rapid increase in infection rate in the large size groups, resulting in a steep curve upwards from the 6 mm.

* *Littorina neritoides* was examined from the Breakwater, Plymouth, the same locality from which Dr Lysaght obtained her material. Metacercaria A was fed in large numbers to laboratory-reared gulls and chicks with negative results.

group (5 mm. for *P. ulvae*) to a maximum of 91 % (100 % for *P. ulvae*) in the 8 mm. group (7 mm. for *P. ulvae*).

The curve for Metacercaria A, on the other hand, does not slope steeply upwards, but increases more or less uniformly to 87 %. In view of the observations made in the wild on *P. ulvae* and the evidence obtained in the laboratory with this species, it is suspected that the dissimilarity in the two curves is due to growth stimulation by Cercaria B. Moreover, assuming that

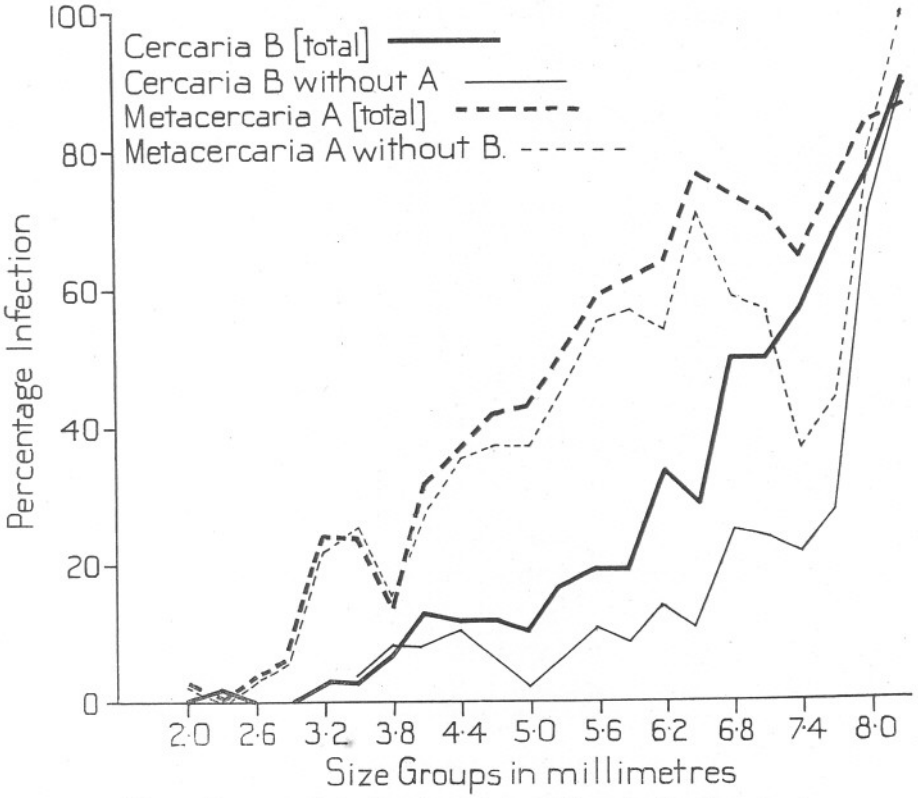

Fig. 1. Percentage infection of population of *L. neritoides*, from data in Lysaght (1941, Fig. 9).

infection occurs at random and increases proportionately with the age of the snail, a far more probable computed growth curve is obtained if it is based on the curve shown for percentage infection of Metacercaria A (see below).

The depression in the upper portion of the curve for Metacercaria A is an anomaly which at present cannot be explained, and it is perhaps idle to speculate as to its possible cause. It does not, however, invalidate the arguments put forward above, as this deviation would, if anything, obscure the contrast obtained for the two curves.

These figures were submitted to G. M. Spooner for criticism and he has very kindly analysed them and made the following comments.

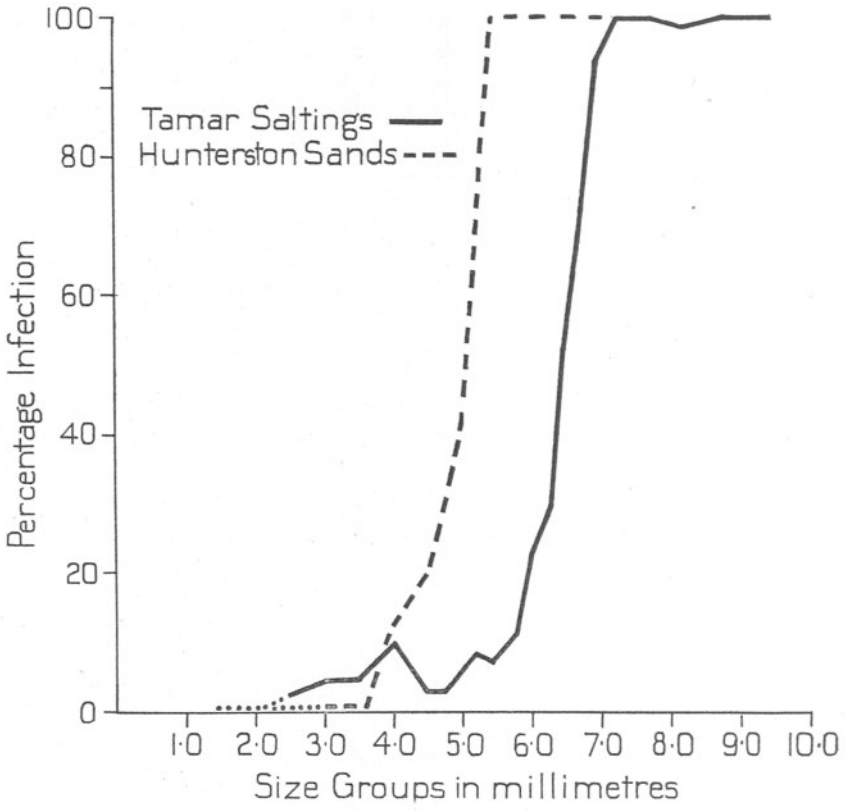

Fig. 2. Percentage infection of 2000 *Peringia ulvae* from Egypt Saltings, River Tamar, and Hunterston* Sands, Firth of Clyde.

Interpretation of the Infection Curves

The curves in Fig. 1 show how percentage infection increases with the size of the snail, or, if the diagram is inverted, how the percentage of the population remaining uninfected decreases with size. Size is a function of age, though the exact relation remains at present unknown. A decrease in freedom from infection as size increases is clearly to be expected, since the longer the snail lives the smaller is the probability that it has avoided contact with the trematode. But does this effect completely account for the shape assumed by both curves?

The method of approaching this question which gives the most instructive results appears to be the following. It is permissible to assume that the average

* Written erroneously as "Hunterdon" in Rothschild (1938).

rate of infection of each trematode remains constant, or at least is independent of the size of the snail. In this event the percentage infection of a population plotted against time gives an ordinary exponential curve:

$$i = 100\,(1-\epsilon^{-at}),$$

in which i is the percentage infected, t is the number of time units, and a is a constant expressing the rate of infection. The formula for the percentage remaining uninfected (u) is of simpler form. From the above,

$$\frac{100-i}{100}=\epsilon^{-at}, \text{ hence } \frac{u}{100}=\epsilon^{-at}.$$

This is a simple logarithmic relation:

$$\log_\epsilon u-\log_\epsilon 100 = -at,$$

hence $$\log u-2 = -0{\cdot}4343at, \quad \text{or} \quad 2-\log u = kt$$

(in which $k = 0{\cdot}4343a$). Thus the logarithm of the percentage infected falls off uniformly with time.

It follows at once that $\log u$ can be used to represent t, and so provide a time scale. If, therefore, size is plotted against $\log u$ (instead of, as in Fig. 1, $1-u$ against size), the snail's growth curve is obtained. This curve, exemplified in Fig. 3, represents the only growth curve from which the particular percentage-infection curve obtained could have arisen. It is, of course, a limitation that the time units in which it is expressed are of unknown value: or rather, the time scale can only be expressed in fractions of a life span, which is of unknown duration. This defect, however, does not prevent a significant test being made—namely, whether the growth curves derived from the percentage-infection curves of the two trematodes are compatible.

The data for Metacercaria A may be considered first. The size intervals are plotted against $\log u$, in descending scale of the latter, and curve A drawn through the points (Fig. 3). If $\log u$ is replaced by $2-\log u$, an ascending time scale is given ranging from 0 to 0·88, this range representing a nearly complete life span of the snail (actually it is the interval between the age at which infection is first possible, presumably during the first few months of life, and the age at which this particular population reaches an average size of 8·3 mm.). If t is time expressed in years, then the scale $2-\log u$ is in units of kt, k being a constant depending on the annual rate of infection.

Curve B is the curve similarly derived from the data of Cercaria B. Its time scale, $2-\log u$, is in units of $k_1 t$. k_1 is not identical with k, since the infection rates of the two trematodes are independent, and indeed, as inspection of Fig. 1 suggests, evidently different, that for Cercaria B being the smaller. For the purpose of comparison the two curves should be superimposed so that the ratio between the units of the two time scales is that of k_1 to k (i.e. of a_1 to a, or the ratio of the two infection rates). If no other factor affects the original percentage-infection curves than the most straightforward conditions which have been assumed, the two growth curves

should then be coincident. In Fig. 3 the curves are actually superimposed so that the two agree closely over a long stretch of the proximal part of their range, the ratio k/k_1 emerging as 4·0. But it will be seen that towards their distal ends they diverge sharply, and the two complete curves have a very different appearance. Curve *B* indicates a life span of almost five times that given by curve *A*. If, on the other hand, they had been superimposed so that their distal ends coincided, giving both an identical range, then the proximal ends would be conspicuously divergent, curve *B* rising much more sharply than curve *A*.

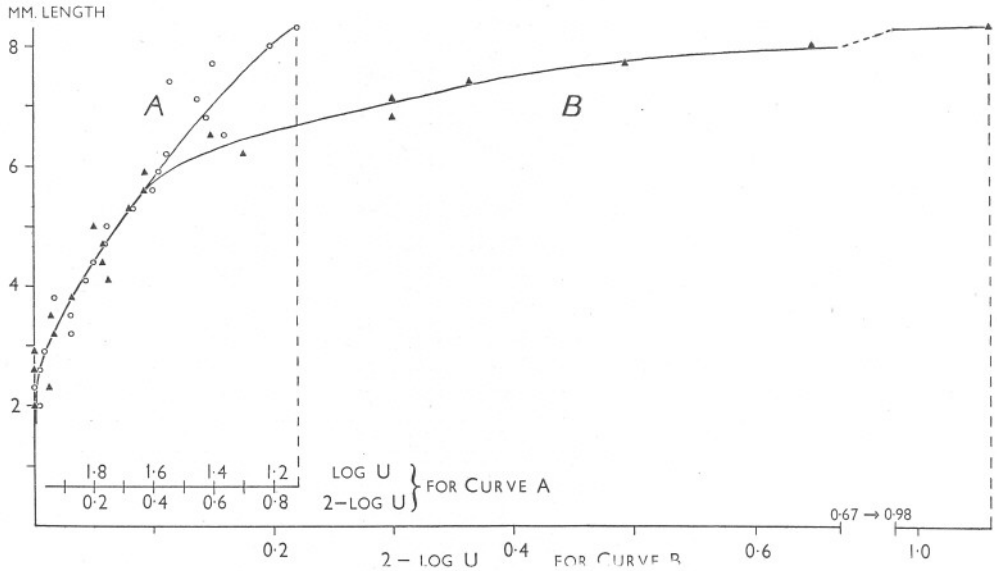

Fig. 3. Theoretical growth-curves of the *Littorina* deduced from the percentage-infection curves of the two trematodes. *A*, curve from the data of Metacercaria A (small circle plots); *B*, curve from the data of Cercaria B (black triangle plots). *u*, percentage of specimens of snail free from infection. For explanation see text.

The growth curves derived from the data of the two trematode infections are thus grossly dissimilar. Both cannot represent the true growth curve of the snail in the population investigated. One at least of the curves must be false; hence one of the original percentage-infection curves requires some special interpretation. This is the first conclusion reached. It is possible to proceed further and enquire which of the two curves is anomalous.

If it is a question of choosing between curves *A* and *B* for the true growth curve of the *Littorina*, there seems little doubt that *A* gives a truer picture than *B*. From what is known of growth-rates in molluscs, and from the available evidence for *L. neritoides* itself, there is little hesitation in assessing curve *B* as extremely improbable. It is, for example, scarcely credible that the snail takes $7\frac{1}{2}$ times as long to grow from 6 to $8\frac{1}{2}$ mm. as it takes to reach

6 mm. On the other hand, there is nothing remarkable about curve *A*. Its form is one which might well have been expected, if it is remembered that the habitat involved is peculiarly favourable to growth. It shows quite an appreciable, and more or less steady, decrease in growth-rate with age, a property which would have been more apparent in the graph itself, had not the time scale been abnormally contracted for the sake of securing space for curve *B*. The second conclusion, then, is that it is the curves derived from the data of Cercaria B which are anomalous: there is clearly an undue concentration of snails infected with this cercaria among the larger size-groups.

This conclusion holds whatever may be the cause of the anomaly. One of the few possible causes (see Discussion) is that the parasites affect the growth of infected snails. On this interpretation the present evidence affirms that Cercaria B stimulates growth, rather than that Metacercaria A inhibits it. This is in complete accordance with evidence from other sources.

It should be noted that the above computations are based on the figures for the percentage *total* infection by each of the two trematodes. In Fig. 1 another pair of curves is plotted, representing the percentage infection, by each trematode, in that section of the population not infected by the other. It happens that the course of this pair of curves consistently lags behind that of the other pair, since combined infections are appreciably in excess of chance expectations, and single infections correspondingly lower. This second pair of curves becomes increasingly unreliable towards the upper end, as the numbers on which the percentages are based are rapidly reduced in the larger size groups, and this loss of accuracy renders these curves much less satisfactory for the treatment given to the first pair, even if the information they contain is considered more important. However, the results obtained from them, as far as they go, are in entire agreement with those given by the total infection data: in fact an even greater contrast between the two trematodes is indicated.

Discussion

In earlier papers the author (Rothschild, 1936, 1938) has briefly discussed the accumulation of specimens infected with trematode larvae (parthenitae and cercariae) among the larger snails—an apparently widespread phenomenon.* This may be due to several causes other than growth stimulation by the parasite:

(1) The young snails may be unattractive to the miracidia and consequently immune to their attack: the infection rate will thus increase with age.

(2) Infections may be lethal to young snails which are consequently killed off.

(3) The growth-rate of the snails may be so greatly slowed down after attaining a certain size, that the time factor alone accounts for the greatly increased percentage of infection in the larger size groups.

* It is of interest to note that in localities where Cercaria B and C were not found in *L. neritoides*, the largest snails (with one exception) did not exceed 6 mm. in height.

In considering all these possibilities the paucity of direct evidence in the wild is a serious handicap. For reasons which will be indicated later experimental evidence, particularly of a negative character, can only be accepted with the greatest caution. It is possible that all these factors may play some part in bringing about the accumulation of infected specimens in the largest size groups, even if the author's view is correct and the direct effects on the growth-rate of the host by the parasite, is the principal explanation of the distribution curves shown in Figs. 1 and 2.

The *immunity of immature snails* to infection was first postulated by Kemp & Gravely (1919) and Manson-Bahr & Fairley (1920). It would appear that these authors tended to overlook the fact that the time factor must account for a much smaller number of young snails becoming infected. When the rate of infection is low, giving a total percentage of about 1 % as in *L. littorea* (L.) for example, one must expect to examine several thousand baby snails before encountering a single infection. Up to quite recent times no examination of large numbers of the smallest size groups was carried out, and a general impression was gained that these were immune.

There is quite a large body of experimental evidence which goes to show that miracidia may exert intra- as well as interspecific selection, at any rate in the laboratory. This interesting fact can account for otherwise inexplicable phenomena encountered in the life histories of trematodes and their hosts. Although young snails have sometimes proved immune, in other cases the immunity appears to be conferred on old snails, thus for example: "The older the snail (*Segmentina nitidellus* Mtd. and *Planorbis schmackeri* Cless) the less liable it is to infection....Old snails hold over from the previous season, but these are scarcely ever successfully invaded by miracidia" (Barlow, 1925). Again "Old snails (*Pomatiopsis lapidaria* Say) could not be infected with the miracidia of *Paragonimus* sp., but an infection of almost 100 % was obtained in young snails of 1 mm. in length..." (Ameel, 1934). Krull (1931, 1934*a*) also found that full-grown snails (*Gyraulus parvus*) could not be infected, but snails of one or two days old were susceptible. There is consequently little experimental evidence to support this theory.

Mortality of Young Infected Snails. The same can be said for the second supposition put forward. As a whole there appears to be a remarkable adjustment between host and parasite, and infected snails undoubtedly survive for long periods. In the laboratory *Littorina littorea* has lived five years (Meyerhof & Rothschild, 1940) and *Peringia ulvae* four years, giving off cercariae throughout that period. However, the literature contains many scattered statements which indicate that as a whole, infected snails of all ages are less resistant than uninfected ones (Thomas, 1883; Manson-Bahr & Fairley, 1920; Sewell, 1922; Wesenberg-Lund, 1934; MacHattie, 1936; Porter, 1938; etc.). A sudden change in environment is more apt to kill off parasitized specimens. There is also little doubt that certain species of trematodes such as the Echinostomes (Rankin, 1939; Rothschild, 1938) have

a more lethal effect than others. On the other hand, Mattes (1936) found that *Zebrina detrina* survived longer when infected than uninfected. It has often been shown that young experimentally infected snails survive to produce cercariae. Krull (1933, 1934*b*), however, found that there was a high mortality of young infected snails and in the case of *Fossaria modicella* Say infected with *Cotylophoron cotylophorum* (Fisch.) and *Fasciola hepatica* L. all died before cercariae producing began. In connexion with the former species he writes: "The snails made little or no growth after having been infected and...it seems reasonable to assume that the amount of food necessary to mature an infection is either not sufficient or does not increase fast enough in a developing snail when infection takes place while the snail is very young."

It must be sufficiently stressed that evidence obtained by laboratory experiments is liable to prove misleading. Again and again failure has resulted from attempts to infect snails with miracidia in artificial surroundings, as apart from other factors, a very slight change in the environment of the snail may render it unsusceptible. Mattes (1936) found it impossible to infect certain snails in his laboratory, but achieved a 100 % infection of the same specimens in his garden. Similarly in the laboratory he successfully infected 100 % of *Helicella candidula* with *Dicrocoelium lanciatum* S. & H., but only 6 % of *Zebrina detrina*, whereas in nature the infection rates were equal. In the laboratory snails may succumb which under natural conditions would survive. Direct evidence in the wild, both in *Peringia ulvae* and *Littorina neritoides*, proves the specimens measuring less than 2 mm. are infected and that these live at any rate until the infections produce cercariae.

Depression of Growth Curve. When considering the third possibility it must be recalled that Sewell (1922) pointed out that Gastropods showed an accelerated growth-rate in the first months of their life. It is also well known that the growth of these molluscs slows down considerably with increasing age. Both Moore (1937) and Lysaght (1941) have demonstrated this slowing down of growth in *L. littorea* and *L. neritoides* in their third and fourth year —a phenomenon much more marked in this genus than in *Peringia*. However, as shown above, an unusual type of growth curve would have to be postulated for *P. ulvae* and *Littorina neritoides* in order to account for the distribution of trematodes throughout the population, supposing infection occurs purely at random.

The Behaviour and Effects of Metacercariae. The facts concerning Metacercaria A recorded by Dr Lysaght agree on the whole with the known observations made on metacercariae which use molluscs as second intermediate host only. Generally such infections appear to occur at random throughout the population, the number of cysts per snail increasing with the time it is exposed to infection. Some examples, however, are reported which clearly indicate selection on the part of the free-swimming cercariae. Thus certain species show a tendency not to re-enter snails infected with their own sporocysts, though readily entering

those infected with other species (Winfield, 1933; Nolf & Cort, 1933). In Metacercaria A it would appear that the free-swimming cercaria is attracted by snails already infected with Cercaria B. A more probable explanation of the high number of these combined* infections is that the sluggish behaviour of infected snails gives the cercariae a better chance to penetrate.

Apart from possible mechanical obstruction caused by the presence of large numbers of cysts, snails appear to be little if at all affected by the presence of metacercariae† using them as second intermediate host only. There is no active destruction of the tissues and sterility does not result. Dr Lysaght draws attention to this fact for Metacercaria A. It is the fact that metacercariae apparently cause no serious histopathological changes in the host, which makes them a suitable subject for comparison with primary infections.

Although no further conclusions can be reached with regard to the actual cause‡ of the large size of snails serving as first intermediate host for trematodes, such a comparison tends to heighten the belief that these parasites induce growth.

Summary

If the number of infections with (*a*) trematode parthenitae and cercariae using *Littorina neritoides* as first intermediate host only, and (*b*) encysted metacercariae using *L. neritoides* as second intermediate host only, are plotted against the size of the snails, two different curves result. The first shows a low rate of infection in the small size groups, but a steep upward slope rising to 91 % in the large size groups. The second shows a curve increasing uniformly to 87 % infection.

Possible interpretations are discussed, and it is concluded that the difference is probably due to the fact that primary infections cause accelerated growth in the host.

* The term "double infection" is reserved for infestations with two primary infections, i.e. two species of cercariae each using a mollusc as first intermediate host. The term "combined infection" is proposed for infections consisting of parthenitae of one species using the snail as first intermediate host and metacercariae of another species using it as second intermediate host.

† This term does not include Tetracotyle which are known to be detrimental to the snail (Van Haitsma, 1930).

‡ The suggestion was originally put forward that castration might account for the increase in size of infected snails. *Littorina littorea*, artificially castrated by treatment with X-rays in doses of 400 r. at 150 kV. and 4 mA., screened with 4 mm. Al., did not grow any faster or any larger than controls.

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OBSERVATIONS ON THE NIGHT TIDAL MIGRANT CRUSTACEA OF KAMES BAY

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CONTENTS

INTRODUCTION

During the year 1936 Mr Richard Elmhirst, Director of the Scottish Marine Biological Station at Millport, carried out a series of night tow-nettings across the waters of Kames Bay* at varying times after nightfall, mainly between the hours of 10 p.m. and midnight. The series was taken in order to ascertain the nature and extent of the faunal immigration into the bay from outside waters, and the nocturnal and vertical movement of the fauna which normally lies buried in the sand during the day. The net employed was an ordinary coarse tow-net supplemented on occasions by a finer net; the latter net, however, captured but few macro-Crustacea, and its results will be neglected in the present paper. The method employed was to walk into the water at the edge of the incoming or outflowing tide to a depth of about 2 ft. and to walk across the bay following the edge of the tide trailing the net about 10 ft. posteriorly and at arm's length into the tidal flow, thus avoiding as far as possible disturbances set up in the water by the walking movement. The length of tow was approximately 100 yards. Thus the position of each sample is determined by the time it was taken in relation to the day of the lunar month, and samples were obtained at all levels from high-water mark to low-water mark. I have previously dealt with the species of the amphipod genus *Bathyporeia* which occurred in these samples (Watkin, 1939). In this paper the remainder of the macro-crustacean fauna apart from the mysids is analysed. I am indebted to Mr Elmhirst for handing over these samples to me for analysis, and for his critical comments during the investigation.

An appreciation of the fauna of the samples is amplified by a knowledge of the fauna which normally lives in the intertidal sand of the bay. This enables

* A map and a brief description of Kames Bay has been given in a previous paper (Watkin, 1939, p. 470).

the distinction to be drawn between those species which perform simple vertical migrations from the sand into the intertidal waters and those which are carried in by the tide into the intertidal area from the various habitats which lie beyond the low-water mark of spring tides. For this purpose a series of sand samples for faunal analysis was taken during the last week of March and the first week of April 1939. It is realized that a period of over two years separates the time when the tow-net samples were taken from that when the sand samples were obtained. It is known, however, that no major differences in the fauna occurred in the meantime, although differences in the density of a particular species may have occurred. The general conclusions are not invalidated by this time difference.

The method of faunal analysis of the sand was to fix stations, at 5-yard intervals, from the high-water mark to the low-water mark of spring tides along a sampling line previously used in the investigations of Elmhirst (1931) and Stephen (1928 and subsequent dates) into the sand fauna of the bay. At each station a block of sand of 1 sq. ft. surface area and of a depth of 6 in. was removed and sieved through a brass wire sieve of 30 meshes to the linear inch. The detailed analysis of this series of samples will form the subject of a separate paper. For the purposes of this paper reference will be made only to the species which also occur in the night tow-net samples.

A comparison of the species which occur in the night tow-net samples with those of the sand samples shows that the night migrant fauna falls into two distinct groups.

(*a*) Those species which normally lie buried in the intertidal sand during the day and perform vertical movements only, retaining their zonation when swimming in the tidal waters. These are the amphipods *Bathyporeia pilosa* Lindström, *B. pelagica* (Bate), *B. elegans* Watkin and *B. guilliamsoniana* (Bate), *Pontocrates norvegicus* Boeck, *P. arenarius* (Bate) and *Urothoë brevicornis* Bate; the isopod *Eurydice pulchra* Leach; and the cumaceans *Pseudocuma cercaria* (van Beneden) and *Cumopsis goodsiri* (van Beneden). The above species represent the dominant forms that occur in the sand, apart from *Haustorius arenarius* (Slabber) which did not appear in the night tow-net samples. Apart from these an occasional specimen of *Nototropis swammerdami* (M.-Edw.), *Megaluropus agilis* Hoek, *Lamprops fasciata* Sars, *Iphinoë trispinosa* (Goodsir) and *Crangon vulgaris* Linn. also occurred in the sand samples.

(*b*) Those species that do not occur in the intertidal sand, but are carried in with the inflowing tide from various habitats beyond low-water mark and thus perform a horizontal, in addition to a vertical, migration. These habitats may be classified as (1) the sand habitats which extend outwards from low-water mark to the deeper waters of the Firth of Clyde, and (2) the algal habitats. The latter harbour during the day species which cling to clumps of seaweed on the sea floor beyond the low-water mark of spring tides, and may also include the algal dwellers of the rock shore, which, until further evidence

is available, may be expected to contribute to the night migrant population. The main species in the second group are the amphipods *Gammarus locusta* (Linn.), *Nototropis swammerdami* (M.-Edw.), *Calliopius rathkei* (Zaddach), *Dexamine thea* Boeck, and *Apherusa* spp.; the isopod *Idotea viridis* (Slabber) and the mysid *Schistomysis spiritus* Norman. Other species which occur only rarely in the samples are *Marinogammarus* spp., *Megaluropus agilis* Hoek, *Stenothoë monoculoides* (Montagu), *Podoceros falcatus* (Montagu), *Metaphoxus fultoni* (T. Scott), *Periculodes longimanus* (Bate & Westw.), *Erichthonius braziliensis* (Dana), *Siphonoecetes colleti* Boeck, *Phtisca marina* Slabber, *Hyale* sp., *Iphinoë trispinosa* (Goodsir), *Lamprops fasciata* Sars, *Diastylis rathkei* (Kröyer) and *Bodotria scorpioides* (Montagu).

The rare appearance of such algal dwellers as *Stenothoë*, *Podoceros* and *Phtisca* is probably due to the drift of bits of algae, and of the tube dwellers such as *Erichthonius* and *Siphonoecetes* to storm action; they cannot at the moment be regarded as night migrants. The sand dwellers, such as *Megaluropus*, *Periculodes*, *Metaphoxus* and the cumaceans, may perform extensive vertical migrations over their respective habitats.

The Fauna of the Sand

The analysis of the crustacean population of the sand samples is given in Table I.

Table I. The Zonation of the Main Species of Crustacea

Station no.	*Eurydice pulchra*	*Urothoë brevicornis*	*Pontocrates norvegicus*	*Cumopsis goodsiri*	Station no.	*Eurydice pulchra*	*Urothoë brevicornis*	*Pontocrates norvegicus*	*Cumopsis goodsiri*	*Pseudocuma cercaria*	*Pontocrates arenarius*
13	1	—	—	—	29	2	24	128	4	—	—
15	35	—	—	—	30	6	33	141	4	—	—
16	8	—	—	—	31	—	22	188	9	—	—
17	13	4	—	—	32	5	40	221	2	—	—
18	5	3	—	—	33	1	26	201	14	4	—
19	8	1	3	—	34	1	17	105	8	—	—
20	3	13	11	—	35	1	18	112	4	2	—
21	10	22	29	—	36	—	30	84	5	7	—
22	16	12	30	—	37	1	25	36	5	—	3
23	3	24	71	—	38	—	25	59	2	5	3
24	4	14	52	—	39	—	31	36	3	2	2
25	2	11	78	—	40	—	42	24	4	17	37
26	3	20	86	—	41	—	19	29	2	22	17
27	3	26	96	—	42	—	6	15	2	34	43
28	7	32	90	7							

High-water neap tide occurs at St. 14, approximate mid-tide at St. 21, low-water neaps at St. 39.

An analysis of the night tow-net samples for the four species of the genus *Bathyporeia* has been given (Watkin, 1939). Consequently the detailed figures of the distribution of these species in the sand samples are omitted. Further, only those species which occur in the night tow-net samples and whose distribution extends over several stations are included. The following species

also occurred: *Lamprops fasciata* St. 35, one; *Iphinoë trispinosa* St. 42, two; *Nototropis swammerdami* St. 42, two; *Megaluropus agilis* St. 42, one; and *Crangon vulgaris* St. 24, one.

The first five stations from the high-water mark of spring tides contained no macrofauna. *Bathyporeia pilosa* appeared at St. 6 with a centre of maximum abundance at Sts. 12 and 13, gradually disappearing to St. 22. *Haustorius arenarius* ranges over Sts. 10–14 and spasmodically to the low-water mark of spring tides. The high-water mark of neap tide occurs at St. 14 (recorded by Mr Elmhirst on May 12 1939, calm sea with a slight north-westerly breeze). *Eurydice pulchra* extends from the upper neap-tide level with a maximum at St. 15 and occurs continuously in varying abundance to St. 37 with a definite tendency to be more abundant in the upper half of the neap-tide range. *Urothoë brevicornis* first appears at St. 17 and continues to the low-water mark of spring tides with a tendency to be more abundant in the lower half of the neap-tide range. The low-water mark of neap tide occurs at St. 39. *Pontocrates norvegicus* extends from St. 19 in gradually increasing abundance to St. 32, to be followed by a gradual decrease to low-water mark. *Bathyporeia pelagica* first appears at St. 24, increases to a maximum over Sts. 31–35 and disappears after St. 40. Thus this species and *Pontocrates norvegicus* have a similar centre of maximum abundance in the lower half of the neap-tide range. The former is distinctly an intertidal species in this bay, but the latter may extend beyond the low-water mark of spring tides. *Cumopsis goodsiri* is never abundant, but is represented at every station from 28 to low-water mark, and thus does not occur above mean sea-level. *Pseudocuma cercaria* does not appear until St. 33 and does not become abundant until St. 40, i.e. below the low-water mark of neap tides. *Bathyporeia elegans* first appears at St. 35 and extends to the low-water mark of spring tides with a centre of abundance near low-water mark. *B. guilliamsoniana* also appears in the last six samples, but is known to be definitely more abundant beyond low-water mark. *Pontocrates arenarius* appears in the last seven samples with a suggestion that its centre of abundance is near low-water mark.

The Fauna of the Night Tow-net Samples

Table II gives the dates on which the samples were obtained, the time the sample was taken, the time of afternoon high tide, the age of the moon in days and the number of individuals of the most abundant species per sample. Table III shows the data for the most important species from the point of view of zonation and also summarizes the results of a detailed analysis of the maturity of each individual.

Pontocrates norvegicus and P. arenarius.

P. norvegicus was present in thirty out of the forty-eight samples and *P. arenarius* in nine, with six samples showing a mixture of the two species. However, in all the six samples containing both species one of the species is

TABLE II. NUMBER OF INDIVIDUALS OF THE MOST ABUNDANT SPECIES IN EACH SAMPLE

Day and month 1936	Age of moon in days	G.M.T. p.m.	Time of high water p.m.	*Pontocrates norvegicus*	*Pontocrates arenarius*	*Nototropis swammerdami*	*Calliopius rathkei*	*Gammarus locusta*	*Idotea viridis*	*Eurydice pulchra*	*Pseudocuma cercaria*	*Cumopsis goodsiri*
7. i.	14	10.00	11.44	—	—	—	—	2	—	3	—	—
15. i.	22	7.30	4.16	117	—	2	—	6	—	—	—	—
21. i.	28	6.45	10.32	28	—	1	—	18	—	2	—	—
12. ii.	20	8.30	3.7	4	28	10	5	25	1	—	76	—
13. ii.	21	7.00	3.37	110	—	1	—	1	—	—	—	—
27. ii.	6	7.40	3.32	11	—	244	2	1656	31	—	—	—
4. iii.	12	11.00	10.38	—	—	—	—	1	—	1	—	—
19. iii.	27	9.00	9.34	—	—	—	—	—	—	—	—	—
24. iii.	2	4.30	1.00	—	—	—	—	—	—	—	—	—
29. iv.	9	10.15	6.53	—	—	—	—	33	—	2	—	—
30. iv.	10	10.15	8.10	125	—	—	—	36	1	4	—	—
1. v.	11	10.15	9.13	10	—	—	—	28	2	1	—	—
2. v.	12	10.15	10.2	2	—	—	—	42	—	7	—	—
3. v.	13	10.15	10.44	2	—	—	1	5	—	9	—	—
9. v.	19	10.15	1.55	91	—	1	1	1	2	12	1	—
14. v.	24	10.15	5.55	—	—	—	—	17	—	17	—	—
15. v.	25	10.15	7.9	59	—	3	—	115	55	2	1	1
16. v.	26	10.15	8.17	42	—	1	—	35	27	12	—	—
17. v.	27	10.15	9.19	13	—	—	—	23	4	15	—	—
21. v.	2	10.15	0.22	19	—	—	—	—	—	22	—	—
1. vi.	13	10.15	10.0	—	—	—	—	—	—	1	—	—
10. vi.	22	11.00	3.49	120	—	—	—	11	1	2	—	1
12. vi.	24	10.30	5.32	6	167	31	—	41	5	1	72	1
16. vi.	28	10.30	9.52	—	—	—	—	—	—	—	—	—
23. vi.	5	1.00*	3.12	—	—	—	—	5	—	1	—	—
26. vi.	8	11.00	5.12	2	219	11	—	42	—	—	90	—
27. vi.	9	1.00*	5.58	479	1	5	—	31	1	1	1	29
2. vii.	14	11.00	10.53	—	—	—	—	2	1	—	—	—
14. vii.	26	11.00	8.23	44	—	—	—	128	2	1	—	—
21. vii.	4	11.00	2.9	786	7	1	—	13	—	—	15	23
31. vii.	14	11.00	10.30	—	—	—	—	6	2	24	—	—
12. viii.	26	11.00	8.11	235	—	2	1	102	3	3	1	9
21. viii.	5	11.00	2.41	21	103	101	1	121	—	2	80	—
31. viii.	15	11.00	11.35	—	5	—	—	6	—	7	2	—
8. ix.	23	9.45	5.11	9	43	7	—	46	2	1	227	—
15. ix.	1	10.00	0.6	150	—	1	—	1	1	18	2	3
24. ix.	10	10.00	5.28	18	—	3	1	2	—	1	1	1
30. ix.	16	10.00	11.50	84	—	—	—	—	—	3	2	7
5. x.	21	10.30	3.9	—	18	99	8	9	—	1	259	—
20. x.	6	10.30	2.41	70	—	3	—	3	1	13	—	4
28. x.	14	10.30	10.38	—	—	—	—	1	—	2	—	—
7. xi.	24	8.30	7.0	—	—	—	—	7	—	3	—	—
12. xi.	29	10.30	11.24	109	—	3	—	503	31	4	3	—
25. xi.	12	8.30	9.14	—	—	—	—	—	—	—	—	—
11. xii.	28	11.45	10.58	—	—	—	—	15	—	2	—	—
14. xii.	2	8.45	0.25	8	—	—	2	10	3	12	—	1
14. xii.	2	11.00	0.25	2	—	—	—	2	1	16	—	—
22. xii.	10	7.30	6.19	—	—	—	—	—	—	2	—	—
Total				2776	591	530	22	3151	177	230	833	80

* 1.00 a.m.

represented by a few individuals only. The samples are reasonably pure to one species. It is to be expected that samples taken towards low-water mark would contain both species, since the analysis of the sand fauna shows that they overlap from St. 37 seawards. *P. arenarius* is present in considerable numbers only in those samples taken between L.W.N. and L.W.S. (Table III), e.g. 12. vi. 36 and 26. vi. 36. The sample of 31. viii. 36 is aberrant, it was taken near the high water of a spring tide and was the only occasion when this species was taken outside its zone, as shown by the sand samples. Similarly, the samples containing *P. norvegicus* in abundance were those taken in the middle and lower third of the neap-tide range, e.g. 21. vii. 36, and 27. vi. 36. The samples taken at high water contain none or very few. Thus both these

TABLE III. SUMMARY OF THE ZONATION AND MATURITY OF SOME SPECIES

	Number of samples	*Pontocrates norvegicus*	*Pontocrates arenarius*	*Nototropis swammerdami*	*Calliopius rathkei*	*Urothoë brevicornis*	*Megaluropus agilis*	*Gammarus locusta*	*Idotea viridis*	*Eurydice pulchra*	*Pseudocuma cercaria*	*Cumopsis goodsiri*
ZONATION												
H.W.S. to H.W.N.	4	2	—	—	—	1	—	45	1	10	—	—
Upper third neap-tide range	15	254	5	3	1	1	—	640	40	75	5	1
Middle third neap-tide range	12	966	—	10	2	3	—	446	91	95	7	20
Lower third neap-tide range	12	1472	154	363	6	8	—	1900	38	35	324	54
L.W.N. to L.W.S.	5	82	432	154	13	1	72	120	7	15	497	5
ANALYSIS OF MATURITY												
Adult males	—	455	22	31	6	6	20	27	Not examined	Not examined	122	12
Females with eggs	—	545	50	54	2	—	28	11			337	17
Adult females without eggs	—	182	56	184	13	6	16	5			202	7
Immature males	—	422	33				8	3108			72	23
Immature females	—	458	109								86	21
Immature—sexes indistinguishable	—	714	321	261	1	2	—				14	—
Total	48	2776	591	530	22	14	72	3151	177	230	833	80

species retain their sand zonation when swimming in the intertidal waters. A comparison with those samples containing *Bathyporeia* (Watkin, 1939) shows that *P. arenarius* is present in the same samples as those containing *B. guilliamsoniana* and *B. elegans* and only partly with those containing *B. pelagica*, whilst *P. norvegicus* overlaps in the main with *B. pelagica* and partly with *B. pilosa*.

Bearing in mind that some of the sample are taken outside its tidal range, the presence of *P. norvegicus* in thirty out of the forty-eight samples suggests that it is migratory throughout the year. Its density, however, on various nights differs considerably.

A detailed examination of the individuals showed that in *P. norvegicus* all stages of maturity are present at all times of the year. Egg-bearing females

and adult males were recorded for each month and the spasmodic appearance of numbers of young forms suggests that broods are produced at definite times. The data are not full enough to draw definite conclusions on the number of broods produced, but they suggest that one brood per month is released. Similar remarks also apply to *P. arenarius*, but no samples, apart from that of 12. ii. 36, were taken within their zone during the first six months of the year.

The totals (Table III) show that the migrant population of *P. norvegicus* consists of 19·6% egg-bearing females, 16·4% adult males, 6·5% non-egg-bearing females, 31·7% immature forms of both sexes and 25·7% young forms. Thus 42·5% are adults. The preponderance of adult males is not nearly so marked as in *Bathyporeia*, where 42% were adult males. The percentage of adult females is, however, somewhat higher, 26·1% as compared with 15%. Comparing these figures with those obtained for the sand population, taken in late March and early April before the production of the new season's broods has reached a high level, when 61% were adults with 5% adult males, it is seen that there is a tendency for adult males to be more abundant in the tow-net samples. The individual samples are somewhat variable in their population, but where the number of individuals in a sample is high the population consists of a mixture of forms in all stages of maturity.

The migrant population of *P. arenarius* shows a smaller percentage of adult males and immature males than *P. norvegicus*, but otherwise retains the same general features.

The data are not sufficient to draw definite conclusions in regard to lunar periodicity. Those given in Table II show irregularity during the first half of the lunar month but become more regular during the last 10 days of the month, with a suggestion that the species becomes more abundant in the periods immediately preceeding the new and full moon.

Fage (1933) records both species in his night tow-nettings "autour d'un foyer lumineux" at Concarneau and Port-Vendres; the numbers are small with adult males predominating.

Urothoë brevicornis (Tables I and III).

It has been noted that this species occurs abundantly in all the sand samples from St. 17 to low-water mark. Its occurrence in the night tow-net samples is, however, very spasmodic. A total of fourteen individuals is recorded from nine samples; they are spread over the whole range in which this species occurs in the sand samples, showing, as in the sand samples, a tendency to be more abundant in the lower third of the neap-tide range. The fourteen individuals comprise six adult males, one adult female, five immature females and two young forms. Fage (1933) records other species of this genus in his night tow-nettings "autour d'un foyer lumineux", particularly at Concarneau. All the specimens were males. Russell (1925) records the genus in samples taken up to 50 m. depth in the waters of the English Channel

on a moonlight night in July, and notes that it differs from other amphipods in appearing in the surface waters at 9 p.m. Tattersall (1913) records *U. marina* and *U. elegans* as night migrants in the Clare island survey. Thus there is considerable evidence to show that species of this genus are migratory at night; but none of the records indicate the presence of egg-bearing females.

The allied form *Haustorius arenarius* is recorded in the sand samples but not in the tow-net samples. Dennell (1933) remarks that "*Haustorius* apparently may forsake the sand...to swim freely" and under laboratory conditions it was observed to do so between the hours of 11 p.m. and 6 a.m. It is to be expected that a species so modified for a swimming habit should have occurred in the samples, but I can find no reference to its occurrence as a night migrant.

Gammarus locusta (Tables II and III).

This species inhabits "water of some fathoms depth" (Elmhirst, 1932) and is usually regarded as living amongst algae. It is thus a migrant into Kames Bay from its known habitat in deeper waters, and is the predominant migratory amphipod from outside waters.

From its presence in forty out of the forty-eight samples it is reasonable to suppose that it is a tidal migrant throughout the year at all phases of the moon. Its abundance is, however, exceedingly variable. Note may be made of the sample of 27. ii. 36 with 1656 individuals and that of 12. xi. 36 with 503 individuals, with many samples containing less than ten. The samples with high numbers do not seem to bear any relationship to the state of the tide at the time they were obtained. They occur in the low-water, mid-tidal and high-water samples. Similarly, they are spread evenly throughout the year. When the data for the whole year are plotted against a lunar month it is seen that there is a distinct tendency for the numbers to increase as the period of new moon approaches and to a less extent towards the period of full moon, if the one exceptional sample of 1656 individuals, taken on the sixth day of the lunar month, is omitted. The numbers fall during the immediate periods of full and new moon.

A striking feature of the results, which is characteristic of every sample, is the dominance of the immature stages and the progressive reduction in numbers as size increases. Thus of 3151 individuals 1495 (47%) are under 3 mm. 1276 (41%) from 3 to 5 mm., 280 (9%) from 5 to 7 mm., 69 (2%) from 7 to 9 mm. and 31 (1%) over 9 mm. Blegvad (1922) in his account of the life history of this species in Danish waters records that males attain full maturity at a size of 10 mm. and some females may attain maturity at 6 mm. Thus this species is characteristically a migrant in its young stages. It should be noted, however, that forty-three, or 1·4%, of the individuals are adults with the males predominating, twenty-seven of the forty-three. Of the sixteen adult females eleven carried eggs in the brood pouch. The presence of a few adults prompts the suggestion that possibly they are more numerous

in the waters over their immediate habitat and that they do not perform such extensive horizontal migrations as the young forms. Further sampling should prove interesting. Fage (1933) records a somewhat similar population at Concarneau, in which the young forms predominate over a few adult males.

Mr Elmhirst is of the opinion that this species comes in when there is much drift algal detritus in the tidal waters.

Marinogammarus spp. occurred in five samples only: No. 8, one; No. 19, one; No. 42, one; No. 46, one; No. 47, four. Of the eight individuals seven were young forms with one egg-bearing female. The data are scanty but the same general features as in *G. locusta* are indicated.

Nototropis swammerdami.

The habitat of this species is amongst the sublittoral algae. Table II shows that it occurred in twenty of the night tow-net samples, which indicates that it is migratory throughout the year; but as with the other species the extent of the migration is very variable. Three of the samples account for 84% of the total number recorded. The samples in which it occurs were taken at all stages of the tide, but it only occurs in abundance in those taken in the lower third of the neap-tide range and those near low water. Continuous sampling in this region would probably show its occurrence to be more regular. All stages of maturity are represented (Table III), with breeding females present only in the samples with a large number of individuals and forming 10% of the total. Adult males are relatively scarce, 6% of the total, with the young forms predominating. Thus this species shows migratory features similar to those of *Gammarus locusta*. Fage (1933) records both *N. guttatus* and *N. swammerdami*, the population consisting mainly of adult males, and Tattersall records *N. vedlomensis* as a night migrant in the Clare Island survey. Other authors also record its pelagic habit.

Calliopius rathkei.

Nine samples scattered over the year contain this species in small numbers. The data are scanty but suggest that it is more numerous during the winter than the summer months, and, as with *Nototropis swammerdami*, it is abundant in the low-water samples. The habitat is amongst sublittoral algae; Sars (1891) records that it occurs in Norwegian waters "in great shoals, swimming actively near the beach, and ascending it according as the tide flows up". Tattersall records it as a night migrant.

Apherusa spp.

This genus is represented by the three species *A. jurinei* (M.-Edw.), ten individuals in seven samples, *A. bispinosa* (Bate), six individuals in three samples, and *A. cirrus* (Bate), one individual, occurring from May to December. It is noteworthy that the individuals are either adults or immature forms and none of the adult females were egg-bearing. Many authors record the pelagic

habit of the species in this genus. Thus Russell (1927) records the abundance of *A. ovalipes* and *A. clevei* in the day-time in the waters of the English Channel; they were absent from the surface layers but abundant from 20 m. depth, 10 min. hauls giving 3480, 6480 and 6940 individuals. In dealing with hauls taken at night-time in summer, he further records (1931), that during 1925 (and probably showing the same behaviour in 1926) there was a marked upward movement at night, the species being evenly distributed from the surface downwards. Samples taken throughout the year 1930 and part of 1931 (Russell, 1934) show the species to be abundant from late June to September, reappearing in April 1931. Fage lists *A. bispinosa* at Concarneau with males and females in almost equal numbers and notes that the species is exceptional in that its abundance is not affected by the light employed.

Other amphipods.

Attention may be drawn to *Dexamine thea*, seventeen individuals from six samples, and *Stenothoë monoculoides*, seven individuals from five samples, as adding to the list of algal dwellers which may be included under the species performing a night migration. The data for the sand dwellers *Megaluropus agilis* (Table III) and *Periculodes longimanus*, six individuals from two samples, does not represent the extent of their migration, since Elmhirst (1932) has shown that samples taken at two fathoms depth near the low-water mark of spring tides yield these two species in considerable numbers. The samples were taken on a night in March and again in June and successive sampling at 3 hr. intervals from 6 p.m. to 6 a.m. gave maximum hauls at 9 p.m. and midnight. *Metaphoxus fultoni* was recorded in one sample only, but its occurrence as a night migrant in the waters of the Firth of Clyde is recorded by Patience (1909) in samples taken during July at one fathom from the bottom. Males were more abundant than females. *Podoceros falcatus*, three individuals from three samples, *Erichthonius braziliensis*, two individuals from two samples, *Siphonoecetes colleti*, two individuals, *Phtisca marina*, one individual, *Hyale* sp. must be regarded as chance occurrences due to storm action.

Eurydice pulchra.

This species occurs in thirty-seven of the samples (Table II). The samples indicate its presence throughout the year and at all tide levels, with a tendency, shown also by its distribution in the sand, to be more abundant in the upper and middle portion of the neap-tide range. It is probable that this species is as equally a day migrant as a night migrant, although actual figures are not available to substantiate this statement. Observations carried out on this species in the laboratory show that it obtains food by capturing other living organisms in the plankton, tearing a rent in their skin and disembowelling them by the use of the anterior peraeopods. On the beach it may be observed that they rise out of the sand with the inflowing tide, proceed to feed im-

mediately and sink again into the sand with the retreating tide. The migration into the tidal waters is thus essentially a feeding one. Details of the annual life cycle are not available but casual observations suggest that two broods, a spring and an autumn, are produced.

Idotea viridis.

The occurrence of this species in twenty-one of the samples suggests that it is migratory throughout the year from its habitat in the littoral and sub-littoral algae. The numbers in the samples are very variable, four of them accounting for 81 % of the total. A notable feature is the dominance of young forms with the numbers rapidly decreasing as size advances. The figures are, under 2 mm. 60, at 3 and 4 mm. 73, at 5 and 6 mm. 32, at 7 and 8 mm. 4, over 8 mm. 8. Thus those under 4 mm. comprise over 75 % of the total. Howes (1939) records that in a saline lagoon in Essex this species attains maturity at 5 mm. in the female and 6 mm. in the male, although very few are mature at this size. Assuming that this population attains similar sizes the absence of the adult stages becomes notable. One egg-bearing female was obtained. When the data for the whole year are plotted against a lunar month it is noted that the species occurs throughout the month but with a definite tendency to be more abundant in the period immediately preceeding the new moon. The migrations of this species recall those recorded here for *Gammarus locusta* and a comparison of the sample numbers shows that the maximum number of both species occurs in the same samples. Elmhirst is definitely of the opinion that the occurrence of *I. viridis* is associated with drift weed in the tidal waters. Thus the amount of algal detritus must be considered as a contributory factor in the migration of both species.

Fage (1933) draws a distinction between the pelagic migration of the Cirolanidae on the one hand and the Idoteidae on the other. In the former the egg-bearing females always remain associated with their "substratum" whatever that may be, and the pelagic migrants are either males or "young" forms, whilst in the latter the thigmotropism which associates them with their substratum during the day is obscured at night-time and all stages of maturity are represented in the night migrant population. This conclusion is partially substantiated by the above observations on *Eurydice pulchra* and *I. viridis*.

Cumopsis goodsiri.

Table I shows that this species occurs in the sand samples from St. 28 to low water mark, and, although never abundant, it occurs in every sample. Table II shows that it was present in eleven of the tow-net samples between May and December but only in numbers during late June and July. The samples in which it occurs were taken mainly within its range as shown by the sand samples, its abundance occurring in the lower third of the neap-tide range; but its absence from many samples suggests that it is spasmodic in its

migratory habits. Of the eighty individuals obtained seventeen were egg-bearing females and twelve adult males, with immature forms of both sexes predominating and young forms absent.

Pseudocuma cercaria.

Of the forty-eight samples sixteen include this species. It will be recalled that it only occurs in sand samples taken near low water. Similarly, it only occurs in numbers in those night tow-net samples taken either at the low-water level of spring tides or in the lower third of the neap-tide range. An occasional specimen occurs in the mid-tidal samples and exceptionally in the upper third of the neap-tide range. It must be regarded mainly as a tidal immigrant from the sand below low-water mark, although the centre of its abundance needs further investigation. It differs from other tidal immigrants in being restricted to low water. Many authors have commented upon the relationship between cumaceans and moonlight. The present data when arranged on a lunar month basis shows two definite peaks of density; the first over the 5th–8th day and the second over the 20th–23rd days, thus suggesting an association with lunar illumination of a certain intensity.

Elmhirst (1932), in a series of samples taken every three hours from 6 p.m. to 6 a.m. on a night in March and again in June, shows that this species is abundant in the surface waters at low tide; but at high tide, when the low-water level is covered by 2 fathoms of water, it is abundant near the sea floor and practically absent from the surface. His data further show that very few are carried in with the tide to high-water mark. The above observations substantiate in part the observations of Elmhirst, but in this investigation no depth samples were taken.

In Table III the sex and degree of maturity of the individuals are shown. The adult males were mainly of the "short antennae" type (Foxon, 1936, p. 388). Very few "fully adult" males were found. The data show that egg-bearing females are present from February to October and that they represent 40% of the total catch. If the adult females without eggs are included, the percentage rises to 65%, adult males accounting for 9% only. Thus adults predominate, with immature males and females constituting the remainder of the catches. Young forms are practically absent. Foxon, giving counts made on previous collections in this area, records males as more abundant than females and Fage makes the same observation. Further work on more extensive collections is necessary before definite statements can be made.

Other cumaceans.

Two of the low-water samples contain *Iphinoë trispinosa*, which occurs in the sand from low-water mark to some depth. *Diastylis rathkei* was recorded once, *Lamprops fasciata* once, and *Bodotria scorpioides* was found in three samples. Russell (1931) records the vertical movement of the last-named species at night-time.

Crangon vulgaris.

Young forms of this species from 4 to 10 mm. in length occurred in eight samples from June onwards. The numbers were small and a total of only twenty individuals was recorded.

Attention may finally be drawn to occasional species other than the Crustacea. Young Pleuronectids less than 12 mm. in length were present in five of the May samples, and other young fishes in some samples from May onwards. Young Nereids of 3–5 mm. were present in the June and July samples and *Scolelepis* adults in four samples. The use of a coarse tow-net avoided most of the usual smaller plankton organisms, but occasional megalopa and zoea larvae, calanoid and harpacticid copepoda and medusae were found.

Of the forty-eight samples thirty-nine contained Mysids, mainly *Schistomysis spiritus*, in varying numbers and varying degrees of maturity, many of the samples containing numerous young forms. It is hoped that these will be analysed and reported on in due course.

Discussion

As far as I am aware this series of samples, collected by Mr Elmhirst for the study of the night migrant macrofauna of the intertidal waters throughout a whole year, is the first of the kind which has been made. The main purpose of the work is to show that this field is a fruitful one for further investigation. It is not proposed to discuss in detail the possible factors which underlie the migration of the species either individually or as a whole, but rather to indicate the problems requiring further investigation and to show how this series of samples demonstrates the positions at which the collection of further samples should be made. The samples were taken, in all cases, at the edge of inflowing or outflowing tide. Thus the position of each sample is determined by the position of the tide when the sample was taken, and they have served to show the general outline of the problems involved. The main point that emerges, apart from the fact that the major part of the night migrant population consists of Crustacea, is that the population falls into two well-marked groups: (*a*) that which normally lives in the intertidal sand of the bay and becomes migrant at night-time, and (*b*) that which is carried in to the bay by the inflowing tide from other habitats. Thus, as an auxiliary study, it is necessary to know the fauna of the intertidal soil and also that of the adjacent deeper water habitats which may be (1) sand or mud habitats, or (2) algal habitats, or both. This investigation shows that both habitats contribute to the migrant population. To complete the analysis of the migrant fauna it is necessary to obtain samples of the microfauna, which in addition to the usual plankton organisms will consist of such forms as Harpacticids (Elmhirst, 1935), and also to obtain a knowledge of the fishes which both as adults and

in their young stages may migrate inshore at night-time in varying numbers at the different seasons of the year (Elmhirst, 1935; Marshall *et al.* 1939). By such studies it will eventually be possible to build up a picture of the extensive activities which occur in intertidal waters at night-time.

The data given in this paper and previously for *Bathyporeia* show that the sand population retains its zonation when migrant in the intertidal waters, but that species which are migrant from outside habitats are distributed over the whole tidal range and show no zonation. Thus, *Pontocrates norvegicus* and *P. arenarius* and the four species of *Bathyporeia* only occur in those samples taken over their immediate habitat, whilst *Gammarus locusta* occurs in practically every sample. The further investigation of the intertidal sand species involves three lines of sampling: (*a*) a series taken above the high-water mark of neap tides which will include as the main species *Bathyporeia pilosa*, (*b*) a series taken just below the mean sea level, i.e. a mid-tidal sample, which is the centre of abundance of *Pontocrates norvegicus* and *Bathyporeia pelagica*, and (*c*) a series at the low-water mark of spring tides to include *Bathyporeia elegans*, *Pontocrates arenarius*, *Pseudocuma cercaria* and *Cumopsis goodsiri* as the dominant species. These three series of samples would also supply much information about the migrants from the deeper water habitats, but they would need supplementing by samples taken over their respective habitats to show whether the population differs at various points along the migratory path. *Gammarus locusta* is a suitable species in this respect. The sampling in deeper waters must include depth samples as well as surface samples; *Pseudocuma*, for instance, is known to remain associated with the water immediately over its habitat and not to rise in numbers to the surface.

Though the data here presented furnish evidence that the behaviour of the species changes at different times of the year, the apparent association of many species with varying lunar light intensities needs as continuous a series of samples as possible. Much further evidence is also required in regard to the time when the species rise, to show if it bears any relationship to the time of the rise of the moon and if it differs on moonlight or moonless nights. This factor may, however, be of considerably less significance than that of the degree of calmness or roughness of the tidal waters. It is probable that there is a close relationship between the calmness of the tidal waters and the degree of emergence of the species from their habitats. In view of all the factors involved, the collection of a perfect series of samples becomes almost an impossibility.

The results for the various species show that their behaviour does not follow any generalized form; but a broad distinction may be drawn, in the amphipods, between the intertidal sand-dwelling forms and the immigrant species. The migrant population in the former, typified by *Pontocrates* and *Bathyporeia*, shows all stages of maturity, whilst in the latter, typified by *Gammarus* and *Nototropis*, there is a predominance of young forms with the adults taking but little part in the migration. In the intertidal sand-dwelling

forms adults tend to predominate over the young, with the adult males showing a stronger migratory tendency than the females. The reasons for this difference in behaviour can only be assumed. It may be imagined that the behaviour in both instances serves as a means of dispersal but with a difference in the age of the dispersal phase. It may be that the sand-living forms migrate to form pairs, while this may be possible amongst algal dwellers without the necessity of migration. A more detailed study of the relationship of the species to their habitat is needed, and of their reproductive habits. The latter are known for *G. locusta* from the work of Blegvad, and it is known that many sand-dwelling species feed whilst buried in the sand, and do not migrate for the purpose of obtaining food. In *Eurydice*, however, which is a day migrant as well as a night migrant, the movement is essentially a feeding one and the absence of egg-bearing females indicates that its main purpose is not that of reproduction.

The behaviour of the various species in regard to the lunar cycle shows that *Pontocrates*, *Bathyporeia* and *Gammarus* are similar; this suggests that a factor other than feeding and reproduction may be causative, and the difference in the time of appearance in the lunar cycle between the species of these genera and *Pseudocuma* suggests that the same factor may affect different species in different ways.

Summary

The faunal analysis of forty-eight samples taken with a coarse tow-net across the intertidal waters of Kames Bay during 1936 shows that the night migrant crustacean population falls into two well-marked groups: (*a*) those species which live in the intertidal sand and perform simple vertical migrations at night-time into the intertidal waters, and (*b*) those which are carried in by the tide into the intertidal area from various habitats which lie beyond the low-water mark of spring tides. In the former group the species of the genera *Bathyporeia* and *Pontocrates* are dominant and they retain their zonation as migrants, the population consisting of individuals in all stages of maturity. This is in sharp contrast to the latter group, typified by *Gammarus locusta* and *Idotea viridis*, which occur over the whole tidal range with a population in which the young immature stages are dominant. The Haustoriids *Urothoë brevicornis* and *Haustorius arenarius* occur as inhabitants of the sand, the former appearing occasionally in the tow-net samples and the latter absent from them. The Cirolanid *Eurydice pulchra* performs both day and night migration for the purposes of feeding.

Discussion of the results indicates the lines along which further investigations may be carried out.

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THE PRESERVATION OF FISHING NETS, TRAWL TWINES AND FIBRE ROPES FOR USE IN SEA WATER

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Introduction

Several papers of this series have already appeared; the last (1936) dealt with nets and its fellow, in collaboration with Prof. J. Purser, with ropes. The best of the methods already tested have now been pitted against new methods or modifications. In particular, preservation by means of cutch, fixed by various processes, received attention.

When considering the best preservative to use, regard must be paid to the thickness of the threads of the net or the diameter of the twines and ropes. With a fine thread, adherence to the relatively large surface may be more important than penetration; whereas with a rope penetration is first and foremost necessary, coupled of course with a low solubility in sea water. Adherence may be improved and leaching away reduced by a subsequent treatment, with tar for example.

The samples were treated in the Laboratory and taken to the sea water basin at Pier Cellars, on the Cornish side of the Sound beyond Plymouth breakwater. This small basin was nearly emptied each tide. In the 1936–7 tests the samples were always totally immersed, being suspended from ropes slung across the basin. In the later tests the ropes were so placed that the samples were out of the water for 3–4 hr. each tide. Some tests were interrupted by the war scare in the autumn of 1938. The samples were replaced in December. All remaining exposures were, however, interrupted by the war in the autumn of 1939.

In order to avoid the use of heavy testing machines a lighter rope than before was used in these tests; all materials were, for uniformity, supplied by one firm, the Gourock Ropework Co., Ltd., as follows:

"Gourock" six thread three strand manila rope, breaking load 700 lb.

Six thread three strand "Yacht" manila rope, breaking load 500 lb., approximately 0·6 in. in circumference.

"Gourock special" manila trawl twine, 150s (namely 150 yards to 1 lb. weight), 160 lb. breaking load.

Cotton netting, 32s/12 ply, 100 mesh deep, 26 rows to the yard. The cotton yarn count is the number of hanks which weigh 1 lb., each hank being 840 yards in length; 32s is therefore 26,880 yards per lb., so with 12 ply the length is 2240 yards per lb.

The strength shown for the new samples is the average value as given by the maker. For samples under 100 lb. tensile strength a spring balance was used; this dial registered the maximum pull. For samples under 200 lb. a dial spring balance was used also, but the needle of this flew back at break, so the figure was hardly reliable to within 10 lb. The ropes tested were so attached, by loops, that only the length under test received any strain. All breaks were clear of the attachments. For samples which did not break in any portion at 200 lb., tension was applied by means of lead weights. Results shown are usually the average of two or three breaks, save with the lead. In some cases, however, one or more portions of sample exceeded the maximum tensile test that could conveniently be applied at the time. Two figures such as 89, 93 and a third over 100 are shown in the tables as an average of >94.

Preservatives and their Application

Coal distillation products

Crude gas-works benzene, used as a solvent for copper soaps; this blackens iron vessels because it contains sulphur compounds.

Motor benzene, a purer solvent, Anglo-American Oil Co.

Creosote oil, purchased locally.

Coal tar from local gas-works; a very thick tar, becomes moderately dry in one month.

Coal tar, "Corroid tar", specially prepared for nets by Messrs Hardman, Hull; a less viscous tar, becomes moderately dry in a fortnight.

"Coalite" low-temperature distillation products

Crude phenol, b.p. 180–230° C., a dark mobile liquid.

A neutral oil, b.p. 170–230° C. ("oil A"). Does not darken much on standing; has been extracted with alkali and with acid; kindly presented by the Director, Chemical Research Laboratory, Teddington, as was also "oil B".

"Oil B", b.p. 225–250° C. at 14 mm. pressure, extracted like oil A.

Coalite neutral oil, b.p. 100–245° C.; sp. gr. 0·971; alkali extracted, darkens on standing. Presented by Coalite Works, Gawber, Yorkshire, as were also other samples.

Coalite heavy neutral oil, b.p. 220–370° C.; sp. gr. 0·975; alkali extracted.

Coalite middle oil, b.p. 180–220° C., with 47% crude tar acids; sp. gr. 0·966.

Coalite heavy oil, b.p. 230–280° C., with 39 % crude tar acids; sp. gr. 1·018.

Coalite low temperature tar, dries moderately in about 3 weeks, rather quicker than the more viscous local tar; all drying rates are approximate and vary with the conditions.

Wood distillation products

Not used in these tests, used formerly, see this *Journal*, 1936, Vol. xx, p. 628.

Petroleum products

White spirit is a distillate between 140–200° C.; it is of low flash point (Shell Co.).

Kerosene or paraffin oil, distils at 150–300° C.; it has a higher flash point, being prepared for domestic use (Shell Co.).

Petrol, as for motor cars (Anglo-American Oil Co.).

Cutch varieties

Cutch from the Bakau and Kenya Extract Co., probably a mangrove extract, but the company's representatives in Glasgow refused all information.

"Forestal brand" cutch, from the heart wood of the South American Quebracho tree, *Quebrachia schinopsis lorentzii*.

"Elephant brand" extract, from the bark of the South African mimosa or black wattle, *Acacia decurrens* var. *mollissima*. These are completely soluble in hot water. For analyses, see Atkins, 1936, p. 629. The samples and analyses were kindly supplied by the Forestal Land, Timber and Railways Co.

Copper compounds

Copper sulphate, crystals, commercial quality. For Olie's (1918) method use a 1 % solution in water and add just enough ammonia solution to redissolve the precipitate; this requires about 44 volumes of ammonia solution (sp. gr. 0·88) for 1000 volumes of copper solution; the resultant liquid is a deep blue; it is used after cutch. Soak 10–15 min., not longer; the solution is nearly decolorized by the net.

Mixed copper soap, containing stearate with oleate, palmitate and laurate, made by Messrs Lever Bros. and sold either ready for use or in a concentrated emulsion. For use with nets it is prepared to contain about 20 % of creosote or of thick mineral oil. We are indebted to Lever Bros. for a number of samples.

Copper oleate, a dark green greasy solid, contains about 2 % of added creosote as supplied by Messrs Wm. Bailey and Sons, Wolverhampton, who also kindly provided samples of resinate and naphthenate.

Copper resinate, a light green dry powder, clean to handle; not very soluble in petrol, soluble in benzol, solvent naphtha and in "oil A" (neutral low-temperature tar distillate).

Copper naphthenate, a dark green greasy solid, sold for use usually in solvent naphtha or various petroleum oils. We have received samples from Messrs Bailey, the Brent Manufacturing Co. in various solvents, and have also obtained it from Scott, Bader and Co. whose source appears to be the Brent Co. It is on the market as "Cuprinol" of various grades. As a result of tests done here a certain proportion of coal tar is now incorporated with the quality sold for nets. It was first manufactured in Denmark many years ago, by Messrs Cuprinol.

A new grade of Cuprinol, specially prepared to give waterproofed fishing lines in the rivers of British Columbia was also tested. This dries with a gloss on the outside of the tin but is not brittle.

Miscellaneous preserving agents

Two organic mercurial preparations, kindly supplied through the "Pest Control Research Committee" and Imperial Chemical Industries, Ltd., were also tried. DS 836 was a miscible oil product, with mercury content 5%. DS 837 was a paraffin oil solution, with mercury content 3·6%. They were used diluted with water, 1 vol. to 100 and 1 vol. to 70 respectively, giving 0·05% Hg.

"Shirlan" was also tried. It is an anti-mildew agent introduced by the British Cotton Industry Research Association for use on sized cloth. It was of course never intended for use in sea water.

A waterproofing process, the Velan treatment, was also tested. The process was applied as directed by the makers, Imperial Chemical Industries, Ltd., who also make Shirlan. Velan PF was used.

"Tectal" is a creosote preservative, prepared by Melanoid, Ltd. of Tipton, one of the Mond group. Through the courtesy of the Belfast Ropework Co., Ltd., we were provided with a sample and analysis, showing its relation to coal-tar oil.

	Coal-tar oil	Tectal
Sp. gr.	1·03	0·99
Flash point	70° C.	90° C.
Boiling range	130–140° C.	200–360° C.
Phenols	10–15%	35%
Viscosity	2·5	1·6

Results of Tests

Experiments of 1937–8: *tests with copper soaps* (Table I)

The aim of the tests shown in Table I was to study the relative merits of copper soaps in various solvents and at various dilutions. A few other preservatives were also tried; the most effective of these on nets was a sample believed to have a modified cutch bichromate treatment, No. 28. This did as well as No. 22, copper resinate in tar, and as Lever's copper soap mixture in creosote oil. Very curiously both outlasted No. 9, copper oleate in tar, which is usually the best on nets. Since No. 28 did so well, special attention

in the waters over their immediate habitat and that they do not perform such extensive horizontal migrations as the young forms. Further sampling should prove interesting. Fage (1933) records a somewhat similar population at Concarneau, in which the young forms predominate over a few adult males.

Mr Elmhirst is of the opinion that this species comes in when there is much drift algal detritus in the tidal waters.

Marinogammarus spp. occurred in five samples only: No. 8, one; No. 19, one; No. 42, one; No. 46, one; No. 47, four. Of the eight individuals seven were young forms with one egg-bearing female. The data are scanty but the same general features as in *G. locusta* are indicated.

Nototropis swammerdami.

The habitat of this species is amongst the sublittoral algae. Table II shows that it occurred in twenty of the night tow-net samples, which indicates that it is migratory throughout the year; but as with the other species the extent of the migration is very variable. Three of the samples account for 84% of the total number recorded. The samples in which it occurs were taken at all stages of the tide, but it only occurs in abundance in those taken in the lower third of the neap-tide range and those near low water. Continuous sampling in this region would probably show its occurrence to be more regular. All stages of maturity are represented (Table III), with breeding females present only in the samples with a large number of individuals and forming 10% of the total. Adult males are relatively scarce, 6% of the total, with the young forms predominating. Thus this species shows migratory features similar to those of *Gammarus locusta*. Fage (1933) records both *N. guttatus* and *N. swammerdami*, the population consisting mainly of adult males, and Tattersall records *N. vedlomensis* as a night migrant in the Clare Island survey. Other authors also record its pelagic habit.

Calliopius rathkei.

Nine samples scattered over the year contain this species in small numbers. The data are scanty but suggest that it is more numerous during the winter than the summer months, and, as with *Nototropis swammerdami*, it is abundant in the low-water samples. The habitat is amongst sublittoral algae; Sars (1891) records that it occurs in Norwegian waters "in great shoals, swimming actively near the beach, and ascending it according as the tide flows up". Tattersall records it as a night migrant.

Apherusa spp.

This genus is represented by the three species *A. jurinei* (M.-Edw.), ten individuals in seven samples, *A. bispinosa* (Bate), six individuals in three samples, and *A. cirrus* (Bate), one individual, occurring from May to December. It is noteworthy that the individuals are either adults or immature forms and none of the adult females were egg-bearing. Many authors record the pelagic

habit of the species in this genus. Thus Russell (1927) records the abundance of *A. ovalipes* and *A. clevei* in the day-time in the waters of the English Channel; they were absent from the surface layers but abundant from 20 m. depth, 10 min. hauls giving 3480, 6480 and 6940 individuals. In dealing with hauls taken at night-time in summer, he further records (1931), that during 1925 (and probably showing the same behaviour in 1926) there was a marked upward movement at night, the species being evenly distributed from the surface downwards. Samples taken throughout the year 1930 and part of 1931 (Russell, 1934) show the species to be abundant from late June to September, reappearing in April 1931. Fage lists *A. bispinosa* at Concarneau with males and females in almost equal numbers and notes that the species is exceptional in that its abundance is not affected by the light employed.

Other amphipods.

Attention may be drawn to *Dexamine thea*, seventeen individuals from six samples, and *Stenothoë monoculoides*, seven individuals from five samples, as adding to the list of algal dwellers which may be included under the species performing a night migration. The data for the sand dwellers *Megaluropus agilis* (Table III) and *Periculodes longimanus*, six individuals from two samples, does not represent the extent of their migration, since Elmhirst (1932) has shown that samples taken at two fathoms depth near the low-water mark of spring tides yield these two species in considerable numbers. The samples were taken on a night in March and again in June and successive sampling at 3 hr. intervals from 6 p.m. to 6 a.m. gave maximum hauls at 9 p.m. and midnight. *Metaphoxus fultoni* was recorded in one sample only, but its occurrence as a night migrant in the waters of the Firth of Clyde is recorded by Patience (1909) in samples taken during July at one fathom from the bottom. Males were more abundant than females. *Podoceros falcatus*, three individuals from three samples, *Erichthonius braziliensis*, two individuals from two samples, *Siphonoecetes colleti*, two individuals, *Phtisca marina*, one individual, *Hyale* sp. must be regarded as chance occurrences due to storm action.

Eurydice pulchra.

This species occurs in thirty-seven of the samples (Table II). The samples indicate its presence throughout the year and at all tide levels, with a tendency, shown also by its distribution in the sand, to be more abundant in the upper and middle portion of the neap-tide range. It is probable that this species is as equally a day migrant as a night migrant, although actual figures are not available to substantiate this statement. Observations carried out on this species in the laboratory show that it obtains food by capturing other living organisms in the plankton, tearing a rent in their skin and disembowelling them by the use of the anterior peraeopods. On the beach it may be observed that they rise out of the sand with the inflowing tide, proceed to feed im-

mediately and sink again into the sand with the retreating tide. The migration into the tidal waters is thus essentially a feeding one. Details of the annual life cycle are not available but casual observations suggest that two broods, a spring and an autumn, are produced.

Idotea viridis.

The occurrence of this species in twenty-one of the samples suggests that it is migratory throughout the year from its habitat in the littoral and sub-littoral algae. The numbers in the samples are very variable, four of them accounting for 81 % of the total. A notable feature is the dominance of young forms with the numbers rapidly decreasing as size advances. The figures are, under 2 mm. 60, at 3 and 4 mm. 73, at 5 and 6 mm. 32, at 7 and 8 mm. 4, over 8 mm. 8. Thus those under 4 mm. comprise over 75 % of the total. Howes (1939) records that in a saline lagoon in Essex this species attains maturity at 5 mm. in the female and 6 mm. in the male, although very few are mature at this size. Assuming that this population attains similar sizes the absence of the adult stages becomes notable. One egg-bearing female was obtained. When the data for the whole year are plotted against a lunar month it is noted that the species occurs throughout the month but with a definite tendency to be more abundant in the period immediately preceeding the new moon. The migrations of this species recall those recorded here for *Gammarus locusta* and a comparison of the sample numbers shows that the maximum number of both species occurs in the same samples. Elmhirst is definitely of the opinion that the occurrence of *I. viridis* is associated with drift weed in the tidal waters. Thus the amount of algal detritus must be considered as a contributory factor in the migration of both species.

Fage (1933) draws a distinction between the pelagic migration of the Cirolanidae on the one hand and the Idoteidae on the other. In the former the egg-bearing females always remain associated with their "substratum" whatever that may be, and the pelagic migrants are either males or "young" forms, whilst in the latter the thigmotropism which associates them with their substratum during the day is obscured at night-time and all stages of maturity are represented in the night migrant population. This conclusion is partially substantiated by the above observations on *Eurydice pulchra* and *I. viridis*.

Cumopsis goodsiri.

Table I shows that this species occurs in the sand samples from St. 28 to low water mark, and, although never abundant, it occurs in every sample. Table II shows that it was present in eleven of the tow-net samples between May and December but only in numbers during late June and July. The samples in which it occurs were taken mainly within its range as shown by the sand samples, its abundance occurring in the lower third of the neap-tide range; but its absence from many samples suggests that it is spasmodic in its

migratory habits. Of the eighty individuals obtained seventeen were egg-bearing females and twelve adult males, with immature forms of both sexes predominating and young forms absent.

Pseudocuma cercaria.

Of the forty-eight samples sixteen include this species. It will be recalled that it only occurs in sand samples taken near low water. Similarly, it only occurs in numbers in those night tow-net samples taken either at the low-water level of spring tides or in the lower third of the neap-tide range. An occasional specimen occurs in the mid-tidal samples and exceptionally in the upper third of the neap-tide range. It must be regarded mainly as a tidal immigrant from the sand below low-water mark, although the centre of its abundance needs further investigation. It differs from other tidal immigrants in being restricted to low water. Many authors have commented upon the relationship between cumaceans and moonlight. The present data when arranged on a lunar month basis shows two definite peaks of density; the first over the 5th–8th day and the second over the 20th–23rd days, thus suggesting an association with lunar illumination of a certain intensity.

Elmhirst (1932), in a series of samples taken every three hours from 6 p.m. to 6 a.m. on a night in March and again in June, shows that this species is abundant in the surface waters at low tide; but at high tide, when the low-water level is covered by 2 fathoms of water, it is abundant near the sea floor and practically absent from the surface. His data further show that very few are carried in with the tide to high-water mark. The above observations substantiate in part the observations of Elmhirst, but in this investigation no depth samples were taken.

In Table III the sex and degree of maturity of the individuals are shown. The adult males were mainly of the "short antennae" type (Foxon, 1936, p. 388). Very few "fully adult" males were found. The data show that egg-bearing females are present from February to October and that they represent 40% of the total catch. If the adult females without eggs are included, the percentage rises to 65%, adult males accounting for 9% only. Thus adults predominate, with immature males and females constituting the remainder of the catches. Young forms are practically absent. Foxon, giving counts made on previous collections in this area, records males as more abundant than females and Fage makes the same observation. Further work on more extensive collections is necessary before definite statements can be made.

Other cumaceans.

Two of the low-water samples contain *Iphinoë trispinosa*, which occurs in the sand from low-water mark to some depth. *Diastylis rathkei* was recorded once, *Lamprops fasciata* once, and *Bodotria scorpioides* was found in three samples. Russell (1931) records the vertical movement of the last-named species at night-time.

Crangon vulgaris.

Young forms of this species from 4 to 10 mm. in length occurred in eight samples from June onwards. The numbers were small and a total of only twenty individuals was recorded.

Attention may finally be drawn to occasional species other than the Crustacea. Young Pleuronectids less than 12 mm. in length were present in five of the May samples, and other young fishes in some samples from May onwards. Young Nereids of 3–5 mm. were present in the June and July samples and *Scolelepis* adults in four samples. The use of a coarse tow-net avoided most of the usual smaller plankton organisms, but occasional megalopa and zoea larvae, calanoid and harpacticid copepoda and medusae were found.

Of the forty-eight samples thirty-nine contained Mysids, mainly *Schistomysis spiritus*, in varying numbers and varying degrees of maturity, many of the samples containing numerous young forms. It is hoped that these will be analysed and reported on in due course.

Discussion

As far as I am aware this series of samples, collected by Mr Elmhirst for the study of the night migrant macrofauna of the intertidal waters throughout a whole year, is the first of the kind which has been made. The main purpose of the work is to show that this field is a fruitful one for further investigation. It is not proposed to discuss in detail the possible factors which underlie the migration of the species either individually or as a whole, but rather to indicate the problems requiring further investigation and to show how this series of samples demonstrates the positions at which the collection of further samples should be made. The samples were taken, in all cases, at the edge of inflowing or outflowing tide. Thus the position of each sample is determined by the position of the tide when the sample was taken, and they have served to show the general outline of the problems involved. The main point that emerges, apart from the fact that the major part of the night migrant population consists of Crustacea, is that the population falls into two well-marked groups: (*a*) that which normally lives in the intertidal sand of the bay and becomes migrant at night-time, and (*b*) that which is carried in to the bay by the inflowing tide from other habitats. Thus, as an auxiliary study, it is necessary to know the fauna of the intertidal soil and also that of the adjacent deeper water habitats which may be (1) sand or mud habitats, or (2) algal habitats, or both. This investigation shows that both habitats contribute to the migrant population. To complete the analysis of the migrant fauna it is necessary to obtain samples of the microfauna, which in addition to the usual plankton organisms will consist of such forms as Harpacticids (Elmhirst, 1935), and also to obtain a knowledge of the fishes which both as adults and

in their young stages may migrate inshore at night-time in varying numbers at the different seasons of the year (Elmhirst, 1935; Marshall *et al.* 1939). By such studies it will eventually be possible to build up a picture of the extensive activities which occur in intertidal waters at night-time.

The data given in this paper and previously for *Bathyporeia* show that the sand population retains its zonation when migrant in the intertidal waters, but that species which are migrant from outside habitats are distributed over the whole tidal range and show no zonation. Thus, *Pontocrates norvegicus* and *P. arenarius* and the four species of *Bathyporeia* only occur in those samples taken over their immediate habitat, whilst *Gammarus locusta* occurs in practically every sample. The further investigation of the intertidal sand species involves three lines of sampling: (*a*) a series taken above the high-water mark of neap tides which will include as the main species *Bathyporeia pilosa*, (*b*) a series taken just below the mean sea level, i.e. a mid-tidal sample, which is the centre of abundance of *Pontocrates norvegicus* and *Bathyporeia pelagica*, and (*c*) a series at the low-water mark of spring tides to include *Bathyporeia elegans*, *Pontocrates arenarius*, *Pseudocuma cercaria* and *Cumopsis goodsiri* as the dominant species. These three series of samples would also supply much information about the migrants from the deeper water habitats, but they would need supplementing by samples taken over their respective habitats to show whether the population differs at various points along the migratory path. *Gammarus locusta* is a suitable species in this respect. The sampling in deeper waters must include depth samples as well as surface samples; *Pseudocuma*, for instance, is known to remain associated with the water immediately over its habitat and not to rise in numbers to the surface.

Though the data here presented furnish evidence that the behaviour of the species changes at different times of the year, the apparent association of many species with varying lunar light intensities needs as continuous a series of samples as possible. Much further evidence is also required in regard to the time when the species rise, to show if it bears any relationship to the time of the rise of the moon and if it differs on moonlight or moonless nights. This factor may, however, be of considerably less significance than that of the degree of calmness or roughness of the tidal waters. It is probable that there is a close relationship between the calmness of the tidal waters and the degree of emergence of the species from their habitats. In view of all the factors involved, the collection of a perfect series of samples becomes almost an impossibility.

The results for the various species show that their behaviour does not follow any generalized form; but a broad distinction may be drawn, in the amphipods, between the intertidal sand-dwelling forms and the immigrant species. The migrant population in the former, typified by *Pontocrates* and *Bathyporeia*, shows all stages of maturity, whilst in the latter, typified by *Gammarus* and *Nototropis*, there is a predominance of young forms with the adults taking but little part in the migration. In the intertidal sand-dwelling

forms adults tend to predominate over the young, with the adult males showing a stronger migratory tendency than the females. The reasons for this difference in behaviour can only be assumed. It may be imagined that the behaviour in both instances serves as a means of dispersal but with a difference in the age of the dispersal phase. It may be that the sand-living forms migrate to form pairs, while this may be possible amongst algal dwellers without the necessity of migration. A more detailed study of the relationship of the species to their habitat is needed, and of their reproductive habits. The latter are known for *G. locusta* from the work of Blegvad, and it is known that many sand-dwelling species feed whilst buried in the sand, and do not migrate for the purpose of obtaining food. In *Eurydice*, however, which is a day migrant as well as a night migrant, the movement is essentially a feeding one and the absence of egg-bearing females indicates that its main purpose is not that of reproduction.

The behaviour of the various species in regard to the lunar cycle shows that *Pontocrates*, *Bathyporeia* and *Gammarus* are similar; this suggests that a factor other than feeding and reproduction may be causative, and the difference in the time of appearance in the lunar cycle between the species of these genera and *Pseudocuma* suggests that the same factor may affect different species in different ways.

Summary

The faunal analysis of forty-eight samples taken with a coarse tow-net across the intertidal waters of Kames Bay during 1936 shows that the night migrant crustacean population falls into two well-marked groups: (*a*) those species which live in the intertidal sand and perform simple vertical migrations at night-time into the intertidal waters, and (*b*) those which are carried in by the tide into the intertidal area from various habitats which lie beyond the low-water mark of spring tides. In the former group the species of the genera *Bathyporeia* and *Pontocrates* are dominant and they retain their zonation as migrants, the population consisting of individuals in all stages of maturity. This is in sharp contrast to the latter group, typified by *Gammarus locusta* and *Idotea viridis*, which occur over the whole tidal range with a population in which the young immature stages are dominant. The Haustoriids *Urothoë brevicornis* and *Haustorius arenarius* occur as inhabitants of the sand, the former appearing occasionally in the tow-net samples and the latter absent from them. The Cirolanid *Eurydice pulchra* performs both day and night migration for the purposes of feeding.

Discussion of the results indicates the lines along which further investigations may be carried out.

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Technical Assistant

Introduction

Several papers of this series have already appeared; the last (1936) dealt with nets and its fellow, in collaboration with Prof. J. Purser, with ropes. The best of the methods already tested have now been pitted against new methods or modifications. In particular, preservation by means of cutch, fixed by various processes, received attention.

When considering the best preservative to use, regard must be paid to the thickness of the threads of the net or the diameter of the twines and ropes. With a fine thread, adherence to the relatively large surface may be more important than penetration; whereas with a rope penetration is first and foremost necessary, coupled of course with a low solubility in sea water. Adherence may be improved and leaching away reduced by a subsequent treatment, with tar for example.

The samples were treated in the Laboratory and taken to the sea water basin at Pier Cellars, on the Cornish side of the Sound beyond Plymouth breakwater. This small basin was nearly emptied each tide. In the 1936–7 tests the samples were always totally immersed, being suspended from ropes slung across the basin. In the later tests the ropes were so placed that the samples were out of the water for 3–4 hr. each tide. Some tests were interrupted by the war scare in the autumn of 1938. The samples were replaced in December. All remaining exposures were, however, interrupted by the war in the autumn of 1939.

In order to avoid the use of heavy testing machines a lighter rope than before was used in these tests; all materials were, for uniformity, supplied by one firm, the Gourock Ropework Co., Ltd., as follows:

"Gourock" six thread three strand manila rope, breaking load 700 lb.

Six thread three strand "Yacht" manila rope, breaking load 500 lb., approximately 0·6 in. in circumference.

"Gourock special" manila trawl twine, 150s (namely 150 yards to 1 lb. weight), 160 lb. breaking load.

Cotton netting, 32s/12 ply, 100 mesh deep, 26 rows to the yard. The cotton yarn count is the number of hanks which weigh 1 lb., each hank being 840 yards in length; 32s is therefore 26,880 yards per lb., so with 12 ply the length is 2240 yards per lb.

The strength shown for the new samples is the average value as given by the maker. For samples under 100 lb. tensile strength a spring balance was used; this dial registered the maximum pull. For samples under 200 lb. a dial spring balance was used also, but the needle of this flew back at break, so the figure was hardly reliable to within 10 lb. The ropes tested were so attached, by loops, that only the length under test received any strain. All breaks were clear of the attachments. For samples which did not break in any portion at 200 lb., tension was applied by means of lead weights. Results shown are usually the average of two or three breaks, save with the lead. In some cases, however, one or more portions of sample exceeded the maximum tensile test that could conveniently be applied at the time. Two figures such as 89, 93 and a third over 100 are shown in the tables as an average of >94.

Preservatives and their Application

Coal distillation products

Crude gas-works benzene, used as a solvent for copper soaps; this blackens iron vessels because it contains sulphur compounds.

Motor benzene, a purer solvent, Anglo-American Oil Co.

Creosote oil, purchased locally.

Coal tar from local gas-works; a very thick tar, becomes moderately dry in one month.

Coal tar, "Corroid tar", specially prepared for nets by Messrs Hardman, Hull; a less viscous tar, becomes moderately dry in a fortnight.

"Coalite" low-temperature distillation products

Crude phenol, b.p. 180–230° C., a dark mobile liquid.

A neutral oil, b.p. 170–230° C. ("oil A"). Does not darken much on standing; has been extracted with alkali and with acid; kindly presented by the Director, Chemical Research Laboratory, Teddington, as was also "oil B".

"Oil B", b.p. 225–250° C. at 14 mm. pressure, extracted like oil A.

Coalite neutral oil, b.p. 100–245° C.; sp. gr. 0·971; alkali extracted, darkens on standing. Presented by Coalite Works, Gawber, Yorkshire, as were also other samples.

Coalite heavy neutral oil, b.p. 220–370° C.; sp. gr. 0·975; alkali extracted.

Coalite middle oil, b.p. 180–220° C., with 47% crude tar acids; sp. gr. 0·966.

Coalite heavy oil, b.p. 230–280° C., with 39 % crude tar acids; sp. gr. 1·018.

Coalite low temperature tar, dries moderately in about 3 weeks, rather quicker than the more viscous local tar; all drying rates are approximate and vary with the conditions.

Wood distillation products

Not used in these tests, used formerly, see this *Journal*, 1936, Vol. xx, p. 628.

Petroleum products

White spirit is a distillate between 140–200° C.; it is of low flash point (Shell Co.).

Kerosene or paraffin oil, distils at 150–300° C.; it has a higher flash point, being prepared for domestic use (Shell Co.).

Petrol, as for motor cars (Anglo-American Oil Co.).

Cutch varieties

Cutch from the Bakau and Kenya Extract Co., probably a mangrove extract, but the company's representatives in Glasgow refused all information.

"Forestal brand" cutch, from the heart wood of the South American Quebracho tree, *Quebrachia schinopsis lorentzii*.

"Elephant brand" extract, from the bark of the South African mimosa or black wattle, *Acacia decurrens* var. *mollissima*. These are completely soluble in hot water. For analyses, see Atkins, 1936, p. 629. The samples and analyses were kindly supplied by the Forestal Land, Timber and Railways Co.

Copper compounds

Copper sulphate, crystals, commercial quality. For Olie's (1918) method use a 1 % solution in water and add just enough ammonia solution to redissolve the precipitate; this requires about 44 volumes of ammonia solution (sp. gr. 0·88) for 1000 volumes of copper solution; the resultant liquid is a deep blue; it is used after cutch. Soak 10–15 min., not longer; the solution is nearly decolorized by the net.

Mixed copper soap, containing stearate with oleate, palmitate and laurate, made by Messrs Lever Bros. and sold either ready for use or in a concentrated emulsion. For use with nets it is prepared to contain about 20 % of creosote or of thick mineral oil. We are indebted to Lever Bros. for a number of samples.

Copper oleate, a dark green greasy solid, contains about 2 % of added creosote as supplied by Messrs Wm. Bailey and Sons, Wolverhampton, who also kindly provided samples of resinate and naphthenate.

Copper resinate, a light green dry powder, clean to handle; not very soluble in petrol, soluble in benzol, solvent naphtha and in "oil A" (neutral low-temperature tar distillate).

Copper naphthenate, a dark green greasy solid, sold for use usually in solvent naphtha or various petroleum oils. We have received samples from Messrs Bailey, the Brent Manufacturing Co. in various solvents, and have also obtained it from Scott, Bader and Co. whose source appears to be the Brent Co. It is on the market as "Cuprinol" of various grades. As a result of tests done here a certain proportion of coal tar is now incorporated with the quality sold for nets. It was first manufactured in Denmark many years ago, by Messrs Cuprinol.

A new grade of Cuprinol, specially prepared to give waterproofed fishing lines in the rivers of British Columbia was also tested. This dries with a gloss on the outside of the tin but is not brittle.

Miscellaneous preserving agents

Two organic mercurial preparations, kindly supplied through the "Pest Control Research Committee" and Imperial Chemical Industries, Ltd., were also tried. DS 836 was a miscible oil product, with mercury content 5%. DS 837 was a paraffin oil solution, with mercury content 3·6%. They were used diluted with water, 1 vol. to 100 and 1 vol. to 70 respectively, giving 0·05% Hg.

"Shirlan" was also tried. It is an anti-mildew agent introduced by the British Cotton Industry Research Association for use on sized cloth. It was of course never intended for use in sea water.

A waterproofing process, the Velan treatment, was also tested. The process was applied as directed by the makers, Imperial Chemical Industries, Ltd., who also make Shirlan. Velan PF was used.

"Tectal" is a creosote preservative, prepared by Melanoid, Ltd. of Tipton, one of the Mond group. Through the courtesy of the Belfast Ropework Co., Ltd., we were provided with a sample and analysis, showing its relation to coal-tar oil.

	Coal-tar oil	Tectal
Sp. gr.	1·03	0·99
Flash point	70° C.	90° C.
Boiling range	130–140° C.	200–360° C.
Phenols	10–15%	35%
Viscosity	2·5	1·6

Results of Tests

Experiments of 1937–8: *tests with copper soaps* (Table I)

The aim of the tests shown in Table I was to study the relative merits of copper soaps in various solvents and at various dilutions. A few other preservatives were also tried; the most effective of these on nets was a sample believed to have a modified cutch bichromate treatment, No. 28. This did as well as No. 22, copper resinate in tar, and as Lever's copper soap mixture in creosote oil. Very curiously both outlasted No. 9, copper oleate in tar, which is usually the best on nets. Since No. 28 did so well, special attention

TABLE I

Tensile strengths (mean of three tests) of manila rope, trawl twine and cotton netting immersed in basin of clean sea water, replenished at half-tide but never dry, near Cawsand, outside Plymouth Sound breakwater. Samples immersed about 8 months after treatment. Time in air after removal, before testing, shown in italics. Immersed 27. viii. 37. Tensile strength in lb. Nets tested by hand (G = good).

Sample no.	Material tested ... ... / Period of treatment ... (months)	"Yacht" manila			Twine				Net	
		6	12+5	%	3	6	12+5	%	2¼	6
25	Untreated, new or kept in air, dry*	500	—	100	160	—	119*	75	—	—
1	Untreated, immersed	0	—	0	24	0	—	0	0	—
2	Lever's copper soap, ready for use	>100	153	31	> 95	53	24	15	0	—
3	Do., conc., diluted with oil A, 1–4 vol.	88	76	15	66	9	0	0	0	—
4	Do., conc., diluted with oil A, 1–9 vol.	54	50	10	58	0	—	0	0	—
5	Do., conc., diluted with creosote oil, 1–4 vol.	>100	149	30	> 85	41	44	27	F.G.	G
6	Do., conc., diluted with creosote oil, 1–9 vol.	>100	168	34	> 99	32	0	0	0	—
7	"Tectal"	60	39	8	47	0	—	0	0	—
8	Copper oleate 1 lb., "Corroid" tar 1 lb., oil A 1 gal.	> 93	77	15	>100	21	0	0	0	—
9	Do., 1 lb., "Corroid" tar 1 gal.	> 98	100	20	>100	20	36	22	V.G.	0
10	Do., 1 lb., "Coalite" tar 2 lb., oil A 1 gal.	>100	80	16	66	21	0	0	0	—
11	"Cuprinol", special British Columbia grade	>100	173	35	>100	**75**	0	0	0	—
12	Do., green for nets, with tar added by makers	>100	**221**	**44**	67	64	0	0	0	—
13	Do., with equal vol. of petrol	>100	84	17	> 81	40	0	0	0	—
14	Copper naphthenate 30% (2·4% Cu) in naphtha, Brent	>100	143	29	82	50	45	28	0	—
15	Do., 30% (2·4% Cu) in white spirit, Brent	>100	100	20	>100	51	0	0	0	—
16	Do., 30% (2·4% Cu) in industrial alcohol, Brent	>100	188	38	> 91	52	55	34	0	—
17	Do., water-resisting mixture in naphtha, Brent	>100	148	30	> 95	69	**64**	**40**	0	—
18	Do., water-resisting mixture in white spirit, Brent	>100	139	28	70	58	55	34	0	—
19	Do., preservative mixture, Brent	69	44	9	54	0	—	0	0	—
20	Do., Bailey 10% (0·8% Cu), "Corroid" tar 1 lb. per gal., in creosote oil	>100	100	20	59	0	—	0	0	—
21	Do., Bailey 10% (0·8% Cu), "Corroid" tar 1 lb. per gal., in oil A	> 95	83	17	71	0	—	0	0	—
22	Copper resinate 1 lb., "Corroid" tar 1 gal.	90	65	13	53	0	—	0	G	G
23	Do., 1 lb., petrol 1 gal.	30	0	0	26	0	—	0	0	—
24	Do., 1 lb., creosote oil 1 gal.	>100	100	20	69	0	—	0	F.G.	0
26	Mercurial compound DS 836, dil. to 0·05% Hg	21	0	0	50	0	—	0	0	—
27	Do., DS 837, dil. to 0·05% Hg	23	0	0	32	0	—	0	0	—
28	Gourock Rope Co., latest cutch bichromate net treatment	—	—	—	—	—	—	0	V.G.	G

* The three surviving nets had rotted after 7 months.

was paid to cutch bichromate methods in the next series, since heretofore these had given occasional good results but were on the whole erratic. It may be seen that only three nets remained sound for 6 months, and none for longer. In practice, however, retreatments at shorter intervals may lengthen life, as described in Atkins, 1936, Table I. On the other hand seven of the trawl twines were still tolerably strong after a total immersion period of a year and then 5 months in air. These did not include either Nos. 22 or 28, but No. 5 is in, fifth on the list with 27%. A copper naphthenate water-resisting mixture in naphtha, No. 17, was so effective that the twine had 40% of its initial strength after this long immersion. These Brent Co. naphthenate samples provided the first four on this list, but the use of copper naphthenate is conditioned by a suitable solvent, for No. 19, with a low temperature tar distillate failed.

The Cuprinol naphthenate mixtures, one of which headed the trawl twine list after 6 months, all perished with the longer period; Lever's concentrate (which is largely oleate) diluted with creosote oil and copper oleate in tar remained relatively strong.

With the closely twisted "Yacht" manila penetration is more important, and Cuprinol and Brent naphthenates take the first three places, with a more dilute (1 to 9) Lever concentrate a good fourth.

Experiments of 1938–9: *tests with cutch, etc.* (Table II)

Table II is occupied with a remarkable array of failures, nearly all modifications of the cutch treatment. The most successful for nets were cutch bichromate methods, six of which survived the first water immersion test, along with twelve with various copper soap or tar treatments similarly exposed and shown in Table III. As all these perished during air storage while wet, they were repeated in 1939 and four bichromate treatments and eight of those in Table III survived a longer period, 27 weeks in the sea and 14 on a gravel path in the open.

For trawl twines the Gourock sample was best but very poor compared with the methods of Table III; next in Table II comes mangrove cutch with Olie's method or hot bichromate. The same held good for "Yacht" manila rope save that as one sample with Olie's method failed the result was taken as zero. For the Gourock manila Olie's method gave 20% of the initial value after the full $14\frac{1}{2}$ months in water and 6 in air; the same was given by No. 16, a bichromate with sulphur dioxide, and four bichromate dips were somewhat inferior. All, however, are far surpassed by results in Table III.

Experiments of 1939: *further tests on various preservatives* (Table III)

Eight samples of netting survived the more extended 1939 test, which was interrupted by the war. It is probably correct to judge between these survivals by taking into consideration the results with trawl twines which had

TABLE II

Tensile strengths of specimens immersed in sea water basin 4. iv. 38–29. ix. 38. Those sound immersed again 12. xii. 38–9. ix. 39. Tested 20. xii. 39. During air storage, 2½ months in 1938, the nets remaining were left wet in error and all rotted. Life of untreated net 14 weeks first set, 16 weeks second, and 12 weeks for 1939 set. Ropes had 14½ months in water and 6 in air; twines had 7½ and 2½. A and B represent two sets treated similarly.

Material tested	Gourock manila rope			Yacht manila rope			Trawl twine	Cotton net
Sample No.	A lb.	B lb.	Mean % Dec. 1939	A lb.	B lb.	Mean % Dec. 1939	Mean % Feb. 1939	Percentage life
48 Untreated new dry	700	700	100	500	500	100	100	—
1 Untreated immersed	22	26	3	0	0	0	0	100
2 Mangrove cutch	23	24	3	0	0	0	0	110
3 Do., with Olie's method	83	191	20	0	56	0*	17†	115
44 Mimosa cutch	55	112	12	0	0	0	4	105
46 Do., with Olie's method	54	100	11	0	0	0	9	115
45 Quebracho cutch	70	57	9	0	0	0	6	100
47 Do., with Olie's method	84	107	14	0	0	0	12	110
6 As 2, then 5 min. in bichromate 15° C.	91	147	17	0	0	0	14†	> 160‡
7 Do., then ½ min. in bichromate 60° C.	70	120	14	42	36	8	17†	> 160‡
8 Do., then ½ min. in bichromate 40° C.	95	125	16	0	0	0	12†	130‡
9 Do., then ½ min. in bichromate 15° C.	95	150	17	0	0	0	12	> 160‡
10 Do., then 5 min. half-neutralized in bichromate 15° C.	0	92	0	0	0	0	7	115
11 Do., then ½ min. half-neutralized in biochromate 60° C.	27	107	10	0	0	0	11	120
12 Do., then ½ min. half-neutralized in bichromate 40° C.	23	117	10	0	0	0	8	135
13 Do., then ½ min. half-neutralized in bichromate 15° C.	0	120	0	0	0	0	9	130
14 As 8, then fresh water, pass SO_2 for 1 min.	36	165	14	0	0	0	8	150
15 As 8, but pass SO_2 into bichromate 1 min. before dip	56	110	12	0	0	0	9	145
16 As 9, continue as 14, viz. at 15° C.	150	137	20	26	0	0	13†	> 160
37 Gourock cutch bichromate treatment	—	—	—	52	63	11	22†	> 160
41 Do., new treatment	—	—	—	—	—	—	—	> 160
42 Untreated control for 41	—	—	—	—	—	—	—	110
38 Velan treatment, 2½% room temperature	45	40	6	0	0	0	2	135
39 Do., dried on water radiator and air oven 5 min. at 120° C.	57	72	9	0	0	0	2	105

* When one value is zero the mean is arbitrarily taken as zero.

† All the second set were rotten after the 7½ months in water, save the six marked. These were put back in water; all were rotten 11 weeks later.

‡ On repetition in 1939 these stood 27 weeks and 14 weeks on a gravel path, namely, a life of over 225% in water. Of one set Nos. 37 and 41 were rotten after the air exposure test. The duplicates were then poor.

TABLE III

Tensile strengths of ropes, trawl twine and cotton net immersed in sea water in among the specimens of Table II, and for the same periods, save that second set of trawl twine lasted longer. Ropes had 14½ months in water and 6 months in air, also second set of twines; first set of twines had 7½ months in water and 2½ months in air.

Material tested ...		Gourock manila rope			Yacht manila rope			Trawl twine		Cotton net Percentage life
Sample No.		A lb.	B lb.	Mean % Dec. 1939	A lb.	B lb.	Mean % Dec. 1939	A Mean % Feb. 1939	B Mean % Dec. 1939	Mean of two
48	Untreated new kept dry	700	700	100	500	500	100	100	100	—
1	Untreated immersed	22	26	3	0	0	0	0	0	100
2	Mangrove cutch	23	24	3	0	0	0	0	0	110
4	Do., then creosote oil cold	190	212	29	57	120	18	36	22	150
5	Do., then "Corroid" tar, cold	250	218	34	82	100	18	36	31	> 160*
21	Creosote oil, cold	175	157	24	26	29	5	25	R 20/4†	115
22	"Corroid" tar, cold	212	166	27	27	35	6	29	R 20/4	155
40	Gourock Rope Co. tar, 3 min. at 49° C.	—	—	—	118	120	24	76	R 3/5	> 160
43	Do., using Plymouth tar	—	—	—	86	160	25	55	M 11/9	140
23	Copper oleate 1 lb. in "Corroid" tar, cold	> 300	> 300	> 43	190‡	195‡	38	> 57	M 11/9	> 160*
24	As 2, then as 23	> 300	> 300	> 43	165‡	190‡	35	> 60	35	> 160*
25	As 3, then as 23	> 300	> 300	> 43	150‡	155‡§	30	50	45	> 160*
26	Copper naphthenate (Bailey) in tar, like 23	> 300	> 300	> 43	77	150	23	56	M 3/5	> 160
27	As 2, then as 26	> 300	> 300	> 43	187	160	35	49	35	> 160*
28	As 3, then as 26	> 300	> 300	> 43	193	280‡	47	53	48	> 160*
29	Copper resinate in tar like 23	> 300	> 300	> 43	132	230‡	36	34	M 3/5	> 160
30	As 2, then as 29	> 300	> 300	> 43	270‡	195‡	46	54	41	> 160*
31	As 3, then as 29	> 300	> 300	> 43	190	190‡	38	49	35	> 160*
32	"Cuprinol" green for nets	> 300	> 300	> 43	98	230‡	33	75	24	160
33	"Cuprinol", British Columbia grade	> 300	> 300	> 43	101	190‡	29	70	21	155
34	As 32, 1 lb. tar extra per gal.	> 300	> 300	> 43	165	175‡	34	75	25	155
35	As 2, then as 32	> 300	> 300	> 43	165	150‡	31	47	35	145
36	As 2, then as 33	> 300	> 300	> 43	210‡	170‡	38	57	48	155
17	Lever's mixture ready for use	> 300	> 300	> 43	160	125‡	30	36	R 20/12	150
18	As 2, then as 17	300	> 300	> 43	174	220‡	39	59	44	> 160
19	As 3, then as 17	> 290	> 300	> 42	97	150‡	25	56	30	150
20	As 2, then as 17‖ in creosote oil, 1–4 vol.	> 270	> 300	> 41	150	195‡	34	53	36	150

* On repetition in 1939 these stood 27 weeks in Cawsand basin and 14 weeks on a gravel path, namely a life of over 225 % in water since untreated control rotted in 12 weeks. One set of No. 40 stood the test, but No. 29 failed. No. 18 was not repeated.

† R 20/4, rotten at this date in 1939; M denotes missing, viz. rotted away.

‡ Stood over 200 lb. on spring balance. Figure given is for weights applied slowly.

§ Gave 155 and 285, latter omitted from average.

‖ The mixture was used in error for the concentrate used in Table I.

the full run from 1938. Nets, twines and ropes all confirm the results obtained by Fillon (1925) with cotton nets and show that a previous cutch treatment is an improvement before the copper soaps or coal distillates are applied. It is advantageous to use tar warm, especially with ropes, as better penetration is secured. There is a great benefit from using copper soaps with the latter as against using the distillates alone or after cutch. To fix the cutch by Olie's method before applying the copper soap mixture seems an advantage with naphthenate, though not with oleate. The best preserved trawl twine and yacht manila had a final strength 44–48 % of the initial and received oleate, resinate or naphthenate mixtures after cutch; but the oleate was good for the twines especially as the penetration is poor with thick ropes.

We were unable to test breaking loads beyond 300 lb., but it is remarkable that every copper soap treatment gave an average value exceeding this limit on the 700 lb. six-thread Gourock manila rope, and only two samples in set A broke below 300 lb. The untreated rope was at this stage valueless, having only 3 % of its initial value as against over 43 %.

These results confirm and extend the earlier tests (Atkins & Purser, 1936) with 2 in. ropes of hemp, manila, sisal and coir, which showed that the preservatives are about equally good on the various fibres. The present tests were accordingly done on manila only.

Taken in conjunction with the previous results, one may conclude that while for ropes of small diameter resinate, oleate and naphthenate copper soaps are all good, yet for thick ropes the more costly naphthenate has the advantage of better penetration.

It is often said that a combination of wet and dry conditions is more destructive to nets and ropes than continual wetness. Table I shows the results of immersion of ropes for a year, and subsequent storage dry. Tables II and III give results where the specimens were out of water every tide, the total immersion being for 14 months. The two sets are not strictly comparable, but the treatments common to both had the final percentage strengths indicated, respectively, oleate in tar, 20 and 38 %; Lever's mixed copper soap, 31 and 30 %; Cuprinol, 44 and 33 %; Cuprinol, British Columbia grade, 35 and 29 %. The results are therefore inconclusive, at least for preserved materials, for which the leaching out of the preservative may offset the advantage, if any, of remaining wet. With trawl twines the evidence was also indecisive and even contradictory. It would be necessary to take a large number of samples for each treatment and to pay special attention to the humidity of the air, viz. the moisture in the fibres, in order to decide this point. Since in practice treatments have to be carried out when required no such differences were taken into account.

The treatments of the nets, which perished during wet storage late in 1938, were repeated early in 1939 and the samples were immersed as before from March 6 to September 11, 27 weeks. Those which survived were then laid out on a gravel path for 14 weeks. The treatments which remained sound are

shown in Tables II and III. In addition certain new treatments stood the test as follows:

No. 54, cutch treatment, then in bichromate at 40° C. for 1 min. with sulphur dioxide bubbling through.

No. 71, green Cuprinol (copper naphthenate solid 12% Cu) in tar, 1 lb. to 1 gal., also 74, as 71 after cutch and 75, after Olie's treatment.

No. 78, copper naphthenate (Brent) with 8% Cu in 95% alcohol, one set good, but (No. 79) both good after cutch.

No. 82. As 78, 1 lb. to 1 gal. tar, after cutch or (83) Olie's treatment.

Nos. 84–87, cutch treatments, including Olie's, followed by dilutions of concentrated Cuprinol with petrol, all failed; this solvent is clearly unsuitable. Similar treatments without cutch also failed.

A series of exposures was also begun to test the suggestion kindly sent by Mr J. S. Tait of Vancouver, B.C., that the addition of boiled linseed oil improved the value of Cuprinol. The samples were immersed on June 29 and had 10½ weeks in the basin before removal, on account of war, on September 11. Those which survived then had 14 weeks on the gravel path.

The untreated control was rotten after the water test. After the air exposure the following were in poor condition: No. 89, linseed oil; No. 98, green Cuprinol; No. 99, Cuprinol, British Columbia grade; No. 92, Cuprinol B.C. with 10% linseed oil; No. 94, Cuprinol with 10% linseed oil; No. 95, ditto with 20% linseed oil. No. 96, Olie's treatment, followed by linseed oil, gave one good and one poor net.

The following remained sound: No. 90, cutch, then linseed oil, and No. 91, as 90 with a further boiling in cutch; No. 93, 20% linseed oil in Cuprinol, B.C. grade; No. 97, copper oleate in tar 1 lb. to 1 gal.

Summary

Manila ropes and trawl twines, and cotton nets, have been immersed in clean sea water for periods up to 14 months, some with alternate wetting and drying, some wet all the time, but in both cases accompanied by storage in air after immersion. All the untreated specimens perished, but the 700 lb. manila ropes retained at least 40% of the original tensile strength in every case in which a copper soap had been included in the treatment. A previous treatment with cutch is a considerable advantage as shown by the 500 lb. manila ropes and trawl twines, though cutch alone is worthless. Coal tar distillates after cutch are, however, more useful than when used alone, and their mixture with copper soaps gives excellent results. Cutch fixed with bichromate gives tolerably good preservation on nets up to 6 months, but is a poor preservative for trawl twines and ropes which are expected to have a long life. The choice of the copper soap used depends upon the material to be preserved. Naphthenate is the most soluble and penetrates thick ropes excellently; on fine nets it leaches out easily. Oleate is cheaper, but its penetration is less; it does very well with tar on twines and nets. Resinate is the least soluble,

but is useful with creosote oil or tar. On account of their greasy nature naphthenate and oleate act as lubricants in ropes.

Immersion tests on other preservatives, kindly suggested by Dr S. G. Barker, are to be begun.

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A NOTE ON THE DETERMINATION OF VERY SMALL QUANTITIES OF HYDROXYLAMINE BY BLOM'S METHOD

By H. Barnes, B.Sc., B.A.

In a study on the possible occurrence of hydroxylamine as an intermediate compound in the oxidation of ammonium salts to nitrites in sea water (see Cooper, 1937), the method of Blom was tried in order to estimate the hydroxylamine. The method consists in the oxidation of the hydroxylamine by a solution of iodine in acetic acid, removal of the excess of iodine with $N/10$ thiosulphate, and estimation of the nitrite so produced by the Griess method; the method has been used by several workers for the estimation of small amounts of hydroxylamine in biological material.

The method had not been used for such small amounts of hydroxylamine as would be expected in sea water, and it was therefore tested at high dilutions. It was found that nitrite itself, however, could not be recovered after treatment with the above reagents, and it was noticed that in many cases a precipitate (probably sulphur) was produced, and a distinct smell of hydrogen sulphide was often apparent. It was thought probable therefore that the loss was due to the interaction of the nitrite or the red dye with the thiosulphate used for removing the excess of iodine. This view was confirmed by noting the removal of the red colour, the appearance of a precipitate, and the smell of hydrogen sulphide when a solution of thiosulphate was added to a solution of the dye.

Experiments were therefore set up to determine the amount of thiosulphate that could be present in excess without interfering with the estimation. Varying amounts of thiosulphate were added to a known concentration of nitrite (30 mg. per $m.^3$), and the colour produced on adding the Griess reagents was then compared with that obtained without the addition of thiosulphate. The solutions were placed in 100 ml. cylinders and matched in the usual manner. The results are shown in Table I.

It is clear from the Table that when the concentration of the thiosulphate is greater than about 1 mg. per litre the nitrite estimation is inaccurate, and that when the concentration is about 6 mg. per litre only 50 % of the nitrite is found. Taking this latter figure for illustration, although it represents a very considerable excess when compared with nitrite present, it is very small in terms of $N/10$ thiosulphate used in the removal of iodine in the normal process. According to these results, if in estimating the strength of solution of hydroxylamine, equivalent to a nitrite production of 30 mg. per $m.^3$,

3/500 of a ml. of thiosulphate more than that required to remove the excess iodine were added, only half the nitrite actually produced would be found. It is clearly very difficult to add the thiosulphate within these limits.

Table I

Conc. of thiosulphate (mg. per litre)	Reading of control	Conc. of thiosulphate (mg. per litre)	Reading of control
0·025	100	1·5	82
0·05	100	2·0	71
0·15	100	3·0	66
0·2	100	4·0	62
0·25	100	5·0	56
0·3	100	6·0	53
0·35	100	7·0	50
0·4	95	8·0	51
0·45	99	9·0	42
0·5	100	11·0	41
0·75	100	14·0	32
1·00	100		

Conc. of nitrite 30 mg. per m.^{3}

I should like to thank Dr Cooper for suggesting this work and for his continued interest during its progress.

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A NOTE ON THE CHANGES IN WATER CONTENT OF THE LOBSTER (*HOMARUS VULGARIS* M.-EDW.) DURING MOULT

By A. G. Lowndes and N. K. Panikkar

From the Plymouth Laboratory

One of the lobsters kept in the tanks of the Plymouth Laboratory moulted on the night of 20 August 1940. This opportunity was taken to examine the changes in water content and osmotic pressure of the freshly moulted as compared with unmoulted lobsters. Though only one recently moulted individual has been examined, the results seem to be worthy of note since so far as we are aware no data are available on the subject in regard to *Homarus*. The biology of moulting among lobsters has received the attention of many investigators (vide Herrick (1895) and Drach (1939) for summary and literature).

The water content was determined by distilling the fresh lobster together with a known weight of sea water under xylol. This method is a modification of that of Dean and Stark which one of us (A. G. L.) has tried on a number of animals and found to give accurate results. The density was estimated by a modification of a method previously described (Lowndes, 1938). Osmotic pressure of blood and the external medium were measured by Baldes's (1934) modification of the Hill thermoelectric technique, as employed by one of us (N. K. P.) in the study of prawns and other crustaceans. The water content of the moulted skin was calculated from its dry weight taken after dehydrating in a hot air oven for 48 hr. at 105° C. Osmotic pressure was measured 17 ± 6 hr. after moult; density and water content after 34 ± 6 hr. The temperature of sea water at which the density was estimated was 17° C. Both lobsters were 4–5 years old as judged by Elmhirst's (1930) growth curve. The results obtained are given in Table I.

The higher values for density and sinking factor are just what one would expect from the highly calcified exoskeleton in the lobster of late intermoult phase. *Homarus* is a stenohaline invertebrate which is isotonic with its surroundings and it is interesting to note that more or less the same degree of osmotic equilibrium with the surroundings is observed in less than one day after moult. Hence, if there is any rapid rise in osmotic pressure prior to moult, as has been observed in some Crustacea, this anisotonicity disappears soon after moulting. The values of water content indicate that a lobster of fresh weight 100 g. loses about 28 g. when its skin is shed, and that it absorbs about 47 g. of water within 34 ± 6 hr. after moulting. Thus an increase in

weight of 19 % is observed in so short a period. Elmhirst (1930) has shown that this increase in weight during the post-moult phase may be as high as 38 %,

TABLE I

	Density g. per ml.	Sinking factor*	Osmotic pressure of blood % NaCl	Osmotic pressure of medium % NaCl
Soft lobster, ♀	1·077	1050	3·410	3·338
Hard lobster, ♀ (late intermoult)	1·158	1128	3·403	3·346

Lobster	Volume ml.	Gross weight g.	Wt. of water g.	% water	% water including moulted skin
Soft: ♀ after moult	110·02	118·47	97·43	82·24	77·30
Moulted skin alone	—	45·14	29·04	64·33	
Hard: ♀ late intermoult	136·13	157·61	105·16	66·82	66·68

* Sinking factor $= \frac{\text{Density of organism}}{\text{Density of medium}} \times 10^3$.

It may be seen from these figures that:
The amount of water in a lobster of dry weight 33·32 g. after moult

$$= \frac{33{\cdot}32 \times 77{\cdot}3}{22{\cdot}7} = 113{\cdot}5 \text{ g.}$$

Therefore the amount of water absorbed $= 113{\cdot}5 - 66{\cdot}68 = 46{\cdot}82$ g.

but it may be noted that the post-moult phase during which it takes place lasts from 15 to 30 days.

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THE OCCURRENCE AND BREEDING OF *SAGITTA ELEGANS* VERRILL AND *SAGITTA SETOSA* J. MÜLLER IN PARTS OF THE IRISH SEA

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(Text-figs. 1–2)

CONTENTS

INTRODUCTION

Investigations in recent years have recognized the fact that certain species of *Sagitta* are associated with particular bodies of water, and that when these species are swept by currents into foreign water masses they exist there for limited periods of time. The relatively large size of *Sagitta* makes them convenient to handle and increases their value as representatives of their respective localities.

There has been no previous prolonged examination of the *Sagitta* in Liverpool Bay with respect to the present classification of the species. Russell (1935, p. 323) has recorded *S. setosa* J. Müller and *S. elegans* Verrill from the north of Ireland and from Port Erin. The present investigation has demonstrated that the *Sagitta* present in Liverpool Bay are *S. elegans* and *S. setosa*. The latter species had not been recorded before from this region. During the period of my study it was the dominant form in these coastal waters.

The work of Russell (1932*a*, *b*, 1933*a*, *b*, 1935), Meek (1928), Wimpenny (1936), and others, on the life history and distribution of the species of *Sagitta*, has placed emphasis on the importance of data from other areas. As a result of their work and of the discovery of *S. setosa* in Liverpool Bay, the problem on which this paper is based is the distribution and relative abundance of *S. setosa* and *S. elegans* in parts of the Irish Sea, and the number and periodicity of their reproductive cycles.

I am indebted to Prof. J. H. Orton for general supervision of my work and for helpful advice. Mr F. S. Russell verified the maturity and classification of a number of specimens sent him. Dr Jenkins, chairman of the Lancashire and Western Sea Fisheries Committee, kindly enabled me to collect from the fishery cutters in Liverpool Bay. Mr Nicholson, operator of the cutter at Liverpool, assisted by making many tow-nettings for me. Dr R. J. Daniel, Director of Port Erin Laboratory, and members of the staff at that station, made it possible for me to study plankton samples from Port Erin. Finally, I wish to thank the various other persons who have aided me in the collection and preparation of this material.

Collecting Stations and Apparatus

Collections were obtained once a week from each of three localities, namely: Pier Head, Liverpool Docks, Liverpool; the outer Mersey Channels; and Port Erin harbour, Isle of Man.

The Pier Head station at the mouth of the Mersey River was selected because it was easily reached, would furnish a plankton sample from estuarine conditions and *Sagitta* were known to be available from there. Two nets were used: a $\frac{1}{2}$ m. stramin net sunk with a weight to an approximate depth of 6 m.; and a fine silk net (104 meshes per inch) $\frac{1}{2}$ m. in diameter suspended just beneath the surface. Both nets were allowed to remain in an ebb tide for $\frac{1}{2}$ hr. The tide at this point flowed at the rate of 1 knot.

The outer Mersey Channels include an area which extends 14 miles into the Bay from the mouth of the river. The samples were usually taken 7 or 8 miles from the mouth of the Mersey in the Queen's and Crosby Channels. Two nets were used: a $\frac{1}{2}$ m. stramin net towed at a depth of 6–8 m. (occasionally in shallower water it was towed just 3 or 4 m. deep); and a $\frac{1}{2}$ m. silk net (64 meshes per inch) towed just below the surface. The period of towing was $\frac{1}{2}$ hr. at the rate of approximately 1 knot.

In both the above stations the depth of the water and the diurnal vertical migration of the *Sagitta* were the chief factors considered in selecting the depth at which the stramin nets were towed. The vertical movement of *Sagitta* has been recorded by several investigators (Michael, 1911; Bigelow, 1924; Russell, 1935). Several tests were made to determine the extent of this movement in the comparatively shallow waters of the outer Mersey Channels. The surface towings made during these trials contained relatively few *Sagitta*. Below a few metres it was difficult to determine at what depth the animals were most numerous. I believe this rather scattered distribution was due to the continual mixing of the water layers by the strong tides in these channels. The water was always heavily silted and of low transparency. I have found on several occasions at the Pier Head, where the water was even more muddy and turbulent than farther out in the Bay, that I have captured almost equal numbers in both nets during one haul.

The third regular station from which weekly collections were obtained was the harbour at Port Erin, Isle of Man. Here two silk nets, 36 cm. in diameter with 64 and 125 meshes per inch respectively, were towed across the harbour behind a rowing boat. These towings were taken just below the surface for a period of 20 min.

Stages of Maturity

Sagitta is hemaphroditic with ovaries in the posterior portion of the body cavity and testes extended in two narrow bands, one on either side of the tail cavity. The testes mature first, filling the tail cavity with clusters of sperm cells in various degrees of development. The early indications of maturity in the ovary are an increase in size accompanied by an apparent increase in the number of eggs. In the final stage the eggs increase rapidly in size, a few at a time becoming distinctly larger than the remainder in the ovary.

Several investigators have recognized stages in the development of the germ cells which may be determined visually in the whole animal. Kramp (1917, p. 37) and Wimpenny (1936, p. 17) have each defined four main stages in the development of the gonads. These stages, though differing in some details, are very similar. Russell (1932*a*, p. 134) has simplified Kramp's divisions, describing three stages of maturity in place of four. Russell's descriptions have appeared to me to be the more suitable and I have classified my specimens according to the stages recognized by him.

These stages, designated as I, II and III, represent progressive sexual development from the young immature individual, through an intermediate form, to the adult and fully mature animal. Quoting from Russell (1932*a*, p. 134): "Stage I included all the youngest *Sagitta* in which not a single sperm mother cell was visible lying loose in the tail cavity. Stage II ranged between those individuals with the first appearing spermatocytes and those in which the tail segment was packed with spermatocytes and spermatozoa, but in which the ovaries, while appearing evident, showed little sign of swelling eggs. Stage III contained those individuals in which the ovaries were fully ripe or ripening" (e.g. contained one or more eggs very much enlarged).

Treatment of Material

Sampling. The *Sagitta* were placed in 10% formalin shortly after capture. Later the total number was counted, the stage of maturity determined and each specimen measured. If the weekly collection exceeded fifty specimens a representative fraction containing about forty individuals was separated for maturity determinations and measuring. The measurement of the body length did not include the caudal fin which is delicate and easily damaged.

Staining. In order to ascertain accurately the maturity of the sperm and ovary it was necessary to stain the animal. A successful method for staining large numbers of *Sagitta* was as follows: groups of specimens (20–30) were transferred gradually from the 10% formalin to 75% alcohol and placed in

small glass tubes ($\frac{1}{2} \times 2$ in.). Three or four drops of a concentrated solution of borax carmine were added to the tubes and gently mixed. A day later the borax carmine solution was poured off and replaced by 75 % alcohol and one drop of concentrated hydrochloric acid. The *Sagitta*, now a light red, were kept in the acid alcohol until by inspection the body wall appeared translucent (20–30 min.); the ovary and testes were still red. At this point the acid alcohol was replaced with 75 % alcohol. A second change was sometimes given if continued fading was noticed. The advantages of this method are that large numbers of specimens can be handled with a minimum of effort, and little or no shrinkage or distortion of the *Sagitta* will take place.

Port Erin *Sagitta*

Port Erin material, 1928–34. The data for *S. elegans* at Port Erin for 1928–34 inclusive, are shown in Table I and Fig. 1. The weekly catches during

Table I. Percentages of *S. elegans* Grouped in Stages I, II and III

Taken from Port Erin 1928–34

Month	Stage I %	Stage II %	Stage III %	No. counted from sample
Jan.	4	69	27	89
Feb.	5	49	46	120
Mar.	14	41	45	46
Apr.	27	50	23	105
May	52	47	1	84
June	60	40	0	122
July	82	16·5	1·5	209
Aug.	91	9	0	192
Sept.	94	3	3	135
Oct.	98	2	0	120
Nov.	78	22	0	108
Dec.	37	63	0	128

these years had been combined in fifty-two grouped samples. Each sample contained the plankton collected in that week for all of the years under consideration. These weekly catches have, for brevity and clarity, been graphed in monthly units.

Fig. 1 presents the relative occurrence of the three maturity stages and their relative percentage frequency. Length (mm.) is plotted on the ordinate of the graph and percentage frequency on the abscissa. Stages I, II and III have been treated separately in each month. The absence of a particular stage in the graph for any month is evidence that such a stage is scarce or wanting in the plankton for that period. A similar graph (Fig. 2) has been drawn of the weekly plankton catches of *S. setosa* taken in the outer Mersey Channels during 1937. The appearance of *S. setosa* at Port Erin and *S. elegans* in the outer Mersey Channels was too sporadic to graph in this manner; however, for a short period in the year they became relatively abundant (Pierce & Orton, 1939).

The graph of *S. elegans* from Port Erin (Fig. 1) shows that the main spawning period is during the months of January, February, March and

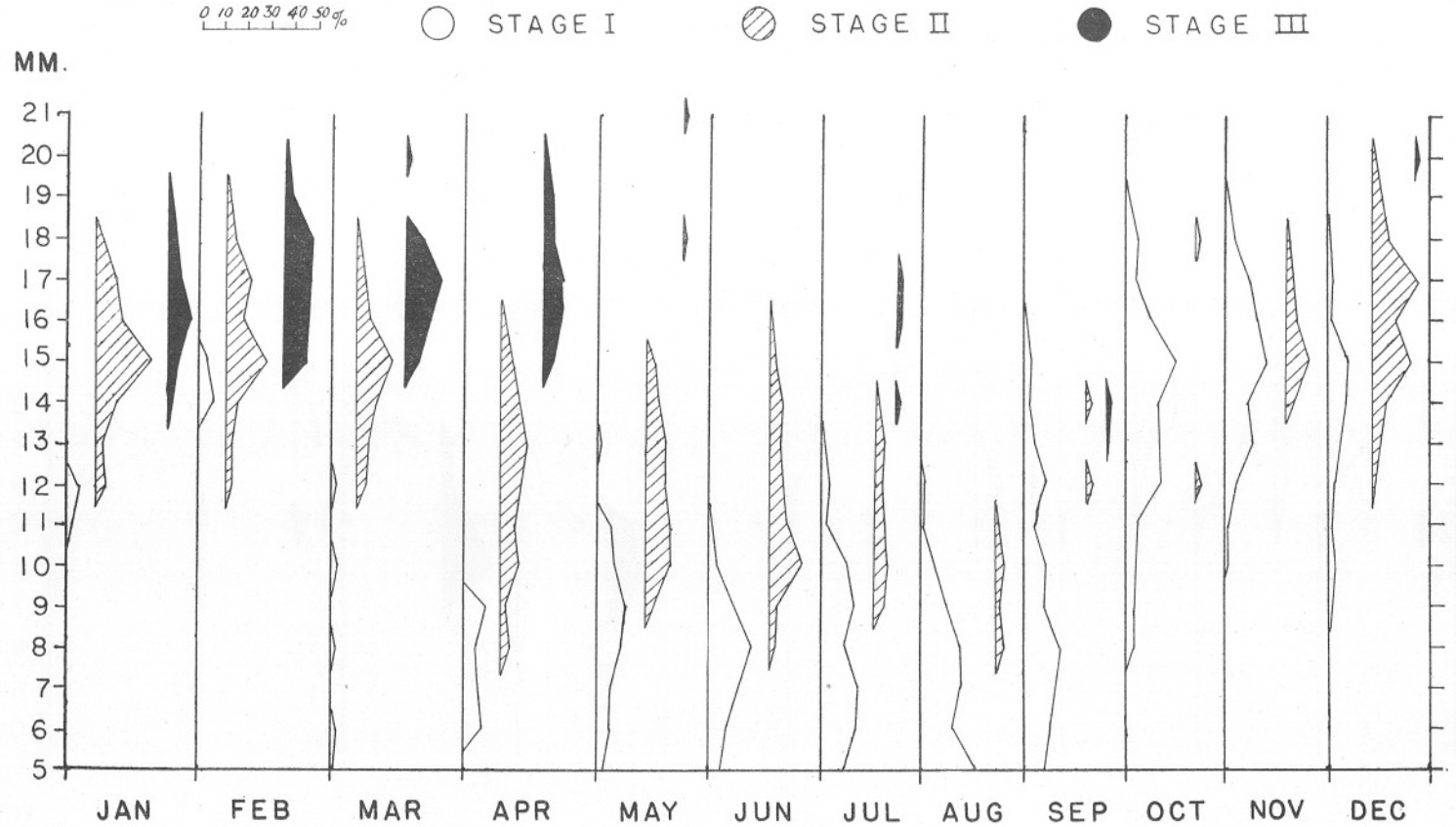

Fig. 1. *S. elegans* caught at Port Erin during 1928–34. Length (mm.) is plotted on the ordinate of the graph and percentage frequency on the abscissa. Stages I, II and III have been treated separately for each month.

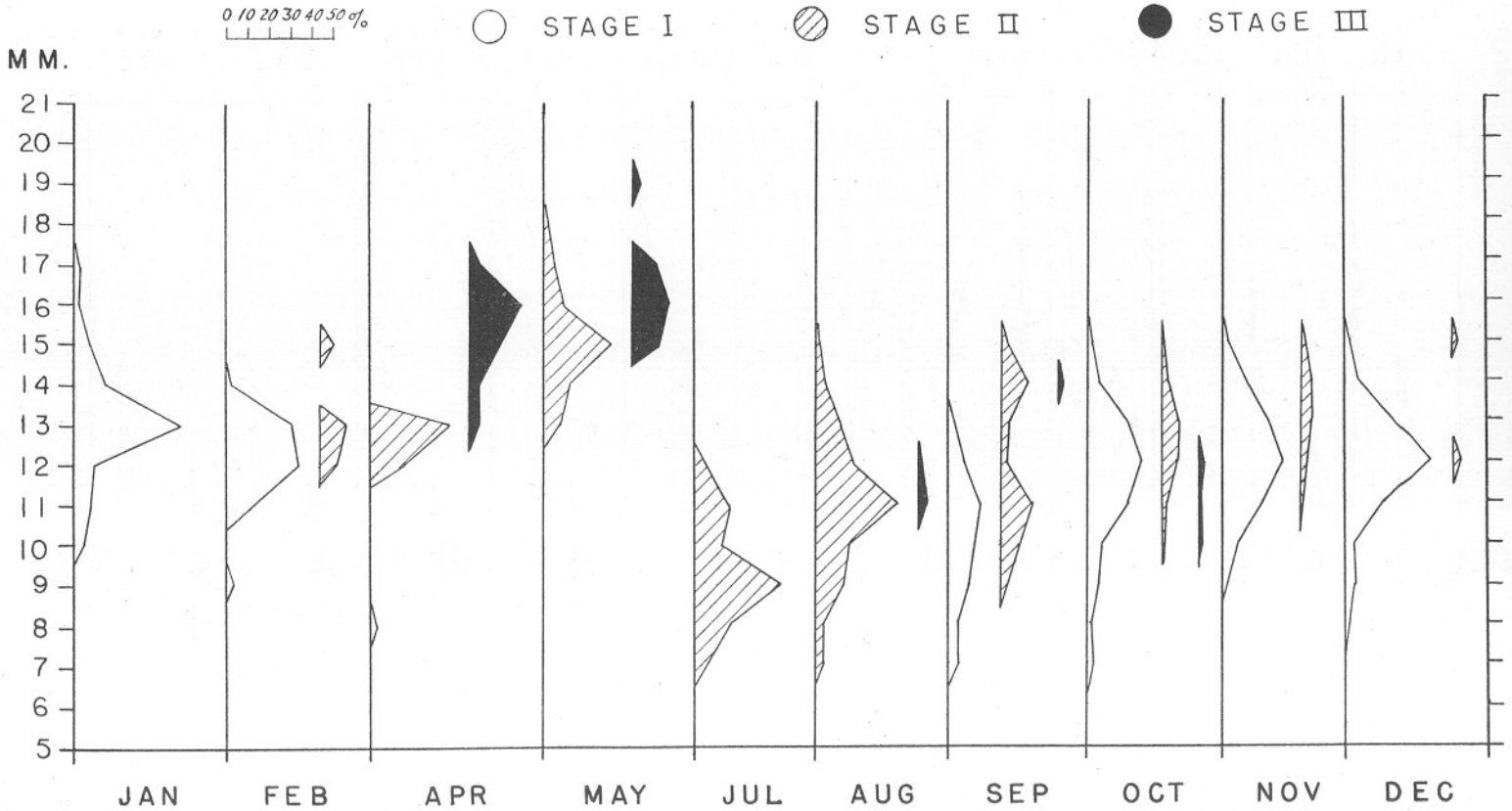

Fig. 2. *S. setosa* caught in the outer Mersey Channels in 1937. Length (mm.) is plotted on the ordinate of the graph and percentage frequency on the abscissa. Stages I, II and III have been treated separately for each month.

April. The stage III *Sagitta* increase from less than 1 % in December to 27 % in January, 46 % in February, and 45 % in March, and decrease to 23 % in April and 2 % in May. Table I contains the complete annual percentages for all three stages. A few mature individuals, as indicated by the small black areas on the graph, were found at scattered intervals throughout the grouped years. Their numbers in these instances were too small to permit recognition of a definite spawning season.

The first young appeared in large numbers in April and from then onward they increased, outnumbering the individuals in the other two stages through November. In November, stage II became noticeable (22 %) and increased to 63 and 69 % in December and January respectively. As indicated above many of the *Sagitta* have become mature by January which thus completes the breeding cycle for the year.

Port Erin material, 1937. Table II of the *S. elegans* collected at Port Erin in 1937 agrees closely with the grouped data for the years 1928–34. A scarcity of specimens in March and October gave few records for those months; however, this does not seriously impair the sequence of the data in the table.

In this year the spawning season began a month later (February) when 18 % of the specimens were mature, and extended through May. The stage II individuals attained their maxima of 73 % in January and 80 % in February, as in 1928–34. The October data are scarce, but the abundance of stage II in November (68 %) indicates that the *Sagitta* began maturing in October, developing into mature individuals in numbers in February and the succeeding months. This completes their annual breeding cycle.

TABLE II. PERCENTAGES OF *S. ELEGANS* GROUPED IN STAGES I, II AND III

Taken from Port Erin in 1937

Month	Stage I %	Stage II %	Stage III %	No. counted from sample
Jan.	23	73	4	66
Feb.	2	80	18	90
Mar.	—	—	—	—
Apr.	4	35	61	138
May	33	33	34	126
June	57	36	7	275
July	94	4	2	87
Aug.	85	12	3	36
Sept.	94	3	3	29
Oct.	89	11	0	9
Nov.	32	68	0	49
Dec.	7	93	0	57

Discussion. In view of the possibility of discrepancies in sampling such a shifting population the close agreement of the data from the grouped samples from 1928–34 and for the single year 1937 is noteworthy. The maxima and minima for stages I, II and III fall in every case within a month of each other. A comparison of Tables I and II reveals a gradual increase and diminution of the individuals in each group. There are no exceptionally large populations

in any month which are not in agreement with the appearances of the *Sagitta* in both the preceding and following months. These are important features, because they substantiate the validity of the sampling methods and support the conclusion that there is but one main season of reproduction for *S. elegans* in the Port Erin region.

Additional collections of *Sagitta* were examined from Port Erin for the years 1935 and 1936. The data from these samples are in essential agreement with the material already discussed and permit of the same conclusions. This information appears useful chiefly as an additional check on the 1928–34 and 1937 breeding cycles and will not be discussed further here.

Russell's data (1932*a*) have indicated four main breeding periods a year for this species in the Plymouth area. These occur in February, May, June-July and September. A comparison of his results with mine reveals that a spawning period in February coincides. After that date and through September no additional breeding periods were identified, as recorded by Russell. In October, November, December, January and February the stages in development appear very similar.

Wimpenny (1936) collected *Sagitta* from the south-west portion of the North Sea. He places one of the breeding periods of *S. elegans* between January and February, which agrees with Russell's and my results; also his data indicate a spawning period between April and August and another tentative breeding in October, which in general is similar to the reproductive periods at Plymouth. In contrast the one long spawning period from January-February to April-May evidenced by my results from Port Erin does not correspond completely with the observations of either Wimpenny or Russell. The great discrepancies appear to lie in the long breeding period from winter to spring of the Port Erin species and the lack of another in the succeeding summer.

Liverpool Bay *Sagitta*

Outer Mersey Channels. The *Sagitta* collected in the outer Mersey Channels in 1937 were with few exceptions *S. setosa*, and the graph (Fig. 2) includes only that species. During January and February this species comprised 95 and 58% respectively of the total number of the two species. Owing to a mishap to the fishery cutter the March data are missing. For the remainder of the year the entire catch consisted of *S. setosa* (Pierce & Orton, 1939).

The first spawning of the year, as indicated in the graph (Fig. 2) occurred in April, May and probably June. During April stage III amounted to 48% of the catch and in May 40% (Table III). In June the presence of the alga *Phaeocystis* in great quantities plus large numbers of the ctenophore *Pleurobrachia pileus* rendered the plankton nets almost useless; moreover, the *Sagitta* themselves appeared very scarce.

Following the April-May spawning the young produced in June must have started maturing rapidly, because all individuals collected were in stage II

in the latter part of July when the first *Sagitta* for that month were obtained in the outer Mersey Channels. By August the first mature individuals from the April-May spawning appeared. The occurrence of these stage III forms, followed by the appearance of numerous stage I specimens, is evidence of a second breeding period despite the scarcity of mature *S. setosa*. During October, November and December stage I continued to increase in relative frequency and by January comprised 100% of the catch. The testes started maturing during February and large individuals ready for spawning appeared in April and May, completing the annual cycle.

It is to be noted that the stage II individuals from February to May (first brood) are larger than the stage II specimens taken between July and November (second brood). The former attained an average length of 13·4 mm. in February, 13·2 mm. in April and 16·0 mm. in May. In the second generation the male stage was first noted in July, when an average length of 9·4 mm. was recorded. By August this had increased to 11·1 mm., in September to 12·0 mm., to 12·6 mm. in October and 13·1 mm. in November. The stage II specimens had almost vanished from this locality by December. The increase in body length found during the colder months (i.e. February, April and May) agrees with the records of Russell (1932*a*) and Bigelow (1924), who have noted a relation between length and temperature; the greater length being found during the colder months. Similar conclusions hold for the stage III *S. setosa* taken; however, in view of the small numbers collected in the summer, details of average length have been omitted.

Pier Head samples. Throughout the year 1937 weekly plankton samples were collected from a pier at the mouth of the Mersey River. Usually the numbers of *Sagitta* caught here were small (Table III). These samples are valuable largely because they confirm the results of the collections taken farther out in the Bay (Fig. 2).

It is of interest to note that during February when mixed catches of *S. setosa* and *S. elegans* were caught in the outer Mersey Channels a similar mixed catch was obtained from the Pier. In March, when the fishery cutter was disabled, towings from the Pier were obtained. The first on March 18 contained a single *S. elegans*. The second sample on March 30 contained nine *S. elegans*; no *S. setosa* were caught during that month. This record agrees with the record of *S. elegans* obtained in Morecambe Bay in March. The remainder of the year produced only *S. setosa*. Collecting at Pier Head was discontinued after the first week in December 1937.

Comparison with previous data. Russell (1932*b*) at Plymouth finds at least six generations of *S. setosa* per year. There is a greater similarity between his results and mine than may at first appear. He records a generation in April and May, and another in June. I believe, in the Liverpool region, that *S. setosa* spawn continuously for these three months, thus combining two of his breeding seasons in one. There was a dearth of mature individuals in July, but there is evidence for a breeding season in August extending into September. This

is also similar to the July-August and September spawnings indicated by Russell. Little evidence was found for a breeding season in October and February, such as he records.

Wimpenny (1936) finds two spawning seasons for *S. setosa* in the south-western portion of the North Sea. The first was in April and the second in July. The earlier season corresponds to that indicated by Russell's data and my own. The July spawning agrees with Russell's records for a brood in July-August and appears to correspond with my evidence for a spawning in August.

Additional Samples

Morecambe Bay. A number of plankton samples were obtained from Morecambe Bay during March and April 1937. The number of *S. setosa* taken is listed briefly as follows: March, stage I, 1 specimen; stage II, 86 specimens; April, stage II, 6 specimens; stage III, 5 specimens.

A graph of the March 1937 collection of *S. setosa* would readily fit between the February and April results from the outer Mersey Channels (Fig. 2), as is evident from the above data. The small April collections agree with those taken in the outer Mersey Channels in the same month.

The number of *S. elegans* found was: March, stage II, 34 specimens; stage III, 105 specimens. None were taken in April. These data agree very well with the 1928–34 and 1937 records from Port Erin.

Anglesey. During the first week in May a trip was made around Anglesey on Board the Lancashire and Western Sea Fishery steamer *Charles MacIver.* Although plankton towings were made completely around the island and in the Menai Strait, *Sagitta* were obtained only from the northern coast in the vicinity of Point Lynas and Moelfre. Relatively few *Sagitta* were taken even here. The total number caught was fifty-eight; of these thirty-eight were *S. elegans* and twenty were *S. setosa.* The large majority of the thirty-eight *S. elegans* were stage III individuals; the remainder were stage II. These specimens are similar both in length and development to the *S. elegans* taken in April and May 1937 from Port Erin (see also Fig. 1). In both species there is a preponderance of stage III forms, indicating a spawning.

There were thirteen stage III specimens as compared to the seven stage II forms among the twenty *S. setosa* caught. These data, though scanty, agree with the May records of the species taken from the outer Mersey Channels some 50 miles east.

Range of *S. setosa*

S. setosa and *S. elegans* are evidently distributed along the west coast of England and Wales from Morecambe Bay to Anglesey, for at least portions of the year. In view of Russell's records (1936, Fig. 6) of *S. setosa* and *S. elegans* from the vicinity of Land's End, and additional records of these two species from the north coast of Ireland, it appears probable that they extend along the entire coast of England and Wales bordering the Irish Sea.

Formerly, *S. setosa* was believed to be indigenous only in the English Channel, North Sea and neighbouring waters. Also it appears that the *Sagitta* at Port Erin, Morecambe Bay, outer Mersey Channels and Anglesey are members of a more or less related population whose breeding periods for each species are approximately the same.

Numbers of *Sagitta* Collected per Month

Table III records the number of *Sagitta* taken per month for the year 1937 at Port Erin, Pier Head and the outer Mersey Channels. Plankton catches from Port Erin taken with a surface tow-net as a rule produced the greatest number of specimens during the summer. This was the period when the young forms were comparatively numerous; later, as winter approached, the catches decreased somewhat, reaching a minimum in January and February. These results are merely indications of the actual quantity of *Sagitta* present during this time. Larger collections taken with nets at greater depths will be required before even general quantitative conclusions may be drawn.

Table III. Total Number of *Sagitta* Caught per Month in 1937

Month	Port Erin	Pier Head	Mersey Channels
Jan.	66	2	69
Feb.	205	19	72
Mar.	—	10	—
Apr.	138	9	75
May	126	3	90
June	590	2	7
July	87	9	57
Aug.	36	4	90
Sept.	34	11	140
Oct.	—	60	1399
Nov.	269	126	377
Dec.	57	16	70

Certain general trends in the increase and decrease of the *Sagitta* in the outer Mersey Channels were more discernible. In June 1937 *S. setosa* had practically vanished from this region. A marked scarcity continued until the latter portion of July when fifty-seven specimens were secured. The noticeable increase in September was due to the presence of the young *Sagitta*. This increase reached a peak in October. After October, although *S. setosa* was present in numbers, no very rich hauls were obtained. The trend from then onward appeared to be one of decrease which would result in a similar scarcity the following summer.

Summary

An investigation has been made of the species of *Sagitta* present in parts of the Irish Sea, their relative occurrence, and the annual number of reproductive cycles of each species. Three stages of maturity as described by Russell (1932*a*) have been used. To determine the maturity the *Sagitta* were transferred to a solution of 75% alcohol and stained with borax carmine.

S. elegans Verrill and *S. setosa* J. Müller were collected in Liverpool Bay and in Port Erin harbour, Isle of Man. The former species was predominant at Port Erin. The coasts of Liverpool Bay have been added to the permanent range of *S. setosa*.

At Port Erin there appears to be but one chief spawning period for *S. elegans* which extends generally from January through May. Following May the young forms appear in numbers and gradually mature through December to repeat the annual cycle.

There appear to be two main breeding seasons for *S. setosa* in the outer Mersey Channels. The first and most noticeable begins in April and extends into June. There is evidence for a second breeding period in August.

Both species were found in the samples taken from Morecambe Bay and Anglesey. The stage of maturity of these agreed with the *Sagitta* caught at the same time at Port Erin and Liverpool.

The total monthly catches of *Sagitta* from Port Erin and the outer Mersey Channels have been recorded.

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OYSTER REARING ON THE RIVER YEALM

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

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In a recent issue of this *Journal* Dr Hughes (1940) published records of a successful attempt to rear oysters in tanks on the River Yealm during the summer of 1939. In this paper he referred to plans for the following year, and it therefore seems desirable to record a few notes on the 1940 season.

Since Dr Hughes left Plymouth I have kept in touch with Mr J. Kingcome, the owner of the fishery, and from time to time have visited his tanks and proffered technical advice. In this I have had the willing co-operation of Mr H. A. Cole of Conway whenever his opinion has been sought. Mr Kingcome has most readily adopted suggestions we have made, and it is to his careful attention and unremitting work that the successful results here recorded are due.

Further History of the 1939 Spat

Dr Hughes mentioned that in August 1939 some of the larger spat were detached from the tiles and placed in cages in the estuary of the river. At the time of writing (mid-October 1940) these range from 4·5 to 8 cm. in diameter. The remainder of the spat spent the winter on the tiles in tank C (Hughes, 1940, Fig. 1), being given almost daily changes of water from the estuary. They were detached from April to July 1940 and placed like the others in wire-meshed cages just above low-water mark spring tides. These oysters have by no means reached the size of those which have been out since August 1939, the size range being 2–4 cm. in diameter.

It is difficult to make a reliable estimate of the number of young oysters now in the cages, all of them from the 1939 spatfall. Mr Kingcome believes there are 20,000–30,000; this figure seems to me to be reasonable. They are in splendid condition and there is every prospect of eventually bringing them to marketable size.

The 1940 Spatfall

Rearing has again been successful under quite different weather conditions. In 1939 there was much rain and heavy cloud, but this year has been outstanding for an almost unbroken period of fine weather from May to September, although heavy rain occurred once or twice during the breeding period. At Conway spat settlement has occurred over a wide range of meteorological conditions (Cole, 1936). As before, tank A was used for breeding and the water in it enriched by Cole's method (1938). The bottom arrangements were

similar to those of last year, the stock oysters lying on slatted trays covered with large flat tiles. Smaller flat tiles were leant up against the sides of the tank at the bottom, while others were propped against one another in rows of inverted V's. In addition some broken curved tiles were piled on the bottom. The tank was flooded from the estuary on June 12 and enrichment with crab meat began a week later. Larvae were first noticed on June 23 (the same date as last year) but may have been present earlier. About this time several bundles of curved tiles were suspended a short distance below the surface. It had been the intention to hang in this way the majority of the limed tiles used for spat collection but unfortunately there was at the time a shortage of curved ones, and for this reason many flat tiles, which are not easy to suspend, were placed on the bottom. Mr Kingcome also scattered a large number of oyster shells after the tank had been filled: most of them reached the bottom white sides uppermost. Some bundles of shells were hung in net bags at the sides of the tank.

The water in the tank was throughout clearer than in 1939 and was so on the day it was put in. Suitable flagellates were present whenever the water was examined, but on July 15 and August 9 the population appeared sparser than usual. On each of these dates two and a half to three litres of a thick culture of Flagellate "I" was poured in. This culture had been prepared—in readiness should it be needed—from a sample culture sent from Port Erin, where the species had proved to be excellent food for oyster larvae (Bruce *et al.*, 1940). Dr Bruce and Dr Parke kindly forwarded this culture at short notice. It is possible to question the value of these additions, but as data for a satisfactory discussion are lacking it can only be remarked that they possibly ensured the presence of a specially good food, in greater or lesser amount, depending on the extent to which multiplication of the added species took place.

Throughout the rearing the *p*H was not known to rise above 8·7 (corrected). Whenever a tendency to increased alkalinity was manifest enrichment was discontinued for a time. Temperatures were not taken regularly.

The first spat settled sometime not later than the first week in July and settlement continued into August. Early in the latter month, before the spat were able to settle too thickly, some of the suspended tiles were removed to tank B. Here they were given daily changes of water from the estuary. About the same time the breeding tank was topped with sea water from the estuary to make up for evaporation loss and leakage. It was emptied on August 15, when the tiles remaining in it were removed to tank C, there to receive daily changes of tidal water. Examination of the tiles during removal amply confirmed the findings of Cole & Jones (1939) that the larvae tend to settle high and in the darker places. The suspended tiles were well covered with spat, but the largest spat, up to 2 cm. in diameter, were on the flat tiles on the bottom. The better the under sides of these latter had been shielded from the light, the more thickly were they covered with spat, although they did not

generally bear as many as did the suspended tiles. Illumination of the under surfaces of some of the flat tiles would be assisted by light reflected from the white oyster shells scattered over the bottom. There were algal growths on the under sides of the tiles with fewest spat. Very few spat settled on the oyster shells lying on the bottom: there were rather more on the shells hung in net bags. In future, after this experience, oyster shells will not be scattered over the tank bottom and every effort will be made to hang the main collectors close to the surface and to keep their under sides well shaded.

At the present time (mid-October 1940) large spat are 3 cm. in diameter with occasional ones as big as 3·5 cm. Some have already been chipped off the tiles and placed in wire cages in the estuary. The majority are, of course, smaller than this; 1–2 cm. across are very common, but many are still only 1 or 2 mm. They will remain on the tiles over the winter, most of them in tank C, but a few bundles have been hung on poles well above the mud near low-water mark.

A few spat have died, but the proportion is insignificant. We believe that this year's spat are more numerous, and on the whole larger at corresponding dates, than last year's.

It is reasonable to expect that the rearing of oysters on the River Yealm will become an annual routine. From a commercial point of view this will considerably enhance the value of the fishery by reducing, perhaps eliminating, the necessity of importing foreign brood; while for the immediate future it will overcome, partially at any rate, difficulties caused by the present impossibility of obtaining brood oysters from Brittany.

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NOTES ON BRITISH AND NORWEGIAN HYDROIDS AND MEDUSAE

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(Text-figs. 1–7)

CONTENTS

The notes collected in this paper are a continuation of earlier observations on British and Norwegian hydroids and their medusae. The observations were made at the Biological Stations of Herdla (Bergen), Millport and Plymouth.

Two of the hydroids described below, *Dipurena ophiogaster* Haeckel and *Tiaropsis multicirrata* (M. Sars), were previously unknown, although their medusae have been known for a long time. The earlier description of the medusa of the hydroid *Trichydra pudica* by Wright (1863) is confirmed and asexual budding in the hydroid *Coryne tubulosa* (M. Sars) is described. Miss Maude J. Delap has kindly allowed me to publish her sketches of the rare hydroid *Tricyclusa singularis* (Schulze).

I am much indebted to Dr Stanley Kemp, F.R.S., for many facilities and much encouragement. I also wish to thank Prof. August Brinkmann and Mr Richard Elmhirst for facilities at Bergen and Millport respectively. The work at Millport was carried out while I was holding a grant from the Royal Society.

Asexual Budding in the Hydroid *Coryne tubulosa* (M. Sars, 1835)

A large colony of *Coryne tubulosa* (M. Sars, 1835), better known as *Syncoryne sarsi* (Loven, 1836), was found growing in a plunger jar kept by Amanuensis D. Rustad at the Biological Station, Herdla, in September 1937. Mr Rustad kindly allowed me to examine the hydroid, which was creeping over the greater part of the bottom of a plunger jar. The colony was of the creeping form (Fig. 1*a*), the stems usually bearing single hydranths, many with medusa buds. Some medusae had been liberated and were

identified as young specimens of *Coryne tubulosa*. The most interesting feature of the contents of the jar, however, were "free hydranths" carrying two whorls of tentacles and sometimes also one or two medusa buds (Fig. 1 *b*, *c*).

A close examination of the hydroid on the bottom of the jar showed that many of these "free hydranths" were developing from the body of the fixed hydranths below the most proximal tentacles. These hydranth buds when liberated showed a striking similarity to the pelagic hydranths of *Margelopsis* (Fig. 1 *c*).

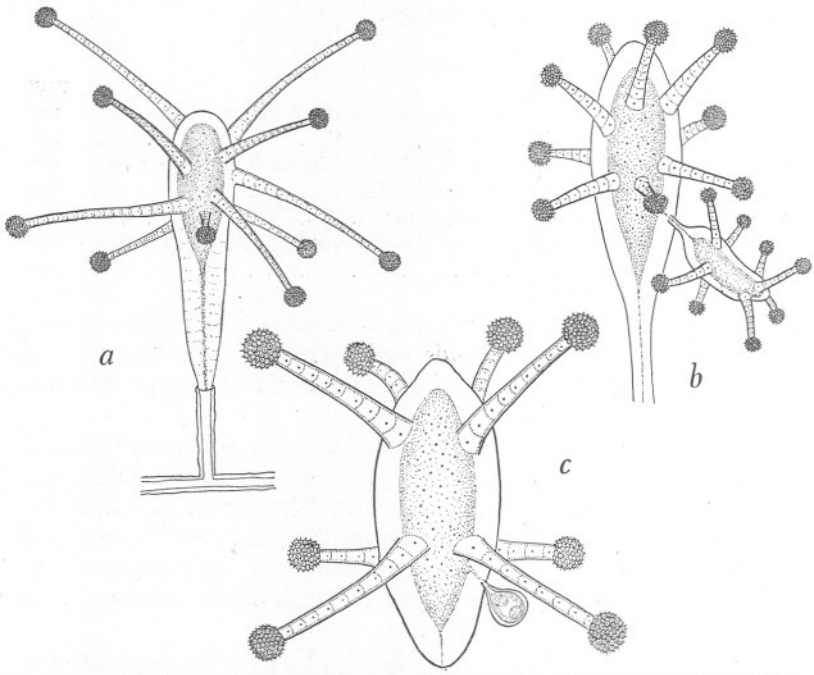

Fig. 1. *Coryne tubulosa*. *a*, Single hydranth from the colony brought back alive to Plymouth from Herdla; drawn 22. iv. 38. *b*, Single hydranth with fully developed bud, drawn from material fixed in formalin. *c*, Newly liberated hydranth bud with a young medusa bud, Herdla, 6. ix. 37.

There was never more than one bud on any hydranth and several buds became free from the parent hydranths during the time they were being examined. Some buds also carried medusa buds. The hydranth buds at liberation were 0·25–0·35 mm. long and 0·15 mm. in diameter. They carried two whorls of four capitate tentacles each, and in some there were one or two medusa buds borne on very short stalks immediately posterior to the proximal whorl of tentacles. The tentacles of the buds were about 0·2 mm. long with capitate terminal knobs 0·05 mm. in diameter.

Budding from the hydranth in this species has been observed by Hartlaub (1916). He figures a bud (p. 103, Fig. 22) similar to those found at Herdla.

Hartlaub also gives many other figures of budding in the same colony but these do not seem to be figures of normal polyps and I am inclined to regard many of them as abnormalities. During the first week of September at Herdla I found one of these "free hydranths" in a plankton haul taken close to the Biological Station. This method of budding "free hydranths" is probably a common feature in the life history of this hydroid when there is an abundant food supply available. A portion of this colony was brought back alive to Plymouth from Herdla, and although it was kept for many months, no further budding of daughter polyps was observed. A few medusae were, however, developed and liberated in May 1938.

The Hydroid of *Dipurena ophiogaster* Haeckel

The hydroid of the medusa *Dipurena ophiogaster* Haeckel was found on the stipe of *Himanthallia loreata* by Miss M. J. Delap at Valentia Island in May 1904. Miss Delap sent the hydroid and the medusae reared from it to the late Mr E. T. Browne. This hydroid, of which there is no published description, is described here from a re-examination of the original colony found by Miss Delap.

The colony was small, consisting of upright stems arising from a creeping stolon and with a total height of about 4 mm. The stems bearing the hydranths arise from creeping stolons, 0·1–0·12 mm. in diameter. Both stems and stolons were covered by a thin perisarc without annulations. In well-developed stems the hydrocaulus reached a height of 2 mm., while in young polyp stems no perisarc was visible. The stems each carried a single hydranth, but short stolons were frequently given off a little distance from the point of origin of the upright stems (Fig. 2*a*). The production of these stolons on the stems was a characteristic feature of the colony.

Mature hydranths with medusa buds were 1–2 mm. long with a diameter of 0·2–0·35 mm. (Fig. 2*b*,*c*). There were two kinds of tentacles, capitate and filiform, present in most hydranths. The capitate tentacles, 10–18 in number, were scattered over the anterior two-thirds of the body; they had a tendency to be arranged in whorls. There was always an oral whorl of four tentacles around the mouth, the remainder being scattered. The capitate heads of the tentacles were 0·07–0·12 mm. in diameter and frequently decreased in size posteriorly.

The filiform tentacles were situated posterior to the capitate tentacles and varied in number in different polyps. There were never more than four on any hydranth (Fig. 2*b*), and frequently only one or two were present. In some hydranths they were absent and in others they formed part of a proximal whorl of capitate tentacles. A closer examination showed that these filiform tentacles always carried a number of nematocysts at the tip, and that transitional stages between capitate and filiform tentacles could be found in one whorl. In this species at least they may be regarded as reduced capitate tentacles (Fig. 2*c*).

Medusa buds were borne singly or in a cluster of two to four buds on the body of the hydranth a little anterior to the posterior whorl of "filiform" tentacles (Fig. 2*b*, *c*). Usually there was only one cluster but sometimes there were two. The young buds were sessile, but as they developed to full size they became stalked with a thin stalk up to 0·2 mm. in length. The largest medusa bud was 0·5 mm. long with a diameter of 0·45 mm. In the largest buds the manubrium, and the four tentacles with their ocelli, could be clearly seen through the thin perisarc covering the bud.

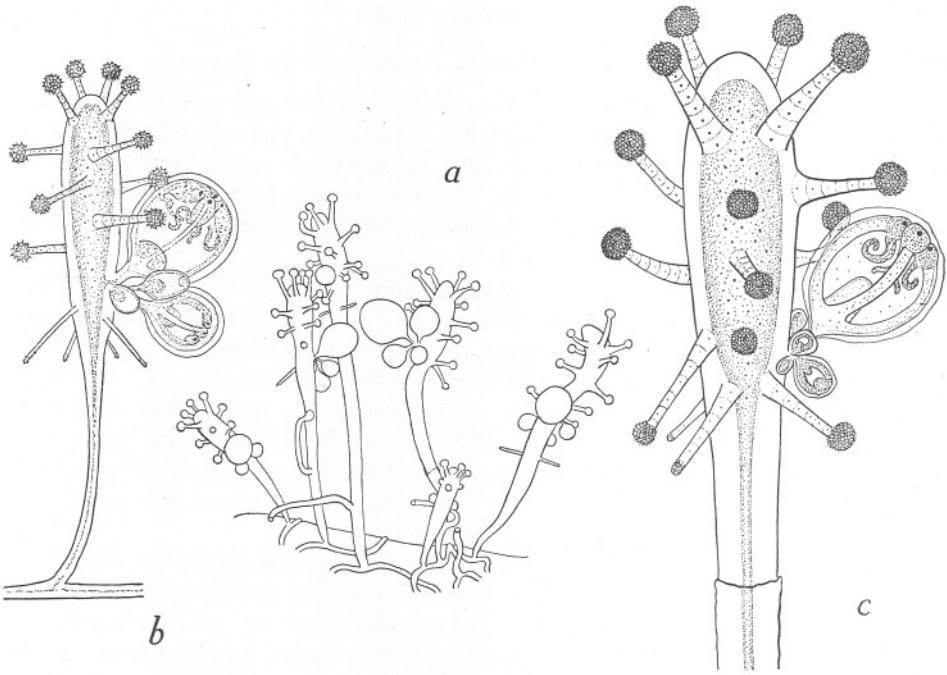

Fig. 2. *Dipurena ophiogaster*. *a*, General appearance of a portion of the colony, drawn from material preserved in formalin. *b*, Single polyp with medusa buds, redrawn from a pencil sketch of a living polyp by Miss M. J. Delap. *c*, Single hydranth, from material preserved in formalin.

The medusae reared from this colony by Miss Delap have been identified by Mr F. S. Russell as *Dipurena ophiogaster* Haeckel. This hydroid bears a superficial resemblance to *Stauridiosarsia* [= *Stauridium*] *producta* (Wright), but in the present hydroid the capitate tentacles are more scattered, there are only four oral tentacles, and the so-called filiform tentacles are really imperfectly developed capitate tentacles. The hydroid of *Dipurena ophiogaster* is also distinct from that of *D. halterata* (Forbes), which has more capitate tentacles, no filiform tentacles, and develops medusa buds singly (Rees, 1939*b*). Although the two hydroids which give rise to *Dipurena* medusae are

well marked, the differences do not justify the allocation of the species to separate genera.

The Hydroid and Free Hydranth of *Tricyclusa singularis* (Schulze, 1876)

The following account of a rare and little known hydroid is based on figures and notes made by Miss Maud J. Delap. Miss Delap has kindly permitted me to publish an account of this hydroid, which I have identified with *Tricyclusa singularis* (Schulze, 1876) (= *Margelopsis stylostoma* Hartlaub, 1903, *syn.nov.*).

The Hydroid. Six specimens with buds were found on a piece of *Zostera* at Reenagiveen Point, Valentia Island, Co. Kerry, on July 19, 1909, and these were kept under observation by Miss Delap until July 30, 1909. The hydroid was attached to the *Zostera* by a short cylindrical stalk. The hydranth itself was more or less flask-shaped, with three whorls of capitate tentacles. Between the middle and oral whorl the body narrows to form a slender neck. The oral tentacles, which are terminal, are four in number, each with a terminal knob of nematocysts. There were six tentacles in the middle whorl. These and the proximal whorl carried two groups of nematocysts on their distal half in addition to the terminal knob. The proximal whorl, situated near the posterior end of the body, had twelve tentacles, disposed in two closely approximated whorls of six tentacles pointing upwards and six tentacles pointing downwards.

In one polyp the hydranth was cut off and the stem grew a new one. Some of the hydranths carried pink or pinkish yellow buds at the posterior end of the body (Fig. 3*a*). These developed into young hydranths which were budded off (Fig. 3*b*).

The young hydranths budded off in this way were identical, and may be regarded as synonymous, with *Margelopsis stylostoma* Hartlaub, 1903. Miss Delap states that "the young when liberated have fewer nematocysts and the tentacles appear longer than in the adult: they use their tentacles to crawl about with." A young specimen after liberation was 1 mm. long and the tentacles were 1·5 mm. long; in another specimen the tentacles were 0·5 mm. long.

The fixed hydroid differs in one respect from the description given by Schulze. There are fewer tentacles in the proximal whorl of the specimen figured by Schulze than in the present species, but their number probably varies with age and I have therefore referred this hydroid to *Tricyclusa singularis*.

Systematic Discussion on the Margelopsidae

The peculiar hydroid described above was first described by Schulze (1876) as *Tiarella singularis*. The name *Tiarella*, however, was preoccupied and Stechow (1919) has given it the new generic name *Tricyclusa*. The hydroid is of an unusual type, which is intermediate between the Tubulariidae and the Corynidae. Its remarkable power of budding young hydranths from the

body, just behind the most proximal whorl of tentacles, was noticed by Schulze. He also observed gonophores developing between the middle and lower whorl of tentacles.

In 1903 Hartlaub published a description of a "schwimmender" hydroid, *Margelopsis stylostoma*, which he referred to his genus *Margelopsis*, of which *M. haeckeli* is the genotype. This latter species is a planktonic hydroid which superficially resembles *M. stylostoma*. Hartlaub drew attention to the marked similarity between his *M. stylostoma* and the hydranth of *Tricyclusa singularis*, and expressed the opinion that they might prove to be the same species. Hartlaub also indicated that the medusa *Margelopsis hartlaubi* Browne, 1903, might be the medusa of *Tricyclusa singularis*. The observations

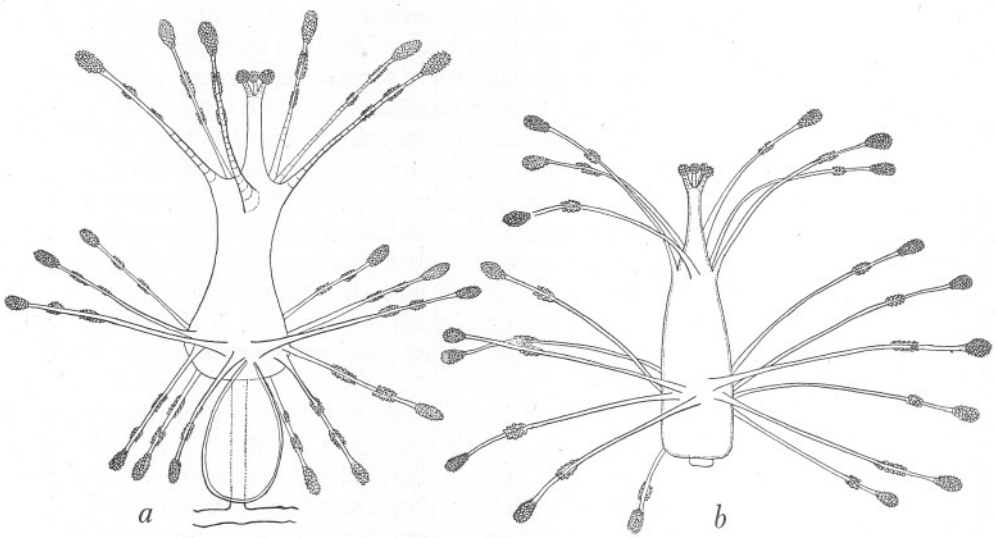

Fig. 3. *Tricyclusa singularis*. *a*, Fixed hydroid. *b*, Free hydranth. From tracings of original pencil drawings by Miss M. J. Delap.

made by Miss Delap show that *Margelopsis stylostoma* comes from the fixed hydroid, *Tricyclusa singularis*.

Mayer (1910) erected a new subfamily of the Codonidae, the Margelopsinae, to take *Margelopsis* and *Pelagohydra* Dendy, 1902. The free hydroids of *Margelopsis haeckeli* and *Tricyclusa singularis* differ in several respects. There are only two whorls of tentacles in *Margelopsis haeckeli*, whereas *Tricyclusa singularis* has a third oral whorl; in the latter all the tentacles are capitate, but they are filiform in the former. These differences have evidently been considered by Stechow (1923), who, in his tables (pp. 37, 49), separates *Margelopsis* (i.e. *M. haeckeli*) from *Tricyclusa* in different families. He places *Margelopsis haeckeli* and *M. gibbesi* (McCrady) in the Tubulariidae in the subfamily Pelagohydrinae, of which *Pelagohydra* is the type; *Tricyclusa* he

refers to the Corynidae. The separation of *Tricyclusa* from *Margelopsis* and the removal of the former to the Corynidae appears justifiable.

Uchida (1927) does not appear to have been aware of Stechow's suggestion and placed *Margelopsis*, *Hypolytus* Murbach, 1899, *Pelagohydra* and *Climacocodon* Uchida, 1924, in his family Margelopsidae. This arrangement appears to be satisfactory if we exclude *Tricyclusa* and *Hypolytus*. I have already indicated (Rees, 1938, p. 29) that *Hypolytus* clearly belongs to the Corymorphinae, if not to the genus *Corymorpha* itself. This species, according to Murbach, is capable of a certain amount of movement, but so are other species of *Corymorpha* (unpublished observations on *C. aurata* and *C. nutans*).

The medusae of *Margelopsis*, *Pelagohydra* and *Climacocodon* are all of the same type and are quite distinct from those of the Tubulariidae and Corynidae and justify the erection of a separate family. As Uchida (1924) has indicated, *Pelagohydra* is probably the only one of these genera that may be regarded as truly pelagic, and it has yet to be shown that the other forms have no fixed hydroid stage in addition to their free hydranths. Dendy has shown that in *Pelogohydra mirabilis* the proximal portion of the hydranth is modified to form a float, whereas a float is either poorly developed* or absent in *Margelopsis* and *Climacocodon*. There are other differences, such as the number and disposition of the tentacles, which indicate that *Pelagohydra* is not so closely related to the other two genera as they are to each other. On the other hand, the structure of the medusa in *Pelagohydra*, which is of the *Margelopsis* type, is proof that these forms are related.

I propose therefore to recognize two subfamilies, the Margelopsinae and the Pelagohydrinae, within the Margelopsidae.

The Margelopsinae may be distinguished by the possession of whorls of tentacles and by the absence of a distinct float. It contains the genera *Margelopsis* and *Climacocodon*.

The Pelagohydrinae may be distinguished by the scattered position of the tentacles all over the body of the hydranth, and by the modification of the proximal portion of the body to form a float. Sole genus: *Pelagohydra* Dendy, 1902.

The Medusa of *Trichydra pudica* Wright

Two well-developed colonies of the hydroid *Trichydra pudica* Wright, 1858, were found on two clinkers trawled off Fairlie Buoy in the Clyde Sea Area on April 11, 1940. This is the first record of the hydroid from this area. Previously it has been reported from the Firth of Forth by Wright (1858), from the English Channel (*Plymouth Marine Fauna*, 1931) and from Valentia Harbour, Co. Kerry (personal communication from Miss M. J. Delap). The hydroid which van Beneden (1866) described as *Eudendrium pudicum* is certainly not the present species (Rees, 1938).

* Leloup (1929) has shown that in *M. haeckeli* the endodermal cells are vacuolated and that the structure of the short stalk of the hydranth resembles early stages in the formation of the float in siphonophores.

Wright (1863) described a medusa which he found in a vessel containing *Trichydra* and which he thought might be its medusa, but he could detect no trace of gonophores on his hydroid colony. On two clinkers from Fairlie there was a heavy growth of this hydroid and no other species were present. Two days later two medusae were liberated. Although a careful daily examination until April 19 revealed no trace of developing or fully developed medusa buds, six more medusae appeared in the bowl during this period. These clinkers with their numerous tiny pockets afford an excellent hiding-place for such buds, which must have been very small. I do not doubt that these tiny medusae came from the *Trichydra*; they agree in structure with those described by Wright except for the presence in Wright's specimens of two or three rudiments of interradial bulbs. Their presence or absence may vary from colony to colony.

A brief redescription of both hydroid and medusa is given below.

The polyps are connected by a creeping filiform stolon which is covered by a thin perisarc and from this stolon the polyps arise at short intervals. At the base of the hydranth there is a collar-like perisarc into which the hydranth can partially contract. This collar varies in length from 0·15 to 0·35 mm. and has a diameter of 0·1–0·14 mm. When disturbed the hydranth can contract so that only the tips of the tentacles show beyond the edge of the perisarc. When expanded, however, the hydranth may reach a height of 1 mm. beyond the edge of the perisarc, and in this state the stem supporting the hypostome and the tentacles is very thin with a diameter of about 0·03 mm. (Fig. 4). Distally the stem broadens to give rise to a whorl of tentacles, and beyond the latter there is a distinct conical hypostome. The tentacles when expanded may reach a length of 1·2 mm.; they carry numerous irregularly disposed nematocysts.

The first medusae were liberated in the laboratory on April 13 and others on succeeding days.

The newly liberated medusae were very small, having a length of 0·4 mm. and a diameter of 0·3 mm. They were of a deep bell shape, higher than wide (Fig. 5). The jelly was uniformly thin and all over the bell there were numerous nematocysts. The velum was well developed. The stomach was short, tubular, 0·14–0·17 mm. in length, and was distinctly broadened at its base. It was difficult to distinguish the stomach proper from the beginnings of the radial canals. The four radial canals were distinct and moderately broad. There were four perradial tentacle bulbs each about 0·05 mm. in diameter. The four perradial tentacles were not observed expanded, but when contracted they had a length of 0·15 mm. The base of the stomach and the tentacle bulbs were yellowish brown or brownish in colour. The medusae did not grow appreciably and did not grow more tentacles during the time I was able to keep them.

This young medusa cannot be identified with certainty with any known medusa because of the lack of any distinctive characters. It is probably a

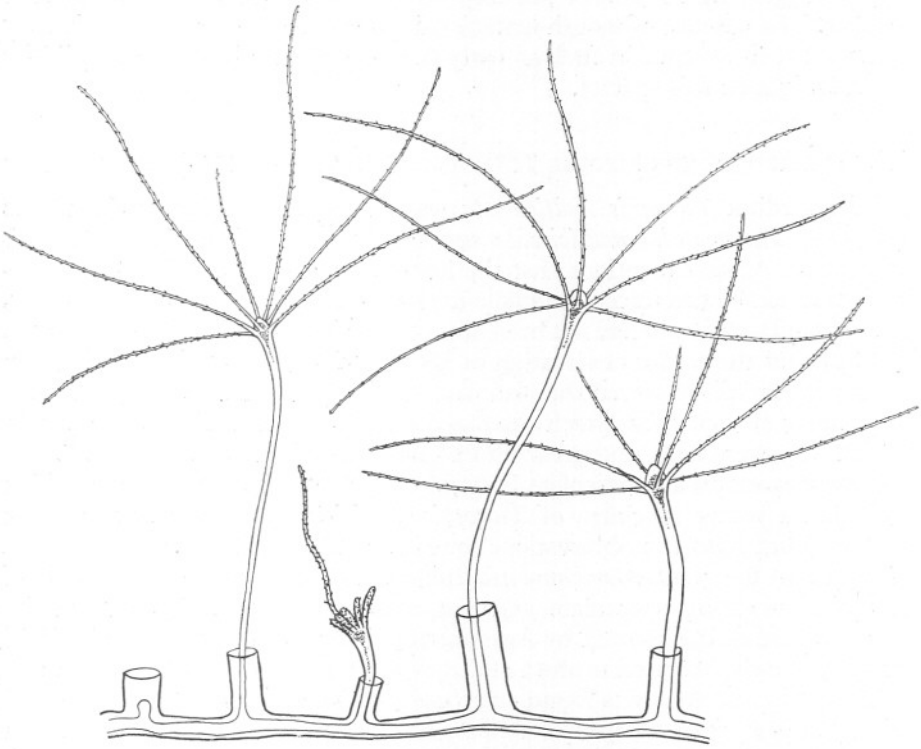

Fig. 4. *Trichydra pudica.* Four polyps from a colony; Millport, 12. iv. 40.

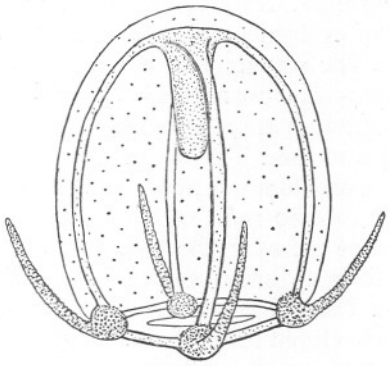

Fig. 5. *Trichydra pudica.* Newly liberated medusa; Millport, 15. iv. 40.

very early stage of a known medusa, and the form and colour of the tentacle bulbs suggest that it might possibly be an early stage of *Lizzia blondina* Forbes. The absence of mouth tentacles, however, does not support this view although their absence in such an early stage does not rule out the possibility that it might be this species.

The Hydroid of the Medusa *Tiaropsis multicirrata* (M. Sars, 1835)

The medusa *Tiaropsis multicirrata* was first described by Michael Sars (1835) as *Thaumantias multicirrata* and later by Louis Agassiz as *Tiaropsis diademata*. Agassiz mentions that the hydroid of this species is a *Campanularia* and that he had traced the whole life history. A. Agassiz (1865), however, stated that the hydroid had not been observed, so it appears that he was in some doubt about the earlier observation of his father. L. Agassiz (1849) definitely states that he had observed the planulae, "recently hatched from eggs, I have seen move slowly, then attach themselves to the solid bodies in the jars in which they were kept, and grow into a Campanularioid polypidom...".

Recent work on an operculate hydroid of the "*Campanulina*" type, which liberated a young specimen of *Tiaropsis multicirrata*, appears at first sight to contradict Agassiz's observations, but it must be remembered that at this time (1849) the genus *Campanularia* consisted of a heterogeneous group of hydroids including operculate and non-operculate forms. Apart from the vague record of the hydroid by Agassiz there is no description of the hydroid or of the newly liberated medusa and they are therefore described below.

The hydroid colony was found on an old *Buccinum* shell dredged off Keppel Pier, Millport, from a depth of about 5 fm. on April 18, 1940. No expanded hydranths were seen and of the few gonothecae present only one contained a medusa. This was liberated in the laboratory and was identified as *Tiaropsis multicirrata*.

Description of the Hydroid. The colony consisted of a large number of hydranths connected by creeping stolons running in all directions over the apical half of the shell. The stolons were 0·05 mm. in diameter and were not annulated. The hydranths were borne singly at short intervals on the creeping stolon and were supported on short imperfectly ringed stalks, which varied in length from 0·06 to 0·10 mm. The total height of the hydranths from the stolon to the tip of the operculum was never more than 1 mm. The hydrotheca itself varied from 0·38 to 0·80 mm. in length and in breadth from 0·1 to 0·13 mm. The perisarc of the hydrotheca was thin but firm and at its distal end became folded to form a distinct conical operculum with seven to eleven outer segments (Fig. 6). The operculum varied in height from 0·16 to 0·25 mm. When the operculum was closed the segments formed a somewhat blunt apex.

When found the colony was dying down after producing medusae and no hydrotheca contained a living polyp. Several gonothecae were present but all except one were empty. One gonotheca contained a single medusa which

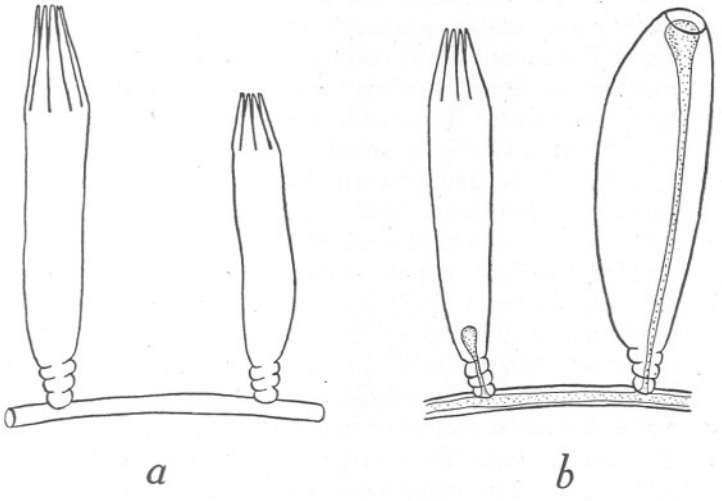

Fig. 6. *Tiaropsis multicirrata*. *a*, Two hydrothecae. *b*, One hydrotheca and a gonotheca; Millport, 19. iv. 40.

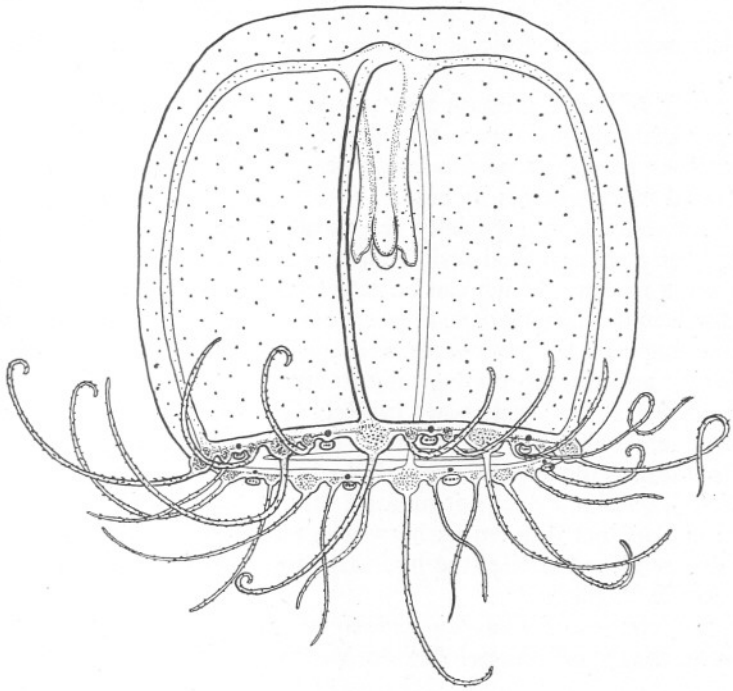

Fig. 7. *Tiaropsis multicirrata*. Newly liberated medusa; Millport, 19. iv. 40.

completely filled it. The gonothecae, like the hydrothecae, were supported on short imperfectly ringed stalks, and were large, elongate oval in shape, with a smooth surface. The mouth of the theca was circular, with a diameter much less than the maximum diameter of the theca itself (Fig. 6*b*).

Description of the Medusa. The newly liberated medusa had a deep bell-shaped umbrella with a thin jelly which was slightly thicker at the apex (Fig. 7). The surface of the umbrella was thickly covered by a large number of small nematocysts. There was a well-developed velum. There was a short quadrangular stomach extending to about half the height of the subumbrellar cavity. The mouth consisted of four well-developed perradial lobes, armed along their free margin by a single row of nematocysts. There were four moderately broad radial canals connecting with the ring canal. The marginal tentacles were many, twenty-three in number, and these were in different stages of development. The four perradial and the four interradial tentacles were equally well developed and when extended reached a length of 1·5 mm. There were also smaller tentacles, one on each side of the interradial tentacles and one on each side of the perradial tentacles. In one quadrant of this medusa (see Fig. 7) one tentacle, immediately adjacent to a perradial tentacle, was missing. Situated adradially and between these younger tentacles were eight prominent black ocelli and eight large oval marginal vesicles. The marginal vesicles measured 0·04 by 0·05 mm. and were adaxial in position on the umbrella margin. The vesicles contained from three to five spherical concretions.

The newly liberated medusa was 1·1 mm. high by 1·1 mm. in diameter. The larger tentacle bulbs were 0·1 mm. in diameter. They were pale brown in colour. The stomach was also faintly brownish in colour with the pigment concentrated more towards its base.

From its characters, especially the adradial position of the eight black ocelli and the eight marginal vesicles, there can be no doubt as to the identity of this young medusa, which can be referred to *Tiaropsis multicirrata*.

The hydroid described above is of the so-called "*Campanulina*" type, and when the shape of the gonotheca and the hydrotheca are taken into consideration, it appears morphologically to stand nearest to *Phialella quadrata* (Forbes, 1848). It has been shown by Rees (1939*a*) that a number of distinct medusa genera belonging to different families all possess "*Campanulina*" hydroids and thus the apparent morphological similarity between this hydroid and *Phialella quadrata* does not indicate that the species are related.

There are distinct differences between this hydroid and *P. quadrata*; the hydranths are all subsessile, the hydrothecae are longer and the gonothecae firmer than in *P. quadrata*.

Young specimens of *Tiaropsis multicirrata* with 25–35 tentacles appeared in plankton caught off Keppel Pier on March 5, 1940.

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ON THE HYDRORHIZA AND CLASPERS OF THE HYDROID *MYRIOTHELA COCKSI* (VIGURS)

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(Text-figs. 1–2)

The Hydrorhiza

The types of hydrorhiza shown by the northern hemisphere species of the hydroid *Myriothela* have been described by Bonnevie (1899) as follows:

I	II	III
Lamellary, expanded with chitinous perisarc	Tentacle-like, attaching filaments which grow from the base of the hydranth	Root-like point with fine attaching filaments, 10–20 mm. long
M. cocksi	*M. phrygia* *M. verrucosa*	*M. gigantea* *M. minuta* *M. mitra*

Among the southern hemisphere species the first type appears to be represented by *M. harrisoni* and the second by *M. australis*, *M. penola*, *M. capensis*, etc. Further details concerning *M. cocksi* were given by Hinks (1868), "the adherent base massive, of a dark horn colour, sending out a few tubular and root-like prolongations"; a small figure is also given, but it shows little detail of the form of the hydrorhiza where it is attached to the substratum. Allman (1875) describes and figures "short sucker-like processes of attachment" arising from the hydrorhiza which lies at right angles to the rest of the polyp.

During a recent examination of some southern hemisphere species of *Myriothela* particular attention has been paid to the manner of attachment of the hydrorhiza to the substratum in those species which show the second type of hydrorhiza (Manton, 1940). Since little is known of the structure and manner of attachment of the hydrorhiza of the first and third types referred to above, an examination of *M. cocksi* has been made with a view to remedying in part this deficiency. I am indebted to the Marine Biological Association for supplying me with well fixed material of *M. cocksi*, and to Dr L. E. R. Picken for carrying out chitin analyses.

The only other species which appears to show the first type of hydrorhiza mentioned above is the Australian *M. harrisoni*, where the cylindrical hydrorhiza "gives off slender rooting processes, expanded and truncated distally, for attachment to the substratum" (Briggs, 1928).

The lower portion of a young expanded specimen of *M. cocksi* is shown in

Fig. 1 *a*; the substratum has been removed from the hydroid. The hydrorhiza is roughly cylindrical in shape, but distorted to fit the irregularities of the substratum. The basal four-fifths of the hydrorhiza is encased in perisarc of a brown colour. The perisarc, unlike that of many hydroids, is everywhere adherent to the surface of the underlying ectoderm; it is fairly rigid, and its presence immobilizes this part of the hydroid. The perisarc is about 6μ thick. It stains red with Mallory's triple stain and black with iron haematoxylin. It is composed of true chitin. The dark colour probably indicates that the perisarc is hardened by impregnation, as is the cuticle of insects (Pryor, 1940 *a*, *b*).

Towards the blastostyle zone the perisarc becomes thinner, losing its staining reactions, and merges into the thin cuticle which covers the ectoderm of the hydranth. This cuticle is well shown in microphotographs of an allied species (Manton, 1940, pl. III, figs. 23 and 25). The zone covered by perisarc is shown by the mechanical tint in Fig. 1 *a*.

Below the blastostyle-bearing zone the axis of the hydrorhiza bears thirteen adhesive tentacles (*a.t.*) attached to the substratum and covered by perisarc. They are of various lengths up to 1·25 mm. One unattached tentacle arises above the zone covered by perisarc (*u.a.t.*), and is invested only by cuticle. Just above this lies the rudiment of another adhesive tentacle (*r.a.t.*), identified as such by sectioning.

The adhesion of the hydrorhiza to the substratum is effected only by the perisarc covering the flattened extremities of the adhesive tentacles (*a.d.*), and the perisarc here appears browner and thicker than elsewhere.

It is probable that growth of the hydrorhiza zone takes place orally, since young adhesive tentacles are found only at the oral unstiffened end of the hydrorhiza. In the region where the perisarc merges into the general cuticle the development of ectodermal musculature in the main axis is more complex than in other parts of the hydroid where these fibres form a regular longitudinal layer. Here the muscle processes lie in a variety of planes forming a network through the inner part of the ectoderm. It is possible that this musculature, besides controlling the position of the upper part of the hydroid, may be used to form local distortions in the flexible upper part of the hydrorhiza so as to produce contact between the young unstiffened adhesive tentacles and the substratum. The subsequent chitinization, thickening and hardening of the cuticle will then fix these distortions. The hydrorhiza figured here is young and simple, but the contorted hydrorhiza of gnarled appearance which is common on old specimens may have grown in this way.

In structure the unattached adhesive tentacle differs little from those of *M. penola* and *M. capensis* (Manton, 1940, text-figs. 6, 7). The tentacle is hollow, its enteric cavity opening directly into the main enteron. The ectoderm of the stem resembles that of other parts of the body and is provided with nematocysts. The terminal ectoderm forms a regular layer of darkly staining narrow cells, and nematocysts are almost absent. These cells do not contain

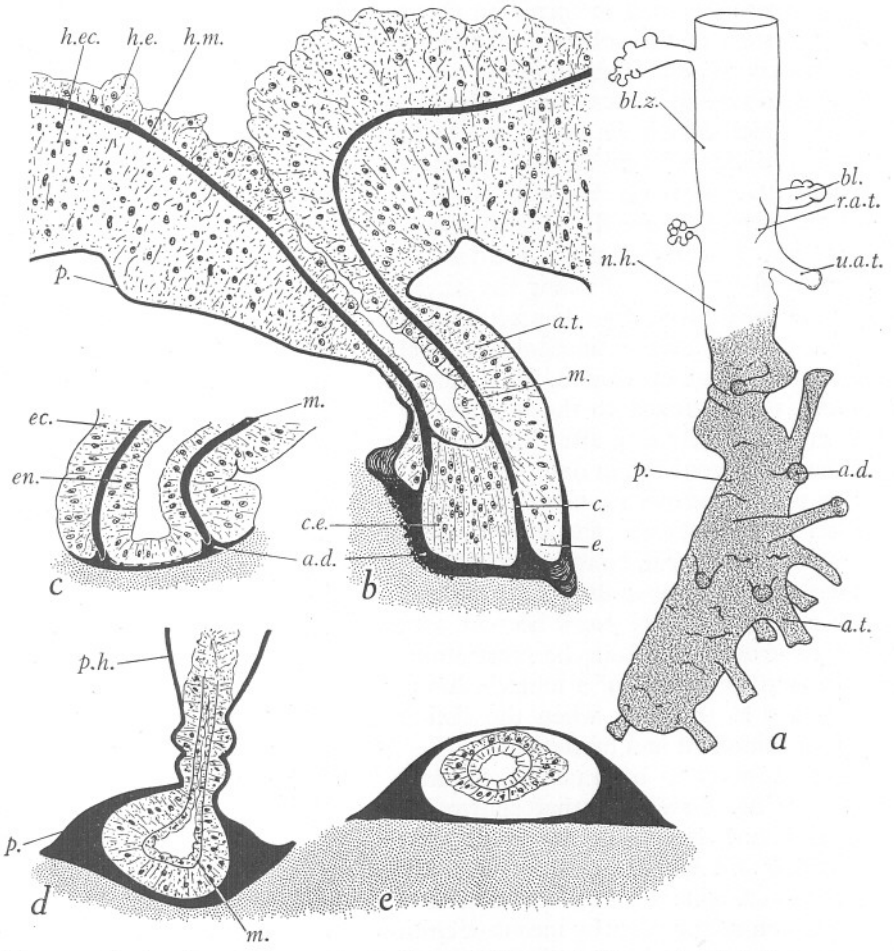

Fig. 1. *a*, the basal part of a young specimen of *M. cocksi*. The mechanical tint represents that part of the hydrorhiza which is covered by perisarc. *b*, sagittal section through an attached hydrorhiza tentacle and wall of the hydrorhiza of *M. cocksi*. The substratum is indicated by mechanical tint. *c*, sagittal section through an attached hydrorhiza tentacle of *M. capensis*. The substratum is indicated by mechanical tint. *d*, vertical section through the junction of hydrocaulus and hydrorhiza of *Obelia*. *e*, transverse section through a hydrorhiza stolon on *Obelia*.

a, × 12 approx.; *b*–*e*, × 110 approx.

a.d., adhesive disk of chitin attached to substratum. *a.t.*, adhesive tentacle of hydrorhiza. *bl.*, blastostyle. *bl.z.*, blastostyle-bearing zone of hydroid. *c.*, annular flange of chitin passing inwards from adhesive disk to unite with mesogloea. *c.e.*, central part of terminal ectoderm. *e.*, lateral part of terminal ectoderm. *ec.*, ectoderm. *en.*, endoderm. *h.e.*, hydrorhiza endoderm. *h.ec.*, hydrorhiza ectoderm. *h.m.*, hydrorhiza mesogloea. *m.*, mesogloea. *n.h.*, part of hydrorhiza not yet covered by perisarc. *p.*, perisarc. *p.h.*, perisarc of hydrocaulus. *r.a.t.*, rudiment of adhesive tentacle. *u.a.t.*, unattached adhesive tentacle.

the intracellular granules, which are present in the two above-named species, and are there destined to form the chitinoid layer. The mesogloea is thick along the stem of the adhesive tentacle, but becomes very thin distally, and here appears to be perforated in places.

The structure of an attached adhesive tentacle is shown in Fig. 1 *b*. The perisarc which covers the axis of the hydrorhiza and the stem of the tentacle is greatly thickened against the substratum. In this particular tentacle the terminal attachment fits into a hollow in the substratum and is humped, but most adhesive disks are flat. The perisarc is particularly thick round the rim of the disk. Just within this rim a deep annular flange of chitin projects into the terminal ectoderm, dividing the latter into a central (*c.e.*) and a lateral (*e.*) part. The mesogloea layer is prolonged into a thick rim projecting into the ectoderm to meet the chitinoid flange, as shown in the sagittal section figured, and the two structures unite. The adherent disk of chitin at the end of the tentacle is thus linked to the mesogloea. The junction between mesogloea and chitin is clearly seen after Mallory's triple stain, as the former stains blue and the latter from red to orange.

The perisarc shows no obvious structure other than a slight stratification parallel with the surface, and in sections it tends to split into upper and lower layers which appear to be identical. The chitin covering the tip of an adherent tentacle shows some slight colour difference from the rest. After Mallory's triple stain the deeper parts become orange red, and the superficial layers which have been torn from the substratum appear a purplish red. The process of adhesion by the tip of a tentacle has not been seen, but presumably this takes place at the time when the cuticle covering an unattached tentacle becomes thickened and hardened.

There appears to be much in common between the type of hydrorhiza shown by *M. cocksi* and that shown by *M. phrygia*, *M. capensis*, etc., a similarity not indicated by the literature. The second type, seen in *M. capensis* and *M. penola*, has been described by Manton (1940). Both types of hydrorhiza adhere to the substratum by the tips of tentacular structures, the adhesion taking place by means of chitinoid material which is also attached to the mesogloea. A sagittal section of an attached adhesive tentacle of *M. capensis* is shown in Fig. 1 *c*. In species showing this type of hydrorhiza a perisarc is usually described as absent, but it is in fact reduced to the small disk capping the bare adhesive tentacle (Fig. 1 *c*, *a.d.*). The naked hydrorhiza of such species is often very short, so that the adhesive tentacles tend to arise close together from the base of the hydranth, instead of at intervals from an elongated axis.

The general perisarc of *M. cocksi* must give some support to the points of adhesion with the substratum, and with the absence of the investing perisarc from species showing the second type of hydrorhiza a stronger attachment of the chitin to the mesogloea is seen. The mode of union between chitin and mesogloea described for *M. cocksi* (Fig. 1 *b*) is clearly repeated by *M. capensis*

(Fig. 1 *c*). The annular flange of chitin (Fig. 1 *b*, *c*.) in *M. cocksi* does not project inwards so far in *M. capensis*. The central portion of ectoderm (*c.e.*), which remains intact in *M. cocksi*, has disappeared in *M. capensis*, these cells breaking down during the formation of the chitinoid disk and leaving the latter closely adherent to the mesogloea right across the tip of the tentacle (Fig. 1 *c*). In *M. penola*, a giant species 850 mm. long, the large adhesive tentacles show a more extensive dove-tailing of the chitinous material into the mesogloea, a feature correlated with the greater size and greater strength needed per unit area of attaching surface.

It has been shown (Manton, 1940) that the chitinoid disks of *M. capensis* and *M. penola* are formed from granules of intracellular material situated in the terminal ectodermal cells, and the bases of these cells in *M. penola* extensively perforate the mesogloea. With the breakdown of these cells and the fusion of their granules chitinoid disks are formed which are thus anchored into the mesogloea. This method of formation of a chitinoid layer is not seen in *M. cocksi*, where intracellular granules are absent and the epithelium persists after chitinization of the cuticle. It is probable that the very unusual method shown by *M. capensis* and *M. penola* is associated with the extreme reduction in the extent of the perisarc, and the necessity for the remaining disk to be correspondingly strongly united with the soft parts of the hydroid. This method of chitin formation may be expected to occur in other species showing this type of hydrorhiza.

The hydrorhiza of many simple hydroids shows no elaboration for attachment such as is seen in *Myriothela*. *Obelia*, for example, possesses a very simple type of hydrorhiza consisting of extensive stolons lying over the substratum and attached to it along their adjacent surfaces. Sections of the hydrorhiza of *Obelia* are given for comparison with *Myriothela*. In Fig. 1 *d* a section is shown which passes longitudinally through the base of the hydrocaulus where it joins the hydrorhiza, and Fig. 1 *e* shows a transverse section of a stolon some distance from the hydrocaulus. Adhesion to the substratum takes place by the perisarc only, and no part of the coenosarc is involved. The perisarc is flattened against the substratum and is thickened along the outer edges of the stolon. The ectoderm may remain in contact with the perisarc, as in Fig. 1 *d*, but the coenosarc shrinks away from the perisarc in many regions situated remote from the hydrocaulus or from the growing tip of the stolon. The mesogloea (*m.*) is very thin and is unconnected with the perisarc (compare Fig. 1 *d* with 1 *b* and 1 *c*).

The perisarc of the hydrorhiza of *Obelia* is thick, but it is not stiff or hard as is that of *Myriothela*. It stains blue with Mallory's triple stain, and is composed of almost pure unhardened chitin. In these hydroids the pure chitin is flexible and pale in colour, just as is the unimpregnated unhardened cuticle in insects (Pryor, 1940*a*, *b*).

Method of Growth of the Hydroid

It has been shown (Manton, 1940) that in *M. penola* increase in size of the polyp takes place from definite growth zones. The tentacle-bearing region elongates mainly from the oral end, and the blastostyle-bearing zone grows orally at the expense of the basal part of the tentacle-bearing zone. The same method of growth is shown by *M. cocksi*, young tentacles are formed round the mouth, and a young specimen shows immature blastostyles arising on the lower part of the tentacle-bearing zone before the tentacles are all absorbed. The hydrorhiza in both species grows in length at its oral end (see above).

The Claspers

The "claspers" of *M. cocksi* have for long been regarded as remarkable or unique structures. Many new species of *Myriothela* have been described recently, but none shows this feature. The appearance and function of the claspers in *M. cocksi* in carrying the fertilized and developing ova has been described by Allman (1875), Benoit (1925), and others. The claspers are tentacle-like structures arising from or near the bases of the blastostyles, and the eggs are carried on their extremities, several claspers often adhering to one egg membrane.

A slight overlapping of the hydrorhiza and blastostyle-bearing zones has been described in *M. penola* and *M. phrygia*, where some of the adhesive tentacles of the hydrorhiza arise from or near the bases of a few of the proximal blastostyles (Manton, 1940). The adhesive tentacles in this position bear a striking superficial resemblance to the claspers of *M. cocksi*. Moreover, inspection shows that the method of adhesion of the claspers to the egg of *M. cocksi* differs little from that of a hydrorhiza tentacle to its substratum.

An unattached clasper in structure resembles a free hydrorhiza tentacle in that the ectodermal and endodermal epithelia are complete, the mesogloea at the tip is thinner, denser, and more darkly staining with Mallory's triple stain, and is here perforated by the bases of some of the ectodermal cells. The tip of a clasper first adheres to the egg membrane by the surface of its ectodermal cells (see Benoit, 1925, text-figs. 24–26), the ectodermal epithelium being intact. Further changes in the clasper are not described by Benoit, but he figures an older clasper with only one layer of cells at its tip (Benoit, 1925, text-figs. 27–28), a feature also shown by Korotneff (1888, pl. 2, fig. 10). A sagittal section through an attached clasper which is older still is shown here in Fig. 2. The mesogloea at the tip has thickened, particularly at the margin of the adhesion, and has united directly with the egg membrane. The ectoderm at the tip of the clasper has disappeared. The only difference between the adhesion of the clasper and that of a hydrorhiza tentacle of *M. capensis* or *M. penola* is the absence of a chitinous disk of adhesion in the former; in both a mesogloea attachment is made and the terminal ectoderm has disappeared (compare Figs. 1 *c*, 2).

Thus the similarity between (i) the position of the claspers of *M. cocksi* and some of the hydrorhiza tentacles of *M. penola* and *M. phrygia*, and (ii) the structure and method of adhesion of the claspers of *M. cocksi* and the hydrorhiza tentacles of other species of *Myriothela*, suggests that the claspers represent a specialized part of the hydrorhiza which has altered its function and now adheres to ova instead of to the substratum.

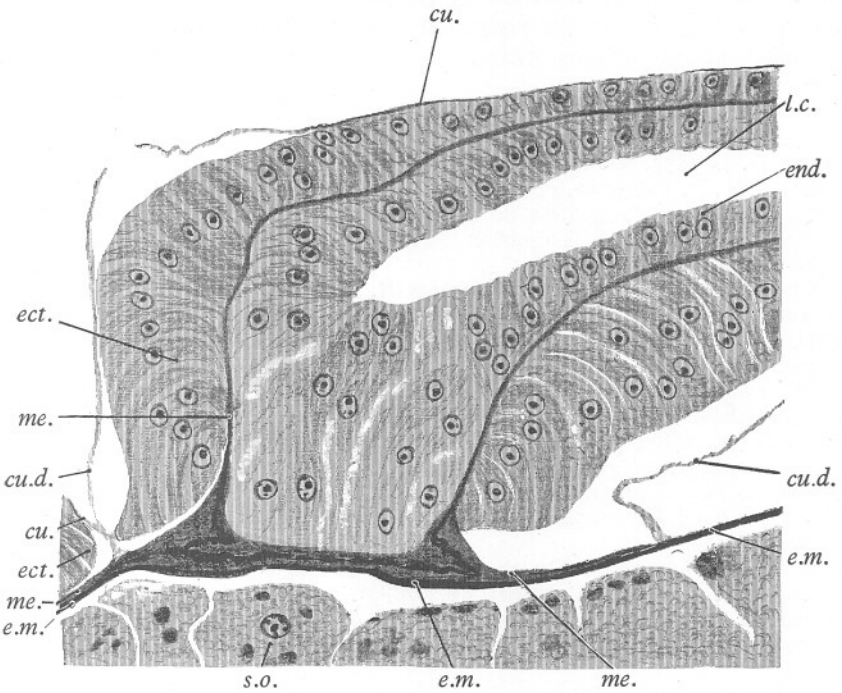

Fig. 2. Section passing sagittally through a clasper and part of the ovum to which it is attached in *M. cocksi*. The edge of a second clasper is seen on the left. The cuticle of the clasper is raised from the epithelium in places (*cu.d.*) owing to shrinkage of the tissues since death. The mesogloea of the clasper is clearly united with the egg membrane, the terminal ectoderm having disappeared.

cu., cuticle. *cu.d.*, cuticle detached from epithelium by shrinkage. *ect.*, ectoderm. *e.m.*, egg membrane. *end.*, endoderm. *l.c.*, endodermal lumen of clasper. *me.*, mesogloea. *s.o.*, segmenting ovum.

Summary

The hydrorhiza of *Myriothela cocksi* is described. It bears adhesive tentacles covered by perisarc, which adhere to the substratum by their flattened extremities.

The chitin forming a disk of adhesion is thick, and is attached to the mesogloea of the tentacle. The terminal ectoderm persists.

The hydrorhiza of *M. cocksi* and of species such as *M. capensis*, *M. penola*, and *M. phrygia*, etc., is built on a common plan. In the latter species the perisarc is reduced to adhesive disks more firmly attached to the mesogloea.

The method of growth of *M. cocksi* is recorded.

The structure and method of attachment of the claspers of *M. cocksi* to the egg membrane is described. The mesogloea at the tip of the clasper fuses with the egg membrane after the disappearance of the terminal ectoderm.

Evidence is given for the view that the claspers of *M. cocksi* represent a specialized part of the hydrorhiza.

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VERTEBRAL VARIATION IN TELEOSTEAN FISHES. II. THE HERRING (*CLUPEA HARENGUS* L.)

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(Text-figs. 1–4)

CONTENTS

INTRODUCTION

In October 1935, investigators from eleven countries represented on the International Council for the Exploration of the Sea met at Lowestoft to discuss the co-ordination of the results of herring research (Cons. Int. 1936, p. 7). The first four of the eight resolutions made at this meeting may be quoted as an introduction to the subject-matter of the present paper:

(1) It is recommended that any group of herring spawning in a given area at a given season from year to year should be defined as the natural "Biological Group". Morphological characters should be used as a practical aid to the identification of these biological groups outside the area and season of their spawning.

(2) It is recommended that work on biological groups and other local and seasonal populations should be continued in order to establish and test the continuity of the morphological characters of the biological groups, so that the members of the group and possibly the products of their spawning may be traced as they occur in the fisheries in later life. This will afford research workers data as to the effect of fishing on particular shoals and material on which to base predictions.

(3) As the biological groups of herrings are in many cases distinguishable by morphological characters, it is recommended that vertebral counts of selected material should be continued, additional characters such as the number of keeled scales being also studied when necessary.

(4) It is recommended that a co-operative study be undertaken on the practicability of utilizing a count of separate portions of the vertebral series in such a way as to draw distinctions between morphologically distinguishable groups with a minimum of labour and material. Mr Ford accepted an invitation to prepare a scheme. Professor R. A. Fisher consented to act in an advisory capacity.

My personal association with resolution 4 was the outcome of my statement at the Lowestoft meeting that there is a well-differentiated group of from four to eight vertebrae at the tail-end of the herring backbone which can be counted with precision; and that the use of this much shorter count as an alternative to the more familiar "total number of vertebrae" in population analyses might perhaps give equally satisfactory results. But, since then, a study of vertebral variation among teleostean fishes in general (Ford, 1937) has revealed an embarrassing lack of information of the kind required for the effective use of vertebral characters in population studies. In the pages which follow, therefore, the main effort has been to draw attention to the changes in form along the length of the herring backbone, and to illustrate by actual data the extent of individual variation which may be expected when working with statistical samples. At the same time, the ultimate purpose of the work, viz. the utilization of counts of separate portions of the vertebral series in such a way as to draw distinctions between morphologically distinguishable groups of herrings (vide Lowestoft resolution 4), has been borne in mind throughout.

Preliminary Considerations

There is no mistaking the backbone of a herring for that of any other fish. For despite the numerous points of agreement in anatomy with the backbones of allied species and genera within the great order Isospondyli and, indeed, with those of other orders as well, the attributes of *Clupea harengus* are discernible not only in the backbone as a composite whole, but in each and every vertebral component throughout its length.

There is at least the possibility that the species *C. harengus* exists in nature in a number of distinct subspecific forms, each with its own bodily characteristics, geographical distribution and established habits of migration, feeding and spawning. If this is so, it might be expected that the backbone, which so plainly reveals specific identity, would also afford clues to subspecific identity. That is to say, one would be able to determine from the backbone alone the particular subspecies to which any individual herring should be referred. And this could be done just as surely for a fish caught outside the area and season of spawning as for one taken from a spawning shoal.

On the other hand, the form of the herring backbone varies to a marked degree from individual to individual—so much so, that in practice it is simply

a matter of routine to resolve any sample of, say, one hundred backbones into one hundred separate backbones, each visibly different in structure from all the rest. Hence, even if the species exists as a number of morphologically distinguishable subspecies, appreciable individual variation in backbone form must be expected in each of them.

Taking these facts into consideration, it becomes clear that a sharp distinction should be drawn between (*a*) a backbone character which, by itself, is definitely diagnostic of the species or subspecies, and (*b*) one which is primarily a measure of vertebral variation, and which only acquires significance as a clue to identity when it is taken in conjunction with corresponding data for other backbones. Characters of class (*a*) may be likened to "hallmarks", which at once establish identity in the individual and will only be seen in *C. harengus*, or in one particular subspecific form of *C. harengus*. It need hardly be said that the study of local populations of herrings and of their migrations would be rendered very much more straightforward if reliable characters of this kind could be determined. The matter has already received preliminary attention, with encouraging results, but it is as yet too early to publish a report. In the meantime, therefore, it is necessary to deal for the most part with backbone characters of class (*b*) which, in contrast with the positive anatomical attributes just referred to, are but statistical measurements. They are the raw data on vertebral variation of a particular kind among the particular group of individuals from which they have been derived. As such, they must be subjected to recognized statistical treatment if they are to yield the special information required. The technique is the routine one of assessing the amount of variation in statistical samples, and comparing the results. For this, counts along the vertebral series in accordance with distinct changes in form are obviously the most serviceable, and the ultimate preferment of one count over another will rest, first, on the degree of precision with which the count can be made, and secondly, on the amount of labour and material involved in its determination.

Seeing that a great deal of work has already been done regarding variation in the so-called "total number of vertebrae", it may be asked why it should be necessary at this late stage to discuss the use of alternative counts? In reply it will probably be sufficient to advance three points:

(1) Experience has shown that in the determination of the total count in each of, say, one hundred herrings, some doubt will arise as to the strict validity of the count in perhaps twenty individuals, because of some observed abnormality in structure (Ford, 1933).

(2) Backbones composed of the same number of vertebrae may nevertheless differ in other respects; conversely, those which differ in the total may yet have other anatomical features in common. Consider, for example, the simple division of the backbone into an anterior part (*a*) and a posterior part (*b*) in accordance with a change in form at the junction of the two parts. The same total of 56 vertebrae is arrived at when (*a*) is 50 and (*b*) is 6, as when

(*a*) is 51 and (*b*) is 5; alternatively, a total of 56 expressed as (50+6) differs from a total of 55 expressed as (49+6), although the value of (*b*) is the same in both.

(3) This point is suggested in part by the examples used above, namely, that in certain circumstances a much shorter count along the backbone may give as much information as the total count. Thus, the difference between a total count of 56 and a second of 55 may prove to be no more than a difference of 1 in the value of (*b*) which is 6 in the one backbone and 5 in the other, the value of (*a*) being 50 in both. When it is remembered that before any direct count along the backbone can be made, the parts to be counted must first be properly exposed to view, whether by X-ray, by dissection, by selective staining, or by preparing a whole skeleton, it will be realized that the shorter the length of backbone to be handled, the less the work of preparation and counting. Apart from this matter of practical economy in working, however, there is another sound reason for thinking that a different system of counting may sometimes yield more conclusive results. This has to do with the basic metamerism of the herring. Investigation has shown that in the anterior part of the body the basic metamerism remains to a large extent unimpaired, so that the vertebrae, ribs, myocommata and certain of the keeled scales along the mid-ventral line of the body are in step with one another. That is to say, a count of the keeled scales, provided that it begins and ends at the right place, is in effect a vertebral count. Details are given later on p. 168, and it will be sufficient here to say that such a count, being an expression of the fundamental constitution of the herring's bodily structure, is one of special interest in present considerations.

The Anatomy of the Herring Backbone

The herring backbone has a characteristic form pattern in consequence of successive alterations in form from vertebra to vertebra along its length. Analysis shows that each of the vertebral components—the centrum, neural and haemal arches and their processes, the zygapophyses, etc.—changes in form from one vertebra to the next in its own appointed way, and that for the most part these form changes are evenly graded. At a number of points along the backbone, however, there is an abrupt change in the form of a component. Thus, at one point the form of the haemal arch will alter appreciably between adjacent vertebrae, while at a second point the form change will be seen in the neural arch, and so on. By determining the position of all such points along the backbone, the primary form pattern can be expressed in terms of a number of secondary patterns, each covering a well-differentiated group of vertebrae within which there is a distinctive gradation of form in at least one vertebral component. Moreover, it may be added that each of these secondary patterns is as characteristic of the herring as is the primary pattern.

Immediate interest centres in the number and serial position of the vertebrae over which the primary and secondary patterns are spread, since these vary from individual to individual within the range shown by the species. In Fig. 1 the left side of a backbone, consisting of a total of 56 vertebrae

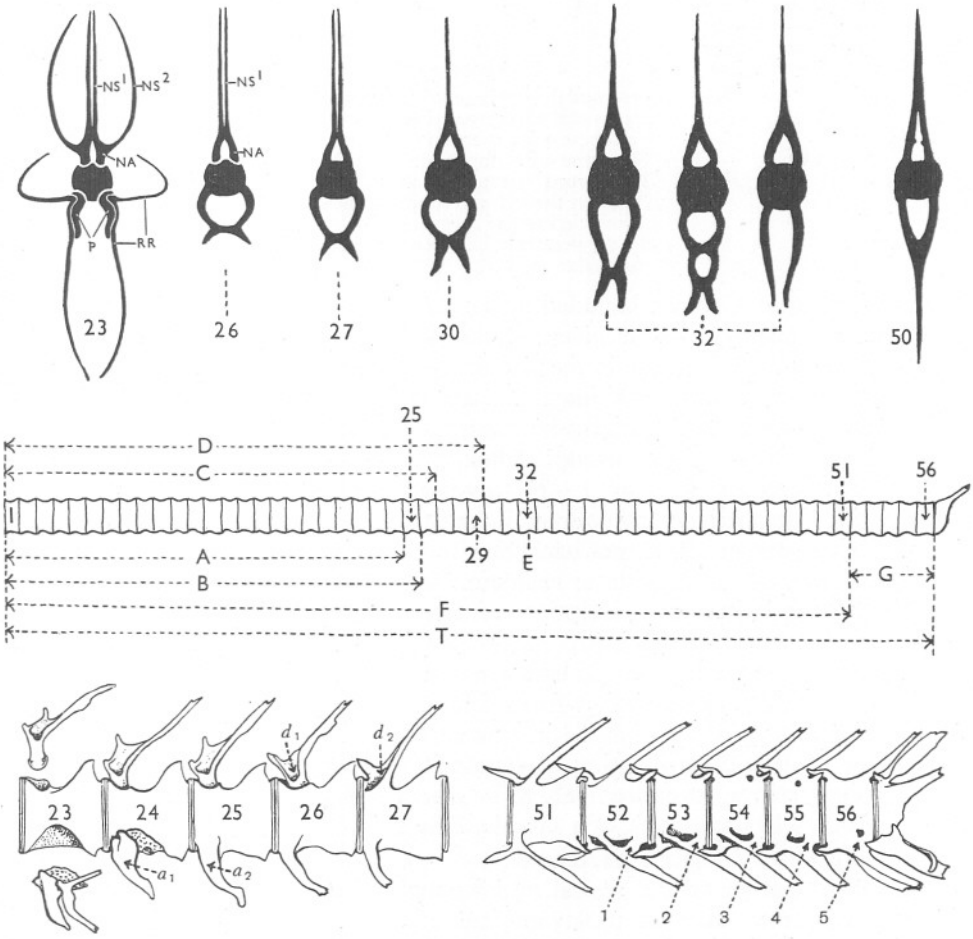

Fig. 1. Above: profiles of key vertebrae; three alternative forms of the 32nd are shown. Centre: diagrammatic outline of backbone viewed from left side. Below: outline of two sections of backbone viewed from left side.

The numbers represent serial numbers of the vertebrae: for particulars of *A*, *B*, *C*, *D*, *E*, *F*, *G* and *T*, see text, p. 156.

between the skull and the terminal urostylar segment, is marked off in accordance with changes of pattern. It so happens that in the particular backbone represented in the figure the right side agrees with the left in the details portrayed, but it is important to note that such complete agreement between the two sides is by no means usual. The known frequency with which bilateral

asymmetry occurs renders it necessary in practice to distinguish between counts along the left side and those along the right. Coming back to Fig. 1, and remembering that in this instance the two sides are in agreement, it is seen that the backbone is composed as follows:

Count denoted by: Left side	Median line	Right side	Group of vertebrae counted	Last vertebra in count
A_l		A_r	Pre-caudal vertebrae with autogenous haemal arch	24
	B		Pre-caudal vertebrae with open haemal arch	25
C_l		C_r	Vertebrae with autogenous neural arch	26
	D		Vertebrae with duplicated neural spine	29
F_l		F_r	The "trunk" vertebrae, i.e. all the vertebrae except those at the tail-end in which the haemal spines are cross-tied to the centra	51
	T		All the vertebrae between the skull and the terminal urostylar segment	56

A further count E is not included in the above summary because it is not of the same category as those given. It marks the vertebra in which there is normally a sudden increase in the size of the haemal canal to provide housing for a blood vessel to the kidney. In the backbone figured this is seen in vert. 32. Reference should also be made here to the fact that the number of vertebrae in the "tail" group, although not specifically indicated in the summary, is given by $G_l = (T - F_l)$ for the left side, and $G_r = (T - F_r)$ for the right. Alternatively, of course, G_l and G_r can be directly determined as a separate count on the actual backbone.

Now it can be stated without hesitation that the above series of counts is a highly discriminating description of any herring backbone. One might examine hundreds of specimens before obtaining two which did not differ in at least one respect. It could hardly be otherwise, seeing that all the counts named are subject to variation from fish to fish, even among those of the same biological group as defined in Lowestoft resolution 1.

In the routine determination of counts in samples of fish, certain irregularities in vertebral form are likely to be discovered which affect one or more of the counts in some 20 % of a sample. The chief of these irregularities are:

(i) Fusions of adjacent vertebrae.

(ii) Duplication of the neural and haemal spines on the two vertebrae immediately preceding the urostylar element.

(iii) Irregularity in character E.

The occurrence of fused vertebrae (see Fig. 2 on p. 157) has been dealt with in an earlier paper (Ford & Bull, 1926). The fusion may occur at almost any point along the backbone, although more often at some points than at others. If these fusions are counted, not as single units but as the number of vertebrae apparently involved in the fusion, the total number of vertebrae is restored to the "normal".

Duplication of neural and haemal spines on the two vertebrae immediately preceding the urostylar element (see Fig. 2 on p. 157) has also been the

subject of an earlier report (Ford, 1933). The counts of the vertebrae in the "tail" group of vertebrae, i.e. counts G_l and G_r, are particularly affected by this irregularity, and it is therefore advisable in statistical work to treat such cases in a class apart from the rest.

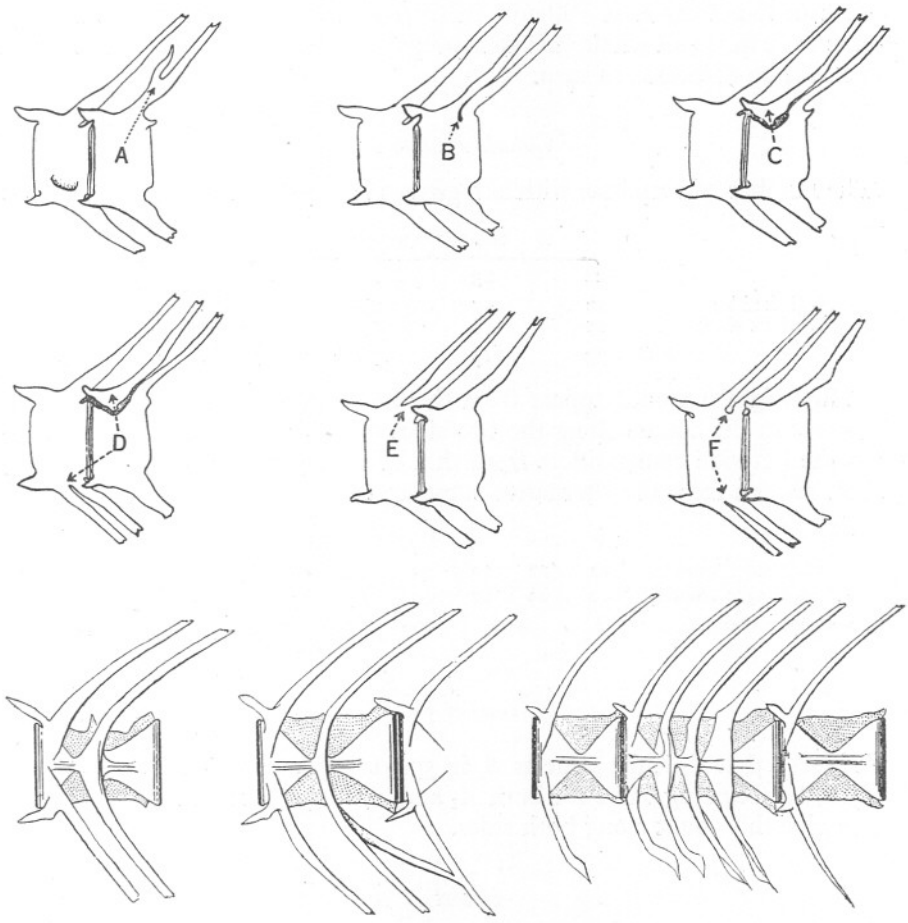

Fig. 2. Above: double-spined vertebrae (*A*, *B*, *C*, *D*, *E* and *F*) at the tail-end of herring, from Ford (1933). In each of the diagrams the two vertebrae represented are those immediately anterior to the terminal (urostylar) segment.
Below: abnormal vertebrae in the herring, from Ford & Bull (1926).

Normality in the secondary count *E* may be described simply as an obvious enlargement of the haemal canal to give easy passage for a blood vessel to the kidney. In some backbones, however, either the closed haemal canal is divided into separate upper and lower compartments, or the canal is open between a large bony loop formed by the haemal arches of the two sides of the vertebra (see Fig. 1).

Individual Variation in Vertebral Counts

The range of variation which may be expected in working through a sample of 100 herrings is satisfactorily indicated by actual data for a sample taken from a drift-net catch at Padstow in Cornwall in December 1935. All the counts were made on whole skeletons prepared by boiling and cleaning. Each count will be discussed in turn.

Counts A_l and A_r

The number of vertebrae with autogenous haemal arches varies as follows:

	No. of vertebrae				Total no. of backbones
	22	23	24	25	
A_l (left side)	12	57	29	2	100
A_r (right side)	11	58	29	2	100
Sum	23	115	58	4	A. mean = 23·215

At first sight it would appear from the above summary that there is little difference in the counts along the two sides of the backbone. Actually, however, the left side count differs from that of the right side in 41 backbones, as will be seen from the alternative summary:

	No. of vertebrae						
$\frac{A_l}{A_r}$ (left side count / right side count)	$\frac{22}{22}$	$\left(\frac{22}{23}\text{ or }\frac{23}{22}\right)$	$\frac{23}{23}$	$\left(\frac{23}{24}\text{ or }\frac{24}{23}\right)$	$\frac{24}{24}$	$\left(\frac{24}{25}\text{ or }\frac{25}{24}\right)$	
No. of backbones	4	15	39	22	16	4	= 100

Total of 59

It is seen that A_l is the same as A_r in 59 backbones, and although the most frequently occurring value for both A_l and A_r is 23, not more than 39 backbones give this count along both sides.

Count B

The number of vertebrae with open haemal arch varies as follows:

No. of vertebrae					Total no. of backbones	
22	23	24	25	26		
3	26	55	15	1	100	A. mean = 23·850

This is a well-known count which has often been made in past work. Objection has been raised to it on the ground that partial bridging across the haemal arches may occur in several vertebrae anterior to the one in which the complete closure is seen. Orton (1916, p. 80), for example, in recording

the serial number of the first vertebra having a complete haemal arch, considered it advisable to state in addition the number of vertebrae having an incomplete but "well-developed" arch—and an arch was recorded as "well-developed" if the haemal processes were almost as large as those of the first complete arch and possessed even the smallest trace of an internal cross-piece. In his opinion, it is not improbable that in the living animal these incomplete but well-developed arches are closed by a cartilaginous cross-piece. Hence, he would seem to favour a statistical count of the number of vertebrae "with potentialities" for complete haemal arches, rather than a count which includes only those vertebrae in which the haemal arch is unquestionably closed by a bony bridge. Certainly, the matter is one which should be borne in mind by any investigator proposing to use the counts in statistical work.

Counts C_l and C_r

The count of the number of vertebrae with autogenous neural arches varies from fish to fish and from side to side. Dealing first with the separate counts C_l and C_r:

	No. of vertebrae					Total no. of backbones	
	24	25	26	27	28		
C_l (left side)	1	11	49	33	6	100	
C_r (right side)	—	12	42	39	7	100	
Sum	1	23	91	72	13	A. mean = 26·365	

As with the counts A_l and A_r, the extent of bilateral asymmetry is best indicated by an alternative summary of the data:

	No. of vertebrae							
C_l (left side count) / C_r (right side count)	$\frac{24}{25}$	$\frac{25}{25}$	$\left(\frac{25}{26}\text{ or }\frac{26}{25}\right)$	$\frac{26}{26}$	$\left(\frac{26}{27}\text{ or }\frac{27}{26}\right)$	$\frac{27}{27}$	$\left(\frac{27}{28}\text{ or }\frac{28}{27}\right)$	$\frac{28}{28}$
No. of backbones	1	5	12	28	23	21	7	3 = 100

Total of 57

The data show that C_l is the same as C_r in not more than 57 out of the total of 100 backbones. The most frequent value for both C_l and C_r is 26, yet only 28 backbones give this count along both sides.

Count D

The number of vertebrae in which the neural spine is duplicated shows the following variation:

No. of vertebrae				Total no. of backbones	
28	29	30	31		
5	32	55	8	100	A. mean = 29·660

Count E

As stated above, it is necessary in making this count to anticipate instances of irregularity in the form of the haemal arch concerned. In the present sample there are 11 backbones in which either the haemal canal is divided into upper and lower compartments, or the haemal arches form a large open loop. The variation in count *E*, shown by (*a*) the 89 normal backbones and (*b*) the 11 irregular ones, is shown below:

	No. of vertebrae				Total no. of backbones	
	31	32	33	34		
Normal	2	47	38	2	89	A. mean = 32·449
Irregular	2	7	2	—	11	A. mean = 32·000
Sum	4	54	40	2	100	A. mean = 32·400

Attention is drawn to the lower average value of the count in the irregular backbones. Although the number of such backbones in the present sample is much too small for statistical purposes, there is reason to believe that the lower average is not an entirely fortuitous result, since it has been observed in a number of other samples. One indication is that the irregular form of haemal arch is more common in backbones with a total of 55 vertebrae, excluding the urostyle, than in those with a total of 56, but, here again, the observation needs statistical confirmation.

Counts F_l and F_r

It will be seen from Fig. 1 on p. 155 that the backbone is divisible into the anterior and larger "trunk" group of vertebrae, followed by the posterior and much smaller group of "tail" vertebrae. Counting along the left side of the backbone, therefore, the total number of vertebrae (T) is the sum of the "trunk" count (F_l) and the "tail" count (G_l). Along the right side, (T) is the sum of (F_r) and (G_r). In the Padstow sample, only 85 backbones were "normal" in the sense that straightforward counts of "trunk", "tail" and "total" vertebrae could be made along both sides. In the remaining 15 this was not possible on account of some irregularity in vertebral form towards the posterior end of the backbone which interfered with the counts. For the normal backbones the values of F_l and F_r varied as follows:

	No. of vertebrae					Total no. of backbones
	48	49	50	51	52	
F_l (left side)	—	8	44	32	1	85
F_r (right side)	1	7	38	36	3	85
Sum	1	15	82	68	4	A. mean = 50·347

The degree of individual discrepancy between F_l and F_r is indicated below in the same manner as before.

$\frac{F_l}{F_r}$	$\frac{48}{49}$	$\frac{49}{49}$	$\left(\frac{49}{50}\text{ or }\frac{50}{49}\right)$	$\frac{50}{50}$	$\left(\frac{50}{51}\text{ or }\frac{51}{50}\right)$	$\frac{51}{51}$	$\frac{51}{52}$	$\frac{52}{52}$
No. of backbones	1	6	2	36	8	29	2	1 = 85

Total of 72

Thus, in 72 out of the total of 85 backbones, the left side count F_l is the same as the right side count F_r, which is a greater proportion than with the counts A and C.

Counts G_l and G_r

The first of the "tail" group is distinguished from the last of the "trunk" group by the fact that in the former the haemal spine is cross-tied to the centrum by a bony strut (see Fig. 1 on p. 155). As with counts A, C and F, there is some measure of bilateral asymmetry, so that it is necessary to distinguish between the left and right side counts G_l and G_r. In the 85 normal backbones for which the values of F_l and F_r have already been given, the values of G_l and G_r are as follows:

	No. of vertebrae				Total no. of backbones	
	4	5	6	7		
G_l (left side)	—	43	38	4	85	
G_r (right side)	2	47	31	5	85	
Sum	2	90	69	9	A. mean = 5·500	

and the extent of bilateral asymmetry:

$\frac{G_l}{G_r}$	$\frac{5}{4}$	$\frac{5}{5}$	$\left(\frac{5}{6}\text{ or }\frac{6}{5}\right)$	$\frac{6}{6}$	$\left(\frac{6}{7}\text{ or }\frac{7}{6}\right)$	$\frac{7}{7}$
No. of backbones	2	40	8	29	3	3 = 85

Total of 72

The data show that of the 72 backbones (*ca.* 85 % of the total of 85 examined), in which G_l is the same as G_r, there are 40 (*ca.* 47 % of the 85 examined) in which the count of "tail" vertebrae is 5 along both left and right sides.

The Total Count (T)

The total count (T) for the 85 normal backbones in the sample varies thus:

No. of vertebrae				Total no. of backbones	
54	55	56	57		
1	19	57	8	85	A. mean = 55·847

With regard to the 15 "abnormal" backbones, 3 show fusions of vertebrae which make it difficult to determine (T) with certainty. In the remaining 12

there is duplication of the neural and haemal spines of one or both of the two vertebrae immediately preceding the terminal urostylar segment, although the centra are normal enough for an uninterrupted count of (T). The results of this count are compared with that for normal backbones:

	No. of vertebrae				Total no. of backbones		
	54	55	56	57			
Backbones with duplicated spines	—	7	5	—	12	A. mean 55·417	Diff. 0·43
Normal backbones	1	19	57	8	85	A. mean 55·847	
Sum	1	26	62	8	97	A. mean 55·794	

It is seen that duplication of spines is associated with a lowering of the total number of vertebrae (T), giving a difference of 0·43 in the value of the mean. If the number of "tail" vertebrae is considered, then it is found that the discrepancy is still more marked:

		No. of "tail" vertebrae				Total no. of backbones	
		4	5	6	7		
Backbones with duplicated spines	G_l	2	9	1	—	12	
	G_r	1	10	1	—	12	
	Sum	3	19	2	—	A. mean 4·958	
Normal backbones	G_l	—	43	38	4	85	Diff. 0·542
	G_r	2	47	31	5	85	
	Sum	2	90	69	9	A. mean 5·500	

By contrast it is to be noted that the mean number of "trunk" vertebrae for the 12 abnormal backbones is 50·459 as against 50·347 for the normal. That is to say, abnormal and normal backbones agree approximately in the number of "trunk" vertebrae, the lowering of the mean value of (T) in association with duplication of spines being almost entirely accounted for by the reduction in the number of vertebrae in the "tail" (cf. Ford, 1933, p. 221).

Variation from Sample to Sample

Having given an idea of the nature and extent of backbone variation among the individuals of an average working sample, it is now proposed to compare the data for a number of different samples. The statistical material to be used in the comparisons was collected and tabulated by Dr A. G. Nichols and colleagues at the Millport Biological Station, to whom I am greatly indebted for their kindly co-operation in a tedious series of observations. The fact that the data were collected by independent workers adds to the interest, since it shows that the successive changes in form along the length of the backbone are sufficiently well defined to be recognized and used by persons other than myself. And so far as I am aware the Millport team experienced no great difficulty in determining with precision the whole series of vertebral counts required. It should be added that the four samples here to be considered were

a deliberate selection from a total of seven which they analysed. That is to say, the comparisons to be made are not to be regarded as a critical examination of the actual herring populations occurring in the regions from which the seven samples were drawn, but rather as an illustration of the variation which investigators may expect to observe in carrying out such a regional study.

General particulars of the four samples are given in Table I.

TABLE I

Serial no. of sample	Locality	No. of fish examined	Length (cm.)	Sexual condition
1	Clyde (from Fairlie)	100	21–27 (mainly 22–24)	Mainly stage II
2	Brown Head, Arran	110	23–28 (mainly 23–26)	Stage VI
3	Isle of Man	217	22–28 (mainly 24–26)	Stages VII–II
4	Isle of Man (Port Erin Bay)	105	21–28 (mainly 23–26)	Stage VII

It may be stated in the first place that each of the four samples included an appreciable proportion of abnormal backbones, mainly those in which there was duplication of the neural or haemal processes of the penultimate or antepenultimate vertebrae (Table II).

TABLE II

Serial no. of sample	No. of backbones with fused vertebrae	No. of backbones with duplicated neural and haemal spines	Remainder (normal backbones)
1	1 (1 %)	23 (23 %)	76 (76 %)
2	—	24 (21·8 %)	86 (78·2 %)
3	4 (1·9 %)	66 (30·4 %)	147 (67·7 %)
4	3 (2·9 %)	15 (14·3 %)	87 (82·9 %)

In consequence of the high percentage of backbones with duplicated neural and haemal spines, the total number of vertebrae (T) for each sample is substantially lowered (Table III).

TABLE III

Serial no. of sample	No. of vertebrae 53	54	55	56	57	58	Total no. of backbones	Total count (T) arithmetic means	and differences
1. Normal backbones	—	—	5	56	15	—	76	56·132	0·436
Backbones with duplicated spines	—	—	7	16	—	—	23	55·696	
2. Normal backbones	—	1	6	61	18	—	86	56·116	0·408
Backbones with duplicated spines	—	—	7	17	—	—	24	55·708	
3. Normal backbones	—	4	51	81	10	1	147	55·680	0·604
Backbones with duplicated spines	1	7	45	12	1	—	66	55·076	
4. Normal backbones	—	2	38	41	6	—	87	55·586	0·186
Backbones with duplicated spines	—	—	9	6	—	—	15	55·400	

Table IV

Count A: No. of Vertebrae with Autogenous Haemal Arch

Serial no. of sample	Count	No. of vertebrae 21	22	23	24	25	26	Total no. of backbones	A. mean
1 (Fairlie)	A_l	—	13	44	40	3	—	100	
	A_r	—	11	52	35	2	—	100	
	Sum	—	24	96	75	5	—		23·305
2 (Arran)	A_l	—	10	62	33	5	—	110	
	A_r	—	10	64	32	4	—	110	
	Sum	—	20	126	65	9	—		23·286
3 (I.O.M.)	A_l	3	33	110	64	6	1	217	
	A_r	2	32	120	55	8	—	217	
	Sum	5	65	230	119	14	1		23·173
4 (I.O.M.)	A_l	2	25	49	26	3	—	105	
	A_r	—	23	58	22	2	—	105	
	Sum	2	48	107	48	5	—		23·029

Count B: Pre-caudal Vertebrae with Open Haemal Arch

Serial no. of sample	No. of vertebrae 22	23	24	25	26	27	Total no. of backbones	A. mean
1 (Fairlie)	1	27	47	17	7	1	100	24·050
2 (Arran)	—	21	58	26	5	—	110	24·136
3 (I.O.M.)	4	81	107	20	5	—	217	23·728
4 (I.O.M.)	4	42	45	13	—	—	104	23·644

Count C: No. of Vertebrae with Autogenous Neural Arch

Serial no. of sample	Count	No. of vertebrae 24	25	26	27	28	Total no. of backbones	A. mean
1 (Fairlie)	C_l	—	13	51	33	3	100	
	C_r	—	14	56	26	4	100	
	Sum	—	27	107	59	7		26·230
2 (Arran)	C_l	2	23	57	26	2	110	
	C_r	2	20	62	22	4	110	
	Sum	4	43	119	48	6		26·041
3 (I.O.M.)	C_l	1	23	86	93	14	217	
	C_r	3	19	91	93	11	217	
	Sum	4	42	177	186	25		26·429
4 (I.O.M.)	C_l	—	9	49	39	8	105	
	C_r	2	11	49	39	4	105	
	Sum	2	20	98	78	12		26·371

Count D: No. of Vertebrae with Duplicated Neural Spine

Serial no. of sample	No. of vertebrae 27	28	29	30	31	32	Total no. of backbones	A. mean
1 (Fairlie)	—	—	31	59	9	1	100	29·800
2 (Arran)	—	2	44	48	15	1	110	29·718
3 (I.O.M.)	1	9	78	96	31	2	217	29·705
4 (I.O.M.)	—	7	41	49	7	1	105	29·562

TABLE IV *continued*

COUNT F: NO. OF VERTEBRAE IN "TRUNK"

Serial no. of sample	Count	No. of vertebrae 47	48	49	50	51	52	Total no. of backbones	A. mean
1 (Fairlie)	F_l	—	—	15	48	35	2	100	
	F_r	—	1	13	46	39	1	100	
	Sum	—	1	28	94	74	3		50·250
2 (Arran)	F_l	1	—	13	46	48	2	110	
	F_r	—	—	15	55	37	3	110	
	Sum	1	—	28	101	85	5		50·291
3 (I.O.M.)	F_l	—	4	35	129	44	5	217	
	F_r	1	1	44	117	51	3	217	
	Sum	1	5	79	246	95	8		50·048
4 (I.O.M.)	F_l	—	3	20	60	18	4	105	
	F_r	—	2	22	60	19	2	105	
	Sum	—	5	42	120	37	6		49·986

COUNT G: NO. OF VERTEBRAE IN THE "TAIL" GROUP. NORMAL BACKBONES ONLY

Serial no. of sample	Count	No. of vertebrae 4	5	6	7	8	Total no. of backbones	A. mean
1 (Fairlie)	G_l	—	20	44	10	2	76	
	G_r	—	25	35	15	1	76	
	Sum	—	45	79	25	3		5·908
2 (Arran)	G_l	—	25	50	11	—	86	
	G_r	—	24	49	13	—	86	
	Sum	—	49	99	24	—		5·855
3 (I.O.M.)	G_l	1	69	75	1	1	147	
	G_r	1	63	77	6	—	147	
	Sum	2	132	152	7	1		5·568
4 (I.O.M.)	G_l	1	34	50	2	—	87	
	G_r	1	31	51	4	—	87	
	Sum	2	65	101	6	—		5·638

THE TOTAL NO. OF VERTEBRAE. NORMAL BACKBONES ONLY

Serial no. of sample	No. of vertebrae 54	55	56	57	58	Total no. of backbones	A. mean
1 (Fairlie)	—	5	56	15	—	76	56·132
2 (Arran)	1	6	61	18	—	86	56·116
3 (I.O.M.)	4	51	81	10	1	147	55·680
4 (I.O.M.)	2	38	41	6	—	87	55·586

Table III on p. 163 also shows that the total number of vertebrae for normal backbones is higher in samples 1 and 2 than in samples 3 and 4. Thus, the arithmetic mean values of (*T*) for the former are approximately greater by 0·5 vertebra than those of the latter. A difference of this magnitude would certainly give grounds for suspecting a real populational difference between the fish from Fairlie and Arran and those from the Isle of Man. For whereas only 7 % of the Fairlie and Arran fish had less than 56 vertebrae, the proportion for the Isle of Man fish was over 40 %. For present purposes, however, this question is of no great moment: the main interest in the comparison is to discover the extent to which vertebral counts other than the total (*T*) also vary from sample to sample. Dr Nichol's determinations of the counts *A*, *B*, *C*, *D*, *F* and *G* (as described on p. 156 of this paper) are summarized in Table IV on pp. 164–5, from which the mean values have been extracted (Table V).

TABLE V

		Serial no. of sample							
		1		2		3		4	
Count	Diff.	A. mean	Diff.	A. mean	Diff.	A. mean	Diff.	A. mean	Diff.
A		23·305		23·286		23·173		23·029	
	(*B-A*)		0·745		0·850		0·555		0·615
B		24·050		24·136		23·728		23·644	
	(*C-B*)	*26·230*	*2·180*	*26·041*	*1·905*	*26·429*	*2·701*	*26·371*	*2·727*
C			3·570		3·677		3·276		3·191
	(*D-C*)	29·800		29·718		29·705		29·562	
D			20·450		20·573		20·343		20·424
	(*F-D*)	50·250		50·291		50·048		49·986	
G	Normal backbones only	5·908		5·855		5·568		5·638	
T		56·132		56·116		55·680		55·586	

It will be seen that there is a pairing off of the samples, 2 agreeing with 1 and 4 with 3. The mean values for counts *A*, *B*, *D*, *F* and *G*, as well as that for the total count (*T*), are all higher in 1 and 2 than in 3 and 4. The same is true of the differences in the means, viz. (*B-A*), (*D-C*) and (*F-D*). Admittedly, the superiority of the sub-counts in 1 and 2 over those of 3 and 4 is not as great as the difference of 0·5 vertebra between the values of the total count (*T*), but it is nevertheless distinct and consistent. It is interesting, too, that the mean number of "tail" vertebrae (count *G*) plainly confirms the difference between the pairs of samples.

But perhaps the most interesting and significant fact to be learned from the above data is that the mean values of count (*C*) and the difference (*C-B*) are not higher but lower—substantially lower—in 1 and 2 than in 3 and 4. Were it not for these exceptions, the data as a whole might well have been explained by the simple hypothesis that the Fairlie and Arran samples (1 and 2) comprised a larger proportion of fish with a total of 56 or 57 vertebrae than the Isle of Man samples (3 and 4). For it would be expected that backbones with a higher total number of vertebrae would, on average, show a higher number of vertebrae in each of its component parts. As matters stand, however, it is necessary to suspect that there is a difference between the fish of the Isle of

Man and those of Fairlie and Arran, *even among those having the same total number of vertebrae*. Accordingly, a comparison has been made to test this, using backbones with a total of 56 vertebrae. The results with regard to the critical count (C) are as given in Table VI.

TABLE VI

Serial no. of sample	Count	No. of vertebrae 24	25	26	27	28	Total no. of backbones	A. mean
1	C_l	2	16	34	9	—	61	
(Fairlie)	C_r	1	14	32	13	1	61	
	Sum	3	30	66	22	1		$C=25{\cdot}902$
2	C_l	—	10	32	14	—	56	
(Arran)	C_r	—	9	35	11	1	56	
	Sum	—	19	67	25	1		$C=26{\cdot}071$
3	C_l	—	7	29	36	8	80	
(Isle of Man)	C_r	—	5	31	40	4	80	
	Sum	—	12	60	76	12		$C=26{\cdot}550$
4	C_l	—	3	18	16	4	41	
(Isle of Man)	C_r	—	4	19	16	2	41	
	Sum	—	7	37	32	6		$C=26{\cdot}451$

It is seen that the mean value of (C) for the Isle of Man samples is definitely higher than that for the Fairlie and Arran samples. There is no need here to give the results of similar comparisons between backbones having a total of 55 or 57 vertebrae, although of course this would be necessary in an actual regional survey.

MERISTIC AGREEMENT BETWEEN THE BACKBONE AND OTHER BODILY ORGANS

All the details and data discussed in the foregoing sections are in respect of individual variation in the form of the backbone itself, apart altogether from variation in other bodily characters. But in the herring, as in any other animal with a segmented body, the relation between successive segments of the backbone and the corresponding segments of other organs is a problem of great interest. For if the bones, muscles, and scales (among other structures) along the full length of the body, or some part of it, are in meristic conformity, then a count of the one is, in effect, a count of the other. And not this alone, for the count itself is a statistic of the basic plan upon which the whole body is organized. Such a statistic might prove of especial service and convenience in the kind of population studies with which this paper is concerned.

Relevant data are given in Fig. 3, which shows the extent of agreement between the backbone, myocommata, fin-radials and keeled scales in a herring which has been dissected and stained in alizarin. It is seen that the backbone consists of 55 vertebrae between the skull and the terminal urostylar segment. Meristic agreement is to be observed in the anterior part of the body. Dorsal to the backbone, the neural spines of the 1st to the 17th vertebrae regularly

alternate with a series of bony rods, described by Hillier* (1932, p. 98) as the root-bones of a fin now submerged. Immediately posterior to the last of these root-bones, where the first of the radials of the dorsal fin makes its appearance, the conformity with the neural spines ceases, so that the whole base of the dorsal fin lies within the span of the neural spines of the 17th to 30th vertebrae. Ventrally to the backbone, the ribs (the first of which is attached to the 3rd vertebra), myocommata, and keeled scales are in step, backward to the anus. Behind the anus, the haemal processes of the vertebrae from the 38th to the 46th or 47th, are out of step with the radials of the anal fin.

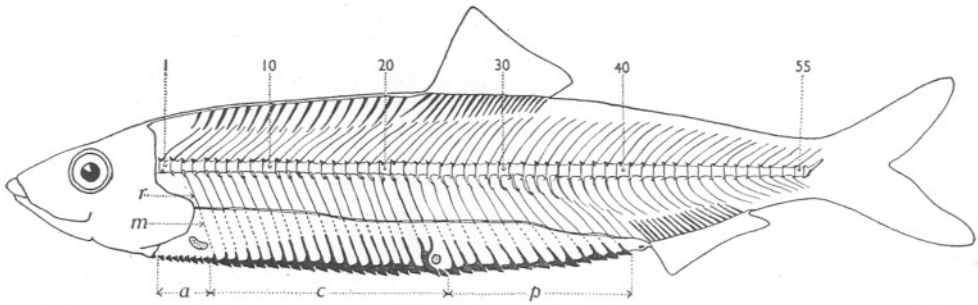

Fig. 3. Left side of a herring to show the extent of meristic agreement between the backbone, fin-radials, myocommata and keeled scales (see text). *r*, rib. *m*, myocomma. *a*, *c* and *p*, anterior, central and posterior groups of keeled scales.

Counts of the Keeled Scales

Along the ventral edge of the body of the herring from the throat backwards to the anus there is a median row of scales. These "keeled scales" have been used in the past as the basis of statistical counts in biometric studies. Usually a distinction has been drawn between the K_1 scales which lie in front of the pelvic fins, and the K_2 scales behind the pelvics. The K_2 count is the one most generally adopted for statistical work, and the first scale to be included in the count is situated between the insertions of the pelvics (see Johansen, 1919, Fig. 9).

Now without in the least degree criticizing the use of K_1 and K_2 counts as statistics of variation within the section of the body in which they are situated, it is of no little interest to consider the number and disposition of the keeled scales in relation to the myocommata, ribs and vertebrae with which they are observed to be in association. In Fig. 3 the keeled scales are marked off into three groups—an anterior group (*a*) of 8, a central group (*c*) of 20, and a posterior one (*p*) of 13, making a total of 41 scales in all between the throat and the anus. For purposes of description it is convenient to deal first with the scales of the central group, which begins at the 9th scale. This 9th scale is

* Hillier's treatise, entitled *A Theory of the Formation of Animals*, contains a very useful and detailed description of the anatomy of the herring, based on personal observations. This footnote will serve to draw attention to a work which may have escaped the notice of many fishery investigators.

seen to be in register with a myocomma, and with the first of the ribs, which is attached to the 3rd vertebra. Proceeding backwards along the series, the 10th, 11th, ..., to the 26th scale are similarly associated with their respective myocommata and the successive ribs of the 4th, 5th, ... to the 20th vertebra. The 27th scale is a compound one having lateral processes which loop round the base of the pelvic fin and, at their distal end break into two and make register with two myocommata and the underlying ribs of the 21st and 22nd vertebrae. There remains the 28th scale from the throat, which appears to be attached anteriorly to the posterior end of the preceding scale. Summarizing, the 20 keeled scales from the 9th to the 28th, both inclusive, form a central group which is in meristic agreement with 20 myocommata and the ribs of 20 vertebrae from the 3rd to the 22nd. It may also be added here that the vertebrae referred to have autogenous parapophyses, the 22nd vertebra being the hindermost one to show this character.

The posterior group of 13 scales commences with the 29th scale from the throat and ends with the 41st just anterior to the anus. Each of these is in register with a myocomma and a vertebra, the first being in register with the 23rd vertebra (the first to have its haemal arches continuous with the centrum and the ribs attached by ligament—the "false" ribs of Hillier, 1932, p. 94) and the last in register with the 35th vertebra.

With the central and posterior groups thus orientated, it is only necessary to state that the anterior group consists of 8 scales of comparatively small size which are without conspicuous lateral processes and are situated in front of the first rib.

The foregoing data relate to a selected specimen from a sample of young herrings of the "O" age-group caught at Plymouth. After removing the scales from the sides of the body in the neighbourhood of the pectoral fins, pelvic fins, and keeled scales, each fish was split longitudinally to expose the backbone and then stained in alizarin. Thus prepared, the keeled scales, myocommata, ribs and vertebrae could be easily counted *in situ* under a dissecting microscope. Only 25 fish in all were examined, but these were sufficient to show that appreciable variation from fish to fish had to be taken into account. The total number of keeled scales varied from 41 to 45, while for the three groups into which the total may be divided the range of variation was from 7 to 11 in the anterior group, 19 to 21 in the central group, and 13 to 16 in the posterior group, with frequencies as shown in Table VII.

But it was also found that in 15 of the total of 25 fish the number of keeled scales in one or other of the central and posterior groups was greater by 1 than the number of myocommata (and ribs) with which the scales were in register. In each instance the breakdown of the normal association of 1 keeled scale with 1 myocomma (and rib) occurred in the region adjacent to the insertion of the pelvics. In 2 of the 15 specimens the last two scales of the central group were in association with a single myocomma, while in the remaining 13 the first two scales of the posterior group were covered by one

myocomma only (see Fig. 4). The significance of these observations in connexion with the K_2 count will not have escaped notice, for it implies that the K_2 count is not a constant function of the number of myocommata and

TABLE VII

		No. of keeled scales					
		41	42	43	44	45	A. mean
No. of specimens:	Total count	6	4	5	6	4	42·92
	Anterior group	7	8	9	10	11	
		1	8	8	7	1	8·96
	Central group		19	20	21		
			1	17	7		20·24
	Posterior group		13	14	15	16	
			10	13	1	1	13·72

vertebrae with which the keeled scales counted are in association. Whether or not this fact affects the results of any particular biometric investigation is immaterial in the present consideration, but it is nevertheless one which should be borne in mind.

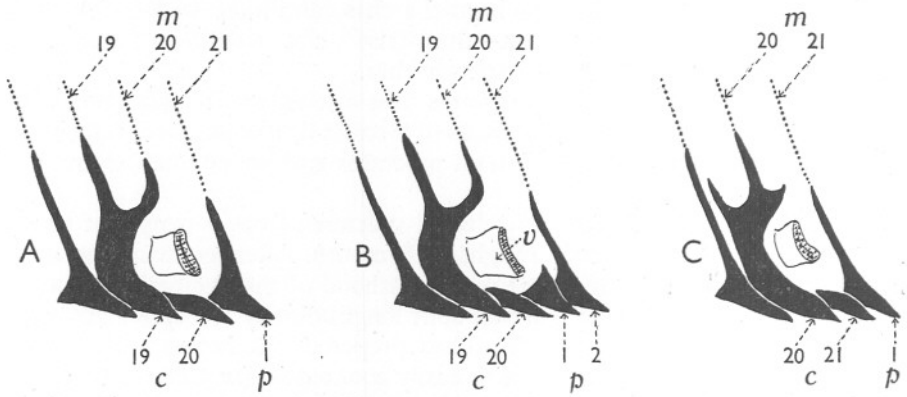

Fig. 4. Keeled scales in the neighbourhood of the pelvic fins. A, the last two scales of the central group (*c*, 19 and 20) and the first scale of the posterior group (*p*, 1) are in register with the 19th, 20th and 21st myocommata; B, a common variation in which the last two scales of the central group (*c*, 19 and 20) and the first two of the posterior group (*p*, 1 and 2) are associated with the 19th, 20th and 21st myocommata; C, a less common variation in which the last two scales of the central group (*c*, 20 and 21) are in register with a single myocomma (20th) instead of two as normally.

DISCUSSION

As a concluding section of this paper, the results given in preceding pages will be considered in their bearing upon the Resolutions adopted by the Lowestoft meeting. An agreed scheme for the detailed study of backbone variation in as many biological groups as possible is clearly desirable. I cannot recommend that the work should be restricted to a selected few of the vertebral counts described above, because I firmly believe that our past persistence in doing so has prevented us from making progress at the rate commensurate

with the amount of solid and tedious labour expended. Long before this we should have undertaken the detailed investigation of the herring backbone in all its parts and of variation from group to group which is only now being contemplated, and without which we cannot make much headway in the future. It is not suggested that past work has been entirely unprofitable, for much useful information has been acquired concerning the variation of the total count (T) in particular, but much of it has proceeded in the absence of an adequate knowledge of the nature and extent of vertebral variation, with a consequent waste of effort and the accumulation of a mass of bewildering data. This, at any rate, is a personal conviction, based on personal experience.

In planning the scheme, considerations of economy in labour and material must be treated as secondary to the requirements for detecting differences between the biological groups. All the alternative counts along the backbone, as well as combinations of counts and differences between counts, should be examined as potential indicators of the differences between groups. The working samples should be fully representative of the biological groups from which they are drawn and large enough to enable comparisons to be made between backbones having the same total number of vertebrae. Recognized statistical methods should be followed in making the comparisons.

Provided these main points are observed, the details of the scheme can with advantage be left to the discretion of the workers who are to carry it through. If all the biological groups are to be studied, as eventually they must, numbers of workers in the different countries interested in the herring fisheries will need to co-operate, but I do not think the amount of work which each must perform should prove excessive. One worker with the aid of a laboratory attendant can prepare 250 backbones by boiling and cleaning in a single day, and the determination of the vertebral counts can be carried out at his convenience on the dried preparations, which will keep in good condition without preservation for many months if necessary. It will be found most helpful for the subsequent analysis of the data to enter all the counts for each fish on a separate card bearing the particulars of the sample and the serial number of the fish. Frequency tables according to any desired criteria can then be quickly compiled by the simple process of dealing out the cards into the correct piles and counting the number in each pile. This can be done without clerical assistance and enables the investigator to try out many alternative comparisons with the minimum of trouble and sub-tabulation.

I think the question of the best use to be made of the count of keeled scales is one of some importance, which should be included in any proposed scheme. The data given in this paper are, of course, inadequate for final decision; but they raise points of great interest, particularly with regard to the basic metamery of the herring and the relation between keeled scale and vertebral counts.

Finally, I strongly recommend that a determined effort should be made to discover the morphological characters which have been referred to in this

paper as the "hallmarks" of the biological groups—those characters which will reveal sub-specific identity by inspection of individual fish, irrespective of circumstances of time and place of capture. Given a representative sample from each of the biological groups, I am of the opinion that careful comparisons, vertebra by vertebra, would bring to light differences of the greatest interest and practical usefulness.

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THE GENITAL DUCTS OF SOME BRITISH STENOGLOSSAN PROSOBRANCHS

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(Text-figs. 1–6)

CONTENTS

Introduction

It has long been known that in the stenoglossan Prosobranchia the ventral pedal gland plays some part in the formation of the egg capsule, but the exact functions of the various parts of the genital ducts have not hitherto been investigated. The ventral pedal gland was originally taken to be the external opening of a water vascular system, and Carrière (1882) was the first to show that this structure was really a gland. Cunningham (1899) ascribed to it the function of producing the chitinous capsules around the eggs which had been passed into it from the oviduct in *Buccinum* and *Murex* (= *Ocenebra*), and of fixing them to the substratum. Simroth (1896–1907) after first agreeing with this opinion ultimately concluded that the capsules were formed in the oviduct and then passed to the pedal gland. His theory was originally rejected by

Pelseneer (1910), who found capsules in the pedal gland of *Purpura* (=*Nucella*) *lapillus* which, owing to their thin, transparent, colourless walls, so unlike the final product, suggested that secretion from the gland was responsible for forming them; this view was quoted by Thiele (1925). Later, however, Pelseneer (1926) obtained capsules from the terminal region of the oviduct of *Nassa* (= *Nassarius*) *reticulata*, which proved that the origin of the capsule must be sought in the genital ducts, though the pedal gland may complete its moulding and harden it. Three years later Ankel (1929) in his observations on *N. mutabilis* and *N. reticulata* compared egg capsules taken from the oviduct with those completed by the pedal gland, and proved conclusively that the gland merely moulds and hardens the secretion which is laid down around the egg mass in the genital ducts. Ankel (1929, 1935, 1937) further suggested that the two sutures easily visible on the surface of the egg case of *N. mutabilis*, *N. reticulata*, *Nucella lapillus* and also of *Lamellaria perspicua* were due to the fact that the ducts in which the capsules are secreted are bilobed. Ankel's conclusions agree in every detail with the observations here described, but his papers include no study of the local manufacturing of the various parts of the egg case nor of the manœuvring of eggs and sperm within the ducts. A complete account of the structure and function of the genital ducts of both sexes is given in the following pages.

The work was carried out at Birkbeck College, Royal Holloway College, and the Plymouth Marine Laboratory. I wish to express my thanks to the University of London and to the British Association for the use of their tables at Plymouth.

The animals of which the genital ducts were investigated included *Ocenebra erinacea* (L.), *Nucella lapillus* (L.), *Buccinum undatum* L., *Nassarius reticulatus* (L.) and *N. incrassatus* (Ström), using the names given by Winckworth (1932). The animals were examined alive by means of a binocular microscope. The tissues were difficult to manipulate owing to their extremely glandular nature, and it was found best to fix them in Susa and Keilin's (1921) modification of Bouin. The distribution of different types of glands in the duct was most easily demonstrated by staining the whole structure in an alcoholic solution of thionin.

The Ducts of the Male

Ocenebra erinacea

From the testis, situated on the columellar side of the visceral mass, the coiled vas deferens passes anteriorly in a superficial position. It leads beneath the gut and the pericardium to the right posterior corner of the mantle cavity and here opens into the prostate gland. The latter runs parallel with the rectum to the opening of the mantle cavity and from it a narrow duct passes along the right side of the head to the penis, which lies behind the right tentacle. On account of histological and physiological differences the duct

leading to the prostate is divisible into two regions—a long coiled posterior part, which in the breeding season is distended with sperm, thus functioning as a vesicula seminalis, and short straight ciliated part leading beneath the intestine and the pericardium to the prostate, and separated from the vesicula seminalis by a sphincter. The two regions correspond to the vesicula seminalis and the vas deferens described by Linke (1933) in *Littorina littorea*, *L. obtusata* and *L. rudis*, and there is close agreement also in histological detail. In the vesicula seminalis the epithelium consists of columnar ciliated cells resting upon a basement membrane, beneath which a few circular muscles are developed. The basal nuclei of the columnar cells are spherical or irregular in outline, each with a nucleolus, and above them the cytoplasm is vacuolated. During the breeding season at least, many of the vacuoles contain lightly staining spherules, whereas in others ingested sperm may be found, for, as in the species of *Littorina* previously mentioned, the vesicula seminalis serves as an area for sperm absorption. The absorbed sperm are digested and the spherules may be regarded as their breakdown products. Relaxation of the sphincter at the entrance to the lower part of the duct, the true vas deferens, allows the contents of the vesicula seminalis, in which the sperm are under pressure, to pass to the prostate. The movement of sperm through the vas deferens is assisted by the thick layer of cilia borne by the columnar epithelial lining. The cilia arise from basal granules, and from these intracellular fibrillae run deeply into the cytoplasm. The epithelium is surrounded externally by circular muscles which are more numerous than in the vesicula seminalis. Close to its opening into the prostate the vas deferens gives off a short diverticulum towards the pericardium, and the blind end of the diverticulum is connected with a slight prominence on the pericardial wall by a band of dense connective tissue and muscle fibres. This strand reaches the pericardial wall close to the renopericardial aperture and lies in a comparable position to the gonopericardial duct of the female. In *Littorina*, Linke (1933) describes a similar connective tissue strand passing from the vas deferens to the pericardium though no diverticulum is mentioned. In *Calyptraea sinensis* (Giese, 1915), animals changing from male to female develop a gonopericardial duct, and this first appears as a strand of dense mesenchyme bridging the gap between the vas deferens and the pericardium. It therefore appears that in the male of *Ocenebra erinacea* this is the remnants of a gonopericardial duct.

The lateral walls of the prostate (Fig. 1) are thickened by a profuse development of glands (CGC) beneath the ciliated epithelium (CE), and in transverse section the lumen (L) appears as an extensive longitudinal slit between these lobes. The vas deferens leads to the narrow ventral surface of the gland and its entrance is guarded by a sphincter. If the mantle cavity of *Ocenebra* be opened to display the prostate it will be seen that the gland communicates with the posterior extremity of the mantle cavity by a slit-like aperture along the thin ventral wall. The aperture lies between two projecting flaps of tissue which in front of it fuse and are continued along the length of the ventral

surface of the gland as a slight ridge. Sections show that the projecting lips of the orifice are ventral extensions of the epithelial lining of the prostate beneath which no glands are present, and anteriorly they are joined one to the other to close the prostate (FE) and to form the projecting ridge. In *Littorina* the prostate is composed of two similar lateral glandular lobes, but it is open throughout its length along the ventral surface. Thus *Ocenebra* demonstrates the formation of a closed prostate from the open type of *Littorina*, and the opening into the mantle cavity is due to the incomplete fusion of the two lobes. The significance of this opening will be dealt with later. In the vicinity of the opening the cilia beat into the prostate, at right angles to the aperture. Elsewhere in the gland they cause an anteriorly directed current.

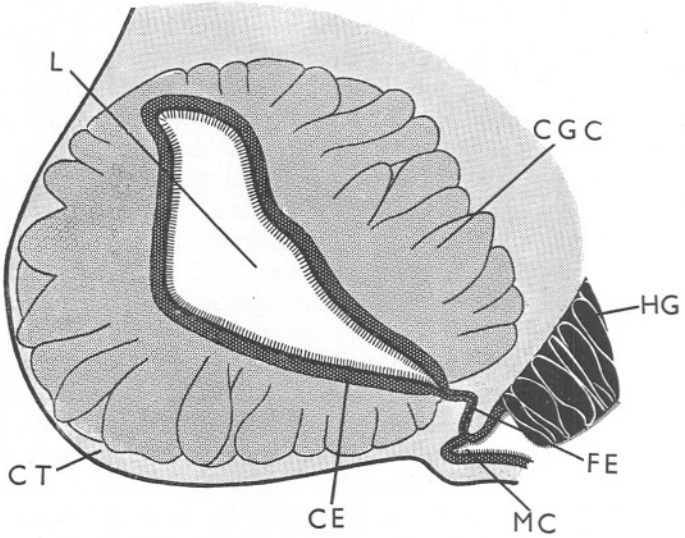

Fig. 1. *Ocenebra erinacea*. Transverse section through the prostate: camera lucida drawing (× 56).

CE, ciliated epithelium; CGC, cluster of subepithelial gland cells; CT, connective tissue; FE, epithelia which fuse to close the prostate; HG, hypobranchial gland; L, lumen of prostate; MC, mantle cavity.

The subepithelial gland cells of the prostate are grouped in spherical clusters (CGC), the ducts from a single cluster running parallel with one another to open between the ciliated cells. Each gland cell has a round basal nucleus with a prominent nucleolus. The cytoplasm is packed with granules which stain lightly with iron haematoxylin, except those around the nucleus which stain more densely. After azan the contents are yellowish in the vicinity of the nucleus and in the upper parts of the cell varying shades of purple. The azan stain shows that between these gland cells are scattered mucous cells. The columnar ciliated cells are compressed laterally by the ducts of the glands; their elongated nuclei lie towards the centre of the cytoplasm. The

cilia arise from basal granules, and intracellular fibrillae pass from these into the deeper regions of the cell, which also contains numerous granules. In the region of fusion between the two ventral lips of the prostate the cells of one side are in close contact with those of the other and no trace of cilia can be seen between, so that, in transverse section, a double row of cells appears to lead from the lumen to the mantle cavity (FE). These cells are cubical, with spherical nucleolated nuclei in the centre of the cytoplasm. At the opening into the mantle cavity the two sheets of epithelium separate; their cells become tall and columnar, like the cells lining the prostate which they resemble in all other features. Among them are a few mucous cells.

From the ventral surface of the prostate arises the ciliated tube which runs up the right side of the head to the penis. In *Littorina* this duct is represented by a deep groove running along a raised muscular ridge, and the edges of the groove can be brought close together to form a closed channel. In *Ocenebra* the edges have fused to form a tube, and evidence of this fusion is seen in sections by the two joined strips of epithelium, which are continuous with those of the prostate and lead from the lumen to the exterior. They are thrown into longitudinal folds and possess the same histological structure as in the previous region. In like manner the channel leading up the penis to its tip has been closed in *Ocenebra*, whereas it is open in *Littorina*.

The duct to the penis runs up the side of the head along a slight ridge which a layer of transverse muscles separates from the underlying tissues. The epithelium is thrown into longitudinal folds owing to the differences in the heights of the columnar ciliated cells of which it is composed. The nuclei are round, oval or irregular and lie towards the middle of the cells which, distally, contain granules; intracellular fibrillae pass from the basal granules of the cilia to the region of the nuclei. Beneath the basement membrane is a well-developed layer of circular muscles.

The penis is slightly flattened dorsoventrally and its duct is not centrally placed, but lies towards the outer edge. The histological structure of the epithelium is similar to that of the preceding duct; no gland cells are present. At its tip the two layers of fused epithelia separate to form the penial aperture. A layer of circular muscles lies beneath the epithelium of the duct and extends beneath the fused strips of epithelium. Throughout the thickness of the penis muscle fibres penetrate the connective tissue—longitudinal muscles run from base to tip, a layer of circular muscles runs under the outer epithelium, and beneath these dorsoventral and oblique muscles are developed. Blood spaces are numerous and the penial nerve occupies a central position.

Nucella lapillus

The gross morphology of the male reproductive system of *Nucella lapillus* is similar to that of *Ocenebra erinacea*, and between the two there is a close correspondence in histological detail. Only the few points in which they differ will be mentioned. In the short vas deferens, which leads from the vesicula

seminalis to the prostate, no trace of a gonopericardial duct can be found, and the muscles underlying the vas deferens are more strongly developed than in *Ocenebra*. The prostate is smaller and the spherules filling its gland cells, of which there is only one type, stain lightly with mucicarmine and blue with azan. The opening of the prostate into the mantle cavity is reduced to a minute aperture, and along the whole length of the genital duct anterior to this point can be seen the two strips of epithelium which fuse to close it. That part of the duct which runs from the prostate up the right side of the head to the penis has, underlying it, a thicker layer of circular muscles, and the penis is more dorsoventrally flattened than in *Ocenebra*.

Nassarius reticulatus

The structure of the male genital duct of *Nassarius reticulatus* differs in some essential features from that of *Ocenebra* or *Nucella*. The upper part of the vas deferens is greatly coiled and functions as a seminal vesicle; in the breeding season it can be traced below the surface of the visceral mass distended with sperm. The epithelium resembles that of *Ocenebra*: in like manner it is capable of ingesting sperm from the lumen. The true vas deferens is a straight duct which leads to the upper extremity of the mantle cavity on the right side, and rarely contains sperm except during the time of copulation. It is separated from the preceding region by a sphincter, and throughout its course a thick coat of circular muscles underlies the columnar ciliated epithelium which lines it. A slight thickening in the connective tissue between the vas deferens and the pericardium suggests the remains of a gonopericardial duct.

From the vas deferens the genital duct leads forward along the right side of the mantle cavity; its course is approximately parallel to that of the rectum. At the opening of the cavity it passes up the right side of the head to the penis. In *Ocenebra* the posterior region, traversing the length of the mantle cavity, is represented by the prostate. It has a much enlarged lumen and thick glandular walls, and the anterior region is a narrow ciliated duct. In *Nassarius* no such differentiation occurs, and from the vas deferens to the penis the duct is narrow, of about the same diameter as the former, and is of uniform histological structure—it is lined by an epithelium of gland cells alternating with ciliated cells and no subepithelial glands occur. The opening of the vas deferens into this anterior glandular region, the whole of which may be termed the prostate, is marked by a projecting circular fold of ciliated epithelium, and a sphincter is capable of closing the aperture completely. From this point, at the posterior extremity of the prostate, a short ciliated duct leads to the mantle cavity and, on dissection, its opening can be seen between the anterior margin of the kidney and the genital duct. It corresponds to the slit-like opening of *Ocenebra*. The duct has thick muscular walls and its external opening may be closed by a sphincter. Anterior to it the genital tract has no connexion with the mantle cavity, and there is no indication of its formation from an open groove as in *Ocenebra*.

Throughout its length the prostate is surrounded by a thick layer of circular muscles, and during copulation the spermatozoa are conveyed with great rapidity along it by peristalsis aided by the cilia. The gland cells which alternate with the ciliated cells of the epithelium have highly vacuolated protoplasm. The vacuoles contain spherules which tend to dissolve on fixation, but which stain lightly with iron haematoxylin and pale blue with azan. The spherical nuclei, each with a prominent nucleolus, lie towards the base of the cytoplasm. The cilia arise from basal granules and from these intracellular fibrillae can be traced to the central region of the cell. Minute orange or yellow pigment granules are scattered in the distal half of each cell and the oval nuclei lie towards the base. That part of the duct which runs up the side of the head to the penis is situated on a slight ridge, and this is separated from the underlying tissues by a sheet of transverse muscles.

The penis is flattened dorsoventrally and its duct is central. The histological character of the lower part of the duct is exactly similar to that of the prostate, but towards the mid region the gland cells disappear, and distally the duct is lined by a columnar ciliated epithelium with cells of uniform height. As in the preceding region of the genital tract a thick layer of circular muscles underlies the epithelium, and spermatozoa are conveyed to the terminal opening by peristalsis and ciliary action. In the subepithelial connective tissue of the terminal part of the duct there are numerous mucous cells, their necks passing between the ciliated cells. The musculature of the penis differs from that of *Ocenebra*: beneath the external epithelium is an outer layer of circular and oblique muscles and an inner layer of longitudinal fibres, and well-developed blood spaces run laterally through the length of the penis. The central region, containing the duct with its thick muscular coat, the penial nerve and other blood spaces, is separated from the outer region by a layer of circular muscles, and dorsoventral muscles penetrate every part of the connective tissue.

Buccinum undatum

The male genital duct of *Buccinum undatum* (Fig. 2) resembles most closely that of *Nassarius reticulatus*. The coiled posterior part of the vas deferens acts as a vesicula seminalis (VS). It is covered by a ciliated epithelium and the cytoplasm of the cells is vacuolated. The distal vacuoles may contain ingested sperm, and in others may be seen brownish granular concretions which, as in *Ocenebra*, are probably the products of sperm digestion. A thick muscular coat is developed below the basement membrane and this consists of an inner circular layer and outer longitudinal fibres. The duct straightens just before it enters the posterior end of the mantle cavity and the musculature increases in thickness. This short region which passes to the mantle cavity is the true vas deferens (VD), into which the sperm are liberated during the breeding season and through which they are passed mainly by muscular activity. Ventral to the kidney aperture the vas deferens opens into a thicker region of the genital duct (PR), which passes forward along the right side of the body,

beneath the rectum (R), and projects from the surface of the floor of the mantle cavity as a prominent ridge. At the mouth of the cavity it passes dorsally to the base of the penis (P) which is situated on the right side of the neck. The region of the duct which passes through the mantle cavity to the penis is of about the same diameter throughout, although there appears fairly constantly

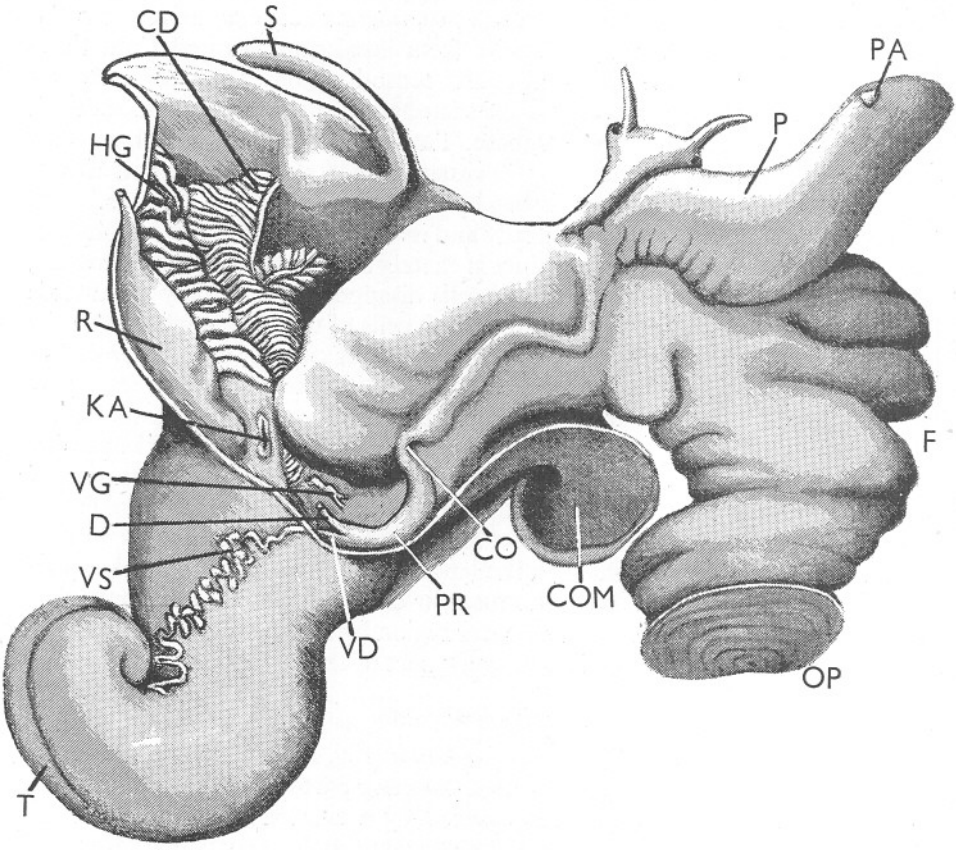

Fig. 2. *Buccinum undatum*. Dissection to display the male genital duct, the mantle cavity having been opened along the right side (× about 1⅔).

COM, columellar muscle; CO, constriction; CD, ctenidium; D, duct leading from the prostate to the mantle cavity; F, foot; HG, hypobranchial gland; KA, aperture of kidney; OP, operculum; P, penis; PA, papilla; PR, prostate; R, rectum; S, siphon; T, testis; VD, vas deferens; VG, visceral ganglion; VS, vesicula seminalis.

a constriction (CO) just about the point where the duct passes on to the side wall of the proboscis sheath.

If the mantle cavity of a male *Buccinum* be opened to expose the prostate (Fig. 2) it will be seen that from the posterior end of this gland and on the left side there arises a narrow duct (D). This passes backwards and to the left to open to the mantle cavity. The opening is alongside the visceral ganglion.

The presence of this structure was not mentioned by Dakin (1912) in his description of the male genital system. It is lined by a columnar ciliated epithelium in which mucous glands are scattered. Beneath the epithelium is a very thick layer of circular and longitudinal muscles. The opening of the vas deferens into the prostate is situated on a small papilla immediately anterior to the opening of the duct. Internally the walls of the prostate are folded longitudinally and covered by a columnar ciliated epithelium. A layer of circular muscles, 200μ thick, underlies the basement membrane, and between the muscles pass the ducts of a still deeper layer of gland cells. The glands are of two types. In one the cytoplasm is filled with small spherules which stain lightly with iron haematoxylin and red with azan. The nuclei are spherical and each has a prominent nucleolus. The second type of cell is a mucous cell. The ducts are long, exceeding 300μ, and they pass between the epithelial cells to open into the lumen of the gland. During the breeding season, when the gland is well developed, the distal tips of the ducts are swollen with secretion and compress the ciliated cells. Circular and oblique muscle fibres pass between the glands and surround the prostate externally.

The duct which passes through the large flattened penis (P) opens at the apex of a papilla (PA) which is subterminal and on its upper edge. The duct is lined by a columnar ciliated epithelium and surrounded by a thick layer of circular muscle. About the middle of the penis the duct measures only 180μ in diameter, but towards the papilla it is further reduced to a very fine tube and the thickness of the muscular coat is correspondingly decreased.

The Ducts of the Female

Nucella lapillus

Owing to the ease of obtaining material the female genital system and the formation of the egg capsules has been studied in greater detail in *Nucella lapillus* (Figs. 3, 4, 5*a* and 6) than in *Ocenebra erinacea*.

The ovary (Fig. 3, O) spreads over the surface of the digestive gland in the visceral mass, and from it a thin-walled oviduct (Figs. 3, 4, OD) leads forwards and ventrally on the right side of the viscera. The anterior region can be seen through the integument and has the appearance of a large blood vessel. At a point below the kidney it opens into the albumen gland (Fig. 3, AG) which turns abruptly dorsalwards, making an acute angle with the oviduct, and then recoils on itself passing ventrally to open into the capsule gland (Figs. 3, 4, OAC). At the junction of the oviduct with the albumen gland arises the gono-pericardial duct. The capsule gland leads forward on the right side of the mantle cavity and, on dissection, it can be seen as an opaque white or yellowish mass which is divided into right and left glandular lobes (Figs. 3, 4, RLC, LLC). These lobes are joined dorsally and ventrally by a comparatively thin and narrow wall forming a dorsal and ventral suture, so that in transverse section the lumen of the gland has the appearance of a dorsoventral slit (Fig. 5*a*, L).

From the narrow ventral wall, where gland cells are absent, arise two longitudinal folds of tissue (Figs. 4, 5*a*, RL, LL). These form between them a longitudinal channel (Fig. 5*a*, VC). The left longitudinal fold (LL) is better developed than the right (RL), over which it bends and which it may completely envelop. Thus the ventral channel may be closed off from the lumen of the capsule gland and form a functionally closed duct. Posteriorly the channel leads through a short duct (Fig. 4, DIG) to a deep brown glandular mass situated between the capsule and albumen glands. This is the ingesting gland (Fig. 3, IG) and its narrow duct is surrounded by a thick muscular coat. The albumen gland opens into the posterior ventral wall of the capsule gland on the right side of

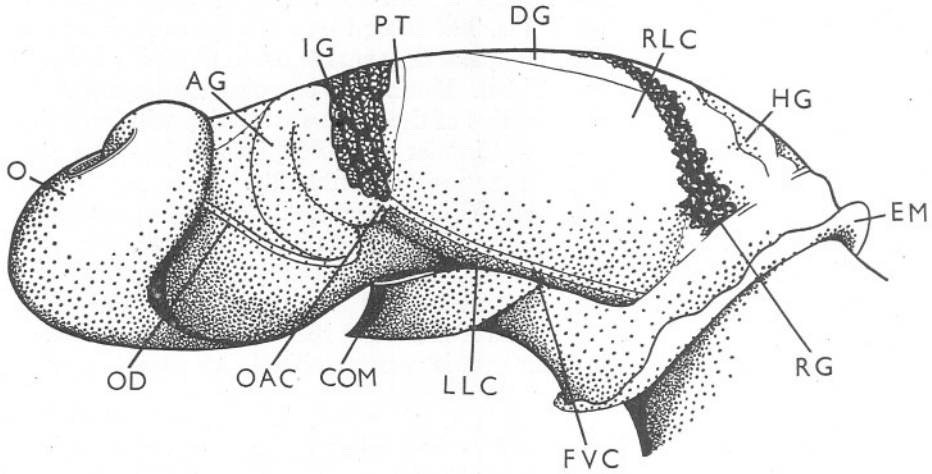

Fig. 3. *Nucella lapillus*. Visceral hump seen from the right side after the removal of the shell (×6).

AG, albumen gland; COM, columellar muscle; DG, gland cells of the dorsal wall of the capsule gland; EM, free edge of mantle; FVC, floor of ventral channel; HG, hypobranchial gland; IG, ingesting gland; LLC, left lobe of capsule gland; O, ovary; OAC, opening of albumen gland into capsule gland; OD, oviduct; PT, posterior tip of capsule gland; RG, rectal gland; RLC, right lobe of capsule gland.

the ventral channel (Fig. 4, OAC). Anteriorly the capsule gland opens into a muscular vestibule (V), and through this the ventral channel leads into the bursa copulatrix (BC), which when filled with sperm bulges into the vestibule. The short vagina (VA), into which the penis is inserted to deposit sperm in the bursa, and from which the fully formed egg capsules pass from the vestibule to the exterior, opens on the right anterior extremity of the mantle cavity, ventral to the anus; the opening is surrounded by a sphincter.

As the oviduct approaches the albumen gland its glandular lining is replaced by a columnar ciliated epithelium, thrown into longitudinal folds by variations in the thickness of the underlying connective tissue. A similar epithelium is found in the gonopericardial duct. This opens into the pericardium by an inconspicuous ciliated funnel, and beneath the basement

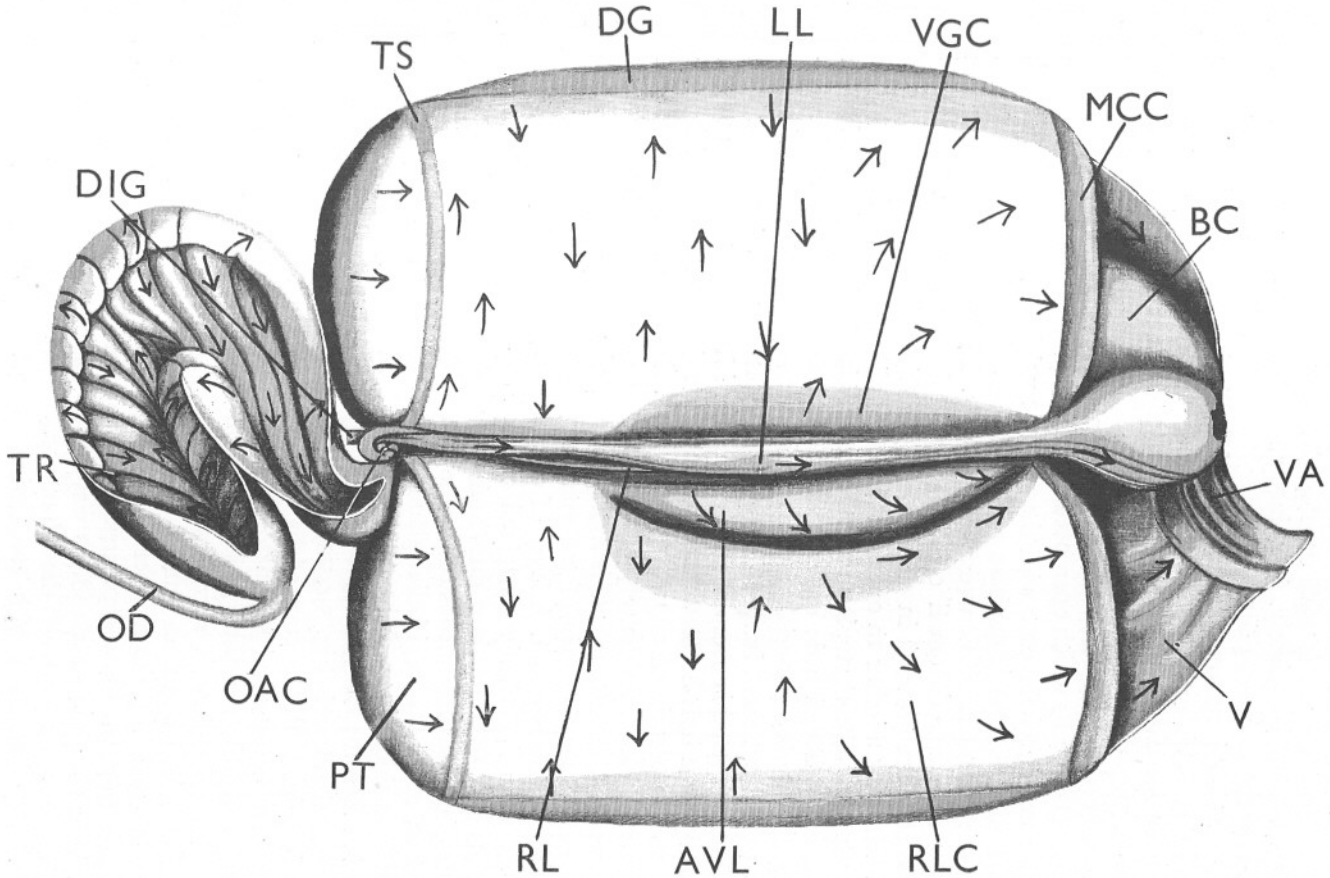

Fig. 4. *Nucella lapillus*. The female genital duct. The muscular vestibule and the capsule gland have been opened by a dorsal longitudinal incision and the albumen gland by a longitudinal incision along the right side. Arrows show ciliary currents. (× about 12)

AVL, anteroventral lobe of capsule gland; BC, bursa copulatrix; DIG, duct of ingesting gland; LL, left longitudinal fold; MCC, mucous cells of the anterior border of the capsule gland; RL, right longitudinal fold; TR, transverse ridges on the wall of the albumen gland; TS, transverse muscular strips; V, vestibule; VA vagina; VGC, anteroventral gland cells. Other letters as in Fig. 3.

membrane of the epithelium are circular and scattered longitudinal muscle fibres; the musculature is well developed around the pericardial opening which it may close completely. A sphincter also surrounds the opening of the oviduct into the albumen gland.

When the shell is removed from a living *Nucella* the opaque, white albumen gland (Fig. 3, AG) is seen through the integument. It is laterally compressed and its walls are ridged transversely (Fig. 4, TR), owing to variations in the thickness of the subepithelial glandular tissue. The gland is ciliated throughout: ciliated cells line the lumen and these are constricted by the ducts of the underlying gland cells which open between them, and by epithelial gland cells which in some parts alternate with them. The nuclei of the ciliated cells are elongated and lie towards the base of the cytoplasm, or they may be pushed towards the distal end of the wedge-shaped cells. Living material shows that the gland cells contain small colourless spherules or granules. The subepithelial cells are grouped in clusters and the ducts from each cluster run parallel with one another to open between the ciliated cells. The nuclei lie towards the base of the cytoplasm and are oval or circular in outline, each with a nucleolus. Although little differentiation between the glands can be distinguished in living material, sections demonstrate the presence of three distinct types, and these have a fairly constant distribution. The outer wall of the albumen gland is composed only of cells with granular contents which stain lightly with iron haematoxylin and mucicarmine, whereas the inner or median wall is composed of two types of cells. In one of these the small secretory spherules stain densely with iron haematoxylin and are unaffected by mucicarmine, and the second less plentiful type is mucus-secreting. These cover a narrow ventral strip of the median wall, though some may have a more scattered distribution. A layer of circular muscles is developed in the connective tissue. The albumen gland opens on to the ventral wall of the capsule gland (OAC) by a short duct lined by a columnar ciliated epithelium with a few interspersed mucous cells. The cilia are long, exceeding the height of the cells, and no subepithelial gland cells are present. The duct is surrounded by a thick layer of circular muscles, which on contraction close the passage between the two glands.

The ventral channel (Fig. 5*a*, VC), which leads posteriorly from the bursa copulatrix (Fig. 4, BC), is covered by a columnar unciliated epithelium. To the cells may be attached spermatozoa, closely packed together with their heads embedded in the distal protoplasm and their tails projecting into the lumen. The epithelium is surrounded externally by a thin inner layer of longitudinal muscles and an outer circular layer; this musculature enables sperm to be passed up the channel by peristalsis. In *Littorina* (Linke, 1933) sperms pass from the bursa copulatrix to the receptaculum seminis, which is embedded in the albumen gland, by way of two longitudinal folds. A ciliary current on the under surface of these transports the sperm balls. Longitudinal folds similarly concerned with conducting seminal fluid are described in

Viviparus bengalensis by Annandale and Sewell (1921). At the posterior end of the capsule gland the ventral channel leads into a duct (Fig. 4, DIG) which passes to the ingesting gland (Fig. 3, IG). The walls of the duct are folded longitudinally and surrounded by a very thick layer of circular muscles, and masses of sperm are invariably attached to the columnar epithelial lining. In

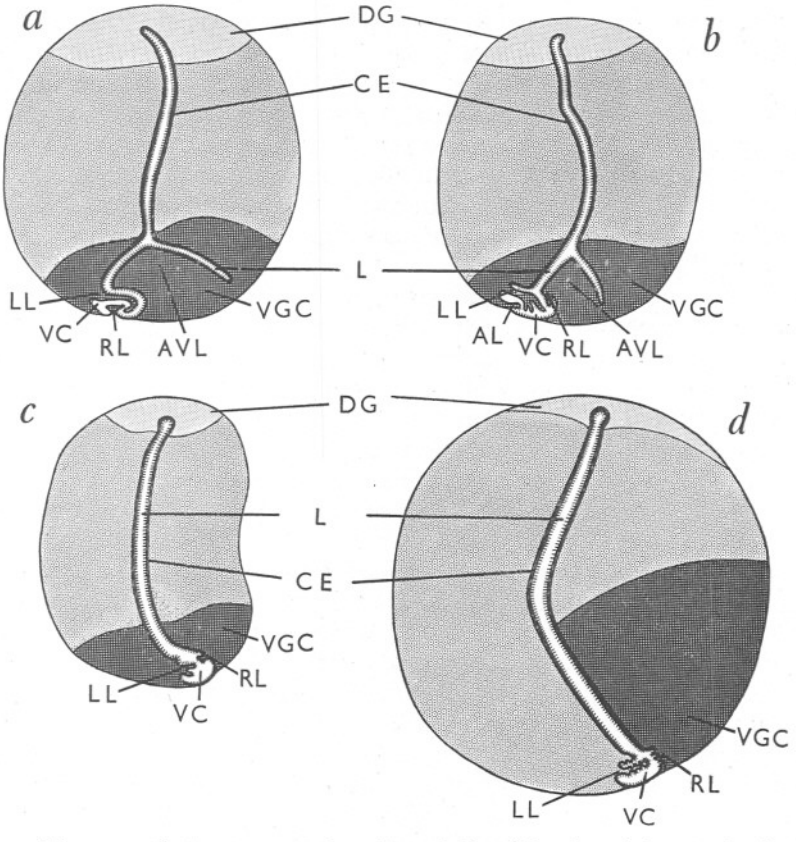

Fig. 5. Diagrammatic transverse sections through the mid region of the capsule gland.

a, *Nucella lapillus* (× 14). *b*, *Ocenebra erinacea* (× 17).
c, *Nassarius reticulatus* (× 23). *d*, *Buccinum undatum* (× 12).

The three types of stippling indicate corresponding glandular areas.

AL, accessory longitudinal fold; CE, ciliated epithelium; L, lumen of capsule gland; VC, ventral channel. Other letters as in Fig. 4.

its relationship to the longitudinal folds and in its role of harbouring sperm this region corresponds to the receptaculum seminis of *Littorina*; posteriorly, however, it opens into the ingesting gland—a brown glandular mass of tissue composed of blind tubules and having the appearance of a digestive gland. Examination of living material shows that the gland is made of only one type

of cell (Fig. 6*a*), which is filled with brown spherical masses (BRM) lying in vacuoles; in the lumina of the tubules large numbers of active unorientated sperm (FS) may be present, but some may lie motionless against the free edges of the epithelium as if trapped in the protoplasm of the cells (SE). In sections it is seen that the sperms are engulfed by the gland cells and lie in vacuoles in the cytoplasm (SV). Within these they are digested and it seems probable that the products or remains of digestion impart to the gland its brown colour. A layer of connective tissue, rich in blood spaces, underlies the ingesting cells and here amoebocytes (AM) are plentiful. Many of these contain brown granules which have the appearance of excretory matter, and it is probably by this means that the gland loses waste. So far as I am aware no such gland has previously been described in the Mollusca: it is, however, present in the four species of Stenoglossa dealt with here. It appears to serve as a mechanism for ridding the animal of unwanted sperm and perhaps of deriving nourishment from them.

The lateral walls of the capsule gland attain 1·75 mm. in thickness and are composed of groups of gland cells lying at various heights and packed tightly together with a very tenuous layer of connective tissue between each group (Fig. 6*b*). As in the albumen gland the ducts of the cells (DGC) run parallel with one another to open between the columnar ciliated cells which line the lumen. This ciliated epithelium covers the narrow dorsal wall, under which a thin layer of gland cells is developed (Fig. 5*a*, DG), and ventrally it spreads over the outer surfaces and free tips of the two longitudinal folds. The inner faces of these folds, forming the dorsal wall of the ventral channel (VC), are not ciliated. If the capsule gland be opened by a dorsal longitudinal incision (Fig. 4) it is seen that the right lateral wall has a ventral longitudinal cleft running from near the middle of the gland to the anterior extremity, and separating an anteroventral lobe (AVL) from the rest of this glandular area. This lobe together with two adjacent longitudinal strips of tissue—one on the right and the other on the left lateral walls—is more translucent than the surrounding areas and of a slightly yellowish hue (VGC). The lobes are composed of gland cells filled with small colourless spherules, which in sections stain lightly with iron haematoxylin and may be faintly tinged with pink by mucicarmine. After azan some spherules are reddish or orange and others blue. It would appear that two types of secretion are produced by these cells since, with azan, the final products in the lumen of the gland stain either deep orange or blue. A longitudinal area around the dorsal wall (DG) has a similar appearance in the living state. In sections of this the cells stain with iron haematoxylin and slightly with mucicarmine; after the azan stain the cytoplasm is pale blue and tiny spherules contained in it are orange in colour. With this stain the secretion is pale blue and orange, suggesting that one type of secretion is present in the cytoplasm and another in the spherules. Near the posterior end of the capsule gland two narrow transverse strips of tissue (TS), one on each side and arising near the opening of the albumen gland, separate

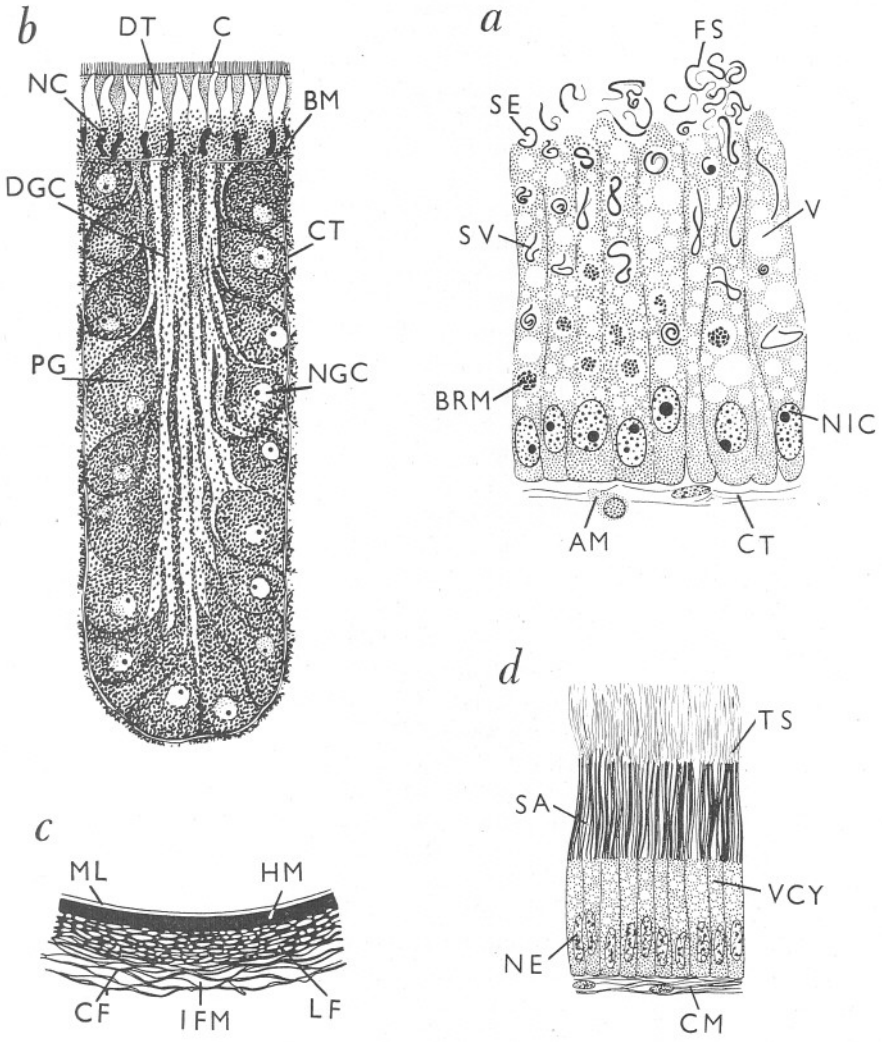

Fig. 6. *Nucella lapillus*. Parts of transverse sections through:

a, the ingesting gland, fixed in Keilin's modification of Bouin's fluid and stained in iron haematoxylin (× about 650).

b, the wall of the capsule gland, showing a single cluster of gland cells (× 200).

c, the wall of an egg capsule (× 200).

d, the bursa copulatrix, fixed in Susa and stained in iron haematoxylin (× 550).

AM, amoebocyte; BM, basement membrane; BRM, brown spherical mass; C, cilia; CF, circular fibres; CM, circular muscles; CT, connective tissue; DGC, ducts of gland cells; DT, distal tip of duct filled with mucoid protoplasm; FS, free unorientated sperm; HM, homogeneous layer; IFM, interfibrillar mucoid substance; LF, layer of longitudinal fibres; ML, inner mucous layer; NC, nucleus of ciliated cell; NE, nucleus of epithelial cell; NGC, nucleus of gland cell; NIC, nucleus of ingesting cell; PG, protein secreting granules; SA, attached sperm; SE, sperm entrapped by protoplasm; SV, sperm in vacuole of cytoplasm; TS, tails of orientated sperm; V, vacuole; VCY, vacuolated cytoplasm.

In the gland cells of *b* and in *c*, the protein secretion is shown in black and the mucoid secretion is left white.

a right and left posterior tip (PT) from the main mass of the gland. Beneath the ciliated epithelium of the strips is a layer of circular muscles and a few muscles radiate outwards; it is this musculature which distinguishes these strips of tissue and constricts them from the surrounding wall. Both they and the posterior tips of the gland are made up of mucous cells, and similar cells border the anterior extremity of each lateral lobe (MCC). The cells constituting the main part of the gland are filled with larger colourless granules which have a rather irregular oval shape (Fig. 6*b*). They stain with iron haematoxylin, but are unaffected by mucicarmine; with azan they are a deep red. The protoplasm has a different staining reaction—it is very slightly affected by mucicarmine but stains deep blue with azan. The distal tip of each duct is filled with this mucoid protoplasm (DT) and no granules are visible, a fact reminiscent of the structure of the cells of the epithelium of the mammalian stomach. Again two types of secretion are produced, one a mucoid and the other a protein. Hence all the gland cells of the capsule gland, except those of the posterior tip and anterior border of each lobe, produce a double secretion and it is the intertwining of these which is responsible for the fibrous structure of the wall of the egg capsule (Fig. 6*c*), an appearance which is obvious if secretion be taken from the gland and examined in sea water.

A layer of dense connective tissue surrounds the capsule gland and through this run muscle fibres. The musculature is best developed beneath the ventral channel and especially near the bursa. Circular muscles surround the dorsal wall and penetrate between the gland cells. Laterally, except in the posterior transverse strips, the muscles are thinly scattered—some circular muscles run below the ciliated epithelium and in the connective tissue surrounding the gland, whilst through the thickness of the wall scattered circular and oblique fibres can be traced. The vestibule, the vagina and the bursa copulatrix are all clothed by a columnar ciliated epithelium. The walls of the bursa are thrown into folds by variations in the depth of the underlying connective tissue, and sperm may everywhere be attached to the epithelium (Fig. 6*d*), whilst a mass of sperm may fill the lumen. Beneath the epithelium is a thick muscular coat, consisting of an outer circular layer with longitudinal and oblique bands beneath the folds. Among the ciliated cells covering the vestibule are a few gland cells filled with spherules which stain black with iron haematoxylin and red with azan. The vestibule and vagina are extremely distensible; the walls are folded longitudinally and the arrangement of the layers of muscle is similar to that of the bursa.

The eggs are liberated from the oviduct by the relaxation of the sphincter at the entrance to the albumen gland. Here they come under the influence of ciliary currents (Fig. 4). The opposing currents drive the secretion from the epithelium and whirl it into the lumen mixing it with the eggs, and at the same time the whole mass is propelled along the gland. It then passes through the short duct which leads into the capsule gland (OAC), being drawn through by the relaxation of the circular muscles and by the action of cilia. In the capsule

gland the forward movement of the mass of eggs is arrested whilst the wall of the capsule is secreted around it. The ciliary currents on the wall of the gland are weak. Mucus secreted by the posterior tips is directed forwards; but anterior to the tips the currents beat at right angles to the long axis of the gland—in some places away from, in others towards, the ventral channel. The currents mix and distribute the various secretions from the gland cells immediately they are poured forth into the lumen. At the anterior end of the gland the currents are directed towards the vagina (VA) and on the longitudinal folds of the ventral channel (LL, RL) they beat outwards. These folds are usually hidden from view by the overhanging glandular lobes. The passage of the egg capsule through the vestibule (V) is effected by muscular means assisted by the action of cilia beating towards the genital aperture.

Ocenebra erinacea

The female genital system of this stenoglossan is built on the same plan as that of *Nucella*. There are, however, the following minor differences in morphology and histology.

The gonopericardial duct appears to be wider and it opens into the pericardium by a very prominent ciliated funnel: so wide is the duct, in fact, that on relaxation of the circular muscles a mature egg may enter it. Only two types of subepithelial gland cells have been observed in the albumen gland. The more plentiful type is filled with spherules which are colourless in life, stain lightly with iron haematoxylin and are a very faint pink after mucicarmine. These cells cover the outer wall in the main part of the gland and spread on to the inner wall, where they are replaced by mucous cells, which in the posterior part of the gland, near the opening of the oviduct, completely encircle the columnar ciliated epithelium. The duct from the albumen gland opens into the ventral channel, and receives near this opening the duct from the ingesting gland. In this gland there is resorption of yolk granules as well as ingestion of spermatozoa. It is possible that these yolk granules have been derived from eggs which for some reason failed to be included in a capsule. This may also occur in *Nucella*, but has never actually been observed. The ventral channel (Fig. 5*b*, VC), which is formed between the two longitudinal folds of the ventral wall of the capsule gland, is subdivided into two regions by a third longitudinal fold of tissue (AL). This arises soon after the channel emerges from the bursa and extends to the opening of the albumen gland. It lies beneath the left longitudinal fold, which completely envelops it, and in the channel formed between them the epithelium is not ciliated. Ciliated cells cover the channel between this third fold, which is not represented in *Nucella*, and the outer or right longitudinal fold. The albumen gland opens into the ciliated region and the transference of sperm is confined to the unciliated part.

The capsule gland is divided into the same regions as in *Nucella*, but there are slight variations in the types of gland cells composing the dorsal (DG) and ventral (VGC) longitudinal strips and the posterior tips of the thick

lateral glandular lobes. The transverse strips of tissue which arise near the opening of the albumen gland, and are constricted off from the surrounding glandular areas, are made up of mucous cells. Posteriorly these are replaced by mucoid cells which often have a pink tinge. In the anteroventral lobe (AVL), separated from the right lateral lobe by a deep cleft, and in the two adjacent longitudinal strips of tissue, the cells (VGC) stain blue with azan and some spherules are reddish. These cells probably produce two types of secretion, but this is less obvious than in *Nucella*. The secretion in the lumen of the gland stains blue with azan and small isolated patches may be reddish or orange. The longitudinal glandular strips surrounding the narrow dorsal wall (DG) are composed for the greater part of mucoid cells, but these produce only one type of secretion and together with the anterior border of each lateral lobe stain purple when the whole gland is opened and placed in thionin. There is, however, a narrow longitudinal band of cells on each side between this dorsal strip of mucoid cells and the main part of the capsule gland which elaborates a second type of secretion, the spherules within the cells and the secretion staining bright orange with azan.

The histology of the bursa copulatrix is of some interest. If this pouch be cut open it may be seen that the white glandular walls are folded transversely and have a velvety appearance. The epithelium is composed of one type of cell, which is elongated, and the free edge is produced into a large number of stiff processes each equal to about a quarter of the total length of the cell. In the proximal half of the epithelium the cytoplasm is vacuolated, and the vacuoles contain small spherules which stain lightly with iron haematoxylin and red with azan. Distally the cytoplasm contains a mucoid substance into which the spherules migrate. The secretion in the lumen of the bursa consists of irregularly shaped mucoid masses with numerous spherules, and sperms introduced into it collect around this secretion. The nuclei of the cells of the epithelium, each with one or two nucleoli, are round or oval in outline. They lie towards the base of the cytoplasm, but migrate to the free tips of the cells when secretion is being liberated.

The musculature and the ciliary currents of the genital duct are practically identical with those described for *Nucella*. Here again the importance of the ciliary currents of the capsule gland appears to be in mixing and distributing the different types of secretion to form the wall of the egg case.

Nassarius reticulatus

Nassarius reticulatus resembles *Nucella* in the main points of the structure of this system, but differs from it in some details; these alone will be dealt with in the following paragraphs.

From the anterior end of the oviduct, near which the gonopericardial duct is given off, the laterally compressed albumen gland widens into a comparatively deep pouch, its dorsal wall being deeply convex and the ventral wall concave. The ciliary currents on the wall of the gland are similar to

those in *Nucella*. The subepithelial glands are of two types only: mucous cells beneath the inner wall and mucoid cells beneath the outer. The albumen gland opens into the ventral channel of the capsule gland and near this opening receives dorsally the duct from the ingesting gland. The duct is longer than in *Nucella* and is somewhat coiled. The gland is less voluminous and amongst the ingesting cells which line the tubules are mucous cells. The posterior tips of the capsule gland may be brownish in colour or may have a rather transparent appearance. They are composed of mucous cells. Anteriorly each lateral lobe of the gland terminates in a reddish glandular area—during life the gland cells are filled with small orange granules. These stain deeply with iron haematoxylin and after azan the granules and the final secretion are red and the cytoplasm around the spherical basal nuclei pale blue. A transverse strip of mucous cells separates this area from the more posterior part of the gland. The right lobe is not subdivided (Fig. 5*c*), and the longitudinal strips of gland cells (VGC), which border the anterior two-thirds of the ventral channel (VC) on each side and surround the dorsal end of the lumen (DG), do not produce a double secretion. The ventral strips are composed of mucoid cells and the dorsal region of mucous cells. The secreting cells, which constitute the main part of the capsule gland, contain granules of the same shape as the corresponding cells of *Nucella*, but they are smaller. They stain deeply with iron haematoxylin and bright orange with azan. Their secretion in the lumen of the gland has a similar staining reaction. The arrangement of the ciliary tracts on the walls of the capsule gland differs slightly from that of *Nucella*. The transverse currents are confined to the upper half of the gland, whilst anteriorly the currents run towards the exterior.

The ventral channel is ciliated throughout and the longitudinal folds which form its dorsal wall (LL, RL) are less pronounced than in the molluscs already described. Anteriorly the capsule gland and the ventral channel lead to the muscular vestibule which is lined by a columnar ciliated epithelium. Mucous cells are interspersed among the ciliated cells and some mucous glands lie in the connective tissue beneath the epithelium. The walls of the vestibule are thrown into deep folds. Muscles radiate from the folds to longitudinal and circular muscles which surround the whole structure. The longitudinal folds of the ventral channel arise at the anterior end of the vestibule beneath the opening of the bursa.

If the mantle cavity of *Nassarius* be opened the genital aperture is immediately obvious, and through it, since it is of large diameter, can be seen two further openings, one dorsal and the other ventral. The dorsal one is the aperture of the bursa copulatrix and the ventral leads to the vestibule of the oviduct. The space between the genital opening and these two inner ones thus represents the vagina. This and the bursa are covered by a columnar ciliated epithelium with an ample supply of mucous cells. The walls of the bursa are folded and beneath the epithelium is a thick muscular coat consisting of circular, oblique and longitudinal fibres.

Buccinum undatum

The gross anatomy of the female genital system of *Buccinum undatum* was described by Dakin (1912), but many details in its structure were not observed. Of these the most outstanding are the bursa copulatrix, the ingesting and resorptive gland, and the gonopericardial duct. The general anatomy of the genital duct conforms to the typical stenoglossan plan and in many respects it approaches most closely to *Nassarius reticulatus*. The albumen gland assumes similar proportions. From the thin-walled oviduct it passes dorsally and enlarges to form a pouch, which is laterally compressed and opens anteriorly into the capsule gland by a wide aperture. The dorsal wall of the pouch is deeply convex and the ventral wall concave. Two types of gland cells are present—mucous cells constitute the thickness of the inner wall and spread on to the outer wall of the gland. Here, except near the opening into the oviduct, they are replaced by cells containing small spherules embedded in the vacuolated protoplasm. The spherules stain deeply with iron haematoxylin and blue with azan; after mucicarmine the protoplasm is faintly pink.

The duct from the ingesting gland opens into the dorsal wall of the genital duct at the junction of the albumen and capsule glands. The walls of the duct are deeply folded and during the breeding season numbers of orientated sperm are attached to the columnar ciliated epithelium. A thick muscular coat which surrounds the walls is chiefly composed of circular fibres, and radial muscles penetrate the folds. The duct opens into the glandular tubules, in which masses of yolk granules and unorientated spermatozoa have been observed during the months of April and May. As in *Ocenebra* the yolk granules and the sperm are taken up by the absorbing cells and apparently digested.

On the lateral walls of the albumen gland the cilia beat away from the narrow dorsal and ventral walls and the current is directed downwards and slightly backwards from the duct of the ingesting gland. Around the opening of the capsule gland the cilia beat posteriorly. The effect of these currents is to mix albuminous secretion with the eggs from the oviduct and probably to direct sperm from the duct of the ingesting gland and from the ventral channel on to the egg mass. Meanwhile the contents of the albumen gland are prevented from passing into the capsule gland. The musculature of the albumen gland is well developed: circular muscles lie beneath the ciliated epithelium and they are also scattered between the groups of gland cells and in the connective tissue surrounding the gland.

The right lobe of the capsule gland (Fig. 5*d*) is not subdivided as in *Nucella* and *Ocenebra*. After the breeding season the glandular tissue is greatly reduced and the lateral walls may be thrown into transverse folds. The posterior tips of the gland are composed of mucous cells, and similar cells underlie the dorsal wall (DG), where they form a narrow longitudinal strip. Anteriorly each lateral lobe is bordered by mucous cells, and mucoid cells constitute the ventral half of the anterior two-thirds of the right lobe (VGC). In living tissue these areas

can be distinguished by their slightly transparent appearance. The main mass of the gland is opaque white and is composed of one type of cell which is filled with small spherules staining deeply with iron haematoxylin and azocarmine. The ciliary currents on the walls of the capsule gland are similar to those of *Nassarius*.

The longitudinal folds which separate the ventral channel from the lumen of the capsule gland are less pronounced than in *Nucella*. The left fold (LL) is obvious on dissection and the ciliated epithelium which covers it, and the wall immediately dorsal, is thrown into longitudinal undulation by variations in the height of the cells and in the thickness of the underlying connective tissue. The right fold (RL) is represented by a number of similar though more pronounced undulations in the ciliated epithelium. Only a narrow strip of cells on the wall of the ventral channel (VC) is unciliated. Mucous cells are interspersed among the columnar cells, especially at the anterior end, and they also occur in the connective tissue beneath the epithelium. Posteriorly in the region of the transverse muscular strips the longitudinal folds terminate and the ventral channel divides into two grooves. One passes to the right and runs dorsally between the albumen and capsule glands to the duct of the resorptive and ingesting gland, and the other takes a similar course on the right side. The ciliary currents on their walls are directed towards the gland.

The muscular vestibule into which the capsule gland opens is covered by a columnar ciliated epithelium. The walls are longitudinally folded. Radial muscles are developed in the connective tissue beneath the folds and these are surrounded by a layer of circular muscles which increases in thickness towards the genital opening. The longitudinal folds of the ventral channel arise near the mid region of the vestibule and in the epithelium which covers them, and in the underlying connective tissue mucous cells are plentiful. Anterior to the origin of the folds mucous cells are distributed throughout the epithelium. Here the lumen of the vestibule is approximately circular in transverse section with a diameter of 0·5 mm., and is surrounded by a layer of circular muscles 1·25 mm. in thickness. The vestibule and the bursa copulatrix open into the vagina. The bursa is a large and very muscular sac, dorsal in position. The walls are deeply folded and covered by a columnar unciliated epithelium which contains yellow pigment granules. Amoebocytes are found between the epithelial cells and in the lumen: they appear to act as scavengers and carry off any available prostatic secretion. Although the longitudinal folds of the ventral channel do not extend to the opening of the bursa the ventral groove runs to this point. Spermatozoa are passed from the dorsal opening of the bursa into the ventral groove and conveyed up the ventral channel of the capsule gland. The channel is surrounded by circular muscles and some longitudinal fibres, and the conduction of sperm is probably assisted by peristalsis, as in *Nucella*, though this has not been observed in *Buccinum*. The short vagina is lined by a ciliated epithelium in which no mucous cells occur. It is surrounded by a sphincter which guards the genital aperture.

The Ventral Pedal Glands

The female *Ocenebra erinacea* has two ventral pedal glands. In anaesthetized animals the anterior one may sometimes be seen as a conical papilla, with a small central cavity, projecting from the surface of the foot. It lies a short distance behind the anterior pedal or pedal mucous gland in the mid line. Usually the gland is not visible. The epithelium of the papilla is very high, attaining 180μ, and is composed of ciliated cells and gland cells. The ciliated cells are narrow at the base and broaden distally; their nuclei are elongated and lie towards the upper half of the cytoplasm. The gland cells arise from the basement membrane to alternate with the ciliated cells. On fixation these glands tend to empty their secretion, leaving within the cells a granular lightly staining cytoplasm. The secretion, often entangled in the short thick layer of cilia, is black after iron haematoxylin. A second, comparatively infrequent type of gland cell is distributed in the connective tissue below the summit of the circular fold—that is around the aperture leading to the central cavity of the papilla—and in the epithelium. It contains spherules which stain deeply with azocarmine and rather lightly with iron haematoxylin. The lips are covered by a columnar ciliated epithelium, which is very low on their inner surfaces. Among the ciliated cells are a few gland cells similar to the second type of gland cell described in the gland, and these are also found in the epithelium covering the surrounding area of the foot.

The second ventral pedal gland is a short distance behind the first. It has the appearance of a pit, which in fixed material measures 2 mm. deep and 0·6 mm. broad and has thick glandular walls thrown into folds parallel to the surface of the foot. The lumen in transverse section is a crescentic slit with a concave anterior surface and a convex posterior surface. The pit is lined by a columnar ciliated epithelium and gland cells are scattered among the ciliated cells. These have basal nuclei and the cytoplasm is filled with small protein secretion granules. Below the epithelium is a dense layer of mucous cells grouped in clusters and in the connective tissue which separates one cluster from its neighbours are developed radial muscles. Circular and longitudinal muscles lie beneath the basement membrane of the epithelium and the ducts of the mucous cells pass between them to open into the lumen of the gland.

In the male there is a single ventral pedal gland identical in structure with the anterior one of the female.

Two ventral pedal glands are present in the female *Nucella lapillus*. These are comparable in position to the two glands described in female *Ocenebra*. In both animals the structure of the anterior gland is similar, but in *Nucella* it has not been seen to project from the surface of the foot, though the musculature suggests that this is possible. It communicates with the exterior by way of a ciliated duct, which has an inconspicuous external aperture lying between the circular opening of the posterior and that of the anterior pedal gland. In

Nucella the posterior gland has the form of a deep conical pit, the walls of which may be thrown into folds running along the long axis of the walls. It is lined by a columnar ciliated epithelium, and among the ciliated cells are a few gland cells with spherules which tend to dissolve on fixation. The cytoplasm stains red with azan and lightly with iron haematoxylin. Beneath the basement membrane of the epithelium is a layer of circular and longitudinal muscles through which pass the ducts of underlying gland cells. These cells form a thinner layer than the corresponding cells in *Ocenebra*: in sections their cytoplasm is vacuolated and the contents of the vacuoles dissolved. The protoplasm stains blue with azan and lightly with iron haematoxylin. It is unaffected by mucicarmine or toluidin blue but the final secretion attached to the cilia and the surface of the epithelium stains lightly with these stains for mucus. Radial muscles penetrate the connective tissue of the folds and pass between the groups of subepithelial gland cells.

In the male only the anterior gland is present.

In male specimens of *Nassarius reticulatus* no pedal gland has been observed, but one is present in the female. It opens in the mid-ventral region of the foot a short distance behind the anterior pedal gland and resembles the posterior pedal gland of *Ocenebra* and *Nucella*. The gland forms a deep but narrow pit, broad laterally and narrow from back to front. At the dorsal end it is rounded. The walls are folded transversely and are covered by a columnar ciliated epithelium. Beneath the basement membrane of this epithelium is a layer of muscles: most of the fibres are longitudinal with respect to the pouch, but a few are circular. A layer of gland cells underlies the muscles, the cells being grouped in small clusters and their ducts passing through the muscle layer and between the ciliated cells to discharge their secretion into the lumen of the gland. After fixation in Susa the cytoplasm of the cells appears highly vacuolated, although the contents of the vacuoles have dissolved. The protoplasm stains blue with azan and lightly after iron haematoxylin; but it is not affected by mucicarmine, although the secretion in the lumen of the gland and that in some of the ducts is stained pink. It thus appears that the cells produce a mucous secretion, the precursor of the secretion not being affected by the recognized stains for mucus. Radial muscles penetrate the folds of the wall and make their way between the groups of gland cells.

The presence of a ventral pedal gland in *Buccinum undatum* has been denied by the majority of previous investigators. Carrière (1882) failed to find one and his results were adopted by Simroth (1907). In 1910 Pelseneer confirmed Carrière's observations for both sexes, stating that the gland was present only in the embryo. Dakin (1912) described the anterior pedal gland (= the pedal mucous gland) and apparently failed to discover the presence of a ventral one. He obviously confused the anterior gland with the ventral and held that the former was homologous with the pedal pore, or opening of the

ventral pedal gland, of other prosobranchs, which had once been considered as the external opening of a water vascular system. He mentioned, without any reference, that in *Purpura* (=*Nucella*) Pelseneer had ascribed to the *anterior* gland the function of secreting the egg capsule and concluded that in *Buccinum* it did the same. But in 1910—before the publication of Dakin's monograph—Pelseneer had figured both an anterior and a ventral pedal gland in *Nucella*, showing the egg capsule in the *ventral* one and had explicitly stated that the capsule was formed there. In a note to *Nature* Cunningham (1899) described egg capsules in the "sole gland" or ventral pedal gland of *Buccinum*, and so far as I know this is the only occasion on which the presence of a ventral pedal gland has been noted in this mollusc. This gland, too, was mistaken by Dakin for the anterior gland. Observations on living animals show that in male specimens there is nothing to correspond to the ventral pedal gland, but in females it can be seen as a shallow pouch some distance behind the anterior gland in the mid line.

The columnar epithelium covering the pouch is ciliated and gland cells are distributed throughout the ciliated cells. In one type of gland, which is very plentiful, the cytoplasm contains small spherules staining red or orange with azan and with varying degrees of intensity with iron haematoxylin; occasionally the spherules stain blue with azan. Mucous cells are numerous in the epithelium, and in the connective tissue below there are small irregularly shaped gland cells with contents staining deeply with iron haematoxylin; their narrow ducts penetrate the basement membrane to open between the epithelial cells. The walls of the pouch are deeply folded by variations in the thickness of the underlying connective tissue and musculature of the foot. Radial muscles penetrate the folds and external to these is a coat of circular fibres.

The whole pouch is covered with an epithelium of the same height and general histological character as is found on the neighbouring area of the foot; in the gland, however, mucous cells are fewer and the other types of gland cell are more numerous.

The Egg Capsules

The egg capsule of *Nucella lapillus* is an erect vase-shaped structure about 8 mm. high. It is circular in transverse section and broadest in the middle where its diameter is about 2 mm. At one end the capsule tapers to form a short stalk which attaches it to a basal disc, and the disc is firmly anchored by cement to the substratum. At the opposite end there is a circular aperture which is filled with a plug of a rather transparent homogeneous substance. Two longitudinal lines of thickening can be traced over the smooth surface, and these are placed so as to divide the wall into two approximately equal halves. Distally the suture of one side meets that of the other over the surface of the plug, which is thus subdivided. The minute structure of the wall has been described by Ankel (1937) who states that it consists of three layers: an

inner layer of a homogeneous transparent substance, and middle and outer layers of fibres orientated in definite ways and separated from one another by distinct spaces. He described the inner fibres as running in a longitudinal direction and the outer fibres as being circular. Transverse sections through the wall of the capsule of *Nucella* (Fig. 6*c*) show this fibrillar appearance clearly and, if the sections be stained with azan, the three regions may be readily distinguished: the inner homogeneous layer (HM) stains red, and in the fibrous layers (LF, CF) the fibres are red, whilst the interfibrillar spaces are filled with a blue staining substance (IFM). Externally the fibrillae are more widely separated by the interfibrillar substance and are thinner. In sections stained with iron haematoxylin the inner homogeneous layer stains deeply and the fibres of the outer layers more lightly. The interfibrillar substance is hardly affected by this stain but is pink after mucicarmine. These results suggest that the wall of the capsule is composed of two substances—a protein which according to Ankel is conchiolin, and, intermixed with the protein in the outer layers, a mucous or mucoid substance. It is the distribution of these two substances which gives the fibrillar appearance to the capsule. When the capsule has weathered for some time the mucus tends to contract leaving the spaces between the fibres observed by Ankel. In the stem and in the basal disc the fibres are more irregularly disposed. The plug is made of mucus and is tightly fitted into the distal aperture of the capsule. A very thin mucous layer also covers the wall internally (ML) and is sparsely distributed over the outer surface. The capsule contains several hundred eggs embedded in an albuminous fluid, but of these only about 15–25 hatch, the remainder being devoured by their fellows (Lebour, 1937).

The egg capsule of *Ocenebra erinacea* is built on the same plan as that of *Nucella*. It is about the same height and a narrow stalk connects it to a basal disc by which it is fixed to the substratum. The capsule is flattened on one surface and is rounded on the other, and the middle of the rounded surface may be produced into a slight keel. In transverse section it is therefore triangular. At the distal end is a circular hole blocked by a mucoid plug. Two longitudinal sutures are visible on the smooth yellowish wall, running up the centre of the convex and concave faces and continuing over the plug. Sections stained in azan show that the microscopic structure of the wall is the same as that of *Nucella*, the inner homogeneous layer occupying a third of the total thickness and the fibrous coats the outer two-thirds. The capsule contains from 12–20 eggs embedded in an albuminous fluid and all may develop into young tingles (Lebour, 1937).

The laying of the egg capsule of *Nassarius reticulatus* has been described by Ankel (1929), and he points out the superficial resemblance between the capsule passed out from the oviduct and its more familiar form attached to the rocks or stones of the seashore. The fully formed capsule is fixed by a basal disc

from which it enlarges into a vase-shaped structure slightly convex on one surface and flattened on the other. It is about 5 mm. high and about 4 mm. across at the broadest point. The walls are thinner and more transparent than in the capsules of either *Nucella* or *Ocenebra*. Examination under a binocular microscope shows that they have a fibrillar structure. The lateral margins of the flattened sides of the capsule are continued out to form a flange on each side, and this is extended over the distal end by a similar flattening of the plug. When the capsule leaves the oviduct the walls have a more opaque appearance than they have in their final state, and there are two longitudinal lines of thickening containing the material for the flanges.

Sections of capsules taken from the vestibule of the oviduct show that the wall is composed of several layers staining blue, red or orange with azan. The inner layer is a mixture of two secretions one of which stains orange and the other blue; the next is a homogeneous layer of orange-staining material and the third resembles the first. Along the longitudinal lines of thickening there is an increase in both types of secretion and the layering is ill defined. Covering the outside is a very tenuous coat of secretion which stains a bright red. Capsules collected from the shore and similarly treated show a surprisingly different structure: the wall appears to be thinner and, except in the region of the flanges, is remarkably homogeneous. It stains orange with azan, but here and there a trace of the blue secretion can be found, mainly confined to the core of the flanges. These differences between the two capsules are due to the moulding action of the ventral pedal gland.

Each capsule contains an albuminous fluid in which float up to a hundred eggs, all of which may develop into free living larvae (Lebour, 1937; Portmann, 1925).

The egg capsules of *Buccinum undatum* are laid in large masses; the lower ones of each mass are fixed to the substratum and the upper ones are piled upon them and attached to them by their bases. The bases are oval and the edges project to form flanges by which the attachment is effected. Each capsule is compressed, one side being flattened and the other convex. It is broadest at the base, which measures 12 mm. and is about 10 mm. in height. The flattened face is smooth, and towards the distal edge, in a subterminal position, is the oval plug, of a different appearance and consistency from the rest of the wall. The convex face is covered by numerous wrinkles which form a reticulate pattern over its surface, and the half of the flange which projects from the base of this face is similarly ridged. From each side of the oval plug a line of thickening passes to the flattened edge, the two lines representing the sutures which, in *Nucella*, divide the capsule into equal halves.

The structure of the wall resembles that of the capsules already described. In section it appears to be made up of four distinct layers compressed together. On the outside is a homogeneous covering and through it can be seen a coat of circular fibres, both these layers staining deeply with azocarmine and iron

haematoxylin: the fibres are separated by a mucous secretion. Next comes a layer of similar but broader longitudinal fibres embedded in a mucoid secretion, and on the inside is a thin mucous sheet. The outer covering is spread over the surface of the plug, which, together with the base, is composed chiefly of mucus.

The egg case contains several hundred eggs embedded in albumen; out of these only about ten come to maturity, the rest being used as food (Portmann, 1925).

The Function of the Female Genital Duct and of the Ventral Pedal Gland

Nucella lapillus

At the time of copulation the male passes the penis through the female genital aperture so that the tip is directed into the bursa copulatrix. Spermatozoa are released into this pouch and attach themselves to the epithelial cells by their heads; these orientated sperms lie closely packed side by side with their tails pointing into the lumen of the bursa, in which unorientated sperm may also lie. After copulation the spermatozoa may be passed up the ventral channel of the uterus by peristalsis, assisted perhaps by their own activity, and they may become attached to the epithelium of the channel or of the duct of the ingesting gland. It is not known how soon after copulation the formation of the egg capsules begins, but evidence suggests that at least on some occasions the two events follow closely upon one another. Several specimens of *Nucella* will often be found associated with a batch of egg capsules: some of these are usually males and others females, and whilst some females may be copulating others will be laying eggs.

The method by which the capsule is manufactured by the genital duct may be partly deduced from the observations given above and verified by the study of living animals. A large number of eggs are passed down the oviduct into the albumen gland and here they are mixed by ciliary activity with the albuminous secretion. At such a time the walls of the gland are greatly distended by the mass of eggs. The exact locus of fertilization is uncertain: if sperms from the ventral channel and the duct of the ingesting gland are passed into the albumen gland on the relaxation of the sphincter muscle which guards its opening, then fertilization will occur in the lumen of this gland. Otherwise spermatozoa may be poured on to the eggs as they enter the capsule gland.

The mass of albumen and eggs is passed into the capsule gland by muscular assisted by ciliary action, and here the process of capsule formation begins. Only on one occasion has a capsule been found within the gland, although numerous specimens have been examined in the hope of finding capsules in various stages of formation. In this case the capsule was near completion and occupied the whole length of the gland, the plug being at the upper end, near the posterior mucous tips, and the base anterior. The longitudinal sutures which divide the capsule into two halves were lying one against the ventral

channel and the other against the narrow dorsal wall. The wall of the capsule was not so smooth as in its final form, nor was it so completely circular in transverse section. The longitudinal sutures were more obvious and the basal disc was represented by a rather irregular fibrous mass. From the orientation of this capsule may be deduced the functions of the various regions of the gland. Since the plug is composed of mucus it is apparently secreted by the posterior mucous tips and the capsule wall by the rest of the gland. As already stated the wall of the capsule is made of three layers: the innermost is composed of a homogeneous substance which stains an orange-red with azan and black with iron haematoxylin, is similar to the more plentiful secretion from the cells of the main part of the capsule gland, and also resembles the non-mucoid secretion from the cells of the dorsal wall and those which border the greater part of the ventral channel—it is therefore presumably derived from them. Outside this layer is a double fibrous coat formed by intermingling this same protein secretion with a mucoid substance. The way in which this occurs and the manner of formation of the egg case as a whole may be reconstructed as follows.

Prior to the entry of the secretion and eggs from the albumen gland the cavity of the capsule gland becomes filled with a mass of secretion from the gland cells in its walls. These secrete first the protein matter and then, in increasing quantities, the mucoid substance which they produce, and the result is that the lumen is filled with a mass of secretion which is almost pure protein in the centre but consists, in its outer layers, of an emulsion in which the mucoid material acts as a dispersed phase in a continuous phase of protein. Because of the steadily increasing quantity of mucus and of the accompanying decrease in the production of protein the size of the mucoid droplets steadily increases from the centre to the periphery of the mass, and the strands of protein which separate the drops gradually decrease in size. The predominantly transverse direction of the ciliary currents on the walls of the gland rotates the mass and draws out the drops of mucoid material into streaks parallel to the transverse axis of the gland, and the protein material separating them is drawn out into strands elongated in the same direction. When the duct between the albumen and the capsule glands is opened, the albumen and the eggs are forcibly passed into the central portions of the secretion lying in the latter, so as to invaginate this into a vase-shaped structure with a round hole at the inner end into which the plug will later be fitted. This process of invagination deposits the eggs and their accompanying albumen in the centre of the mass of secretion occupying the capsule gland, which is composed of unmixed protein material, and from this is formed the innermost layer of the capsule. It has also the effect of drawing the outer emulsion of protein and mucoid secretion into sheets around the inner homogeneous layer, in which the direction of elongation of the mucoid droplets now lies parallel to the direction of movement of the eggs, that is, parallel to the long axis of the gland: from this results the longitudinal direction of the strands of the inner part of the fibrous coat. The outer part of this layer, being still

exposed to the ciliary currents on the wall of the gland, retains the original alignment of the drops and so gives rise to the outer part of the fibrous coat in which the fibres are circular in direction. With the disappearance, on exposure, of the mucous dispersed phase the space occupied by it is left as a series of lacunae separating what now appear as strands of fibrous material. The mucus which lines the wall internally is secretion from the posterior tips, which was dragged along with the mass of eggs when the latter passed into the capsule gland. These tips continue to pour out secretion while the wall of the capsule is being elaborated by the more anterior parts of the genital duct. The mucus forms an accumulation which is fitted into the hole in the upper part of the capsule by the muscular action of the transverse strips which border the mucous tips anteriorly. These press the upper edge of the wall of the capsule on to the mass of mucus so that the cavity within is securely closed. The suture which divides the plug into two equal halves demarcates the limit of the secretion produced by each posterior tip.

The egg capsules are passed from the oviduct to the posterior ventral pedal gland along a groove situated in the right anterior portion of the foot and temporarily formed for that purpose. When examined in this position, it can be seen that the gland fits tightly over the capsule, and only the tip of the basal disc is protruded from the sole of the foot. The wall of the capsule is compressed and moulded to the final, smooth, vase-shaped outline. The stalk is constricted from the basal disc and the latter finally pressed out and fixed to the substratum. The mucous secretion from the subepithelial cells of the gland acts as a lubricant during the fashioning of the egg case. Secretion from the second type of gland cell may have a similar function, or may, in some way, be concerned with the hardening of the wall.

The anterior ventral pedal gland is equally developed in both sexes. Its function is obscure. Since, however, a corresponding gland is present in *Ocenebra erinacea* and both animals are carnivorous feeders, obtaining their food by boring the shells of other molluscs, it is possible that the gland may be concerned with their specialized feeding mechanism (Graham, 1941).

Ocenebra erinacea

Since the structure of the female genital duct of this mollusc and of the egg capsules produced by it so closely resembles those of *Nucella lapillus*, it may be concluded that the mode of functioning of the system is similar in the two animals.

The shape of the completed egg capsule of *Ocenebra* differs from that of *Nucella*, and this is due to a difference in the shape of the ventral pedal gland which moulds it. In the former the capsule is much more drastically changed by this gland than in *Nucella*. In the final state the two longitudinal sutures which are formed in the genital duct are situated one in the middle of the concave surface and the other in the middle of the convex. From this it may be deduced that the orientation of the capsules in the pedal gland must always be the same.

Nassarius reticulatus

The functioning of the female genital ducts of *Nassarius* agrees with that of *Nucella*, but there are some differences in the structure of the capsule which need explanation. When the capsule is being formed it does not occupy the whole length of the capsule gland, with the effect that as it passes outwards successive layers of secretion are poured over it. The plug is formed by the posterior mucous tips and the wall is moulded around the plug by the transverse muscular strips. Anterior to these the ciliary currents beat at right angles to the long axis of the gland, and they mix the mucous and mucoid secretions from the cells overlying the dorsal wall and bordering the ventral channel with that from the rest of the gland. In this way the inner layer of the capsule wall is formed. Over the anterior part of the gland the ciliary currents are directed forwards and there is little mixing of the secretion. That produced by the mucous or mucoid secreting cells is mainly confined to the dorsal and ventral lines of thickening, whilst the homogeneous secretion from the rest of the gland forms the second layer of the wall. Mucus is then mixed with this secretion as the capsule is passed to the anterior tips of the gland, since these are bordered posteriorly by a strip of mucous cells. Finally the anterior tips coat the wall with yet another thin layer which stains deeply with azocarmine and iron haematoxylin. The muscular vestibule then expands to receive the capsule and it is passed to the genital aperture. At this stage the case is biconvex and two longitudinal lines of thickening extend from the plug to the thick basal plate. The capsule is directed to the ventral pedal gland along a groove in the foot, and here a mucoid secretion is poured upon it which may act not only as a lubricant but as a hardening mixture. The walls are compressed and the flanges are formed from the longitudinal lines of thickening. At the same time the basal disc is constricted from the capsule, which assumes its final flattened shape in correspondence with that of the lumen of the pedal gland.

Buccinum undatum

Some knowledge of the functioning of the female ducts of *Buccinum* has been obtained by studying specimens during the process of egg laying and also by dissecting such animals. Unfortunately only one capsule, and that fully formed, was found still within the oviduct. This differed in several respects from the finished cases which are fastened to the rocks on the shore. The capsule was broadly oval in shape and its surface was smooth; the plug occupied an approximately terminal position and the fins around the base were thicker. Microscopically the walls were more loosely compacted.

On leaving the genital duct such a capsule is passed along a temporary groove of the foot, which runs from near the genital aperture to the ventral pedal gland. Within the latter it is retained for several minutes and is meanwhile kneaded by the pedal musculature which flattens the capsule and stamps

the reticulate pattern on to the convex face. The flanges are compressed and anchored to the substratum.

The manner in which the four layers making up the wall of the capsule are laid down around the mass of eggs appears to be as follows. The three inner layers are similar to the layers of the capsule wall in *Nucella* and are formed in a corresponding manner except that the secretion is derived from the upper part of the gland only—the capsule occupying only about half the total length of the gland during its formation. Whilst this secretion is taking place a mass of mucoid and protein material is produced from the walls of the whole lower section of the gland. On the completion of the formation of the wall of the capsule in the upper half, the capsule is pushed against this material, which is thus collected into a heap situated at the base of the capsule—in this way the material for the basal disc and its flanges is brought into its correct position in relation to the rest of the wall of the egg case, and even at this stage the rudimentary basal disc and flanges can be separately discerned in it. When the capsule is pushed through the lower half of the gland, collecting the material for its base as it goes, a second period of secretion is initiated and a layer of almost pure protein secretion is applied over the already formed walls and also over the top of the plug embedded in them.

Discussion

In the majority of the British Stenoglossa the development of which has been studied, there is complete suppression of the free living larval stage, the young emerging from the capsule as a miniature of the adult. In some of them, however, such as *Nassarius*, the capsule contains up to a hundred eggs and these develop into planktonic larvae. In *Ocenebra* about a fifth of this number of eggs is present in one capsule and there is sufficient nourishment for all to develop as far as the crawling stage. The newly laid egg capsules of *Nucella* and of *Buccinum undatum* contain several hundreds of eggs, but the supply of nourishment within any one capsule is insufficient for all the eggs to complete development, and, as a result, the most precociously developed embryos feed on the less advanced. In *Littorina* (Linke, 1933) and the majority of other prosobranchs each egg is surrounded by its own supply of nutrient albumen with which it is encased in a protective shell: it is the loss of this individual shell—uniting all the eggs in a common chamber—which has permitted the evolution of embryonic cannibalism in the Stenoglossa and has, among other factors, contributed to the suppression of a free larval stage.

The egg capsules of the Stenoglossa which have been investigated are very similar in structure. The variations in shape are due not to any fundamental differences in the structure of the genital ducts themselves, but to differences in the shape of the ventral pedal gland which moulds the capsules passed to it in an unfinished condition from the capsule gland. The wall of the capsule is highly elastic and has a fibrillar appearance due to the mixing together of the various secretions from the capsule gland. One end is anchored to the

substratum and at the opposite end is a circular aperture in the wall which is filled by a mucous or mucoid plug. Ankel (1937) has shown that in *Nucella* this plug is dissolved by the young animals when they are ready to hatch, and it is probable that in the other species the animals have a similar means of escape, for in empty, discarded, capsules the wall is always intact and the plug gone.

The ingesting and resorptive gland of the female genital system is one of the more interesting features which call for discussion. The phenomenon of sperm and yolk ingestion does not appear to have been previously described in the Mollusca, although the ingestion of sperm has been demonstrated in other invertebrate phyla. In the bed bug, *Cimex*, Abraham (1934) has shown that the majority of sperms in the female are normally absorbed in the "Resorptionsorgane", previously known as the spermatheca (Cragg, 1923). Here they become motionless and disappear. Sperms are also taken up by leucocytes as they traverse the haemocoel on their way from the body wall to the genital tract. In *Peripatopsis* (Manton, 1938) there is no special sperm ingesting organ, but absorption takes place in the ovary and the sperm provides the ova with some of the nutriment necessary for growth. In both these instances there appears to be some special significance attached to the process, for it has been suggested that the normal development of the ova is dependent on sperm absorption (Cragg, 1923; Manton, 1938). Copulation is of frequent occurrence in both animals. An ingesting gland is well developed in *Nucella lapillus*, an animal in which copulation and capsule formation continue throughout the year; examination shows that an excess of sperm is often present in the female, whilst the frequency with which copulating pairs can be collected suggests that copulation is frequent in this species too. The excess sperms are absorbed as previously described, but whether the development of eggs to maturity is in any way dependent upon the amount of sperm absorbed, or whether absorption is merely to empty the ducts of unwanted sperm, is as yet unknown. In *Nassarius reticulatus* the gland is smaller and probably of less importance in the functioning of the reproductive system. Specimens of *Buccinum* which were collected and sectioned during April show that the number of sperms in the gland is small as compared with the quantity of yolk present. During the breeding season the sperms in the genital duct of a female *Buccinum* are comparatively fewer than in *Nucella* and consequently the need for sperm ingestion may be less. The gland, however, is not reduced in size, since a second task—that of resorbing unused yolk granules—has been imposed upon it. This yolk must originate from eggs which for some reason are not included in a capsule. In *Ocenebra* during the breeding season yolk has also been found in the lumen of the gland and in the resorptive cells, but not in such quantities as in *Buccinum*. Yolk resorption may occur in *Nucella* and *Nassarius*, but has never been observed.

In the male system there is also a means of resorbing sperm. In the vesicula seminalis the epithelial cells frequently contain sperm in various stages of

digestion. Linke (1933) observed this in *Littorina* and stated that the process continued during the whole period of sexual activity. This suggests that the production of sperm by the testis may be in excess of requirements, or that too great a number of sperms in the seminal vesicle may in some way upset the functioning of the system. The cells may have the ability of resorbing only senile sperm (though the presence of senile sperm so close to the testis seems improbable) and thus by a selective mechanism maintain within the duct an effective stock, or the absorption may be haphazard with the intention of safeguarding the duct against blockage. In neither male nor female is the ingestion of sperm restricted to that of apyrene spermatozoa: in both sexes, where two kinds do occur, each type is ingested.

The opening of the prostate into the mantle cavity is another character of the male genital system which needs some comment. In *Littorina* the male duct, anterior to the opening of the vas deferens into the prostate, is open throughout its length. The lower Stenoglossa, *Nucella* and *Ocenebra*, show evidence of the method by which this duct was closed during the course of evolution, but in them the closure is incomplete at one point, and a slit-like communication with the posterior end of the mantle cavity remains—in *Ocenebra* this is of quite considerable size. The cilia which direct the sperm through the prostate beat away from this opening and during the actual transference of sperm to the female there is no leakage into the mantle cavity. In *Nassarius* and *Buccinum*, in which the prostate is in the form of a narrow and highly muscular duct, there is an opening in a corresponding position, but it lies at the end of a short duct which leads from the prostate to the mantle cavity. In *Buccinum* the opening of the vas deferens into the prostate is well in front of this duct, so that normally the sperm, which is rapidly passed forward by peristalsis, is prevented from escaping. Although there is an evolutionary trend towards the complete closure of the male duct the persistence of the opening in these higher forms at once suggests that it plays some important role. It is conceivable that it functions as a safety valve, for if during the act of copulation the male is disturbed and forced to withdraw within its shell, sperm distending the prostate would be enabled to escape into the mantle cavity, so reducing the pressure in the gland and facilitating a more speedy withdrawal to safety. There is no evidence that excess sperm liberated from the vas deferens is at any time absorbed by the cells lining the more anterior regions of the male duct; it may be that it is always released to the mantle cavity. On one occasion when the shell of a male *Buccinum* was removed by bone forceps sperm was actually seen to escape in this way.

In the female the gonopericardial duct opens at the junction of the oviduct with the albumen gland. It is found in a comparable position in female *Littorina*. In the Stenoglossa and *Littorina* it is absent in the male, as also in *Calyptraea sinensis* and *Crepidula unguiformis* (Giese, 1915). In the mature male of *Ocenebra erinacea* there is evidence of its previous existence in the presence of a short diverticulum given off from the vas deferens and connected

to a prominence on the pericardial wall by a band of dense connective tissue and muscle fibres. In *Littorina* there is no diverticulum, but a similar strip of connective tissue is developed. Linke (1933) suggests that the persistence of this duct in the female is connected with the fact that the eggs are too large to pass through it, and that it has been abolished in the male to prevent sperm escaping. This may explain its distribution in the Stenoglossa, but in *Ocenebra* sections of the duct show that its dimensions when the muscles are relaxed would allow the passage of eggs, and in one specimen of *Buccinum*, which admittedly was under abnormal conditions (affected by the strain of having the shell removed), eggs were seen to pass from the oviduct to the pericardial cavity.

The gross structure of the male genital systems of the stenoglossan prosobranchs described here agrees in yet other respects with that of the male systems of the above-mentioned mesogastropods. In *Calyptraea*, *Crepidula* and *Capulus* (Giese, 1915), and in the three species of *Littorina* described by Linke (1933), the upper part of the vas deferens functions as a seminal vesicle, and from this, during copulation, sperm is liberated to the true vas deferens, a short ciliated duct. In all of these molluscs, however, the seminal duct anterior to the vas deferens is represented by an open groove. A bilobed prostate is developed in *Littorina* and this is homologous with the prostate of the Stenoglossa.

So far as the female is concerned the genital systems of the Mesogastropoda and the Stenoglossa conform to the same fundamental plan—a narrow proximal oviduct opening into a wide glandular distal section with a spermatheca lying near the point of junction. It may be pointed out that the male tract can be split into the same two divisions and, with the exception of the males of *Nassarius* and *Buccinum*, the thickening of the walls of the glandular parts in both sexes is restricted to the lateral walls, leaving narrow dorsal and ventral areas where few glands occur. In animals with an open genital groove the dorsal area appears as a groove separating the right and left glandular lobes, along the free edges of which runs on each side a thinner marginal strip, representing the ventral areas. When fusion of the lips of the groove has converted it into a closed tube the former persists as the narrow dorsal wall of either the prostate or capsule gland, and the two latter join one another to form the ventral channel. In the mesogastropods the receptaculum seminis is situated at the posterior end of the glandular uterus; in *Littorina* it is in the form of a small pouch embedded in the albumen gland; in *Calyptraea* and *Crepidula* it is represented by a number of blind tubules. No mention is made of any sperm-ingesting epithelium in these snails, so that there would appear to be no method of utilizing the waste genital products. The ingesting gland of the Stenoglossa occupies a comparable position and is homologous with the receptaculum—the duct of the gland still functions as an area for the storage of spermatozoa, but at its distal end a large number of glandular tubules are developed and in the walls of these sperm and also yolk granules may be digested.

The various types of gland cells of the thick-walled uterus are in each genus mapped out according to a definite plan. In *Calyptraea* the cells are of three types: some pour a fibrous secretion over the eggs, which may be similar to the conchiolin from the capsule gland of the Stenoglossa, and others are mucous cells. Giese was unable to trace the various types of secretion in the fully formed capsules. In *Littorina* the albumen gland occupies a posterior position. It is homologous with that of the Stenoglossa, and fertilization occurs in both within the lumen of the gland. The fertilized eggs of *Littorina*, each coated with albumen, pass next to the shell gland, a structure which is not developed in the Stenoglossa, for in them the individual eggs are not enclosed in a shell, but lie freely in a common mass of albuminous secretion. In *L. littorea* and *L. obtusata* the jelly gland, which lies anterior to the shell gland, is homologous with the capsule gland of the Stenoglossa. In *L. rudis* the jelly gland has been modified to form a brood pouch in which the embryos develop into miniature adults. Whereas in the Stenoglossa the wall of the capsule is secreted around the egg mass in the capsule gland, Linke states that in *L. littorea* the jelly gland secretes a gelatinous fluid around the eggs, which have already been enclosed in a shell, and that the outer wall of the egg case is formed in and moulded by the ovipositor, which is situated on the right side of the head. The wall is tough and shows spiral markings. Sections of the jelly gland of this species show that it is made up of cells producing a protein secretion and of some mucous cells—hence in histological structure it resembles the capsule gland. In the Stenoglossa there is no definite structure to which the name ovipositor may be applied, but the same region at the right side of the head passes the capsule to the ventral pedal gland and so may be regarded to some extent as its homologue. The ventral pedal gland takes over the task of moulding the capsule. A bursa copulatrix lies at the anterior end of the jelly gland in *Littorina* and sperms are conducted from this pouch to the receptaculum by way of two longitudinal folds: these are ciliated and the sperm travels beneath them in the direction of the ciliary currents. In the Stenoglossa similar longitudinal folds separate a ventral channel from the lumen of the capsule gland, and along this the sperms are passed by peristalsis, assisted by their own activity, to the duct of the ingesting organ. No bursa is developed in *Calyptraea*, *Capulus* or *Crepidula*, for in each of them the penis deposits the sperm directly into the receptaculum.

So far as the interrelationships of the various gastropods dealt with in this paper are concerned, the conclusions which can be drawn from the comparative structure and function of the reproductive system are the same as have been arrived at by a study of other systems—that *Nucella* and *Ocenebra* belong to a more primitive group than *Buccinum* and *Nassarius*. This is seen particularly clearly in the persistence of indications of an open male duct in the two former genera, and, in *Ocenebra*, in the presence of a well-formed vestige of a gonopericardial duct in the male. In other respects the two groups appear to have attained a very close degree of similarity and this extends even to the habit of embryonic cannibalism. Since some members of each group

have this habit and others have not this must be an example of parallel evolution.

Nassarius appears to have retained a primitive feature in still possessing a free-swimming veliger, although in other respects, such as the ventral pedal gland, it appears to be less primitive than *Buccinum*, but the gland in the latter may owe its primitive structure to degeneration. The other members of the group have sacrificed the benefit of wider distribution conferred by free larvae for the greater certainty of the young developing to a crawling stage and of reaching the correct habitat for adult life; this is ensured, first by the provision of eggs as food for the precociously developing embryos, and secondly by the fixation of the capsules on the shore in a suitable position for the young snails to start independent life.

So far as the remaining groups of the Stenoglossa, with the exception of the Toxoglossa, are concerned, little in the way of comparison can be made. The Volutacea include a large number of mollusca of the anatomy of which very little is known. The work of Küttler (1913) on *Oliva* indicates that there is a close similarity between this animal and the Buccinacea. In the Volutids, on the other hand, the brief note by Woodward (1901) would suggest that the conditions of the male genital tract are rather more primitive than occur elsewhere in the Stenoglossa, since he describes an open seminal groove running across the mantle cavity and along the penis. The description is too short to allow one to decide whether the condition resembles that found in *Calyptraea* or that in *Nucella*.

Taking all into consideration, however, the fact remains that the Stenoglossa are a highly specialized group of prosobranchs. This can be seen not only in the highly modified genital system, in the specialization of the egg case and embryonic mode of life, but also in the structure of the nervous system (Bouvier, 1887), in the elongation of the proboscis (Amaudrut, 1898) and in the complexity of the oesophagus (Graham, 1941).

Summary

The foregoing pages include an account of the anatomy and histology of the male and female genital ducts of *Ocenebra erinacea*, *Nucella lapillus*, *Nassarius reticulatus* and *Buccinum undatum*. Observations have also been made on the mode of functioning of the ducts and the formation of the egg capsules.

In both male and female it is possible to divide the genital ducts into a narrow and thin-walled proximal section which leads from the gonad and opens into a thick-walled glandular distal region, and in this respect the Stenoglossa agree with the mesogastropods. Near the junction of these two portions, in the female, arises the gonopericardial duct, which puts the genital duct into communication with the pericardial cavity; in males this structure is lost or reduced to a vestige lying in a similar position.

In males the upper part of the proximal region of the genital duct is used as a vesicula seminalis and the epithelium is capable of taking up and digesting effete or superfluous sperm. Sperms are passed from it into the anterior, distal region during the act of copulation, and secretion from the glands is mixed with them and provides the medium in which they are transferred to the female. In *Ocenebra* and *Nucella* this glandular region, the prostate, extends only as far as the opening of the mantle cavity, from which a continuation of the duct, without glandular walls, runs to the penis. The entire distal half of the male duct shows evidence of having been derived from an open seminal groove such as is found in *Littorina*. The transformation is incomplete at the posterior end, where the prostate opens directly to the mantle cavity. In *Nassarius* and *Buccinum* the prostate extends to the base of the penis and there is a similar communication in the form of a narrow duct. In all the species, seminal fluid may, if necessary, be lost through this opening.

In females the whole of the proximal part of the oviduct serves to carry eggs from the ovary to the glandular distal section, a sphincter preventing their entry into the gonopericardial duct. The distal region may be divided into (i) the albumen gland; (ii) the capsule gland; (iii) the vestibule; (iv) the vagina; (v) between the albumen and capsule glands, the spermatheca, and (vi) the bursa copulatrix.

The albumen gland produces an albuminous fluid by which the eggs are surrounded, and fertilization occurs in this region. The capsule gland secretes around the mass of eggs and albumen the walls of the egg case composed of mixed protein and mucoid materials, the process of capsule formation being described in detail. The plug, of mucus, is produced by localized regions of the gland, the posterior mucous tips, and is moulded into position in the capsule by special muscular strips. The bursa copulatrix receives the seminal fluid from the male in copulation. The sperm becomes attached to the walls and, in *Buccinum* at least, the prostatic secretion is absorbed by amoebocytes. Later the sperms migrate, partly by their own activity, partly by muscular or ciliary action on the part of the female, along the ventral channel of the capsule gland to the spermatheca. They are stored here by being attached to the wall until required, and some storage may also occur in the upper end of the ventral channel. The spermatheca is provided with several tubular outgrowths distally, and in these ingestion and destruction of superfluous spermatozoa occur. In *Ocenebra* and *Buccinum*, and probably in the two others as well, a resorption of stray particles of yolk occurs in the same epithelium. No connexion between this and the maturation of the eggs has been noticed, nor is the ingestion limited to apyrene spermatozoa. No shell gland is present and the eggs are therefore enclosed in a common mass of albumen, a fact which permits of embryonic cannibalism.

The egg capsules, roughly formed by the glands at the base of the oviduct, are passed along a temporary groove on the right side of the foot, perhaps

homologous with the ovipositor of mesogastropods, to the ventral pedal gland in the middle of the sole of the foot. Here they are manipulated into their definitive shape, their walls are hardened and they are cemented to the substratum. The gland occurs in females only. In both sexes in *Ocenebra* and *Nucella* a second ventral pedal gland of obscure function lies directly in front of it.

The relationships of the Stenoglossa amongst themselves and with the lower gastropods are discussed.

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ABSTRACTS OF MEMOIRS

RECORDING WORK DONE AT THE PLYMOUTH LABORATORY

The Resistance of Nerve in Relation to Interpolar Length

By J. F. Danielli

Journ. Physiol., *Vol.* xcvi, 1939, *pp.* 65–73

Assuming that a nerve may be regarded as a conducting core surrounded by a resistant sheath, lying in a conducting medium, conductivity experiments have been made following Rushton's treatment, by which the several resistances can be determined. Errors, probably caused by uneven distribution of water over the surface of the nerve and by uneven contact with the electrodes, are so large that a rigorous test cannot be obtained for this hypothesis. The results obtained, however, are compatible with this theory.

Very large errors also enter into the measurement of R, the resistance across a nerve sheath. It has, however, been possible to show that for frog nerve the maximum change in R for a pH change from 6 to 8 is less than $\pm 10\%$ of the value at pH 7. Addition of Ca or K to bring the total in Ringer to ten times normal does not change by more than $\pm 30\%$ of the value found in normal Ringer. Both Ca and K in these concentrations have very marked effects on the excitability of the nerve, so that it seems probable that the membrane on which these ions act gives rise to a relatively insignificant part of the total sheath resistance. J. F. D.

Factors in Cation Permeability

By H. Davson and J. F. Danielli

Biochem. Journ., *Vol.* xxxii, 1938, *pp.* 991–1001

The possibility that the high concentration gradient of K^+ maintained by the erythrocytes of many species against their surrounding plasma is due to an active metabolic process has been investigated. Metabolic poisons, such as CN, CO, urethane, and accelerators such as methylene blue and pyocyanine had no influence on the K^+ content of the non-nucleated erythrocytes of the rabbit and the nucleated cells of the goose and dogfish. Fluoride caused a small loss of K^+, but it was concluded that this is not associated directly with the inhibition of glycolysis produced by this substance.

The extent to which losses of K^+ may be caused by centrifuging the cells from serum or saline was studied. Direct proof of such losses was obtained

with the erythrocytes of the dogfish and ox. The possible bearing of these effects on earlier work is discussed.

The question as to whether haemolysis, however produced, is preceded by a state of cation permeability was studied. Subhaemolytic concentrations of amyl alcohol, the dihydric phenols and guaiacol caused losses of K^+ from the rabbit erythrocyte; digitonin, Na cholate and oleate caused losses only when in haemolytic concentrations (these losses were over and above those due to the haemolysis itself); saponin produced no loss of K^+ in all the concentrations studied. Acidity and alkalinity were only effective under haemolytic conditions, whilst raising the temperature caused considerable losses of K^+; the penetration of K^+ into the erythrocytes of the ox from strongly hypotonic aqueous KCl was demonstrated. The haemolytic action of silver is preceded by an induced permeability to cations. J. F. D.

The Colour Changes and Colour Patterns of *Sepia officinalis* L.

By William Holmes

Proc. Zool. Soc. London, A, Vol. cx, 1940, *pp.* 17–36

The cuttlefish, *Sepia officinalis*, has the power to change its colour more strikingly developed than any other animal known. As the result of the variety of its chromatophore pigments, and the neuro-muscular nature of the chromatophore control, it can show a number not only of colours but also of patterns of colour on the surface of its mantle and head; and each pattern appears under specific conditions of stimulation. And its colour behaviour is made still more impressive by the fact that one pattern can be changed for another entirely different in times of less than a second.

The weight of evidence is in favour of the view that its powers of colour change and pattern production endow *Sepia* with a system of protective coloration unique in its complexity. Protection is afforded chiefly by various concealing patterns, each produced in the appropriate environment. But there are also patterns which may well be directed towards "terrifying" a predator. Further, it is suggested that in its power to change conspicuous patterns rapidly *Sepia* is provided with a protective colour device which does not fall into any category of Poulton's classification. This device depends on the fact that the pattern change gives the impression of rapid movement, and this movement will probably cause a "flight reaction" in the predator. For it is commonly observed, in fish for example, that any sudden movement in the visual field causes the animal to withdraw. W. H.

The Myenteric Nerve-plexus in some Lower Chordates

By P. Kirtisinghe

Quart. Journ. Micr. Sci., Vol. LXXXI, 1940, *pp.* 521–39

Preparations of the myenteric plexus in a few teleosts, in *Scylliorhinus canicula*, and in *Amphioxus*, stained chiefly with methylene blue and silver nitrate methods, showed a much simpler arrangement than in the higher forms. The neurons of the plexus in teleosts belong to Dogiel's types I and II, in *Scylliorhinus* only those of type II were found. In *Amphioxus* bipolar nerve cells are definitely present in addition to the stellate ganglion cells described by Boeke. Synapses between (*a*) the pre-ganglionic fibres and the enteric neurons, and (*b*) the enteric neurons themselves are figured and described. No connexion between the system of "interstitial cells" of Cajal and the enteric nerve-plexuses was observed. The enteric plexuses of fish and *Amphioxus* are not in the form of a nerve-net. It is not possible to compare the enteric plexus of *Amphioxus* with the system of "interstitial cells" of the higher chordates. The stellate ganglion cells of *Amphioxus* are comparable to the neurons of type I in the higher forms. P. K.

Reproduction of the Dogfish

By H. Metten

Phil. Trans. Roy. Soc. London, B, Vol. CCXXX, 1939, *pp.* 217–38

Migration of ova from the ovary to the coelomic opening of the oviducts in *Scylliorhinus canicula* is entirely dependent upon ciliation, as it is in Amphibia. The entire peritoneal wall and many abdominal viscera of an adult female are ciliated. The cilia, which are absent in the male and immature female, direct a current of coelomic fluid towards the ostium. An ovum excised from the ovary of one adult female and inserted through an abdominal incision into the peritoneal coelom of another will undergo migration towards the ostium. The speed of the migration depends upon the region into which the ovum is introduced. An ovum placed in the bridge joining the two liver lobes will traverse the hepatic sinus, enter the ostium and descend an oviduct as far as the top of the oviducal gland, in three hours. There are no muscular movements of any of the organs concerned.

In addition to its function of secreting albumen and the egg-case, the oviducal gland of the dogfish is a receptaculum seminis. By triturating a portion of the shell-secreting zone of the gland in saline solution, active spermatozoa can be seen at all times of the year. There does not seem to be any sharply defined breeding season, but an increase in breeding activity is noticed in the spring. The oviducal glands of all adult females contain spermatozoa, but the sperm

content is very variable. In preparations of resting glands, spermatozoa can be seen in the shell-secreting tubules, whilst in actively secreting glands, a proportion of these spermatozoa are emitted in the shell material. In this way fertilization of an ovum is practically ensured. H. M.

Algal Production and the Food Requirements of a Limpet

By H. B. Moore

Proc. Malacol. Soc., Vol. xxiii, 1938, *pp.* 117–18

On the outer wall of the new swimming pool at Tinside, Plymouth, a thick algal felt had developed, and in this a number of limpets (*Patella vulgata*) had eaten clear patches. By measuring the sizes of the cleared areas and of the limpets on them it was estimated that in their first year these individuals require an area of about 75 sq. cm. per c.c. of limpet to support themselves, food being provided both by clearing the edges and by cropping the already cleared area. H. B. M.

The Colonization of a New Rocky Shore at Plymouth

By H. B. Moore

Journ. Anim. Ecol., Vol. viii, 1939, *pp.* 29–38

A newly made stony beach and a concrete wall at Tinside, Plymouth, were kept under observation for two years after their completion. The time of arrival, abundance and growth-rate of the colonizing species of animals and algae were noted and compared with a neighbouring long-established beach. The results indicated rapid colonization by a few hardy species and very slow colonization by most others. It appeared further that the latter were deterred, not by overcrowding, but by some environmental condition particularly unfavourable to the young stages, since those individuals which succeeded in establishing themselves showed a quite normal growth rate. H. B. M.

Further Observations on the Colonization of a New Rocky Shore at Plymouth

By H. B. Moore and N. G. Sproston

Journ. Anim. Ecol., Vol. ix, 1940, *pp.* 319–27

The state of colonization of the flora and fauna on a new concrete wall and stony beach at Plymouth after six years is described, for comparison with a previous survey made during the first two years (Moore, 1939: see above). Fourteen species of Algae and seventy-one species of animals were found. The highest and lowest zones of the beach appear to have developed more quickly towards a climax than the intermediate zone, in which environmental conditions are less favourable than in the others. N. G. S.

Some Observations on the Growth of *Peringia ulvae* (Pennant) 1777 in the Laboratory

By Anne Rothschild and Miriam Rothschild

Novitates Zool., *Vol.* XLI, 1939, *pp.* 240–7

A comparison was made between the growth-rate of *Peringia ulvae*, a brackish water Gastropod, collected from two different habitats and kept in the laboratory in (*a*) glass bowls, and (*b*) glass tubes. It was found that the snails kept in the bowls grew considerably faster, and that their size, consequently, is no criterion of their age. It was also found that apart from the different rapidity of increase in size the specimens in bowls and tubes displayed certain differences in their growth curve. When reared in the laboratory specimens collected from the mud-flats and saltings, which in nature differ from each other in size, shell shape, shell colour and shell texture, show no such variation, and it therefore seems probable that these differences are due to environmental rather than genetic factors. The snails parasitized by trematodes grew faster than uninfected specimens, thus supporting the theory that these infections cause increased growth. It was also found that uninfected females grew faster than uninfected males, and it seems probable that the larger size of females in nature is due to increased growth-rate rather than a longer life. M. R.

A Note on the Life Cycle of *Cryptocotyle lingua* (Creplin) 1825 (Trematoda)

By Miriam Rothschild

Novitates Zool., *Vol.* XLI, 1939, *pp.* 178–80

The life cycle of *Cryptocotyle lingua* was demonstrated experimentally in the laboratory. The cercariae were found parasitizing *Littorina littorea*; a number of fish, more especially in-shore forms such as wrasse, rockling, blennies and gobies, served as the intermediate host. The cercariae encysted in the fins and skin, and in those fish which are probably the natural hosts, stimulated the formation of pigment deposits round the cysts. The infected fish were kept in the laboratory a fortnight, and then fed to laboratory-reared albino rats, ducks and black-headed gulls. The adult worms were recovered from the intestine of the latter birds a month later. It was found that the behaviour of the cercaria is of importance for distinguishing between closely related species. The fertility of single infections proved to be very high. *Littorina* in the laboratory emitted cercariae for periods extending over three years, averaging about 300 cercariae per day. M. R.

Electrolyte Content and Action Potential of the Giant Nerve Fibres of *Loligo*

By D. A. Webb and J. Z. Young

Journ. Physiol., *Vol.* xcviii, 1940, *pp.* 299–313

Previous attempts to discover the physico-chemical basis of the resting and action potentials of nerve fibres have been handicapped by the presence in ordinary nerve trunks of connective tissue and intercellular fluid, which reduce the potentials by short-circuiting and introduce into the analyses an error of considerable but unknown magnitude. With the giant fibres of *Loligo* it is possible to isolate a single fibre, measure its resting and action potentials, and then submit it to chemical analysis. It is shown that the observed action potentials approximate closely to the diffusion potentials which would be produced if the bounding membrane of the axoplasm were permeable only to potassium ions, except during the passage of the impulse, when it is presumed to be freely permeable to all ions. The potentials may therefore be attributed largely, though not entirely, to the high concentration of intracellular potassium (0·28 *M*, as against 0·01 *M* in sea water) and the differential permeability of the axon membrane. Chloride is present in the axoplasm at a concentration of 0·11 *M*, which, though only a fifth of the concentration in sea water, is far higher than the values reported for the cells of vertebrates. The electrolyte balance-sheet of the axoplasm reveals large osmotic and anion deficits, indicating the presence in considerable quantity of anions (and perhaps non-electrolytes also) whose nature is not yet known. D. A. W.

Observations on the Coelenterate Nervous System

By the late H. H. Woollard and J. A. Harpman

Journ. Anatomy, *Vol.* lxxiii, 1939, *pp.* 361–2

Discontinuity in the Nervous System of Coelenterates

By the late H. H. Woollard and J. A. Harpman

Journ. Anatomy, *Vol.* lxxiii, 1939, *pp.* 559–62

The histology of the nervous system in *Cyanea lamarcki* and *Chrysaora isosceles*, and in the tentacles of *Actinia equina* and *Tealia felina*, has been studied by the methods of methylene blue and gold chloride. In the jelly-fishes, nerve cells and fibres are most abundant in the sub-umbrellar region close to the sense organs.

The nerve cells are usually bipolar; multipolar cells are infrequent. The cells contain granules (stainable with methylene blue) which extend for a short

distance into the cell processes. There is no differentiation into dendrites and axon, and no neurilemma is present.

The fibres usually appear varicose. The larger varicosities, at least, are due to toxic effects of the methylene blue. The fibres may be thick or thin, the distinction depending on the distance of the fibre from the parent cell. At the cell all the fibres have the same thickness.

The fibres may run parallel, cross each other obliquely or transversely, or commonly one fibre twists itself round another. Where the fibres cross each other they may lie in intimate contact, one of them showing a thickening. Fibres may also lie in close contact with the surface of nerve cells. Sometimes an ending resembling a "bouton" was seen. Intertwining between the fibres is a characteristic and frequently observed relation. Fusion does not occur, no true nerve net being formed. The intertwining and other intimate contacts between nerve fibres and fibres and cells are believed to be of synaptic significance.

Pericellular nerve endings on muscle occur; they are comparable to the endings on unstriped muscle cells in mammals. Neuro-sensory cells were also observed, but the relation of their processes to the general nerve plexus could not be determined.

The present observations confirm the histological work of Schäfer (1878) and Bozler (1927) and correlate favourably with the physiological findings of Pantin (1935). They are not in accordance with those of the majority of observers, whose descriptions have led to the general acceptance of the faulty notion that the coelenterate nervous system is a nerve net. J. A. H.

On the Mantle Cavity and its Contained Organs in the Loricata (Placophora)

By C. M. Yonge

Quart. Journ. Micr. Sci., *Vol.* LXXXI, 1939, *pp.* 367–90

Study of the course of the water currents in the mantle cavity of three species of the Chitonida and one species of the Lepidopleurida revealed that inhalant openings are created anteriorly or laterally by local raising of the girdle. The single exhalant opening is always posterior and confined to the region between the last pair of gills. The exhalant current carries with it the genital and excretory products and, in the Chitonida, the faeces. The functional division of the mantle cavity into inhalant and exhalant chambers is brought about by the bridging of the pallial grooves in the region of the pallial folds by the post-anal (and adanal) gills. Though modified the gills possess the typical structure and ciliation of true ctenidia. They are to be regarded as multiplied ctenidia and not as secondary structures. Four possible tracts of mucous glands in the pallial grooves are concerned with the consolidation of sediment; of these

the pallial tracts are possibly homologous with the hypobranchial glands in the Prosobranchia. Osphradia, possibly homologous with those in the Gastropoda, occur in the majority of the Chitonida; in the Lepidopleurida they are replaced by branchial and lateral sense organs. All are similar in structure and as likely to be concerned with the estimation of sediment as with olfactory functions previously ascribed to them. The Loricata probably evolved between tide-marks, their characteristic structure being admirably fitted for life on the shore.

C. M. Y.

The Protobranchiate Mollusca; a Functional Interpretation of their Structure of Evolution

By C. M. Yonge

Phil. Trans. Roy. Soc. London, B, Vol. CCXXX, 1939, *pp.* 79–147

The Protobranchia represent the one unquestionably natural group within the Class Lamellibranchia. The large foot permits movement into and through a soft substratum. Feeding, except in the modified Solenomyidae, is by means of the palp proboscis which collects organic detritus. In these respects the structure of the Protobranchia probably corresponds closely to that of the primitive Lamellibranchia, the evolution of the palp proboscides permitting retreat of the mouth from the substratum and the enclosure of the body within the bivalve shell. This involved life on a soft substratum, so that the apparently specialized foot is probably primitive for the Lamellibranchia.

The Nuculidae are the most primitive of existing Protobranchia, having an anterior inhalant current, primitive ctenidia essentially respiratory in function, and hypobranchial glands. Conditions are essentially similar in the Solenomyidae, but the ctenidia are enlarged as feeding organs. The Nuculanidae possess highly specialized "pumping" ctenidia forming delicate septal membranes, the filaments being united by complex ciliated junctions to each other and to the siphonal septum. The inhalant current is posterior and siphons occur which in different species show interesting stages in the conversion of ciliary into tissue junctions. Rejection of sediment from the mantle cavity is by cilia, except in the Solenomyidae, where it is brought about by the intucking of the ventral, uncalcified regions of the shell.

The alimentary canal is correlated in structure with the nature of the food particles collected by the palps. There is a dorsal crushing region lined with chitin and a ventral "style-sac" region which secretes mucus. Particles are embedded in this to assist triturition and the formation of faeces. There is no amylase and so no extracellular digestion. The digestive diverticula are organs of intracellular digestion. They consist of paired masses except in the Nuculanidae, where there is an additional mass of wide diverticula opening near the

entrance of the oesophagus, and into which larger particles enter. There are no wandering phagocytic cells. The intestine and rectum are concerned exclusively with the consolidation of faeces.

The nature, interrelationships, systematic position and evolution of the Protobranchia are discussed. C. M. Y.

Fused Neurons and Synaptic Contacts in the Giant Nerve Fibres of Cephalopods

By J. Z. Young

Phil. Trans. Roy. Soc. London, B, Vol. ccxxix, 1939, *pp.* 465–503

A full description is given of the system of giant nerve fibres by means of which *Loligo* produces its rapid movements through the water. The whole system is operated by a pair of very large cells which lie in a hitherto undescribed lobe, the lobus magnocellularis. This lobe contains other large cells controlling the movements of the arms, and thus constitutes a higher motor co-ordinating centre. A peculiar feature of the giant fibre system is that in two places the processes of separate nerve cells fuse completely, contrary to the doctrine of the neuron theory. But in other parts of the system there are synaptic junctions at which it is very clear that no fusion takes place. The neurons between which fusion does occur always work together in life, and the case is therefore the exception which proves the rule of the neuron theory, showing that nerve fibres can fuse, but normally do not do so unless they invariably work together. The whole giant fibre system shows the extreme development of a neuromuscular mechanism for producing movement rather than tonus. Contractions are initiated by the action of the minimum possible number of motor units, and a single impulse is able to set the whole system in action. Such a system, though not well suited for the production of finely graded movements, allows the development of few, large and hence rapidly conducting fibres. The combination of speed with fine gradation of movement is only possible in animals, such as Vertebrates, in which rapid conduction is obtained by thickness or special structure of the myelin sheath, rather than by increased diameter of the fibres. J. Z. Y.

THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM

THE ASSOCIATION was founded in 1884 to promote accurate researches leading to the advancement of zoological and botanical science and to an increase in our knowledge of the food, life, conditions and habits of British fishes. The work of the Association is controlled by a Council elected annually by its subscribing members.

Professor T. H. Huxley took the chair at the initial meeting held in the rooms of the Royal Society and was elected the first President. Among those present were Sir John Lubbock (afterwards Lord Avebury), Sir Joseph Hooker, Professor H. N. Moseley, Mr G. J. Romanes, and Sir E. Ray Lankester who, after Professor Huxley, was for many years president of the Association. It was decided that a laboratory should be established at Plymouth where a rich and varied fauna is to be found.

The Plymouth Laboratory was opened in June 1888. The cost of the building and its equipment was £12,000 and, since that date, a new library and further laboratory accommodation have been added at an expenditure of over £23,000.

The Association is maintained by subscriptions and donations from private members, scientific societies and public bodies, and from universities and other educational institutions; a generous annual grant has been made by the Fishmongers' Company since the Association began. Practical investigations upon matters connected with sea-fishing are carried on under the direction of the Council, and from the beginning a Government Grant in aid of the maintenance of the Laboratory has been made; in recent years this grant has been greatly increased in view of the assistance which the Association has been able to render in fishery problems and in fundamental work on the environment of marine organisms. An account of the Laboratory and the scope of the work undertaken there will be found in Vol. xv, p. 735 of this *Journal*.

The Laboratory is open throughout the year and its work is carried out under the supervision of a Resident Director and with a fully qualified research staff. The names of the members of the staff will be found at the beginning of this number. Accommodation is available for British and foreign scientific workers who wish to carry out independent research in marine biology and physiology. Arrangements are made for courses for advanced students to be held at Easter and in September, and marine animals and plants are supplied to educational institutions.

Research work at sea is undertaken by the steam drifter "Salpa" and by a motor boat, which also collect the specimens required in the Laboratory.

TERMS OF MEMBERSHIP

		£	s.	d.
Annual Members	per annum	1	1	0
Life Members	Composition fee	15	15	0
Founders		100	0	0
Governors		500	0	0

Members of the Association have the following rights and privileges: they elect annually the Officers and Council; they receive the Journal of the Association free by post; they are admitted to view the Laboratory at Plymouth, and may introduce friends with them; they have the first claim to rent a place in the Laboratory for research, with use of tanks, boats, etc.; and have access to the books in the Library at Plymouth.

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