THE FUNCTIONAL MORPHOLOGY AND GENERAL BIOLOGY OF THE BRITISH SPECIES OF VENERACEA WITH PARTICULAR REFERENCE TO VENUS STRIATULA (DA COSTA).

by

ALAN D. ANSELL.

ProQuest LLC.
789 East Eisenhower Parkway
P.O. Box 1346
Ann Arbor, MI 48106 – 1346

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I. General Introduction.

The original plan for this work was to study the general biology of members of the British Veneracea with reference to those factors which determine their spatial and geographical distribution. It was realised however, that this plan could not be adequately achieved in the time available and, therefore, certain aspects of the biology, especially of Venus striatula, have alone been studied.

The work falls naturally into three sections; the first deals with the functional morphology of the adult, the second with breeding and larval development, and the third with certain ecological considerations. In the first section an attempt has been made to bring together the scattered accounts of various aspects of the anatomy of the British species of the Veneracea and to re-examine these in the light of recent views of the functional significance of bivalve structure. Twelve of the seventeen British species have been examined. In the further two sections attention has been limited in the main to a single species - Venus striatula. This is one of the commonest of the British species, and was chosen

for study, partly for this reason, but also because it's range is mainly in the sublittoral zone, the bivalves of which have received less attention than those of the shore.

II. Acknowledgements.

The writer is indebted to Professor C.M. Yonge, C.B.E., F.R.S., for providing facilities to carry out this work and for his constant help and encouragement.

Grateful acknowledgement is also given to Mr. G. Owen, and other members of the staff of the Department of Zoology, Glasgow.

The writer also wishes to thank Dr. C.H. Mortimer, F.R.S. for facilities kindly placed at his disposal at the laboratory of the Scottish Marine Biological Association, Millport, and to express his appreciation to members of the staff there for assistance and encouragement.

The work was carried out while the writer was in receipt of a grant from the Development Commission.

III. The Functional Morphology of the Adult.

1. Introduction.

The Veneracea comprises the three families: the Veneridae, the Petricolidae, and, as has been recently confirmed by Owen (1959), the Glaucomyidae. Of these the Veneridae has sixteen British species (including Mysia undata) representing seven genera, and the Petricolidae one, namely, Petricola pholadiformis, an introduced North American species which has become common in some areas of the British coast (Burton 1957). There are no British representatives of the Glaucomyidae. Members of the Veneracea inhabit every type of soft substratum in all seas and Theile (1934) lists 33 genera. The Veneracea are therefore an important and successful group of eulamellibranchs. This section is based on a study of twelve of the British species including representatives of all British genera except Callista and Irus. The nomenclature adopted throughout is that of Winkworth (1932).

The localities from which the various species were obtained are listed below together with brief notes on their normal habitats.

Dosinia exoleta (L.). Occasional specimens of this species were obtained from various localities near Millport, Isle of Cumbrae, Firth of Clyde. It is recorded from depths from L.W.S.T. to about 50 metres (Haas, 1929-40), but in the Clyde it usually occurs between 10 and 40 metres, on gravelly or stony substrata with some mud.

Dosinia lupinus lincta (Montagu) was obtained from Kames Bay, Millport where it occurs in sand and muddy sand at a depth of 5 - 20 metres. Larger specimens were collected from grounds offshore of the Lion-rock, Isle of Cumbrae, from fine shell gravel with mud at a depth of 10 - 20 metres. Haas (1929-1940) says that this species is found at depths of from 25 to 150 metres. It is generally associated with a finer grade of substratum than Dosinia exoleta.

Gafrarium minimum (Montagu) was obtained from various grounds off the Isles of Cumbrae, together with Venus casina (L.), Venus ovata (Pennant) and Venus fasciata (da Costa). All these four species are found in the Clyde on stony or coarse gravelly grounds with some admixture of mud.

Callista chione (L.). Not examined.

Venus verrucosa (L.). Not examined.

Venus striatula (da Costa) was obtained in abundance from three localities; small specimens were collected from fine sand at a depth of from 4 to 10 metres in Kames Bay, Millport. Larger specimens were obtained from Hunterston Sands, Ayrshire, and from Loch Creran, Argyll, from littoral populations occurring from below L.W.S.T. to just above L.W.N.T. This species is normally found on clean, sandy bottoms although it may be found elsewhere in small numbers.

Paphia aurea (Gmelin) was collected from various places on the shores of West Loch Tarbert, Argyll, and Loch Sween, Argyll, where it occurs together with Paphia decussata fusca (Gmelin). Both species were found in a narrow belt from about L.W.N.T. to just below L.W.S.T. P. decussata is normally found burrowing in coarse gravel, while in the situations described here P. aurea was only rarely found buried. This may be abnormal, however.

Paphia pullastra (Montagu) was collected from the Cross Houses Beach, Millport. The occurrence of P. (= Venerupis) pullastra on this beach and its habitat have been described by Quayle (1952).

Paphia rhomboides (Pennant) was collected in small numbers offshore of the Lion-rock, Isle of Cumbrae,

at a depth of 10 - 20 metres. This is the only species of Paphia occurring in this country which is normally found at depths greater than 10 metres (Haas, 1929-40).

Paphia saxatilis (Fleurieu). Not examined.

Irus irus (L.). Not examined.

Mysia undata (Pennant) was found burrowing in muddy shell gravel at 10 - 20 metres depth off the Isle of Cumbrae.

Petricola pholadiformis (Lamarck). Specimens of this species were kindly supplied from Burnham-on-Crouch, Essex, by Mr. G. D. Waugh, to whom the author wishes to express his thanks.

Where possible drawings have been prepared from relaxed and preserved specimens. Magnesium sulphate, or propylene phenoxytol (Owen, 1955), was used as the relaxing agent. Accurate drawings were prepared first and details of the ciliary currents added later.

Ciliary currents were studied by the use of carborundum powder Grade 3F, carmine suspensions, and, in some instances, suspensions of algae (Phaeodactylum).

Where necessary, sections have been prepared from tissues fixed in Bouin's fluid in sea water and imbedded

in Ester wax (Steedman, 1947). These were stained with Ehrlich's Haemotoxylin and eosin, Azan, or Mallory's Triple Stain.

2. Veneridae.

The Shell.

The shell and hinge teeth of the Veneridae have been described by several authors including Forbes and Hanley (1853) and Jeffreys (1863). In the British species there are normally three well-developed cardinal teeth in each valve, one or more of which is bifid. A low ridge on the anterior side is usually regarded as a reduced lateral tooth, but well-developed lateral teeth are present only in the genus Gafrarium. The descriptions of the hinge teeth of the Veneridae given by Jeffreys (1863) are confusing; those of the left valve being described as the right and vice versa.

Owen (1953a) has discussed the form of the shell in Bivalves and he suggests that growth may be considered as the resultant of three components: (a) a radial component radiating from the umbones and acting in the plane of the generating curve, (b) a transverse component acting at right angles to the plane of the

generating curve, and (c) a tangential component acting tangentially to and im the plane of the generating curve. The resultant shape of the shell is determined by the relative magnitude of these three components. The form of the shell valves should therefore be considered with reference to the outline of the generating curve, the spiral angle of the normal axis (Owen 1953), and the form of the normal axis. Where the three components are all present they combine to produce a shell in which the normal axis is in the form of a turbinate spiral. This is well illustrated by Glossus humanus (Owen, 1953b), but occurs in many groups of Bivalves, including the Veneridae, where the direction of the tangential component is such that the umbones are inclined anteriorly. The effect of this on the ligament will be dealt with later.

The shape of the generating curve depends largely on the magnitude of the radial component around the mantle margin. Asymmetry of the generating curve about the normal axis is increased if the region of greatest marginal increase lies anterior to,

or posterior to, the normal axis. In the Veneridae this effect is greatest in some species of Paphia where the region of greatest marginal increase is situated posteriorly.

The external surface of the shell is covered with a thin, clear periostracum. The details of the structure of the various shell layers have been described by Bøggild (1930).

The ligament and mantle isthmus.

The structure of the ligament in the Veneridae is characteristic and shows little variation from species to species. This account is of the ligament of Venus striatula, but applies equally well to the other species examined. The nomenclature used is that of Owen, Trueman and Yonge (1953) and of Yonge (1957).

The relationship of the ligament, mantle and shell valves is shown in figure 1 (B - H). These drawings form a series taken from the extreme posterior end of the animal to a region anterior to the umbones, as shown in figure 1A. Figure 1A is a dorsal view of the ligament of a decalcified specimen. Figure 2 is a view of the ligament split in the mid-line.

Figure 1.

Figure 1. Venus striatula: Diagrams to show the relationships of the ligament, mantle and shell valves.

A. Dorsal view of the ligament and mantle margin in a decalcified specimen.

B-H. Transverse sections through the ligament, shell valves and mantle. The positions of the sections are shown in A.

AOL. Anterior outer layer.

FL. Fusion layer.

FMF. Fused middle folds.

FOF. Fused outer folds.

IL. Inner layer.

M2. Outermost of middle folds.

MI. Mantle isthmus.

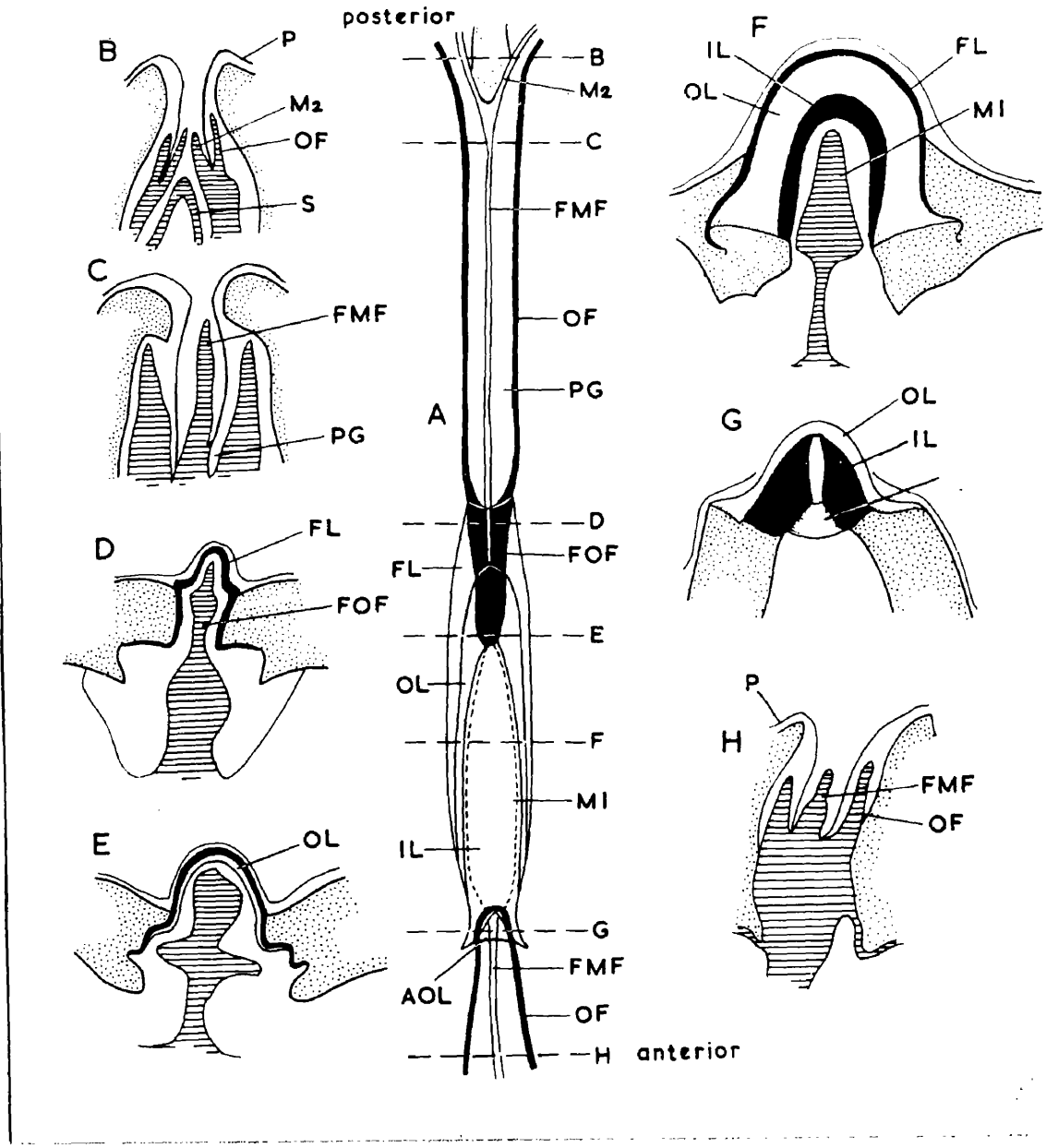
OF. Outer fold.

OL. Outer layer.

P. Periostracum.

PG. Periostracal groove.

S. Siphon.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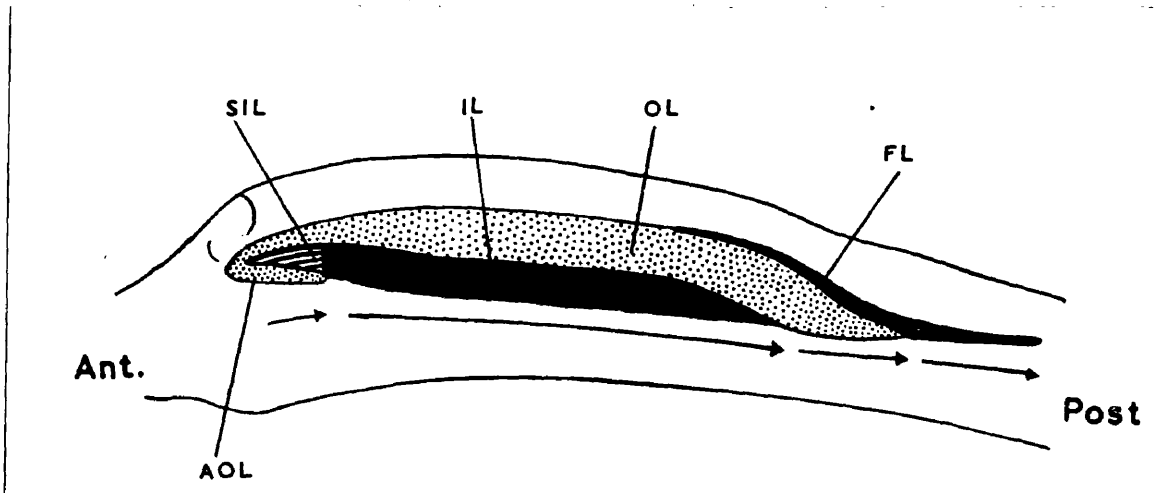


Figure 2. Venus striatula: Diagrammatic vertical longitudinal section of the ligament.

AOL. Anterior outer layer.

FL. Fusion layer.

IL. Inner layer.

OL. Outer layer.

SIL. Split portion of inner layer.

The arrows indicate the direction of growth of each of the layers.

Figure 1B represents a section taken at the extreme posterior end of the animal in the region of the siphons (S). Here the inner folds of the mantle edge and part of the middle folds (see later) are fused to form the siphons while the outer folds (OF) and the remainder of the middle folds (M), on either side of the periostracal grooves, remain separate. Anteriorly the middle folds fuse to form a single median ridge (FMF, figure 1C) lying between the periostacal grooves (PG). This represents the extent of fusion of the mantle edges occurring along the whole of the dorsal edge posterior to the functional ligament; there is no region of periostracal fusion.

Posterior to the ligament (fig. 1D) the outer surfaces of the outer mantle folds fuse (FOF) and a thin layer of conchiolin-like material is secreted from the fused surfaces. This is the fusion layer (FL) which forms a secondary extension of the primary ligament posteriorly (Yonge 1957). As growth proceeds, the fusion layer becomes split in the mid-line over the anterior region of the ligament. The mantle edge immediately posterior to mantle

isthmus secretes additional material on the inner surface of the fusion layer, forming the outer layer of the primary ligament (OL fig. 1E). Finally the inner layer (IL) is secreted by the epithelium of the mantle isthmus (MI, fig. 1F).

Owen (1953b) has discussed the effect of the tangential component of shell growth on the form of the ligament of Glossus humanus, and the same considerations apply here. In bivalves in which there is no tangential component affecting the form of the valves, as in Glycymeris, growth of the mantle/shell anterior to the umbo takes place anteriorly. In the Veneridae, as in Glossus humanus, however, growth of the valves is affected by the tangential component, which, in the region anterior to the umbo, acts in the opposite direction to the radial component. Since the tangential component is stronger than the radial component in this region growth of the mantle/shell takes place posteriorly, with the result that the anterior end of the ligament between the umbones is progressively split as growth proceeds (fig. 1A). Anterior to the umbones there is no fusion of the outer mantle folds and hence no fusion

layer. The mantle edge at the anterior end of the ligament secretes an anterior outer layer between the split portions of the inner layer of the ligament (fig. 1G; AOL).

Apart from these effects the ligament of Venus striatula and of other members of the Veneridae is that of a typical bivalve possessing an external, opisthodetic ligament and is similar to that of Glossus humanus (Owen 1953b). In the Veneridae, as in this genus, the fusion layer is split in the mid-line over the anterior region of the ligament, the ligament is split anteriorly and there is no region of periostracal fusion.

The Mantle Edge and Mantle Fusion.

In the Bivalvia the mantle margins are thrown into three folds (Yonge 1957). The outer fold secretes the two outer layers of the shell. The middle fold is sensory and may carry tentacles and eyes, while the inner fold is typically muscular and controls water movements into and out of the mantle cavity.

The form of the mantle edge in the Veneridae presents some special features in which it differs

from such a typical bivalve. The free mantle margin is split into four folds: a typical outer fold (OF), concerned in secreting the shell and periostracum from its outer and inner surfaces respectively; and three others, the innermost of which is a small, flap-like fold directed dorsally (fig. 4A).

The homologies of these folds with those in other Bivalves may be interpreted in two ways:

Yonge (1957) has suggested that the middle fold of the mantle edge in the Veneridae is duplicated. In this case the inner fold would be here represented by the small flap (fig. 4A, FF). The two middle folds described here would represent the separated inner and outer surfaces of the typical bivalve mantle edge middle fold, the innermost having taken over the function of the inner fold in sealing the mantle cavity. Alternatively, the three outermost folds may be regarded as homologous with the three folds of the typical bivalve mantle edge and the small, flap-like innermost fold as a fold of the inner surface of the mantle similar to those which occur in certain members of the Tellinacea (Yonge, 1949). In the Veneracea, however, they do not inclose a waste canal and have no function in the disposal of pseudo-faeces.

Figure 3.

Figure 3. Diagrammatic stereogram to show the details of fusion of the mantle folds in the Veneracea.

AAM. Anterior adductor muscle.

ESM. Exhalent siphonal membrane.

EX. Exhalent siphon.

FMF. Fused middle folds.

FMIF Fused middle + inner folds.

FOF. Fused outer folds.

IF. Inner fold.

IN. Inhalent siphon.

ISM. Inhalent siphonal membrane.

M1. Innermost middle fold.

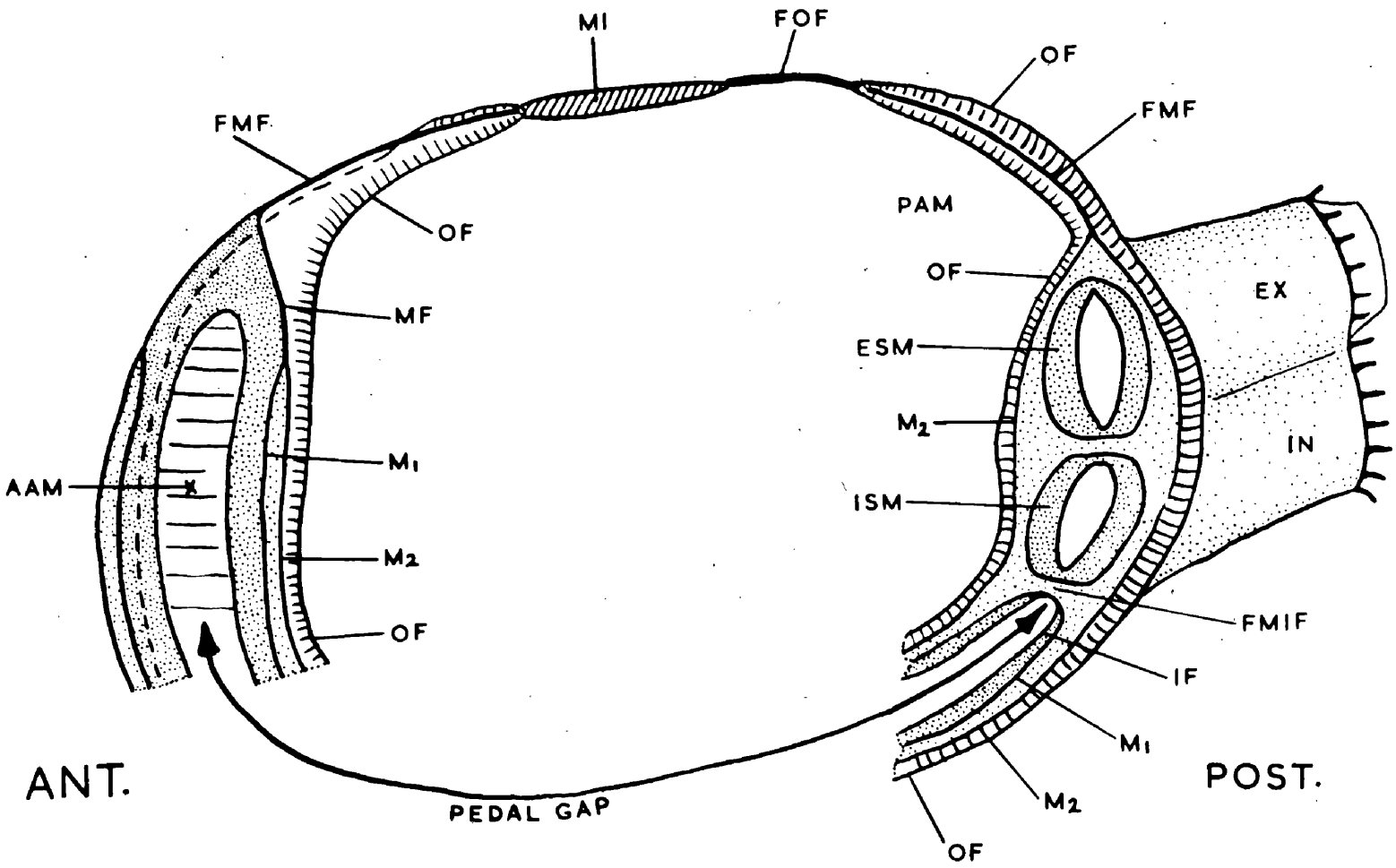
M2. Outermost middle fold.

MF. Middle fold.

MI. Mantle isthmus.

OF. Outer fold.

PAM. Position of posterior adductor muscle.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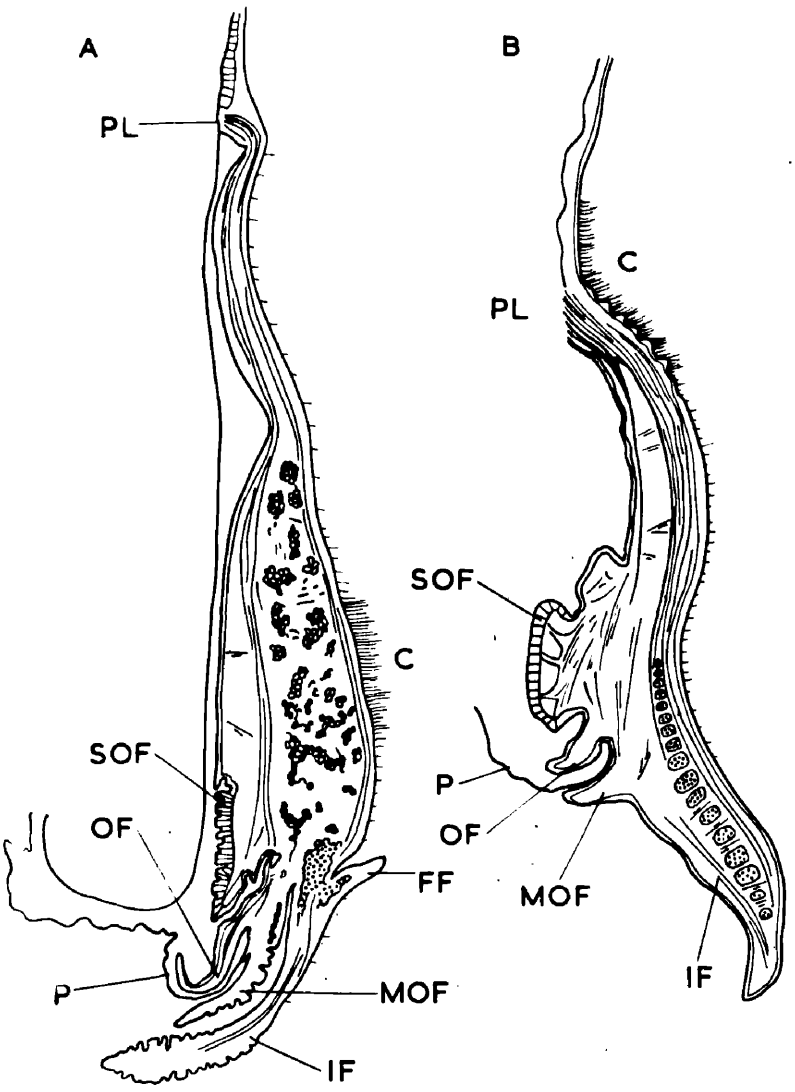


Figure 4. Transverse sections of the ventral mantle margins of A Venus striatula; B Cardium norvegicum.

C. Cilia of the main rejection tract.

FF. Flap-like inner fold.

IF. Innermost middle fold.

MOF. Outermost middle fold.

SOF. Secretory area of outer fold.

OF. Outer fold.

P. Periostracum.

PL. Pallial line.

The details of the fusion of the mantle folds anterior to the pedal gap (fig. 3) suggests that the first of these alternatives is the correct interpretation. The small flap-like folds may be traced around the pedal gap until the folds from either mantle lobe fuse dorsal to the anterior adductor muscle. They clearly differ therefore from the folds of the inner mantle surface in some other bivalves, which do not extend so far anteriorly and never fuse in the mid-line. The fusion of the middle two folds supports the view that they together represent the middle fold of the mantle edge of a typical bivalve, since these two folds on each side fuse together to form a single fold on each side, which then fuses in the mid-line. It appears that the folds must therefore be interpreted as: (1) a typical outer fold (OF), (2) and (3) duplicated middle folds (M1 & M2) representing separated inner and outer surfaces of the typical bivalve middle fold, and (4) a reduced inner fold, the normal functions of which have been taken over by the innermost part of the middle fold.

The fusion of the mantle folds posteriorly to form the siphons is of type B (Yonge, 1957). As in the Solenacea and the Cardiacea, the entire region between the ridge bordering the inner side of the periostracal groove, and the siphonal tentacles is to be regarded as formed from the middle fold of the mantle edge, in this case from the innermost of the duplicated middle folds.

A constant feature of the siphons of the species of Veneridae examined is the presence at the proximal ends of the siphons of valve-like structures - the siphonal membranes. In some species, e.g. Venus striatula (fig. 5A), these membranes are simply low ridges, in others, e.g. Venus ovata (fig. 5B) and Gafrarium minimum, they show much greater development and appear to be capable of closing the inner apertures of both siphons. In Venus casina there is a double ridge at the base of the inhalent siphon. Similar siphonal membranes occur in Pholadidae loscombiana (Purchon, 1955a), Petricola pholadiformis (Purchon, 1955b), and Petricola carditoides (Yonge, 1958). Kellog (1915) recorded similar structures in many

Figura 5.

Figure 5. Drawings to illustrate the form of the siphonal membranes.

A <u>Venus striatula</u>:

Internal view of base of the inhalent siphon.

EX. Exhalent siphon.

FF. Inner fold.

IF. Innermost middle fold.

IN. Inhalent siphon.

MOF. Outermost middle fold.

SM. Siphonal membrane.

SRM. Siphonal retractor muscle.

B <u>Venus ovata</u>:

View into base of the siphons from the mantle cavity.

AP. Anal papilla.

C. Ctenidia.

ESM. Exhalent siphonal membrane.

IF. Inner fold.

ISM. Inhalent siphonal membrane.

M1. Innermost middle fold.

M2. Outermost middle fold.

MC. Mantle cavity.

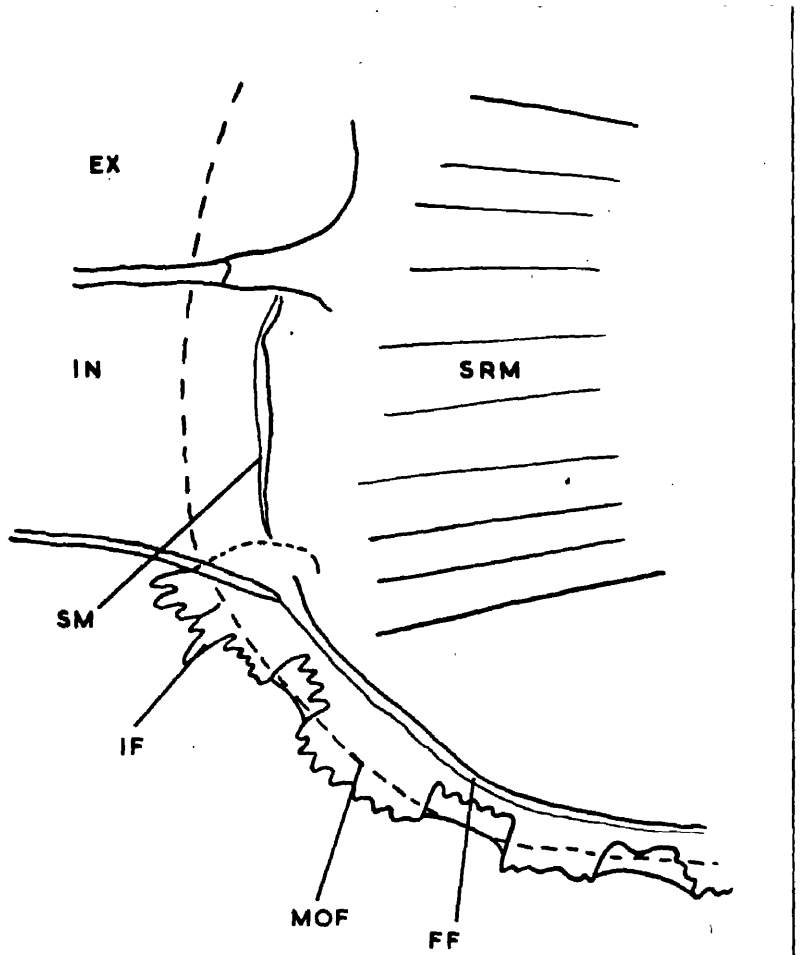
OF. Outer fold.

P. Periostracum.

PAM. Post adductor muscle.

SC. Suprabranchial chamber.

SS. Siphonal septum.


EX
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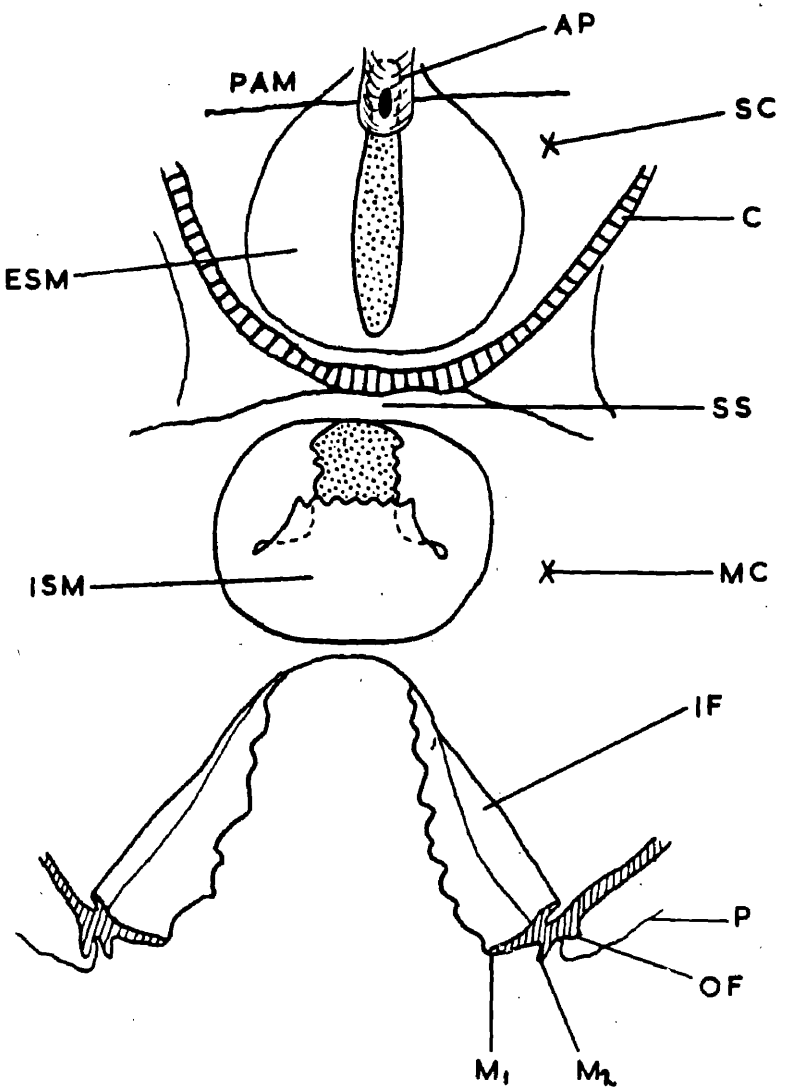
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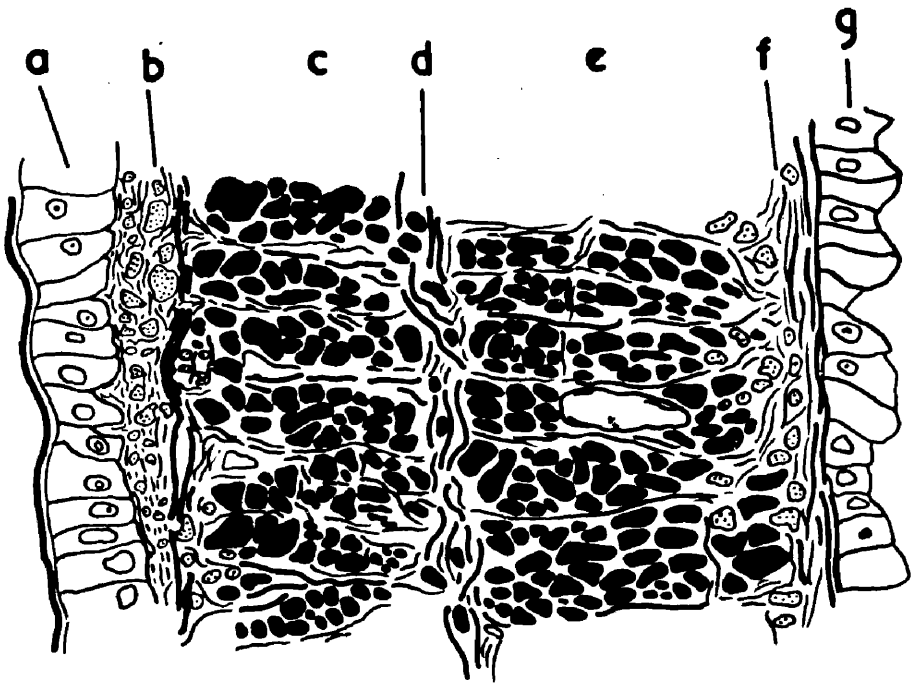


Figure 6. Venus striatula: Diagram representing a transverse section through part of the wall of the siphon.

a. Outer epithelium with thin cuticle.

b & f. Circular muscle, connective tissue, and collagen fibres.

c 5 e. Longitudinal muscle blocks, and radial muscle strands.

g. Inner epithelium.

d. Radial muscle strands.

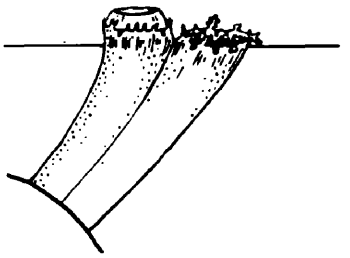
American species, and Haas (1929-40) states that they occur at the bases of the siphons in many groups of bivalves. In some species of the Tellinacea (Yonge, 1948) the inhalent siphonal membrane is associated with a covered waste canal and directs the inhalent current ventrally in the mantle cavity. In the Veneridae, however, the opening between the membranes is normally slit-like, but in some species (e.g. Venus ovata) the membrane may apparently direct the current dorsally. It is probable that the membranes function in controlling the water current passing into and out of the mantle cavity.

The siphons of the species examined are all similar in structure and pigmentation. Figure 6 represents a transverse section through part of the wall of the siphons of Venus striatula. Distinct blocks of longitudinal muscle occur, separated by radial and circular muscles, and other material thought to be collagen fibres. The inner and outer surfaces of the wall are covered by a layer of cubical epithelium, with, on the outer surface a thin cuticle. No trace of mucus secreting cells was seen on the outer surface.

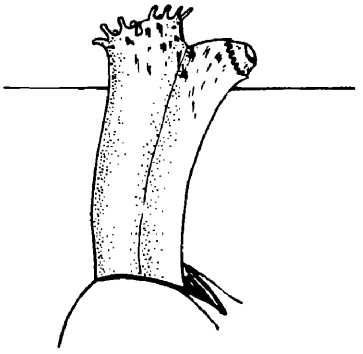
Figure 7.

Figure 7. The appearance of the siphons of some members of the Veneridae. (The species here labelled *Circe minima* is referred to in the text as *Gafrarium minimum*).

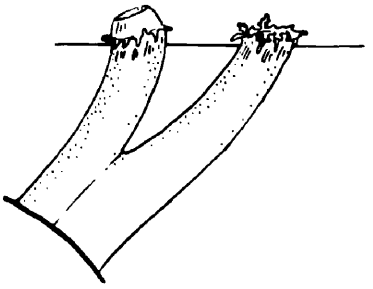
CIRCE MINIMA



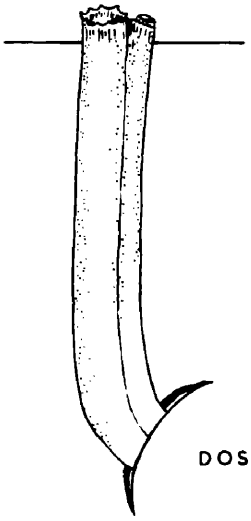
PAPHIA PULLASTRA



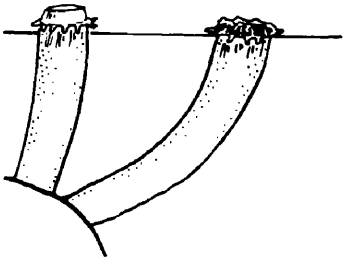
VENUS STRIATULA



PAPHIA AUREA



DOSINIA LUPINUS



PAPHIA DECUSSATA

Near the ends of the siphons irregular patches and streaks of reddish-brown pigment occur in the outer surface. Elsewhere the surface of the siphons is a smooth, creamy white, this appearance being caused by the presence of opaque, white patches on the inner surfaces.

The appearance of the siphons in various species is shown in figure 7. The species vary in the length of the siphons, the extent of fusion, and the development of tentacles around the free apertures, as follows:

Gafrarium. The siphons are short, fused, and extend only slightly outside the shell. The tentacles are well-developed, simple, and sensory in function.

Venus. The siphons vary in length from species to species, being longest in Venus striatula. Tentacles are normally present around both apertures, and are simple and sensory in function. The siphons are fused except for a short region near the tip, which allows the exhalent aperture to be directed at right angles to the inhalent.

Dosinia. The siphons are long and capable of

extension to two or more times the length of the shell. They are fused throughout their length. The apertures are fringed by small papillae only. Paphia. The siphons of the members of this genus are interesting because of the range of variation of form which they show. In Paphia pullastra and Paphia rhomboides the siphons are fused, apart from a small region near the tip. In Paphia aurea the siphons are fused for only half their length, whilst in Paphia decussata the siphons are completely separate. In all species tentacles are well-developed being simple round the exhalent aperture, and pinnate around the inhalent aperture, where they function as strainers as in other suspension-feeding Bivalves.

In all species of the Veneridae the distal end of the exhalent aperture is provided with a valve, or primary exhalent siphon, by means of which the exhalent flow can be confined and directed away from the inhalent aperture.

The differences in form of the siphons reflect important differences in the habitats of the different species. In Venus striatula, Dosinia

lupinus and D. exoleta, the tentacles surrounding the apertures are poorly developed. These three species are found typically in clean, sandy or gravelly bottoms offshore where the amount of detrital material in suspension may be expected to be low. V. striatula occurs in the littoral zone only on beaches which are well sheltered and subject to little wave-action. The remaining species of Venus, and Gafrarium minimum, occur normally on gravelly or stony bottoms with some admixture of mud and organic debris. In these species tentacles are well-developed. Finally the greatest development of tentacles and their use as a straining mechanism occurs in Paphia. The species of this genus, with the exception of Paphia rhomboides, are normally littoral or slightly sublittoral and occur on beaches where considerable amounts of organic debris may at times be brought into suspension by wave-action.

The Organs of the Mantle Cavity.

Topography.

The disposition of the organs in the mantle cavity of Venus casina is shown in figure 8. Detailed description of this and other species is

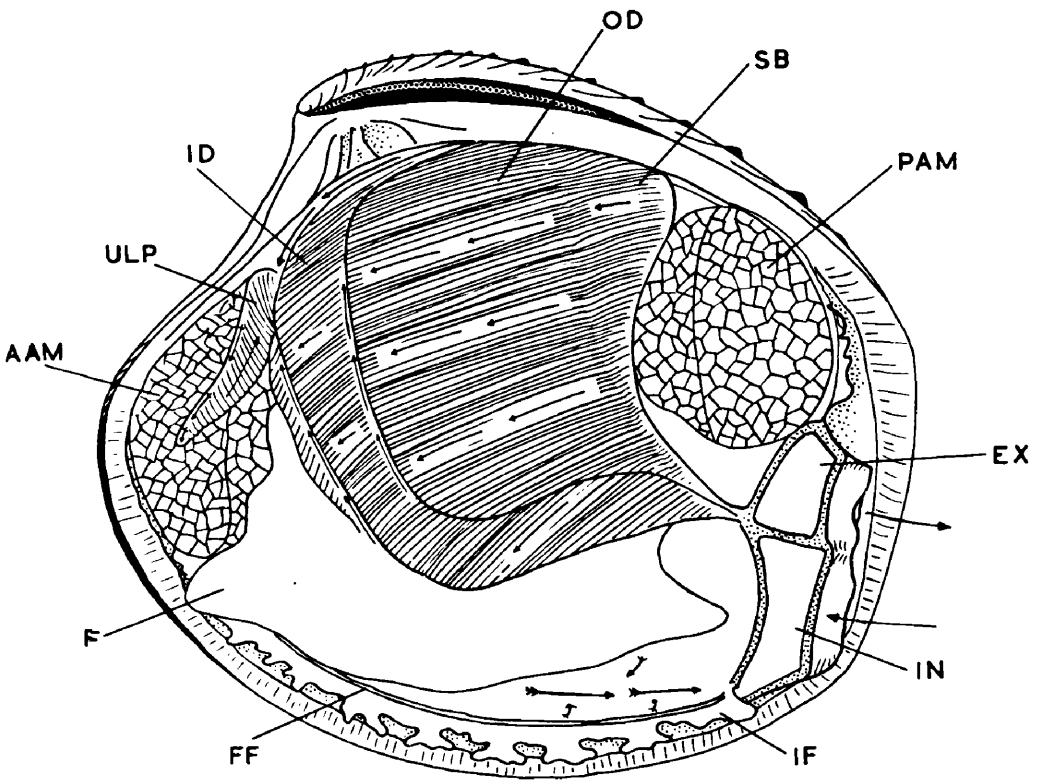


Figure 8. Venus casina: Disposition of the organs in the mantle cavity.

AAM. Anterior adductor muscle.

EX. Exhalent siphon.

F. Foot.

FF. Inner fold of the mantle edge.

ID. Inner demibranch.

IF. Innermost middle fold of the mantle edge.

IN. Inhalent siphon.

OD. Outer demibranch.

PAM. Posterior adductor muscle.

SB. Supra-axial extension of the outer demibranch.

ULP. Upper labial palp.

unnecessary but some points of comparison should be noted.

The outer demibranch of the ctenidia in all species is about half the depth of the inner. A large supraxial extension of the ascending lamella of the outer demibranch is present in all species.

The palps are small in area compared with the ctenidia. This point will be discussed later.

The ventral margins of the mantle are free, forming a long pedal gap. The foot is large and muscular in all genera, but notably so in Dosinia.

The Ctenidia.

The form of the ctenidia and the general course of the currents upon them has already been figured (fig. 8). Ridewood (1903) and Atkins (1937a, 1937b) have described the form of the ctenidia and their ciliation, and present observations confirm their work.

In the Veneridae the inner demibranch is always well-developed and, as already stated, is about twice the depth of the outer. Ciliary currents on both the ascending and descending lamellae of the inner demibranch carry particles to the free edge where they are conveyed forward to the palps by the cilia of the

marginal groove. At the extreme dorsal edge of the descending lamella, particles may be carried dorsally to an oralwards current between the bases of the demibranchs.

On the outer demibranch some variation occurs between species, and even between different specimens of the same species. These variations are in the strength of the current at the free edge carrying particles towards the palps, and in the direction in which particles are moved on the descending lamella (Atkins, 1937b). In general the currents fall into one of the two types shown in figure 9 (A & B) which is based on two of Atkins figures. Paphia pullastra and Paphia decussata have ctenidial currents of type C (2). All the other species examined have currents of type C 1(b) (Atkins, 1937b).

Groups of guard cilia are developed at the free edge of the inner demibranch in all the species examined except Venus striatula, Dosinia lupinus, D. exoleta and Paphia decussata (Atkins, 1937a). These cilia separate the groove into two channels. Fine particles travel safely in the depths of the

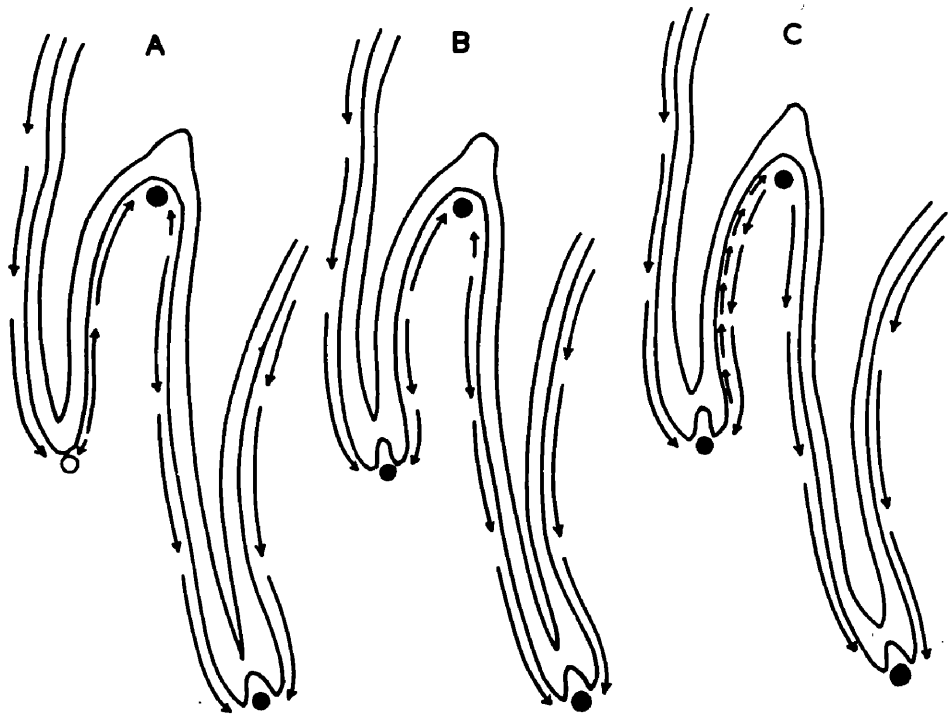


Figure 9. Diagrams showing the form in transverse section of, and the major ciliary currents on, the ctenidia of:

A *Venus*, *Dosinia*, *Paphia aurea*, *P. rhomboides*, *Mysia undata*.

B *Paphia decussata*, *P. pullastra*.

C *Petricola pholadiformis*.

Arrows indicate the direction of major currents, solid circles oralward currents, hollow circles incipient oralward currents.

groove, while larger particles and material bound in strings of mucus travel superficially and may fall off to be rejected by the mantle currents. In the Veneridae there is no clear relationship between the possession of guard cilia and the substratum in which the animal lives, but it is noteworthy that the three species which inhabit the cleanest substrata are three of the species which lack guard cilia.

Towards the posterior end of both demibranchs long cirri are present, beating intermittantly outwards from the marginal groove. Similar cirri are present in many bivalves. They possibly remove large particles or other obstructions from the groove.

In suspension feeding bivalves such as the Veneridae where normally little material enters the mantle cavity with the water current, the primary function of the ctenidia is to maintain a considerable water current and to transfer material to the palps. Sorting by the ctenidia is of secondary importance. The large size of the ctenidia compared with the palps, and the presence of a considerable supraxial extension of the outer demibranch may therefore be regarded as an adaptation for maintaining and filtering a large

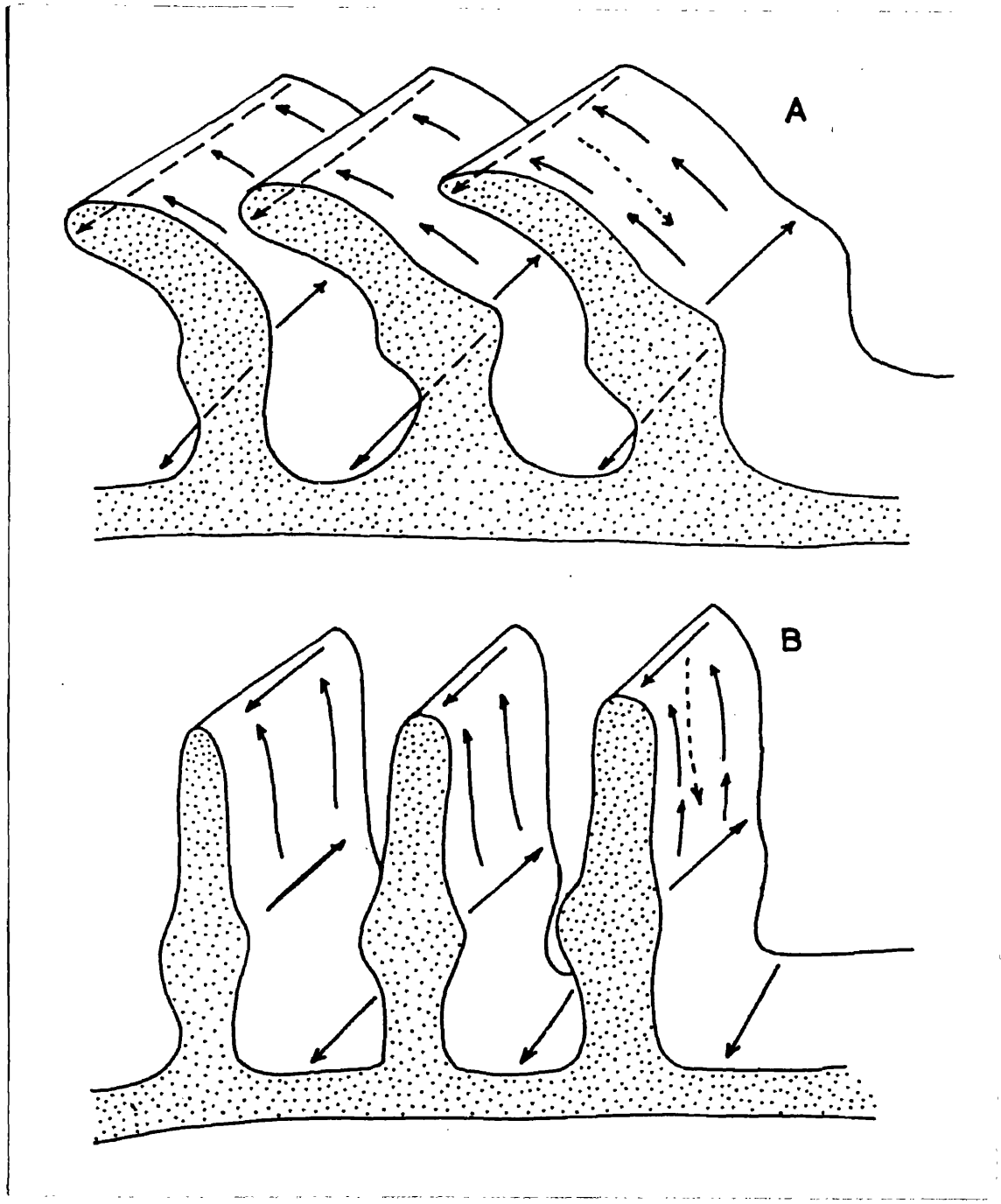


Figure 10. Paphia pullastra: Diagrams to show the main ciliary currents of, and the effect of muscular activity on, the folds of the labial palps.

A Folds relaxed and overlapping, oralwards currents predominant.

B Folds erect, sorting and re-sorting currents predominant.

flow of water. The lack of special sorting mechanism on the ctenidia means that the bulk of material collected is transferred to the palps, the main pathway being by way of the marginal groove of the inner demibranch, since material passing to the edge of the outer readily falls off on to the inner demibranch, or the mantle.

The Labial Palps.

The general structure of the inner ridged surfaces of the labial palps is shown in figure 8. In order to study the currents which occur, the palps were removed from freshly dissected specimens and stretched over small pieces of plasticine after being pinned out in a dissecting dish. Ciliary currents were then studied by application of suspensions of carborundum, carmine, and various algae. The detailed structure of the palps and the ciliary currents, are shown in diagrammatic form in figure 10.

The ciliary currents on the palps can be considered under three headings (Purchon, 1955a): (1) Rejection currents. In all species the main rejection current is on the floor and sides of the lower half of the groove. Here the cilia beat

ventralwards, carrying particles out of the grooves on to the unridged ventral edge where there is a strong current towards the tip of the palps.

(2) Acceptance currents. Oralwards currents occur on the upper half of the folds, carrying particles rapidly forward from fold to fold.

(3) Resorting currents. These occur on the upper halves of the ridges. Dorsalward currents occur on the upper surface of the distal shelf and ventralward currents on the crest of each ridge. These ciliary currents were similar in all the species examined.

In considering the action of the labial palps in sorting food particles, muscular as well as ciliary activity must be taken into account. The palps of the Veneridae are relatively active, two main types of reaction occurring:

(1) The ridges on the inner surface may be erected, or laid flat, (fig. 10). In the erect position the strong rejection currents beneath the distal and proximal shelves in the depths of the grooves are revealed, and the palps exert their full sorting action. When the ridges are relaxed and overlap the

rejection currents and resorting currents are covered and little sorting takes place.
(2) The palps may be contracted into a spiral form bringing the ventral edge with its strong rejection currents into contact with the ridged surface. When this occurs, all the material brought to the palps is caught in the rejection current, carried to the tip of the palp, and rejected on to the mantle.

When small amounts of material are presented to the palps little sorting takes place. The ridges are relaxed and overlap and the majority of particles are carried rapidly oralwards by the exposed ciliary tracts on the upper distal faces of the ridges. Larger amounts of material elicit various degrees of muscular activity resulting in greater efficiency of sorting. With moderate amounts of material the ridges undulate gently exposing the various re-sorting and rejection currents. Large particles fall into the depths of the grooves and are rejected, while smaller particles are carried oralwards bound in mucus. These particles are subjected to the sorting currents and

only a small proportion of them reach the proximal end of the palps. Excessive amounts of material brought to the surface cause the palps to react strongly, as described earlier, by contraction into a spiral form. Under these conditions most, or all, of the material is rejected. The selection of material by the palps appears to be dependent only on the size of the particles and not on their chemical nature.

Material which reaches the proximal end of the palps is carried towards the mouth by the cilia of the proximal oral groove. On the unridged outer surface of the palps the ciliary currents are directed to the dorsal edge, so that material coming into contact with this surface is carried upwards, and around the dorsal edge on to the ridged inner surface.

In considering how far the palps are adapted in each species to its particular way of life three things are important: (1) The complexity of the ciliary currents and the amount of muscular activity, (2) the number and size of the ridges on the inner surface, (3) the relative sizes of the palps and

ctenidia. The ciliary currents and muscular activity of the palps have already been described. All the species examined appear to be similar in respect to these. The palps of Paphia species, however, differ from those of the other genera in being relatively larger and possessing numerous, small, transverse ridges. This difference may be related to the different habitats of these species; the simpler palps of the majority of species being adapted to a sublittoral life with little suspended material entering the mantle cavity. This view has some support from the studies of Purchon on the Teredinidae (1941) and the Pholadidae (1955a), and of Yonge (1949) on the Tellinacea. In the Pholadidae and Teredinidae the palps of "oceanic" species are smaller and possess fewer ridges than those of comparable intertidal species, while of the Tellinacea, Yonge says, "There is a general tendency ... for the palps to be larger in mud-living species where much fine material is taken into the mantle cavity."

The Visceral Mass and Foot.

The foot in the Veneridae is characteristically

large and wedge-shaped, being adapted for burrowing in soft substrata. There is a correspondingly extensive pedal gap. In the adult, the cilia which clothe the foot of the larval stages are completely absent, and there are no ciliary movements on the surface of the foot. Quayle (1949) has described the sequence of digging movements which occur in Paphia (=Venerupis) pullastra. This sequence appears to be similar in many groups of bivalves. In the Veneridae observed, the sequence of digging movements is identical with that described for Paphia pullastra, although differences occur in the timing of the sequence. Greater efficiency in digging appears to be the result of quicker repetition of the characteristic sequence and increase in the number of consecutive movement sequences, rather than of any change in the basic mechanism.

The byssal gland is reduced in most species and is non-functional. In the genus Paphia, however, it is functional at settlement (Quayle, 1953) and sometimes in the adult, the foot of which is provided with a byssal groove.

The ciliary currents on the surface of the visceral mass differ from those of many other bivalves in being directed ventrally and anteriorly, thus moving material falling on to the visceral mass towards the palps. The area which is covered by the inner palp appears to be without ciliary activity. The unusual direction of the ciliary currents of the visceral mass may result in more material reaching the labial palps since any material which is lost from the marginal groove of the inner demibranch may still be carried forward by the cilia of the visceral mass.

Ciliary Currents on the Surface of the Mantle.

In studying the ciliation of the inner surface of the mantle, the visceral mass and ctenidia were removed and the preparation left for some time to allow the pallial muscles to relax. The siphons were never seen to extend in preparations from which one shell valve had been removed, and it was impossible to obtain drawings of the mantle with the siphons extended.

The surface of the mantle is covered with short cilia, the general trend of particles carried by them

being anterior and ventral towards the strong rejection tract lying near the ventral margin and running posteriorly from a point near the anterior adductor muscle to the base of the inhalent siphon. The cilia forming this tract are longer than those of the general mantle surface (fig. 4). Mucus is supplied to the mantle surface by cells situated below the inner epithelium, and opening on to the surface through ducts which run between the cells of the epithelium. The contents of these secreting cells, together with their secretion, which remains as a layer on the surface after fixation, colour blue with Alcian Blue 8GS (Steedman, 1950) - a mucin stain. Masses of pseudofaeces collect at the base of the inhalent siphon and are rejected through it in the normal way by sudden partial closure of the shell valves.

Unciliated areas of the mantle have not been noticed in the species examined except that the surface of the siphonal retractor muscle is without cilia. Cilia are usually absent on areas overlain

by the labial palps. In the Veneridae these areas are small and may have been missed.

Apart from the mucus-secreting cells already described, and secretory cells associated with the formation of the shell and periostracum, the mantle also possesses numerous spaces filled with granular material. These extend in a band near the ventral margin from near the anterior adductor muscle to the siphons. The contents are acidophil, fail to stain with Alcian Blue, and appear to be similar to material occurring in the same position in Glossus humanus (Owen, 1953b). In Venus striatula the contents are discharged through ducts opening between the two middle folds of the mantle edge.

Musculature.

The adductor muscles are inserted into the shell in the normal position ventral to the hinge line. They are sub-equal, the posterior being slightly larger than the anterior, which is inserted slightly deeper.

The anterior pedal retractor muscle is inserted posterior to the anterior adductor muscle. Some fibres radiate over the foot superficially, but the

bulk of the fibres radiate posteriorly in the foot, internal to the posterior retractor muscle. Distally, within the foot, the fibres from either side cross over and mingle.

The posterior pedal retractor muscle is inserted into the shell anterior and dorsal to the posterior adductor muscle. The bundles from either side join below the pericardium and fibres from the right and left cross over. Where it enters the foot the bundles separate again and the fibres radiate anteriorly and ventrally into the foot.

These pedal muscles constitute the extrinsic musculature of the foot (Graham, 1934), and are of constant occurrence throughout the Veneridae. Protractor and elevator pedis muscles are never developed. In addition to the extrinsic musculature, a varying amount of intrinsic musculature is also present in the visceral mass and foot: immediately below the epithelium of the visceral mass and proximal part of the foot, there are a number of circular muscle strands running antero-posteriorly and completely surrounding the visceral mass. In the distal part of the foot a number of fibres run

transversely and in the visceral mass numerous transverse fibres occur, arising in the epithelium and running either to the walls of the alimentary canal or to the opposite epithelium. These fibres are mainly concentrated in bands which pass between the viscera. In particular bands of transverse muscle occur posterior to, and anterior to, the ascending coil of the hind-gut, and anterior to the combined style-sac and intestine.

The Alimentary Canal.

General Structure.

The alimentary canal varies only in minor details in the species examined. A short oesophagus opens into the anterior ventral wall of the stomach, the structure of which is described in the next section. The combined style-sac and intestine passes backwards and downwards towards the heel of the foot. The mid-gut passes from the distal end of this wider tube, coils on the ventral side of the stomach, and then passes backwards to ascend posterior to the style-sac as the hind-gut. The hind-gut passes through the pericardium penetrating the ventricle and posterior aortic

bulb, and passes dorsally round the posterior adductor muscle to end in an anal papilla in the normal way.

Structure of the Stomach.

The structure of the stomach has been studied in living animals using various suspensions of living and non-living matter to trace the course of the ciliary currents. In some cases it was found possible to remove most of the digestive diverticula and other material covering the walls of the stomach, without damage, and thus observe the functioning of the intact organ. These observations have been augmented where necessary by studies of the stomach of living animals opened in various ways. In describing the structure and functioning of the stomach in the Veneridae the nomenclature suggested by Graham (1949) and modified by Owen (1953b) and Purchon (1955a) will be used throughout.

The anatomy of the stomach is in the main similar throughout the Veneridae, so that a description of one species is sufficient, points of difference being noted where they occur. Venus

casina was chosen for study in the greatest detail, mainly on account of its greater size. Graham (1949) has described the stomach of Venus fasciata and that of Venerupis (= Paphia) pullastra.

The stomach consists of the usual two parts (Graham, 1949): a large, globular anterior region, lying dorsally in the visceral mass and a posterior elongated style-sac, with which is combined the intestine. The style-sac opens from the postero-ventral wall of the globular region and lies towards the posterior end of the visceral mass running dorso-ventrally. The style-sac and anterior globular region of the stomach are, therefore, lying at right angles to each other and the crystalline style, which in the intact animal projects into the anterior region, is curved. The appearance of the stomach exposed and opened dorsally is shown in figure 11.

The greater part of the left wall and the roof of the globular part of the stomach is covered by the cuticular gastric shield (fig. 11A GS). Two wings of the gastric shield project into the openings of the dorsal hood (DH) and the left pouch

Figure 11.

Figure 11. Venus casina: Drawings to show the structure and main ciliary currents of the stomach and right and left caeca.

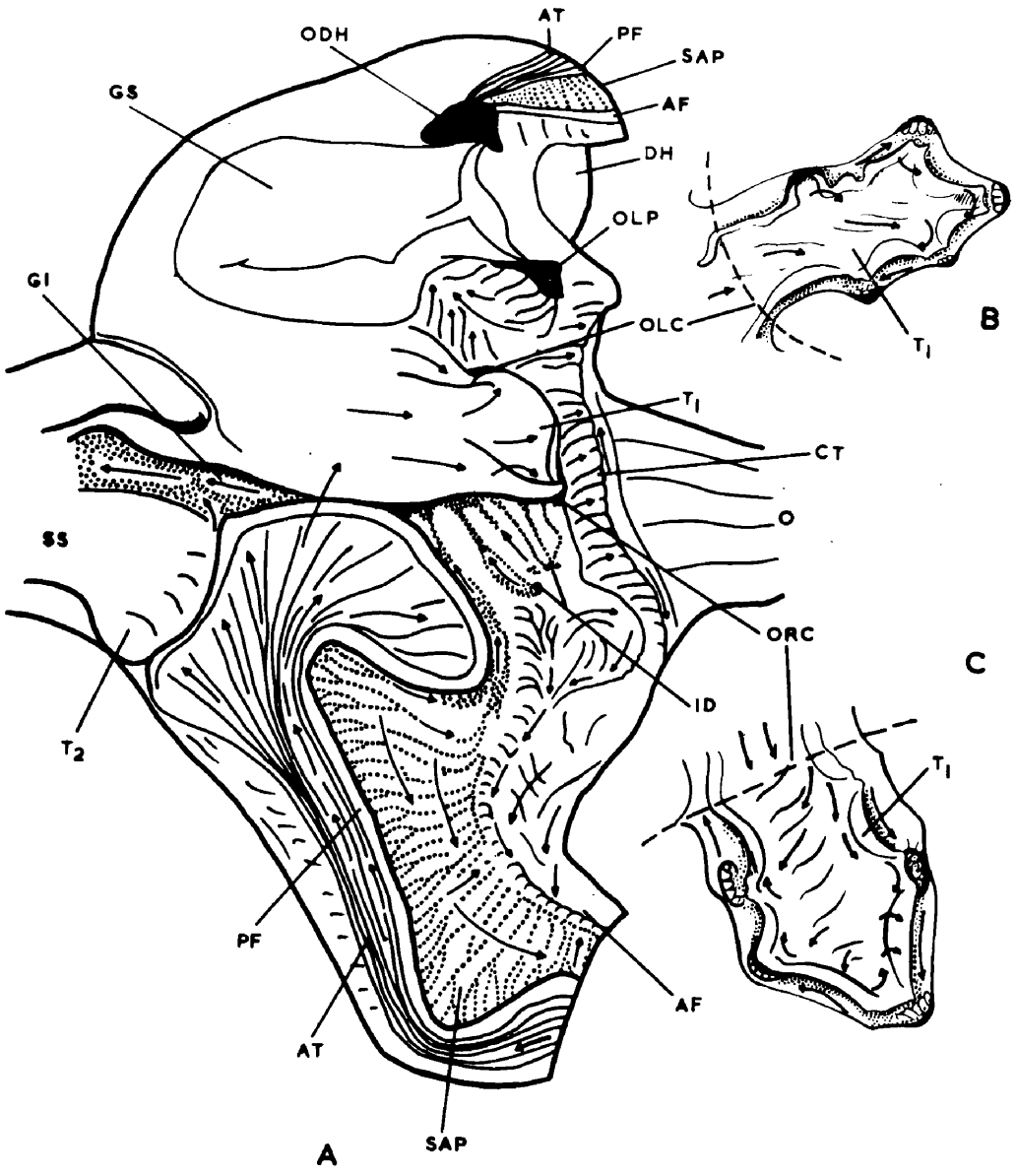
A. The stomach opened dorsally.

B. Left caecum.

C. Right caecum.

AF. Anterior fold.
AT. Acceptance tract.
CT. Circular tract.
GI. Intestinal groove.
GS. Gastric shield.
ID. Isolated ducts from the right digestive diverticula.
O. Oesophagus.
ODH. Opening of the dorsal hood.
OLC. Opening of the left caecum.
OLP. Opening of the left pouch.
ORC. Opening of the right caecum.
PF. Posterior fold.
SAP. Posterior sorting area.
SS. Combined style-sac and intestine.
T1. Major typhlosole.
T2. Minor typhlosole.

Arrows indicate the direction of the main ciliary currents.


AT
ODH
PF
SAP
GS
AF
DH
OLP
GI
OLC
B
T_1
T_1
CT
O
SS
ORC
C
ID
T_2
T_1
PF
AF
AT
SAP
A

(LP) respectively. Along its axis, the gastric shield is strengthened by a low ridge which bears a small tooth at the anterior end.

The oesophagus enters on the anterior ventral side above the openings of the right and left caeca, which lie on either side of the floor of the stomach at its anterior end. Around the opening of the oesophagus there is a low folded ridge, the anterior collecting area. The dorsal hood opens from the right anterior wall of the stomach and curves round over the roof, its tip lying on the left side. The digestive diverticula form a dense mass of greenish-brown tubules around the anterior part of the stomach, into which they open by a series of ducts via the left and right caeca and the left pouch. A number of isolated ducts may also open directly into the anterior region of the stomach. The details of the arrangement of these ducts vary from species to species.

The style-sac and intestine are only partially separated by the major and minor typhlosoles. The major typhlosole lies along the right wall, continues across the floor of the stomach, loops into

the right and left caeca and ends just inside the stomach after emerging from the left caecum. The intestinal groove lies along the right hand side of the major typhlosole throughout its length. The minor typhlosole lies along the left wall of the style-sac and ends at the junction of the combined style-sac and intestine with the globular region of the stomach.

The right wall of the globular region of the stomach, and the walls of the dorsal hood bear a complex system of ciliated ridges and folds, forming the posterior sorting area. This will be described in the section which follows.

Sorting Mechanisms of the Stomach.

The functioning of the Bivalve stomach and digestive diverticula has been investigated and described in detail by Owen (1953b, 1955, 1956). Observations made in the course of the present study confirm these observations made on other Bivalves.

Material entering the stomach from the oesophagus is carried dorsally by the cilia of the circular tract and collects just below the opening of the left pouch (fig. 11 OLP). From here it is

probably transferred to the posterior sorting area by the rotating crystalline style. The action of the crystalline style has not been observed in adults of the Veneridae. In the larva and young bottom stages of Venus striatula, however, the rotation of the style is clockwise when viewed from the anterior end of the animal, and the direction taken by particles of carmine in the style-sac of the adult animal confirms that the rotation is the same here. The direction of rotation is therefore the same as in all other species of bivalve observed. As noted by Graham (1949), the posterior sorting area is well-developed in the Veneridae and lies on the right wall of the stomach extending dorsally onto the floor and sides of the dorsal hood. The movement of the cilia on the ridges and grooves of this sorting area exert a quantitative influence on material in the stomach, fine particles being carried by cilia on the crests of the ridges into the dorsal hood (DH) while coarse particles fall into the grooves and are carried to the main rejection tract of the stomach, the intestinal groove. Within the dorsal hood fine particles pass

into the acceptance tract and are carried across the right wall of the stomach, over the intestinal rejection tract, and on to the floor of the stomach. In this region the intestinal groove is covered by the flaplike major typhlosole (Owen, 1955). Ciliary currents on the floor of the stomach carry material to the openings of the right and left caeca (ORC, OLC). Particles which fail to enter the caeca are carried anteriorly by the cilia of the anterior collecting area and returned to the general circulation of the stomach by way of the circular tract (CT) around the oesophagus.

Within the right and left caeca the major typhlosole has the form of a tube within a tube (Owen, 1955) with extensions into the openings of the ducts of the digestive diverticula. Ciliary currents on the surface of the typhlosole within the caeca serve to retain material but are not directed into the openings of the ducts from the diverticula, (fig. 11 B & C). Similar lack of ciliary currents into the ducts of the diverticula was found in Glossus humanus, Cardium edule and Zirphea crispata by Owen (1955) who suggests that

this is a characteristic feature of the stomach of all Bivalves. This view is further supported by the observations of Purchon (1955a) on the Pholadidae, where the currents on the surface of the typhlosole within the caeca are similarly not directed into the openings of the ducts.

Between the opening of the left pouch and that of the left caecum is a small ridged area. This extends onto the floor of the left pouch, and ciliary currents on the ridges and in the grooves direct particles dorsally to a point just outside the opening the opening of the left pouch and just ventral to the gastric shield. No ciliary currents appear to be directed into the ducts of the digestive diverticula which open into the left pouch.

Waste material from the diverticula, together with the material rejected by the posterior sorting area passes into the intestinal groove and hence to the intestine.

The stomach of the Veneridae therefore has the structure of, and functions as, that of a typical suspension-feeding Bivalve. It is similar in all important respects to that described by Owen (1953b)

for Glossus humanus, and to that of Cardium edule (Owen, 1955b). Within the stomach food material is kept in motion by the combined action of the rotating crystalline style and the ciliated walls, and is subjected to the sorting action of the posterior sorting area. In considering the action of the Bivalve stomach, some workers, and especially Purchon (1955a), have designated as sorting areas any region where the wall bears ridges and grooves, thus implying that such areas exert a quantitative influence on material passing over them. Many of these areas however direct particles indescriminately in one direction only, and can, therefore, have no sorting function, but are collecting areas. In the Veneridae sorting occurs only on the posterior sorting area, where different grades of particles are carried in different directions on the ridges and in the grooves.

The Pericardium.

The heart was studied on living specimens and in specimens fixed in formalin and preserved in propylene phenoxetol, (Owen and Steedman, 1956). This method shows up the structure of the heart

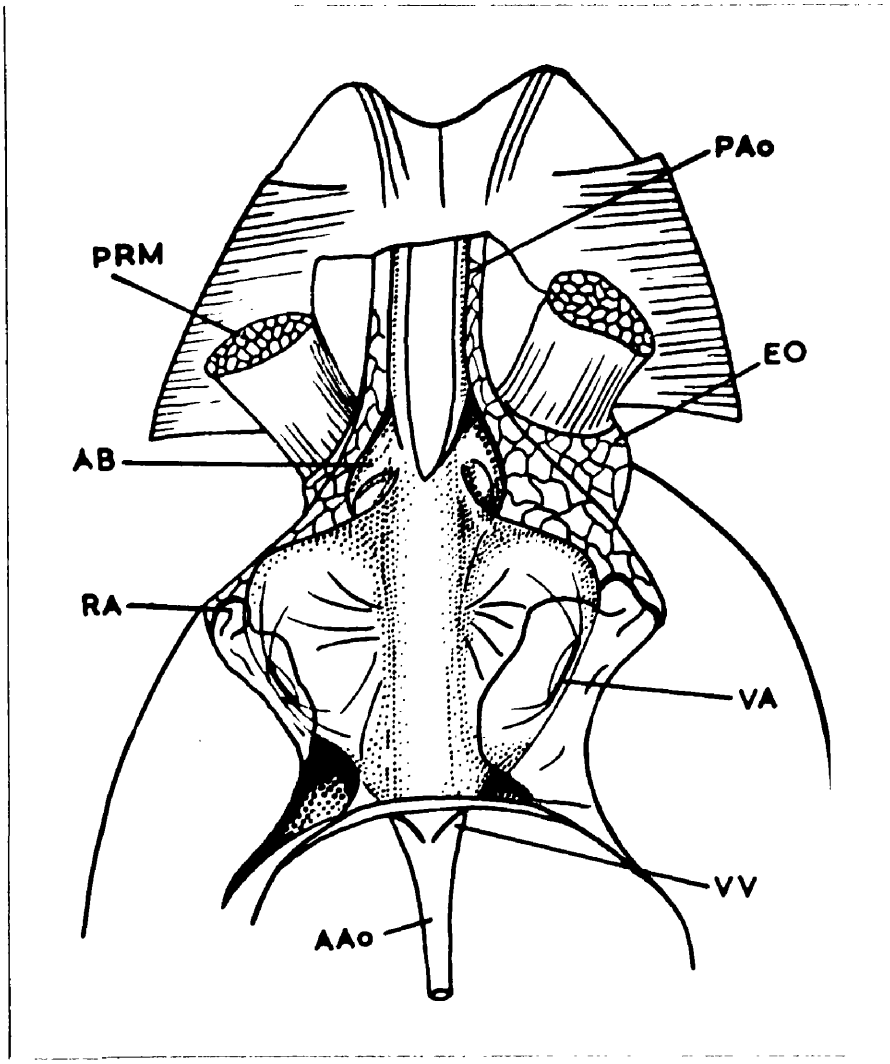


Figure 12. Venus striatula: Dorsal view of the contents of the pericardium.

AAo. Anterior aorta.

AB. Posterior aortic bulb.

EO. Excretory organ - kidney.

LA. Left auricle.

PAo. Posterior aorta.

PAM. Posterior adductor muscle.

VA. Auriculo-ventricular valve.

VV. Valve at origin of anterior aorta.

particularly well.

The pericardium is situated dorsally between the supraxial extensions of the outer demibranchs of the ctenidia. The ventricle (fig. 12) is large and spherical, communicating on either side with the cone-shaped, thin-walled auricles, by way of slit-like auriculo-venticular valves. Anterior and posterior aortae open from the ventricle and there is a large posterior aortic bulb. Blood is prevented from returning to the ventricle from the anterior aorta by a simple, annular valve at the junction of the two. The hind-gut runs through the ventricle and the posterior aortic bulb.

White (1942) has described the position of the pericardial glands in the Bivalvia, including several members of the Veneridae. The pericardial glands may lie either in the pericardial investment of the auricles (auricular pericardial glands), or in the dorsal and ventral anterior regions of the pericardium and neighbouring areas of the mantle (pericardially situated pericardial glands). In the Veneridae the glands occur in both these positions in some species (Gafrarium) while in others they

appear to be restricted to the pericardial situation. In all species, however, the greatest development of the glands is in the anterior region of the pericardium and in the mantle.

The kidneys of the Veneridae lie dorsal to the posterior adductor muscle and are partially overlain by the posterior aortic bulb. The two kidneys communicate by way of a large median aperture. The reno-pericardial pores open into the posterior ventral corners of the pericardium.

The Nervous System.

The nervous system has been briefly studied by dissection in Venus striatula only.

The cerebral-pleural ganglia are of simple, fusiform shape and lie just behind the anterior adductor muscle. The cerebro-pedal connective passes obliquely backwards through the anterior pedal retractor muscle and enters the anterior face of the pedal ganglion. The cerebro-visceral connective penetrates the base of the anterior pedal retractor muscle and then passes back through the tissues of the visceral mass. A large nerve on either side runs round the ventral side of the anterior adductor

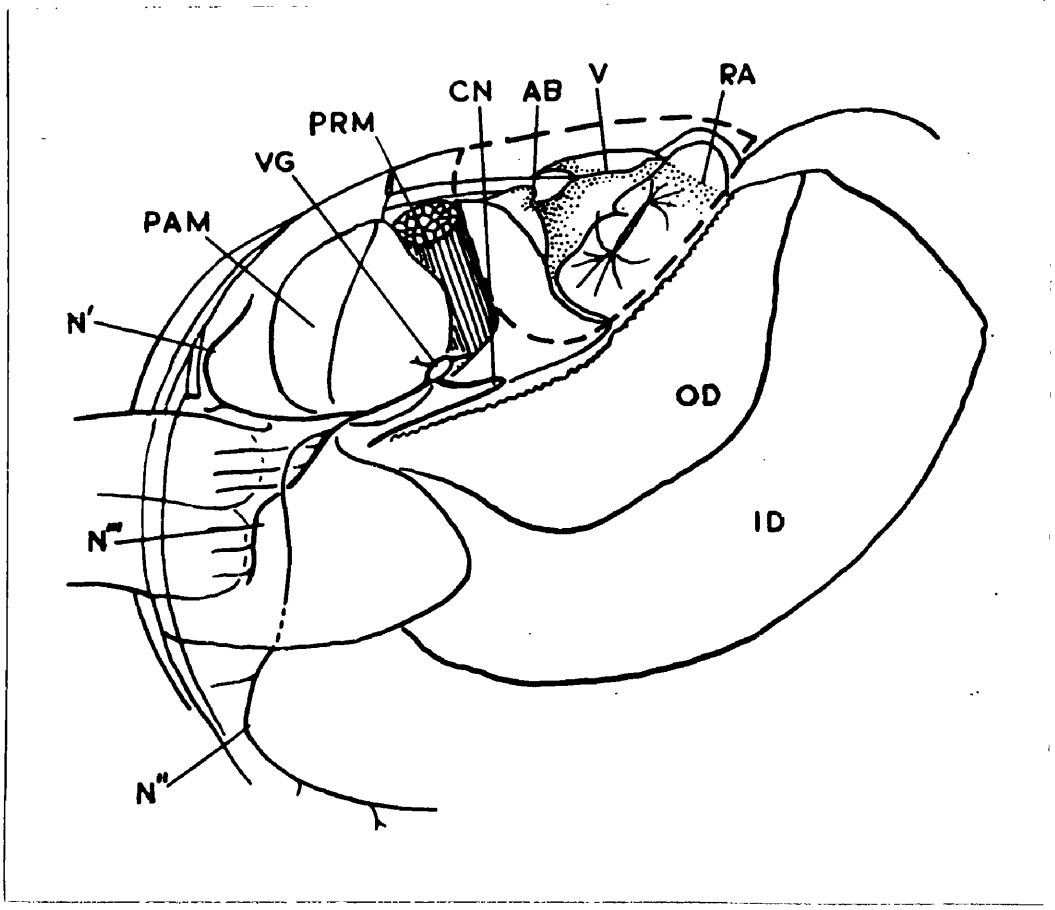


Figure 13. Venus striatula: Lateral view of the contents of the pericardium and of the posterior part of the nervous system.

AB. Posterior aortic bulb.

CN. Ctenidial nerve.

ID. Inner demibranch.

N', N'', N'''. Nerves to mantle and siphons.

OD. Outer demibranch.

PAM. Posterior adductor muscle.

PRM. Posterior pedal retractor muscle.

RA. Right auricle.

V. Ventricle.

VG. Visceral ganglion.

muscle and branches to supply the anterior and ventral regions of the mantle edge. Other nerves run to the anterior adductor muscle and the dorsal region of the visceral mass.

The pedal ganglia are fused to give rise to a large, rounded ganglion which lies in the mid-line just ventral to the coils of the intestine. Two large nerves pass ventrally on each side into the foot.

The visceral ganglia lie at the anterior surface of the posterior adductor muscle. Three main nerves leave these ganglia on either side: a ctenidial nerve, a nerve to the posterior adductor muscle, and a nerve to the siphonal process and posterior part of the mantle. This last named nerve divides ventral to the posterior adductor muscle to give separate branches to various regions of the mantle (fig. 13).

The Reproductive System.

The genital aperture lies on the postero-dorsal surface of the visceral mass, and opens into the epibranchial space above the inner demibranch. In the ripe condition, the gonad occupies most of

the space between parts of the alimentary canal in the visceral mass, but does not extend into the mantle. All the British species are normally unisexual. The development of the gonad, and the breeding of certain species is described later.

(3) Mysia undata

The systematic position of Mysia undata has been the subject of some disagreement in the past, being placed by some authors in the Veneridae, and by others in the Petricolidae. It will therefore be considered separately here and its systematic position discussed.

The shell of Mysia undata is equivalve and inequilateral. The shape is sub-orbicular, the form of the normal axis being a turbinate spiral. The shell is thin and fragile and the periostracum transparent. Internally the adductor muscle scars are well-marked, the posterior being slightly larger than the anterior. The pallial line is distant from the edge of the shell and sinuous (fig. 14). There is a deep pallial sinus, extending about two-thirds of the way to the umbones. The valve margins are not crenulated.

The hinge is well-developed, with three cardinal

Figure 14.

Figure 14. Mysia undata: A. Disposition of the organs in the mantle cavity. B. Internal view of the left shell valve showing hinge teeth.

AAM. Anterior adductor muscle.

EX. Exhalent siphon.

F. Foot.

ID. Inner demibranch.

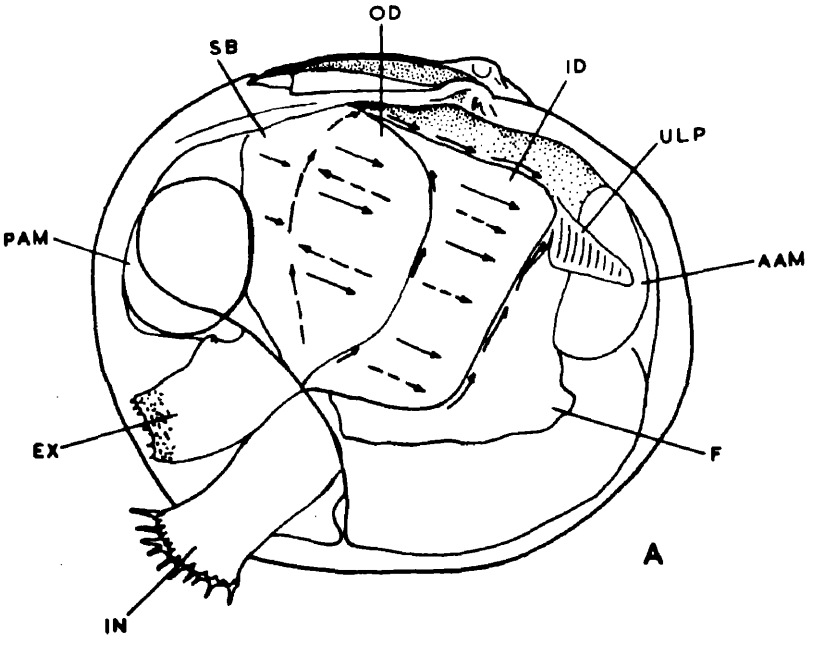
IN. Inhalent siphon.

OD. Outer demibranch.

PAM. Posterior adductor muscle.

SB. Supra-axial extension of outer demibranch.

ULP. Upper labial palp.


OD
SB
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ULP
PAM
AAM
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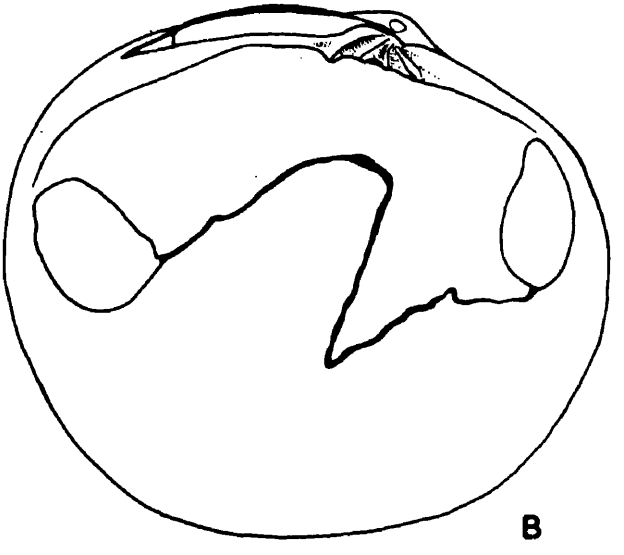

B

teeth in the left valve, the centre one of which is bifid. In the right valve there are two cardinal teeth, the posterior one being bifid. The ligament is identical in structure with that already described for the Veneridae.

The mantle margins are free ventrally forming a large pedal gap through which the well-developed muscular foot may be protruded. Posteriorly the mantle margins fuse to form the siphons, the fusion being of type B (Yonge, 1957). The siphons are long and separate, the exhalent being slightly shorter than the inhalent. The opening of the inhalent siphon is ringed by a double row of simple tentacles, while the exhalent is ringed by a single row of short tubercles. In life the siphons are protuded a little above the substratum and undergo little movement except when disturbed. Mysia undata is a true suspension feeder - a view which is confirmed by the structure of the stomach, which does not differ in essentials from that of the Veneridae.

The organs of the mantle cavity (fig. 14) are similar to those of Venus. The outer demibranchs

Table 1. Comparison of characteristic features of *Venus*, *Paphia*, *Petricola* and *Mysia undata*.

	Venus	Paphia	Mysia	Petricola
Shell	3 cardinal teeth left 3 cardinal teeth right Closes completely not lengthened posteriorly	3 C teeth left 3 C teeth right Closes completely lengthened posteriorly	3 C teeth left 2 C teeth right Closes completely not lengthened posteriorly	3 C teeth left 3 C teeth right Gapes lengthened posteriorly
Siphons	Fused Tentacles simple	Separate or partly fused Tentacles pinnate	Separate Tentacles simple	Separate Tentacles pinnate
Ctenidial currents	C1(b)	C1(b) or C(2)	C1(b)	C(1c)

of the ctenidia are about half the depth of the inner. There is a large supraxial extension. Ciliary currents on the ctenidia are of type C 1(b) (Atkins, 1937b), with well marked oralwards currents at the free edge of the inner demibranch and at the axis of the two demibranchs, and a weak oralwards current at the free edge of the outer demibranch. Guard cilia are present. Ciliary currents on the inner surface of the mantle, the visceral mass, and the palps are similar to those of Venus.

Internally there are no important differences in structure between Mysia and undoubted members of the Veneridae.

In table 1, the characteristic features of the genera Venus and Paphia representing the Veneridae, and of the Petricolidae, are summarised and compared to those of Mysia undata. The characters of the Petricolidae have been taken from the papers of Purchon (1955) and Yonge (1958) on Petricola pholadiformis and Petricola carditoides respectively. As is seen from this table, Mysia resembles the Petricolidae especially in the form of the siphons

and the pallial sinus, but the form of the hinge teeth suggest that this species should be classified with the Veneridae rather than the Petricolidae. The number of hinge teeth is not regarded as important in this connection since, although all other British species have three teeth in each valve, a number of foreign genera occur in which the number of teeth is different. For example Gemma has three teeth in the left valve and two in the right, as does Cyclina (Adams & Adams, 1958).

(4) Discussion.

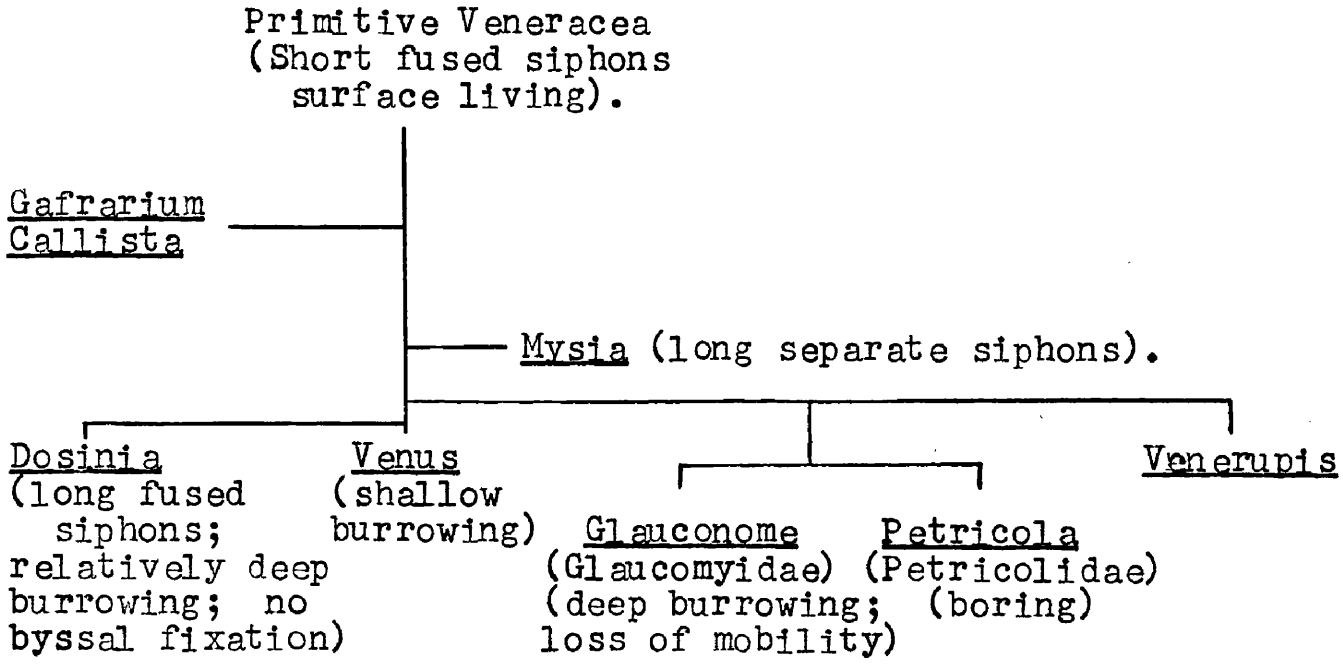
From the foregoing account of the functional morphology of the Veneracea it is clear that within this group the Veneridae form a central family of closely related forms, mostly living close to the surface in relatively soft substrata, and all with a suspension-feeding habit, but without many special adaptations. This lack of special adaptations may itself be connected with the habit and habitat of the animals since under suspension-feeding conditions much of the material entering the mantle cavity is normally utilisable as food, making adaptations of

the ctenidia and mantle, such as are found in deposit feeders, unnecessary. Further Owen (1959) has suggested that many of the adaptations of more specialised suspension-feeders (e.g. Solenidae, Myidae) are connected with a deep-burrowing habit and loss of horizontal mobility, whereas the Veneridae retain their mobility and are, in general, shallow burrowing forms. Among the suspension-feeding Bivalvia the Veneridae may be regarded as a group which have evolved along unspecialised lines although their world-wide distribution on all types of substrata shows that they are none the less highly successful.

In considering the relationships of the Veneracea with other groups of bivalves the most important anatomical features are those connected with the burrowing and the suspension-feeding habits, notably the form of the siphons and foot, and the structure of the stomach. Certain members of the Veneridae such as Gafrarium and some species of Venus have short fused siphons. Such siphons may be regarded as primitive in the Veneracea so that within the Eulamellibranchia related forms

must be sought among these groups with similar siphons. Such groups include the Astartacea, Isocardiacea and Cyprinacea. Of these the Isocardiacea and Cyprinacea show many points of similarity with the Veneracea, especially with the genus Gafrarium.

Within the Veneracea the least specialised condition is found in the genera Gafrarium and Callista, which have short fused siphons associated with a surface-living habit. Only slightly more specialised is Venus, the members of which range from near-surface-living forms, like Venus fasciata, to deeper burrowing forms with longer siphons, such as Venus striatula. Among the other members evolution appears to have taken a number of lines, one possible course being indicated below:



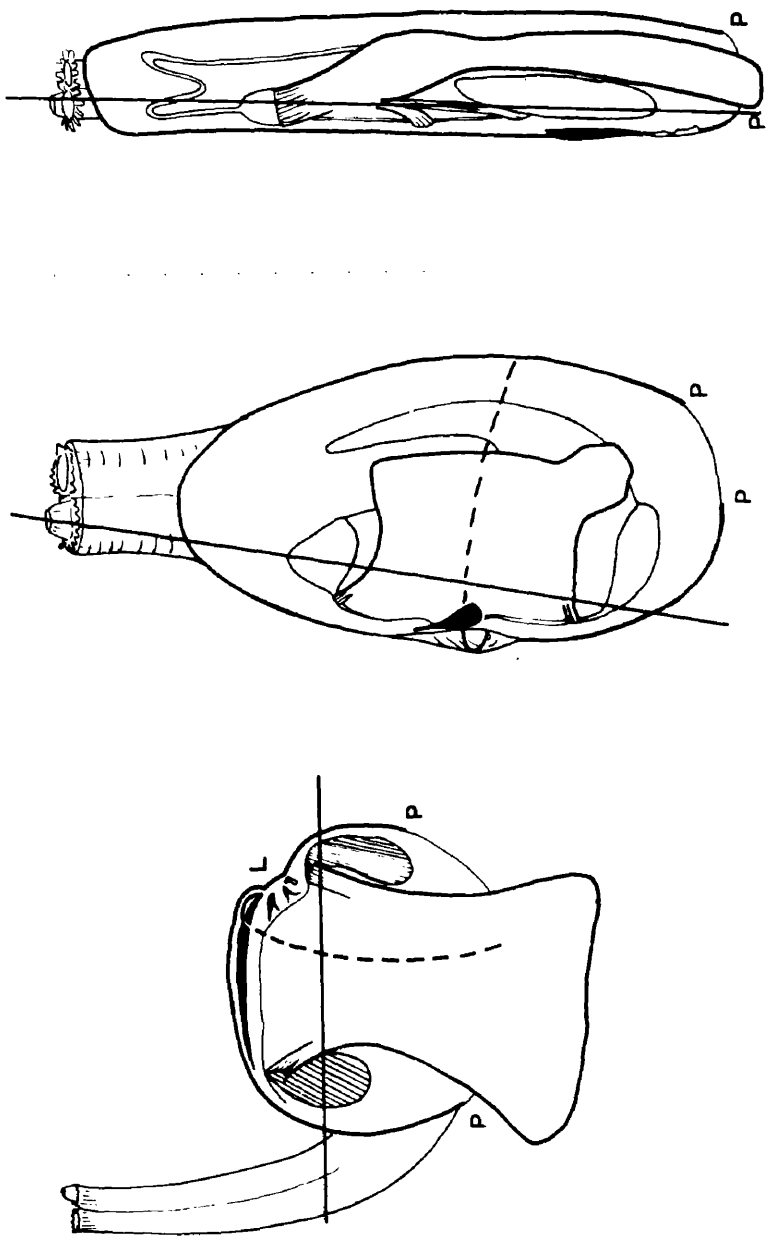
The genus Dosinia has taken a somewhat different course, being adapted for what is a relatively deep burrowing habit when compared with a typical Venerid such as Venus casina. This end point has, however, been reached by a different route from that taken by the other deep burrowers. In these burrowing is associated with elongation of the shell by a shift in the location of the zone of greatest marginal increase away from the region where the demarcation line meets the shell edge. The animals lie vertically in the substratum with the posterior end uppermost. In those genera such as Ensis which move in their burrows the foot is protuded anteriorly. In others such as Mya, the foot is reduced and the animal occupies a permanent position deep below the surface. In contrast to these the shell of Dosinia is almost circular, and lies normally with the ligament more or less parallel to the surface. The foot is protruded ventrally in digging and the anterior and posterior sets of pedal muscles perform equal work in the digging process. Burrowing is possibly assisted by the flattened lunule acting as a pressure plate preventing the animal from moving

Figure 15.

Figure 15. Diagrams to show the normal position in life of A. Dosinia, B. Mya, and C. Ensis. The extent of the pedal gap, the antero-posterior axis through mouth and anus, and the demarcation line are shown.

L. Lunule.

P - P. Extent of pedal gap.


P
P
P
P
L
P
P

upwards as the foot is extended. The normal position of Dosinia in life is shown in figure 15, together with that of Mya and Ensis for comparison.

The two families, the Glaucomyidae and the Petricolidae show the result of divergence from the central venerid type in two different directions, which have recently been discussed by Owen (1959) and Yonge (1958) respectively. Glauconome is adapted by the possession of long, united siphons, extensive fusion of the mantle margins ventrally, and reduction of the foot, to a deep-burrowing life in soft substrata. It presents a further contrast with Dosinia. The Petricolidae, as represented by Petricola pholadiformis (Purchon, 1955) and Petricola carditoides (Yonge, 1958) are adapted in varying degrees to a rock-boring habit, and have long, separate siphons, and ventral mantle fusion. Both the Glaucomyidae and the Petricolidae show special adaptations of the ctenidia allowing them to deal with particles of sand and mud entering the mantle cavity, and both possess shells which are elongated by displacement of the zone of greatest

marginal increase posteriorly. As Owen (1959) has suggested, members of the genus Paphia show features in common with both these groups.

The evolution of the rock-boring habit in the Bivalvia has taken place along a number of lines. Yonge (1951) has suggested that it would appear to have been preceded by specialisation, in some cases for byssal attachment in crevices, or "nestling", in others for deep-burrowing into soft substrata. The first of these is exemplified by Botula and Lithophaga (Yonge, 1955), the other by Platyodon (Yonge, 1951). If the Petricolidae are regarded as evolved from a Paphia-like ancestry, the possibility exists that the boring habit may have been acquired by either of these two routes, since within the genus Paphia both relatively deep burrowing, (P. decussata) and nestling (P. pullastra) forms exist. By nestling is here meant the attachment of the young animal within crevices in rocks by means of a byssus, a process which occurs in Paphia pullastra and may result in abnormal growth due to the restriction of the shell by the surrounding rock.

The Petricolidae are less specialised for the boring habit than are many other groups. Their main adaptations consist of the elongation of the shell posteriorly, the development of sharp ridges on the shell especially at the posterior end, and elaboration of the ciliary currents of the ctenidia. These adaptations are developed to their fullest extent in Petricola pholadiformis (Purchon, 1955), but in other members the link with the genus Paphia of the Veneridae may be seen more clearly. In Petricola lapicida (Otter, 1937) the shell is similar to that of the venerids, (e.g. Paphia pullastra), but with serrations developed especially at the posterior end where they form a rough, jagged border to the shell. Boring is mechanical as in all the Petricolidae, but the burrow is shallow. Otter considers that the opening and closing of the shell valves would be sufficient to enlarge the burrow as growth proceeds. The internal anatomy of Petricola lapicida has not been described in detail and it would be interesting to see how it compares with other members of the Petricolidae, especially in

regard to the ciliary currents of the ctenidia. In the Petricolidae, as in Hiatella (Hunter, 1949) the byssus is not used in burrowing by the adult, as it is in Botula and Lithophaga (Yonge, 1955). The burrowing movements are developed from the normal locomotory activities of the animal and more especially from the cleansing movements of the shell valves. The well-developed hinge-teeth and the long ligament make rocking movements of the shell valves, such as occur in the Pholadidae (Purchon, 1955a), impossible. Thus the evidence suggests that the boring habit of the Petricolidae has been made possible by the previous adaptation of Paphia-like ancestors to a nestling rather than to a deep burrowing habit.

IV. Breeding and Larval Development.

1. Introduction.

The work described in this section is concerned with the breeding and larval development, mainly of Venus striatula.

The study of the breeding cycle was originally undertaken as a preliminary to attempts to identify the larva in plankton collections. However, the small size at which larvae of the Veneridae set and metamorphose makes specific identification from mixed plankton collections difficult, especially in areas where several different species are present together and where the exact spawning periods of the adults are not known. Early attempts to separate types of larvae from such collections were therefore abandoned, and most of the work described here was carried out in larvae cultured in the laboratory from natural spawnings. The study of the breeding cycle was continued, however, for comparison with similar studies by other workers in other parts of the world.

2. The Reproductive Cycle of Venus striatula.

In the early stages of the investigation, the condition of the gonad in individuals was studied by means of sections. For this purpose the visceral mass and foot were removed and imbedded in ester wax (Steedman, 1947). With large specimens a piece of gonad tissue, approximately 0.5 mm square, taken from the side of the visceral mass, was used. Bouin's fluid in sea-water was used as a fixative. Sections were cut at ten or twelve microns and stained with Ehrlich's haematoxylin and eosin. Each block was numbered separately so that further sections could be prepared later if required. This material has been used for the qualitative description of the state of development of the gonads and for the quantitative work in 1957. The labour and time involved in cutting sections limited the number of animals which could be examined in each sample. For this reason the method was dispensed with in later stages of the investigation and the animals were ascribed to the groups described later, on the macroscopic appearance of the gonad and by the

examination of smear preparations. In conjunction with observations of the spawning of animals brought into the laboratory this method gives an accurate estimate of the time and duration of spawning during the year.

Samples for study were taken from the population of Venus striatula in Kames Bay, Millport, described later, which consisted largely of young individuals. Daily temperature records were available for the period covered by the investigation, from Keppel Pier, Millport. These are given in figure 15.

The female gonads were assigned to one of the following three groups:

Stage A. The gonads included in this group were those which were generally unripe, but nevertheless contained some ripe cells. This group therefore included all stages of development from that immediately following spawning to that at which ripe ova predominated. Stage A ovaries were relatively small in volume being restricted to the ventral part of the visceral mass, and the ova were difficult to separate in smear preparations.

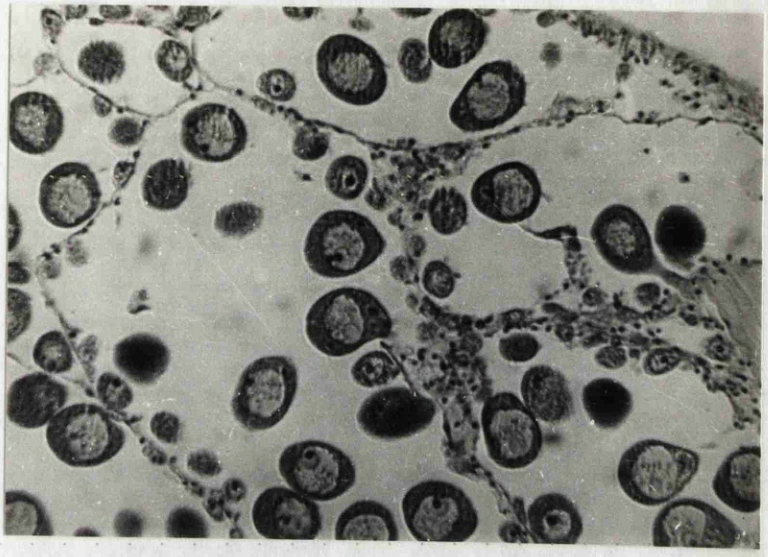
Plate 1.

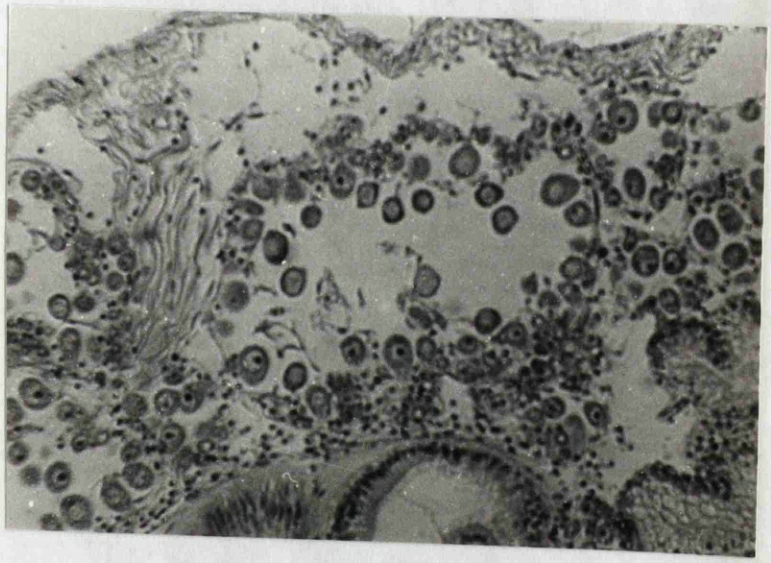
Plate 1. *Venus striatula*: Photomicrographs of sections through the gonad.

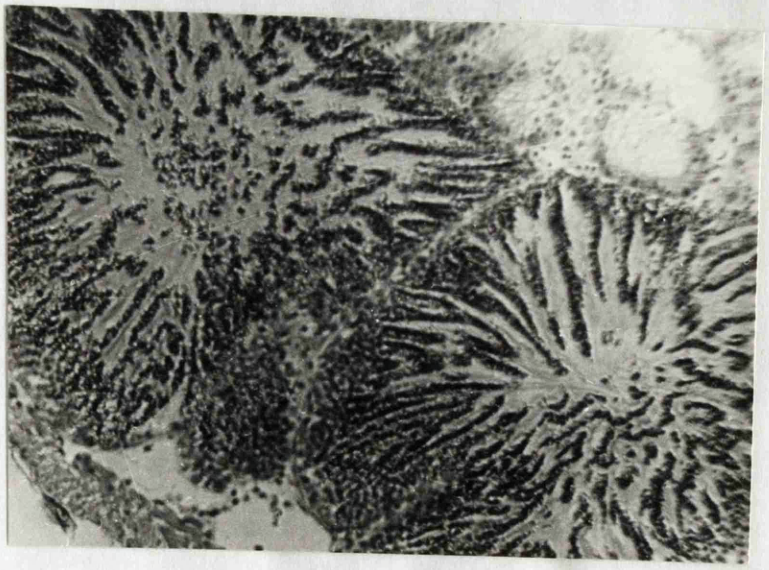
A. Female. Spawned out. August 1957.
Young ovocytes and residual ova are present.

B. Female. Developing. Stage 1. October 1956.
Numerous young ovocytes are present.

C. Male. Developing. April 1957.
The lumina of the follicles contain spermatozoa.







Stage B. The animals in this group were ripe morphologically, but as far as could be told had not begun to spawn. This group may possibly have included some early spawning stages since the discharge of ova in the early stages of spawning may not noticeably affect the ovary.
Stage C. This group consisted of partially spawned animals.

The male gonads were assigned to one of the two groups: ripe or developing, or spawning.

The annual cycle in the female.

The period just before spawning commenced forms a convenient point to begin a description of the annual cycle. During 1957 this condition was reached in late April to early May, when the temperature recorded at Keppel Pier was about 9.0 C. Ripe females were characterised at this stage by extended follicles containing almost exclusively large, ripe ova. The follicles were closely packed, with little connective tissue between them. The ovaries formed a creamy-white area in the visceral mass and extended dorsally and anteriorly over the digestive diverticula. In the fully-ripe

ovary the ovocytes were detached from the follicle wall and occupied the centre of the lumen.

The numbers of females in each stage during the period October 1956, to September 1958, is shown in table 2 and figure 16. Spawning in 1957 began in May and continued into August. The first animals showing signs of spawning appeared in the collection of May 20th. Before this, however, numerous animals had spawned on being brought into the laboratory indicating that the bulk of the population was both morphologically and physiologically ripe. In 1958 spawning took place a little later than in 1957.

In the female, spawning takes place at intervals during the season and is never complete, some residual ovocytes remaining in the ovary at the end of the spawning season. Similar residual ovocytes have been recorded in Venerupis pullastra, (Quayle, 1953), in Venus mercenaria (Loosanoff, 1937), Cyprina islandica (Loosanoff, 1953) and in several other bivalves. In Venus striatula, as in Venerupis pullastra, these residual ovocytes persist throughout the winter and spring without being resorbed. Their

Table 2. *Venus striatula*: Percentage of animals in each stage of the gonad cycle. 1956-58.

	Females					Males					
Date	Dev. I	Dev. II	P.S.?	P.S.	Total ♀	Dev.	P.S.?	P.S.	Total ♂	Total	% ♀
23.10.56	69	31	0	0	13	100	0	0	17	30	43.3
30.11.56	61	39	0	0	13	100	0	0	17	30	43.3
1. 2.57	36	64	0	0	11	100	0	0	19	30	36.7
13. 3.57	28	72	0	0	18	100	0	0	12	30	60.0
3. 5.57	0	100	0	0	24	100	0	0	15	39	61.5
9. 5.57	0	100	0	0	21	100	0	0	20	41	51.2
20. 5.57	0	77	23	0	17	76	16	4	24	41	41.5
22. 6.57	0	18	48	30	22	40	32	24	12	34	64.7
19. 7.57	63	0	0	37	19	40	33	27	15	34	55.9
21. 8.57	100	0	0	0	15	100	0	0	24	39	38.5
26. 9.57	92	8	0	0	25	100	0	0	30	55	45.5
30.11.57	88	12	0	0	25	100	0	0	34	59	42.4
14. 1.58	56	44	0	0	25	100	0	0	17	42	59.5
27. 2.58	60	40	0	0	25	100	0	0	20	45	55.6
21. 4.58	4	96	0	0	20	100	0	0	20	40	50.0
3. 6.58	0	85	5	10	20	94	0	6	13	33	60.6
25. 6.58	0	20	28	52	25	50	31	19	16	41	61.0
15. 7.58	44	0	0	56	25	42	29	29	24	49	51.0
14. 8.58	100	0	0	0	25	100	0	0	28	53	47.2

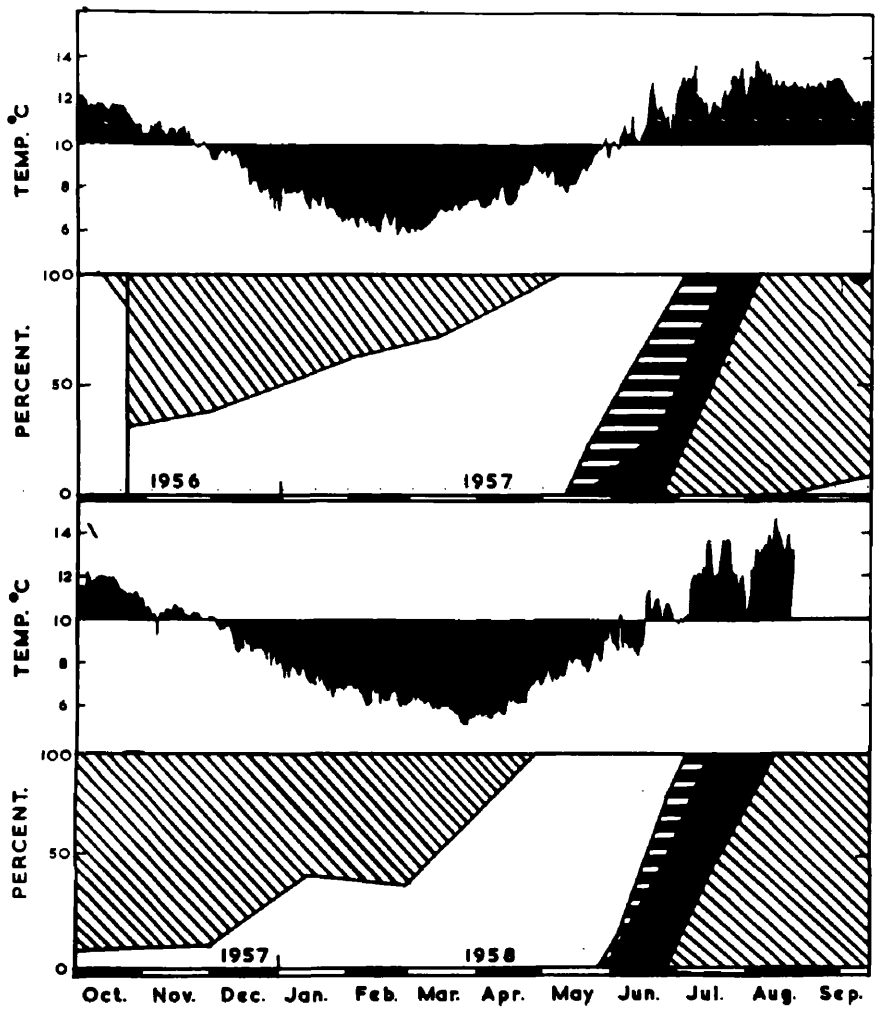


Figure 16. Venus striatula: Diagram to show the percentage of females in each stage of the gonad cycle during the period October 1956 - September 1958. Daily temperatures taken at Keppel Pier are also shown.

Cross-hatched	Development Stage 1.
Unshaded	Development Stage 2.
Horizontally shaded	Spawning?.
Shaded	Partially spawned.

ultimate fate is unknown, but it is probable that they are spawned with the ovocytes of the following year.

The development of young ovocytes in the ovary begins before spawning ends, so that the ovary passes directly from the spawning condition to an early stage of development. Immediately following spawning the follicles may in some cases become filled with vacuolated cells but the follicle walls do not collapse. Development at this stage is rapid and by September some of the animals may have passed into the second stage of development (Stage B) with the follicles filled with relatively large ovocytes. At this time, however, the ovary is still fairly small and restricted to the ventral regions of the visceral mass.

Ovogenesis continues throughout the winter, although at a reduced rate. In late February and early March, development is accelerated and the gonad extends dorsally and anteriorly. The ovocytes continue to increase in size and assume a pear-shaped form with a thin stalk-like attachment

to the follicle wall. By the end of April the ovaries are both morphologically and physiologically ripe.

In 1958 the sea-water temperature as recorded at Keppel Pier reached its lowest point towards the end of March, about a month later than in 1957. In spite of this the development of the gonads followed the same pattern in both years. The proliferation of the gonad which takes place in the months of February and March coincides with the period when the phytoplankton in the water is increasing. At this time the digestive diverticula of the animals take on a deep green colouration, quite distinct from the rather pallid appearance they have during November and December. From the information available from the two years studied it appears that the proliferation of the gonad takes place in response to increased food supply rather than to increasing temperature. Apparently, proliferation of the gonad does not involve the use of glycogen or other material stored throughout the winter, but takes place whenever the amount of food obtained by the animal is sufficient to exceed the amount

required by other metabolic processes. Under these circumstances, an increase in phytoplankton, or an increase in temperature leading to an increased rate of water filtration by the bivalve, would accelerate the rate of proliferation of the gonad.

The cycle in the female consists therefore of a brief period of recuperation following spawning, followed by rapid development of the ovogonia into ovocytes. This development in many cases overlaps the spawning phase. Development of the gonad is continuous until maturity in early May. This cycle is similar to that found in Venerupis pullastra (Quayle, 1948) and to that of many North American species including Venus mercenaria (Loosanoff, 1937) and Paphia staminia (Quayle, 1943). It differs considerably from the cycle in many oysters where a period of fattening follows spawning, and where development of the gonads does not start until the following spring.

The annual Cycle in the Male.

In the male gonad immediately before spawning the follicles are closely packed and are filled

almost exclusively with ripe spermatozoa. These spermatozoa are typically arranged with the heads together forming dense bands within the follicles, an appearance which is particularly noticeable in sections, but also, in some cases in smear preparations. In spawning animals the spermatozoa lie free in the follicles. Spawning apparently takes place at intervals, since animals opened immediately after spawning for some time in the laboratory still contained large numbers of spermatozoa. In some cases the gonads of such individuals were difficult to distinquish from those of fully ripe animals which had not spawned. When spawning is completed a number of spermatozoa are left in the gonad and in fact, ripe spermatozoa may be found at any time of the year. Immediately after spawning there is a development of vacuolated cells in the follicles although the presence of these may be masked by the spermatozoa which remain. Spermatogenesis begins rapidly and by early September the gonads have reached a considerable degree of development with spermatogonia and spermatocytes lining the walls of the follicles and

spermatozoa filling the lumen. Spermatogenesis continues throughout the winter, and the early months of the year are marked by an increase in the volume of the gonad. The animals are ready to spawn in late April.

The cycle in the male is therefore similar to that in the female, with gametogenesis continuous from August to April, although reduced in rate during the winter. As in the female the spring is marked by proliferation of gonadial material which spreads dorsally and anteriorly in the visceral mass.

Sex Ratio.

Of the 765 animals examined in the course of the study of the breeding cycle of Venus striatula, 388 were females and 377 males, showing that the sexes are present in equal proportions. An examination of a large sample of adults of different ages from Hunterston Sands indicated that the sex ratio remains the same at all ages. No hermaphrodite individuals were found.

3. Spawning.

Observations of the spawning of various members

of the Veneridae have been made on numerous occasions. It was found that when the animals were ripe, bringing them into the laboratory was often sufficient stimulus to cause a large percentage to spawn, the stimulus probably being rise of temperature, but possibly also mechanical disturbance. Natural spawnings induced in this way were used as a source of gametes for fertilisations in the larval-rearing experiments described later, and for obtaining information on the breeding season of those species where the annual cycle of the gonad was not followed in detail. These observations, made in the laboratory, also give some information on factors influencing spawning in nature.

In the spawning experiments the animals were brought into the laboratory and placed in filtered sea-water in flat pyrex dishes of about one litre capacity. With Venus striatula, 40 or 50 animals were used in each dish, but with most of the other species animals were used as they became available, usually in fairly small numbers. As far as possible specimens of each species were examined,

monthly. The rise of temperature to which the animals were subjected varied according to the season but was, in general, about 5°C in summer and up to 10°C in winter. The animals were examined at short intervals and any seen to be spawning were removed to separate dishes. The time after the start of the experiment at which each animal started spawning was recorded.

Spawning Period.

The months in which natural spawning was observed in each of the species examined are shown in table 3.

The observations for Venerupis pullastra agree with those of Quayle (1953), who observed this species spawning at Millport during May, June and July, and found larvae in the water during July, August and September. Lebour (1938) records that this species breeds at Plymouth in June and July, and also in September and October. In the North Sea, larvae which were probably of this species (Rees 1950, 1951, 1954, ? Paphia) occurred in the plankton in September, October, November and December. In each case therefore this species

Table 3. Months in which natural spawning was observed in members of the Veneridae.

	J	F	M	A	M	J	J	A	S	O	N	D
Venus striatula	0	0	0	0	X	XXX	XXX	X	0	0	0	0
Venerupis pullastra	0	0	0	0	0	XX	XX	0	0	0	0	0
Gafrarium minimum	0	0	0	0	0	X						0
Venus ovata	0	0	0	0	X	0	0					0
Venus casina	0	0	0	0	X	0	0					0
Venus fasciata	0	X	X	X	0	0	X					0

breeds during the period when the sea temperature is at, or approaching, the annual maximum.

The larvae of Venus striatula occur in the North Sea in September, October and November (Rees 1951, 1954, Venerid B) when the sea temperature is at its maximum. Lebour (1938) states that this species breeds at Plymouth in February, March and May. Jørgensen (1936) has recorded larvae of this species from the Øresund from September 1941 to February 1942 and in August and September 1942. The larvae were most numerous in October and November at about the time when the water temperature was at its maximum.

These two species of the Veneridae for which most information on the breeding season is available, therefore conform with the generalisation of Orton (1920) that species near the lower limit of their geographical range of temperature should breed during the warmer months of the year.

From these observations, it appears that the spawning season of Venus fasciata occurs earlier in the year than that of the other species for which information was obtained, and there is a suggestion

that it may be split into two peaks. However, the number of observations of spawning in this species is insufficient to draw any definite comparison, and the changes in the gonad were not followed.

The Spawning Act.

The sexual products are first extruded into the suprabranchial chamber and are then discharged through the exhalent siphon, being carried by the exhalent stream for some distance. In male Venus striatula the sperm may reach a distance of six to eight cms. from the siphon. The distance depends on the size of the animal and on the strength of the exhalent current. Numerous observations have indicated that this may vary considerably from individual to individual, and in one individual at different times. Shell movements play no part in the act of spawning in any of the Veneridae examined, an observation which agrees with that of Quayle (1953) on Venerupis pullastra and of Loosanoff (1937) on Venus mercenaria. Shell movements are important in spawning only in those bivalves, such as female oysters, in which

the gametes pass through the gills, and where special shell movements associated with spawning are developed from the normal cleansing movements of the shell valves.

Spawning in both the male and the female is repeated at intervals throughout the spawning season, but no precise information on the length of the refractory period has been obtained. Quayle (1948) found that the refractory period in Venerupis pullastra was two to three days in both the male and the female.

Intensity of Spawning at Different Times during the Season.

A large number of observations of spawning were made on Venus striatula, especially during 1958. The results indicate that the intensity of spawning builds up to a peak in the middle of the spawning period and then drops. In figure 16 17 the intensity of spawning in animals brought into the laboratory on different dates is indicated by plotting the number starting to spawn in each half hour period from the start of the experiment.

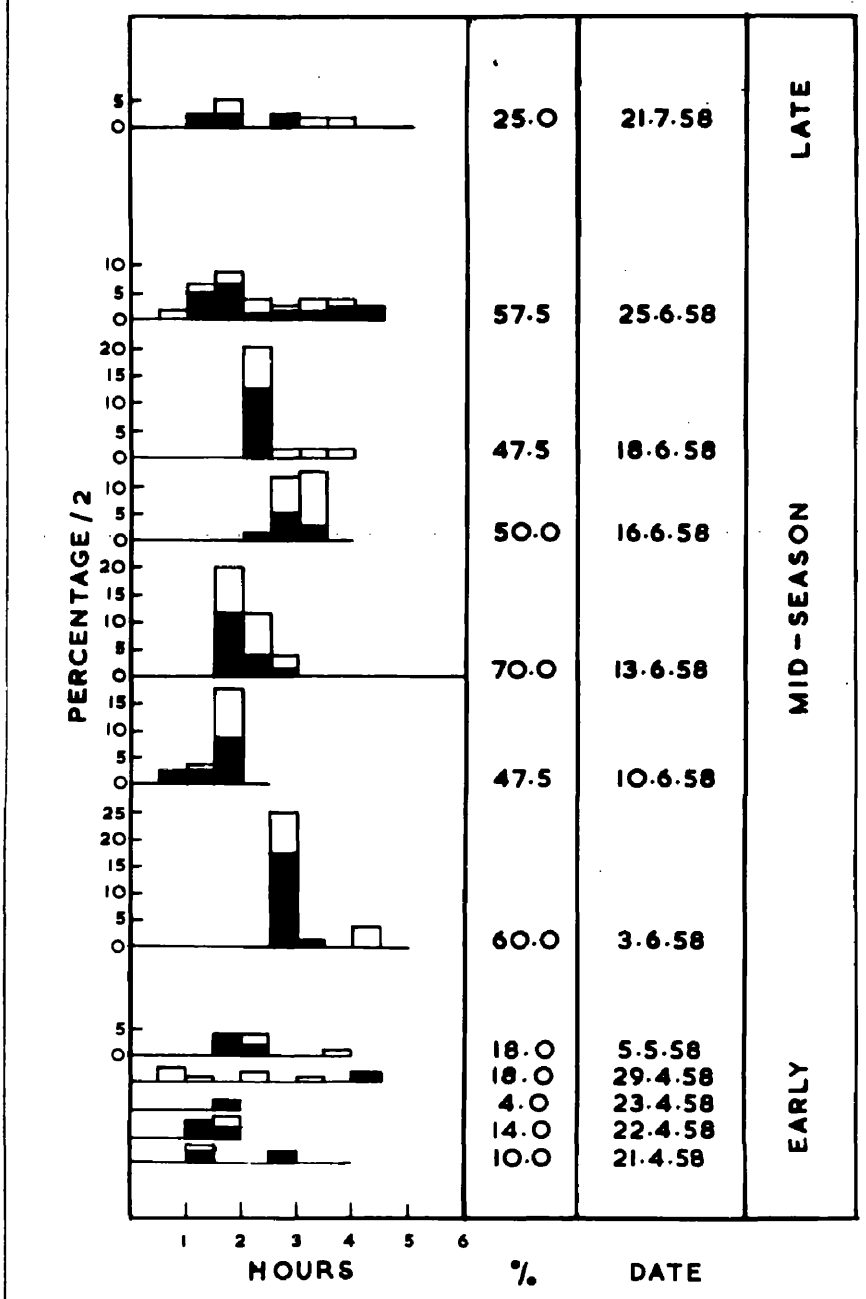


Figure 17. Venus striatula: Diagram to show the intensity of spawning throughout the season. The histograms show the number of animals starting to spawn in each half-hour period from the start of the observations.

Shaded. Males.
Unshaded. Females.

Early in the season the percentage number of animals which were induced to spawn in each group was low, and the time intervals between individual animals beginning to spawn, fairly long. As more animals in the population became physiologically ripe later in the season the percentage spawning rose, and the time intervals became shorter until "epidemic spawning" (Thorson, 1946) took place in most of the samples examined. The factors producing epidemic spawning will be discussed later.

The time which elapsed between bringing the animals into the laboratory (i.e., the stimulating rise of temperature) and the first spawning, varied considerably, but was in most cases between 1.5 and 2 hours (fig. 16). During this period some physiological change must occur in the animals which eventually results in spawning. The nature of this change is unknown. In the female an important change in the eggs takes place between stimulation and the onset of spawning: in the ovary the eggs possess an intact germinal vesicle. Before spawning this breaks down and a maturation division

takes place. The eggs are spawned when this has occurred. If the eggs are removed artificially from the ovary they do not mature, and artificial fertilisation is therefore impossible. The stimulus initiating the maturation division is thought to be a rise in temperature.

Considerable variation occurred in the time pattern of these experiments from day to day, and in different batches of animals collected at the same time but examined at different times on the same day. These variations could not be explained im relation to changes in the conditions of the experiment. In some cases the variation was extreme: some samples giving 50 - 60% spawning while other samples from the same collection gave none. Since these variations occurred in the middle of the spawning period as well as early and late, they cannot be explained by the suggestion that the batches which failed to spawn were unripe physiologically. It seems that there is some other factor affecting spawning in these animals. A series of observations made on June 18th, 1958, suggested spawning might take place with a tidal

rhythm, but later experiments did not confirm this. More experiments are necessary before the factors controlling spawning in these bivalves can be fully understood.

Epidemic Spawning.

The animals in the experimental dishes were exposed to stimulation by sexual products after the first animal had spawned, although each animal was removed as it was seen spawning. Under these conditions "epidemic spawning" occurred, that is, a large number of the animals present were stimulated to spawn in a short time. In many experiments over 50% of the animals present spawned within an hour of the first. Table 4 is a record of such an experiment. The effect of the sexual products in stimulating spawning in bivalves is well established, but the work of Galtsoff (1938, 1940) should be mentioned. Epidemic spawning is the result of continued mutual stimulation between males and females and may, in Venus striatula, be initiated by either males or females. In experiments where the first animal spawning was definitely seen, 13 were started by males and 11

Table 4. *Venus striatula*: Record of typical spawning group, June 13th, 1958.

Sex	Time	Sex	Time	Sex	Time	Sex	Time
♂	3.45	♂	4.02	♂	4.09	♂	4.33
♀	3.46	♀	4.03	♂	4.09	♀	4.34
♂	3.53	♂	4.04	♀	4.12	♀	4.39
♂	3.55	♀	4.05	♀	4.12	♀	4.39
♂	3.58	♀	4.06	♂	4.19	♂	5.10
♂	3.59	♀	4.07	♂	4.20	♀	5.11
♀	4.01	♀	4.07	♀	4.25	♀	5.12

Experiment started 2.12 p.m. 40 animals.

by females.

Critical Spawning Temperature.

In the course of these experiments no animals were found to spawn at temperatures lower than 11°C. Observations on the reproductive cycle of Venus striatula recorded earlier suggest that in nature spawning may take place before the temperature reaches this point, since signs that some animals had spawned were seen when the sea temperature recorded at Keppel Pier, was still at about 9°C only.

4. Identification of the Veliger.

Adult animals collected during the spawning period and placed in flat dishes of sea water in the laboratory usually spawned the same day if ripe, as described earlier. When the animal was seen to be spawning, it was removed from the dish and placed in a separate vessel containing filtered sea-water. This procedure rarely disturbed the animal greatly and spawning usually restarted within a few minutes. Naturally-spawned eggs and sperm were thus obtained relatively free from detritus and other contamination.

Fertilisations were made by adding a little sperm suspension to the egg suspension in a 500 ml. or 1 litre beaker, stirring continuously to avoid polyspermy and to insure fertilisation of all the eggs. The water was changed several times after fertilisation to remove any unfertilised eggs or excess sperm.

The fertilised eggs were kept mainly in two-litre vessels containing water collected from Keppel Pier and filtered through Whatman No. 3 filter paper. For some fertilisations sea-water filtered through a Berkfield bacterial filter was used in an attempt to restrict bacterial growth. The water in the vessels was changed at intervals of a few days.

After the larvae had reached the shelled stage with the gut developed they were fed daily by the addition of a few mls. of a culture of Monochrysis lutheri Droop. When larvae were observed crawling, a small dish of sand was placed in the vessel. Larvae settled in the sand, but some settlement also took place on the glass bottom of the culture vessel.

In cultures to which no sand was added the larvae settled normally on the bottom of the vessel.

Larvae and young bottom stages were observed living and vitally stained with neutral red. For sectioning, the larvae were fixed in Bouin's fluid and imbedded in paraffin or ester wax. Sections were cut at 3μ, 4μ, or 6μ. For the preparation of photographs of the shell, the valves were separated by immersing the larvae in a solution of sodium hypochlorite (Rees, 1950), or in a weak solution of neutralised hydrogen peroxide. As far as possible the valves were cleaned before being photographed, by the use of fine glass needles. The valves were photographed lying flat on a slide as recommended by Quayle (1952). This view gives the true shape of the shell and is more useful for comparison than views of the intact larva where the curve of the shell may cause it to lie at an angle and so give an erroneous impression of the shape.

Description of the Veliger.

Larvae attributed to Venus striatula have been described by Jørgensen (1946) from the Øresund, and

by Rees (1950, 1951) from the North Sea. The identification of the larva by Rees was tentative, but is confirmed by observations made here.

The characteristics of bivalve larvae which are useful for identification purposes are confined almost entirely to those of the shell, in particular, the shape, sculpture and hinge teeth. Colour is generally not a good character, since, as noted by Loosanoff, Miller and Smith (1951) the colour is dependant on the food taken by the larva and may change in a few hours. Also the colour is lost in preserved specimens.

Considerable difficulty was experienced in seeing the structure of the hinge plate in the larva of Venus striatula. It was confirmed however that the hinge was of type C (Rees, 1950) although exact details could not be seen.

The most generally useful characters for the identification of the larva of Venus striatula are the shape of the larval shell and its sculpture. A series of photomicrographs were taken to illustrate these characteristics in larvae of different sizes (Plate 2). Prodissoconch 1 is immediately

Plate 2.

Plate 2. Venus striatula: Photomicrographs to show the shape and sculpture of the larval shell.

A. larva: 85μ.

B. larva: 90μ.

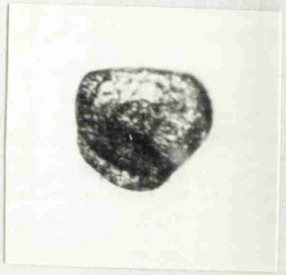
C. larva: 175μ.

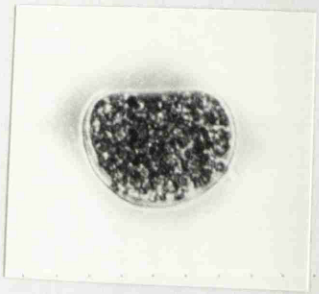
D. larva: 185μ.

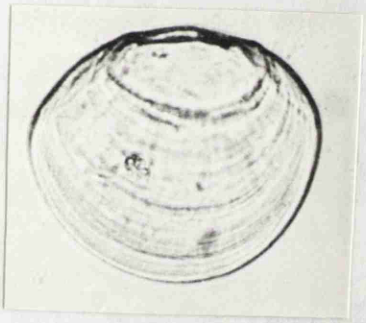
E. larva: 195μ.

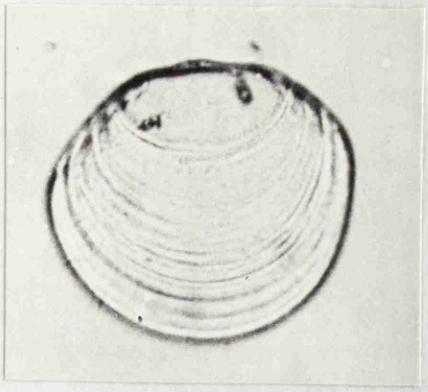
F. spat: 300μ.

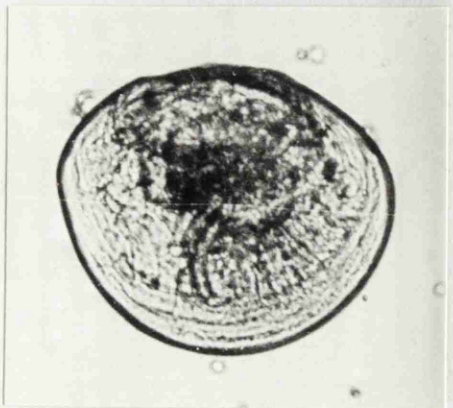
G. spat: 640μ.

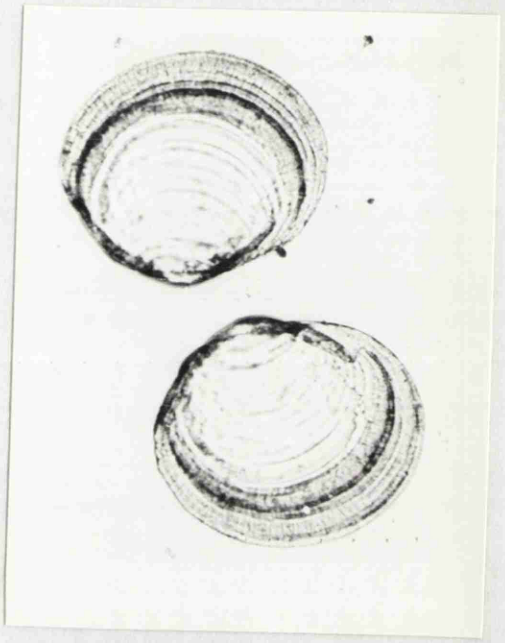


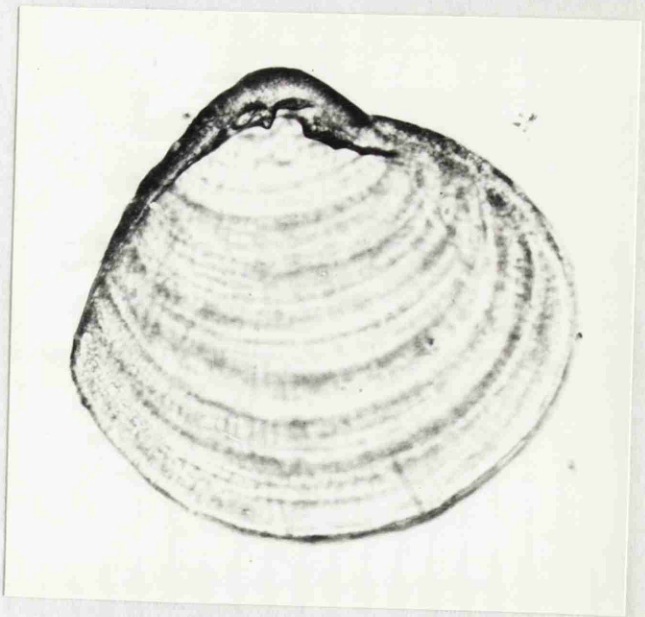












distinguishable from the later formed prodissoconch II. The former bears small, punctate markings and is 90 - 110μ long. Prodissoconch II bears concentric lines of varying degrees of clarity, but most are well-marked. Especially towards the ventral edge, the shell may be of a light, brownish-orange colour.

Setting occurs when the larvae have reached a length of 200 - 220μ, although some larvae may set when only 190μ long. A few remain in the plankton until 280μ long. Jørgensen (1946) found young bottom stages with prodissoconch II, 210 - 225μ long and a single one with prodissoconch II, 280μ long.

Complete success in rearing the larvae through from the fertilised egg to metamorphosis was obtained only in the case of Venus striatula. Natural spawnings were obtained also from V. fasciata, V. ovata, and Gafrarium minimum, and the larvae reared to the straight hinge state. In the case of V. fasciata and G. minimum the larvae were taken to a size of about 160 μ. However, up to this stage, characteristic differences in the larvae were not

obvious enough for useful descriptions to be given. Measurements of prodissoconch 1 showed no significant difference in the relative proportions of height and length.

Development.

The egg is surrounded by a gelatinous membrane within which cleavage takes place (Plate 3). Cleavage is of the typical bivalve type and the trochophore larva is formed within 24 hours of fertilisation. At this stage the gelatinous membrane is shed and the larva becomes free-swimming. The secretion of the larval shell by the shell gland during the second day following fertilisation brings the larva into the straight-hinge veliger stage. Up to this point the source of nutriment for the developing larva has been the yolk stored in the egg, but on the third to fourth day following fertilisation the gut becomes fully formed and the larva begins to feed on nanno-plankton organisms. Growth is then continuous until settlement.

5. Effect of Temperature on Growth of the Larva.

Numerous authors have made general statements concerning the effect of temperature on the rate

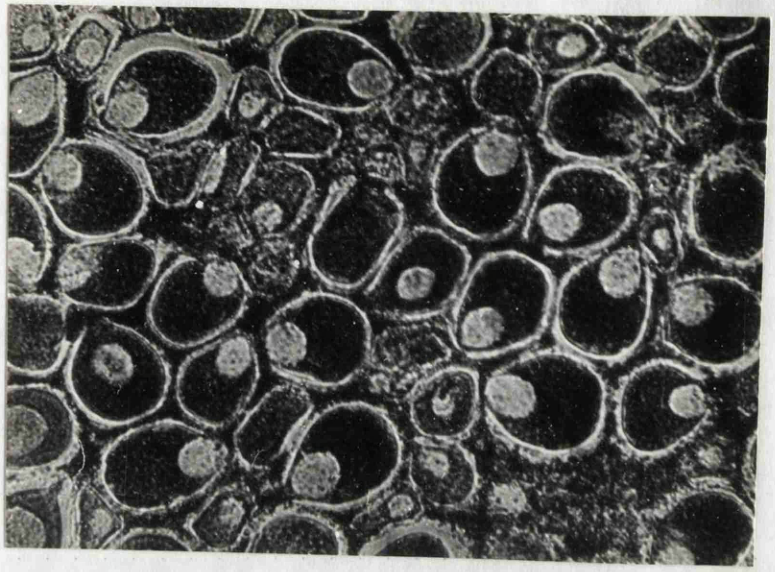
Plate 3.

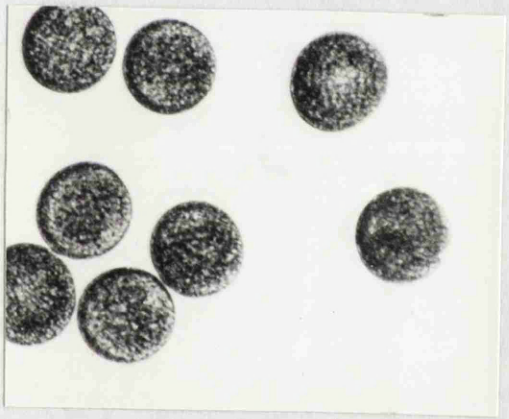
Plate 3. Venus striatula:

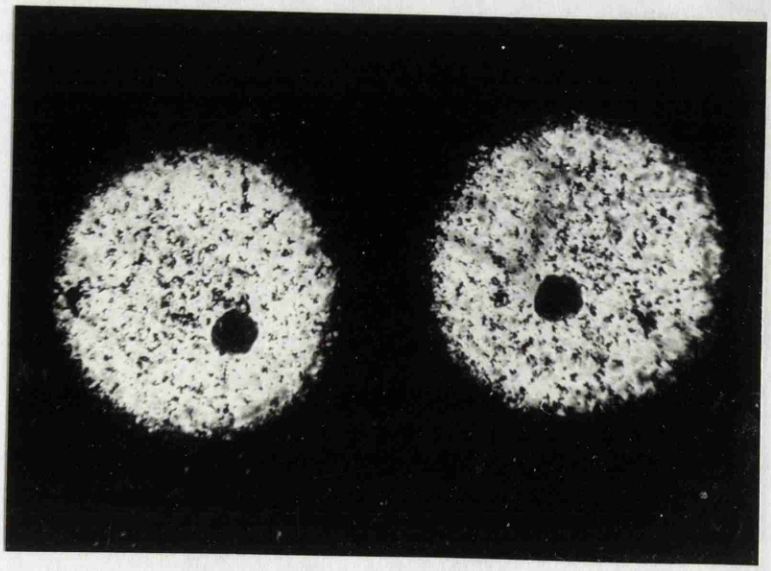
A. Photomicrograph of smear preparation of ripe female gonad. Note the germinal vesicle.

B. Photomicrograph of eggs obtained from natural spawning. No germinal vesicle is present.

C. Photomicrograph of developing eggs mounted in a suspension of carbon black to show the large surrounding gelatinous sheath.







of development and growth of bivalve larvae, but few of these have been based on experiments in which the conditions were controlled. Korringa (1941) states that larvae of Ostrea virginica require thirteen days at 23.0 - 25.0°C, fifteen days at 21.0 - 22.0°C, and seventeen days at 20.0°C for development to the setting stage. The same author also states that the pelagic stage in Ostrea edulis lasts six days at 22.0 - 23.0°C, seven days at 21.0°C, twelve days at 19.0°C and fourteen days at 16.0°C. Medcoff (1939) concluded that larvae of Ostrea virginica require 24, 26 and 30 days to reach maturity at temperatures of 21.0, 20.0 and 19.0°C respectively. Recently Loosanoff, Miller and Smith (1951) have thoroughly investigated the effect of temperature on growth and setting of the larvae of the clam, Venus mercenaria in laboratory cultures, and have shown that at 30.0°C setting began as early as seven days after fertilisation, at 27.0°C - nine days, at 24.0°C - eleven days, at 21.0°C - fourteen days, and at 18.0°C - sixteen days.

The bulk of these observations were made on

species which develop at relatively high temperatures compared with those at which many British bivalves develop. Little information is available on the rate of growth of larvae which normally occur at temperatures in the range of 10.0°C - 16.0°C or lower, and it is thought therefore that the results obtained here on the rate of growth of the larvae of Venus striatula, although incomplete in some respects, may be usefully recorded.

Eggs and sperm of Venus striatula were obtained in the laboratory as described earlier. Fertilisations were made and the larvae allowed to develop at room temperature (about 15.0°C) for two days, that is until the veliger stage was reached and the larval shell had grown to length of 100 - 120μ. The larvae were then divided at random between the eight 600 ml. beakers which were used during the experiment, to give a density of about 10/ml. in each vessel. Throughout the experiment, the sea-water present in the vessels was removed every second day through a stainless steel mesh filter, and fresh sea-water added.

The sea-water used was collected from Keppel Pier, Millport, and filtered through Whatman No. 3 filter paper to remove the larger planktonic organisms and debris.

To obtain a range of temperature, a large galvanised iron bath, divided into ten separate compartments by iron sheets, and containing fresh water, was used. The temperature at one end of this bath was controlled at 30.0°C by means of a heating coil, stirring unit, and thermostat, and at the other end a temperature of 5.0°C was maintained by means of a thermostatically controlled refrigerating coil. Each compartment was stirred individually by a stream of air bubbles. Before use the bath was run for several days to allow a temperature gradient to be set up, and it was found that the temperature in each compartment remained fairly steady, within 1.0°C on either side of the mean temperature of the compartment. The difference in temperature between one compartment and the next remained very steady. The beakers used were suspended in the various compartments of this bath to give experimental

temperatures of 5.0, 10.0, 12.0, 14.0, 16.0, 20.0, 22.5, and 26.0°C.

Aliquots of a culture of Monochrysis lutheri Droop, were added to the cultures each day to maintain a concentration of approximately 500 cells per ml. of water.

Results.

The results of the two experiments carried out are shown in figure 18, the curves of which are based on the mean lengths of the larvae as determined by measurements of representative samples of the populations taken on the third, fifth, seventh, tenth, twelfth and sixteenth days following fertilisation (table 5). In the first experiment a sample of larvae was also taken on the fourteenth day. On the sixteenth day, the fastest growing larvae in the cultures were beginning to set and the experiment was carried out with larvae from a fertilisation made on June 14th, 1958, the second with larvae from a fertilisation made on June 30th, 1958. Prior to these several experiments had been carried out in which newly fertilised eggs had been transferred to different temperatures.

Table 5A. Venus striatula: Mean lengths of larvae in cultures. Experiment 1.

days	3		5		7		10		12		14		16	
Temp.	N	l	N	l	N	l	N	l	N	l	N	l	N	l
5°	50	115.3	30	117.8	50	117.6	33	117.1	30	117.3	*	*	50	117.7
10°	30	113.4	50	116.3	50	118.8	30	119.2	30	123.6	30	127.7	30	123.5
12°	40	117.8	50	124.4	50	133.9	30	139.2	30	146.9	30	154.8	30	158.0
14°	50	121.8	50	132.0	40	138.5	30	148.9	30	159.2	30	162.2	30	164.7
16°	50	123.1	50	136.2	30	152.7	50	164.5	30	166.8	30	186.9	30	192.4
20°	50	122.6	30	140.5	30	148.8	30	152.8	30	162.4	30	174.3	30	183.7
22.5°	50	125.0	30	138.5	30	136.7	31	142.9	30	150.5	30	155.8	*	*
26°	50	117.2	30	121.2	30	118.9	*	*	30	122.5	*	*	*	*

Table 5B. Venus striatula: Mean lengths of larvae in cultures. Experiment 2.

days	3		5		7		10		12		16	
Temp.	N	l	N	l	N	l	N	l	N	l	N	l
10°	30	115.7	30	122.2	30	125.6	30	130.5	30	135.8	30	135.3
12°	30	120.9	30	129.5	30	136.4	30	148.7	30	152.5	30	167.2
14°	30	121.3	30	132.8	30	146.6	30	156.0	30	157.8	30	177.9
16°	30	123.1	30	136.4	30	147.8	30	156.8	30	158.4	30	174.2
20°	30	124.0	30	140.7	30	150.0	30	163.3	30	172.2	30	189.3
22.5°	*	*	30	137.1	30	147.5	30	156.8	30	161.7	30	183.6
26°	*	*	30	123.9	30	123.1	30	124.4	*	*	*	*

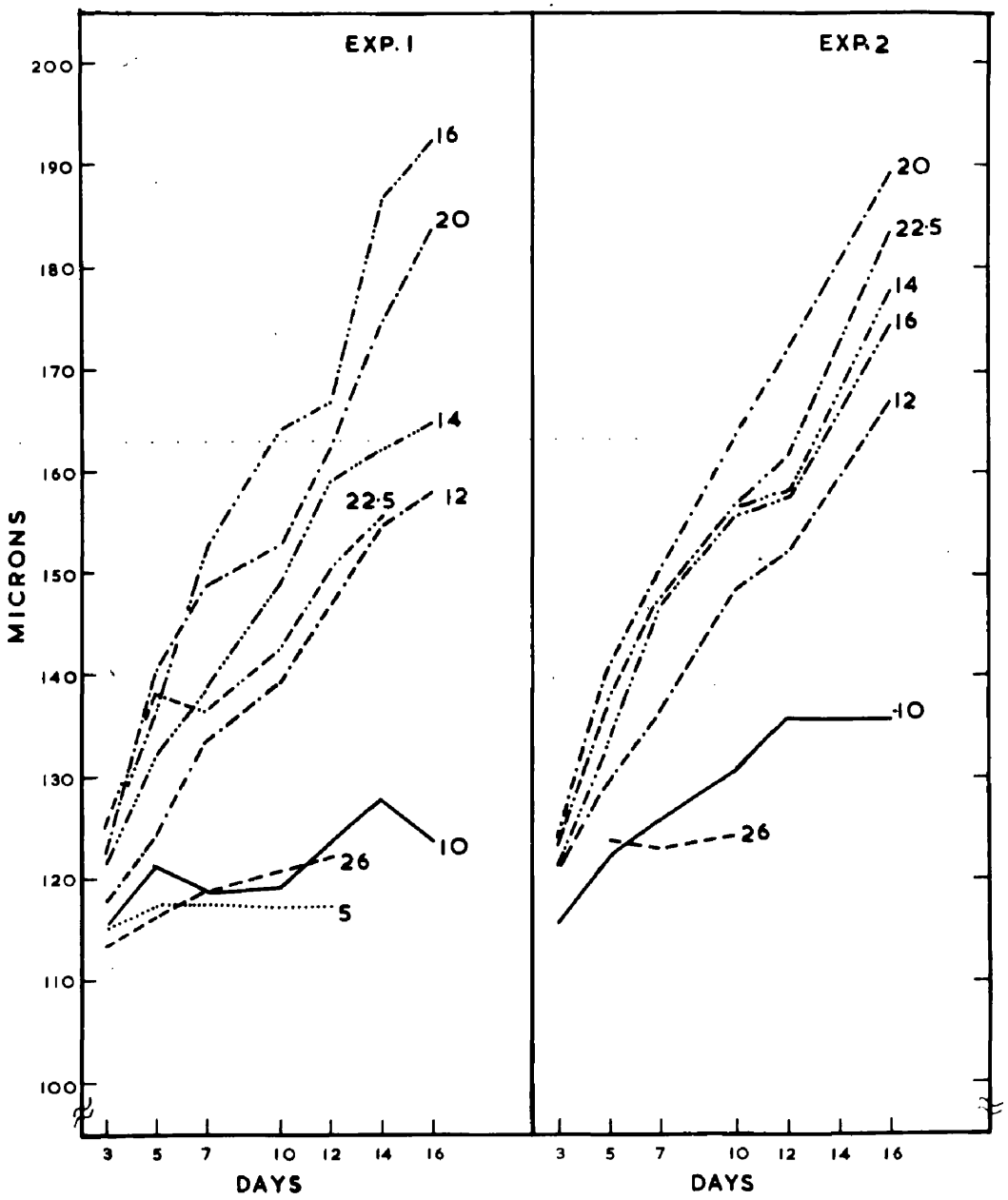


Figure 18. Venus striatula: Graph to show increase in length of larvae at different temperatures in laboratory cultures.

The larvae in cultures kept at temperatures between 10.0°C and 22.5°C inclusive behaved normally. They swam vigorously and remained in suspension in the sea-water without mechanical agitation of the cultures. Cells of Monochrysis could be seen being actively moved by the cilia and crystalline style in the stomach, while the digestive diverticula were coloured green by the ingested food particles.

Larvae kept at 5.0°C in experiment 1 failed to grow. These larvae swam sluggishly and were very transparent, with little or no food in the gut. Some of the larvae at this temperature were alive at the end of the experiment, 16 days after fertilisation, but mortality occurred in the cultures kept at 26.0°C although in these food was observed in the stomachs of the larvae. In spite of this, little growth occurred, and it is probable that this temperature is near the upper limit of temperature tolerance for these larvae.

Mortality in cultures kept at temperatures between 10.0°C and 22.5°C was low. In those kept at 12.0, 14.0 and 16.0°C mortality was estimated at the conclusion of the experiments as not more

than 10%. At 10.0°C and at 22.5°C mortality was higher, an observation which agrees with that of Loosanoff et al (1951) who found that mortality was greatest in those cultures of Venus mercenaria in which the growth of the larvae was slowest. It is to be expected that mortality in cultures will be greatest at temperatures closest to the tolerance limits of the species.

Only the fastest growing larvae in the cultures reached metamorphosis before the experiments were concluded, so that no information is available on the size at metamorphosis at the different temperatures. Loosanoff et al (1951) found no indication that larvae of Venus mercenaria grown at lower temperatures were reaching a larger size before setting than those grown at higher temperatures.

The two experiments showed agreement in general although there are some discrepancies. In particular, larvae in the culture kept at 16.0°C in the first experiment grew considerably faster than those in the similar culture in the second experiment, and in fact grew faster than the larvae kept at 20.0°C.

Without further experiments it is impossible to account for these differences. It is possible that the conditions in the cultures may have varied in some factor which was not controlled, possibly in some property of the sea-water at different times or in the bacterial flora which developed. A number of workers have suspected that such differences may occur between sea-waters and affect the growth of larvae grown in cultures. Of particular interest in this connection is the work of Wilson (1951) and Wilson and Armstrong (1952, 1954, 1958) on the development of the larvae of Echinus esculentus in waters of different origin, and that of Walne (1958) on the effect of the bacterial flora on growth in laboratory cultures of the larvae of Ostrea edulis. In addition Loosanoff et al (1951) found differences between cultures of Venus mercenaria grown under controlled conditions, and suggest that differences in micro-plankton, or in "certain dissolved substances which ..... affected the rate of development of bivalve larvae" in the sea-water used, may have been responsible. Dr R.H. Millar

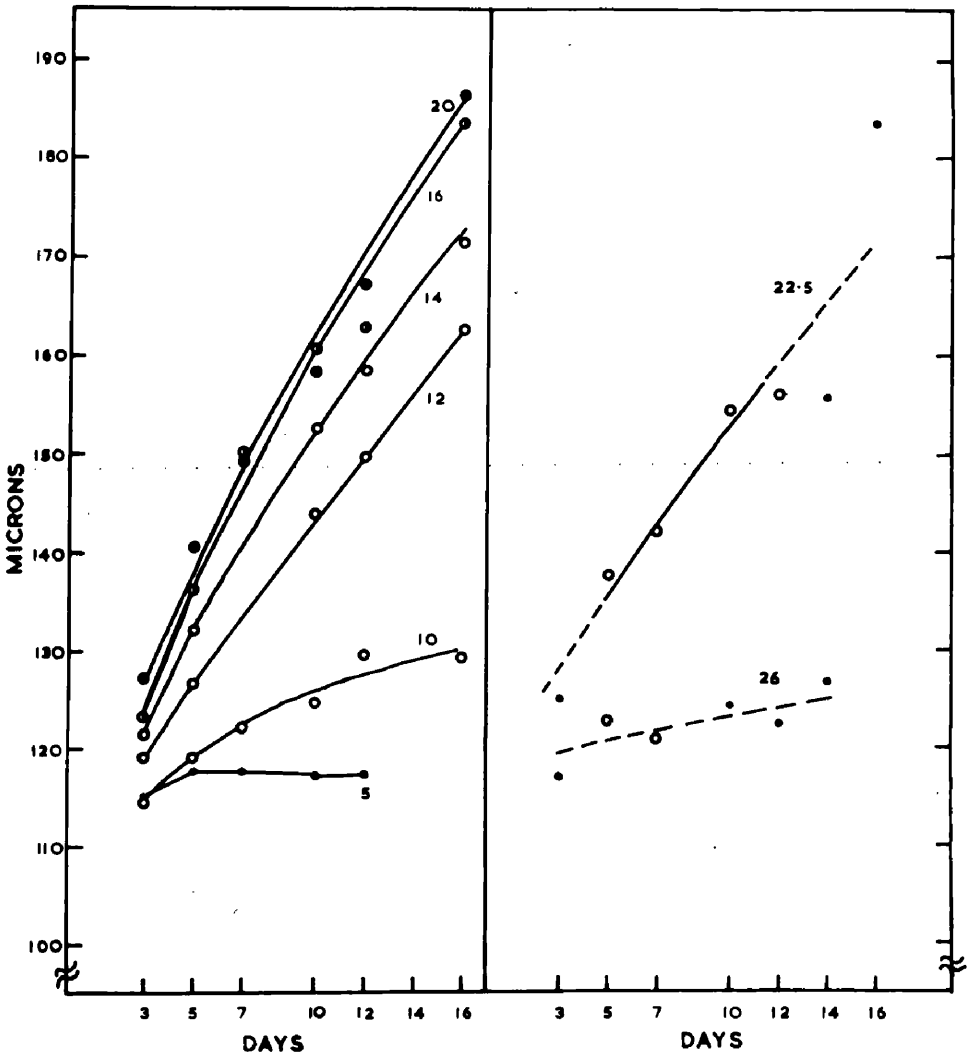


Figure 19. Venus striatula: Graph showing the general trend of increase of length of larvae grown at eight different temperatures in laboratory cultures.

Based on two experiments.

(personal communication) finds similar differences between cultures of the larvae of Ostrea edulis.

To summarise the results of the two experiments the arithmetic mean of all the results for each temperature on each day when measurements were taken have been calculated. The results are summarised graphically in figure 19. The curves show that growth of the larvae increased with increase in temperature in the range 5.0°C - 16.0°C. Growth at 20.0°C is similar to that at 16.0°C and it seems likely therefore that the maximum mean growth of larvae might occur at about 18.0°C. At temperatures above 20.0°C growth of the larva is retarded. Significant amounts of growth were obtained in the range 12.0°C - 22.5°C.

In all cultures it was found that there was considerably variation in size of the larvae. In table 6 are given the maximum and minimum lengths of larvae at each temperature on each day on which measurements were taken, the table being based on the combined results of the two experiments. In figure 20 these values are compared graphically for the 10.0, 16.0 and 20.0°C cultures. It will be seen that the extent of variation is not the

Table 6. Maximum and Minimum lengths in microns of larvae of V. striatula in cultures.

Based on two experiments.

DAYS	TEMPERATURE															
	5°C		10°C		12°C		14°C		16°C		20°C		22.5°C		26°C	
	Max	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max	Min
3	125*	100*	129	100	129	102	131	110	130	108	132	108	131*	108*	128*	105*
5	125*	108*	130	103	136	105	140	121	145	120	152	120	151	118	130	110
7	126*	110*	135	108	145	120	150	125	165	135	170	121	160	120	130	110
10	125*	110*	140	108	161	125	170	131	185	130	181	120	175	125	135+	115+
12	125*	110*	145	110	170	132	178	135	190	145	200	121	190	121	130*	115*
16			148	110	190	135	200	153	220	160	230	140	210+	145+		

* Based on Experiment 1 only.
\+ Based on Experiment 2 only.

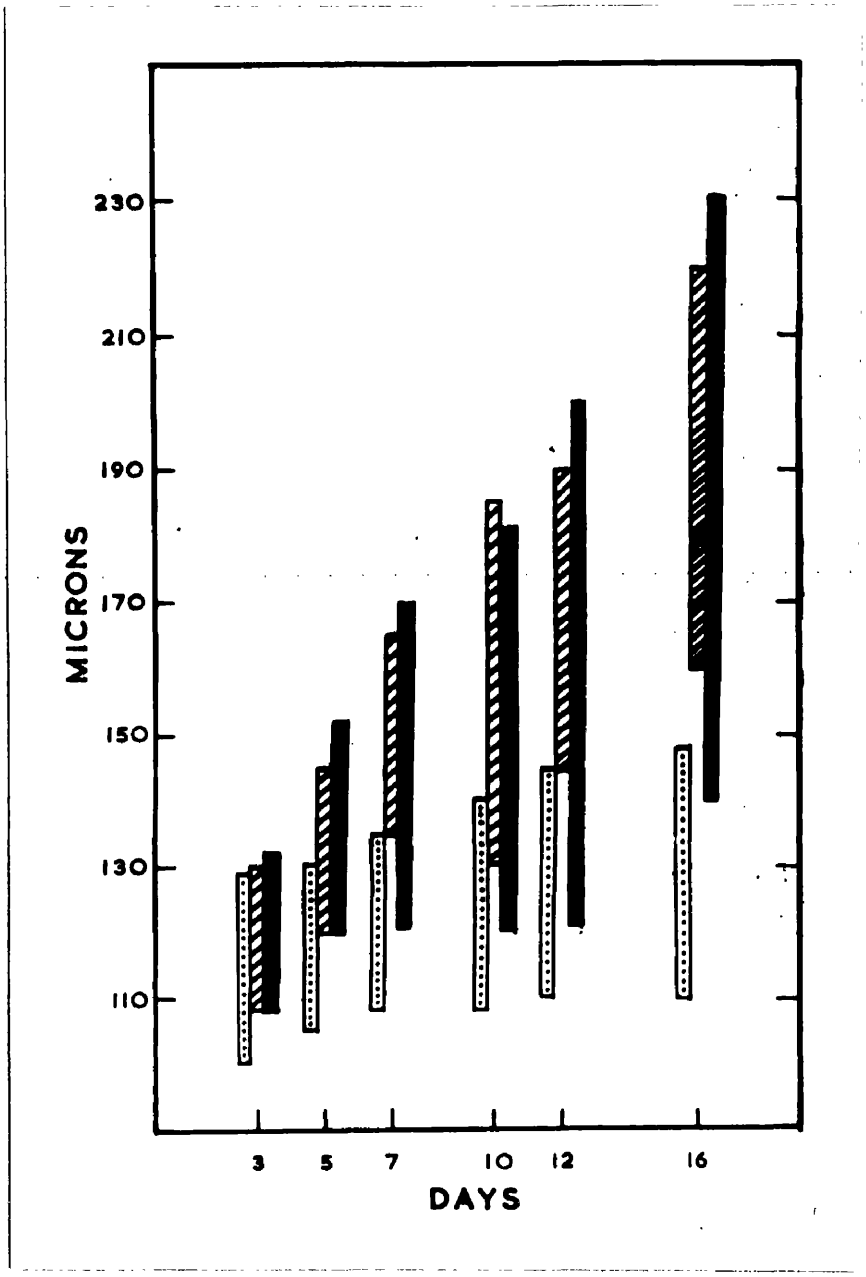


Figure 20. Venus striatula: Extent of variation in length of larvae on different days of cultivation.

Based on measurements of larvae grown at 10.0, 16.0 and 20.0°C in two experiments.

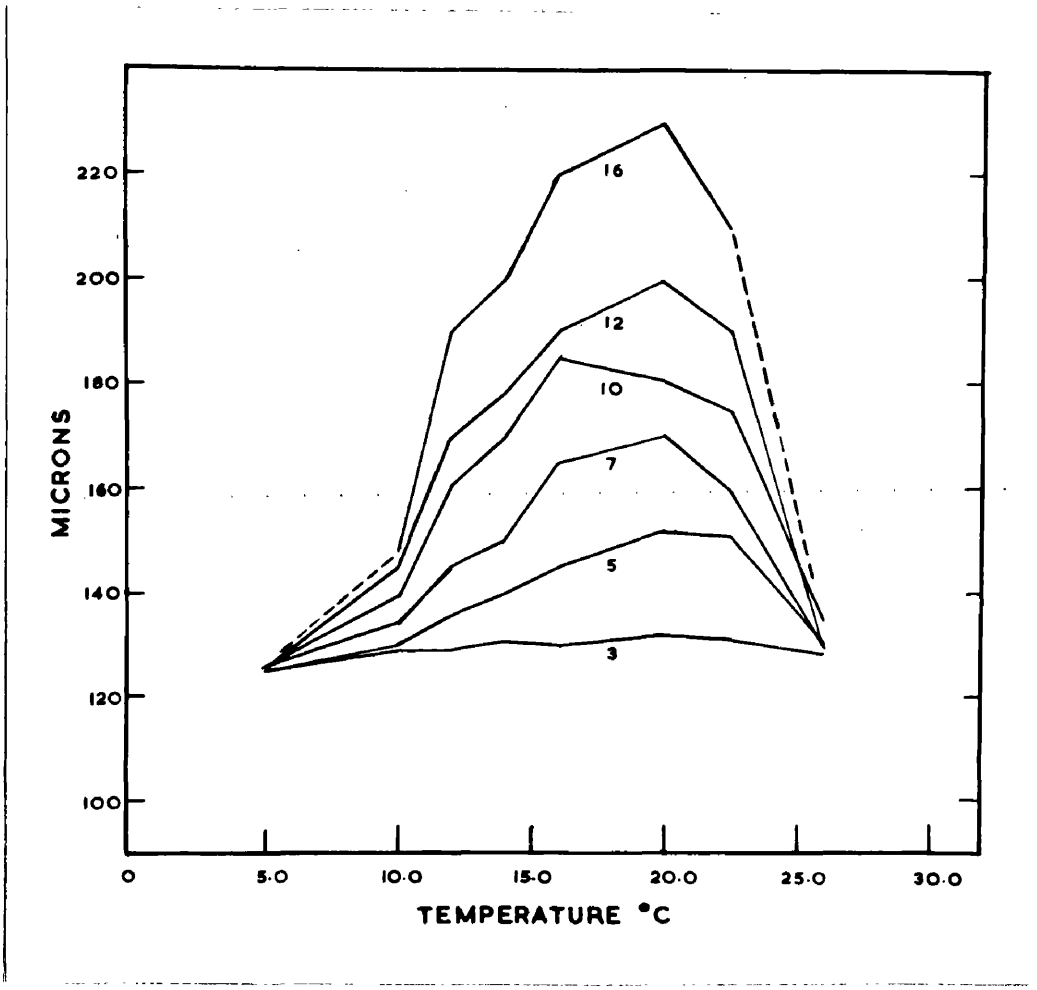


Figure 21. Venus striatula: Maximum lengths of larvae in cultures at different temperatures on different days after fertilisation.

Based on two experiments.

same at each temperature. If the 16.0°C and 20.0°C cultures, where the mean rate of growth is similar, are compared, this effect is best seen. The range of length of the larvae at 20.0°C is greater than that of the larvae at 16.0°C, with the result that, although individual larvae at 20.0°C grow faster than those at 16.0°C, a considerable number also show a slower growth rate, the mean rate being the same. The cause of these wide differences in individual rates between larvae of the same spawning, kept under identical conditions, is at present unknown.

If the maximum size obtained by individual larvae on different days at each temperature is plotted (fig. 21), the effect of temperature on the individual rate of growth is clearly seen. From these figures it is clear that the highest individual rate of growth occurred in the 20.0°C culture.

Examples of the length/frequency distribution of the larvae in the cultures are given in figure 22, which is based on measurements of the larvae grown at 10.0, 12.0 and 20.0°C in experiment 2. The tendency for some of the distributions to be bi-modal

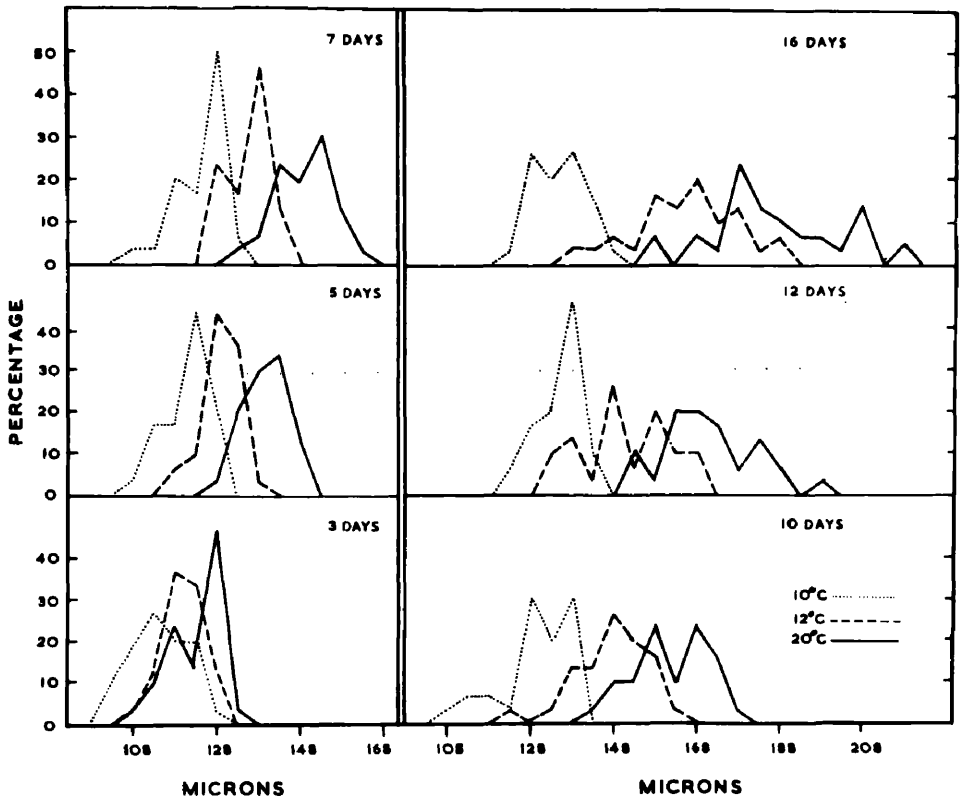


Figure 22. Venus striatula: Length/frequency distributions (expressed in percentages) of larvae of different ages, grown at temperatures of 10.0, 12.0 and 20.0°C, in experiment 2.

suggests that the sample size used may have been too small, but even so, these distributions give a clear picture of the effect of temperature on the rate of growth of the larvae. As will be seen from figure 22 there is a tendency, which has been noted earlier, for the range of size to increase as the larvae grow older.

The two experiments described were carried out on the shelled larvae of Venus striatula. Earlier experiments were attempted in which newly-fertilised eggs were transferred to different temperatures and their subsequent development followed. Although rather incomplete, these observations are included here, since they indicate that the temperature tolerance of the earlier stages of the development may be different to that of the veliger larva.

Eggs fertilised at room temperature (about 15.0°C) and then transferred with gradual rise of temperature to 26.0°C failed to develop normally. Segmentation was interfered with, small pieces of the eggs became completely detached, and in some a bubbling appearance of the cytoplasm developed.

The eggs soon died. At 22.5°C the same processes occurred.

At the other end of the temperature scale, at 5.0°C, the eggs were apparently not injured and cell division occurred, though at a very much reduced rate. Most of the trochophore larvae produced were, however, abnormal, and mortality was almost 100% before the shelled-larva stage was reached. Between the range 10.0 - 18.0°C development was normal, but the time between the first and second, and the second and subsequent divisions, was greater at lower temperatures. At 20.0°C there was some interference with the normal course of early development, and a large proportion of the larvae produced were abnormal.

These observations on the early development of Venus striatula at extreme temperatures are in agreement with results found for other bivalves. Seno, Hori and Kusakabe (1926) found that at 16.0°C few of the eggs of Ostrea gigas would develop to the shelled larva, and that the larvae which were produced were abnormal and soon died. At 14.0°C segmentation was so abnormal that no shelled larvae

were produced. In Venus mercenaria, Loosanoff et al (1951) found that eggs placed in water at 15.0°C within three hours of fertilisation would not develop normally. Some would develop into trochophore larvae, usually of abnormal appearance. At 33.0°C an abnormal development and heavy mortality occurred if fertilised eggs were immediately transferred to such a high temperature.

In the course of these experiments measurements were made of a large number of larvae of different sizes. The measurements of the larvae grown at 16.0°C in the two experiments, together with some of those of larvae grown at 20.0°C have been used to construct table 7 and a curve (fig. 22) showing the relationship between length and height of the larva from the straight-hinge stage of metamorphosis. The numerals on the curve represent the frequency of occurrence of larvae of various heights and lengths. The curve closely approaches a straight line indicating that the relationship is simple and direct with no radical change in shape with age. Dispersion is slight, and is partly due to differences in the positions in which the

Table 7. Length/height relationship. Larvae.
V. striatula.

Mid point length	No. of specimens	Mean height	Height/ length
108	4	088	0.815
113	4	094	0.832
118	17	094	0.797
123	30	098	0.797
128	41	103	0.805
133	14	111	0.835
138	46	113	0.819
143	25	119	0.832
148	40	123	0.831
153	44	128	0.837
158	43	132	0.835
163	22	137	0.840
168	49	145	0.863
173	38	149	0.861
178	46	155	0.871
183	35	159	0.869
188	27	166	0.883
193	15	169	0.876
198	26	176	0.889
203	11	180	0.887
208	21	185	0.889
213	7	188	0.883
218	10	195	0.894
223	2	198	0.888
228	2	206	0.903
233	1	208	0.893

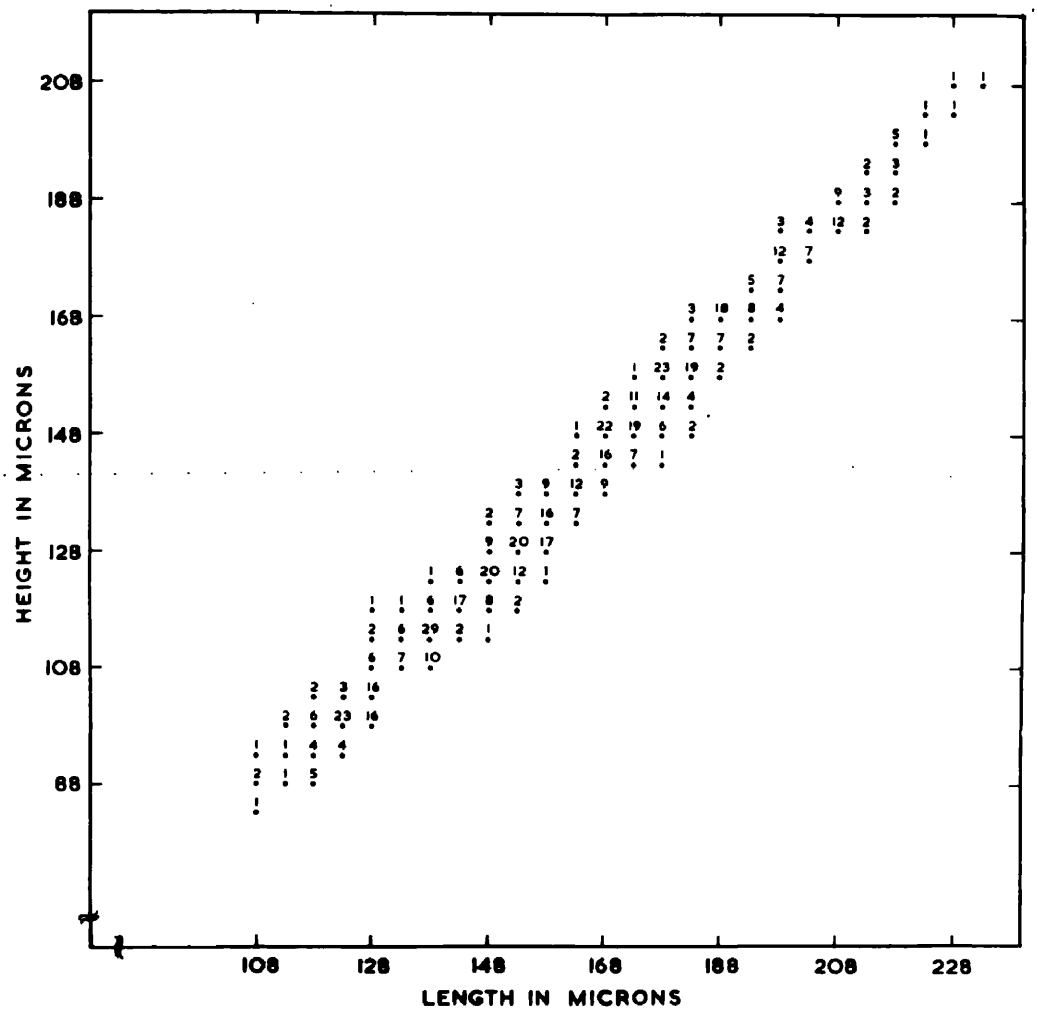


Figure 23. Venus striatula: Length/height relationship of the larva.

The numerals represent the number of larvae of each size measured.

Based on measurements of 620 larvae.

larvae lie on the slide; especially in larger larvae the curved shell causes them to lie obliquely.

The size of the smallest larva shown in the curve was 108 × 83μ, the largest 235 × 210μ.

6. Anatomy of the Veliger: Venus striatula.

The shell.

The first appearance of the larval shell occurs on the second day following fertilisation. It is composed of a thin layer of conchiolin-like material secreted by the shell gland and is at first uncalcified. Later it becomes calcified. The first formed region of the shell, secreted by the shell gland (Prodissoconch 1) is distinguishable in larvae of all ages. The rest of the larval shell is secreted in the normal way by the outer fold of the mantle edge. This outer region (Prodissoconch 11) is thicker than prodissoconch 1 and bears the concentric markings already described.

The observations of Jørgensen (1946) and of Rees (1950) on the hinge of Venerid larvae were confirmed. Venus striatula has a hinge of type C (Rees, 1950). When fully developed the provinculum

of the left valve carries two low ridges which, on closure, lie on either side of a single ridge in the centre of the provinculum of the right valve. Anteriorly on the left valve there is a long projection which on closure is applied to a solid tooth on the right valve.

The ligament is a small structure about 15μ long in the fully developed larva. It is difficult to distinguish in sections, but appears to consist of a single layer, presumably secreted by the mantle isthmus and continuous with the product of the shell gland (Prod. I), and hence homologous with the inner layer of the adult ligament.

The Mantle.

The mantle edge of the fully developed larva consists of only two folds. The outer surface of the outermost of these secretes the shell, while the periostracum is secreted from its inner surface. The innermost fold represents the inner and middle folds of the adult, but these do not separate until considerably later in development when the animal has become bottom-living.

The mantle is one cell thick except at the

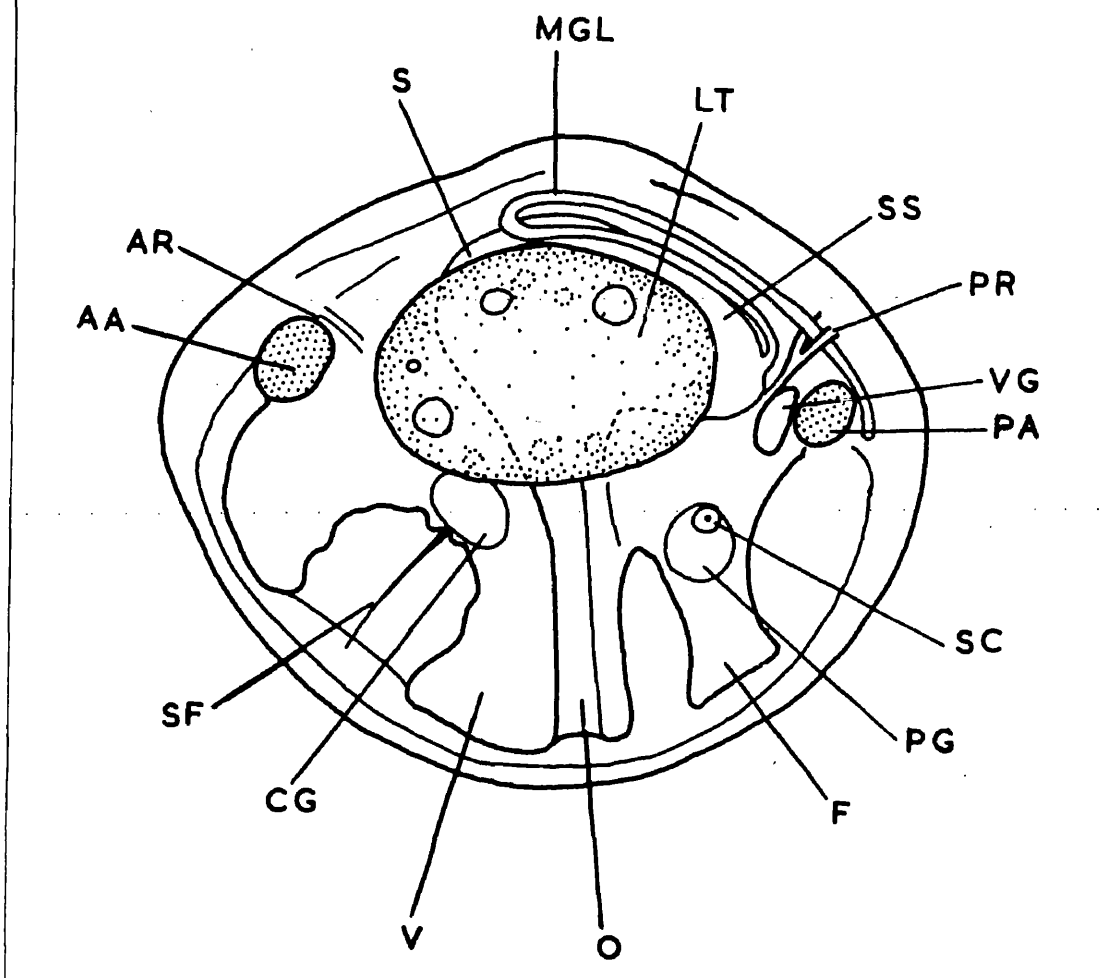


Figure 24. Venus striatula: Disposition of the organs in the veliger. Drawing from life.

AA. Anterior adductor muscle.
AR. Anterior pedal retractor muscle.
CG. Cerebral ganglion.
F. Foot.
LT. Left digestive tubule.
MGL. Anterior loop of mid-gut.
O. Oesophagus.
PA. Posterior adductor muscle.
PG. Pedal ganglion.
PR. Posterior pedal retractor muscle.
S. Stomach.
SC. Statocyst with statolith.
SF. Anterior sensory flagellum.
SS. Style-sac.
V. Velum.
VG. Visceral ganglion.

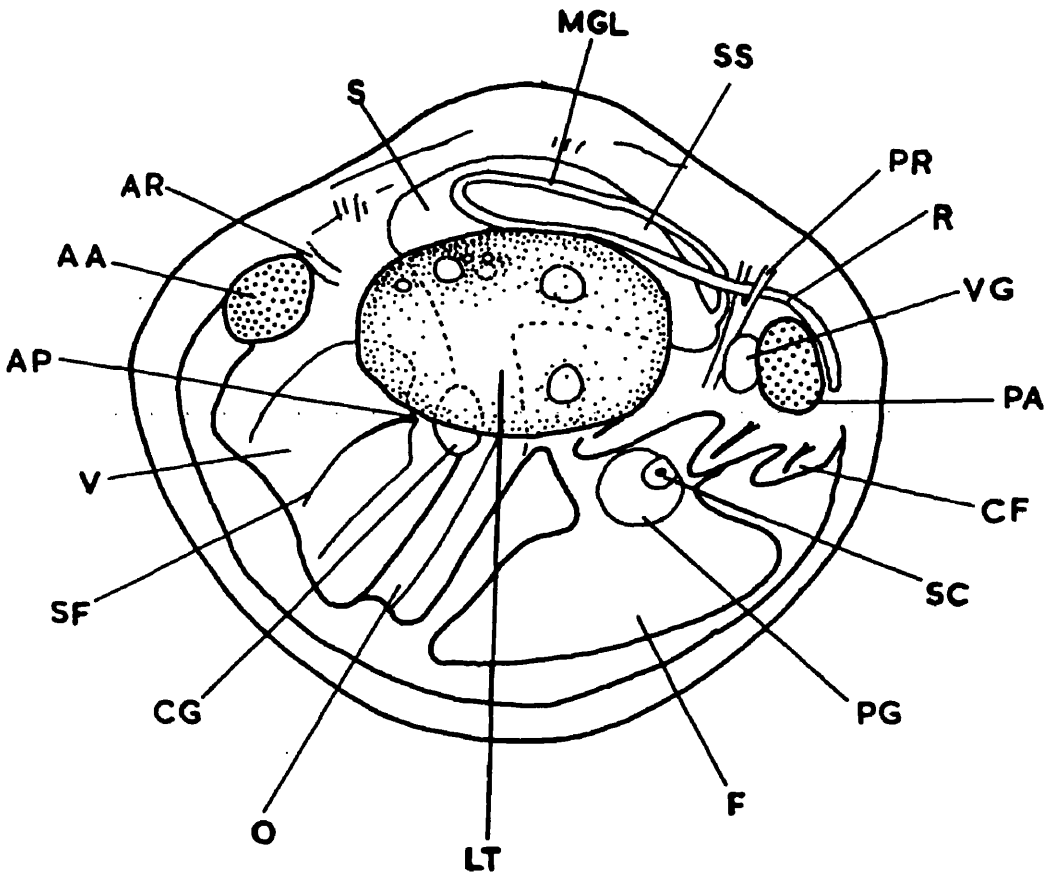


Figure 25. Venus striatula: Disposition of the organs in the pedo-veliger. Drawing from life.

AP. Apical plate.
CF. Ctenidial filament.
R. Rectum.

Other lettering as in figure 24.

edges where it becomes three cells thick, the inner and outer cell layers continuing into the two folds of the edge.

On its inner surface the mantle bears a row of cilia which follow the same course as the cilia of the main rejection tract of the mantle of the adult. These cilia are not lost at metamorphosis and probably represent the first appearance of the mantle rejection tract.

The mantle edges of the larva are separate except for a small region posteriorly, where in the fully developed larva they fuse to form the siphonal septum.

The Ctenidia.

The filaments of the inner lamella begin to form when the larva is 190 - 200μ in length, that is about 14 days after fertilisation, at 16°C, being budded off from a block of tissue in the region of the siphonal septum. The most recently formed filaments are therefore posterior. In the fully developed larva, three or four filaments may be present. Active cilia are present between the filaments at this stage, but the ctenidia do not

take over the function of food collection until after settlement, that is, until after the velum is lost.

The Foot.

Throughout most of the larval life, the foot is a small organ occupying the posterior end of the mantle cavity. Shortly before settlement the foot increases rapidly in size and is used in crawling on the surface of the substratum. At this time there is a period - the pedo-veliger stage (Carriker, 1956) - which may last several days, when both the foot and the velum are functional. The surface of the foot is covered with long cilia, and when on the surface of the substratum with the foot extended, the animal is dragged forward by their action. At the base of the foot, the very large pedal ganglion and the statocysts are obvious in the fully developed larva (fig. 24).

The pedal musculature is poorly developed in the larva, but both the posterior and the anterior retractor muscles can be distinguished, each consisting of a few muscle strands only. The

posterior pedal retractor muscle runs from the heel of the foot, anterior to the visceral ganglion and is inserted into the shell above the posterior adductor muscle, on either side of the rectum. The anterior retractor muscle runs from the anterior part of the foot to be inserted just above the anterior adductor muscle.

No sign of a byssus gland has been seen in sections and no evidence of byssal secretion found in living material. Venus striatula apparently never attaches itself to the substratum at any stage of its life.

The Velum.

The velum is the characteristic swimming and food-collecting organ of bivalve larvae. When expanded, the velum of Venus striatula is circular, and bears a ring of long cilia at the circumference. At the centre of the disk lies the apical plate which is intimately associated with the cerebral ganglia. From the centre of the apicle plate protrudes a long single sensory flagellum, about 50 - 60μ in length. This anterior sensory flagellum is present throughout the larval life from the trochophore

stage until settlement. In the swimming larva, contact of this flagellum with an obstacle causes retraction of the velum. Re-expansion of the velum is preceded by the appearance of the flagellum from between the partly open shell-valves. A similar anterior flagellum is present in the larvae of Gafrarium minimum, Venus ovata, and Venus fasciata (personal observation) and in Venerupis pullastra (Quayle, 1953), and appears to be characteristic of the larvae of the Veneridae, although it also occurs in some other groups.

The velum is retracted by means of two pairs of velar retractor muscles. When retracted into the shell it is thrown into folds (fig. 24) and occupies the anterior half of the mantle cavity.

The Digestive System.

Food collected by the cilia of the velum is passed into the mouth, which lies immediately posterior to the velum. The oesophagus passes dorsally into the visceral mass and opens into the anterior ventral region of the stomach. The walls of the oesophagus are lined with cells bearing cilia, those closest to the opening into

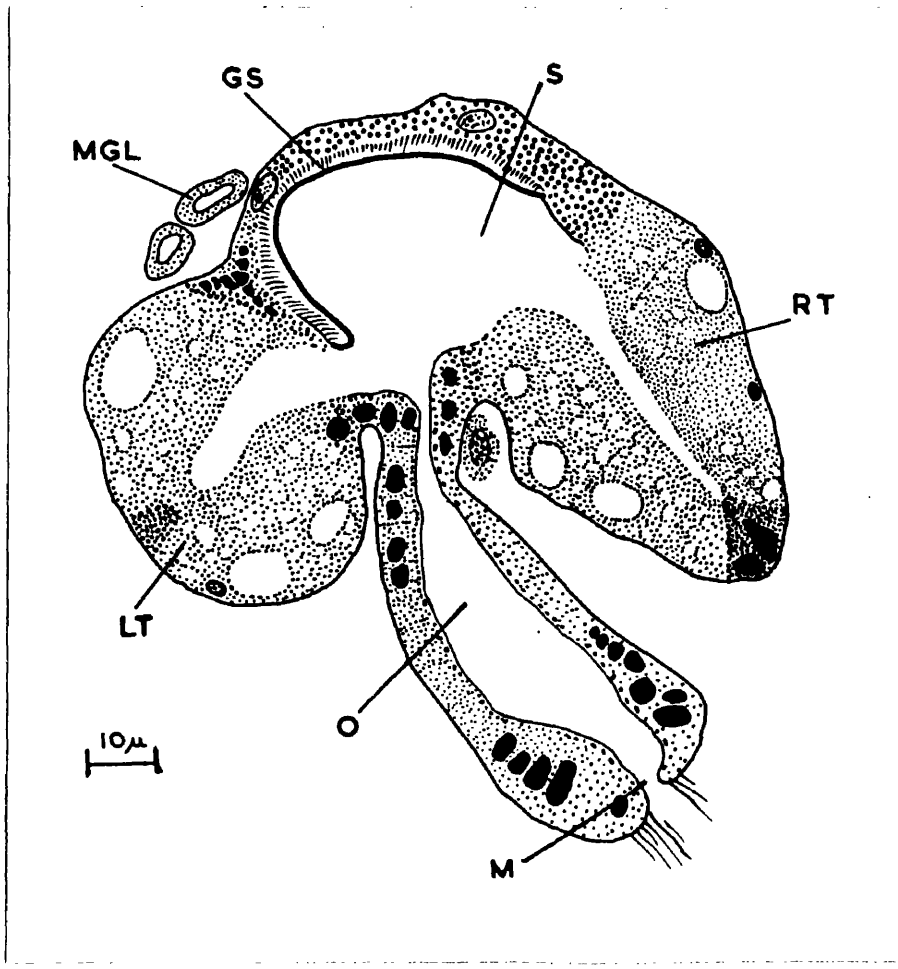


Figure 26. Venus striatula: Larva: transverse section of the oesophagus and stomach, showing the openings from the digestive tubules on either side.

GS. Gastric shield.
LT. Left digestive tubule.
M. Mouth.
MGL. Anterior mid-gut loop.
O. Oesophagus.
RT. Right digestive tubule.
S. Stomach lumen.

the stomach being especially long.

The stomach is a globular organ, situated between the umbones in the dorsal region of the visceral mass. Posteriorly it is elongated to form the style-sac, the posterior end of which lies just anterior to the posterior adductor muscle. The walls of the stomach are ciliated except for the roof and left side which bear the smooth gastric shield (fig. 26 GS). The style-sac is lined with dense cilia which have the same characteristic appearance in section as those of the adult. The digestive diverticula lie on either side of the stomach and open separately through its anterior latero-ventral wall, on either side of the opening of the oesophagus (fig. 26). In the larva the lumina of the diverticula open directly into the stomach and there are no ducts present to compare with the system of primary and secondary ducts of the adult (Owen, 1955). The ducts develop later when the diverticula become branched and complex.

Functioning of the Digestive System.

Movement of food in the gut of larvae ready to

metamorphose has been observed under the microscope in larvae fed on a thick culture of Monochrysis. The mechanism of food movement within the gut is similar to that observed in the larvae of Ostrea edulis by Millar (1955). Food material passing from the oesophagus into the stomach becomes entrapped in a mass of material wrapped in mucus around the head of the crystalline style. This material is rotated in a saggital plane by the action of the cilia of the floor and anterior walls of the stomach, and is also subjected to rotation by the crystalline style, which rotates in a clockwise direction when viewed anteriorly. The digestive diverticula on either side of the stomach contact alternately, drawing material to rejoin the mass in the stomach, as they contract. The process may be seen in swimming larvae moving on the surface of the substratum by means of the foot, but apparently stops when the velum is retracted. The same process has also been observed in young post-larval stages.

The structure of the diverticula of the larva is similar to that of a single tubule of the adult

diverticula. Most of the wall is lined with large, vacuolated absorptive cells, but at the ends, small numbers of deeply-staining cells occur similar to the flagellated cells which occur in this position in adult tubules (Owen, 1955). No flagella were distinguished in sections.

The Nervous System.

In the larva of Venus striatula the nervous system is represented by large masses of deeply-staining cells forming the ganglia. The cerebral ganglia lie anterior to the oesophagus, and posterior to the apical plate of the velum. The cerebral commisure is present connecting the two ganglia. Ventral to the cerebral ganglia and connected to them by connectives, lie the pleural ganglia. The fused pedal ganglia are very obvious in the proximal region of the foot, with, on either side in the fully developed larva, the stato-cysts, each with a single large statolith. The visceral ganglia lie anterior to the posterior adductor muscle.

Musculature.

The adductor muscles occupy the same relative positions as in the adult. The pedal musculature

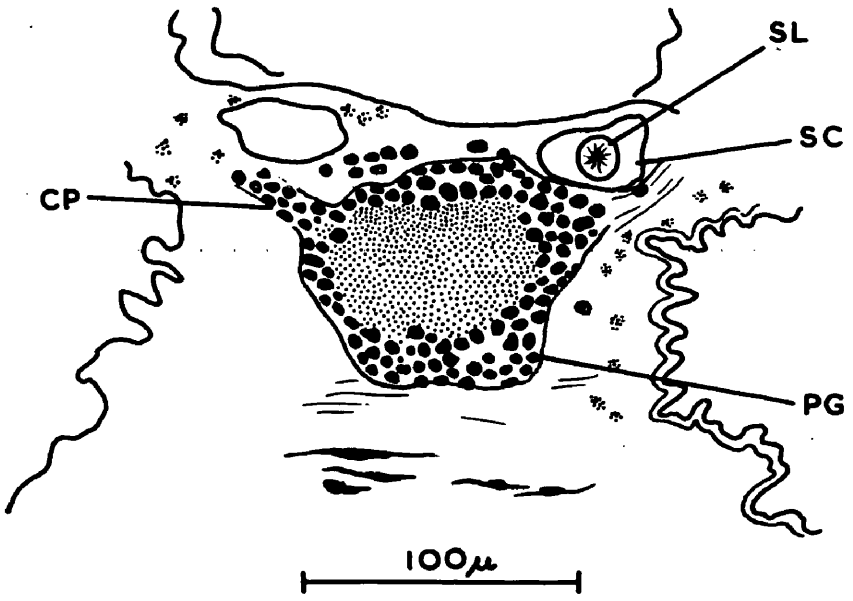


Figure 27. Venus striatula: Transverse section of the proximal end of the foot of a young post-larva to show the pedal ganglion and statocysts.

CP. Cerebro-pedal connective.
PG. Pedal ganglion.
SC. Statocyst.
SL. Statolith.

has already been described in relation to the foot, so that all that remains to be described here are the anterior and posterior pairs of velar retractor muscles. The anterior pair are inserted into the shell anterior to the anterior adductor muscle and the posterior pair anterior to the hinge ligament. The muscles branch to give multiple insertions into the shell, while the distal ends branch and radiate over the surface of the expanded velum.

Setting and Metamorphosis.

The changes occurring at metamorphosis have not been studied in detail, but some points of particular interest should be noted. In Venus striatula as in Venerupis pullastra (Quayle 1953) metamorphosis is a fairly gradual process extending over a number of weeks, and not a rapid change such as occurs in Ostrea edulis (Cole, 1938a, 1938b). The processes of metamorphosis may be regarded as starting in the pedo-veliger stage, with the increase in size of the foot, after which there is a continuous development of organs until the full adult form is reached. Setting occurs early in this process and is marked by the loss of the velum, and

a subsequent re-arrangement of the internal organs. In Venerupis pullastra (Quayle, 1953) and Venus mercenaria (Carriker, 1952) setting also involves attachment to the substratum by means of a byssal secretion, but this has not been observed in Venus striatula. It is possible that permanent settlement is not reached until some time later since the animal may be transported by water currents even after the velum has been lost, as is the case in Cardium edule (Baggerman, 1953).

The changes succeeding the loss of the velum involve a rotation of the organs of the visceral mass, and foot, so that the mouth comes to lie immediately posterior to the anterior adductor muscle. This rotation involves changes in the orientation of the stomach and alimentary canal, and of the ctenidia, while the cerebral and pleural ganglia are carried forward with the oesophagus until they lie in the adult position posterior to the anterior adductor muscle.

Following the changes at setting the ctenidia continue to develop by the addition of more filaments postero-ventrally, while the palps develop

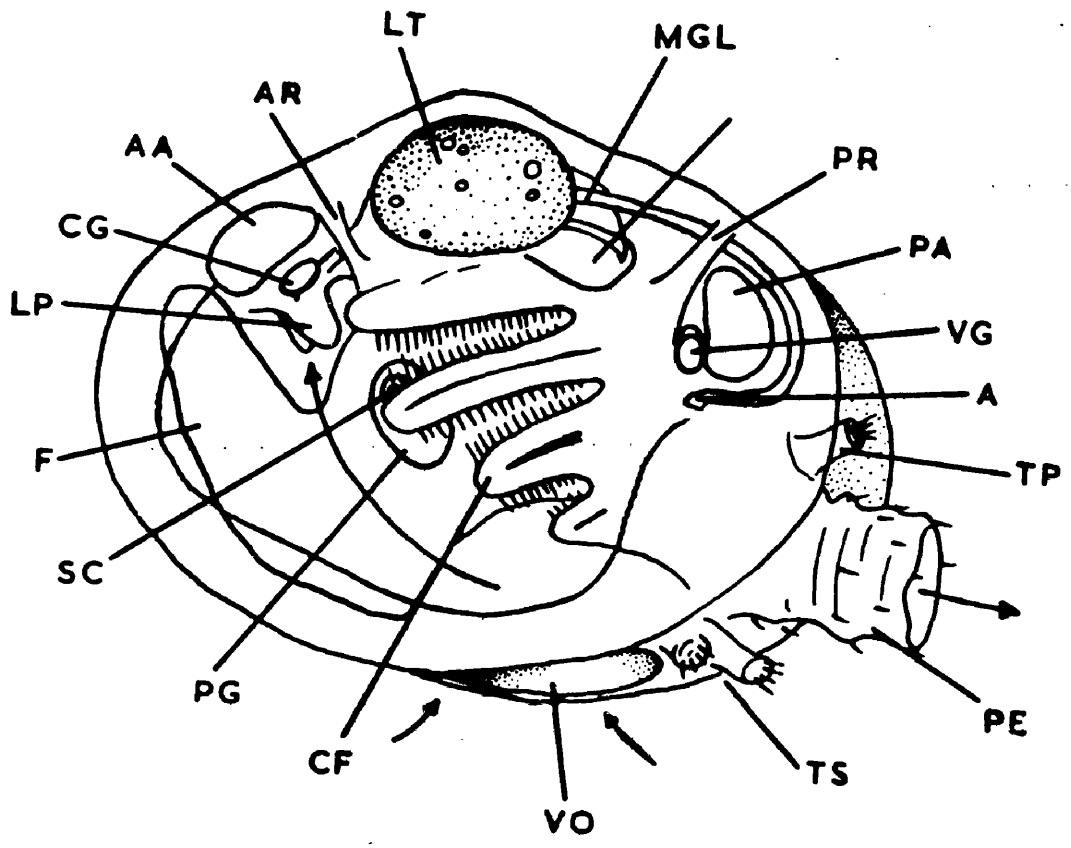


Figure 28. Venus striatula: Lateral view of a young post-larva to show the disposition of the organs and especially the appearance of the siphonal structures at this stage. Drawing from life.

A. Anal papilla.
LP. Labial palp.
PE. Primary exhalent siphon.
TP. First formed siphonal tentacle.
TS. Second formed pair of siphonal tentacles.
VO. Ventral opening of pedal gap.

rapidly. At this stage the beating of the lateral cilia of the ctenidia cause a water current to enter the mantle cavity around the ventral gap. This water current carries particles in suspension forward in the mantle cavity around the sides of the proximal end of the foot, parallel to the free edge of the ctenidia, so that they impinge on the palps, which at this stage are relatively large. The further development of the food collecting mechanism of the mantle cavity has not been followed.

The siphonal apparatus makes its first appearance very early in the post-larval life of the animal. This takes the form of the development of short tentacles of the mantle edge dorsally, posterior to the posterior adductor muscle. The mantle margins are already fused posteriorly to form the siphonal septum, in the pedo-veliger, and a short, thin-walled primary exhalent siphon soon develops dorsal to this, with a ring of at first three and later five tentacles around it. The young spat is extremely sensitive to mechanical disturbance, to which it responds by closing the shell. The primary

exhalent siphon is apparently extended and kept extended by the pressure of the exhalent water stream and is withdrawn rapidly prior to closure of the shell, by inversion. The mechanism by which this occurs is apparently as follows: prior to closure of the shell the ventral mantle margins are drawn together, thus effectively stopping the flow of water through the mantle cavity. This stoppage causes the primary exhalent siphon to collapse and so seal off the mantle cavity completely. Any slight opening of the shell valves would then set up a reduced pressure inside the system, which would in turn cause the collapsed siphon to invert into the mantle cavity. The primary exhalent siphon is retained in the adult at the distal end of the true exhalent siphon, and functions in the same way, that is, it is withdrawn by inversion into the siphon. The early appearance of the primary exhalent siphon is necessary in order to direct the exhalent stream away from the current entering around the general ventral margin.

The first appearance of the inhalent siphon

takes the form of pairs of tentacles ventral to the siphonal septum. When several pairs of these tentacles have been formed the mantle edges fuse ventrally and the true exhalent and inhalent siphons are formed by local growth of the posterior mantle edges.

V. Ecology.

1. Introduction.

The work described in this section deals with some aspects of the ecology of Venus striatula, and in particular, is a study of a single year's spatfall in Kames Bay, Millport, Isle of Cumbrae. This population was sampled regularly over the period October, 1956 to January 1957, the samples being taken generally by means of a Robertson Mud Bucket, or an anchor dredge (Forster, 1953). Neither of these two pieces of gear provide information on the density of animals in relation to area of bottom, and attempts to obtain such information by the use of a Van Veen grab proved fruitless due to the inability of the jaws of the grab to penetrate the tightly packed sand on the bottom. The bottom sampler designed by Holme (1949) was also tried but suffered from the same disadvantage. Density of animals on the bottom is therefore only described in relative terms.

2. Bottom communities.

The study of the animals of the level sea-bottom in terms of communities originated with the

classic work of Petersen and Jensen (1911), and Petersen (1913, 1914, 1915, 1918) on the distribution of animals in Danish waters. Since then this work has been extended to other seas by various workers among whom should be mentioned Blegvad (1922), Davis (1923, 1925), Ford (1923), Jones (1940, 1951, 1952) and Holme (1953). Members of the Veneracea characterise what are known as Venus communities (Thorson, 1957) of which the "Venus gallina community" and the "Venus fasciatum - Spisula elliptica - Branchiostoma community" are important in British waters. Parallel communities to these occur in other parts of the world (Thorson, 1957).

Such communities form a broad basis for the comparison of bottom fauna in different areas. Under local conditions, however, certain members of the community may be dominant and it is possible, when dealing with a number of closely related species, to subdivide the communities, on the basis of these dominant animals, into groups characteristic of slightly differing although related environments. Thus, in the Firth of Clyde

Table 8. Distribution of some Venerid species with regard to bottom deposits.

LITTORAL			SUBLITTORAL		
P. pullastra	P. decussata P. aurea	V. striatula	V. striatula (D. lupinus)	Venus fasciata (P. rhomboides) (D. exoleta)	V. casina V. cvata G. minimum (D. lupinus)
Loosely packed rocks, with muddy gravel	Coarse gravel	Sand	Clean sand	Coarse gravel	Mixed stones shell gravel and mud. Generally hard.
	Mya arenaria	Mya truncata Tellina tenuis Spisula subtruncata Ensis ensis Echinocardium cordatum	Tellina fabula S. subtruncata Mya truncata Natica alderi Echinocardium cordatum		Astarte sulcata
		"Venus gallina community"		"Venus fasciata - Spisula elliptica - Branchiostoma community".	

and neighbouring areas, the members of the Veneracea, including those which occur on the shore, may be regarded as belonging to the scheme of sub-communities shown in table 8.

Venus striatula is normally most abundant on bottoms of fine, clean sand. Samples of soil were taken from several areas where Venus striatula occurred and were subjected to grade analysis by the method used by Holme (1954). The results have been expressed in the form of a cumulative curve for each deposit, and examples of these are shown in figure 29. The curves for those soils in which Venus striatula occurred in greatest numbers are very similar to each other, while curves of soils supporting fewer V. striatula depart more or less from them. Holme (1954) found that species of Ensis were associated with particular types of substratum, and that the density of the population was usually greater in sands approaching the mean grade of the samples for that species. The importance of substratum in influencing the distribution of marine bottom invertebrates has recently been stressed

Table 9. Grade composition of soils.

		GRADE MMS.							
	Arith. Mean (mm)	>2.0	1.9-1.0	1.0-0.5	0.5-0.23	0.23-0.19	0.19-0.14	0.14-0.03	0.03-0
A.	0.183	0.0	0.02	0.303	3.48	33.43	55.9	6.73	0.01
B.	0.213	0.25	1.19	2.99	13.94	19.30	28.56	33.43	0.34
C.	0.369	0.45	3.03	3.28	72.5	2.76	8.08	8.31	1.48
D.	0.355	0.17	0.6	1.67	85.7	4.74	4.56	2.99	0.28
E	1.209	23.5	14.0	31.9	14.3	5.09	3.72	5.84	1.46

A. Kames Bay
B. Loch Creran — V. striatula abundant.

C. West Loch Tarbert
D. West Loch Tarbert — V. striatula frequent.

E. West Loch Tarbert — V. striatula rare.

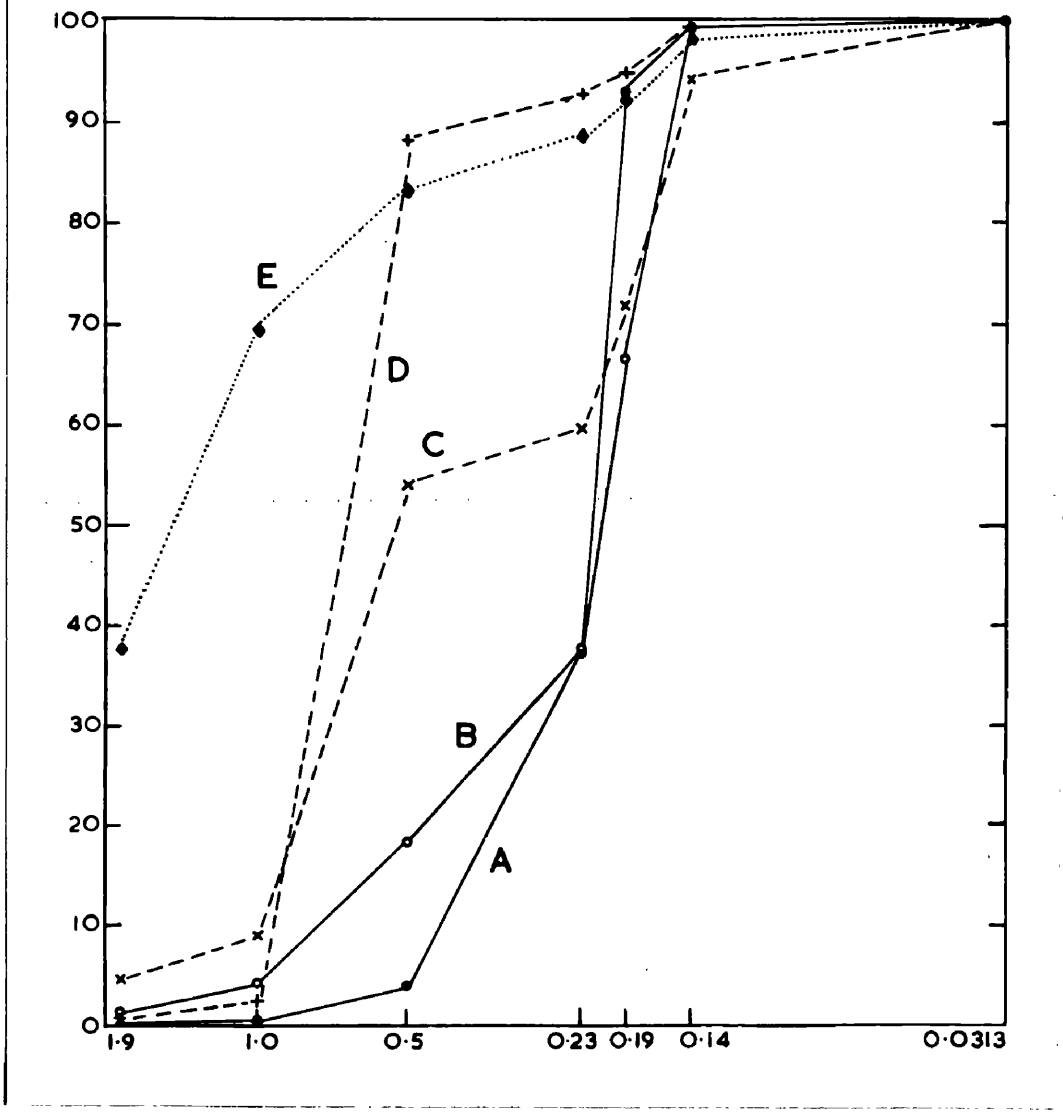


Figure 29. Cumulative curves for bottom deposits.

A Kames Bay.
B Loch Creran. — V. striatula abundant.

C West Loch Tarbert.
D West Loch Tarbert. — V. striatula occasional.

E West Loch Tarbert. — V. striatula rare.

by Rasmussen (1958) in an interesting paper on the changes in density of population of Venerupis pullastra in Danish waters.

3. General Description of the Kames Bay Population.

Before dealing with the results of the ecological study in detail it is necessary to describe the population dealt with since it shows certain characteristics which make it especially suitable for a study of this sort.

The population occurred on a bottom of fine, clean sand in Kames Bay, Millport, at depths from 3 - 4 metres to about 20 metres. Kames Bay is a small bay, facing south, and therefore exposed to the prevailing winds which are from the south-west (Barnes, 1955). Wave action is moderate at all times and probably for this reason Venus striatula does not occur on the shore here, although elsewhere its range may extend above L.W.S.T. The fauna of the sublittoral region of the bay has been described by Clarke and Milne (1955) from two surveys, in 1938 - 1939 and 1949. Since these surveys however, certain changes in the fauna have occurred, of which the most noticeable is the

Figure 30.

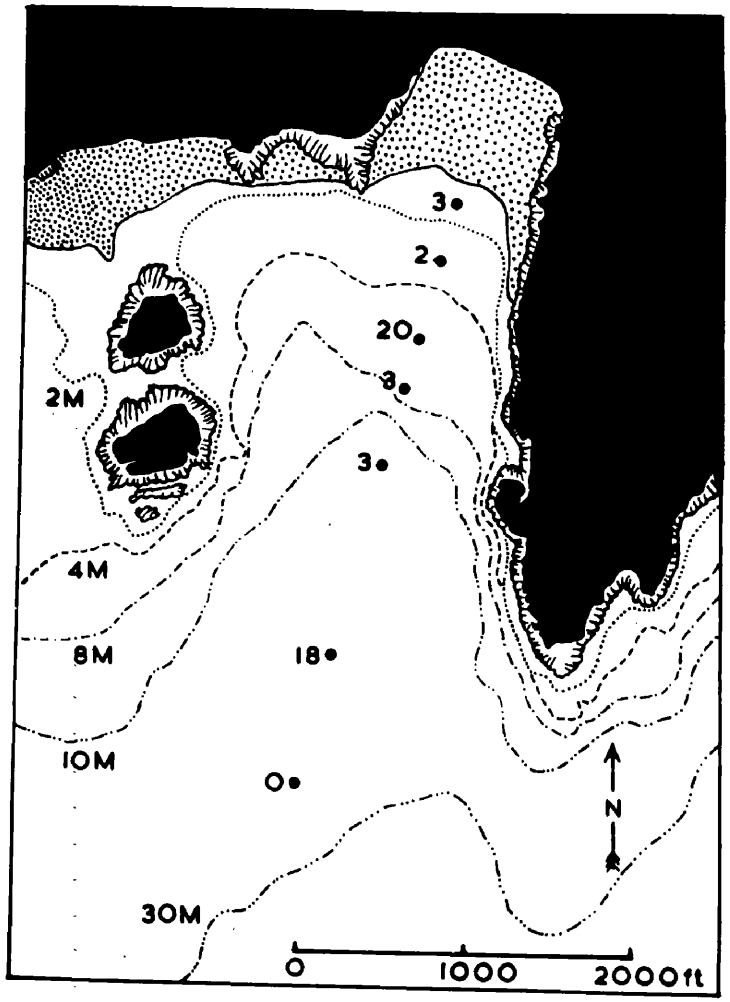
Figure 30. Distribution of Venus striatula in Kames Bay, Millport.

Left. From Clarke & Milne (1955).

Right. Distributions found in the present survey.

The figures are number of Venus striatula found in ten hauls with a mud bucket.

× Position of main sampling station for series of samples for growth.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2
20
3
2M
3
4M
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18
10M
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N
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0
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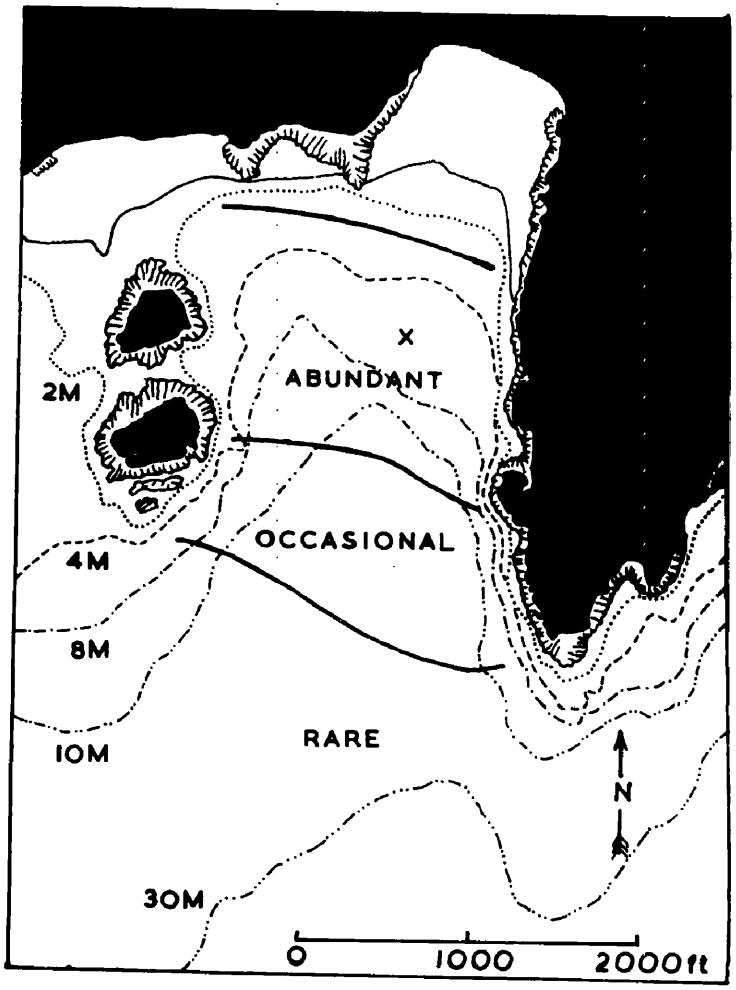
X
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2M
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considerable increase in the numbers of Venus striatula. Probably associated with this increase, although there is no direct evidence since no surveys were carried out in the period from 1949 to 1956, is a change in the carnivorous gastropod fauna, but this will be discussed later (Appendix 1).

Distribution.

The distribution of Venus striatula in Kames Bay is summarised in figure 30. Map A has been prepared from the figure and tables in Clarke and Milne's paper (1955), while Map B shows the general distribution found by the author in the course of this study. The numbers found are difficult to compare directly due to the difficulty experienced in obtaining any accurate quantitative measure of the population density, but sampling with a Robertson Mud Bucket (as used by Clarke and Milne) suggest that the increase in population density was in the region of a hundredfold. The region of the bay where the greatest population density was found, was similar in both cases.

The reason for the sudden increase is

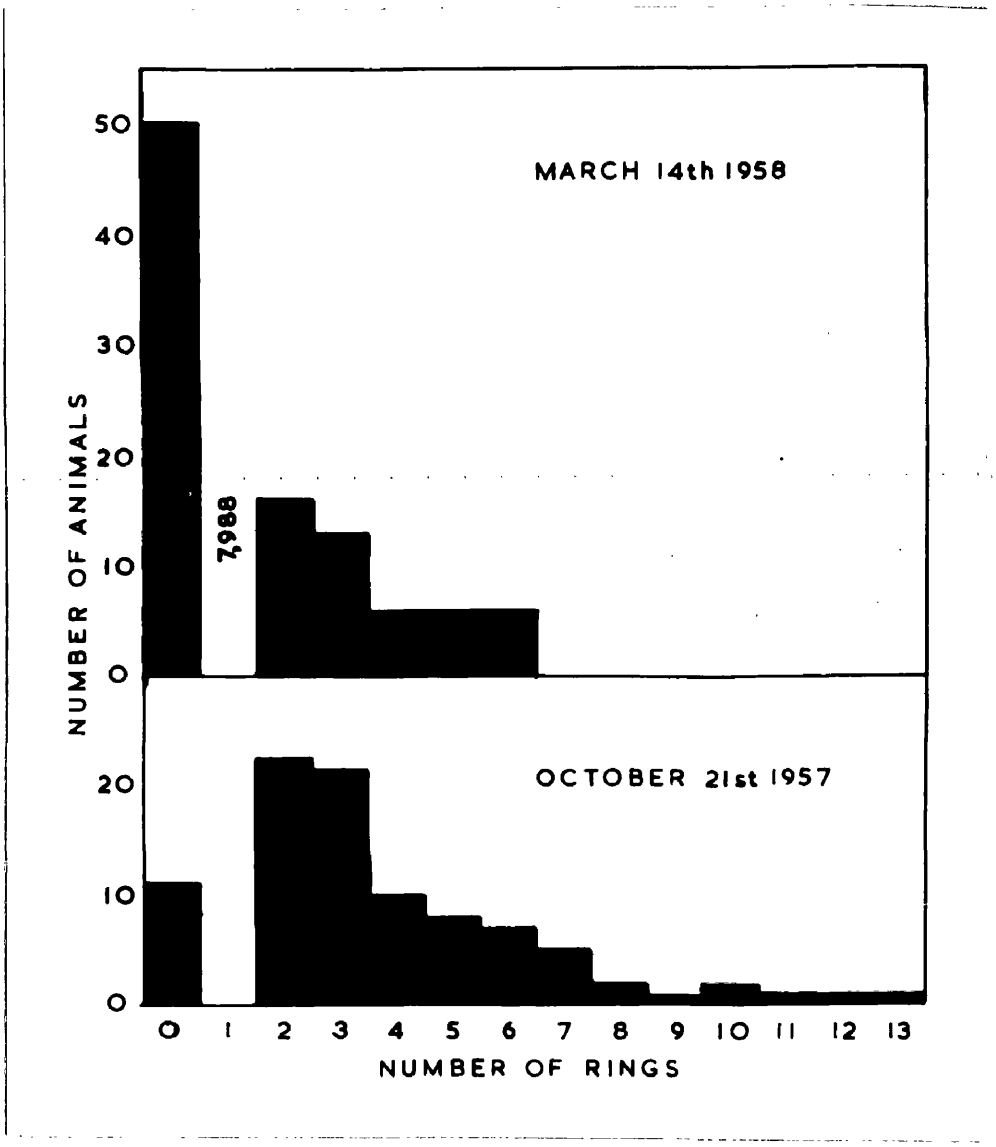


Figure 31. Venus striatula: Age frequency distribution for the Kames Bay population.

immediately obvious if the size or age distribution of the animals in the population is examined. Age distributions of the population are given in figure 31. From this it will be seen that the bulk of the population is composed of animals from the settlement which occurred in 1955. The size distribution (fig. 34A) shows a single peak formed by animals derived from this settlement, and the population may be regarded, in practice, as composed of a single year group. In this it clearly differs from most populations of bivalves of similar life-span, which normally show a complex, multimodal size/frequency distribution from which it is difficult or impossible to separate year classes (Quayle, 1953; Green, 1957). Examples of more typical size/frequency distributions for Venus striatula are given in figure 34B & C, the graphs in which are derived from measurements of animals from Hunterston Sands, Ayrshire, and Loch Creran, Argyll.

The factors which may limit the distribution of Venus striatula have already been briefly touched upon. In Kames Bay the upper limit is

probably set by wave-action disturbing the stability of the sand, and thus making permanent settlement of spat difficult. As depth increases towards the mouth of the bay, the bottom deposits become gradually more and more silty and eventually grade into mud. The bulk of the population is thus limited to the shallower region of the bay, which has a fairly undisturbed bottom of fine, clean sand.

Dispersion.

The results of sampling at a number of stations in the bay indicate that the density of Venus striatula is not uniform even within the area where it is greatest. Two series of replicate samples were taken during 1957 and the results of these are given in table 10. The first series was taken with the Robertson Mud Bucket, the second with a small dredge consisting of two "buckets" mounted on a frame, designed to give smaller samples than those taken with the mud bucket. To test whether the distribution on the sea bed is random Fisher's "coefficient of dispersion" has been calculated for the results of these two series of samples. A discussion on the use of this, and other, measures of dispersion in animal ecology is given in the paper of Clarke and

Milne (1955). The coefficient of dispersion is given by the formula:

$$c.d. = \sum (x - \bar{x})^2 / \bar{x}(n - 1),$$

where $\sum (x - \bar{x})^2$ is the sum of the squares of the deviations of the individual units (x) from the mean ($\bar{x}$) of all the units (n) comprising the sample. The coefficient leads to unity when the population is randomly distributed, is less than one if the population is over-dispersed (i.e. more or less evenly distributed), and greater than one if it is under dispersed (i.e. more or less aggregated). The significance of the departure from unity is tested by:

$$1 \pm 2 \times \sqrt{[2N/(n - 1)^2]},$$

where, again, n is the number of units in the sample. In the two present series of samples, n = 20 and the limits of the coefficient, for random distribution, are 1.6658 and 0.3342. A coefficient greater than 1.6658 may therefore be taken as significant evidence of aggregation, while a coefficient smaller than 0.3342 would

Table 10. Coefficient of dispersion for three series of samples of *Venus striatula*.

Locality	Kames Bay	Kames Bay	West Loch Tarbert
Date	15/4/57	24/5/57	24/7/57
Gear	Mud bucket	Bucket dredge	Bucket dredge
No. of hauls	20	20	20
Mean No. per haul	301.1	10.6	5.5
Coefficient Dispersion	60.5	10.6	1.86

indicate a significant degree of over-dispersion.

The results from both series of samples give a coefficient far greater than 1.6658 indicating that Venus striatula is aggregated in this population. This result is in agreement with that of Clarke and Milne (1955) who also found significant evidence of aggregation in this species, (referred to in their paper as V. gallina). Young V. striatula in West Loch Tarbert, Argyll, also showed evidence of aggregation (table 10).

The results obtained in studies such as this will depend to some extent on the size of the sample unit used. Evidence for aggregation may disappear if the size of the sample unit is reduced, since this results in the reduction of the mean number found in each sample (Evans, 1952). Moreover, if a small sample unit is used and samples are taken close together, a result which indicates random distribution or over-dispersion may be obtained from a population which in fact consists of large, more or less isolated aggregations. Obvicusly when studying the relationship between animals of the same species on the sea-bed, it is

desirable to collect information concerning both these levels of distribution, that is, the wide-scale distribution over the area, and, in populations which are thus shown to be aggregated, the local distribution within a single group. The first might be expected to reveal distributional patterns based on such factors as settlement preferences, etc., while the second might indicate any reaction by individual adult animals to their neighbours.

In natural sublittoral populations it is impossible to study the small-scale distribution directly - unless by diving - but it is possible in populations occurring on the shore, where small areas can be mapped directly. Holme (1950) found that the distribution of the deposit-feeding bivalve Tellina tenuis was over-dispersed in a population in the Exe estuary, and concluded that this distribution was the result of the individual's reaction to it's neighbours caused by the activity of the sweeping inhalent siphon. The distribution became random at higher population densities.

In artificial populations of Venus striatula in boxes containing sand, kept in a large outdoor tank (see later), the author found that the individuals were dispersed at random at population densities of less than 5,000/sq. metre while in populations of 5,000/sq. metre and 10,000/sq. metre the animals were over-dispersed. In these two artificially high densities however, over-dispersion is more or less inevitable since the cross sectional area of the animal (calculated roughly as mean length × mean breadth) accounted for 22.5% and 45% respectively of the area available.

4. Growth.

There is a continually expanding amount of literature on the rate of growth of various bivalves, since with their hard shells, which in many cases bear annually produced rings, these animals offer ideal subjects for such studies. Much of the literature in this field, however, concerns the commercially important oysters and clams, and until recently, few of the common small bivalves of the British coasts had been studied in this way. In many cases such small bivalves form

a considerable part of the food of bottom living fish (Ford, 1925; Hunt, 1925) and contribute substantially to the productivity of the areas of the sea-bed where they occur (Jensen, 1919; Blegvad, 1925). Obviously therefore study of the rates of growth and of the mortality of such bivalves is of importance in both these fields, as well as being of interest in itself, or in comparison with similar studies in other areas.

In general there are three ways of studying the rate of growth in bivalve mollusca in their natural habitat. These are (1) by means of marking experiments, (2) by the study of annual markings on the shell, and (3) by the study of random samples taken from the population at various times.

The first of these methods, that of marking the shell, returning the animal to its normal habitat, and subsequent recovery, is generally of more use in the study of bivalves living in the littoral zone, than in the sublittoral, since the former are more easily recoverable. This method has been used by some workers to confirm that shell

markings are in fact formed annually (Orton, 1926; Quayle, 1953). The method has certain disadvantages, one being that the animals are disturbed each time measurements are made. Such disturbances may temporarily stop growth with the formation of disturbance rings (Orton, 1926; Weymouth, 1923). In sublittoral populations this method has the additional drawback that successive measurements are not normally possible.

The second method, the study of annual markings on the shell, may provide the most information but its use is limited to those bivalves where shell markings can be shown to be of an annual nature. It must therefore be used in conjunction with either or both of the other methods discussed. Once the rings in any species have been shown to be annual a considerable amount of information may be obtained both of individual and mean rates of growth. The comprehensive paper of Weymouth (1923) on the life-history and growth of the Pismo clam, Tivela stultorum, established the usefulness of this method for the study of the rate of growth of marine bivalves.

In this paper Weymouth reviewed previous literature and went on to show beyond doubt that markings on the shell of Tivela are formed annually. Since then a number of workers have used the method, among them McMillan (1923), Orton (1923), Ford (1925), Fraser & Smith (1928) and Newcombe (1936) and more recently Quayle (1952) and Green (1957).

The third method, the study of random samples of the population, is useful only in certain types of bivalve population. It is essential that the sample can be split into age groups, either from peaks in the size/frequency distribution, or from ring measurements. This method together with the measurement of annual rings on the shell has been used in the present work, since the population of Venus striatula studied was particularly suitable for this treatment.

Throughout the study, length has been used as the measure of growth since this is the most easily determined, and appears to be as good as, or better than any other measurement. Height (dorso-ventral measurement) and thickness, or breadth (greatest lateral measurement) have been used only

to establish their relationships with length. Where ring number is referred to rather than age, age may be determined by adding one half to the ring number, since the true first ring, formed a few months after settlement, is rarely noticeable and has not been included in the ring counts.

In the course of this study, numerous animals have been sexed prior to measurement, but in no case has any significant difference in size been found between males and females. Venus striatula is therefore similar to many other bivalves in showing no difference in rate of growth between the sexes. Thus Fraser and Smith (1928) found no difference between the sizes of males and females of similar ages in Paphia staminea and Saxodomus giganteus, nor did Weymouth, McMillan and Rich (1931) with the razor clam, Siliqua patula. Quayle (1952) stated that in Venerupis pullastra no striking differences between the sizes of males and females were observed.

Shells were measured with a vernier calliper reading to 0.1 mm. Measurements have in most cases been grouped subsequently to summarise the

data. The length is taken as the greatest distance between the anterior and posterior ends of the shell (fig. 32A, L), the height is the distance from the umbo, or from a line along the hinge margin of the shell, to the most ventral part of the shell, and was measured at right angles to the length (H). The thickness, or breadth, is the greatest lateral distance across the tightly closed shell (fig. 32B, W). Ring length is the greatest distance along the longitudinal axis of the shell as it was when the ring was formed (fig. 32A, R1). Shells too small to be measured with the callipers were measured under a binocular microscope with a micrometer eyepiece.

Results from random sampling.

The results obtained from repeated random sampling over the period October, 1956, to December, 1958 are summarised in table 11 and figure 33, in which are given the mean size of the dominant year group together with its standard deviation for the various days on which samples were taken. These results do not include

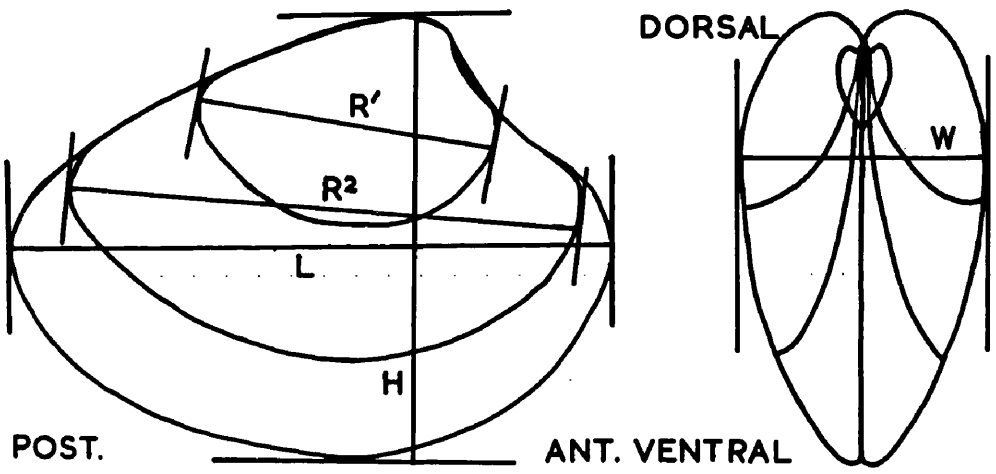


Figure 32. Diagram to show the measurements made on the shells of adults.

H. Height.

L. Length.

R1. Ring 1.

R2. Ring 2.

W. Width, or thickness, or breadth.

Figure 33.

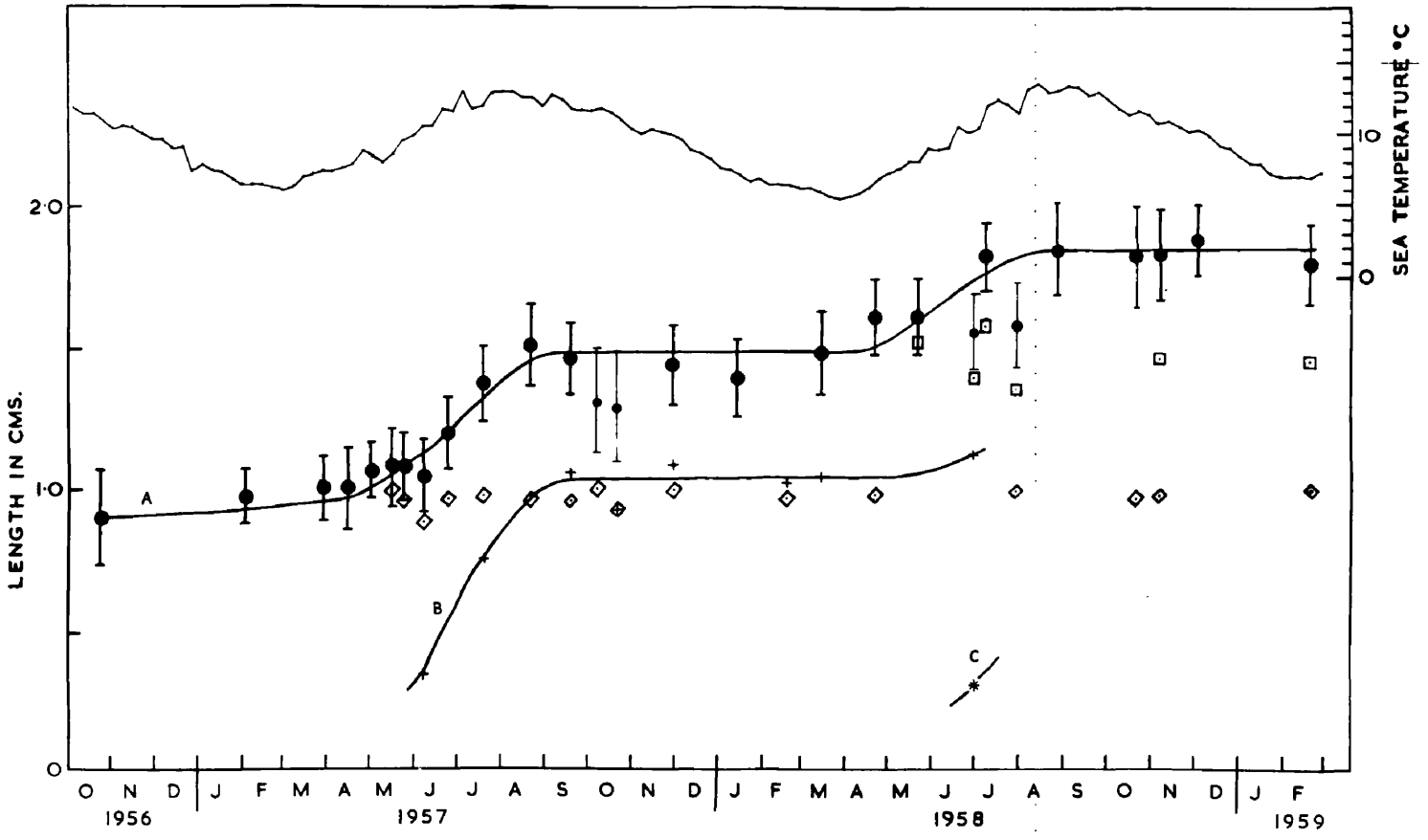
Figure 33. Growth of young Venus striatula in Kames Bay, Millport.

A. 1955 settlement.

B. 1956 settlement.

C. 1957 settlement.

The mean length of Ring 1 (triangles) and Ring 2 (squares) for the 1955 settlement are also shown.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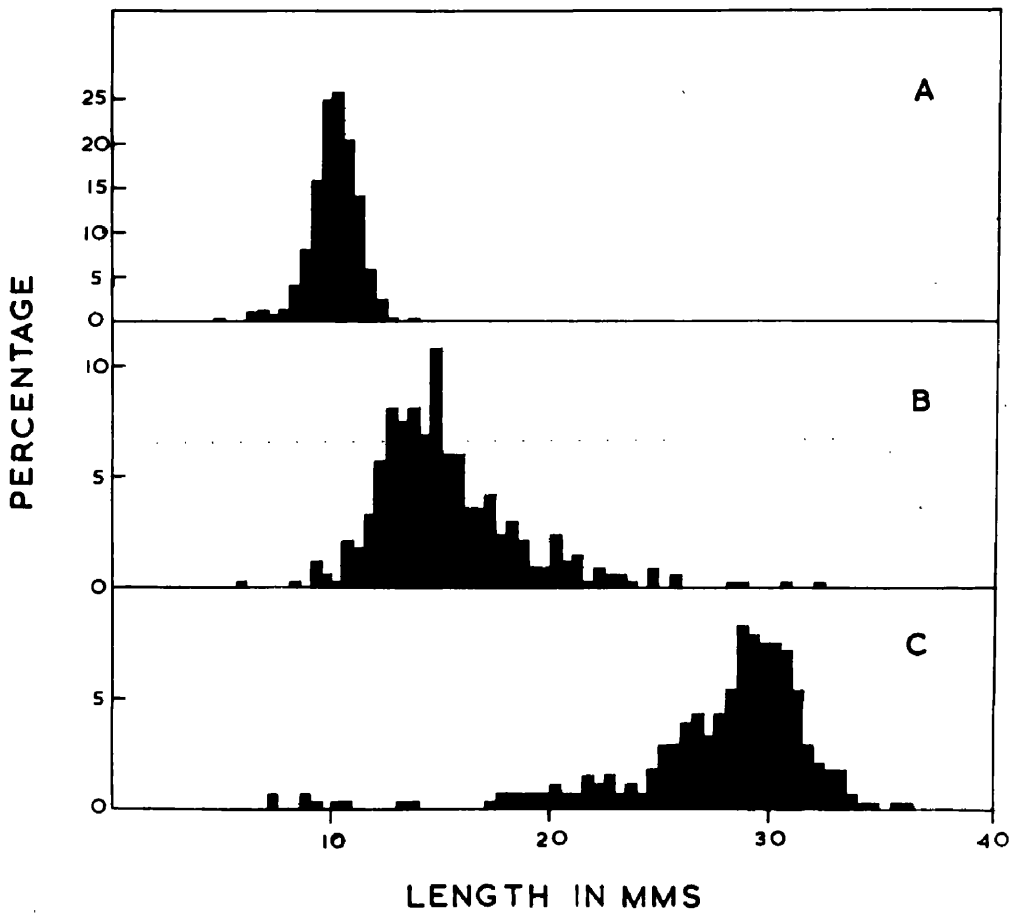


Figure 34. Venus striatula: Size/frequency distributions for three populations.

A. Kames Bay, Millport. March 12th, 1957.

B. Hunterston Sands, Ayrshire. April, 1957.

C. Loch Creran, Argyll. March 18th, 1957.

Table 11. Venus striatula: Summary of data from random sampling. 1955 settlement. Kames Bay.

Length

Date	N	Range	Mean length	Standard deviation
23.10.56	714	21-120	89.85	16.61
1. 2.57	170	59-118	97.82	9.67
29. 3.57	630	48-137	100.98	11.28
15. 4.57	774	24-134	100.96	14.31
3. 5.57	350	77-137	107.54	9.72
16. 5.57	92	61-134	108.27	13.88
24. 5.57	281	46-142	108.28	11.95
7. 6.57	121	53-128	105.60	12.97
24. 6.57	409	70-160	120.70	13.12
19. 7.57	335	89-175	138.12	13.15
21. 8.57	207	108-185	151.55	14.47
8. 9.57	518	114-186	147.18	12.32
7.10.57	323	81-185	131.78	18.38
21.10.57	405	71-198	129.27	19.89
30.11.57	440	113-189	144.64	13.95
14. 1.58	360	99-173	139.89	13.69
17. 2.58	499	104-175	138.92	13.14
14. 3.58	1151	106-191	148.77	14.51
21. 4.58	614	123-200	161.50	13.25
21. 5.58	454	124-205	161.46	13.34
30. 6.58	179	133-193	156.35	12.63
8. 7.58	320	145-215	182.61	11.49
30. 7.58	541	124-215	158.88	14.86
26. 8.58	309	148-218	184.82	13.21
22.10.58	138	135-220	182.54	14.81
7.11.58	212	144-235	183.02	15.80
3.12.58	66	158-224	188.10	12.49
18. 2.59	215	151-222	179.40	13.88

Measurements in one tenth of a millimetre.

Table 11 (contd.). Venus striatula: Summary of data from random sampling. 1955 settlement. Kames Bay.

Length of R1.

Date	N	Range	Mean length	Standard deviation
3. 5.57		Not measured		
16. 5.57	91	61-124	100.53	12.48
24. 5.57	281	46-130	97.61	11.44
7. 6.57	120	32-110	89.37	13.49
24. 6.57	399	42-134	97.74	12.57
19. 7.57	322	40-136	98.67	13.06
21. 8.57	207	53-125	97.42	13.30
8. 9.57	519	50-129	96.50	10.43
7.10.57	223	59-128	101.09	9.79
21.10.57	334	62-125	93.48	10.12
30.11.57	442	68-128	100.98	9.81
14. 1.58		Not measured		
17. 2.58	505	55-120	97.23	9.50
14. 3.58		Not measured		
21. 4.58	613	48-128	98.60	10.55
21. 5.58	455	43-125	98.20	10.03
30. 6.58		Not measured		
8. 7.58		Not measured		
30. 7.58	539	55-120	100.16	9.69
26. 8.58		Not measured		
22.10.58		Not measured		
7.11.58	212	66-125	98.86	3.87
3.12.58		Not measured		
18. 2.59	215	68-126	100.02	8.77

Measurements in one tenth of a millimetre.

Table 11 (contd.). Venus striatula: Summary of data from random sampling. 1955 settlement. Kames Bay.

Length of R2.

Date	N	Range	Mean length	Standard deviation
21. 5.58	454	116-194	152.30	13.16
30. 6.58	180	115-178	140.50	12.77
8. 7.58	324	124-192	158.66	12.27
30. 7.58	541	101-185	136.96	12.90
26. 8.58		Not measured		
22.10.58		Not measured		
7.11.58	212	114-190	147.03	8.01
3.12.58		Not measured		
18. 2.59	215	119-176	146.72	11.10

Measurements in one tenth of a millimetre.

information on growth during the first year following settlement, but this information has been obtained from the few samples collected of the spat of 1956, 1957 and 1958. These results have not been included in detail since they do not form a complete sequence, but they indicate that after settlement in the summer months, the young spat grow to a length of between 0.1 and 0.3 mm. before their first winter, when growth slows or ceases completely. The main year group dealt with here is therefore that of the settlement of 1955, which in October, 1956 was between one year two months and one year five months old.

The results show clearly that noticeable growth is restricted to the summer months of May, June, July and August. In table 12 and figure 35 the mean increment/day added by the animals between each sampling date during 1957 is shown. Growth is slow during May, increases during June and reaches its maximum rate during July. Thereafter the rate is reduced and

Table 12. *Venus striatula*: Daily increments in length of 1955 settlement during 1957.

Period		days	A	B		
From	To		Mean length - Mean Rl Start	Mean length - Mean Rl End	B - A increment	increment per day
15. 4.57	16. 5.57	31	0	07.74	07.74	0.250
16. 5.57	24. 5.57	8	07.74	10.67	02.93	0.366
24. 5.57	7. 6.57	14	10.67	16.23	05.56	0.397
7. 6.57	24. 6.57	17	16.23	22.96	06.73	0.396
24. 6.57	19. 7.57	25	22.96	39.45	16.49	0.660
19. 7.57	21. 8.57	33	39.45	54.13	14.68	0.445

Measurements in one tenth of a millimetre.

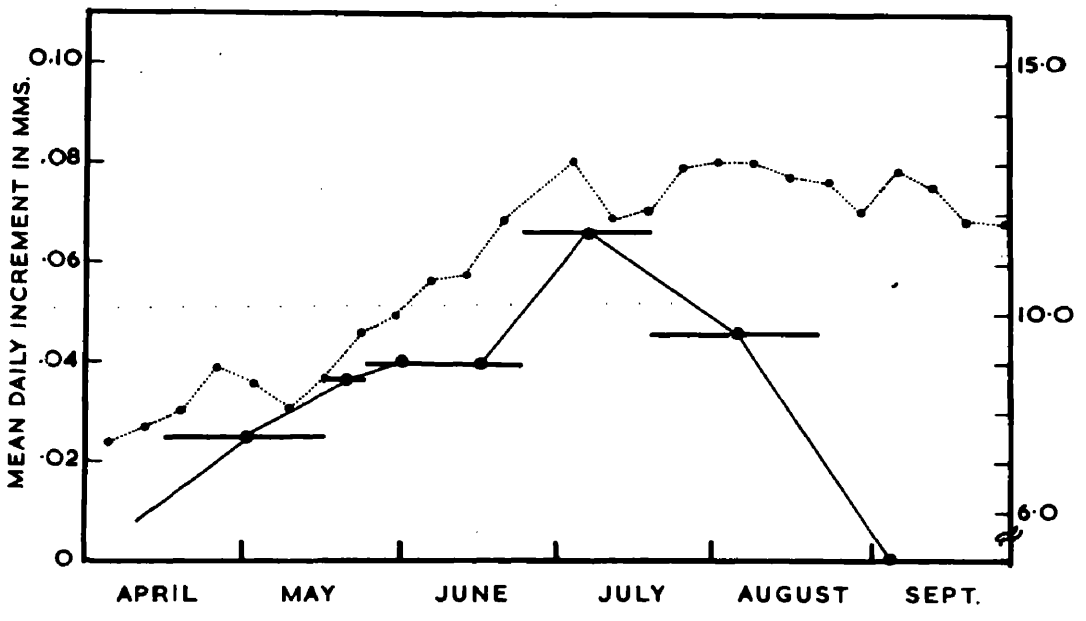


Figure 35. Venus striatula: Daily increments in length of the 1955 settlement in Kames Bay, during 1957.

The weekly mean temperature for the period is also shown.

throughout the winter months it is nil. During the early part of the growing season the growth increment curve follows the temperature curve closely, but the increment curve drops in August although the temperature is then at its highest for the year. This condition is similar to that for the Pismo clam - Tivela stultorum (Weymouth, 1923; Coe, 1947) where there is also an increase in the rate of growth with the spring increase in temperature until August when growth falls off, and to that of Venerupis pullastra (Quayle, 1952). Both Weymouth and Quayle consider that the falling off of growth at a time when the water temperature is still high, is connected with breeding, and this view was also put forward by Orton (1928) who found that growth of the shell of Ostrea edulis took place in the spring and autumn, but not in the summer, when the animals were breeding. He suggested that there is a physiological antagonism between reproductive activities and shell growth. With Venus striatula this is not the case. Ripening of the gonads takes place throughout the winter although at an increased rate in March and April.

Spawning occurs in May, June and July (see earlier), that is, during those months when the animals are also actively growing.

The same trend of growth also takes place in the two species of Mytilus found in California and in other invertebrates there (Coe and Fox, 1944). They suggest that food supply is the factor which controls the rate of growth rather than small changes of temperature. At Millport, a diatom increase occurs in the spring (Marshall and Orr, 1927). This coincides with the period of proliferation of the gonad of Venus striatula as noted earlier, while growth does not start until about a month later, when it follows closely the increase in temperature of the sea-water.

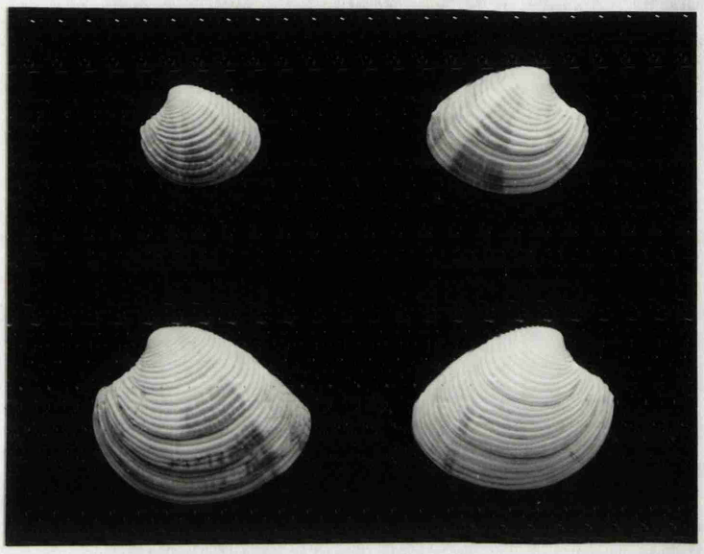
The shell of Venus striatula bears a number of more or less well-defined rings on the surface (plate 4). The results of the series of random samples taken of the settlement of 1955 show clearly the annual nature of these rings, and their usefulness therefore as indications of the age of any particular individual. The measurements of the rings in the samples are

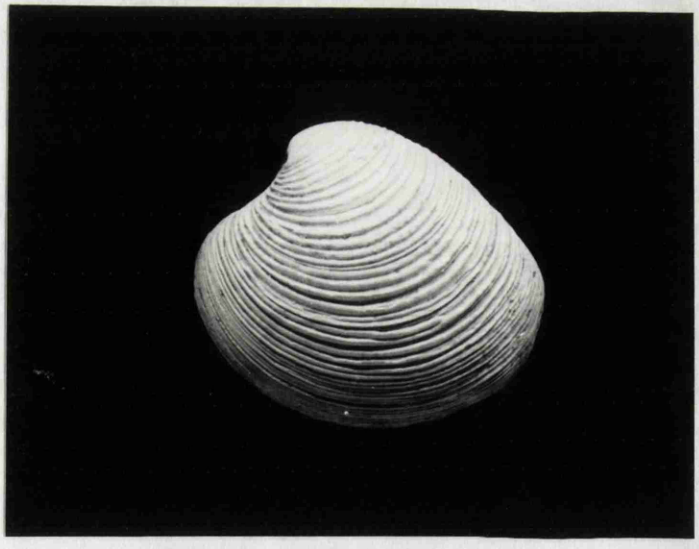
Plate 4.

Plate 4. Venus striatula:

A. Shells from the Kames Bay population to show the annual rings.

B. Shell from the Loch Creran population, to show closely packed rings in older specimens.





summarised in table 11 and figure 33, which show the mean length of each ring in each sample together with the standard deviation. In 1957, the first sign of renewal of active growth after the winter months occurred in the collection taken on May 16th. In this collection some animals showed a small edge of obviously new growth marked off from the previously formed shell by a ring. By June 7th, all animals in the collection were showing a similar edge of newly formed shell, and a ring was distinguishable in each. The mean length of this ring in these and subsequent samples corresponds to the mean length of the animals in the collections taken during the winter of 1956 - 1957. A similar ring, corresponding in length to that of the animals in the winter of 1957 - 1958 became apparent when growth restarted in 1958. No rings were formed on the shell between these two dates. One ring only therefore is formed each year which becomes apparent at the recommencement of growth after the winter, and such rings may be used for the determination of the age and rate of growth of individual animals.

Growth from Ring Measurements.

The series of random samples has indicated the seasonal variation in the rate of growth, and demonstrated the annual nature of the rings formed on the shell. The series gives information concerning the first three years of the animals life only. To determine the form of the general growth curve of the species, measurements of the annual rings on the shells of older individuals from Kames Bay have been used.

As the animal ages the annual growth increment in length lessens, so that the later formed rings are closely packed. For this reason it is usually impossible to distinguish the later-formed rings in old shells. However shells have been found in which ten rings were distinguishable, so the duration of life may be ten or eleven years and probably in some cases more.

In all 372 measurements of annual rings in older shells from Kames Bay have been made. These are grouped according to ring number in table 13 and the mean length of each ring is given in table 14. These figures have been used to construct the curve

Table 13. Venus striatula: Ring measurements in Kames Bay.

Mid point	R1	R2	R3		Mid point	R4	R5	R6	R7	R8	R9	R10
043	1				163	1						
048	1				168	1						
053	6				173	2						
058	4				178	7						
063	11				183	8						
068	9				188	6	1					
073	10				193	11	1					
078	6				198	2	3	1				
083	12				203	5	4	0				
088	9				208	6	5	0				
093	4				213	3	2	0				
098	4	3			218	1	2	2				
103	4	1			223	2	1	3				
108	2	4			228		0	2				
113	3	4			233		2	3				
118	1	9			238		1	0	1			
123	1	12			243		1	0	1			
128	1	11	1		248			1	2			
133	0	8	1		253			0	0	1		
138	0	13	1		258			1	0			
143	0	8	1		263			1	0			
148	1	7	6		268			1	1			
153		3	11		273				1		1	
158		2	8		278							
163		4	15		283							1
168		1	12									
173			5									
178			10									
183			3									
188			8									
193			3									
198			4									
203			1									

Table 14. A. Venus striatula: Ring measurements. Kames Bay. Means.

Ring No.	1	2	3	4	5	6	7	8	9	10
N	90	90	90	55	23	15	6	1	1	1
Mean length (cms.)	0.78	1.32	1.68	1.93	2.11	2.33	2.53	2.54	2.75	2.84

B. Venus striatula: Mean of all measurements for each ring (random samples).

Ring No.	1	2
N	5262	1711
Mean length (cms.)	0.98	1.47

C. Venus striatula: Mean total length animals during winter (random samples).

Winter No.	1	2	3
N	2288	3792	278
Mean length (cms.)	0.97	1.45	1.84

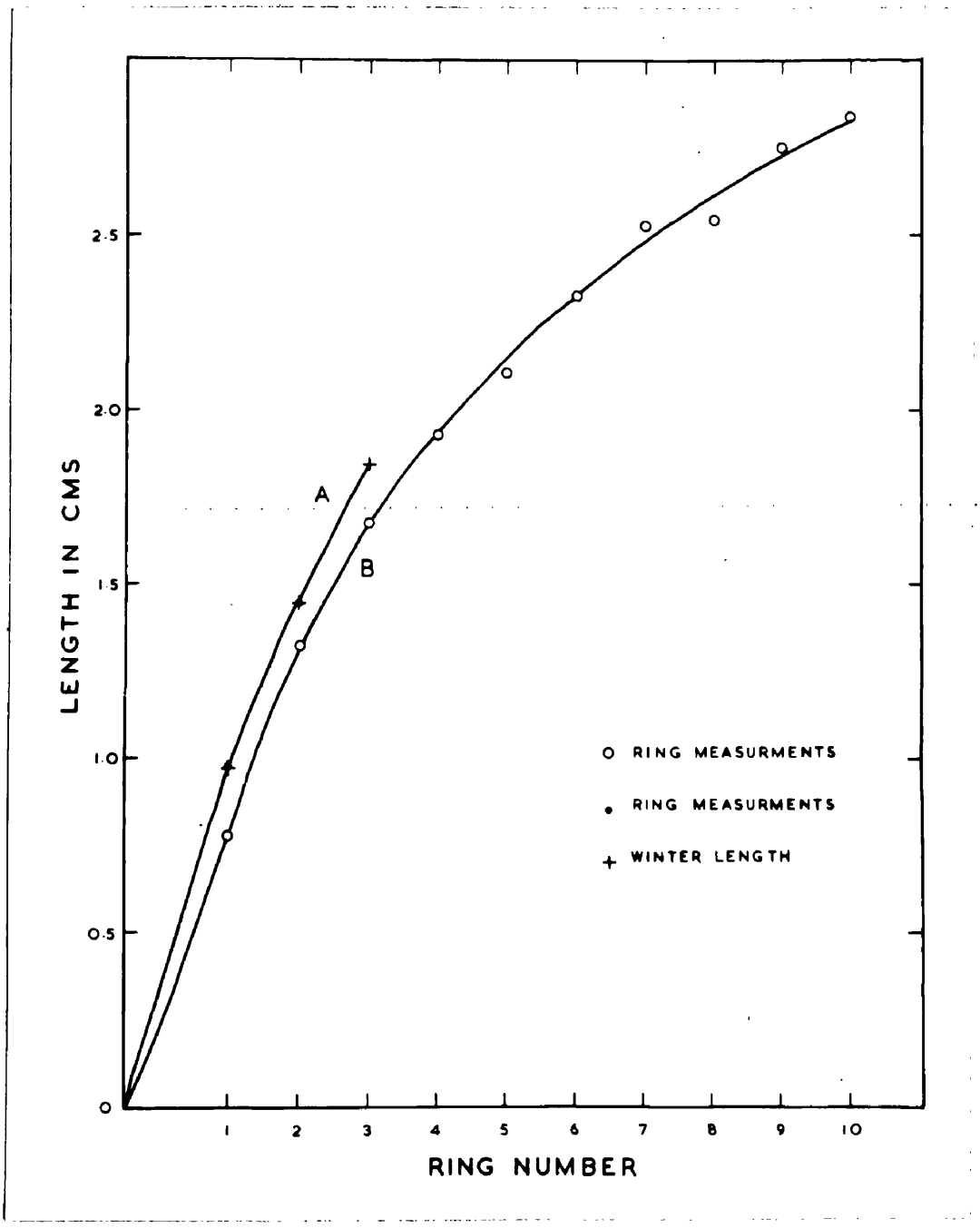


Figure 36. General growth curve (Length/Number of rings) for Venus striatula in Kames Bay.

A. Based on measurements of the 1955 settlement.

B. Based on measurements of annual rings in older shells.

shown in figure 36B. Since the measurements for each ring include those of a number of different year classes, the curve shows the mean trend of growth, unaffected by annual variations in rate caused by short term environmental fluctuations. Also in figure 36 (A) are shown the mean values of the length for each ring for the 1955 settlement. These values have been derived from two sources, firstly, the mean of all measurements for each ring, (table 14B) and secondly the mean total length of the animals during the corresponding winter (table 14C). These two sets of measurements for the 1955 settlement agree almost exactly, demonstrating again the validity of the ring measurements, but there is some difference between the rate of growth of the 1955 settlement and that of the rest of the population as shown by the general growth curve: the 1955 settlement has shown a higher mean rate of growth than that of earlier spatfalls.

Examination of the measurements taken showed that there is a considerable variation in the rate of growth from one individual to another. This is partly the result of annual variations in the rate

of growth of the population as a whole, but even between animals of the same year group there is still a wide range of variation. This may be ascribed to three sources: firstly, there is a period of approximately three months in the summer during which settlement may take place, so that animals of the same year group may in fact differ in age by as much as three months, secondly, the rate of growth of individuals may be affected by local, small-scale differences in the environment, in Kames Bay this factor is probably not very important since the area is small and very uniform. Thirdly, the observed differences in the rate of growth may be the result of inherited physiological factors.

Annual-ring measurements have also been made on Venus striatula from two other localities in Scotland; Hunterston Sands, Ayrshire, and Loch Creran, Argyll. These measurements are given in tables 15 and 16, and in figure 37 where they are compared with those for Kames Bay. The trend of growth is similar in all three cases but minor differences occur which are probably the result of

Table 15A. Venus striatula: Ring measurements: Fairlie Shore.

Mid Point	R1	R2	R3
043	2		
048	12		
053	7		
058	12		
063	8		
068	13		
073	11		
078	9	1	
083	6	0	
088	9	3	
093	5	1	
098	5	8	
103	0	13	
108	0	9	
113	0	9	1
118	1	18	0
123		13	2
128		8	1
133		6	1
138		3	4
143		2	5
148		0	2
153		0	5
158		1	10
163			7
168			2
173			5
178			5
183			2
188			2
193			2
198			

Mid Point	R4	R5	R6	R7
158	1			
163	0			
168	0			
173	0			
178	1			
183	1			
188	0			
193	1	1		
198	0	0		
203	2	0		
208		0		
213		0		
218		3		
223			2	
228				
233				1
238				1
243				
248				
253				

Table 15B. Venus striatula: Length of shells with 2 - 8 rings: Fairlie.

Mid Point	2	3	4	5	6	7	8
113	1						
118	0						
123	0						
128	2						
133	1	2					
138		3					
143		4					
148		4	2				
153		6	1				
158		5	1				
163		6	2				
168		4	6				
173		2	2				
178		2	6				
183		1	5				
188			5				
193			2				
198			7				
203			2	1			
208			2	1			
213			2				
218			1				
223			2				
228			0				
233			1		1		
238					0		
243					1		
248					0		1
253					1		1

Table 16A. *Venus striatula*: Ring measurements: Loch Creran.

Mid Point	R1	R2	R3
058	2		
053	1		
068	2		
073	8		
078	10		
083	7		
088	15		
093	15		
098	14		
103	12		
108	14		
113	15	1	
118	8	3	
123	10	5	
128	3	3	
133	2	7	
138		12	1
143		13	1
148		17	0
153		16	0
158		16	4
163		13	2
168		6	3
173		12	4
178		6	8
183		3	16
188		2	16
193			17
198			14
203			15
208			7
213			5
218			3
223			1
228			0
233			1

Mid Point	R4	R5	R6	R7	R8
168	2				
173	0				
178	1				
183	0				
188	1				
193	3				
198	5	1			
203	4	1			
208	5	0	1		
213	22	1	0		
218	14	1	1		
223	17	2	0		
228	7	10	0		
233	6	11	0	1	
238	6	13	3	0	
243	1	10	7	0	
248	1	4	5	2	
253	1	6	5	0	
258		2	5	2	
263		2	1	3	
268			1	0	1
273			3	0	1
278			1	3	0
283				2	0
288				1	0
293					0
298					1
303					

Table 16B. *Venus striatula*: Length of animals with 1 - 9 rings. Loch Creran.

Mid Point	1	2	3
073	2		
078	0		
083	1		
088	1		
093	1		
098	3		
103	0		
108	2		
113			
118			
123			
128			
133		1	
138		2	
143		1	
148		0	
153		0	
158		0	
163		0	
168		0	
173		1	1
178			3
183			1
188			2
193			2
198			3
203			1
208			1
213			1

Mid Point	4	5	6	7	8	9
208	2					
213	3					
218	1	1				
223	2	1				
228	1	0				
233	2	0				
238	1	1				
243	0	0		1		
248	1	1	1	1	1	
253		0	0	1	0	
258		1	1	0	1	
263		0	1	2		
268		0	1	1		
273		1	0			1
278			0			
283			1			

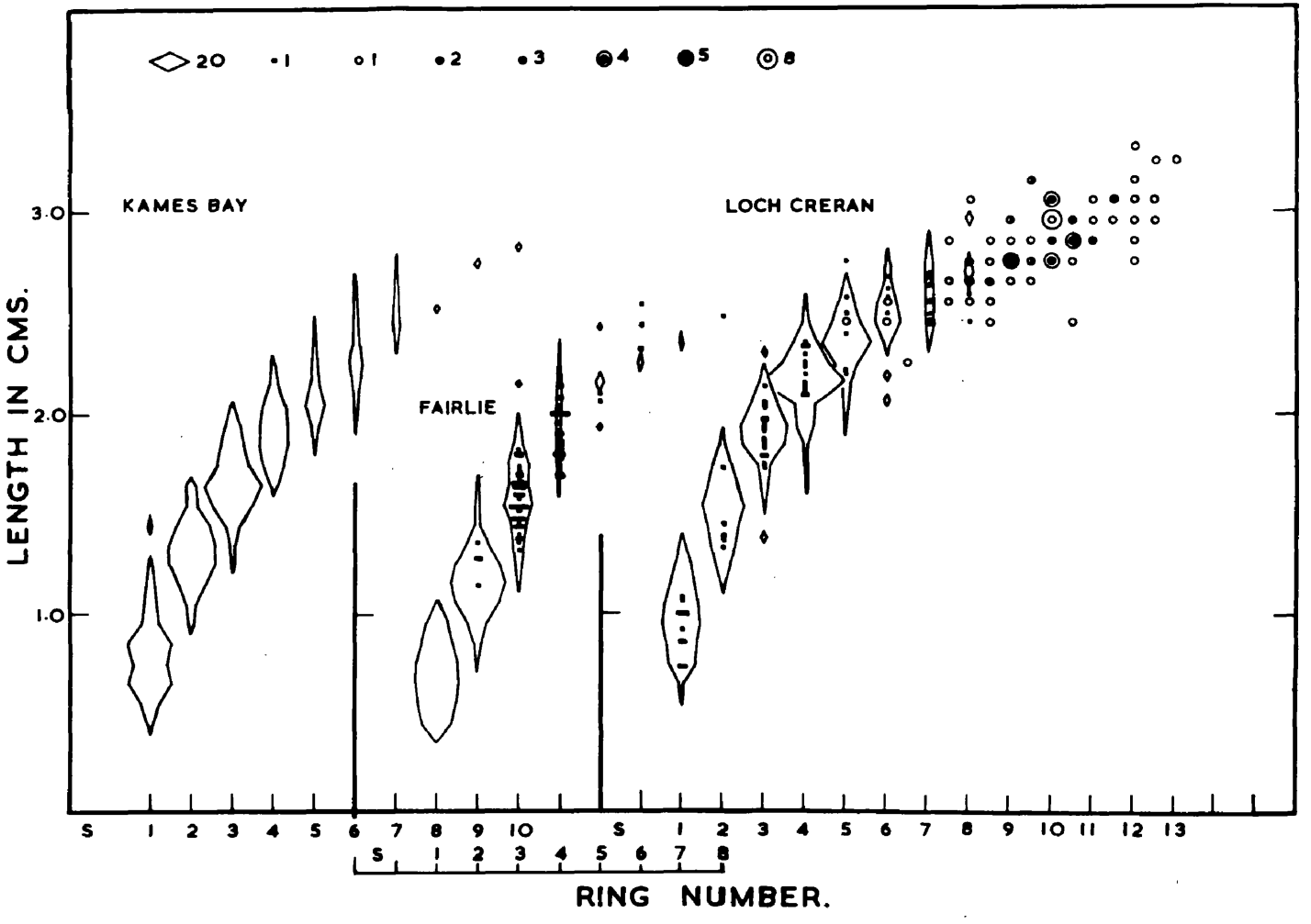
Table 16C. Venus striatula: Estimated age/length. Loch Creran.

Mid Point	Mid Point Estimated Age.															
	5	6	6.5	7	7.5	8	8.5	9	9.5	10	10.5	11	11.5	12	12.5	13
215																
225			1													
235																
245	1	1		1			1				1					
255		1		0	1	1	1									
265				1	1	3	2	1	1							
275				0	0	1	1	4	2	3	1	1		1		
285				1	1	0	1	2	1	3	4	3		1		
295						0		2	0	8	3	1	1	1	1	
305						2			0	5	1	1	3	1	1	
315									2					1	0	
325														0	1	1
335														1		

Figure 37.

Figure 37. Venus striatula: Summary diagram showing annual ring measurements for three localities: Kames Bay, Millport, Hunterston (Fairlie) Sands and Loch Creran.

Kites.	Measurements of annual rings.
Shaded histograms.	Measurements of lengths of shells with 1, 2, etc., rings.
Circles.	Measurements of shells of estimated age.


20
1
1
2
3
4
5
8
KAMES BAY
FAIRLIE
LOCH CRERAN
LENGTH IN CMS.
3·0
2·0
1·0
S 1 2 3 4 5 6 7 8 9 10 S 1 2 3 4 5 6 7 8 9 10 11 12 13
S 1 2 3 4 5 6 7 8
RING NUMBER.

differences in the period of maximum settlement, and in the length of the growing season during the summer.

Height/length and Thickness/length Relationships.

In table 17 are shown the height/length and thickness/length relationships for animals between 0.35 and 3.65 cms. in length. Earlier (table 7 and fig. 23) the similar relationships for the larva were given. During the early post larval stage the ratio of height to length changes from that typical of the larva to that of the adult. In the adult the ratio of height to length and of thickness to length remains relatively constant as size increases, and there is little variation from the mean ratio, except in extremely large individuals where growth tends to become completely transverse, resulting in increase in the thickness without a corresponding increase in the length. The two curves approximate closely to straight lines showing that there is no radical change of shape with age. A similar straight line relationship was found by Weymouth (1923) for the Pismo clam - Tivela stultorum, and also by Crozier

Table 17. *Venus striatula*: Height/length and Thickness/length relationship.

A. Balloch Bay.

Mid Point length	No. of specimens	mean length	mean height	mean thickness	Height/ length	Thickness/ length
0.35	10	0.366	0.337	0.197	0.921	0.538
0.45	13	0.452	0.394	0.232	0.872	0.513
0.55	11	0.545	0.485	0.285	0.890	0.523
0.65	2	0.665	0.570	0.360	0.857	0.541

B. Kames Bay.

Mid Point length	No. of specimens	mean length	mean height	mean thickness	Height/ length	Thickness/ length
0.75	4	0.779	0.668	0.362	0.858	0.465
0.85	10	0.886	0.744	0.417	0.840	0.471
0.95	10	0.967	0.810	0.469	0.838	0.485
1.05	10	1.053	0.881	0.502	0.837	0.477
1.15	10	1.131	0.922	0.548	0.815	0.485
1.25	10	1.253	1.045	0.639	0.834	0.510
1.35	10	1.369	1.158	0.685	0.846	0.500
1.45	10	1.465	1.249	0.749	0.853	0.511
1.55	10	1.548	1.313	0.810	0.848	0.523
1.65	10	1.650	1.403	0.846	0.850	0.513
1.75	10	1.761	1.490	0.930	0.846	0.528
1.85	6	1,875	1.588	0.982	0.847	0.524
1.95	10	1.940	1.647	1.040	0.849	0.536
2.05	9	2.041	1.695	1.044	0.830	0.512
2.15	5	2.158	1.804	1.120	0.836	0.519
2.25	1	2.240	1.930	1.130	0.862	0.504

Table 17. Venus striatula: Height/length and thickness/length relationship.

C. Loch Creran.

Mid Point Length	No. of specimens	mean length	mean height	mean thickness	Height/ length	Thickness/ length
0.75	2	0.750	0.670	0.380	0.893	0.507
0.85	2	0.885	0.780	0.455	0.881	0.514
0.95	1	0.940	0.800	0.500	0.851	0.532
1.05	2	1.050	0.935	0.555	0.890	0.529
1.15						
1.25						
1.35	2	1.375	1.190	0.735	0.865	0.535
1.45						
1.55						
1.65						
1.75	3	1.770	1.540	0.933	0.870	0.527
1.85	4	1.855	1.610	1.010	0.868	0.544
1.95	4	1.955	1.670	1.020	0.854	0.522
2.05	5	2.042	1.714	1.056	0.839	0.517
2.15	6	2.178	1.908	1.152	0.876	0.529
2.25	7	2.267	1.989	1.219	0.877	0.538
2.35	5	2.364	2.014	1.218	0.852	0.515
2.45	6	2.485	2.115	1.366	0.851	0.550
2.55	10	2.541	2.189	1.378	0.861	0.542
2.65	15	2.652	2.323	1.494	0.876	0.563
2.75	12	2.762	2.399	1.573	0.869	0.570
2.85	24	2.862	2.487	1.590	0.869	0.556
2.95	25	2.952	2.552	1.647	0.865	0.558
3.05	26	3.051	2.632	1.660	0.863	0.544
3.15	15	3.149	2.671	1.679	0.848	0.533
3.25	10	3.262	2.829	1.840	0.867	0.564
3.35	7	3.340	2.799	1.793	0.838	0.537
3.45	2	3.450	2.885	1.790	0.836	0.519
3.55	1	3.600	3.010	1.800	0.836	0.500
3.65	1	3.610	3.020	2.060	0.837	0.571

Table 17. Venus striatula: Height/length and thickness/length relationship.

D. Fairlie Shore.

Mid Point length	No. of specimens	mean length	mean height	mean thickness	Height/ length	Thickness/ length
0.95	2	0.940	0.845	0.510	0.899	0.543
1.05						
1.15	3	1.187	1.053	0.643	0.887	0.542
1.25	5	1.244	1.080	0.688	0.868	0.553
1.35	7	1.366	1.203	0.759	0.881	0.556
1.45	10	1.460	1.282	0.815	0.878	0.558
1.55	6	1.542	1.355	0.845	0.879	0.548
1.65	2	1.685	1.500	0.935	0.890	0.555
1.75	9	1.757	1.557	0.972	0.886	0.553
1.85	9	1.850	1.623	1.024	0.877	0.554
1.95	3	1.967	1.723	1.097	0.876	0.558
2.05	11	2.049	1.773	1.091	0.865	0.532
2.15	5	2.132	1.832	1.144	0.859	0.537
2.25	5	2.225	1.924	1.220	0.865	0.548
2.35	3	2.340	2.030	1.250	0.868	0.534
2.45	3	2.490	2.140	1.340	0.859	0.538
2.55	2	2.570	2.200	1.440	0.856	0.560
2.65						
2.75						
2.85	2	2.855	2.525	1.485	0.884	0.520
2.95						
3.05	1	3.100	2.820	1.850	0.910	0.597
3.15						
3.25	1	3.230	2.820	2.020	0.873	0.625

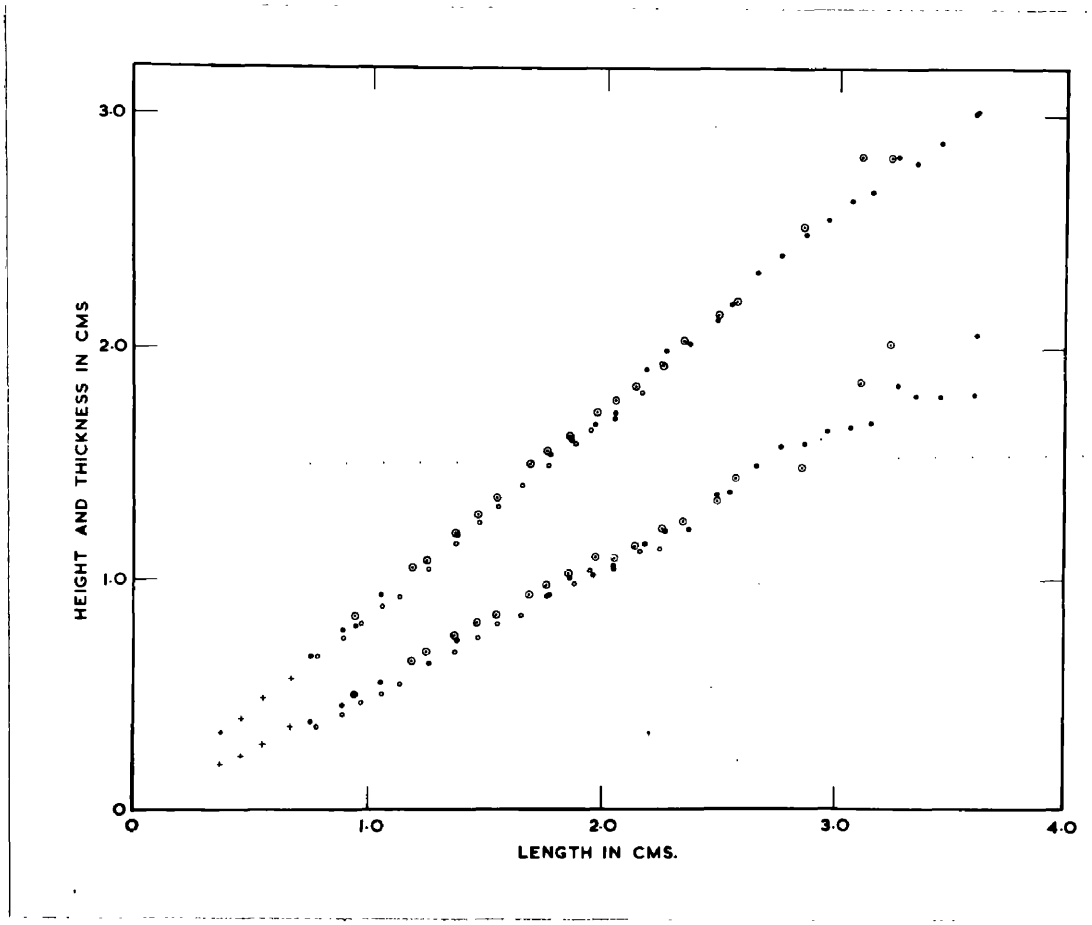


Figure 38. Venus striatula: Height/length and thickness/length relationships for adults.

Crosses. Balloch Bay, Cumbrae.

Open circles. Kames Bay, Millport.

Dotted circles. Hunterston Sands, Ayrshire.

Closed circles. Loch Creran, Argyll.

(1914) for Dosinia discus, and Quayle (1952) for Venerupis pullastra.

5. Mortality.

The difficulty of obtaining accurate quantitative samples in hard sand such as occurs in Kames Bay has already been briefly mentioned. Because of this difficulty, and of the aggregated distribution of Venus striatula in the Bay, the series of random samples gave no direct information on the intensity of mortality. However a rough estimate of the mortality which had occurred prior to sampling could be obtained from counts of the number of dead shells present in the samples, compared with the number of living animals. The presence of one dominating year group in the population meant that it was possible to assume that the majority of the dead shells found were derived from this year group, and this assumption was supported by the appearance of such shells, which were almost entirely clean and unworn. In practice it was found that older shells were easily picked out from those derived from the 1955 settlement.

Only one cause of mortality was definitely established - that of predation by the gastropod drill Natica poliana alderi (Forbes). During the first year of life of the bivalve, Natica was responsible for the death of about fifteen per cent of the population in the area studied. This figure represents about 40% of the total mortality during this period. Quayle (1953) studying a population of young Venerupis pullastra in Balloch Bay, Cumbrae, found that approximately 5% of the dead shells found were drilled by a gastropod, probably Natica.

During the second year of life of the bivalves the importance of Natica as a cause of mortality lessened. Only about 5% of the animals remaining alive at the end of the first year were bored during the second year of life. This figure represents only about 15% of the total mortality during the period. In the third year of life of the bivalves the intensity of predation is again much less (1 - 2%). Natica is therefore an important predator only during the first year, or possibly two years of the life of Venus striatula.

Apart from the mortality due to the activities of Natica alderi, there was a considerable "residual" mortality, the causes of which are unknown. In the period from the time when the bivalves reached a length of about 2 - 3 mms. until October 1956 (approximately the first year of life) this residual mortality accounted for the death of about 25% of the population. The total mortality during this period was therefore about 40%. During the second year of life of the bivalves the total mortality was about 33% of the animals remaining alive at the end of the first year, of which only about 5% was caused by Natica. During the third year of life, the percentage mortality was of the same order.

These figures indicate that there is a fairly high mortality during the early years after settlement and that few of the animals originally present live to complete the maximum life span possible. A similar mortality has been found to occur in Tivela stultorum (Weymouth, 1923) although there, mortality was largely the result of human predation, since T. stultorum is an important food species in the United States.

The figures obtained for the rate of mortality apply only to those causes which leave the empty shell intact in the same position which it occupied in life. Another possible cause of mortality which does not fulfil this condition is that of predation by bottom feeding fish, many of which are known to take bivalves. However fish are not abundant in Kames Bay and their affect on the population of Venus striatula is probably small.

It was thought that the mortality might in some way be the result of the high density of the 1955 settlement, since it is known that the mortality of some animals is markedly affected by their population densities. A series of experiments was therefore carried out during 1957 in a large outdoor tank at Millport which had originally been used for the tank breeding of oysters. Wooden boxes, approximately 0.1 sq. metre in area and 22 cms. in depth, were filled with sand to a depth of about 10 cms., and placed on the bottom of the tank, which was then filled with sea-water to a depth of about three feet. The sand was obtained from Kames Bay, and sieved before use.

Table 18. Venus striatula: Growth and mortality at different artificial population densities.

Population density per $^{1}/_{10}$ sq. m.	Mean Length	Mean Length R1	% growth	% mortality
10	1.22	0.99	23.2	0
30	1.29	1.05	22.9	6.67
30	1.19	1.01	17.8	6.67
100	1.23	1.04	18.3	9.0
100	1.24	1.02	21.6	8.0
200	1.26	1.05	20.0	6.67
500	1.26	1.08	16.7	
1000	1.25	1.06	17.9	7.0
Kames Bay	1.21	0.98	23.5	

Venus striatula from Kames Bay were placed in the boxes to give artificial population densities of 10, 30, 100, 200, 500, and 1,000 per/one tenth of a square metre. These populations were set up on March 31st, 1957, and the experiments were brought to a close on June 28th, 1957, when all animals both alive and dead were preserved.

The results obtained are summarised in table 18. Over the range of population density from 300/sq. M to 10,000/sq. M. the percentage mortality during the three months of the experiment was apparently not affected by population density in any way.

The animals in the experimental populations were measured at the beginning and end of the experiment, and the percentage growth increment for each group is shown in table 18. The measurements were too small to show whether there is any significant density affect on growth, but were similar to those which occurred in members of the natural population over the same period.

In a similar experiment with Venerupis semidecussata, Ohba (1956) found that percentage

mortality increased with population density and that there was a linear relationship between the two in populations of less than 5,000/sq.M. Moreover individual growth was less in the denser populations. However, the mortality recorded in his experiments was much higher than that recorded here (68.8% in a population of 10,000/sq.M.) so that the conditions were apparently more stringent.

VII. Summary.

1. The functional morphology of the main organ systems of twelve of the seventeen British species of Veneracea is described and figured.

2. The functional morphology of Mysia undata is described and compared to that of the Veneridae and the Petricolidae. The systematic position of Mysia undata is discussed.

3. Adaptation and evolution within the Veneridae and the origin of the boring habit in the Petricolidae, are discussed.

4. Seasonal changes in the gonads of both sexes of V. striatula were followed by macroscopic and microscopic examination, or study of sections, in over 700 animals. The sex ratio was approximately equal, and no hermaphrodite individuals were found.

5. The time and duration of the spawning period of V. striatula during 1957 and 1958 were found.

Spawning in both males and females takes place at intervals throughout this period. Intensity of spawning builds up to a peak near the middle of the season and then drops. In laboratory experiments, no animals spawned at temperatures below 11.0°C. Spawning may be induced by rise of temperature or stimulation by sexual products. "Epidemic spawning" may be initiated by either males or females.

6. Natural spawning was observed in six species of the Veneridae. Shell movements play no part in the spawning act.

7. Artificial fertilisation is impossible since eggs removed from the ovary still possess the germinal vesicle intact, and this is not broken down in sea-water.

8. The veliger larva of V. striatula has been cultured from eggs obtained from natural spawnings fertilised in the laboratory, and reared until settlement took place.

9. Laboratory experiments were carried out to find the effect of temperature on larval development and growth. Larvae were grown in two experiments at temperatures between 5.0 and 26.0°C and observations on the development of the eggs were also made.

10. The organs of the veliger and pedo-veliger stages are described and figured. The main changes occurring at metamorphosis are briefly described and discussed.

11. A population of V. striatula in Kames Bay, Millport, consisting mainly of animals from one year group, is described.

12. The rate of growth of young V. striatula was found from a series of random samples taken over the period October 1956 to January 1959. The growing season was found to be restricted to the summer months of May, June, July and August.

13. Certain markings on the shell of V. striatula are shown to be of an annual nature, and a

general growth curve has been constructed from measurements of 372 of these. This follows the usual sigmoid form.

14. The rate of mortality among the 1955 spatfall in Kames Bay is described.

15. In artificial populations, mortality was found to be independent of the population density.

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Appendix 1.

A Note on Predation of Venus striatula by Natica poliana alderi.

As described earlier an increase in the numbers of Venus striatula in Kames Bay has occurred since 1949, the increase being attributed particularly to the spatfall of 1955. Of the dead shells from this population a number show holes bored by the gastropod drill, Natica poliana alderi (Forbes) (Plate 5). Clarke and Milne (1955) stated that this gastropod was not present in Kames Bay, although it was present in the nearby White Bay. At the time of their survey Philine aperta was the important carnivorous gastropod in Kames Bay. During the course of the present study, numerous samples of the fauna of Kames Bay have been taken over the area studied by Clarke and Milne, and Philine aperta has not been found. On the other hand Natica poliana alderi is now common, both adults and young specimens, as well as egg collars, having been taken on many occasions. The apparent coincidence of this change in the carnivorous gastropod fauna with the increase in numbers of Venus striatula is striking. This note

Plate 5.

Plate 5. Photograph of specimens of *Natica poliana alderi* and various bivalves from Kames Bay with holes bored by this species.

left. *Venus striatula*: the lower four show incomplete borings.

centre. from top to bottom:

Montacuta ferruginosa

Nucula turgida

Thyasira flexuosa

Spisula subtruncata

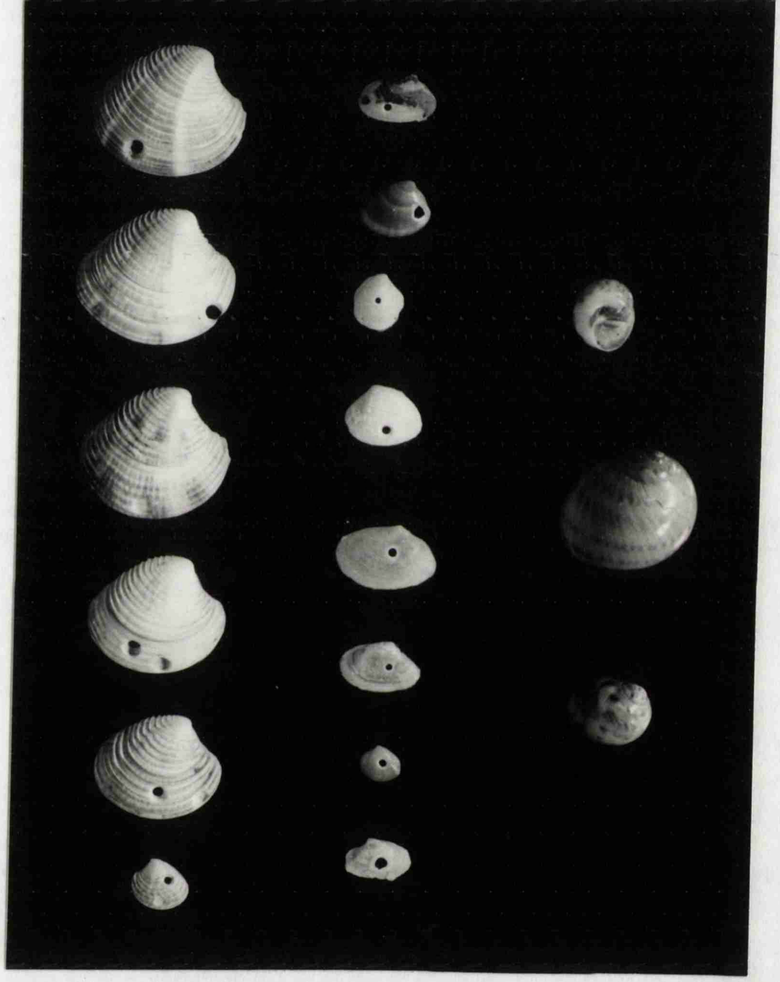
Tellina tenuis

Tellina fabula

Cyprina islandica

Thracia sp.

right. *Natica poliana alderi*.



discusses certain aspects of the relationship of these two species in the area.

Studies of the predation of bivalves by boring gastropods have been carried out by a number of workers, but such studies have for the most part concerned the commercially important oysters and clams, and drills such as Urosalpinx and Oceanebra belonging to the Muricidae. These gastropods may cause considerable damage to natural and cultivated oyster beds, especially among the young spat. Thus Nelson (1923) found that in Delaware Bay, U.S.A., 33% of the spat from one oyster bed, 41% from another, and 50% from a third had been drilled. More recently Hancock (1954) has shown that Urosalpinx cinerea on Essex oyster beds may consume at least 58% of the young oyster spat in three months from the time when the spat reach a length of 4 - 5 mm. He estimated that 540,000 spat were destroyed by Urosalpinx in an area of only 6,250 square metres of oyster ground. Carriker (1955) has reviewed the subject of predation by the drills Urosalpinx and Eupleura.

Comparable information on the damage caused to natural populations by Natica is not available.

The mortality caused by Natica poliana alderi in Kames Bay has been described earlier. During the first year of life of the bivalves, Natica was responsible for the death of about fifteen per cent of the population in the area studied. This figure represents about 40% of the total mortality from all causes during this period. Quayle (1953) studying a population of young Venerupis pullastra in Balloch Bay, Cumbrae, found that approximately 5% of the dead shells found were drilled by a gastropod, in this case probably also Natica.

During the second year of life of the bivalves, the importance of Natica as a cause of mortality lessened. Only about 5% of the animals remaining alive at the end of the first year were bored during the second. This figure represents only about 15% of the total mortality during the period. In the third year of life of the bivalves, the intensity of predation was again much less (1 - 2%). Natica is therefore an important predator only during the first year or possibly two years of the

life of Venus striatula.

The factors which might affect the intensity of predation by a predator such as Natica alderi on a single species, may be summarised under four headings, as follows:

(1) Food preferences of the predator.

(2) Availability of alternative food.

(3) Density of prey.

(4) Density of predator.

The evaluation of the effects of these factors would require a lengthy study, but some indications of the importance of some of them have been gained, and although these are incomplete, it is thought that they may be usefully included here.

(1) Food preferences and availability of alternative food.

The species of Bivalve which have been found bored by Natica in the Millport area are given below:

Species found bored by Natica alderi in Kames Bay.

Nucula turgida Leckenby & Marshall

Nucula tenuis (Montagu)

Thyasira flexuosa (Montagu)

Montacuta ferruginosa (Montagu)

Dosinia lupinus (Montagu)

Venus striatula (da Costa)

Venerupis pullastra (Montagu)

Tellina tenuis da Costa

Tellina fabula Gmelin

Gari fervensis (Gmelin)

Cultellus pellucidus (Pennant)

Spisula subtruncata (da Costa)

Corbula gibba (Olivi)

Thracia sp.

Additional species found bored by Natica sp. in the Clyde.

Gafrarium minimum (Montagu)

Venus fasciata (da Costa)

Of these, by far the commonest bored shell in Kames Bay was Venus striatula, but this is to be expected since this species was the commonest bivalve in sand in the sublittoral region. Natica will apparently attack any bivalve in the sand provided it is of suitable size.

A number of laboratory experiments were attempted to see if Natica would select one species of bivalve in preference to others, but considerable

difficulty was experienced in keeping the animals alive and healthy under laboratory conditions. In one experiment, one large specimen of Natica drilled seven V. striatula and one Nucula turgida, but did not attack Tellina fabula, Spisula subtruncata and Thracia sp. which were also present. Smaller specimens of Natica were found to be apparently unable to attack the size of Venus used in the experiments (average length about 1.0 cm.) and drilled Tellina, Nucula, small Spisula, and Thracia with no apparent discrimination. No definite conclusions could be drawn from the experiments, apart from that the size of the prey was an important factor in influencing predation.

(2) Density of prey and predator.

Information on the importance of this factor was obtained only indirectly, from a consideration of the connection between the size of the predator and the size of the bivalve bored. As is shown in table 19 and figure 39, there is a direct, although loose relationship between the size of the hole (and hence the size of the drilling gastropod) and the size of the shell bored. A similar relationship

Table 19. Relationship between the size of holes bored by Natica poliana alderi and the length of the shell of Venus striatula in which they were bored.

			Mean diameter		
Mid Point length	Mean length	N	Inside	Outside	I/O
0.15	0.19	2	0.340	0.560	0.607
0.25	0.27	17	0.398	0.647	0.615
0.35	0.35	22	0.507	0.867	0.585
0.45	0.46	16	0.647	1.042	0.621
0.55	0.55	28	0.703	1.161	0.605
0.65	0.66	21	0.710	1.229	0.578
0.75	0.77	21	0.745	1.250	0.596
0.85	0.86	23	0.840	1.400	0.600
0.95	0.95	37	0.936	1.560	0.600
1.05	1.06	20	1.018	1.672	0.609
1.15	1.16	27	1.105	1.862	0.593
1.25	1.26	28	1.140	1.913	0.596
1.35	1.35	19	1.179	1.960	0.602
1.45	1.46	12	1.297	2.097	0.619
1.55	1.54	2	1.180	1.920	0.614

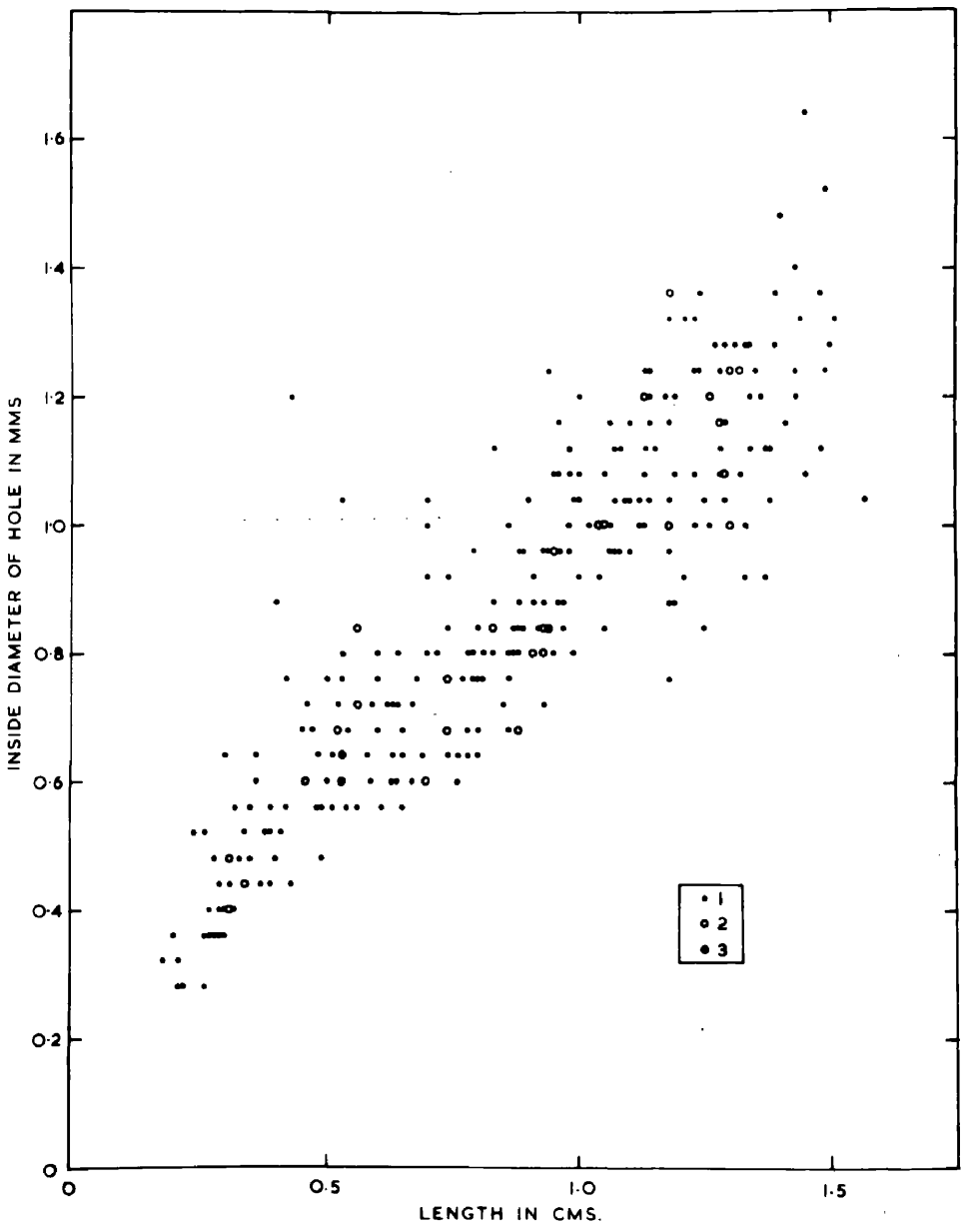


Figure 39. Scatter diagram showing the relationship between the size of the hole bored by Natica poliana alderi and the length of the shell of Venus striatula in which it was bored.

was found by Pieron (1933) for Donax and Mactra bored by Natica. The largest specimens of Natica alderi are unable to drill shells of Venus striatula of length much greater than 1.5 cms. and therefore bivalves larger than this are not subject to predation from this cause. During their second year of life a fair proportion of the Venus population grew to a length greater than 1.5 cms. and the majority were above this size throughout their third year. The drop in intensity of predation after the first year may therefore be explained by the fact that increasing numbers of the bivalves were becoming too large to be successfully attacked, thus effectively reducing the population density of the prey species. At the same time, mortality of the Natica themselves would result in there being fewer large specimens capable of attacking the larger Venus.

Another result of this size limitation is that predation on the older age groups of Venus becomes progressively more selective in that those bivalves of two or more years old which are bored tend to be the smallest of their age group. The

size distribution of the dead shells collected shows this clearly, since the mean size of the dead bored shells is less than that of the corresponding group of dead unbored shells. Examination of the annual rings on the shells confirmed that this distribution was the result of selective mortality rather than of any particular seasonal distribution of mortality from predation.

A suggested explanation for this size limitation is that Natica may be unable to bore through the thicker shells of the larger specimens of Venus.

Behaviour of Natica.

The distribution of holes over the shells of certain bivalves drilled by members of the Naticidae has been taken by some authors to indicate that the animal chooses the site of its hole in some way in relation to the internal organs of the bivalve. In most cases the holes are distributed, not at random, but grouped in some particular region of the shell. Scheimenz (1891) found in 61 cases out of 79 that the hole bored by Natica josephina was anterior to the umbones and in most cases in the dorsal region of the shell. Pelseneer (1924)

recorded the distribution of holes in the shells of Donax vittatus and Tellina tenuis bored by Natica alderi, and in Mytilus edulis bored by Purpura lapillis. He found in the two former cases that the holes were grouped in the umbonal region of the shell. In Mytilus the holes were scattered over the whole of the surface of the shell with the exception of a narrow belt around the margins. He showed that the area of distribution of the holes was that area of the shell overlying the gonads in all three cases. Loppens (1926) found that in Donax vittatus 70%, Tellina balthica 86%, Mactra subtruncata 86%, and Mactra solida 100%, of the holes bored were in the umbonal region of the shell. Pieron (1933) examined numerous valves of Mactra solida and of Donax trunculus and found in both cases that the majority of the holes were a little more than a quarter of the distance from the umbones to the margin of the shell. Verlaine (1936), after describing the distribution of borings in Tellina balthica, Mactra subtruncata and Donax vittatus suggested that the site of boring is chosen by the predator and that, moreover, a

learning process occurred in juveniles enabling them to chose the most suitable site for the hole.

Among other boring gastropods, it has been shown that shells of Ostrea edulis were bored by Murex erinaceus between the adductor muscle and the hinge (Fischer, 1865), or with regard to the "visceres essentiels" (Issel, 1882). Federighi (1931) found that holes were drilled by the American oyster drill, Urosalpinx cinerea, in any part of the shell of the oyster, but that 73% were over or near the place of muscle attachment (presumably of the adductor muscle). In shells of Venerupis phillipinarum bored by the "drill oyster" 201 out of 217 perforations were in the beak cavity, that is in the dorsal region of the shell ventral to the hinge plate (Hotta and Tamuri, 1953).

The distribution of the holes drilled by Natica alderi in the shells of Venus striatula was found by plotting their positions on outline drawings of the shell. A typical result is shown in figure 40 which records the positions of 150 holes. This represents only one such group examined but is typical of all. The holes are situated mainly around the margin of

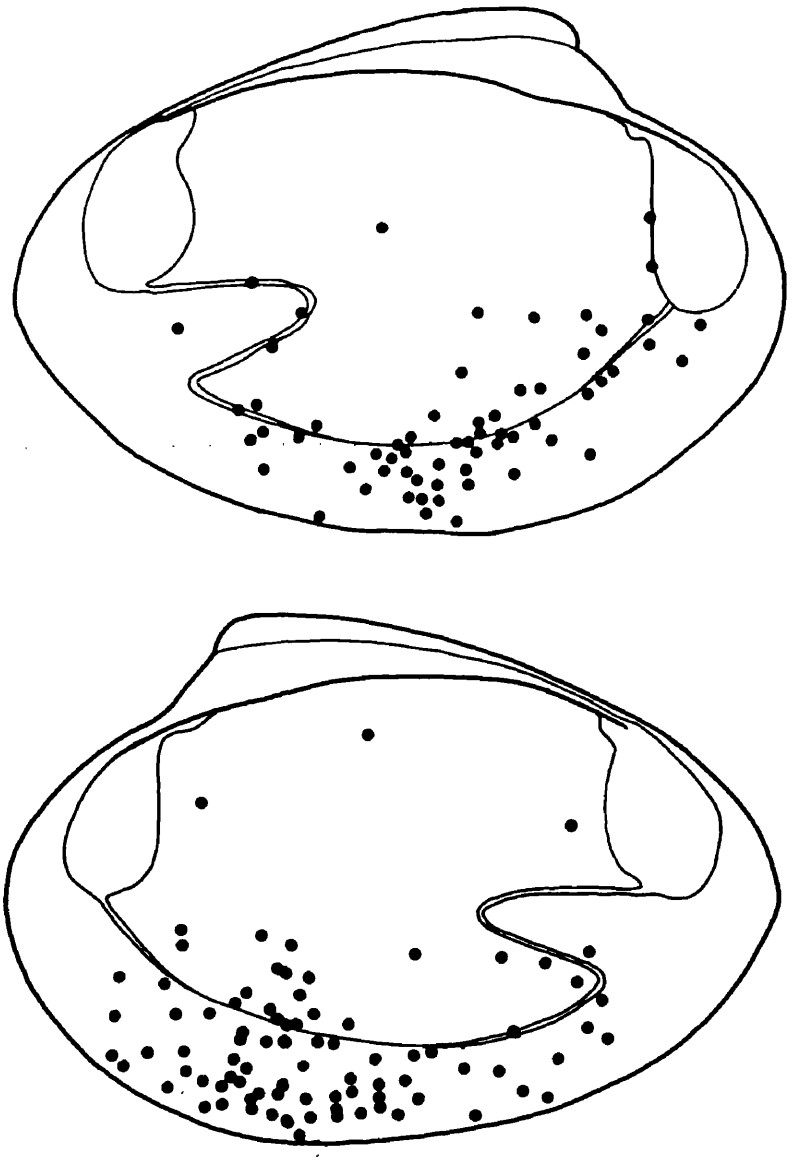


Figure 40. The distribution of 150 holes bored by Natica poliana alderi in the shells of Venus striatula.

The position of the centre of the hole only is marked in each case.

the shell ventral to a line running antero-posteriorly at the ventral limit of the adductor muscle scars. A large proportion of the holes perforate the shell outside the pallial line. Most of the holes, therefore, penetrate the shell in its thinnest region.

The observed distribution of the holes appears to be the result of a stereotyped behaviour pattern involving recognition of the prey and adoption of a particular attitude whilst boring. A possible suggestion is that the prey is found by random wandering and that suitable bivalves are distinguished from unsuitable objects such as dead shells or stones by thigmotactic response to slight movements of the shell valves or the siphons, and/or by olfactory stimuli; that recognition of the prey acts as a releasing mechanism resulting in the gastropod taking up the feeding position with the bivalve surrounded by the foot, and that the position adopted by the predator in relation to the prey during feeding depends both on the predator species and on the shape of the prey. The relative positions would be likely to be similar in all cases

where a particular predator attacked a particular prey species, with the result that the holes bored would show a non-random distribution over the shell. The region in which the density of holes bored was greatest might be expected to differ for different predator and prey combinations, as has been shown to be the case.

This hypothesis would explain the observed distribution of the holes bored in the shells of Venus striatula, and suggests another explanation for the size limitation recorded earlier. This is that larger bivalves are not 'recognized' as suitable objects for boring, since the gastropod is unable to adopt its normal feeding position with regard to them. Also large Natica would not 'recognize' very small bivalves, for the same reason.

Method of Drilling.

No new evidence on the method of drilling by the Naticidae has been found by the author. Animals kept in the laboratory never drilled bivalves unless both were completely buried in sand, so that it was impossible to observe the process.

The inability to drill unless buried suggests that the position of the bivalve and its orientation in respect to the gastropod might be a factor important in the recognition of its prey by Natica, and tends to support the suggestion outlined above that the behaviour of Natica is highly stereotyped.

Early work on the method by which carnivorous gastropods drill their holes led to three theories being put forward: (a) Mechanical drilling, by means of the radula, (b) Action of acid or other secretion from the salivary glands or from the "boring glands", (c) A combination of both these methods. This work has recently been reviewed by Jensen (1951) and Turner (1953), both of whom present evidence that the Naticidae are able to bore by mechanical means alone. Jensen has found egg capsules of the Ray, Raia, from the Davis Strait which had been bored in the manner typical of the Naticidae and where the edges of the holes showed marks apparently caused by the radula teeth. Similar holes were found by Thorson (1935) in the egg capsules of the snail Sipho (= Colus) curtus from East Greenland. Both these

types of egg capsules are acid resistant and hence such holes must have been drilled by mechanical means alone. Jensen concludes that the radula and possibly the jaws are the tools used for drilling in this group. This view is supported by Turner who found that the American clam drill Polynices duplicata was able to perforate the shell of Mya arenaria even after this had been covered with layers of histological paraffin wax, or with Plaster of Paris (partially dehydrated calcium sulphate). The evidence indicates that under these circumstances the Naticidae are able to drill through the shells of their prey by mechanical action alone, unaided by any chemical secretion, but does not necessarily confirm that this is normally the case.

Carriker (1943) has shown that among other boring hastropods, Urosalpinx probably uses a softening agent whilst drilling, the softening agent being secreted in this case from a gland in the foot - the accessory proboscis. Rasping by the radula and softening by secretion from the accessory proboscis take place alternately during the drilling process. It is at least possible that the boring process in

the Naticidae is similar, with the boring gland on the proboscis secreting a softening agent, possibly in the form of a calcium chelating agent, or of some agent which acts on the organic matrix of the shell.

Discussion.

It is tempting to postulate some connection between the appearance of Natica poliana alderi in Kames Bay and the great increase in the density of Venus striatula in the bay as the result of the abnormally high spatfall in 1955, although there is no direct evidence to show when Natica appeared. Clarke and Milne made their main survey in 1938 - 1939, but also sampled after 1949. They state that Natica was not present (Clarke & Milne, 1955 pp. 168 & 177). Dr. R.B. Pike (personal communication) found Natica alderi during 1951 (1 specimen in 6 hauls with mud bucket) and 1952 (6 specimens in 6 hauls), which indicates that Natica may always have been present although in small numbers. During 1956, 1957, and 1958 the numbers found were of the order of 10 - 50 per mud bucket (personal observation), an increase of up

to fiftyfold from 1951. Before 1950, Natica was also present in areas close to Kames Bay, for example in White Bay (Clarke and Milne l.c.) and in Balloch Bay (Quayle, 1953). Elmhirst (1936) recorded a local increase in numbers of the species, similar to that described here, on Hunterston Sands, Ayrshire, in 1934, where "it was decimating the + 1 year group of Cardium edule (1933 brood)".

Extension of the local range of Natica might take place by two methods: by migration of adult animals, or by dispersal of the planktonic larval stage. Nothing is known about the extent of migrations by individual adult Natica, but Carriker (1955) concludes that the American oyster drill Urosalpinx moves about only to a rather limited degree. Local movements of drills might however lead to aggregation in areas where there was an abundant food supply even although they were not directly attracted by it. Since young Venus striatula form a readily acceptable source of food for Natica alderi, this process might have resulted in the observed distribution.

Thorson (1946) states that the larva of Natica alderi (= N. nitida) hatches when the shell is 195μ across, and since larvae of 750μ (Thorson, 1946) and 800 - 1,000μ (Lebour, 1937) have been found in the plankton, the planktonic stage must be fairly long, and the opportunity for wide dispersal, great. At Millport, egg collars were found in May, June, July and early August, and larvae hatched from here agreed well with Thorson's description. Dispersal by this planktonic larval stage might lead to aggregation locally in areas where food was particularly abundant if settlement were influenced by density of suitable food organisms on the bottom, perhaps in response to ectocrines released by the bivalves. Adult Urosalpinx are known to find their food by a positive chemotactic response to the external metabolites of their prey (Carriker, 1955), but nothing is known of the responses of young drills, or of larval Naticidae. The larvae of certain polychaetes respond to characteristics of the substratum at settlement (Wilson 1932, 1937, 1955; Day & Wilson, 1934). Larval Ostrea edulis are influenced by characteristics of the surface with which they come into contact,

and especially by the presence of settled spat (Cole & Knight-Jones, 1949). The successful metamorphosis of Adalaria proxima depends on its establishing contact with a live colony of the polyzoan Electra pilosa during a searching phase of the larval life, and many marine invertebrates, including Natica (Lebour, 1937), have a swimming-crawling stage preceding metamorphosis during which a choice of substratum could be made. It is possible therefore that larval Natica might discriminate between areas of high and low bivalve population density in setting. Alternatively the observed distribution could be the fortuitous result of local hydrographic conditions affecting both types of larvae.

A long term study in a small local area such as Kames Bay, of the fluctuations of numbers of Natica in relation to the number of bivalves should give much interesting information on predator prey inter-relationships, while more laboratory and field experiments are necessary before these inter-relationships, especially in regard to setting, are fully understood.

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