THE INFESTATION OF MOLLUSCS BY *POLYDORA* SPP.

BY

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DECLARATION

This work has not been accepted in substance for any other degree, and is not concurrently being submitted for any other degree.

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SUMMARY

The ecology of *Polydora*,spp was reviewed and the infestation of molluscs by the boring, spionid polychaete, *Polydora ciliata*, was studied in detail.

X-radiography showed that.*P.ciliata* infested a wide variety of molluscan substrates, but it occurred in greatest abundance on large, rough-surfaced, epibenthic shells, which were collected from the sublittoral zone and the level of extreme low water spring tides, of shores sheltered from wave action. *P. ciliata* was contagiously dispersed on mussel shells. Monthly radiographs of mussels indicated that maximum settlement of *P. ciliata* larvae in the river Fowey, occurred in May.

The effect of heavy infestations of *P. ciliata* on limpets (*P.vulgata*), mussels (*Mytilus edulis*), and oysters (*Crassostrea gigas*), was investigated.

At certain times of the year, heavy infestations of *P. ciliata* reduced the dry weight condition and fecundity of limpets and mussels, but did not seem to adversely affect *C. gigas*.

Compression tests showed that *P. ciliata* weakened mussel shells. Predation experiments, with *Cancer pagurus*, indicated that this might increase the mussels' vulnerability to predation.

Heavy *P. ciliata* infestation also reduced the mussels' resistance to loads which tended to force the mussels' valves apart. This may decrease the mussels' physico-chemical tolerance, and increase their vulnerability to starfish predation.

Limpet adhesion, measured on the shore with a simple dynamometer, was impaired by *P. ciliata* infestation. This may reduce the limpets' resistance to wave action, and increase their vulnerability to predation.

Reasons for the adverse effects of *P. ciliata* infestation on limpets and mussels are suggested, and the ecological and commercial implications of the infestation are discussed.

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PREFACE

The cultivation of marine molluscs is making an increasing contribution to man's insatiable demands for food. If we are to get the maximum benefit from mollusc cultivation, it will be necessary to reduce the loss of stock due to pests. As new species of molluscs and new areas are used for commercial cultivation, there is a greater risk of disastrous losses due to pests; pests which are at present regarded as relatively innocuous may prove to be very harmful under new conditions of cultivation. It is therefore imperative that we are aware of the pests associated with molluscs and that we learn more about them so that we can anticipate the damage that they may cause to commercial molluscs. This work started as a general examination of the pests of molluscs, but, after collecting some mussels from the river Fowey, it soon developed into a detailed study of one pest; Polydora ciliata. The mussels were riddled with the tubes of this spionid polychaete. Heavily infested mussels seemed to be in poor health; their shells were friable, and their tissue was watery, transluscent, and flaccid. I searched the literature to find out more about the effects of this worm on mussels and other molluscs, but there was a great deal of confusion and argument concerning its effects. Prompted by the lack of agreement concerning the effects of P. ciliata, I attempted to resolve some of the confusion, and this thesis is the result of that attempt.

The thesis is divided into four sections. The first section is a literature review of the ecology of Polydora spp. It seemed pertinent to assess the present state of our knowledge concerning this genus, before pursuing with new research. The second section describes some aspects of the distribution of Polydora ciliata; it aims to answer the question " which molluscs are most vulnerable to P. ciliata infestation?" The third section attempts to evaluate the effects of P. ciliata on molluscs at the whole-organism level. Mussels (Mytilus edulis)were chosen because of their initial involvement in the project, and because of their commercial importance; limpets (Patella vulgata)were chosen because of their prominence and importance on rocky shores; and the Japanese oyster (Crassostrea gigas)was chosen because of its recent introduction as a commercially important bivalve, in South-west England. The fourth section ties together the results of the other sections, and attempts to assess the ecological and commercial implications of P. ciliata infestations.

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SECTION I

THE ECOLOGY OF POLYDORA SPECIES :

A literature review.

THE ECOLOGY OF POLYDORA SPP.

A literature review

INTRODUCTION

The ecology of Polydora spp. is of interest not only to the ecologist, but also to the geologist, the coastal engineer, the shellfisherman, and the fisheries biologist. The geologist is interested in the bore holes created, in the distant past, by Polydora spp. in rocks and shells; these bore holes may be valuable palaentological clues to the geological history of the substrate. The coastal engineer is interested in the destructive power of Polydora spp. which bore holes into coastal installations: lighthouses, breakwaters, and harbour walls. The shellfisherman is interested in Polydora spp. which bore through the shells of his stock and adversely affect its production. Finally, the fisheries biologist is interested in the prolific nature of many species of Polydora, which may result in their total dominance of the plankton or benthos.

In this review, I intend to discuss the life history of Polydora spp.; their geographical, ecological, and geological distribution; their relationships with other organisms; their method of burrow formation; and the effect that burrow formation has on the living and non-living substrate. However, first, it is necessary to discuss the confusion surrounding the systematics of Polydora spp.

SYSTEMATICS AND MORPHOLOGY

The systematics of the genus *Polydora* has been in a state of confusion since 1802, when Bosc first described *Polydora*. Systematists have been inconsistent in their choice of generic characteristics. Unfortunately, no one arrangement has been generally accepted; therefore, genera such as *Bocaardia*, *Carazzia*, and *Pseudopolydora* have, on more than one occasion, been brought out of synonymy and used as genera or subgenera.

Specific diagnosis is not much better. In many cases, new species have been described on the basis of only a few specimens in poor condition; for example, *P. narica* is described on the basis of only one specimen (Light, 1969). Sometimes, the criteria used to differentiate species are not constant. Rasmussen (1973) discusses the separation of *P. ciliata* from closely related polydorids. He showed that the characteristic used for separation, the number of modified bristles on the fifth setigerous segment, is not stable, even in *P. ciliata* from the same region. Therefore, he suggests that some other species of *Polydora*, such as *P. ligni*, *P. websteri*, *P. cirrosa*, and *P. muchalis*, may prove to be only varieties of *P. ciliata*.

So, it is sometimes difficult to understand the literature and gain insight into the ecology of *Polydora* spp., because of the many contradictory statements concerning their identification. However, among the most useful keys for identifying *Polydora* spp. are those of Berkeley and Berkeley (1952), Blake (1969a and 1971), Day (1967), Fauvel (1927), Foster (1971), Kirkegaard (1959), Okuda (1937), and Rainer (1973). These keys also give many morphological details, and

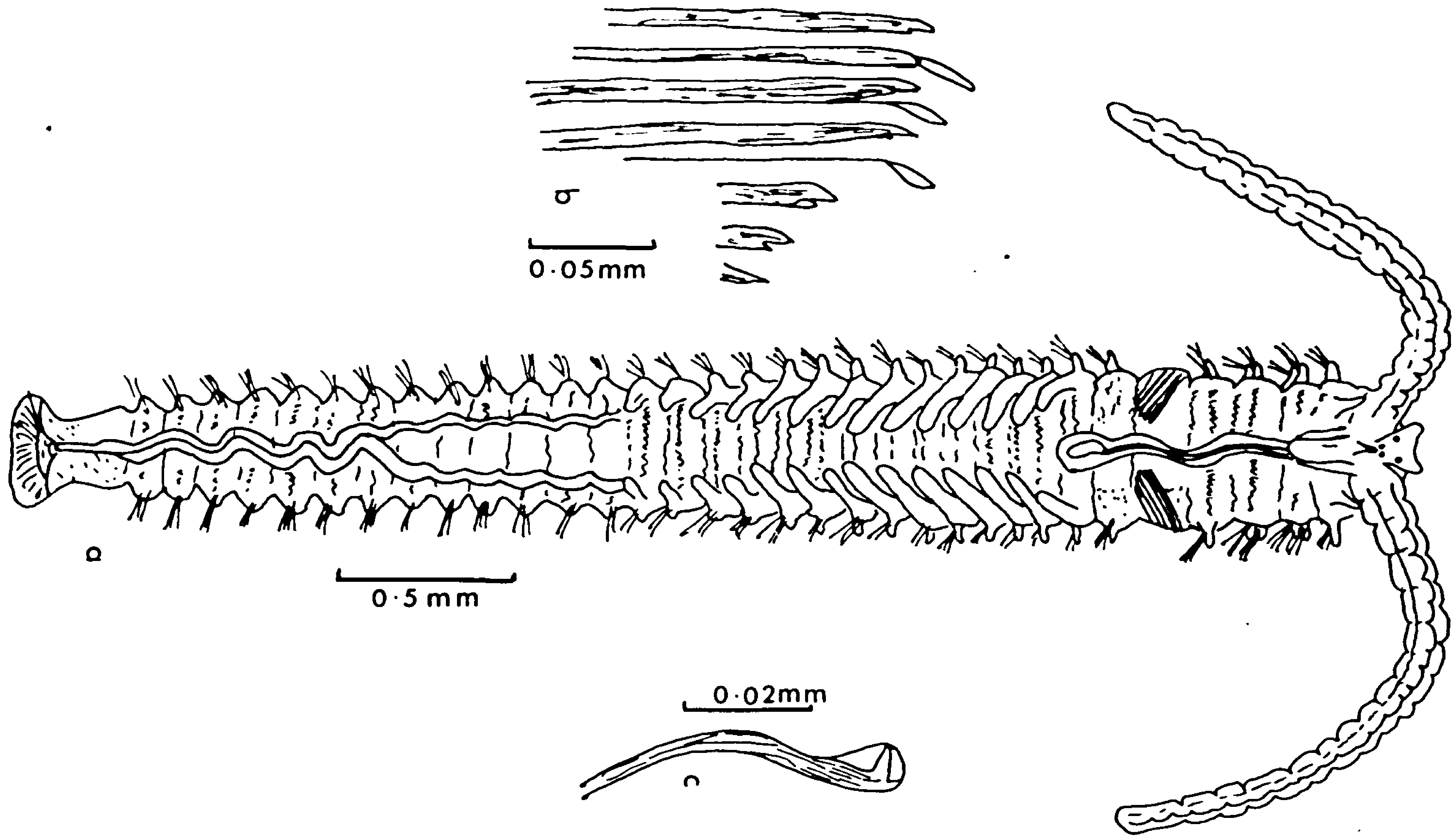
Hempel (1957), Orrhage (1964) and Soderstrom (1920) give fuller accounts of the morphology of Polydora. Figure 1 shows the external features of Polydora.

Figure 1.

The external features of Polydora ligni.

a) Young bottom stage (dorsal view).
b) Modified bristles from segment 5.
c) Ventral hooded crochet.

(Redrawn from Hannerz,1956).


b
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c

LIFE HISTORY

SPAWNING

Soderstrom (1920) and Dorsett (1961a) give detailed descriptions of the development of polydorid gonad cells. Gonad cells arise just inside the ventral epithelium and later migrate to the gonads. Then they are released into the coelom and transported to the region of maturation. After maturation, the gonads are released through modified nephridia.

An increase in temperature is thought to initiate spawning of some *Polydora* (Blake,1969b; Dorsett,1961a). However, the spawning periods of *Polydora* spp. are variable, and depend on the species of *Polydora* and geographical locality. Most species that have a long planktonic phase, such as *P. ciliata* (Daro and Polk,1973; Dorsett,1961a; Hannerz,1956; Wilson,1928; Wolff,1973), *P. ligni* (Watling,1975) and *P. websteri* (Blake,1969b), have their main spawning period in spring or early summer, with sometimes a secondary spawning maxima in autumn. This probably allows the planktotrophic *Polydora* larvae to take advantage of the spring and autumnal phytoplankton blooms. Those species that have a short planktonic phase, such as *P. hoplura* (Wilson,1928), *P. nuchalis* (Woodwick,1960) and *P. quadrilobata* (Blake,1969b), often spawn maximally in late autumn or early winter; the larvae are not so dependant on phytoplankton for food, as the mother would have been able to accumulate food reserves in the summer, to be used later by the larvae. The precise date of spawning depends on the geographical locality of the *Polydora*. For example, *P. ciliata* from Kiel spawn from April to October, with maximum spawning in July; while P. ciliata from Plymouth spawn from January to October, with maximum spawning in March (Thorson,1946).

FERTILIZATION AND DEVELOPMENT OF THE EGG

Fertilization of Polydora eggs is generally preceded by copulation (Hannerz,1956; Wilson,1928; Woodwick,1960). However, protandry and neoteny have been reported for P. hermaphroditica (Hannerz,1956) and P. nuchalis (Woodwick,1960). A reciprocal transfer of eggs occurs between two protandric male P. nuchalis; the sperm is stored and fertilizes the eggs which develop in the later female stage (Woodwick,1960). Other species of Polydora may also store sperm (Skeel,1975). After fertilization, cleavage of polydorid eggs is complete but unequal (Woodwick,1960).

Leschke (1903) thought that the fertilized eggs are released from the parental burrow, to drift freely about on the sea-bed. However, the eggs are laid in capsules which are deposited in strings and fastened onto the walls of the mother's burrow. The burrow, at this time, is known as the brood tube. It may be quite different from the dwelling tube; it is often reinforced with mucus, as in P. ciliata; or it may be reinforced with ferric hydroxide, as in P. redeki and P. quadrilobata (Hempel,1957). The female remains in the brood tube after oviposition and aerates her eggs by producing a respiratory current through the tube, with movements of the parapods and abdominal cilia (Daro and Polk,1973).

There are two main types of egg development. The first is exemplified by P. ciliata. Figure 2 shows that each of its eggs develops into a larva, which hatches at about the three-setiger stage and has a long planktonic phase (Dorsett,1961a; Wilson,1928). The second type of egg development is exemplified by P. hoplura. Figure 3 shows that only a small proportion of its eggs, less than one in ten, develop into larvae; the other eggs, the nurse eggs, are used as food for the developing larvae; a form of feeding known as adelophagia (Wilson,1928). Adelophagia allows P. hoplura larvae to remain within the protective brood tube longer than P. ciliata larvae, and P. hoplura pass through a short planktonic stage, if any, before settling and metamorphosing. P. quadrilobata may have either type of development, depending on its geographical locality; a characteristic known as poecilogony (Blake,1969b).

The pelagic phase of Polydora larvae may be as long as six weeks, as for P. ciliata (Dorsett,1961b; Wilson,1928) and P. commensalis (Hatfield,1965); or it may be a few hours, or even ommitted, as in P. hoplura (Wilson,1928). Larvae which have a long planktonic phase may be carried great distances. Hannerz (1956) estimated that larvae, such as P. ciliata and P. commensalis, that spend a month or more in the plankton, could be carried more than 670 kilometres from their brood tubes by currents with speeds as low as 1 knot per hour.

Many Polydora spp. have the potential to produce vast numbers of larvae which may dominate the plankton. For example, P. ciliata has dominated the meroplankton of Scandinavian waters (Schram,1968, 1970), Copenhagen harbour (Smidt,1944), Lake Veere (Bakker and Pauw,1973) and Ostend oyster beds (Daro and Bofill,1972). Rasmussen (1973) estimated that, in May in Iselfjiord, there were more than 1,375

Figure 2.

Portion of a chain of egg-sacs of Polydora ciliata Johnston. Larvae in process of liberation. Sketch from life. x 65.

Figure 3.

Portion of a chain of egg-sacs of Polydora hoplura Claparede, showing early larvae and yolk, masses. Sketch from life. x 65.

(Both figures redrawn from Wilson,1928).

Figure 2

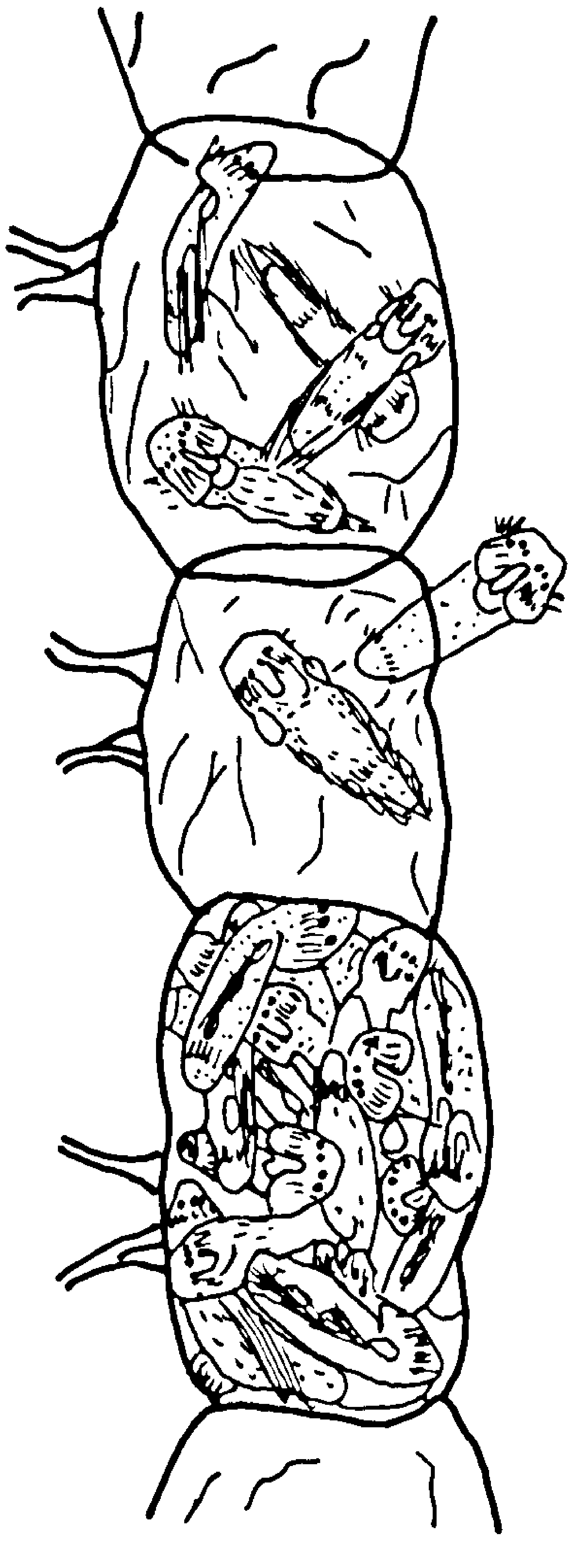
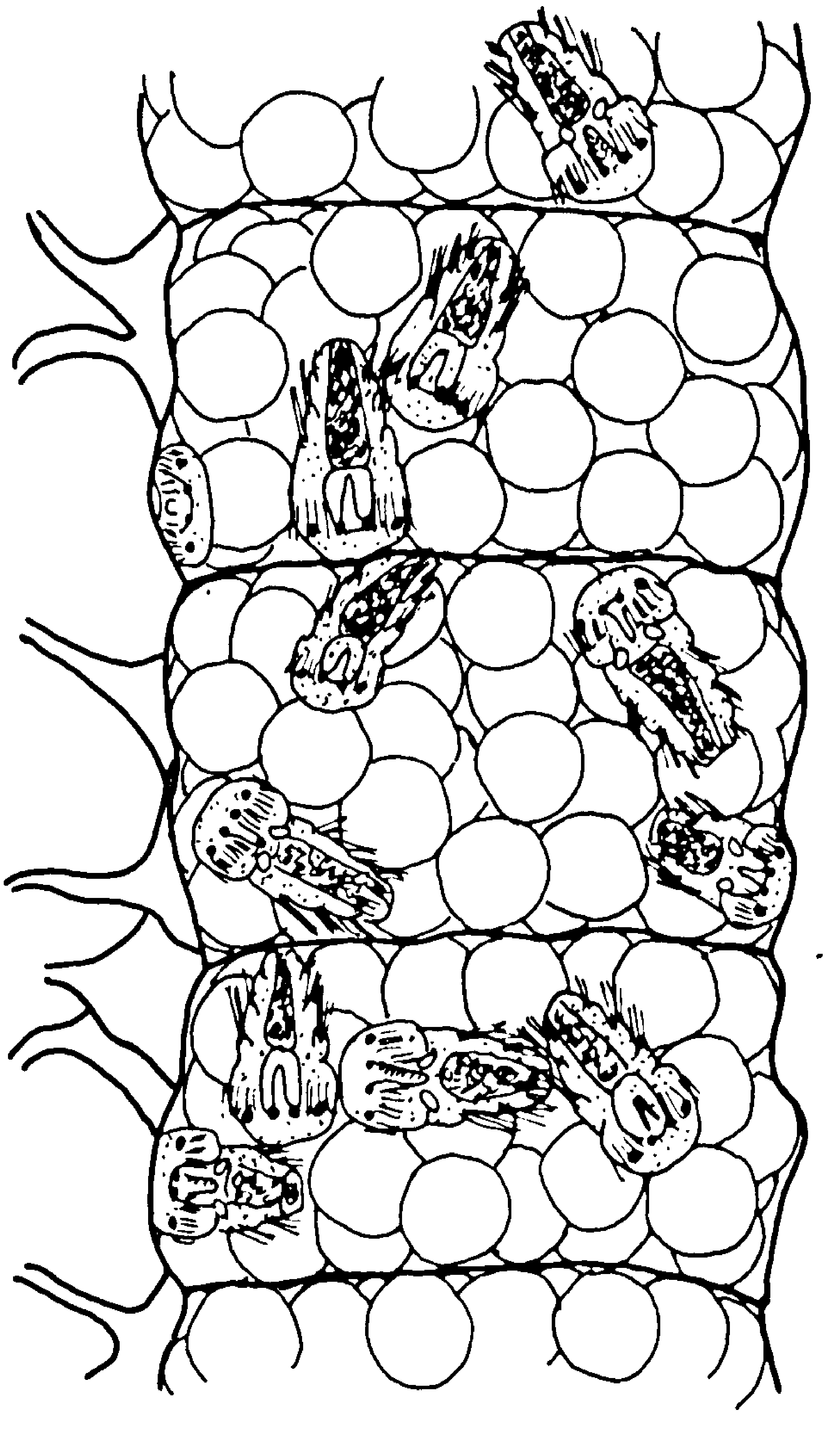


Figure 3



P. ciliata larvae for each cubic metre of water; while Dorsett (1961a) estimated that P. ciliata, in each square metre of substrate at Whitstable, produced 3 x 10^6 larvae.

Because they occur in such large numbers, planktonic Polydora larvae are an important part of pelagic food-webs. Polydora larvae are omnivorous; for instance, P. ciliata larvae eat barnacle larvae, lamellibranch larvae, phytoplankton, and detritus. All the food seems to be within the size range 50 to 150 microns (Daro and Polk,1973). The Polydora larvae may be eaten by fish or by planktonic carnivores. The pressure of predation on planktonic Polydora must be great; but the setae which become erect when Polydora are disturbed (Gravely,1909) may offer some protection, and P. ciliata does exhibit escape reactions when disturbed (Singarajah,1975).

Blake (1969b), Dorsett (1961a), Hannerz (1956), Wilson (1928) and Woodwick (1960) give more detailed accounts of the development of Polydora larvae; and Blake (1969b) and Hannerz (1956,1961) provide keys for the identification of the larvae. Figures 4-6 show the development of P. nuchalis from egg to sixteen-setiger stage larvae.

SETTLEMENT AND METAMORPHOSIS OF THE LARVAE

The settlement of planktonic Polydora larvae plays a big part in determining the distribution of the species. For a long time it was thought that meroplanktonic larvae of benthic organisms settled randomly; only those that drifted onto a suitable substrate survived. Now it is known that most larvae search for suitable substrates on which to settle, thus reducing their mortality (Meadows and Campbell,1972).

Larvae of many Polydora species exhibit active habitat selection (Blake,1969b; Daro and Polk,1973; Dorsett,1961b; Evans,1969; Hannerz, 1956; Hatfield,1965; Kiselva,1967; Wilson,1928). Some species, such as P. flava which settles only in the presence of lithothamnium crusts, are specific in their search for a permanent home; others, such as P. ciliata which settles on a wide variety of substrates, are less specific in their search (Hannerz,1956).

Many Polydora spp. are able to delay metamorphosis until a suitable habitat is found, these include P. ciliata (Dorsett,1961a; Wilson,1828) P. commensalis (Hatfield,1956), P. flava, P. coeca, P. ligni, and P. hermaphroditica (Hannerz,1956). A number of factors direct Polydora larvae to a suitable habitat, or induce metamorphosis once a suitable habitat is reached. Light first attracts larvae, just released from the brood tube, up into the surface layers of the sea; later light repels them downwards into the benthos, when the larvae are ready for metamorphosis (Hempel,1957; Thorson,1946). The clearest indication to the larvae of the suitability of an area for settlement, is the presence of adults of the same species. It is, therefore, not surprising that some polydorid larvae, such a P. ciliata prefer settling near P. ciliata adults (Blake,1969b; Kiselva,1967). Also, the settlement of some larvae induces the settlement of others of the same species, thus resulting in a gregarious distribution (Blake,1969b; Gulliksen,1975).

Water currents may carry larvae from one area to another. They may, since at least P. ciliata larvae can respond to currents (Singarajah,1975), affect the settlement of Polydora larvae. For example, P.websteri settles best in the presence of a weak current produced by shellfish or other P. websteri (Haigler,1969). The feeding and respiratory currents of bivalves may also direct Polydora larvae to settle in the incurrent area of the bivalve shell (Seilacher,1969).

The nature of the substrate plays a crucial role in the settlement of many polydorids (Hannerz,1956). The presence of a bacterial film on the substrate induces metamorphosis of P. ciliata larvae (Bourget and Lacroix,1973; Daro and Polk,1973), and these larvae settle preferentially on substrates with a mean particle size diameter of 2 phi (phi = $-\log_2$ of the particle diameter in millimetres). This preference is independent of the type of substrate, since P. ciliata settles equally well in sand, ground glass, and ground shell (Dorsett, 1961b; Kiselva,1967). P. ciliata larvae settle more in cracks and crevices in the substrate, than on smooth surfaces (Daro and Polk,1973; Orrhage,1969; Wilson,1928).

The vast numbers of Polydora in the plankton often result~~s~~ in the settlement of large numbers of metamorphosing individuals, and the fouling of man-made structures (Cory,1967; Graham and Gay,1945). Bourget and Lacroix (1973) estimated that 2,661 P. ciliata settled on each square decimetre of their test panels. However, as many as 37 per cent of the larvae which settle, may die before metamorphosis (Dorsett, 1961a). Most of the mortality of newly settled larvae may be due, in the summer, to interspecific and intra-specific competition; while in the winter it may be due to adverse physico-chemical conditions (Bourget and Lacroix,1973).

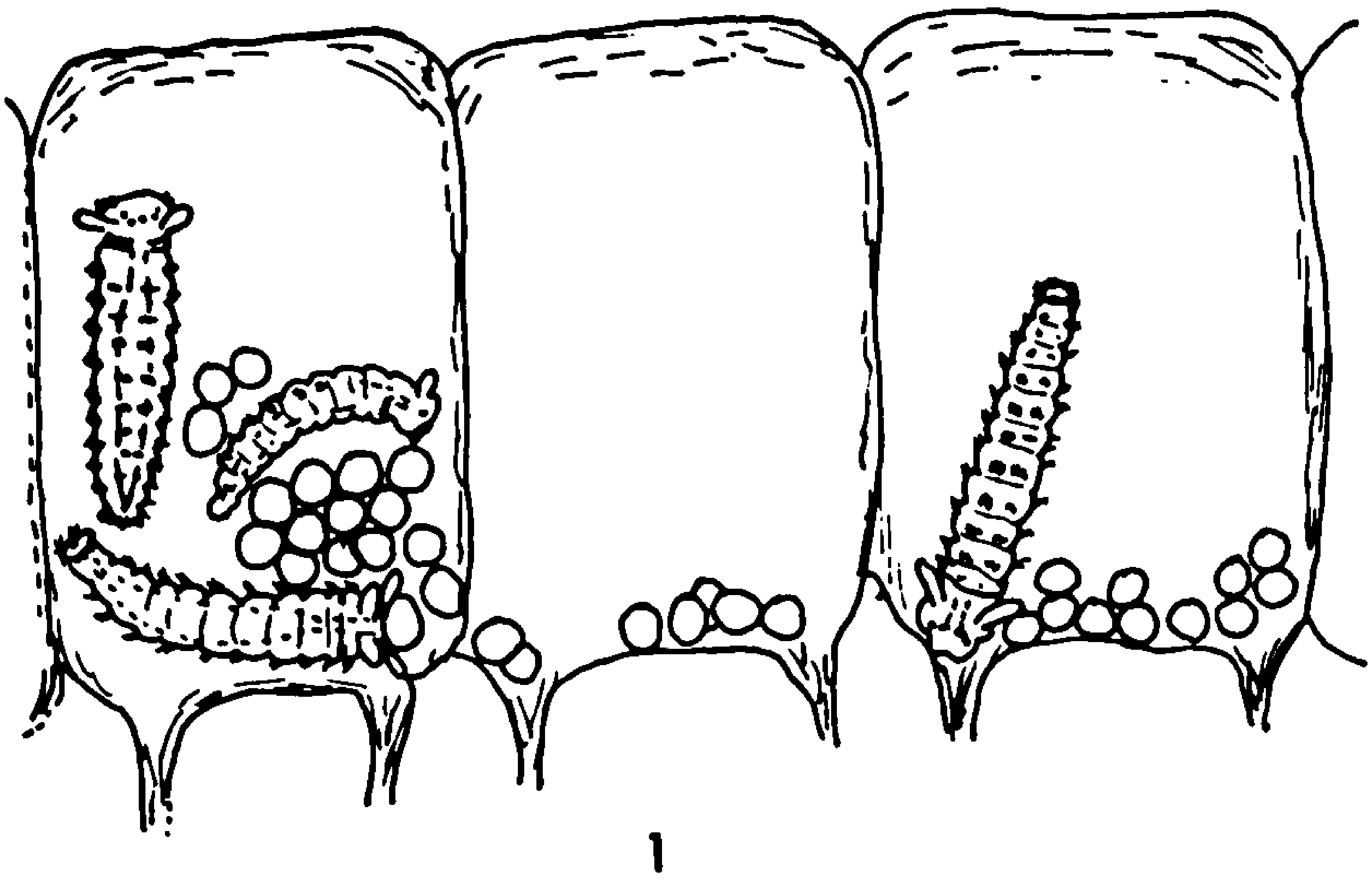
Hannerz (1956) describes the morphological changes of some metamorphosing Polydora species. After metamorphosis, the Polydora grow

Figure 4.

The development of Polydora nuchalis.

1. Egg capsules and larvae.
2. Egg, 0.12 mm.
3. Early larva (18 hours) 0.18 mm.
4. Early larva (36 hours), 0.12 mm.
5. Late presetiger larva (72 hours), 0.20 mm.

(Redrawn from Woodwick,1960).



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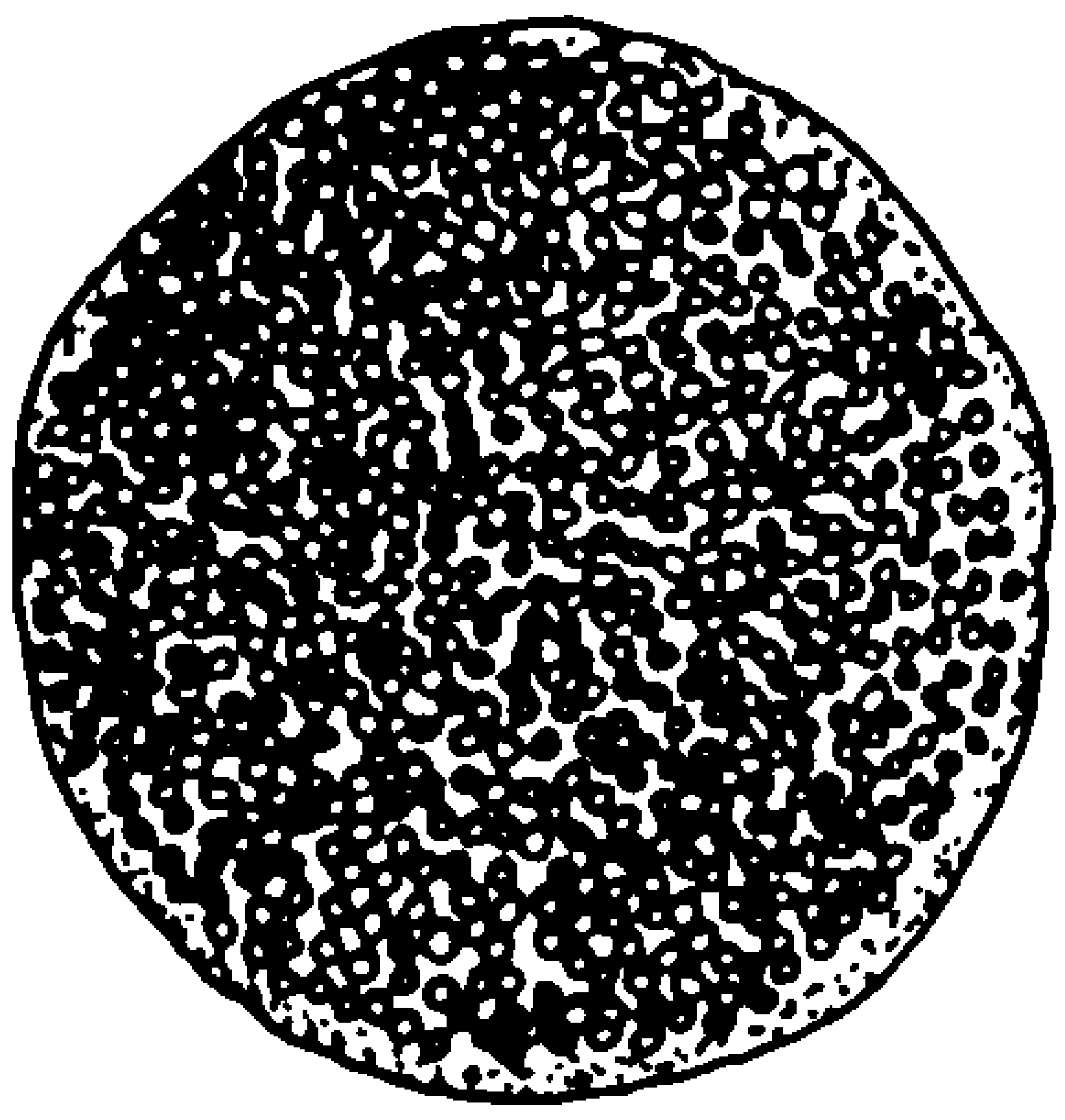

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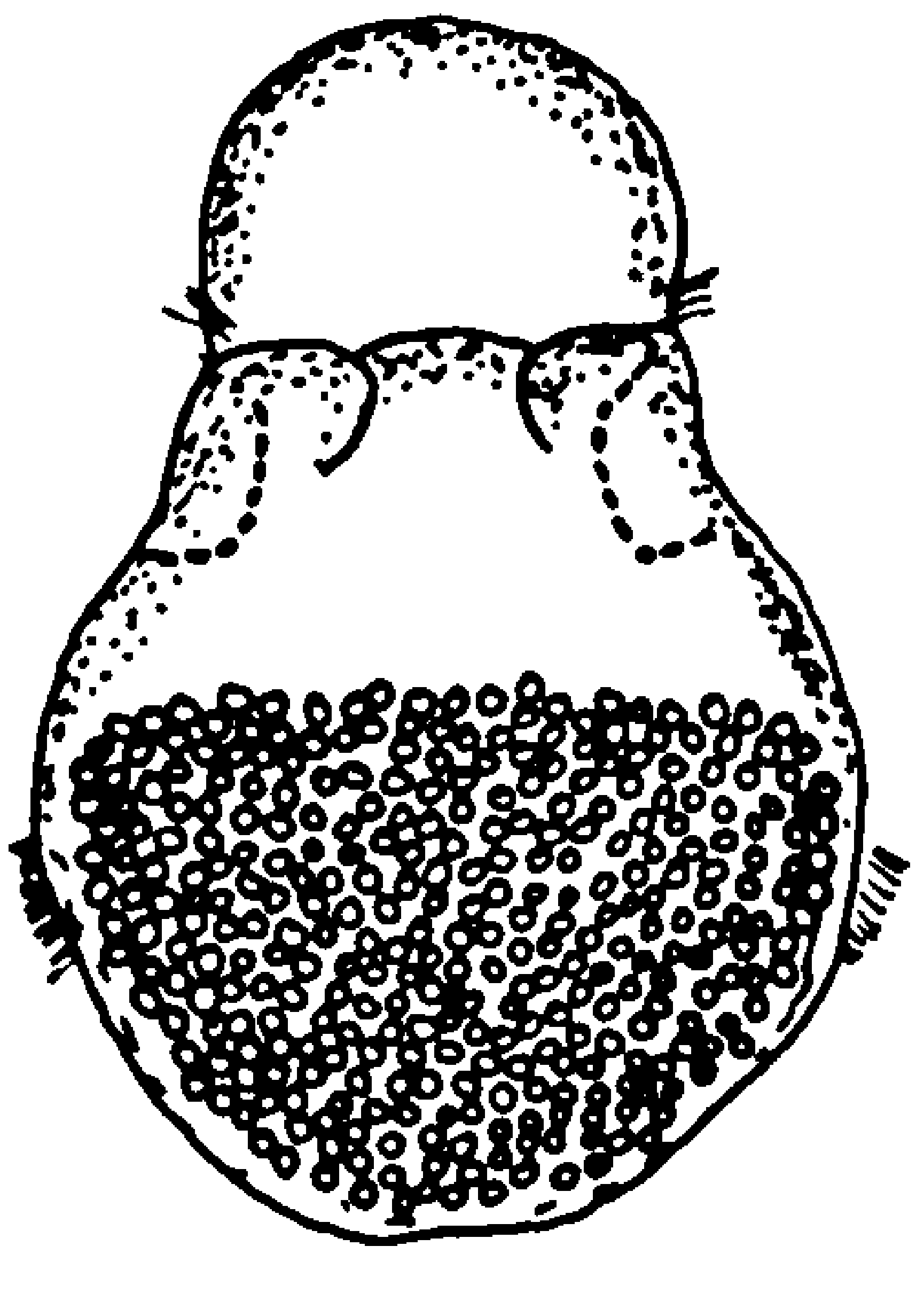

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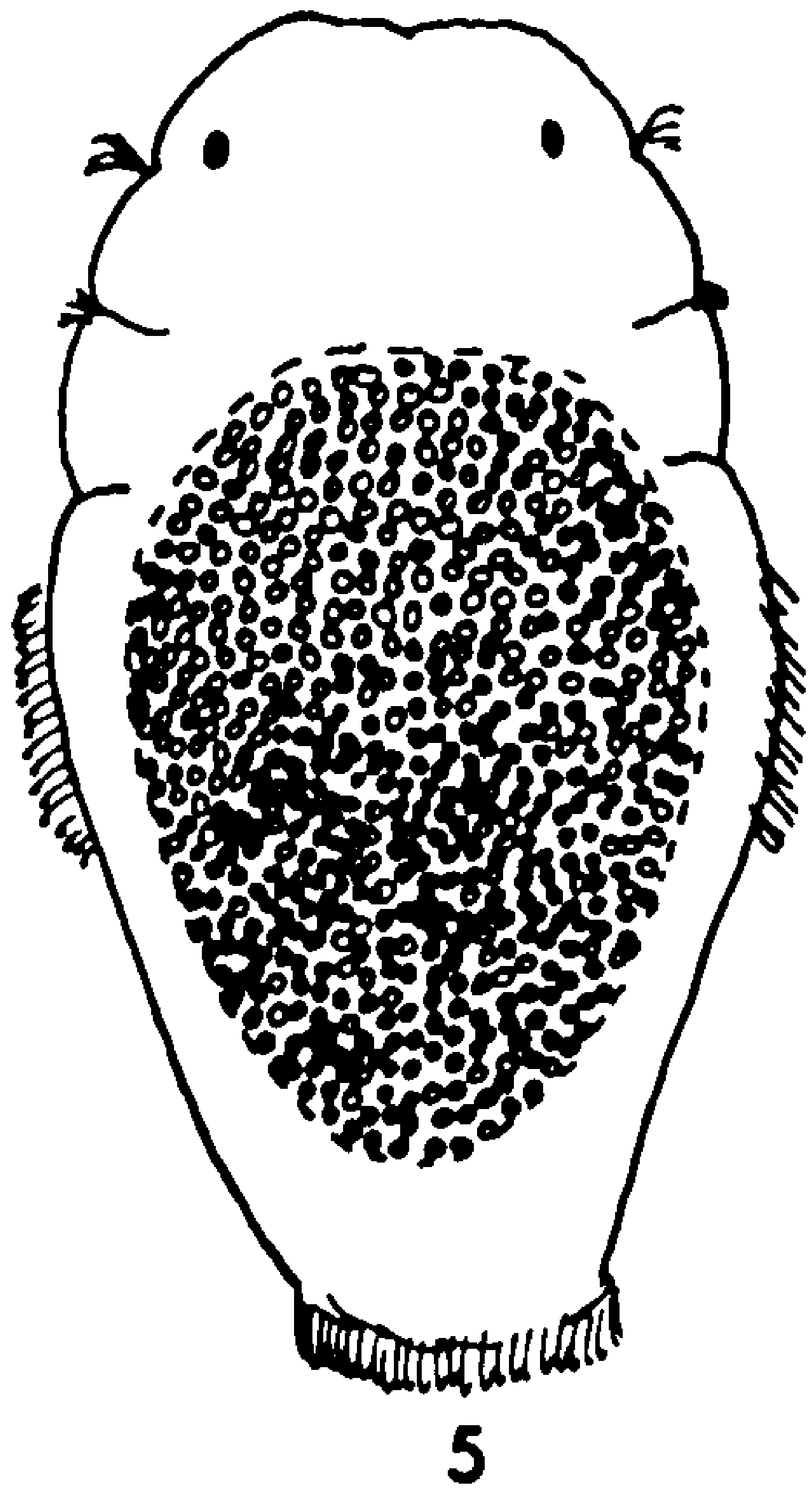

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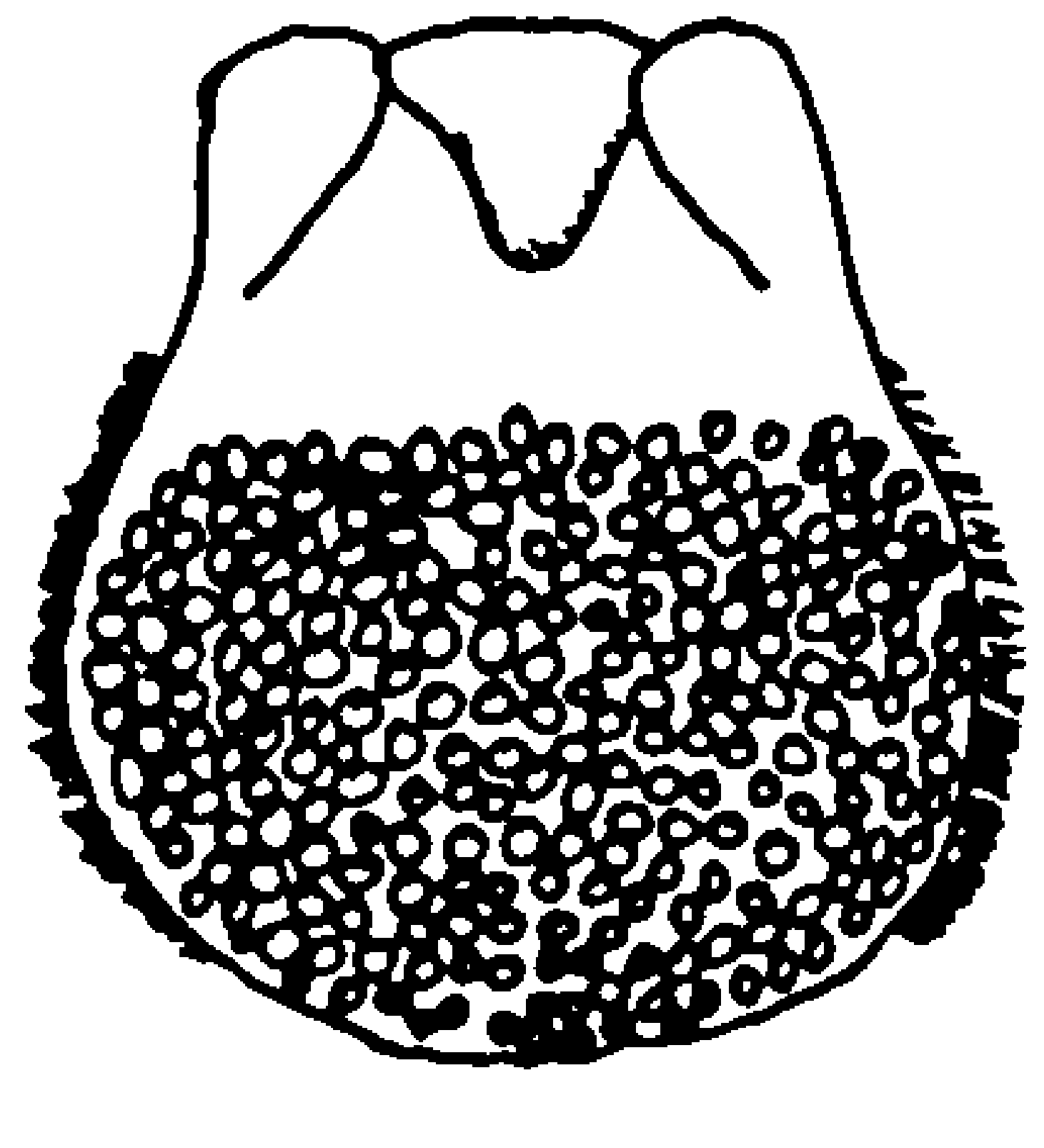

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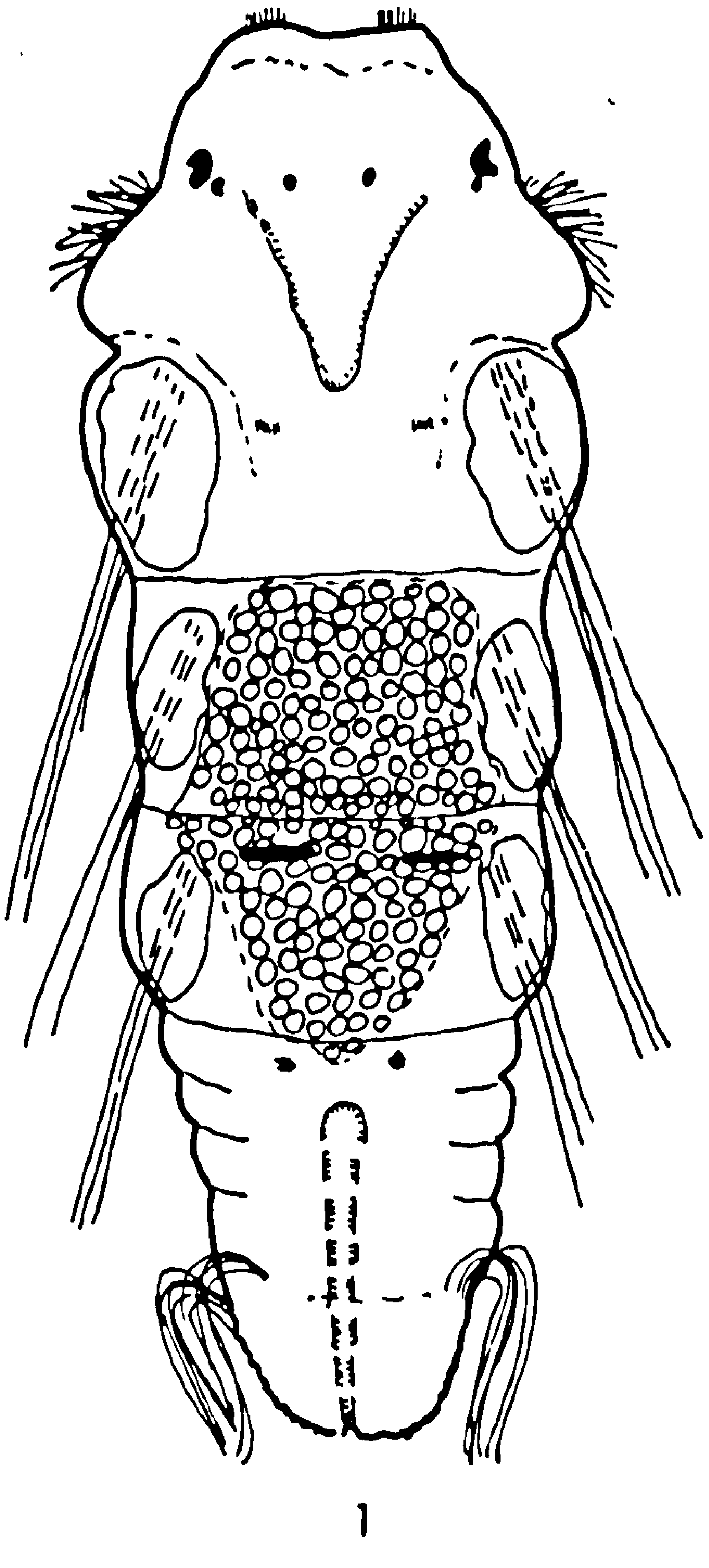
Figure 5.

The development of Polydora nuchalis.

1. 3-setiger larva (6 days), 0.30 mm.
2. 10-setiger larva (two weeks), 0.65 mm.

(Redrawn from Woodwick,1960).



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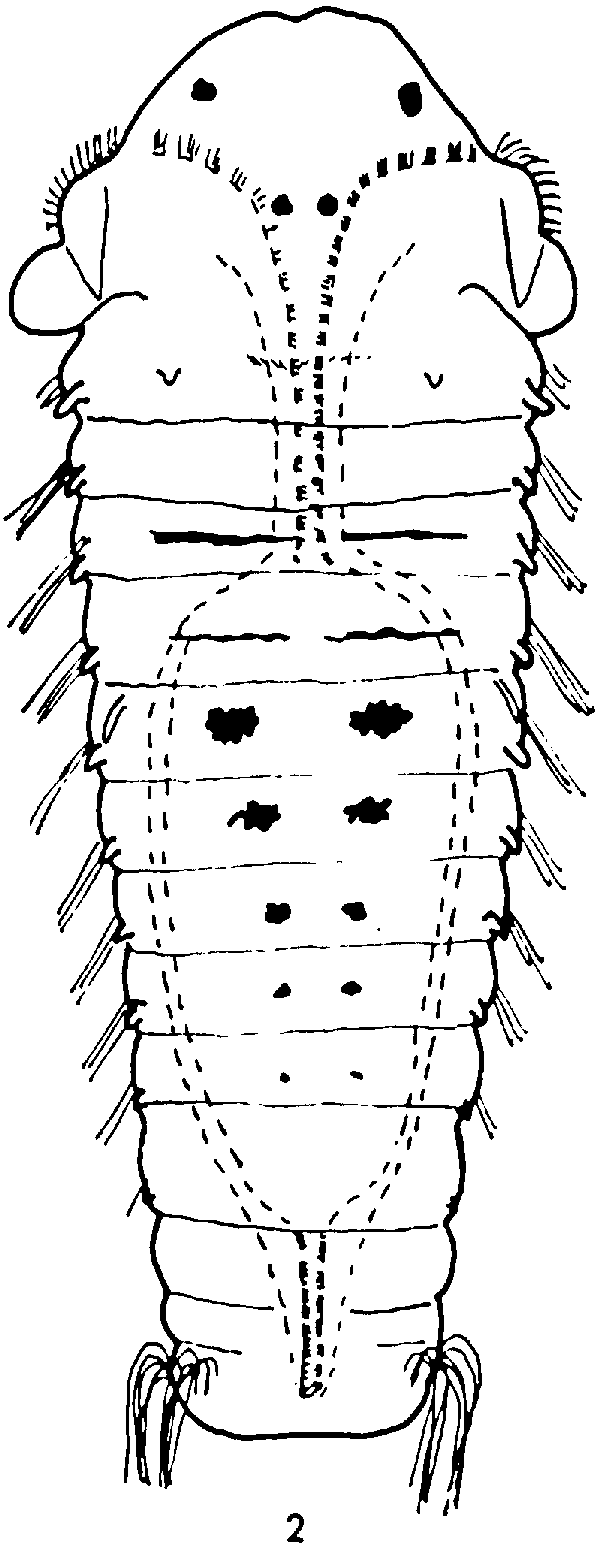

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Figure 6.

The development of <u>Polydora nuchalis</u>.

15-setiger larva, the settlement stage,
(three weeks), 0.90 mm.

(Redrawn from Woodwick,1960).

mainly by increasing their segment number. P. ciliata, which settles after about three weeks in the plankton when it has reached 16 segments, may grow at the rate of one segment per day. It may lay eggs about three weeks after settlement, when it has reached 40 segments. Thus, P. ciliata may complete its life-cycle in 6 weeks. P. ciliata may lay a second batch of eggs two weeks after the first batch, then it usually dies (Daro and Polk,1973).

Polydora species, such as P. ligni and P. ciliata, have an opportunistic life history (Grassle and Grassle,1974). They are able to exploit open habitats, because of their high birth rate and high dispersal ability. This characteristic makes many Polydora species potential pests if they are introduced to new areas which have no competing species. It may explain the devastation caused by polydorids on oyster beds in Australia, in the late 1880's (Roughley,1922; Whitelegge,1890).

DISTRIBUTION

GEOGRAPHICAL DISTRIBUTION

Representatives of Polydora are found off the coasts of all the continents: Europe (Andreu,1957; Clark,1960; Fauvel,1927; Harris,1971; Hannerz,1956; Hempel,1957; Marine Biological Association,1957; Muus, 1967; Rasmussen,1973); Africa (Day,1967; Kirkegaard,1959); America, north (Berkeley and Berkeley,1936,1952; Blake,1969a,1969b,1971; Hartman,1941; Pettibone,1954; Treadwell,1948) and central (Foster, 1971; Rioja,1943); Asia, including Ceylon (Perera and Arudpragasam, 1966), Indonesia (Pillai,1965) and Japan (Imajima and Hartman,1964; Okuda,1937); Australasia (Rainer,1973; Roughley,1922; Skeel,1975; Whitelegge,1890); the Arctic (Davis,1967; Wesenburg-Lund,1950); and the Antarctic (Hartman,1953).

Certain species are cosmopolitan; P. ciliata is found from latitude 60° north to 60° south (Dorsett,1961a). Other species, such as P. narica (Light,1969), have been recorded from only one locality.

ECOLOGICAL DISTRIBUTION

Table 1 shows the wide variety of substrates on which Polydora may be found. Some species, like P. ciliata, are found on many different organic and inorganic substrates; other species, such as P. maculata are restricted to a few calcareous substrates (Blake and Evans,1973). Actively crawling molluscs and highly mobile substrates are rarely inhabited by Polydora, even though the substrates are accessible to settling larvae. Deep- burrowing molluscs are also

TABLE 1

The Substrates Inhabited by

Polydora spp.

SPECIES	SUBSTRATE	REFERENCES
	BIVALVES	
P. cavitensis	*Ostrea virginica*	Pillai,1965
P. ciliata	*Cerastoderma edule*	Amanieu & Cazaux,1963; Hertweck,1971
	dead *Mya arenaria*	Boekschoten,1966.
	Mytilus edulis	Crowley 1972; Field,1922; Hempel,1957; Lebour,1907; Rasmussen,1973; Williams,1968.
	Ostrea cucellata	Mc.Intosh,1902; Roughley, 1922; Whitelegge,1890.
	Ostrea edulis	Dollfus,1921; Fauvel,1927; Korringa,1951,1952; Leloup,1937; Mc.Intosh,1896, 1915; Wilson,1928.
	Scrobicularia plana	Hempel,1957.
	Pecten irradians	Plaine,1952.
P. coeca	*Glycimeris* sp.	Southward,1957.
	Ostrea edulis	Southward,1957.
P. concharum	*Placopecten magellanicus*	Blake,1969b.
P. dorsomaculata	*Ostrea lutaria*	Rainer,1973.
P. giardi	*Ostrea lutaria*	Rainer,1973.
	Modiolus sp.	Southward,1957.

TABLE 1 continued.

SPECIES	SUBSTRATE	REFERENCES
	BIVALVES contd.	
P. hermaphroditica	*Ostrea edulis*	Hannerz,1956.
P. hoplura	*Ostrea edulis*	Fauvel,1927; Korringa, 1951,1952; Wilson,1928.
P. ligni	*Crassostrea virginica*	Lunz,1941; Nelson and Stauber,1940.
	Mytilopsis sallei	Ganti et.al.,1975.
	Ostrea edulis	Hannerz,1956.
P. pacifica	*Pinctada margaritifera*	Takahashi,1937.
P. quadricirrata	*Ostrea lutaria*	Rainer,1973.
P. socialis	*Placopecten magellanicus*	Blake,1969b.
P. vulgaris	*Pinctada margaritifera*	Mohammad,1972.
P. websteri	*Aequipecten gibbus*	Wells and Wells,1962; Wells et.al.,1964.
	Crassostrea gigas	Kavanagh,1940.
	Crassostrea virginica	Frey,1946; Galtsoff,1964; Hartman,1945,1966; Hopkins,1958; Loosanoff and Engle,1943; Mackin and Cauthron,1952; Needler,1941; Owen,1957.
	Mya arenaria	Pearse and Gunter,1957.
	Mercenaria mercenaria	Landers1967; Jefferies,1972.

TABLE 1 continued.

SPECIES	SUBSTRATE	REFERENCES
	BIVALVES contd.	
P. websteri contd.	Patinopecten caurinus	Hartman,1961.
	Placopecten magellanicus	Blake,1969b,1971;Evans,1969.
	Ostrea lurida	Hartman,1961.
	Pecten irradians	Turner and Hanks,1959.
	Ostrea permollis	Forbes,1966.
	GASTROPODS	
P. armata	Haliotis iris	Rainer,1973.
P. bioccipitalis	Murex gemma	Blake and Woodwick,1972.
	Ocenebra poulsoni	Blake and Woodwick,1972.
	Olivella biplicata	Blake and Woodwick,1972.
	Polinices reclusianus	Blake and Woodwick,1972.
P. capensis	Turbo sarmaticus	Day,1955.
P. ciliata	Buccinum undatum	Hempel,1957.
	Crepidula fornicata	Hempel,1957.
	Gibbula cineraria	Ankel,1936.
	Haliotis sp.	Lamy and Andre,1937.

TABLE 1 continued

SPECIES	SUBSTRATE	REFERENCES
	GASTROPODS *contd*.	
P. ciliata contd.	*Littorina littorea*	Ankel,1936; Dollfus,1932. Eliason,1920; Hannerz,1956; Hempel,1957; Lelcup,1937; Orrhage,1969; Rasmussen,1973; Soderstrom,1920,1923; Thorson,1946.
	Littorina obtusata	Ankel,1936.
	Nassarius reticulatus	Codreanu and Mack-Fira,1961.
	Neptunea antiqua	Eliason,1920.
	Patella vulgata	Ballantine,1961b; Hannerz, 1956; Lamy and Andre,1937.
	Thais lapillus	Moore,1938; Pelseneer,1928.
	Thais lamellosa	Berkeley and Berkeley,1952.
P. commensalis	*Buccinum undatum*	Hatfield,1965.
	Buscyon canaliculata	Hatfield,1965.
	Cerastoma nuttali	Woodwick,1963.
	Littorina littorea	Blake,1969; Hatfield,1965.
	Lunatia heros	Hatfield,1965.
	Nassarius obsoletus	Andrews,1891a; Berkeley and Berkeley,1936; Hatfield,1965.
	Olivella biplicata	Woodwick,1963.
	Polinices duplicata	Hatfield,1965.
	Thais emarginata	Woodwick,1963.
	Thais lamellosa	Berkeley and Berkeley,1936.

TABLE 1 continued

SPECIES	SUBSTRATE	REFERENCES
	GASTROPODS contd.	
P. convexa	Diodora aspera	Blake and Woodwick,1972.
	Olivella biplicata	Blake and Woodwick,1972.
	Tegula brunnea	Blake and Woodwick,1972.
P. elegantissima	Olivella biplicata	Blake and Woodwick,1972.
P. hoplura	Thais lapillus	Fischer,1930.
P. moculata	Bullia laevissima	Day,1963.
P. websteri	Littorina littorea	Blake,1969,1971.
	PORIFERA	
P. caeca	Microciona plumosa	Dollfus and Rullier,1965; Hornell,1892.
P. hoplura	Halichondria panicea	Southern,1914; Southward,1956.
	COELENTERATES	
P. armata	Lepastrea purpurea	Ima-jima and Hartman,1964.
P. pacifica	Montipora sp.	Takahashi,1937.

TABLE 1 continued

SPECIES	SUBSTRATE	REFERENCES
	POLYCHAETES	
P. caulleryi	Pomatoceros sp.	Fauvel,1927.
P. ciliata	serpulid tubes	Southward,1956.
	CRUSTACEANS	
P. ciliata	Balanus sp.	Dollfus and Rullier,1965.
	CORRALINE ALGAE	
P. armata	Lithothamnion sp.	Fauvel,1927; Mesnil,1896; Okuda,1937.
P. caulleryi	Lithothamnion sp.	Southward,1956.
P. ciliata	Lithothamnion sp.	Dollfus and Rullier,1965; Fauvel,1927; Hannerz,1956; Lamy and André,1937; Mesnil,1896; Woodwick,1963.
P. coeca	Lithothamnion sp.	Fauvel,1927; Hannerz,1956.
P. flava	Lithothamnion sp.	Fauvel,1927; Hannerz,1956; Mesnil,1896; Southern,1914.
P. giardi	Lithothamnion sp.	Fauvel,1927; Mesnil,1896; Southward,1956.

TABLE 1 continued

SPECIES	SUBSTRATE	REFERENCES
	WOOD	
P. ciliata		Dorsett,1961b.
P. ligni		Foster,1971; Hartman,1945.
P. redeki		Eliason and Haatela,1969.
	ROCK	
P. ciliata	sandstone	McIntosh,1915.
	hard clay	Dorsett,1961b.
	limestone	Anon,1904; Calman,1936; Clark,1906;1960; Daro and Polk,1973; Dorsett,1961b; McIntosh,1868; Marine Biological Association, 1957.
P. flava	limestone	Anon,1904.
P. hoplura	limestone	Anon,1904; Calman,1936.
P. redeki	hard clay	Hempel,1957.
	SAND AND MUD	
P. caulleryi	sand	Hannerz,1956.
P. ciliata	muddy-sand	Abbott,1946; Agassiz,1866; Dorsett,1961b; Kiselva, 1967; Percival,1929; Smidt,1944.

TABLE 1 continued

SPECIES	SUBSTRATE	REFERENCES
	SAND AND MUD contd.	
P. hermaphroditica	sand	Hannerz,1956.
P. ligni	sand and muddy	Galstoff,1964; Hannerz,1956.
	sand	Hartman,1945; Rasmussen, 1973.
P. plena	sandy silts	Foster,1971.

uninhabited by Polydora (Boekschoten,1966).

There is little information on the salinity requirements of most Polydora species. However, P. ciliata and closely related species, such as P. ligni, P. redeki and P. websteri, are most abundant in brackishwater (Abbott,1946; Bakker and Pauw,1975; DeCoursey and Vernberg,1975; Eliason and Haatela,1969; Galstoff,1964; Muus,1967; Percival,1929; Rasmussen,1973; Wolff,1973). P. ciliata is found in water with only 4°/oo salinity (Percival,1929) and 1-3°/oo cholorinity (Wolff,1973). P. redeki is found at 6°/oo salinity (Eliason and Haatela,1969).

Little more is known about the oxygen requirements of polydorids, than their salinity requirements. But, at least P. ciliata is tolerant of low oxygen concentrations (Bakker and Pauw,1975; Cognetti, 1972). Other species may also be tolerant of poorly oxygenated water, since they possess bright red gills (Day,1955), which might indicate oxygen-carrying pigments.

Polydora species have been used in toxicity tests of pollutants (DeCoursey and Vernberg,1975). P. ciliata and P. ligni are abundant in areas of organic enrichment, and are regarded as indicators of organic pollution (Cognetti,1972; Schram,1968,1970; Wass,1967).

GEOLOGICAL DISTRIBUTION: fossil Polydora

It is difficult to identify fossil borings with any degree of certainty. Many of the borings are ascribed to Polydora-like individuals on insufficient evidence. Bather (1910) reviewed the early literature. He discussed how some borings were ascribed to Polydora solely on the basis of the superficial resemblance of the entrance of the fossil boring with that of present-day borings. Nevertheless, a number of credible accounts of fossil Polydora-like borings have been reported (Boekschoten,1966,1967; Cameron,1967,1969; Gripp,1969; Hempel,1957; Kern et.al.,1974; Prell,1925). Fossil polydorids have been reported from Miocene deposits, Miocene fossil bivalve and gastropod shells, and Cameron (1967) found a fossilized Polydora-like worm, with its external features clear, in deposits from the Devonian period of the Palaeozoic era. Fossil borings give us the rare opportunity of ageing, geologically, soft-bodied invertebrates.

Fossil polydorid borings give valuable clues to the ecology of the fossil hosts, since we know something about the ecological requirements of Polydora. For instance, geologists can determine the orientation of fossil bivalves by the distribution of the borings on the shell, because Polydora can only settle on the parts of the shell above the substrate surface (Boekschoten1966,1967; Cameron,1969).

RELATIONSHIPS OF POLYDORA SPP.

Polydora have a number of different relationships with the molluscs they infest. In many cases, Polydora bore into the mollusc shell without causing the host any harm; they merely use the shell as a refuge. On other occasions they bore through the shell, weaken it, and debilitate their hosts; Polydora may compete for the food carried in the incurrent of the host (Hempel,1957 ; Hopkins,1957). I do not wish to enter the debate concerning the classification of such relationships. The classical terms are inadequate to define relationships between animals, which may be on any part of a continuum from total independence to total metabolic dependence (Cheng,1967).

A classical form of commensalism occurs between P. commensalis and pagurids, such as Eupagurus longicerpus and E. pollicans (Andrews,1891a1891b; Berkeley and Berkeley,1936; Hatfield,1965). The pagurid-spionid relationship may have persisted since the Pleistocene period (Kern et.al.,1974). P. commensalis is not known to live freely (Hatfield,1965). P. ciliata is sometimes associated with the pagurid Diogenes pugilator, but the relationship is not obligatory (Codreanu and Mack-Fira,1961).

Polydorids have many loose associations with other animals. For example, P. ciliata is found associated with Jassa falcata or Corophium insidisus, depending on the hydographical conditions of the locality (Daro,1970). Polydora often occupy the same burrow as other animals, such as Limnoria tripunctata (Sleeter and Coull,1973).

Polydorids may compete for space with other animals. Pearce and Chess (1970) give some evidence of the competition between *P. ligni* and *Tubularia caeca*. Also, Williams (1968) found an inverse relationship between the infestation of *P. ciliata* and *Mytilicola intestinalis* in *Mytilus edulis*. He tentatively suggested that mussels with heavy polydorid infestations were unable to support *M. intestinalis* because *P. ciliata* debilitates its host. Hempel (1957) found that *P. ciliata* in shells, may be suffocated by secondary infestation of encrusting animals, such as *Hydractinia panicea* and *Halichondria panicea*.

Figure 7 shows three ways in which *P. ciliata* may acquire food. Most of the reports of the feeding habits of *Polydora* refer to *P. ciliata*. *P. ciliata* feeds on a variety of organisms: plankton; occasionally, meiobenthos; harpacticoid copepods; decaying *Balanus* sp., *Crepidula* sp., and hydroid corals; and detritus (Brayko,1954; Daro and Polk,1973; Hempel,1957; Losovskaya,1973). Hempel (1957) suggested that *P.ciliata* creates weak water currents by waving its tentacular palps; it then captures plankton which is carried along the palps by cilia to the mouth. In addition, *P. ciliata* may collect plankton carried in the strong feeding currents of bivalves (Hempel,1957; Hopkins,1958). Daro and Polk (1973) and Losovskaya (1973) regard *P. ciliata* as, primarily, a detritus feeder.

Enemies of *Polydora* include the predators *Psammechinus miliaris* (Hancock,1957), *Echinus asculentus* (Krumbein,1974), and *Zygonemertes virescens* (Marsh,1973); and at least one parasite, *Polyrhabdina polydorae*, which infests *P. flava* in Plymouth Sound (Mackinnon and Ray,1931).

Figure 7.

Nutrition of Polydora ciliata by scraping particles of the substrate with its palps (a), by grazing directly with its mouth (b), and by collecting the decomposed material of a dead Balanus (c).

(Redrawn from Daro and Polk,1973).


a
b
c

BURROW FORMATION AND BURROW STRUCTURE

There are three main ways Polydora species form their burrows: they may adhere to, but not penetrate, the sediment and agglutinate particles around themselves to form a tube; they may settle on a mollusc and be embedded by nacreous material produced by the mollusc; or they may actually penetrate the substrate by mechanically or chemically boring their way through it.

P. ciliata (Daro and Polk,1973; Korringa,1952; Personne,1965) and P. ligni (Galtsoff,1964; Haswell,1886; Lunz,1941; Mortensen and Galtsoff,1944) can form a tube on the surface of substrates by the agglutination of sediment. Figure 8 shows how a tube might be formed by P. ciliata on a glass slide.

Embedding does not involve any penetration. Polydora larvae swim into the mantle cavity, or between the mantle and the shell, of the mollusc, where they accumulate mud. The mud irritates the mollusc which tries to isolate the mud by secreting a nacreous layer of shell around it. Figure 9 shows the mud-blister which may result from embedding of polydorids. Examples of Polydora which become embedded in shell are P. websteri (Korringa,1951), P. vulgaris (Mohammad1972) P. ligni (Lunz,1941) and P. hoplura (Korringa,1951).

Boring Polydora larvae first attach themselves to the substrate by mucus. Then they make their way into the substrate and form a pouch. This pouch may be converted into a U-shaped tube, as shown in Figure 10. The penetration into the shell may be mechanical or chemical (Hempel,1957; Schafer,1972).

Figure 8.

The settlement of Polydora ciliata on a substrate. The worm starts to make two traces of mucus (a), then constructs a mucus ring (b), and finally encrusts mucous ring and mucous traces with mud particles (c).

(Redrawn from Daro and Polk, 1973).

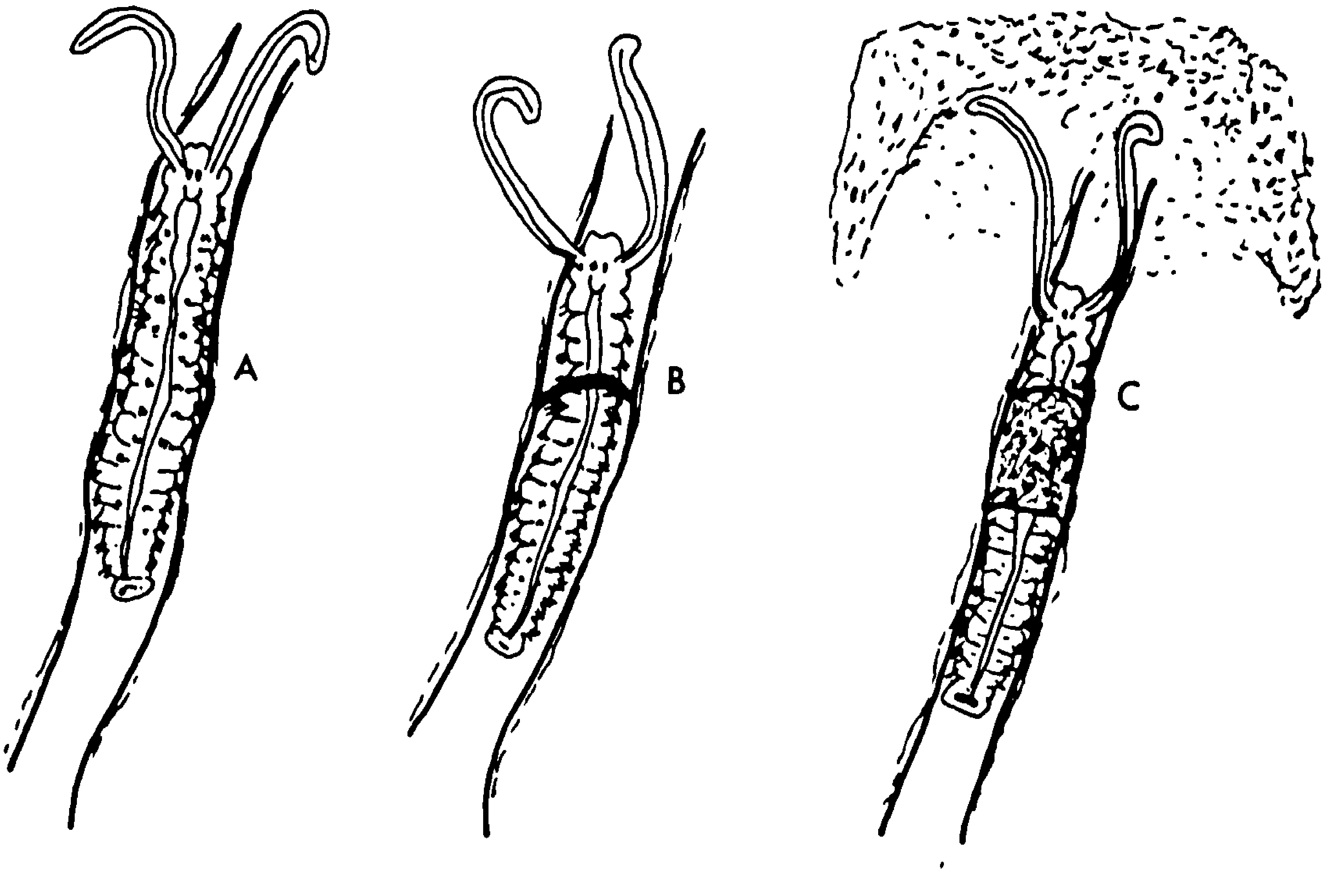

A
B
C

Figure 9.

Diagrammatic section through the shell of an oyster and a mud-blister.

(Redrawn from Lunz,1941).

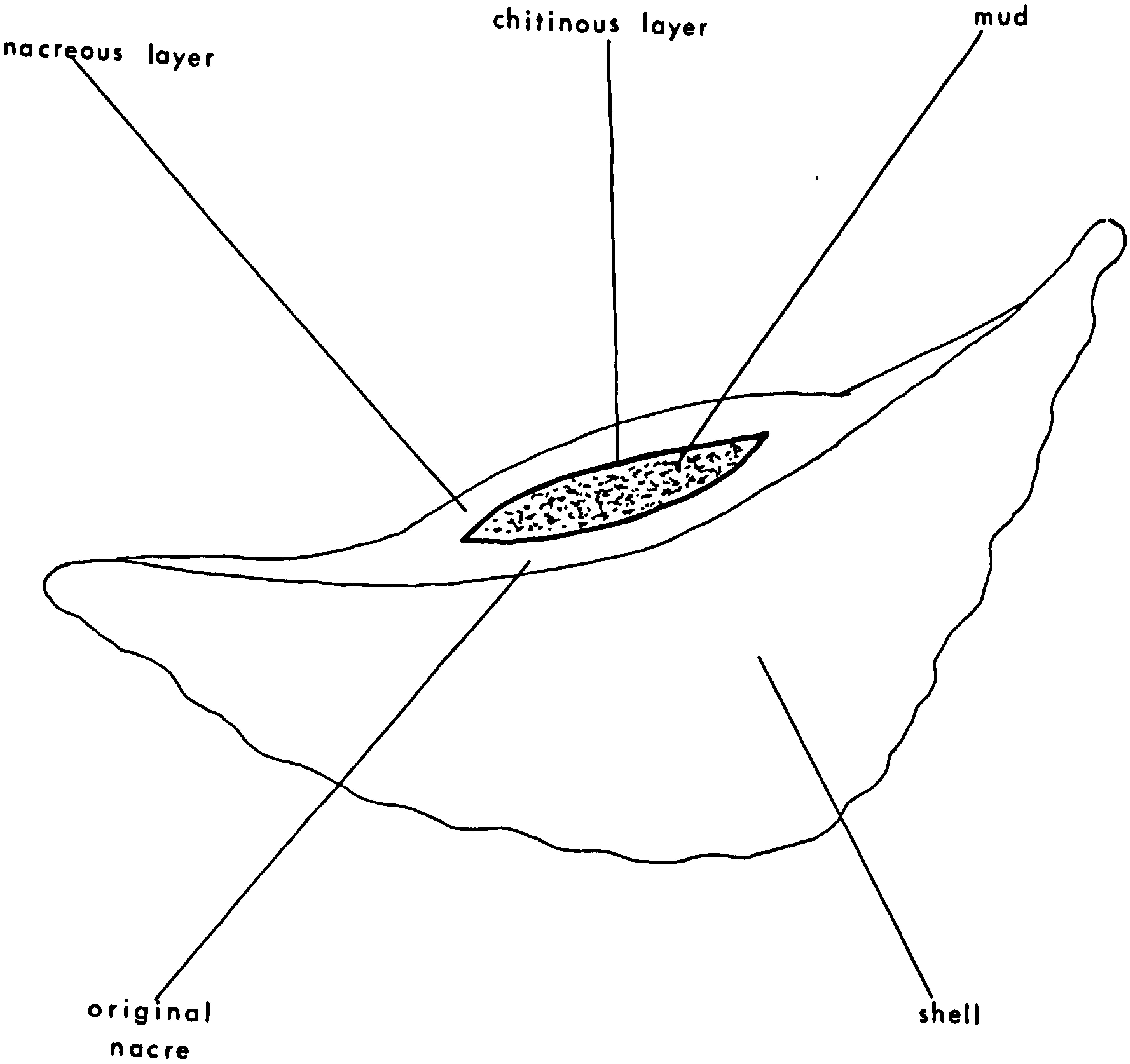
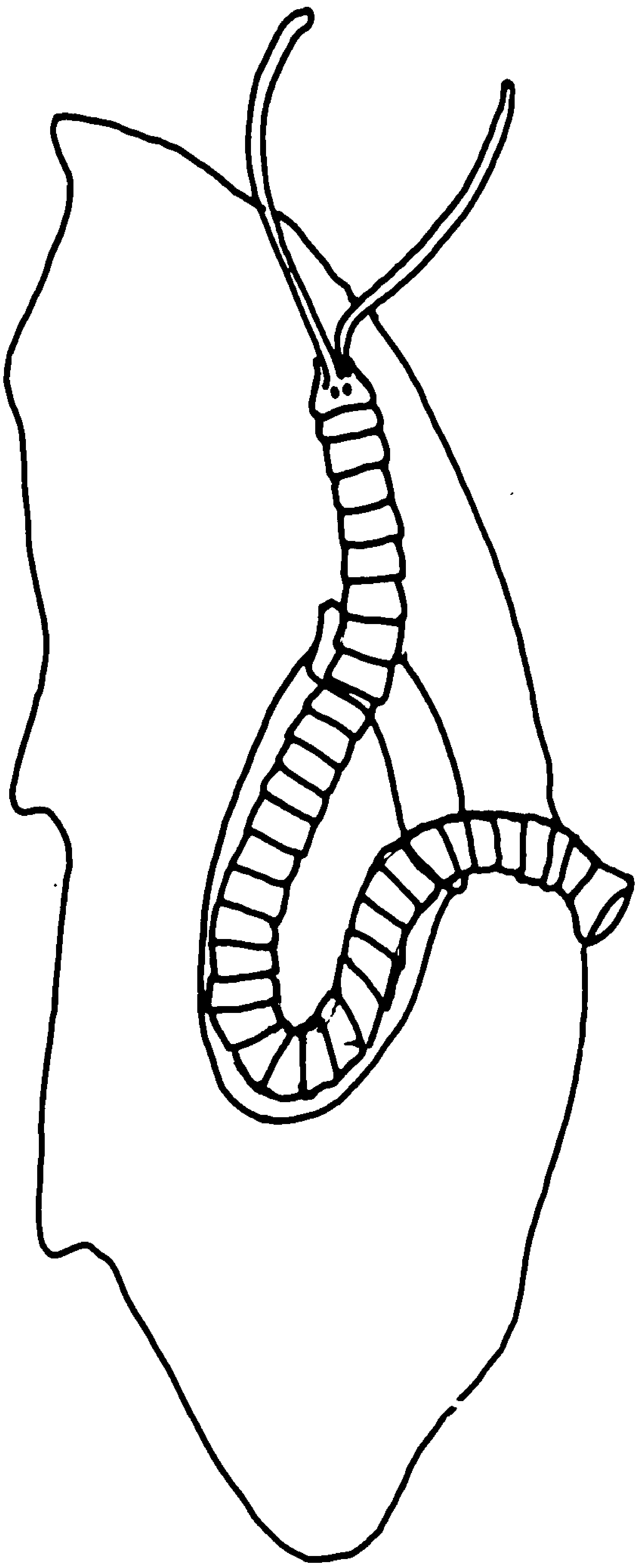

nacreous layer
chitinous layer
mud
original nacre
shell

Figure 10.

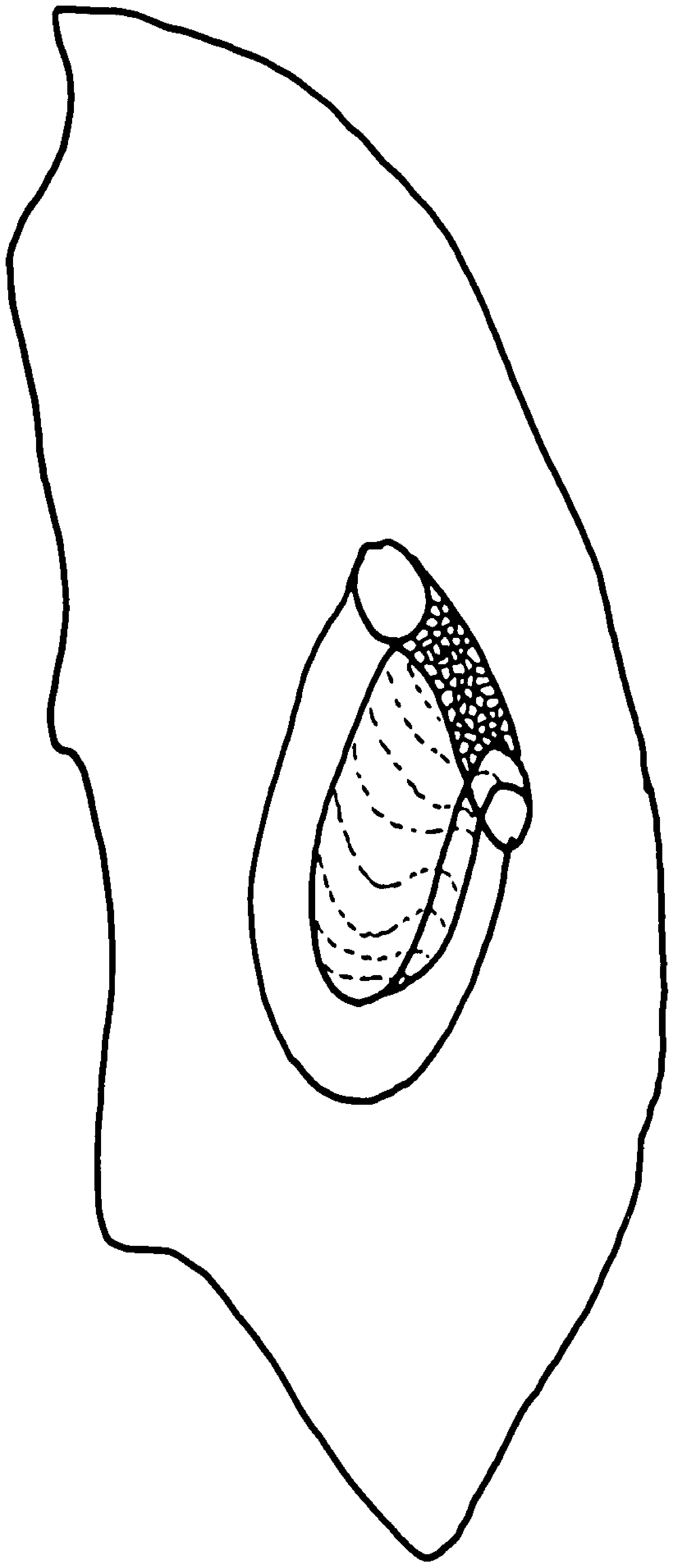
Burrow of Polydora ciliata in a calcite shell.

1. A pouch is formed by dissolving calcite.
2. The pouch is converted into a U-shaped tube by infilling with a septum made of cemented sediment grains.

(Schematic drawing, adapted from Schafer,1972).



1



2

Mechanical penetration of the substrate by Polydora is thought to involve the giant setae of the fifth segment with its powerful musculature (Dorsett,1961b; Hannerz,1956; Hempel,1957; Soderstrom, 1920). However, Soderstrom (1923) suggested that the setae were used merely for anchoring Polydora to the walls of their tubes. Other evidence for the mechanical penetration of the substrate by Polydora, are: abrasion of the setae of boring species (Hempel,1957); scratch marks on the walls of the burrows (Hempel,1957); some observations of boring individuals using their setae in penetration (Hannerz,1956; Hempel,1957); and the penetration of non-calcareous substrates, such as wood and siliceous rocks (Dorsett,1961b; McIntosh,1868,1902). However, the giant setae are probably too weak to facilitate penetration of hard substrates; and the removal of the setae does not stop P. websteri from boring into calcareous material (Dorsett,1961b; Haigler,1969). Therefore, chemical penetration must be responsible for some borings.

Evidence for the chemical penetration of substrates by Polydora has relied mainly on finding polydorid secretions which dissolve substrates. Claparede (1870) described acid-producing glands, the "poches glanduleuses", in P. ciliata. These were thought to enable P. ciliata to penetrate limestone (Lankester,1868). Unfortunately, non-boring Polydora species also possess these glands. Hannerz (1956) describes other acid-producing glands, which lie ventral to the setae of the fifth segment in P. ciliata larvae, which may aid the penetration of shells. Also, Haigler(1969) demonstrated acid production by P. websteri. However, in all these cases, it is impossible to be sure that the acid is used in substrate dissolution.

Kuhnelt (1935) suggested that acid is used in penetration because the middle wall of P. ciliata burrows contain precipitated calcium carbonate. Chemical penetration of mollusc shells by Polydora may involve the dissolution of the non-calcareous, organic interprismatic and interlamellar matrices of the shell (Travis and Gonsalves, 1969; Zottoli and Carriker,1974). This would loosen the calcareous crystals which could be dissolved or mechanically removed.

The method of boring by Polydora is not yet fully resolved. It seems likely that chemical and/or mechanical penetration can be used, depending on circumstances.

The depth of Polydora burrows depends on the stability of the surrounding sediment: the worms do not penetrate deeply into substrates surrounded by mobile sediment, but they may build chimney-like extensions beyond the surface of the substrate; worms surrounded by stable sediment generally burrow deeply into the substrate (Boekschoten,1966; Schafer,1972).

The shape of Polydora burrows is very variable, even for the same species in the same locality (Hempel,1957). Figure 11 shows a number of different burrow shapes, from the simple U-shaped burrows of P. ciliata and P. commensalis, to the complex branched burrows of P. concharum (Evans,1969). Some of the branches may be used for storing faecal pellets (Schafer,1972) or as brood tubes (Hempel,1957).

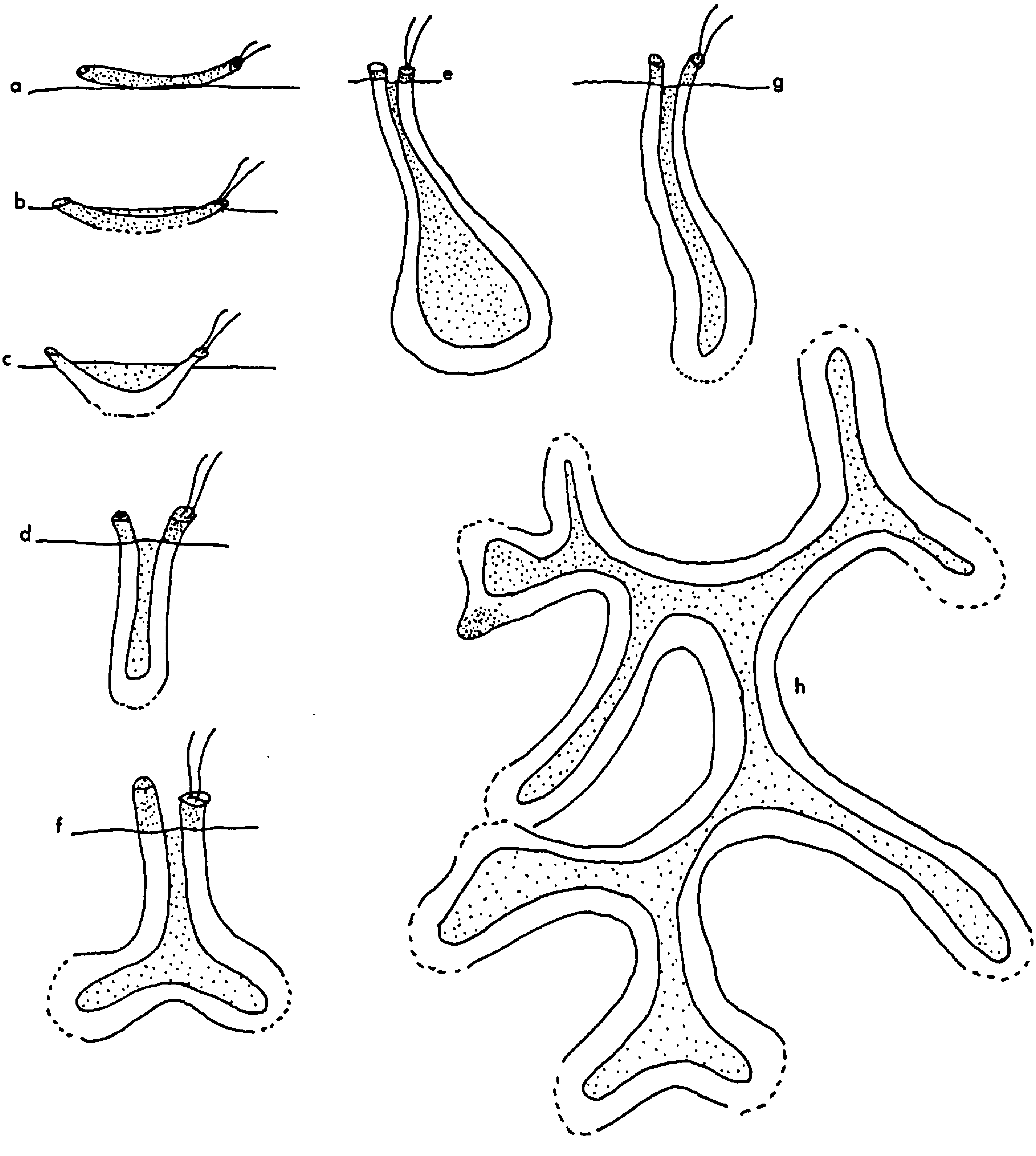
Polydora burrows have walls composed of sediment collected from the sea, carried to the mouth by ciliary grooves on the tentacular palps, and cemented together with mucus (Hempel,1957; Schafer, 1972). The particle size of the sediment on the wall may be quite

Figure 11.

Diversity of burrow structure of Polydora spp.

a) Tube of just settled larva.
b) Initial boring activity of worm, this stage is reached by Polydora commensalis.
c) An extended boring of P. commensalis.
d) U-shaped boring, such as that formed by Polydora ciliata.
e) Pear-shaped burrow formed by P. websteri.
f) Single branched burrow formed by P. websteri in Placopecten shells.
g) Multiple branched burrow of Polydora concharum from shells of Placopecten magellanicus.

(Redrawn from Evans, 1969).


a
b
c
d
e
f
g
h

different from that of the surrounding sediment; <u>Polydora</u> are able to select particles according to their size (Dorsett,1961b; Kiselva, 1967) their texture, or their weight (Hempel,1957).

THE EFFECT OF POLYDORA INFESTATIONS AND THEIR POSSIBLE CONTROL

Even planktonic Polydora larvae may be harmful to molluscs since they feed on lamellibranch larvae (Breese and Phibbs,1972; Korringa,1951) making them pests over oyster beds and in oyster hatcheries (Breese and Phibbs,1972).

Polydora are probably most damaging to shellfish when they bore into and weaken shells, making them more susceptible to predation, more difficult to clean, and more difficult to transport (Dollfus,1921; Forbes,1966; Korringa,1952; Leloup,1937).

Most Polydora borings do not penetrate the shell completely. But those that do, physically stimulate the mollusc to seal off the perforation. A layer of conchyolin is secreted around the invading worm or around the perforation; after which, nacreous material is laid down and a pearly blister is formed on the interior of the shell (Korringa,1951; Malek and Cheng,1974). However, if Polydora penetrate the shell near the posterior adductor muscle of bivalves, the shellfish are unable to seal off the hole. Consequently the muscle may be weakened (Lebour,1907; Turner and Hanks,1959) or the perforation may allow entry of microbes (Dollfus,1921).

The formation of a nacreous blister may have far reaching consequences for the molluscs. Some authors suggest that the energy used in blister formation reduces the energy available for growth and fattening (Hoek,1902; Lamy and André,1937; Owen,1957; Williams,1968) or pearl formation (Takahashi,1937). Other authors suggest that only shellfish in poor condition or with an exceptional number of blisters are adversely affected (Korringa,1951; Loosanoff and Engle,1943; Mackin,1950; Menzel and Hopkin,1950). Both views are based mainly on qualitative observations or inadequately controlled experiments. For instance, Loosanoff and Engle (1943) found that Polydora infestations were higher in oysters in trays above the sediment-bed than in oysters lying on the sediment; but the tray oysters were still in good condition. It is possible that the different conditions above the sediment-bed compensated for any deleterious effect of Polydora.

There are a number of ways Polydora-induced blisters may adversely affect shellfish: they reduce the living space of the mollusc (Korringa,1952); they disrupt the smooth interior of the shell, which may disturb the filtering current of bivalves (Korringa,1951); they may deform the underlying mantle and reduce the fecundity of bivalves (Pillai,1965); they deform the shell margin and interfere with valve closure, thus making the occupants of the shell more susceptible to predators, noxious chemicals, and desiccation (Leloup,1937); and the blisters also make the shells unsightly and reduce the marketable value of the shellfish (Medcof,1946; Needler,1941; Thomson,1954).

Polydora which cause mud-blisters, or are surface foulers of molluscs, may be a greater hazard than boring species. They tend to accumulate mud which decomposes and produces hydrogen sulphide, which is injurious to molluscs (Galtsoff,1964; Korringa,1951; Lunz,1940,1941; Mortensen and Galtsoff,1944; Nelson and Stauber,1941; Owen,1957; Whitelegge,1890).

Another possible cause of the decrease in growth of Polydora-infested bivalves is that the Polydora may compete with the bivalves for planktonic food; they may even steal plankton carried in the bivalves' feeding currents (Hopkins,1957; Whitelegge,1890).

Polydora may also indirectly affect the mortality of molluscs, due to predators destroying the mollusc to get to the *Polydora*. For example, the sea-urchin *Psammechinus asculentus* may destroy *Ostrea edulis* shells to get at *P. ciliata* (Hancock,1957) and *Carcinus maenas* may destroy oyster spat on lime-covered collecting tiles, in order to get at *P. ciliata* (Korringa,1951).

Polydora also affect non-molluscan substrates. They may be a direct cause of coastal erosion wherever they bore into limestone rocks or coral reefs (Borley,1909; Hartman,1954; Takahashi,1937); or where their predators destroy the rock to get at them (Krumbein,1974). They may also change the constitution of the sediment by accumulating mud or fragmenting shells into fine grains (Cameron,1969; Galtsoff, 1964; Schafer,1972P. *Polydora* are among the worst foulers of man-made structures (Graham and Gay,1945; Personne,1965). They can create a 10 - 12 centimetre-thick mud-carpet on wooden piles (Rao and Shyamasundari,1963) and they can increase the weight of the structure by more than one kilogram per square foot.

There are a number of methods aimed at controlling polydorid infestations. The most mentioned method is to bathe the substrate in a poison, such as phenol (Owen,1957), di-nitro-ortho-cresol (Korringa, 1951), di-chlorobenzene (McKenzie and Shearer,1961) or saturated salt solution (Korringa,1951 ; Loosanoff,1957); this is supposed to kill *Polydora* without harming bivalves. However, some bivalves, such as *Pecten irradians*, which can not keep their valves tightly shut, will be injured by the poisons (Turner and Hanks,1959). Thomson (1954) suggests avoiding polydorid infestation by planting bivalves away from areas of Polydora settlement. This method certainly controlled the infestation of Australian oysters, but often the most favourable areas for oyster growth coincide with areas of Polydora settlement. Polydora larvae which infest oyster hatcheries are easily controlled by filtering the seawater before it enters the hatchery (Breese and Phibbs, 1972).

In most circumstances, it may not be economically advantageous to control Polydora; and even if they are killed, the abundance and duration of most Polydora in the plankton would necessitate their continual removal from shells.

SECTION II

THE SETTLEMENT AND DISTRIBUTION OF *POLYDORA CILIATA*.

THE SETTLEMENT AND DISTRIBUTION OF POLYDORA CILIATA.

INTRODUCTION

The settlement and distribution of P. ciliata on a variety of molluscan substrates is described in this section. The factors considered are monthly patterns of larval settlement; type of molluscs infested; the dispersion of polydorids on individual shells; and the distribution of P. ciliata in relation to tidal height and exposure.

The aim is to show which molluscs are most vulnerable to polydorid attack, and where and when the attacks are most likely to occur.

The results are based on radiographs taken of molluscan shells from a variety of shores. The degree of infestation was assessed for each shell by counting the polydorid tubes on the radiographs. The radiographic conditions were, unless otherwise stated, current, 5mA; voltage, 40 KeV; and exposure tine, 1 minute. Details of other methods are described in the relevant subsections.

SETTLEMENT OF POLYDORA CILIATA

Two methods were used to analyse the monthly settlement pattern of Polydora ciliata on mussels in the river Fowey. Firstly, 100 uninfested Mytilus edulis of between 6.0 and 6.5 cm length, were selected from the river Fowey mussel bed. The mussels were placed in a nylon bag and laid down alongside undisturbed mussels in the river, at the level of mean low water spring tides. Each month, the mussels were removed and X-radiographed; the number of new P. ciliata settling on each shell was recorded. In the second method, the monthly radiographs of previously undisturbed mussels, used in the condition analyses, were examined, and the percentage of tubes of less than 0.2 mm maximum length was recorded.

Both methods suffer from disadvantages. In the first method, the disturbance of the mussels may affect the settlement of polydorids. Also, the lack of any adults on the shells at the start of the experiment may inhibit new settlement, since P. ciliata is generally regarded as gregarious (Blake,1969a; Kiselva,1967). In the second method, not all the tubes of less than 0.2 mm will represent recently settled P. ciliata; some of them will have resulted from past settlers which have died, or which have failed to grow. Despite these disadvantages, the two methods do reveal the general pattern of settlement. Figures12a and12b show that maximum settlement occurred in May, but settlement continues for a long period.

The results seem to conform with what is already known of the life history of P. ciliata. P. ciliata may spawn several times in the year, but maximum spawning occurs from March to April. The larvae hatch from the egg at the three-setiger stage, then they spend up to six weeks in the plankton, after which they settle and metamorphose into the benthic form. Maximum settlement of P. ciliata larvae occurs between May and June (Daro and Polk,1973; Dorsett,1961a; Wilson,1928).

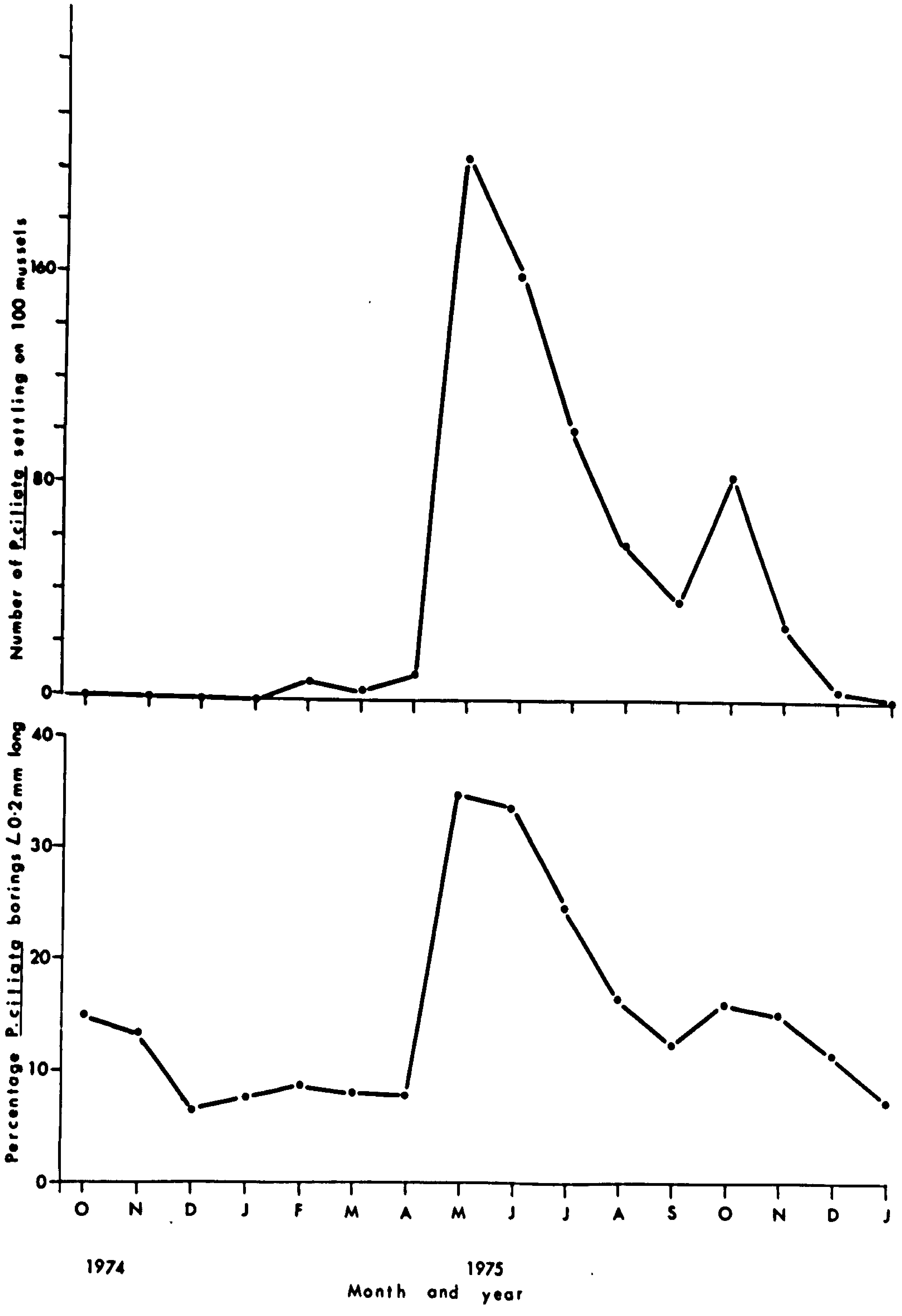
MOLLUSCAN SUBSTRATES INFESTED BY P. CILIATA

A wide variety of live molluscs were examined by radiography for polydorid infestation. A sample of the worms were extracted for

Figure 12

The monthly settlement pattern of *Polydora ciliata* on

(a) initially uninfested mussels and
(b) on undisturbed mussels.


Number of P.ciliata settling on 100 mussels
160
80
0
Percentage P.ciliata borings ∠0·2mm long
40
30
20
10
0
O
N
D
J
F
M
A
M
J
J
A
S
O
N
D
J
1974
1975
Month and year

specific diagnosis. Table 2 shows those molluscan species which harboured P. ciliata within their shells. Plates 1A - F are radiographs of some of the shells. Shells of dead Haliotis sp. were examined since, during the period of this study, there was a restriction on the collection of ormers in Guernsey. However, I believe that P. ciliata also infests live Haliotis.

Some molluscs were uninfested even in areas where P. ciliata was otherwise common. These molluscs included Trivia monacha, Mya arenaria and Scrobicularia plana. T. monacha avoids infestation by folding its mantle around its shell; and M. arenaria and S. plana escape polydorid infestation because their shells are buried in the substrate. However, dead shells of M. arenaria and S. plana lying on the substrate surface were infested by P. ciliata.

DISPERSION OF POLYDORA CILIATA

The dispersion pattern of P. ciliata tubes on M. edulis shells was analysed in detail to determine if the polydorids were gregarious and if they preferred any particular areas of the shell. First, radiographs of 5 left valves and 5 right valves of mussels, were carefully taken, so that the film conformed to the shape of the shell and recorded a 1:1 image. Figure 13 shows tracings of the valves with the position of the entrances to the polydorid tubes plotted. It is assumed that the entrances represent the initial settling site of polydorid larvae, since their tubes are generally extended backwards from the entrance (Schafer, 1972). The valves were randomly chosen from 100 mussels which had between 10 and 50 P. ciliata per shell.

The tracings of the valves were divided into 0.5 cm squares, and

Table 2

MOLLUSCS INFESTED BY POLYDORA CILIATA

SPECIES	LOCATIONS
GASTROPODS	
Buccinum undatum	Rivers Truro, Fowey and Yealm.
Crepidula fornicata	Rivers Fowey and Truro.
Gibbula cineraria	Porthpean.
Gibbula magus	Porthpean.
Gibbula umbilicalis	Porthpean.
Haliotis sp. (dead)	Guernsey.
Littorina littorea	Porthpean, Charlestown, Fowey and Yealm, Menai Bridge.
Nassarius reticulatus	Rivers Truro and Yealm.
Nucella lapillus	Porthpean, Charlestown, Fowey and Yealm, Menai Bridge.
Ocenebra	River Fowey.
Patella vulgata	See figure 17
Patella aspera	Porthpean, Charlestown.
Turitella communis	River Yealm.
BIVALVES	
Cerastoderma edule	Rivers Fowey and Tamar.
Chlamys opercularis	Plymouth Sound.
Mytilus edulis	See figure 18
Ostrea edulis	Rivers Fowey and Truro.
Venerupis decussata	River Fowey.

Plate 1

Radiographs of some gastropod and bivalve molluscs infested with *Polydora ciliata*.

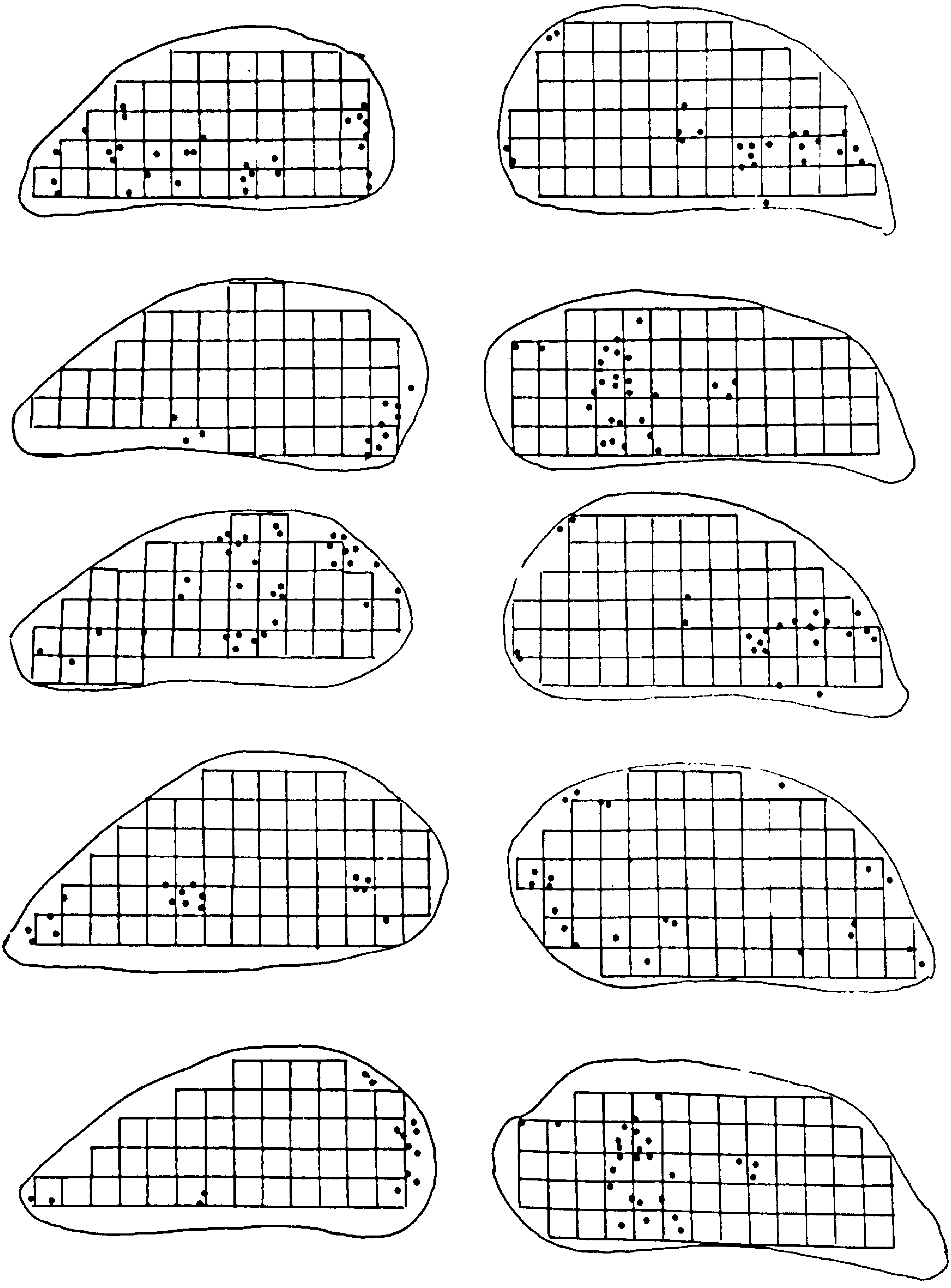
A *Buccinum undatum*
B *Thais lapillus*
C *Littorina littorea*
D *Crepidula fornicata*
E *Chlamys opercularis*
F *Ostrea edulis*
G *Cerastoderma edule*


A
B
C
D
E
F
G

Figure 13 .

THE DISPERSION OF POLYDORA CILIATA ON MYTILUS EDULIS:

Ten valves of *Mytilus edulis* were divided into 0.5 cm. squares and the position of *P. ciliata* burrow entrances, represented by dots in the figure, were plotted.



the number of polydorid tube entrances within each square was recorded. The dispersion of the entrances was then statistically analysed to see if it conformed to a Poisson distribution. Table3 shows that the variance was larger than the mean, which indicates that the entrances are contagiously dispersed. That is, that the presence of one individual *P. ciliata* on the shell tends to result in other *P. ciliata* settling near it.

This aggregation of polydorids complicates an analysis of their relationship with the different parts of the shell. To avoid this complication, the relative positions of tube entrances on mussels with only one *P. ciliata* were recorded; these are shown in figure 14. This figure is semi-diagrammatic and shows only the relative position of the entrances; there is no exact quantitative relationship between the points, therefore statistical analysis of the distribution was not undertaken. However, the figure does suggest that *P. ciliata* can settle on almost any part of the shell, and it does not seem to prefer one particular area on which to settle.

Examination of radiographs of *C. gigas* and *O. edulis* did not reveal any clear preference of *P. ciliata* for a particular area of the shell. Therefore, *P. ciliata*, unlike some other polydorids (Seilacher, 1969), does not seem to prefer to settle in the incurrent area of bivalves. Plate 1G is a radiograph of *C. edule*. The apparent preference of *P. cilata* for the incurrent area of *C. edule* is merely the result of the mode of life of the cockle; it usually lies buried in the substrate with only its posterior margin exposed to settling polydorid larvae.

Table 3.

ANALYSIS OF THE DISPERSION OF POLYDORA CILIATA ON MYTILUS EDULIS.

Mussel	No. P. ciliata per square	Observed frequency	Expected frequency	Chi-squared	p	Coefficient of dispersion
A	0	29	27.36	10.61	0.005	1.35
	1	14	15.36			
	2	3	4.32			
	3	1	0.86			
	4	1	0.10			
B	0	48	43.71	30.36	0,005	2.66
	1	1	7.52			
	2	2	0.71			
	3 & 4	1	0.04			
C	0	31	28.21	4.91	0.100	1.87
	1	10	14.40			
	2	4	3.62			
	3	2	0.60			
D	0	54	49.6	9.13	0.005	1.99
	1	5	11.8			
	2,3 & 4	4	1.4			

Table 3 Continued

Mussel	No.*P.ciliata* per square	Observed frequency	Expected frequency	Chi-squared	p	Coefficient of dispersion
E	0	42	40.4	11.74	0.005	1.58
	1	2	5.3			
	2	2	0.3			
F	0	50	45.2	22.07	0.005	2.12
	1	6	12.7			
	2	2	1.8			
	3	1	0.05			
G	0	41	36.4	27.34	0.005	1.60
	1	11	16.9			
	2	2	2.9			
	3	4	0.5			
H	0	48	43.7	6.08	0.050	2.1
	1	8	13.8			
	2	3	2.2			
	3,4 & 5	1	0.2			
I	0	60	58.6	1.47	0.250	1.2
	1	10	12.8			
	2	3	1.4			
J	0	44	37.9	15.28	0.005	1.6
	1	6	16.7			
	2	7	3.7			
	3	2	0.5			

Figure 14

The relative position of 100 P. ciliata entrances on mussels with only one polydorid.

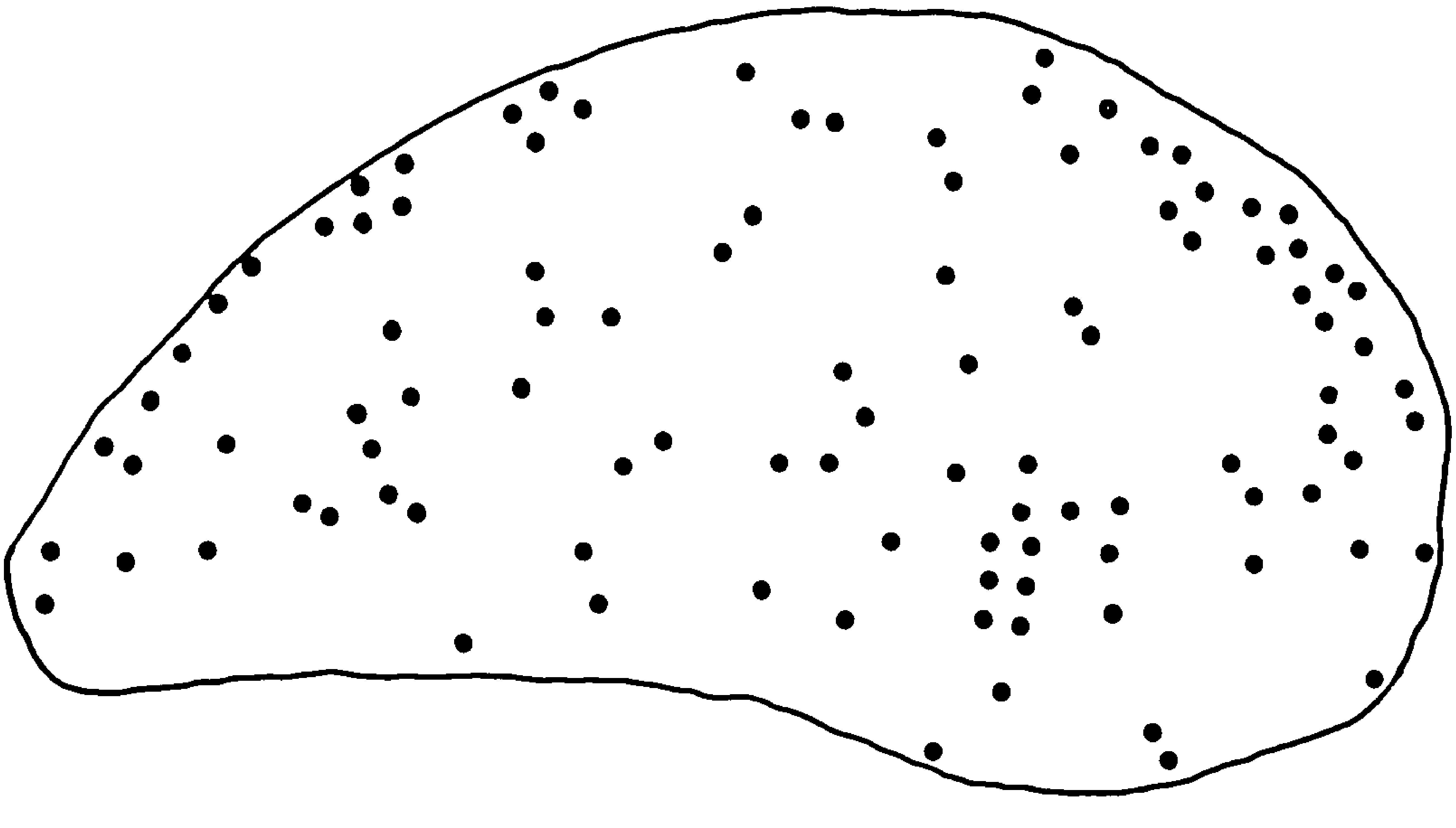


Figure 15 is based on radiographs and microscopical examination of a shell of Littorina littorea. The polydorids seem to settle preferentially in the suture lines of the shell. These lines are mainly in the apex of the shell and, of 100 infested shells examined, 57 per cent had P. ciliata only in the apex of the shell; while only 3 per cent had no polydorids in the apex. The aggregation of P. ciliata in the apex of littorinid shells often results in the destruction of the apex. P. ciliata seems to also settle preferentially in the suture lines of other gastropods, such as Buccinum undatum, Nassarius reticulatus, Nucella lapillus, and the top shells, Gibbula cineraria, G. magus, and G. umbilicalis.

Figure 16 shows the results of an analysis of 50 shells of Crepidula fornicata from the river Fowey. It seems that ~~the slipper limpet~~ POLYDORA CILIATA prefers the margin of the right side of the shell, which is where the feeding current enters the shell. Again, this apparent preference of P. ciliata for a particular area of the shell is probably due to the mode of life of its host. C. fornicata usually lives in chains, as shown in figure 16B, and, in the majority of the slipper limpets, the outer margin of the right side of the shell is the area most exposed to polydorid attack.

EXPOSURE

The distribution of Polydora ciliata in relation to exposure to wave action was studied by collecting mussels and limpets from a number of shores and comparing the degree of infestation of the molluscs.

Lewis (1964) stated that "waves are probably the most important factor determining shore populations and influencing their distribution".

Figure 15

The position of Polydora ciliata on a shell of the winkle, Littorina littorea. The polydorids seem to have a preference for the suture lines of the shell.

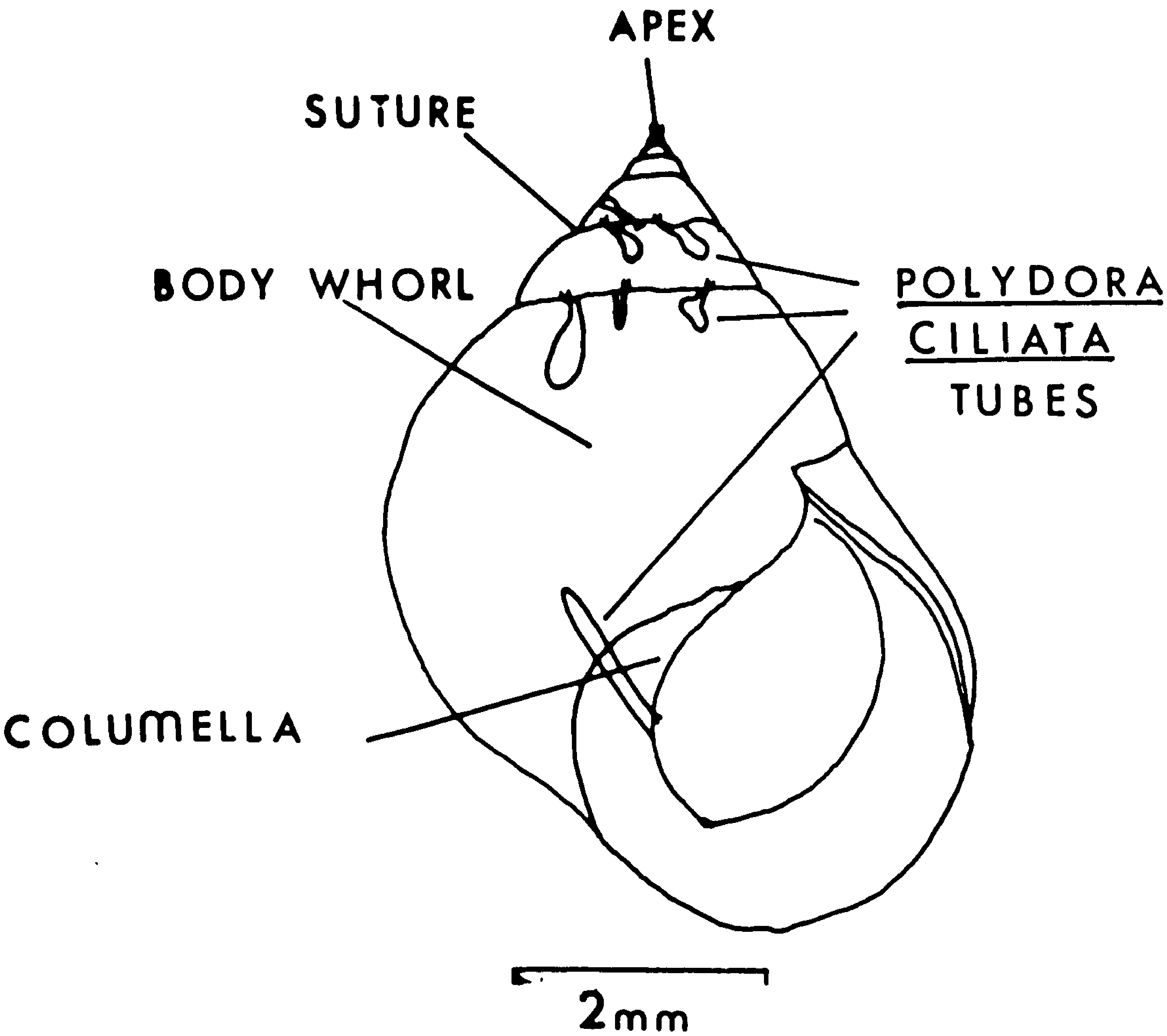

APEX
SUTURE
BODY WHORL
POLYDORA CILIATA TUBES
COLUMELLA
2mm

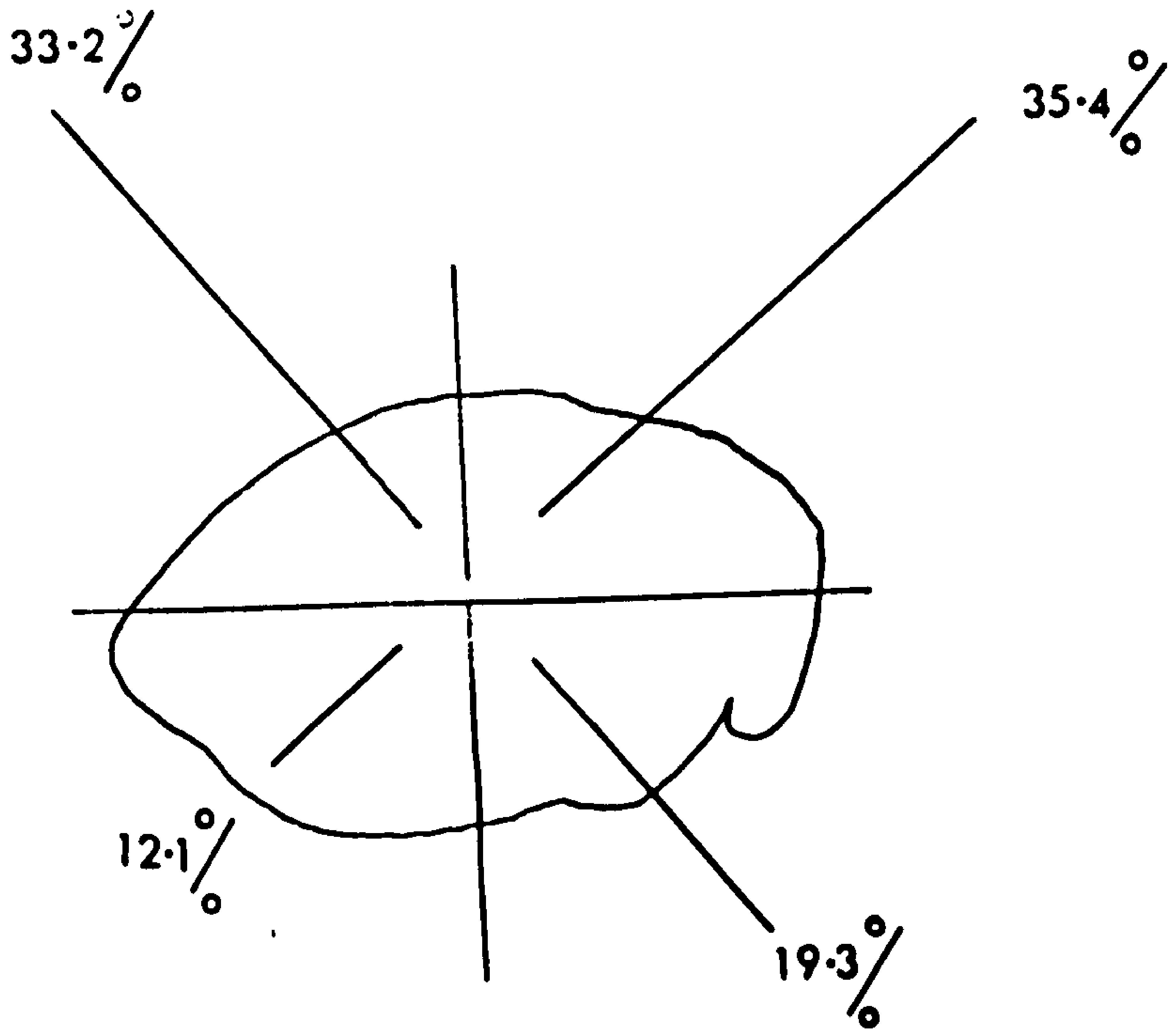
Figure 16

A. Diagram of Crepidula fornicata showing the the percentage infestation of 4 shell areas.

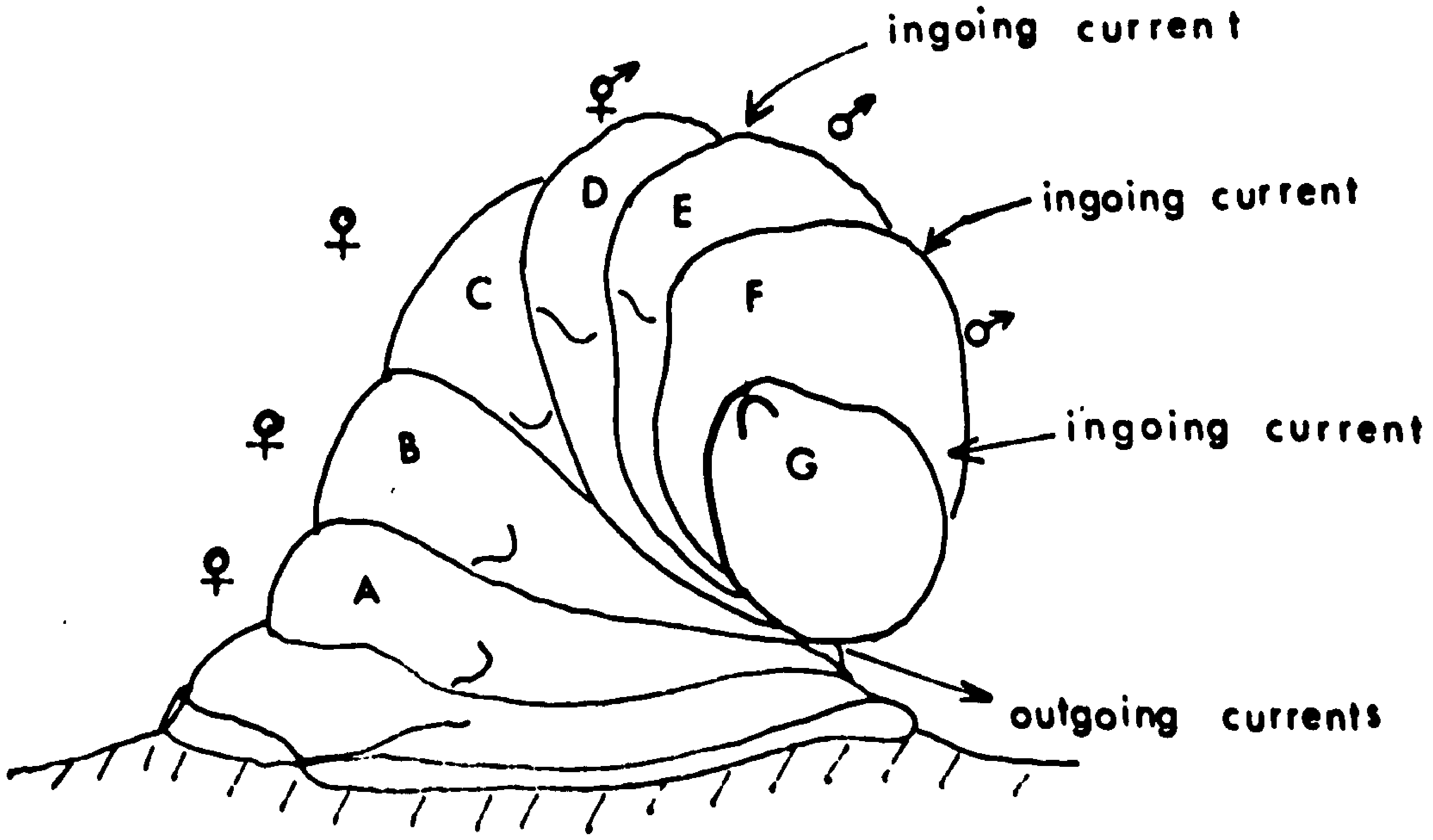
B. Postero-lateral view of a chain of seven C. fornicata, to show that the outer right margin of the shell is the area most exposed to the settlement of Polydora ciliata.

(From Orton, 1910-1911)

A


33·2%
35·4%
12·1%
19·3%

B


ingoing current
⚥
♂
ingoing current
♀
D
E
C
F
♂
♀
ingoing current
B
G
♀
A
outgoing currents

But he goes on to discuss the difficulty of obtaining objective evaluations of specific shores. The best indicators of exposure seem to be presence or absence of certain shore animals (Ballantine,1961a; Lewis,1964). This is the basis of biological exposure scales. I used the scale described by Lewis (1964), which is an adaptation of Ballantine's exposure scale (Ballantine,1961a).When classifying the shores according to this scale, I bore in mind Lewis' comment that "In assessing exposure by biological indicators the entire character of the shore should carry more weight than the density of single species" (Lewis,1964).

100 P. vulgata and/or 100 Mytilus edulis were collected at their lowest level on the shore. The collections were made during spring tides. Each shell was radiographed, and the number of infested shells was recorded.

Figures17&18 clearly show that P. ciliata is absent in limpets and mussels from exposed shores, and is generally more frequent in molluscs from sheltered locations. A number of factors complicate a more detailed analysis of the results. Firstly, the density of the molluscs was not the same at each locality. One would expect that the greater the density of the host, the greater the chances of P. ciliata finding a host. Secondly,the size of limpets and mussels tends to be influenced by the exposure of the shore. Limpet shells are generally smaller and thinner, with ribs more pronounced, in exposed situations; mussel shells attain a greater length on sheltered shores than on exposed shores. Figures19A&B show that the degree of infestation of limpets and mussels tends to increase with increased size of the molluscs. This may partly explain

Figure 17 .

The percentage infestation of Patella vulgata from shores with different degrees of exposure to wave action. The letters refer to the name of the shore, and the numbers refer to the exposure of the shore.

EXPOSURE SCALE : 1 = very exposed; 2 = exposed; 3 = semi-exposed ;
4 = sheltered; 5 = very sheltered.

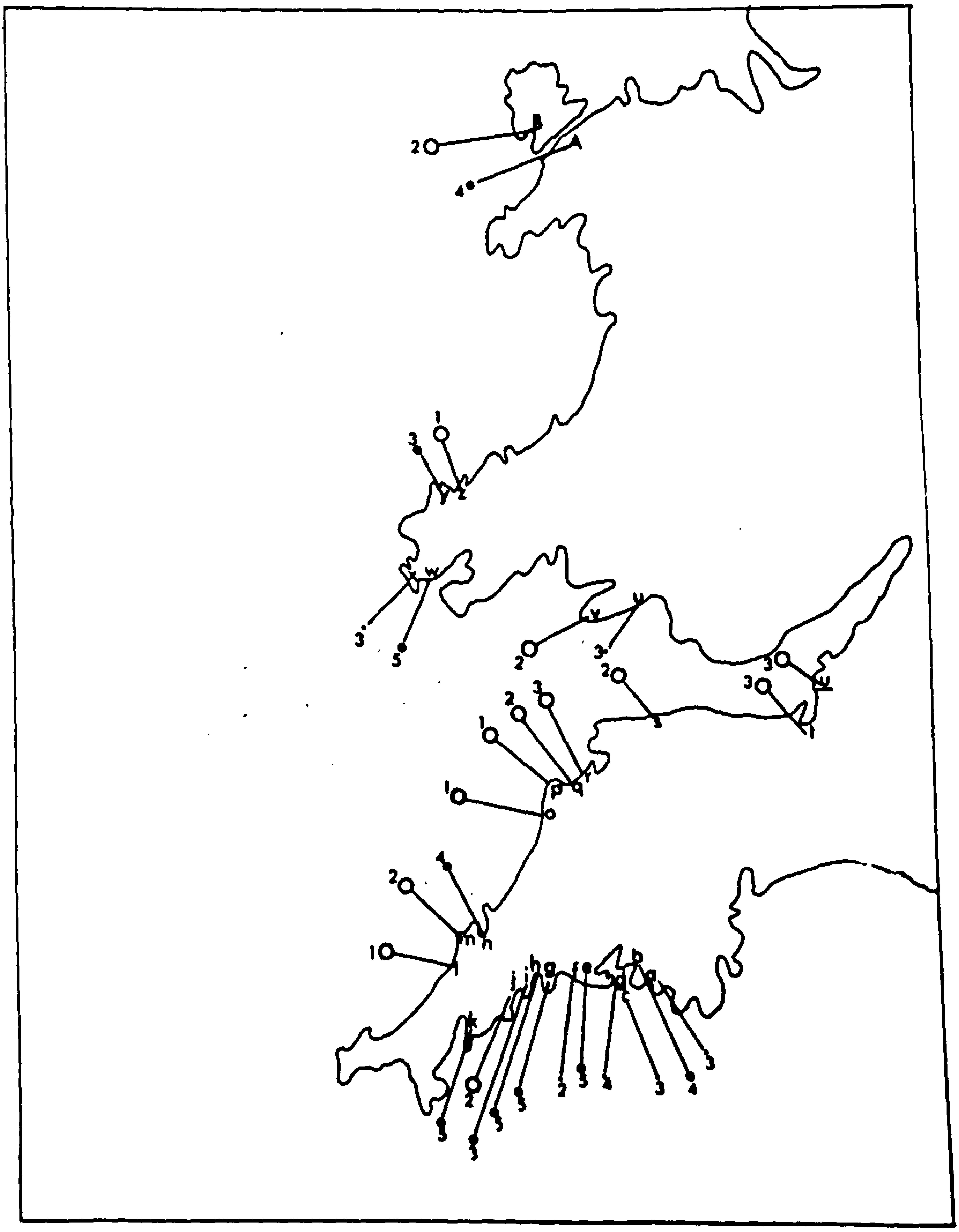
	% infestation		% infestation
a : Fort Bovisand	14	p : Hartland Quay	0
b : Jennycliffe	65	q : Lynmouth shore	0
c : South breakwater	12	r : Lynmouth harbour	5
d : North breakwater	23	s : Appledore	0
e : Cremyll	56	t : Burnham	0
f : Whitsand Bay	7	u : Weston-Super-Mare	0
g : Fowey	27	u : Bracelet Bay	0
h : Charlestown	76	v : Oxwich Bay	0
i : Porthpean	55	w : Dale mud flats	45
j : Caerhays	0	x : Dale Fort	17
k : Amsterdam Point	62	y : Fishguard	28
l : Porthcothan	0	z : Pwllgweelod	0
m : Padstow estuary	0	A : Menai Bridge	32
n : Padstow harbour	45	B : Aberfraw	0
o : Bude	0		

Key to symbols

-o = 0% infestation

- = less than 25% infestation

-• = more than or equal to 25 % infestation



B
A
2
4
1
3
y
z
x
w
3
5
v
u
2
3
3
3
t
s
2
w
1
2
3
1
p
q
r
1
o
4
2
m
n
1
l
h
g
f
e
b
a
d
c
j
i
k
2
3
3
5
5
2
3
4
3
4
3

Figure 18

The percentage infestation of Mytilus edulis collected from shores with different degrees of exposure to wave action.

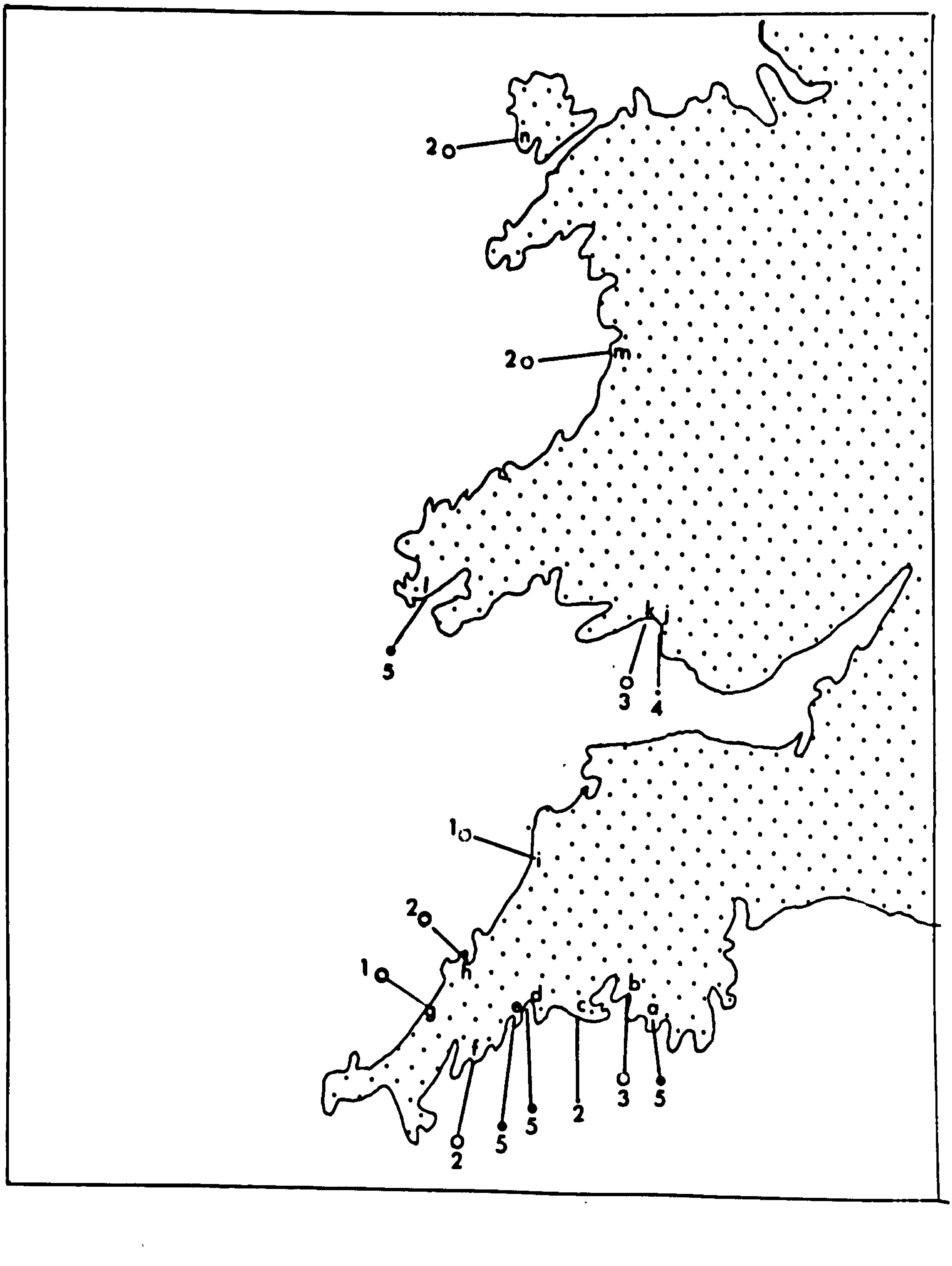
Shore exposure : 1 : Very exposed
2 : Exposed
3 : Semi-exposed
4 : Sheltered
5 : Very sheltered.

Name of the shore	% infestation
a) River Yealm	30
b) Fort Bovisand	0
c) Whitsand Bay	18
d) River Fowey	60
e) Charlestown harbour	40
f) Caerhays	0

Name of shore	% infestation
g) Porthcothan	0
h) Padstow estuary.	0
i) Bude	0
j) Swansea Bay	5
k) Oxwich Bay	0
l) Dale mud flats	41
m) Borth	0
n) Aberfraw	0

The percentage infestation is represented by the following :

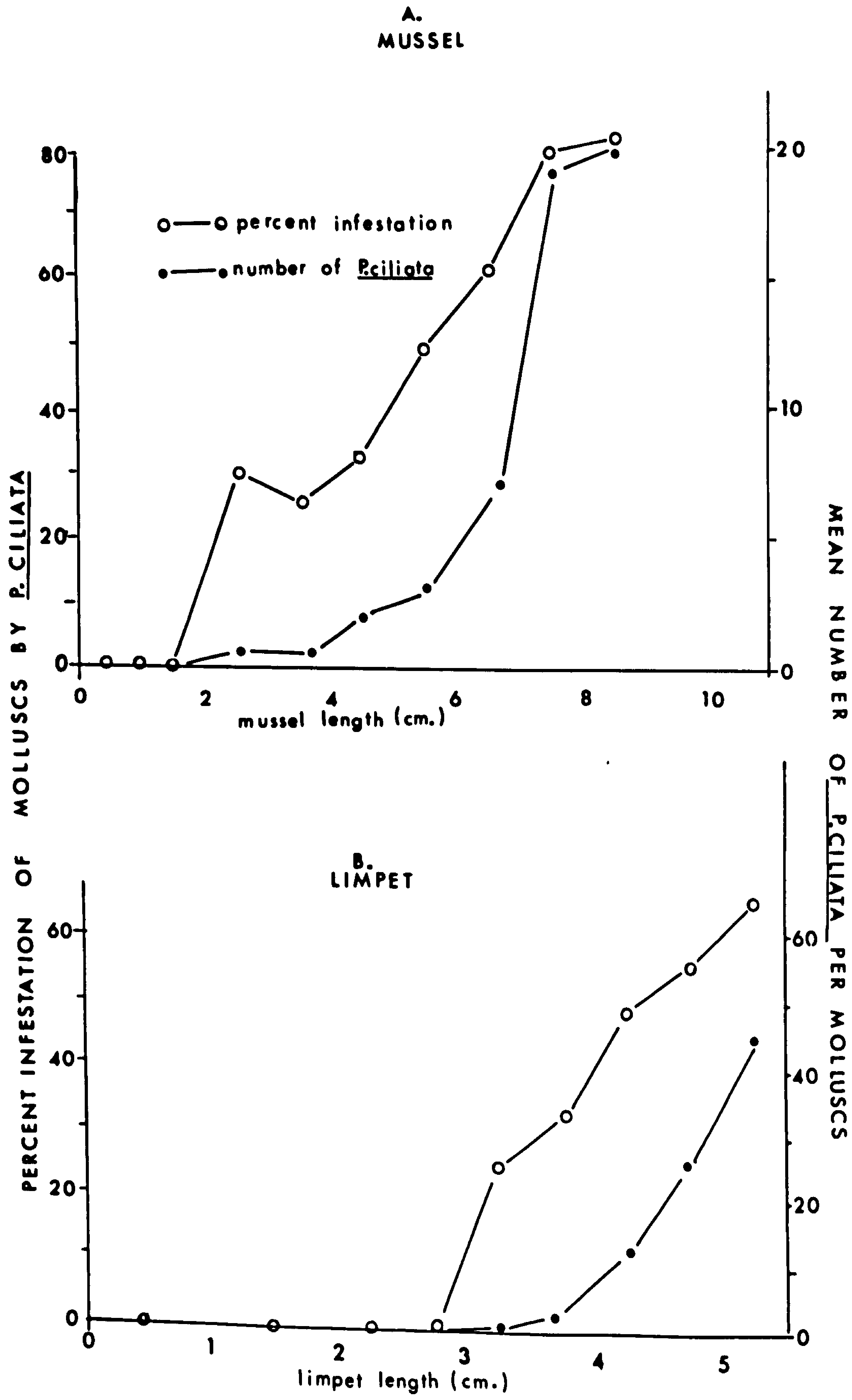
0 %	○—
1 - 25 %	—
more than 25 %	●—



2
n
2
m
5
l
k
j
3
4
1
i
2
h
1
g
f
e
d
c
b
a
2
5
5
2
3
5

Figure 19

The relationship between polydorid infestation and size of (A) mussels; (B) limpets .


A.
MUSSEL
o—o percent infestation
•—• number of P.ciliata
80
60
40
20
0
20
10
0
0
2
4
6
8
10
mussel length (cm.)
B.
LIMPET
60
40
20
0
60
40
20
0
0
1
2
3
4
5
limpet length (cm.)
PERCENT INFESTATION OF MOLLUSCS BY P. CILIATA
MEAN NUMBER OF P.CILIATA PER MOLLUSCS

the lower levels of infestation of molluscs from exposed shores. However, the total absence of polydorids from exposed shores shows that this is not the only explanation. A number of other factors may stop P. ciliata settling on molluscs on very exposed shores : the sheer physical violence of waves on exposed shores may remove settling larvae; the water in exposed localities is usually less turbid than water in sheltered areas, and might not contain enough detritus to sustain polydorids, which use detritus as food and in tube building; the physico-chemical conditions associated with exposed shores (eg., better aeration and less extreme temperatures than on sheltered shores, Lewis,1964) may be detrimental to Polydora ciliata. Any of these factors, alone or in combination, may limit P. ciliata to sheltered shores.

TIDAL HEIGHT

The density and size of the molluscan hosts of P. ciliata may change with the tidal level of the shore. This makes it difficult to establish a quantitative relationship between the distribution of P. ciliata and tidal height. Limpets were unsuitable substrates to analyse because they tended to be absent from the lower levels of sheltered shores where there was excessive competition with algae, or where the substrate was unstable. However, Littorina littorea are abundant from the lowest levels of the shore, to just above the level of mean high water neap tides, at Yealm Ferry; a very sheltered shore near the mouth of the river Yealm. Therefore, the mean number of P. ciliata per littorinid shell was estimated by analysing radiographs of 50 L. littorea at 0.5 metre intervals up the shore.

The level of the shore was estimated using a method described by Evans (1947).

Figure 20 shows that P. ciliata is most abundant at the lowest intertidal levels and that it does not extend as far up the shore as its host.

Other molluscs were collected from other shores, and the presence of P. ciliata at different levels is shown in figure 21. P. ciliata did not extend as far up exposed shores as up sheltered shores. This is opposite to the effect of exposure on most intertidal animals (Lewis, 1964). However, more molluscan substrates are available on sheltered shores; while P. aspera, which is confined to the lower levels of the shore, is the main host of P. ciliata on moderately exposed shores.

The absence of P. ciliata from levels above mean high water neap tides, may be due to a number of factors associated with emersion, such as desiccation and restricted feeding time. It is possible that the tolerance of adult polydorids, which can partly avoid adverse conditions by withdrawing into their tubes, is greater than the tolerance of their settling larvae.

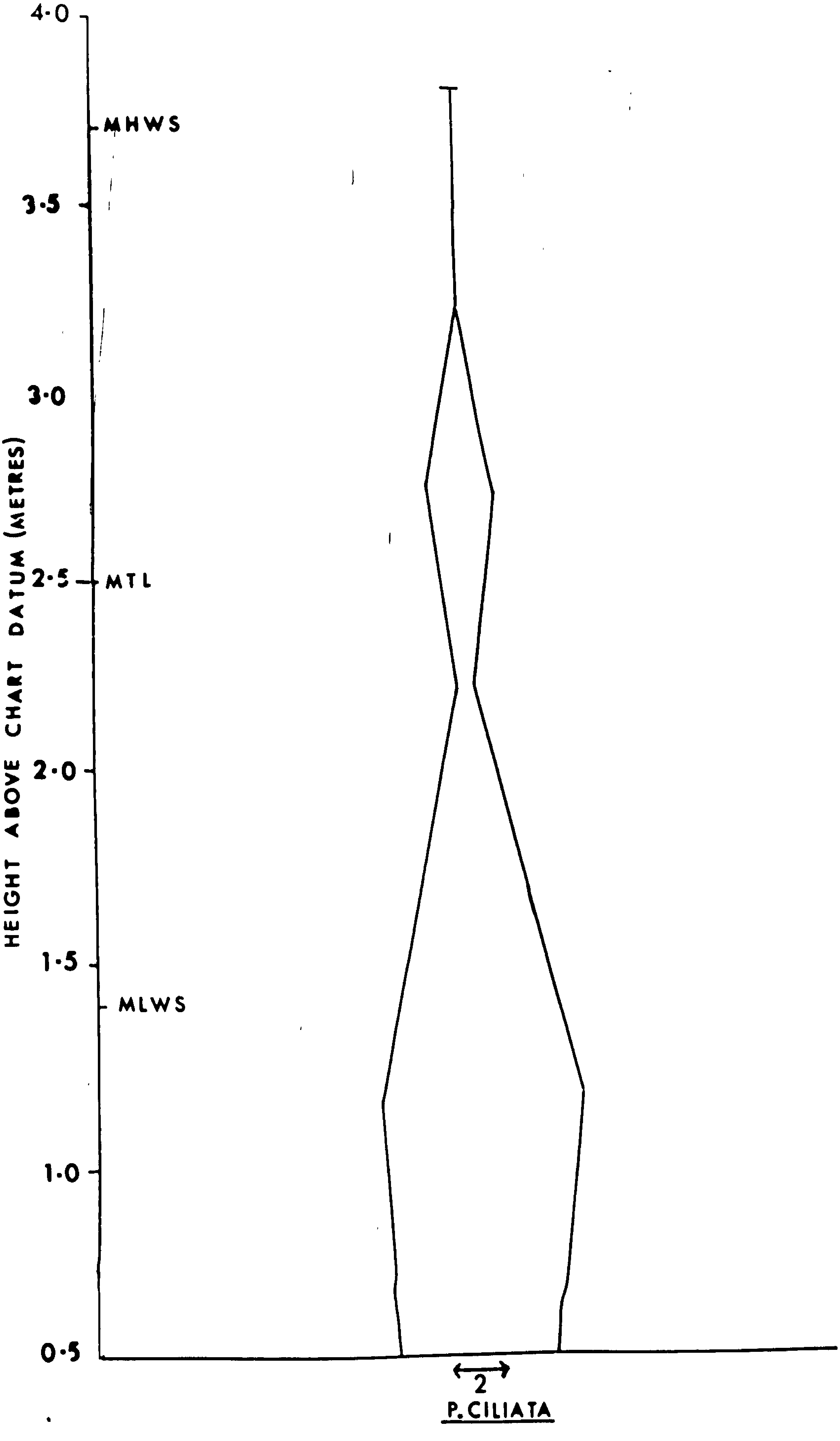
CONCLUSIONS

From the above results, one can make some tentative predictions concerning the vulnerability of molluscs to polydorid infestation.

Molluscs will be mainly liable to P. ciliata infestation in the spring and early summer, when the larvae seek out a substrate on which to settle. The molluscs which will be most liable to the infestation are those which already have some P. ciliata boring within their shells, since the worm seems to be gregarious. Large

Figure 20

The degree of infestation of <u>Littorina</u> <u>littorea</u> at different tidal heights at Yealm Ferry.



MEAN NUMBER OF <u>P. CILIATA</u> ON <u>L. LITTOREA</u>

Figure 21

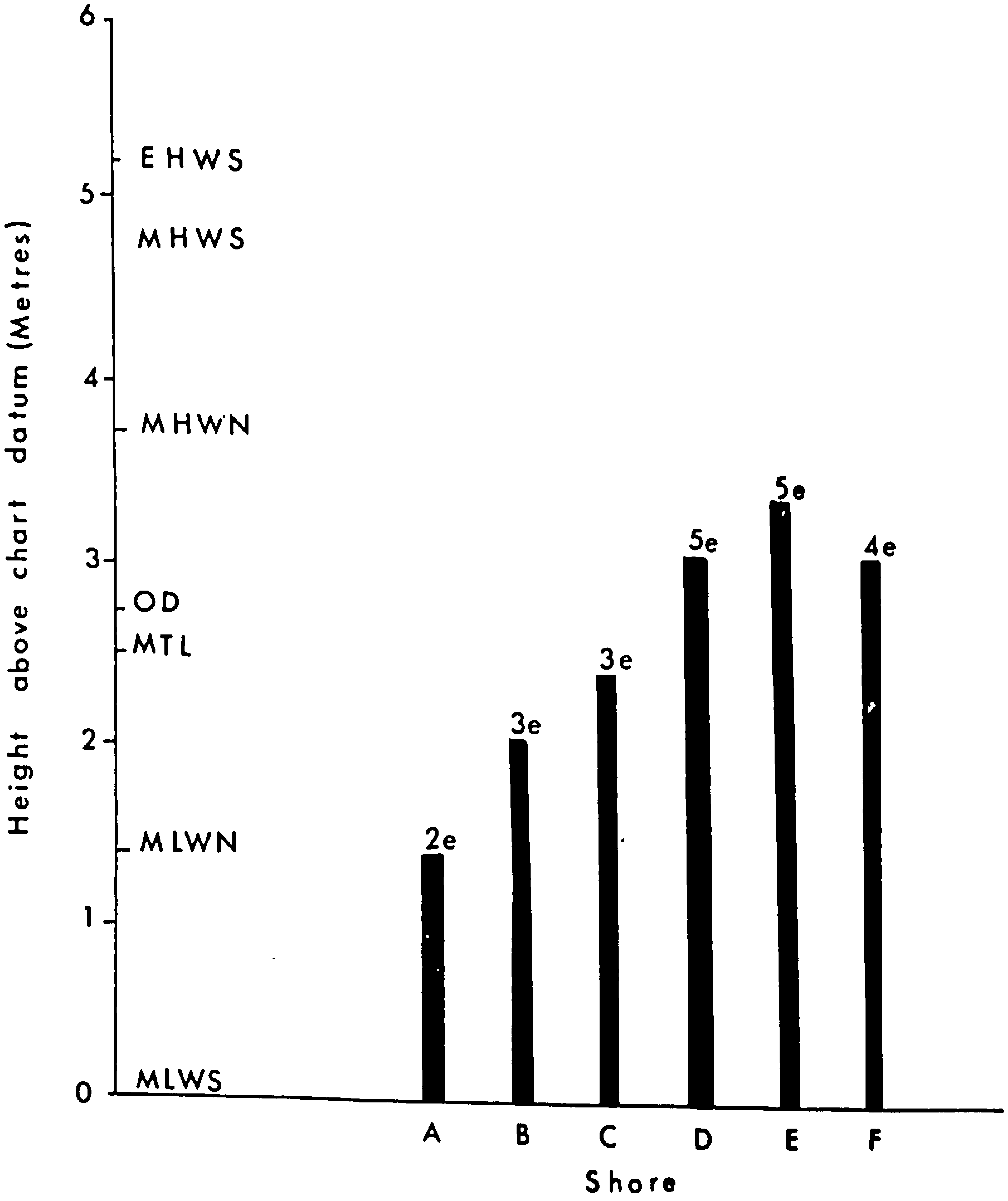
The presence of P. *ciliata* on molluscs collected from different tidal heights on shores of varied exposure.

2 : exposed shore

3 : semi-exposed shore

4 : sheltered shore

5 : very sheltered shore


6
EHWS
5
MHWS
4
MHWN
3
OD
MTL
2
MLWN
1
0
MLWS
Height above chart datum (Metres)
2e
3e
3e
5e
5e
4e
A
B
C
D
E
F
Shore

shells which have plenty of cracks, such as suture lines of gastropods or the imbricated shell layers of some bivalves (eg. *C. gigas* and *O. edulis*) will be more likely to be attacked by *P. ciliata* than are small, smooth shells. Finally, molluscs living at low tidal levels on sheltered shores will be most likely to become infested by *Polydora ciliata*.

It is unfortunate that the places which are most suitable for *P. ciliata* settlement are also the places where the molluscs grow the best; otherwise shellfishermen could transplant their molluscs to areas which are free from polydorids. However, figure 19 suggests that young shellfish are less likely to be attacked than are older shellfish, which have a larger shell area and have had a longer exposure time to *P. ciliata* settlement. Perhaps, if *P. ciliata* was considered a bad enough pest, it might be possible to market the molluscs before they became heavily infested.

SECTION III

THE EFFECT OF POLYDORA CILIATA INFESTATION ON ITS MOLLUSCAN HOSTS

THE EFFECT OF POLYDORA CILIATA INFESTATIONS ON THE CONDITION OF PATELLA VULGATA, MYTILUS EDULIS, AND CRASSOSTREA GIGAS.

INTRODUCTION

Table 1 shows that P. ciliata can infest a variety of molluscs. However, despite the large number of reports of its infestation of molluscs, there have been few attempts at objectively evaluating the effect of P. ciliata on its hosts. Most reports are subjective, or only allude to the possible damage that P. ciliata might cause its hosts, without giving any substantiating evidence. An example is Boekschoten's comments that " ... several borers, such as blue-green algae, sponges and polychaete worms, are a nuisance to the living mollusc and may even endanger its life... " (Boekschoten,1966). He goes on to describe the infestation of molluscs by P. ciliata, but he offers no quantitative evidence to support his comments. Some reports of the potential danger of polydorid infestations are conflicting. For example, Lebour (1907) regarded P. ciliata as a "real evil" of mussel beds; while Crowley (1972) gives the impression that P. ciliata is relatively innocuous. He suggests that, although P. ciliata infestation may affect the muscular development of M. edulis, it does not affect the meat content, or the mussel's fecundity. However, he did not compare uninfested and infested mussels from the same locality.

In this section, I have tried to evaluate the effect of P. ciliata on three of its molluscan hosts: the limpet, Patella vulgata; the mussel, Mytilus edulis; and the oyster, Crassostrea gigas. I have used an objective criterion of the condition of the molluscs: the ratio between the dry tissue weight and the total volume of the limpets; and the ratio of the dry tissue weight and space between the valves of the bivalves. These indices were used to determine how harmful P. ciliata infestations are to the molluscs.

MATERIALS AND METHODS

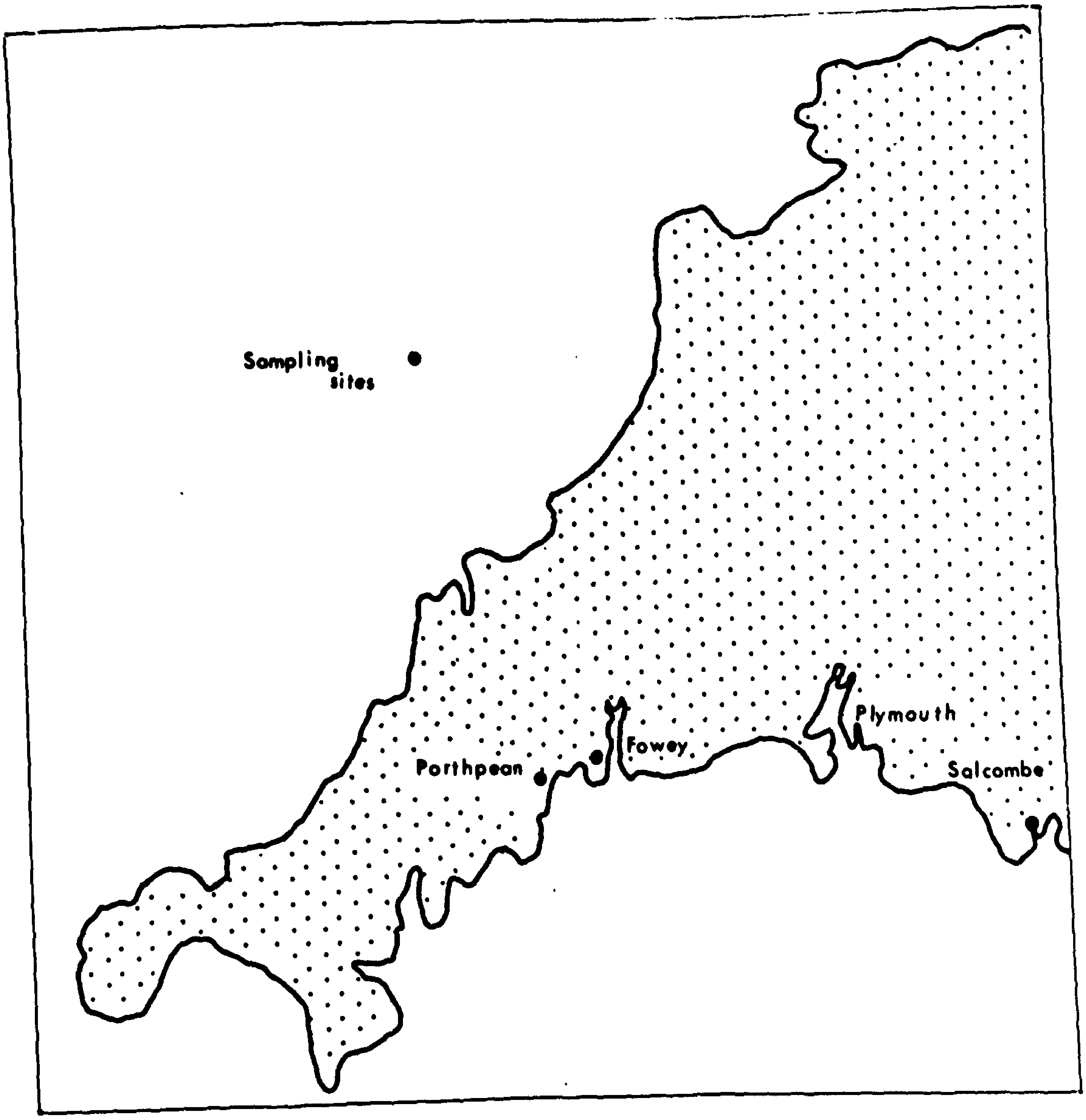
Several samples of limpets, mussels, and oysters, with varying degrees of polydorid infestation, were collected at different months and their condition analysed. Great care was taken to ensure that the samples of infested and uninfested molluscs were comparable. The molluscs were collected from the same shore, at the same tidal level, and had the same restricted size range.

Approximately 40 limpets were collected at monthly intervals from Porthpean Beach, which is on the south coast of Cornwall, in St. Austell Bay. The location of the collection area is shown in Figure22. The limpets were removed from rocks on the eastern part of the beach, at a level halfway between extreme low water neap tides and mean low water spring tides. This level was determined using tide tables and noting the position of the water's edge at different times on specific days. The method is more fully discussed by Evans (1947). The tidal level at which the first sample was collected was marked with a bolt; each subsequent sample was collected along the water's edge when the tide reached the bolt, thereby ensuring that all the limpets were collected at the same level on the shore. The collection area is semi-exposed, according to Ballantine's (1961a) exposure scale. Only limpets within the size range 40 - 50 mm shell length were collected.

Approximately 40 mussels were collected at monthly intervals from the River Fowey, in Cornwall. The location of the collection area is shown in Figure 22. The mussels were removed from stones at the bottom of a railway embankment, at approximately the level of

Figure 22

The sites from which the molluscs were collected. Patella vulgata were collected from Porthpean, Mytilus edulis from the river Fowey, and Crassostrea gigas from the Salcombe estuary.


Sampling sites
Porthpean
Fowey
Plymouth
Salcombe

extreme low water neap tides. The method of determining the tidal level was similar to that for limpets. Only mussels between 65 - 70 mm shell length were collected, and any mussels which were clearly *M. galloprovincialis* were discarded. The salinity at the collection site varied, over one tidal cycle, from 22 - 29 °/oo salinity. The shore is very sheltered.

The oysters were supplied by J. Lamble from his oyster farm at Kingsbridge. All the oysters came from the same tray, which was laid in a drainage channel at the level of extreme low water spring tides, in a very sheltered area of Salcombe estuary.

The sexes of all the molluscs were analysed together.

After collection, the molluscs were transported in plastic bags to the laboratory where they were kept overnight in filtered seawater; this enabled the molluscs to clear their guts of food which might have invalidated the condition analyses. The following day, the condition of each mollusc was evaluated.

On first examining molluscs infested by *P. ciliata*, I found that they often looked more emaciated than uninfested individuals. For example, the tissue of heavily infested mussels was often watery and flaccid, and the mantle was thin and semi-transparent. However, it is not possible to objectively evaluate the effect of *P. ciliata* on mollusc from such subjective and qualitative descriptions. Therefore, the first requirement of this study was to find an objective criterion of the relative health, or condition, of molluscs.

Unfortunately, it is not easy to define health or disease of individuals. Perfectly healthy individuals, free from infestations and genetic abnormalities, and living in optimal environmental conditions, are probably hypothetical animals which rarely exist. Disease has been defined by Sinderman (1970) as " ... any departure from normal structure of function of the individual ...". This all-embracing definition can mean whatever one wants it to mean and has little practical value.

Bayne (1976) has given much thought to the problem of defining factors which diminish the condition of molluscs; he calls these factors "stress" factors. He defines stress as " ... a measureable alteration of a physiological (or behavioural, or biochemical, or cytological) steady state which is induced by environmental change ...". He goes on to say that the change must be for the worse and " ... must be shown to render the animal (or the population) less able, directly or indirectly, to compensate for further enviromental change ..." (Bayne,1975).

What Bayne did not make clear is what he meant by normal. He could have meant that the animals were without any pathological features, or that they represented the average condition; but normal can not mean both these things at once (Simpson et. al.,1960). A dictionary definition of normal is "according to standard". Ideally I have regarded the molluscs with no <u>P. ciliata</u> borings as my standard, and their condition as being normal; molluscs with different degrees of infestation have been compared to this standard.

Another point that Bayne did not emphasize is that a disadvantage at one level, say the whole organism level, may not be a disadvantage at another level, such as the population level. It is therefore necessary to state which level is being considered in the evaluation of the effect of a factor. I have limited my evaluation of the effect of P. ciliata infestation to the whole organism, although I have felt free to speculate as to the possible effect of P. ciliata at other levels.

The clearest indication of the harmful effect of a factor on molluscs is if death is associated with the presence of the factor, but what is most often required is a measurement of the sublethal effect of the enviromental factor on the condition of molluscs; this is certainly the case with P. ciliata infestations.

Almost any measureable activity of molluscs, whether it be cytological, physiological, or behavioural, can be used as an indication of the condition of molluscs. However, Bayne (1976) suggests that the most useful indicators are the "integrated" physiological processes, and that the more integrated the process, the more general will the symptom be of a deterioration in the animals' condition, and the more evident will be the concomitant degree of disadvantage. He espouses the use of a bioenergetic approach, such as "scope for growth" or the O:N ratio. The scope for growth is the physiologically useful energy that remains to the animal from the ingested ration after losses due to defaecation, excretion, and respiration have been accounted for. The O:N ratio is the ratio of the oxygen consumed by the animal, to the ammonia nitrogen produced; this ratio indicates the balance between the animal's catabolism of protein, carbohydrate, and lipid substrates.

/ Other indices of condition of molluscs include growth rate (Black, 1973), rate of heart beat (Walne,1972), rate of byssus thread production (Martella,1974) glycogen content (Gabbott and Bayne,1973; Robson and Williams,1971; Walne,1970; Williams,1968), relative size of the digestive gland (Thompson,1972; Thompson et.al.,1974) molar ratio of taurine to free glycine (Jefferies,1972), and amoebocyte count (Moore, pers. comm.).

I did not use any of these condition indicators because they all suffer from some disadvantage. The biochemical analyses are very time-consuming, and would restrict the analyses to a few individuals. The O:N ratio and "scope for growth" necessitate the disturbance of the molluscs which may upset their condition before analysis, and make the effect of P. ciliata difficult to evaluate. The variability of certain indicators, such as heart rate and byssus thread production, cannot be interpreted simply (Bayne,1976; Martella,1974), and they have limited application.

I have used the ratio of dry tissue weight to total volume of limpets, and the ratio of dry tissue weight to between shell volume of bivalves, as my main indicators of condition. Hereafter, these condition indicators will be referred to as condition indices. I believe that this is the first time that such indices have been used to evaluate the effect of a possible stressor on limpets. However, condition indices have been used extensively for bivalves (see Walne,1970, for a review).

I suggest that there is an optimal relationship between the size of molluscan tissue and the size of its shell. This is a hypothetical concept and is difficult to define exactly. But it is likely that there are physical restrictions on the relationship: for example, the limpet has to carry its shell around during feeding excursions and if the shell:tissue ratio is too large, movement might be impaired. Bivalves need to be able to control the gape of their valves; this ability may also be affected by the shell:tissu~~r~~e ratio.

As well as the theoretical justification of the use of the condition index, there is much empirical support. Molluscs which have a low condition index usually look emaciated; their glycogen content is usually low (Gabbott and Stephenson,1974; Walne,1970; Yonge,1960; Zwann and Zandee,1972), but not always low (Ingle,1949); their taste and nutritive value is impaired (Medcof and Needler,1941; Tally,1936); their growth rate is low (Baird,1966); and, most important to the shellfisherman, their commercial value is lower than molluscs in good condition (Walne,1970).

Glycogen is one of the most important energy reserves of limpets (Barry and Munday,1959) and bivalves (Baird,1966; Gabbott and Bayne, 1973; Gabbott and Stephenson,1974; Walne,1970). Since there is, generally, a good relationship between glycogen content and condition index, a low condition index could indicate a diminution of energy reserves.

A major criticsm of the use of condition indices is that most authors have not regarded the shellfish as a growing animal (Walne, 1970). A change in the ratio of meat to volume of the shell suggests that as one part increases the other part decreases. In reality, what might be happening is that one constituent is increasing at a faster rate than the other.

There are two reasons why I believe that, in my analyses, a change in condition index represents a change in tissue size rather than shell size. Firstly, I used only adult molluscs which have a slow growth rate of the shell. Secondly, there is some evidence to suggest that tissue growth precedes marginal increments of the shell.

These increments are produced by the mantle edges, and therefore must depend on the size of the mantle (Blackmore,1969a; Wilbur and Owen,1964). I therefore suggest that molluscs increase their total volume in response to tissue growth, so as to accomodate the tissues, and that a low condition index indicates a regression of the tissue.

The weight of molluscan shells depends not only on the total volume of the mollusc, but also on the thickness of the shell. Thickening of the shell may occur independently of marginal increments; it proceeds inwardly by the laying down of nacreous material and may be undertaken by most of the mantle surface (Seed,1973).

Another criticsm of the condition index is that it is not precise enough, and that it suffers from too much variability (Williams,1968). I suggest that this variability is not a consequence of the method of measuring condition, but stems from the inherent variability of the molluscs. All the molluscs examined in this study have planktonic larvae, and the adults I collected may have originated from a variety of localities. This suggests that they will be genetically variable. In addition, mussels, at least, are phenotypically labile (Seed1968,1969a) and their condition may be affected by their microhabitat. Therefore, variability of the condition index is not surprising, and any indicator of condition will probably suffer from a similar variability.

In addition to condition indices, I used another measurement of condition. This was the water content of the molluscan tissues. A number of authors have used this in conjunction with other condition indicators, but, although most imply that high water content is indicative of poor condition, no one has stated why this should be.

I suggest that an animal which is not able to maintain its body-form with solid material (due to insufficient consumption or increased catabolism) may minimise the disruption of its physical shape by accumulating water. Although this would reduce the physical disruption of the mollusc, it may not ameliorate the effect of loss of solids on the molluscs physiology, especially its catabolic potential.

The condition index of limpets was determined using the following formula:

$$\frac{\text{Total dry weight of limpet tissue (g)}}{\text{Total volume of limpet (ml)}} \times 1000$$

The condition of mussels and oysters was determined using this formula:

$$\frac{\text{Total dry weight of bivalve tissue (g)}}{\text{Volume between the valves (ml)}} \times 1000$$

This is the first time that a condition index has been used to evaluate the effect of a possible stressor on limpets. However, condition indices have been used extensively for bivalves. The main difficulty is that the formula used to determine the condition index of bivalves is not standardized. Other formulae include weight of oyster meat/bushel (Ingle,1949); wet meat volume/shell cavity volume (Baird, 1958); and dry flesh weight/total dry weight (Ansell et. al.,1964).

Dry weight determinations of molluscs also lack standardization, and the different methods give different results (Crisp,1971; Giese, 1967; Shaw et. al.,1967). In this study, the molluscan tissue was freeze-dried; it was placed in a refrigerater at -20°C for 12 hours then dried in a Freeze Dryer, supplied by the New Brunswick Co., U.S.A., for 18 hours to ensure complete drying. The dried tissue was weighed immediately after removal from the dryer, to minimise the uptake of atmospheric moisture.

The total volume of the limpet was measured by first determining the volume of shell material and adding this to the volume of the space within the shell. The shell volume was determined using an application of Archimedes principle, which states that "A substance immersed in a fluid is buoyed up by a force equal to the weight of fluid displaced" (Gucker and Siefert,1967). The shells were first weighed in air, then in water, and the difference in the weights is equivalent to the volume of shell material, thus:

Volume of shell material (ml) = shell wt. in air - shell wt. in water (g)

The volume of the space within the shell was measured by pouring sand of particle size diameter 40 - 100 microns, into the shell until the sand was level with the shell's margins. The sand was then poured into a measuring cylinder and its volume recorded. The above method of measuring limpet volume seems to be better than the previous methods described by Crapp (1970) and Blackmore (1969a).

The volume of the space between the valves of mussels and oysters was determined by subtracting the total volume of the bivalves from their shell volume. The total volume and shell volume determined by applying Archimedes principle, and using the following formulae:

$$\text{Total vol. of bivalve (ml)} = \text{wt. bivalve in air} - \text{wt. bivalve in water (g)}$$

$$\text{Shell volume (ml)} = \text{wt. of shell in air} - \text{wt. of shell in water (g)}$$

Care was taken to ensure that no air was trapped between the valves of the bivalves when they were weighed in water.

Giese (1969) discusses the advantages of considering the separate body components in biochemical analyses. Therefore, in addition to finding the condition of the whole mollusc, the condition of certain body components of limpets and mussels was determined. Figure23 shows the three body components of limpets which were analysed: the foot; the visceral mass, mantle and head; and the gonad. In the mussel, the mantle and non-mantle tissue were analysed separately. The body component indices of the limpets were determined using the formula:

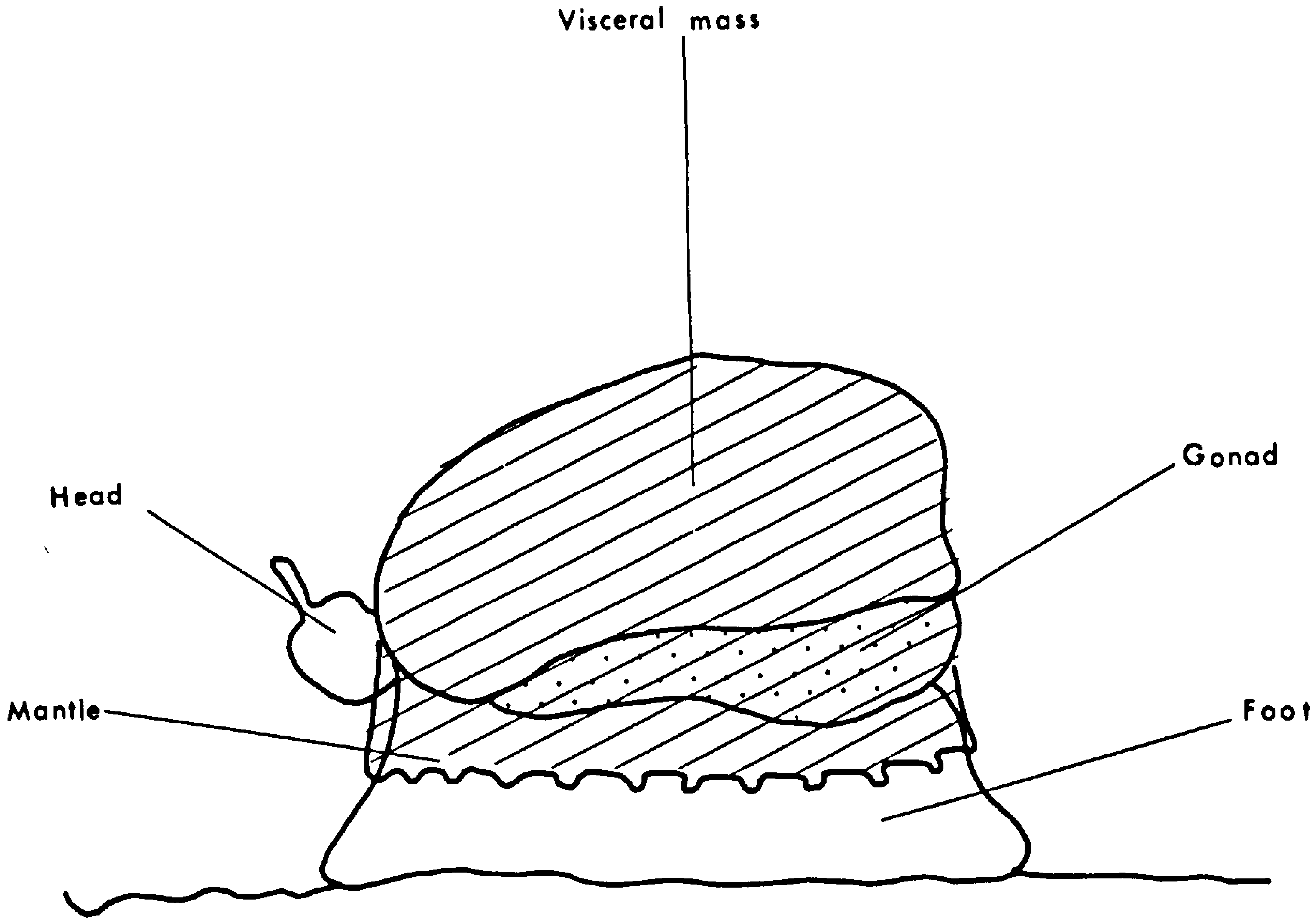
$$\frac{\text{Dry weight of component}}{\text{Total volume of limpet}} \times 1000$$

The body component indices of the mussels were determined using the formula:

$$\frac{\text{Dry weight of component}}{\text{Between shell volume}} \times 1000$$

Figure 23 .

The three body components of Patella vulgata: the viscera (head, visceral mass, and mantle), the gonad, and the foot.


Visceral mass
Head
Gonad
Mantle
Foot

Also, the relative size of each component was determined using the formula:

$$\frac{\text{Dry weight of component}}{\text{Total dry weight}} \text{ X } 100$$

The water content of the molluscs was determined using the formula:

$$\frac{\text{Wet weight of mollusc - dry weight}}{\text{Wet weight}} \text{ X } 100$$

The wet weight of the limpets was estimated after removing the limpet from its shell, wiping the excess water off its surface, and weighing the tissue to the nearest 0.1 g. The wet weight of the mussel was estimated by first opening the shell by forcing the valves apart and cutting the posterior adductor mussel; draining off the mantle fluid; weighing the shell and the tissue together; then removing the tissue and weighing the shell on its own. The wet tissue weight is equal to the weight of the tissue and shell, minus the weight of the shell. This method of determining water content includes the extrapallial fluid and minimises the loss of body fluid due to cutting the tissue. The extra-pallial fluid is produced by the mussel, and does not come into contact with seawater (Wiejsma,1975), so it should be regarded as part of the body fluids.

The degree of polydorid infestation of the molluscs was determined by counting the number of borings on radiographs taken of each shell. Plate 2-5 give examples of some radiographs and photographs of shells. The X-ray apparatus was supplied by Marconi Co. The radiographic conditions were voltage 40 KeV; current,5 mA; and exposure time, 1 minute. The number of Polydora borings in the radiographs does not necessarily correspond to the number of Polydora living in the mollusc shell; but it is a summation of past and present infestation. I did not estimate the number of living P. ciliata, because I could not find any reliable method of extracting the worms. Vermifuges, such as dichlorobenzene and phenol, gave inconsistent results; and the fracture of the shells to free the worms resulted in the destruction of a large number of the worms. However, some polydorids were extracted from the shells, using 100 ppm. dichlorobenzene as a vermifuge, to ensure that all the polydorids belonged to the species P. ciliata.

Figures24 and 25 show some of the preliminary analyses of the results which indicated that there was little effect of low infestations of Polydora on the condition of limpets or mussels. Therefore, to get the maximum benefit from the analyses, I grouped the mildly infested individuals together, and compared their condition with that of heavily infested individuals. Limpets with less than 50 P. ciliata per shell and mussels with less than 25 P. ciliata per individual were little affected by the infestation, so these limpets and mussels were regarded as mildly infested.

The results of the condition analyses of the mildly infested and heavily infested molluscs were compared, using a Students 't' test, to evaluate the effect of P. ciliata infestation; the Null hypothesis adopted was that the condition of the heavily infested molluscs did not differ significantly from that of mildly infested molluscs.

Plate 2

Comparison of an uninfested valve (left) and a heavily infested valve (right) of Mytilus edulis.

A Photograph of external surface of uninfested valve

B Photograph of internal surface of uninfested valve

C Radiograph of uninfested v valve

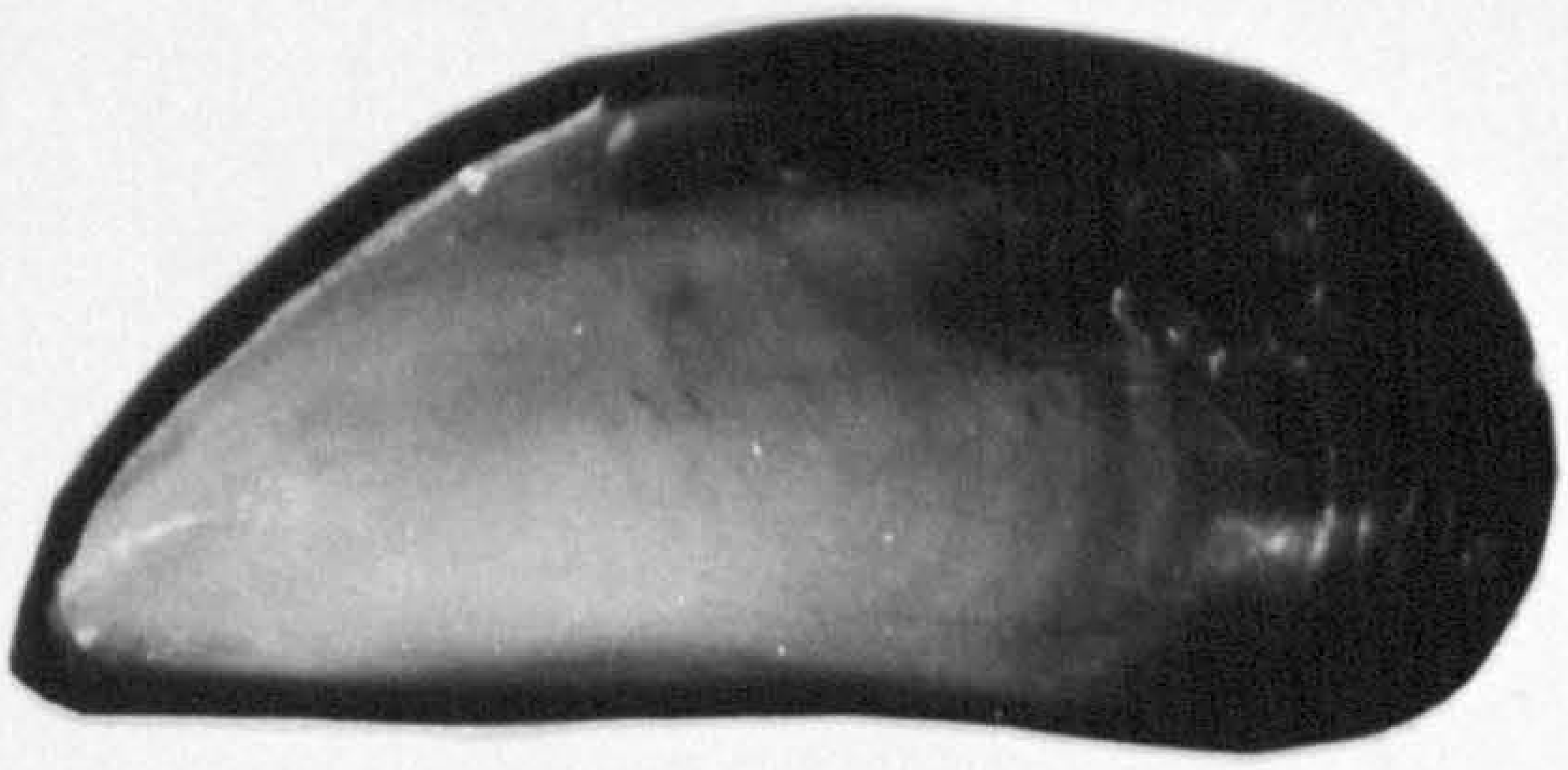
D Photograph of external surface of heavily infested valve

E Photograph of internal surface of heavily infested valve

F Radiograph of heavily infested valve

A

B



C

D

E

F

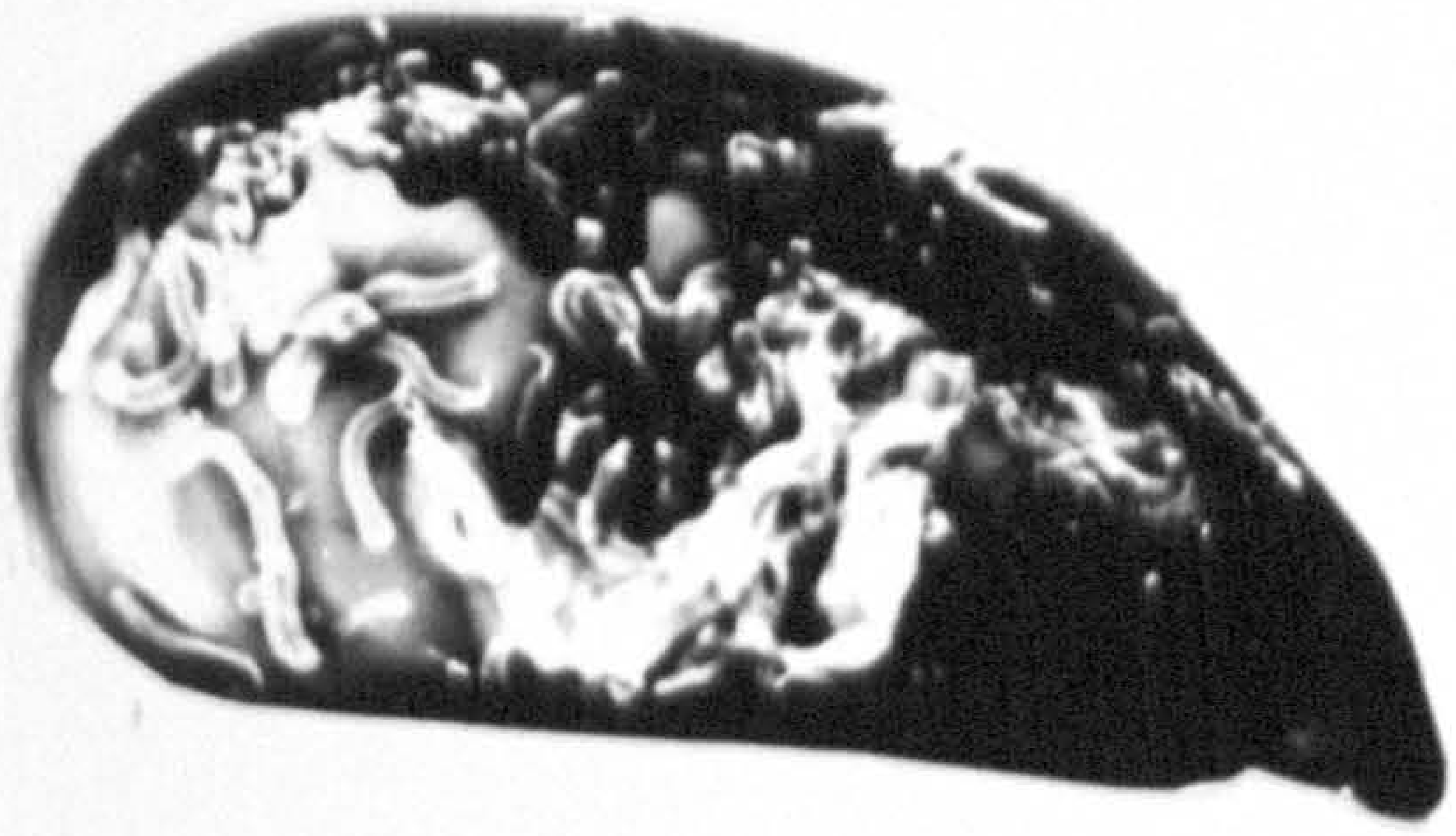


Plate 3

Enlarged (3X) radiograph of _Mytilus edulis_, showing two _Polydora ciliata_ tubes.

Plate 4 .

Comparison of uninfested (left) and heavily infested (right) shells of the limpet, <u>Patella vulgata</u>.

A Photograph of external surface of uninfested shell.

B Photograph of internal surface of uninfested shell

C Radiograph of uninfested shell

D Photograph of external surface of heavily infested shell.

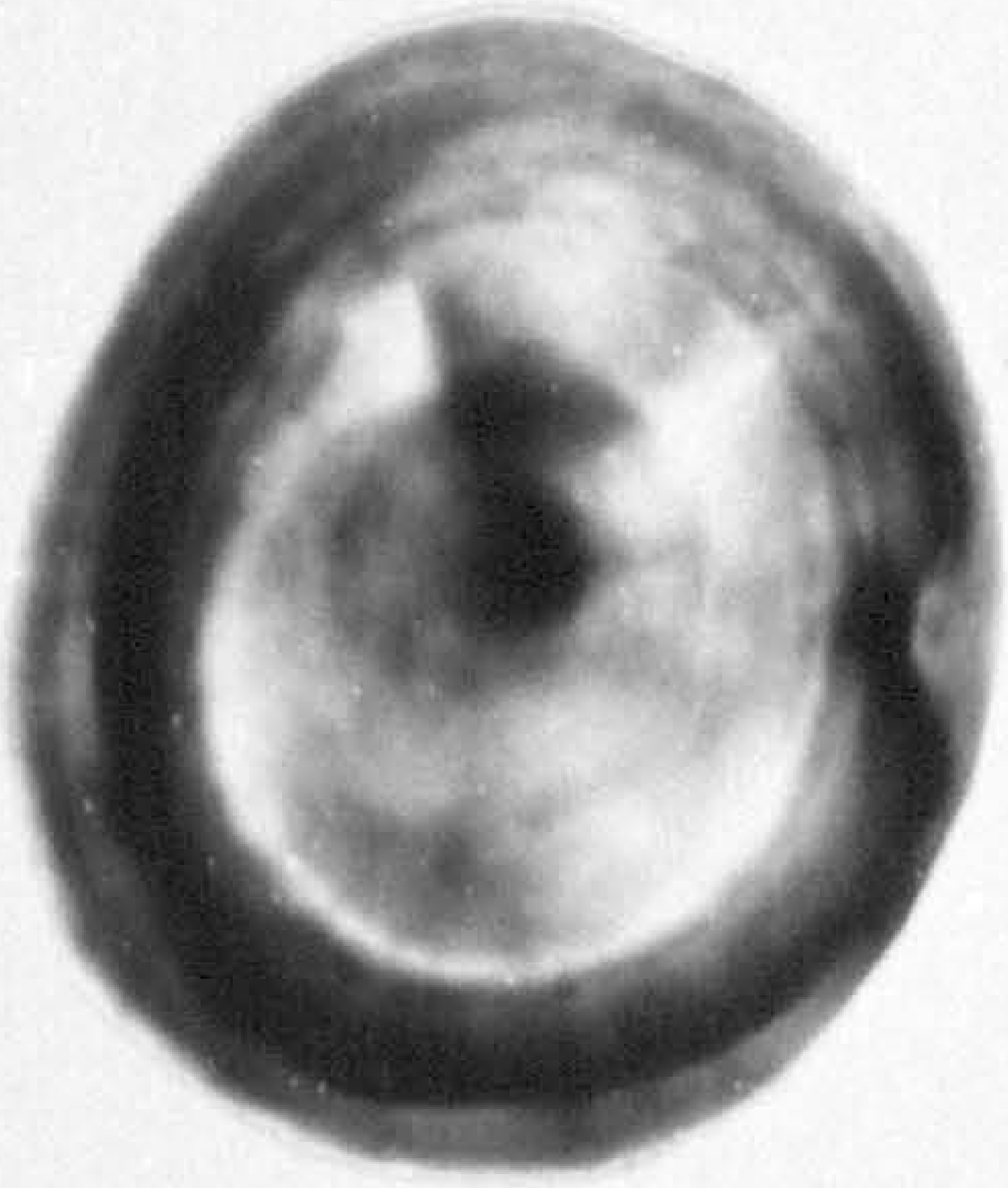
E Photograph of internal surface of heavily infested shell.

F Radiograph of heavily infested shell.

A

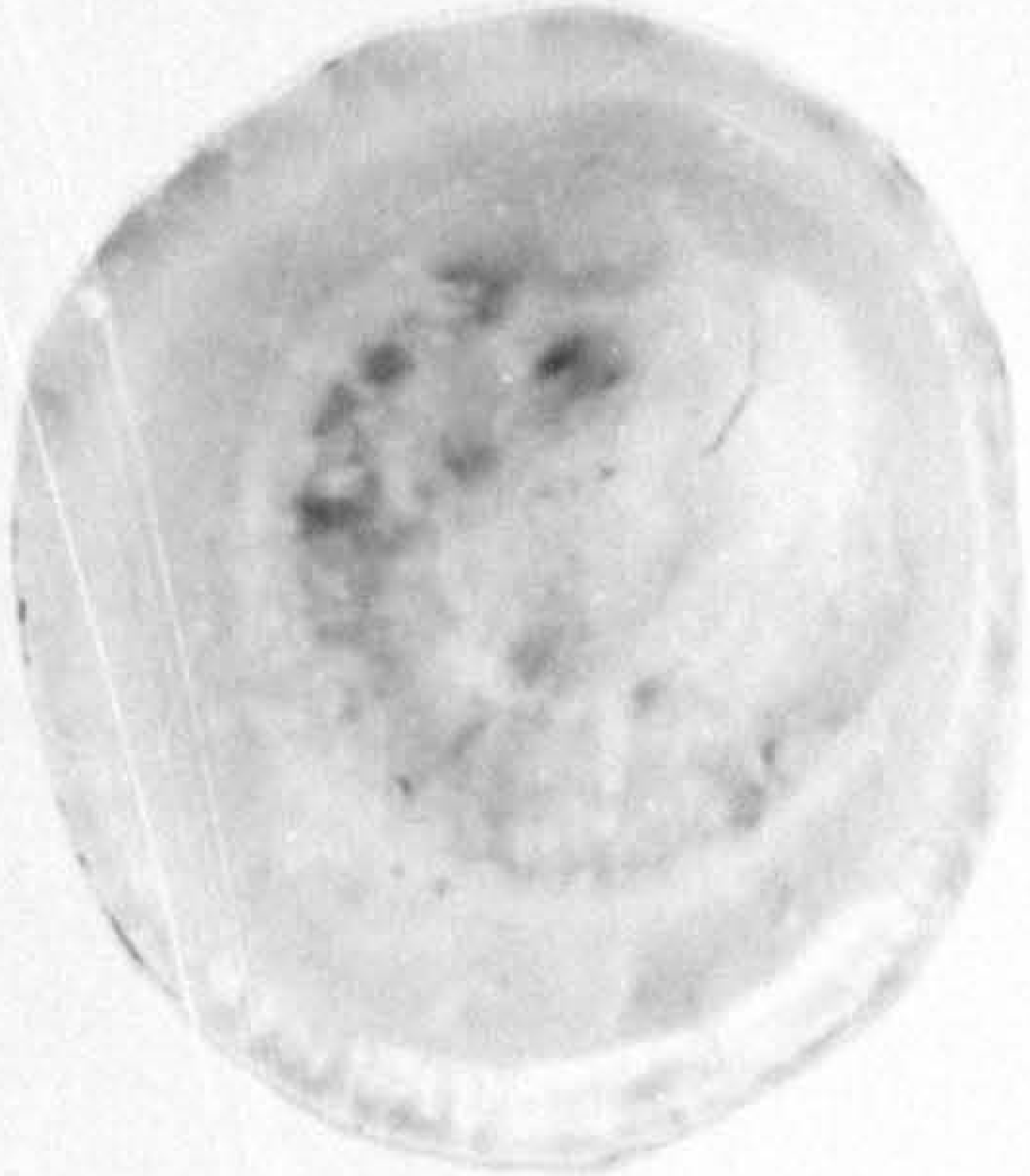
B

C



D

E



F

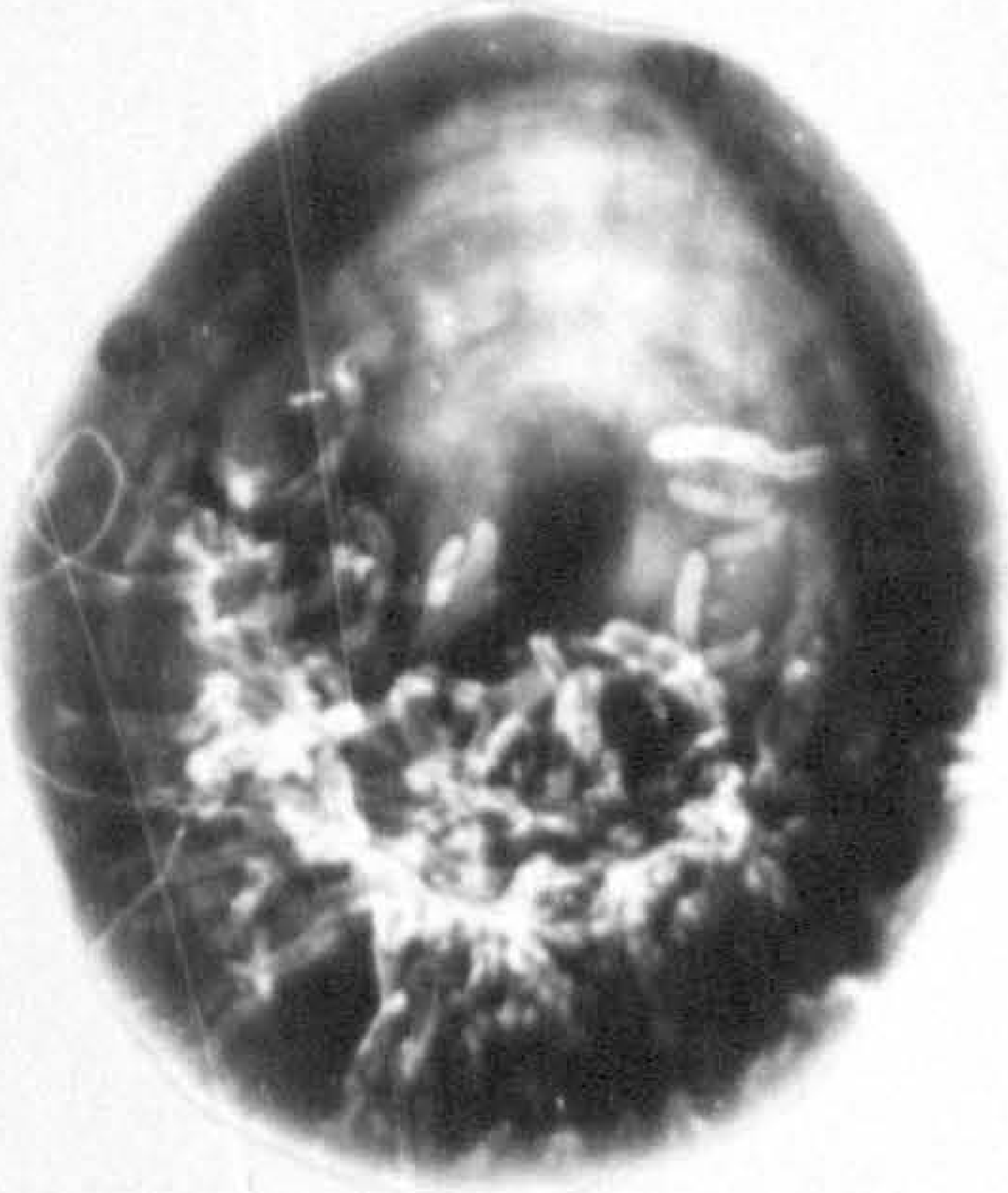


Plate 5 .

Photographs and radiographs of the shells of the Japanese oyster, *Crassostrea gigas*.

A External surface of bottom valve

B Internal surface of bottom valve

C Radiograph of the bottom valve

B External surface of top valve

E Internal surface of top valve

F Radiograph of the top valve

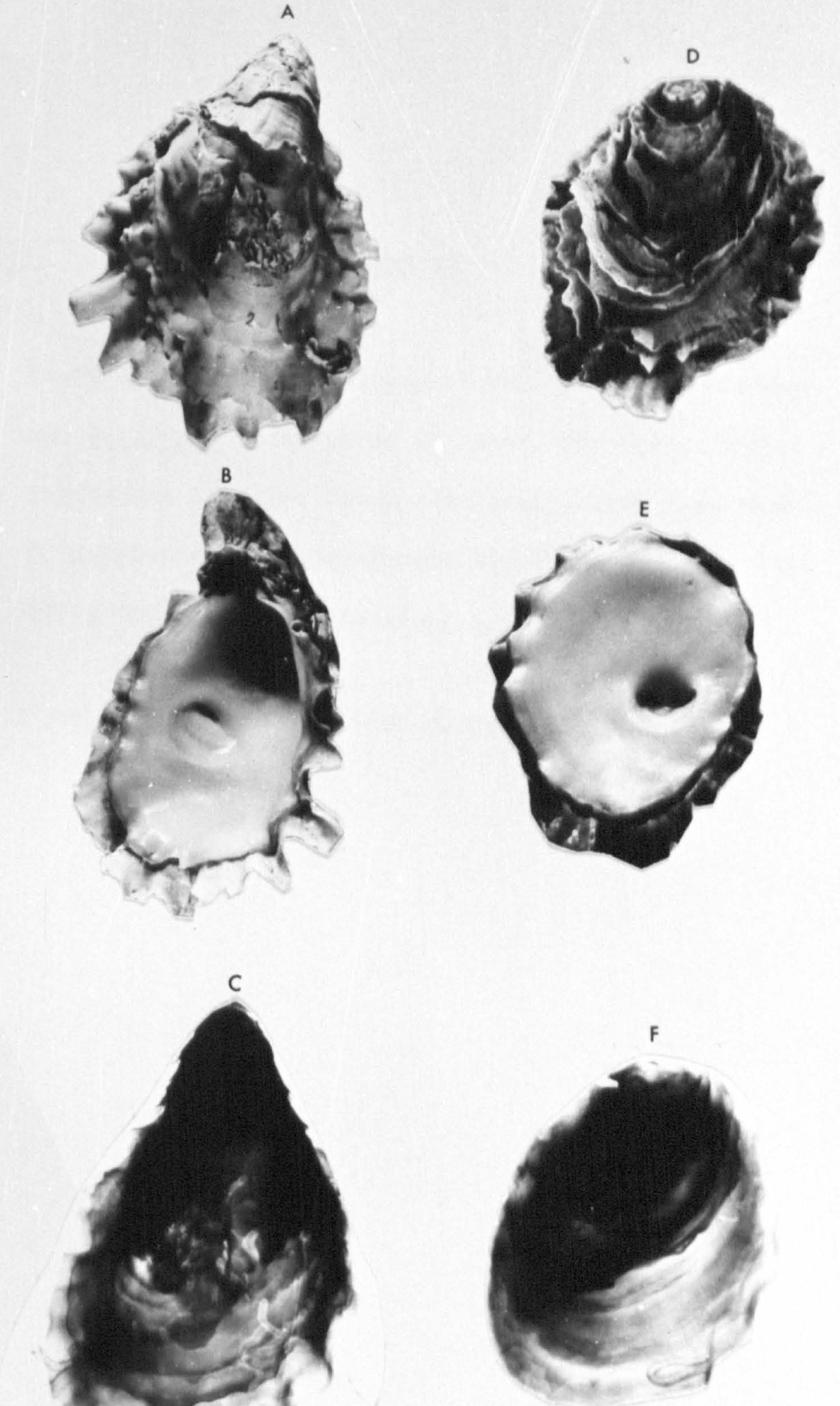

A
D
B
E
C
F

Figure 24 .

Graph showing the relationship between body condition and P. ciliata infestation for September 1975. The regression line was drawn for limpets with less than 50 polydorids per individual. Limpets with more than 100 polydorids per individual have been grouped.

$r = -0.157$; not significant at the 5% level.

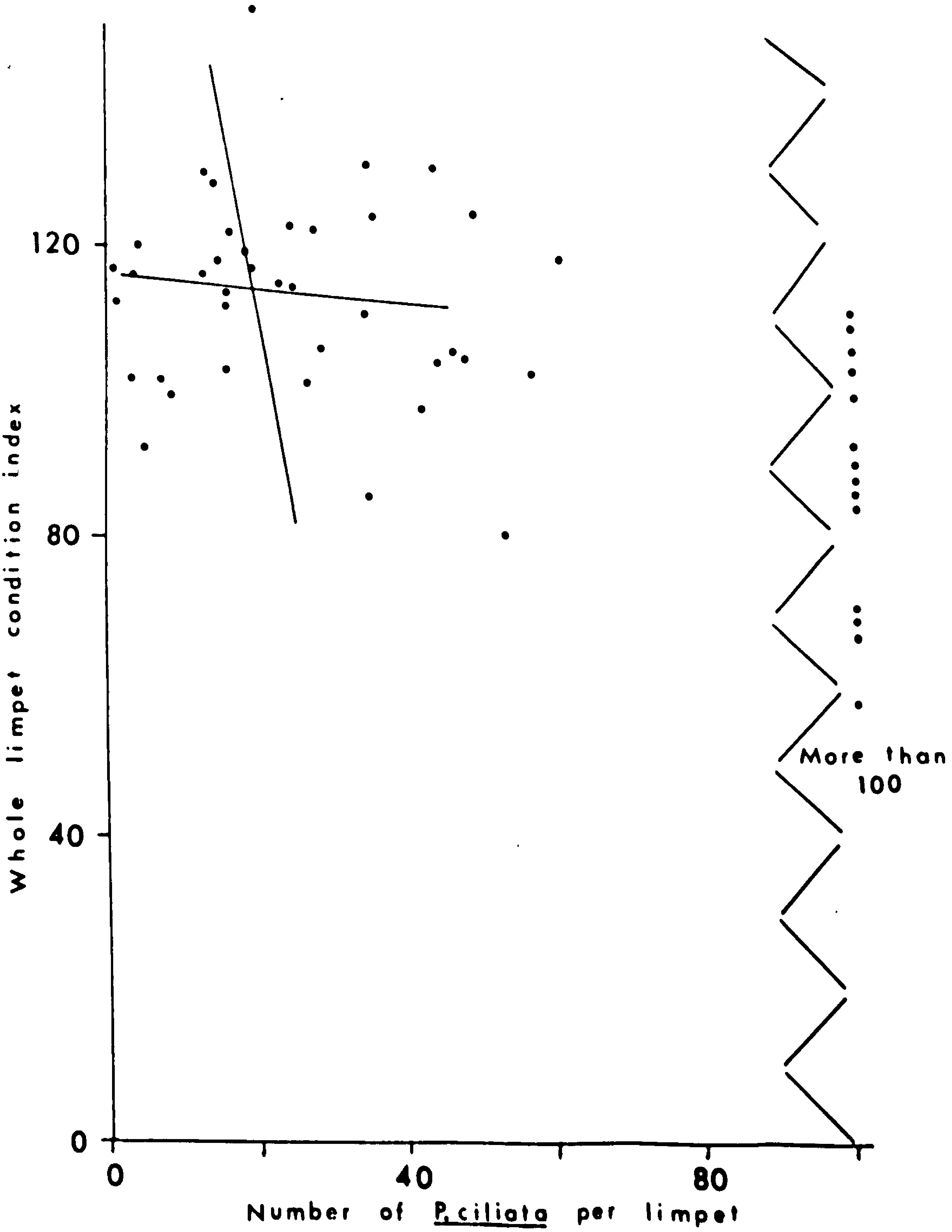
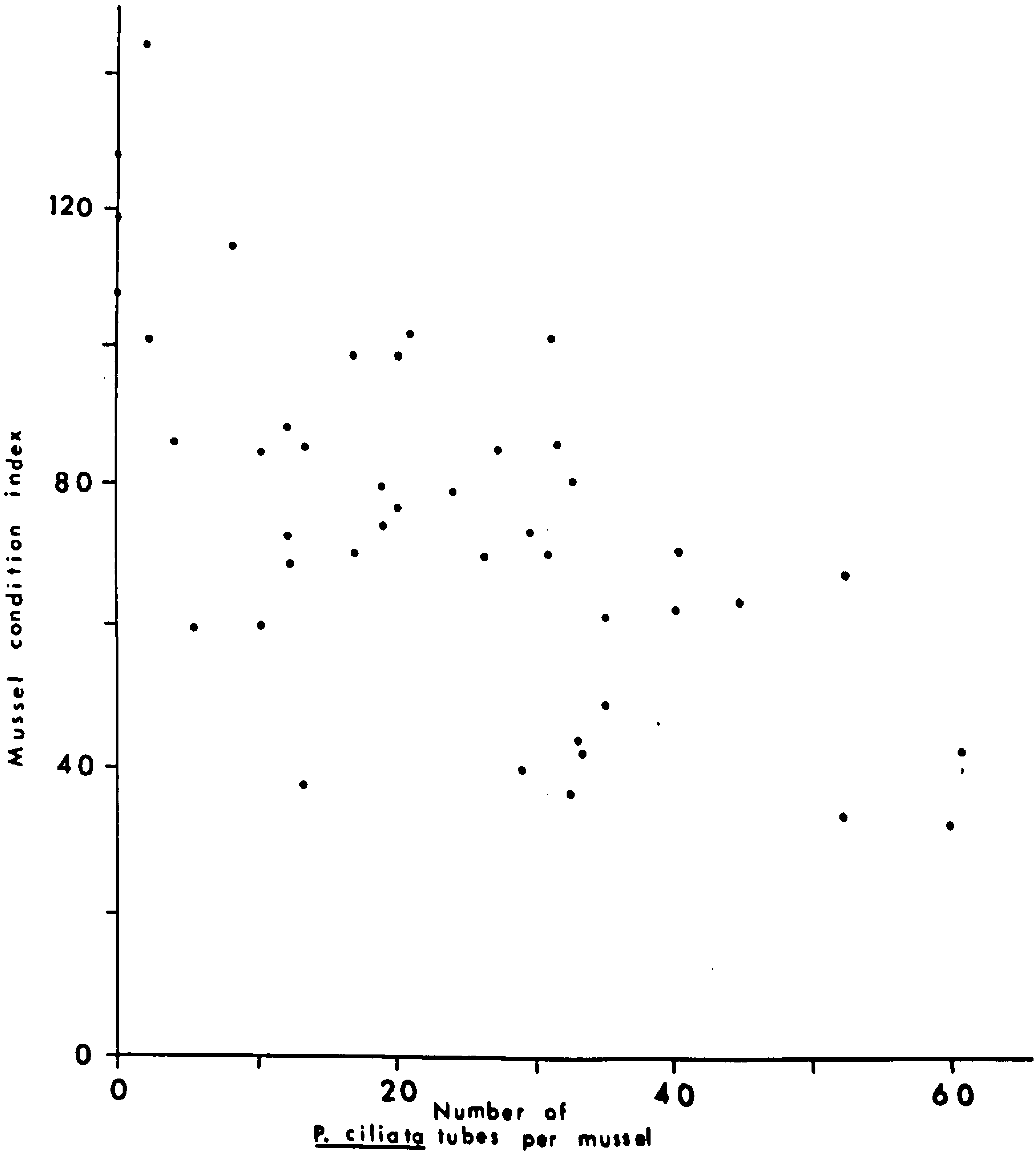

Whole limpet condition index
120
80
40
0
0
40
80
More than 100
Number of P. ciliata per limpet

Figure 25 .

Scatter diagram showing that the effect of Polydora ciliata on the condition of mussels, is very variable and only becomes clearly detectable when the infestation is high. The mussels were collected in October, 1974.


Mussel condition index
120
80
40
0
0
20
40
60
Number of
P. ciliata tubes per mussel

As well as determining the condition of molluscs, I also assessed the effect of borings on mussels. Mussels were collected from Fowey, with the usual monthly sample. Their condition indices were estimated at the start of the experiment. Then the mussels were randomly separated into two groups. One group had 4 holes drilled, with a high-speed dentist's drill, into the extrapallial cavity; the other group had holes drilled partly into the shell. The mechanical disturbance due to drilling and handling was similar for both groups. The holes were covered with filter paper soaked in adhesive. The adhesive was "Simplex", a non-toxic, fast-setting, acrylic supplied by Dental Fillings Ltd., London N16. Without something covering the holes, the mussels with the drill holes penetrating into the extrapallial cavity died. Both groups of mussels were placed in filtered seawater for 3 weeks, after which their condition was analysed.

RESULTS

The results of the condition analyses are presented in the form of graphs. The data from which the graphs were compiled, and the significance of the differences between the means of condition of heavily and mildly infested limpets, are shown in tables in the appendices.

Figure 26 shows that the condition indices of heavily infested limpets were consistently lower than those of mildly infested limpets, although the differences between the means were not significant for every month. The condition of ~~mussels~~ limpets seemed to be most adversely affected by P. ciliata infestation in autumn and winter, when the condition had reached its peak and was declining.

Figure 27 shows that all the body components were adversely affected by polydorid infestation. The low gonad condition of heavily infested limpets suggests that the fecundity of limpets may be reduced by P. ciliata infestation; however, there is no evidence to suggest that the development of the gonad is impaired by the infestation. The sharp decrease of gonad condition between January and February may indicate spawning of the limpets.

The monthly trends of changes in body component condition varied with each component. The gonad grew when the viscera and foot regressed; this may indicate that the gonad grew at the expense of the visceral and foot condition. Superficially, the changes of visceral and foot condition are similar, but closer examination of Figure 27 reveals that the growth of the viscera preceded that of the foot, and visceral growth seemed to be completed before that of the foot.

Figure 26 .

Graph showing the monthly changes in the condition of whole limpets. A significant difference (at the 5% level) between the means of the heavily infested and mildly infested limpets is indicated by * .

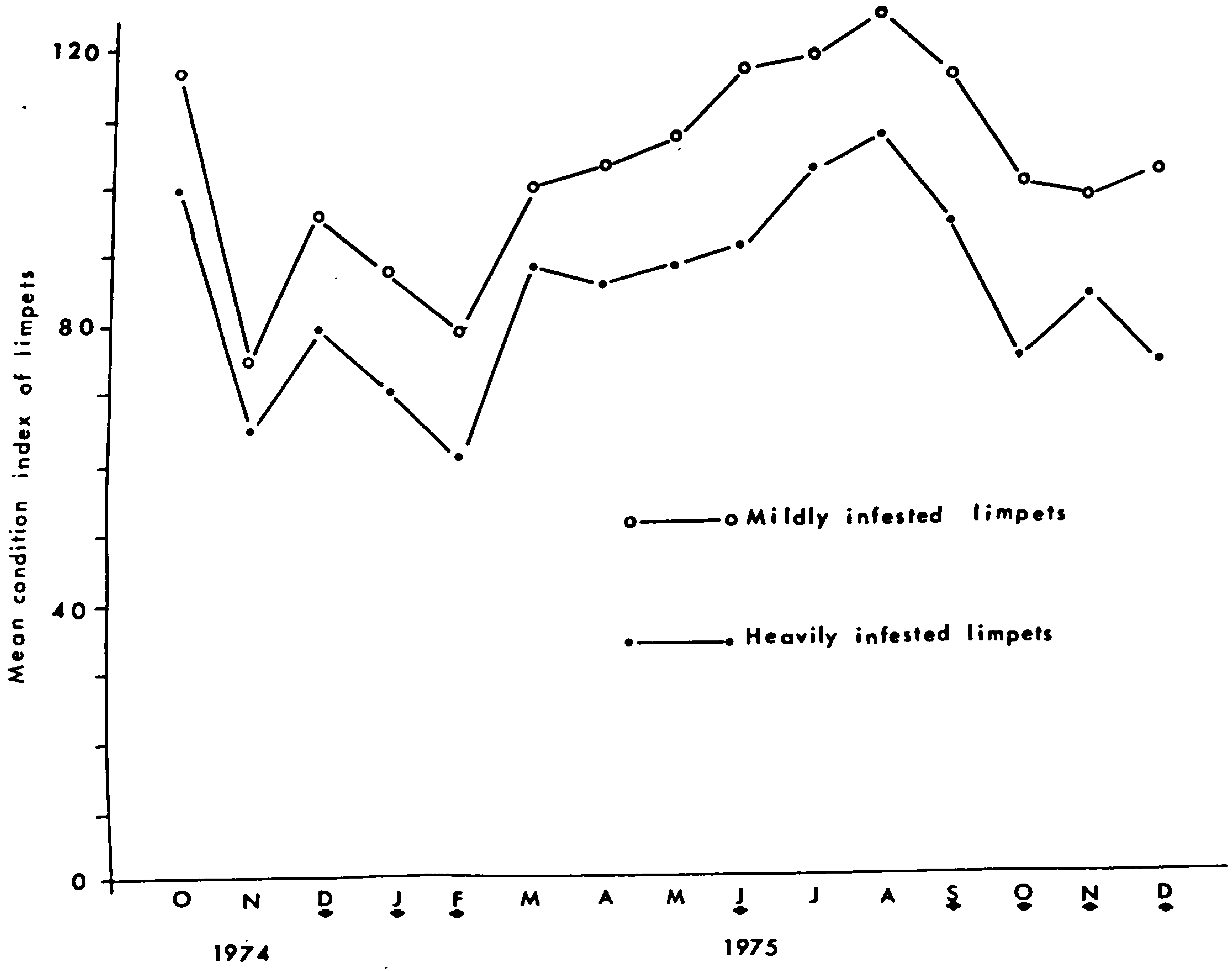

120
80
40
0
Mean condition index of limpets
O
N
D
J
F
M
A
M
J
J
A
S
O
N
D
1974
1975
Mildly infested limpets
Heavily infested limpets

Figure 27 .

Graphs showing the monthly changes in the condition of the body components of limpets. A significant difference between the means ($p = \angle 0.05$) of heavily infested and mildly infested limpets is indicated by. •

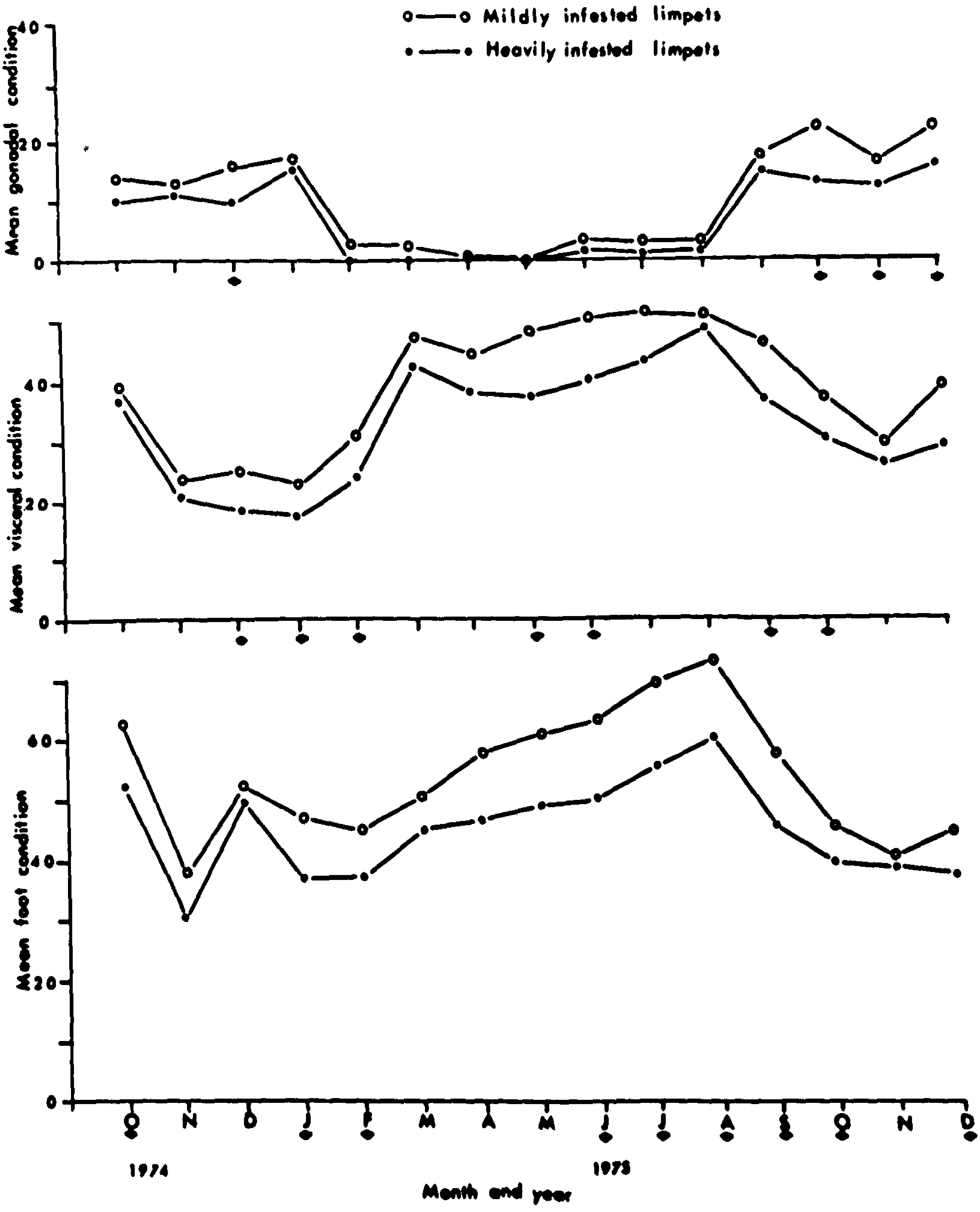

o——o Mildly infested limpets
•——• Heavily infested limpets
Mean gonadal condition
40
20
0
Mean visceral condition
40
20
0
Mean foot condition
60
40
20
0
O
N
D
J
F
M
A
M
J
J
A
S
O
N
D
1974
1975
Month and year

Figure 28 shows that the proportions of the body components were little affected by polydorid infestation, despite the adverse affect of P. ciliata on the body component indices.

Figure 29 shows that as the condition of limpets improved, their water content decreased. This supports the view that high water content is indicative of poor condition. Heavily infested limpets are likely to have a high water content since they generally have a lower condition index than mildly infested limpets.

Plate 4 shows that the shells of heavily infested limpets may be larger than those of mildly infested limpets. This is probably due to the limpets secreting extra nacreous material around the polydorid boring to block the entry of P. ciliata into the extra-pallial cavity. The increase in shell secretion, induced by polydorid borings, may act as a drain on the energy reserves of limpets, thus contributing to the lowering of their condition.

Figure 30 shows that heavy infestations of P. ciliata impaired the condition of mussels. Each month, the condition index of heavily infested mussels was lower than that of mildly infested mussels. However, the differences were not significant every month. The condition of heavily and mildly infested limpets seem to have undergone similar cyclical changes; they both reached a peak in autumn and early winter, and fell to a minimum in late winter and early spring.

Figure 31 shows that both the mantle and non-mantle condition were adversely affected by heavy polydorid infestation; however, P. ciliata had a greater effect on the mantle than the non-mantle condition. Both components exhibited similar cyclical changes which correspond with those of the whole organism, but the changes in the mantle condition were greater than those of the non-mantle condition.

Figure 28 .

Graphs showing monthly changes in the proportions of each limpet body component. Significant differences (at the 5% level) between the means of heavily infested and mildly infested limpets is indicated by ◆ .

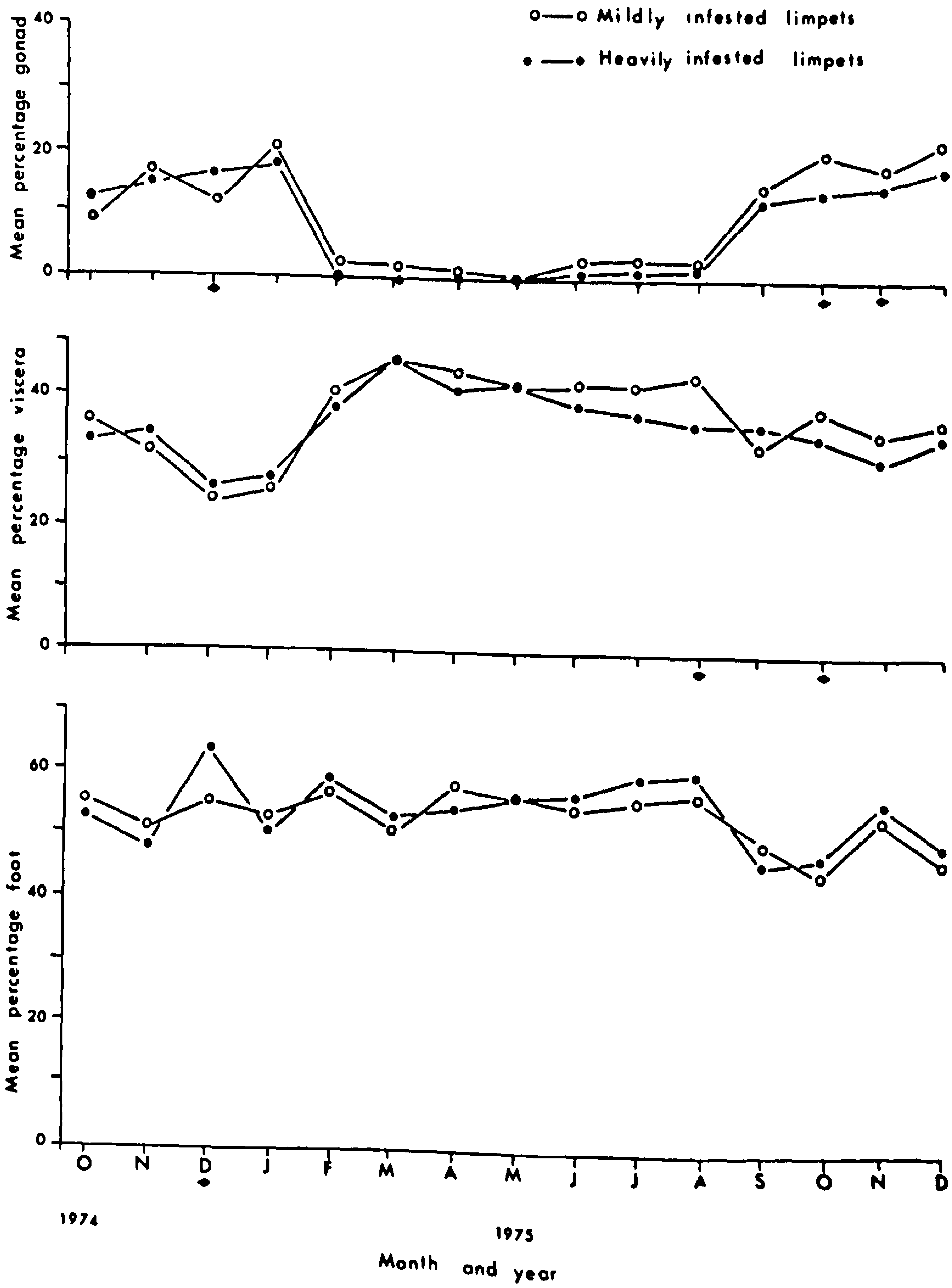

o—o Mildly infested limpets
• —• Heavily infested limpets
Mean percentage gonad
40
20
0
Mean percentage viscera
40
20
0
Mean percentage foot
60
40
20
0
O
N
D
J
F
M
A
M
J
J
A
S
O
N
D
1974
1975
Month and year

Figure 29 .

Graph showing the relationship between water content and condition of Patella vulgata, for September 1975. The regression lines were calculated using arcsin transformations of the percentage data. $r = -0.943$; $n = 29$. $Y_{est} = -5.921X + 485.93$. The regression coefficient is significant at the 5% level.

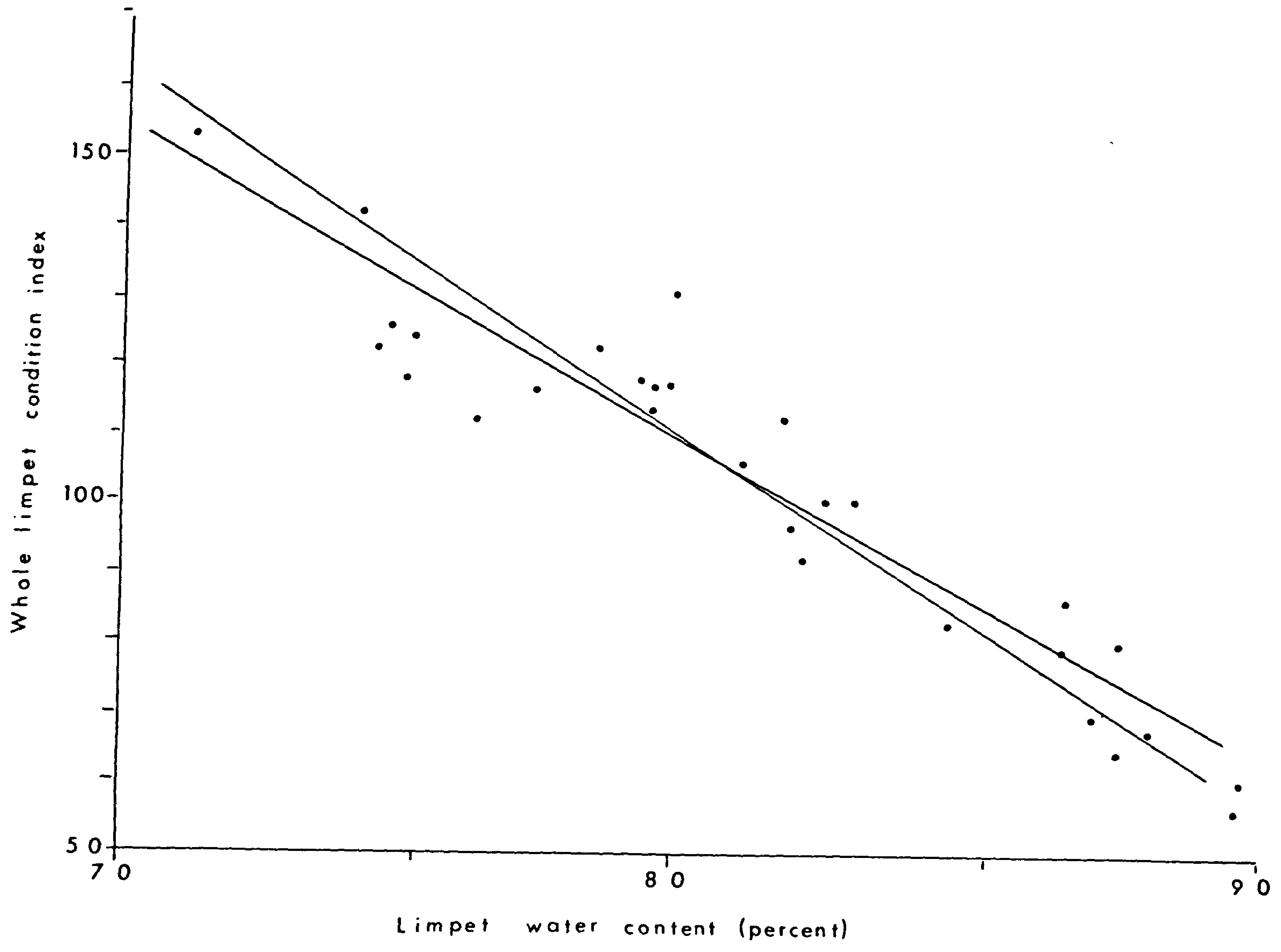

Whole limpet condition index
150
100
50
70
80
90
Limpet water content (percent)

Figure 30 .

Graph showing the monthly changes in the condition of mussels. A significant ($p = \leq 0.05$) difference between the means of heavily and mildly infested mussels is indicated by ✦ .

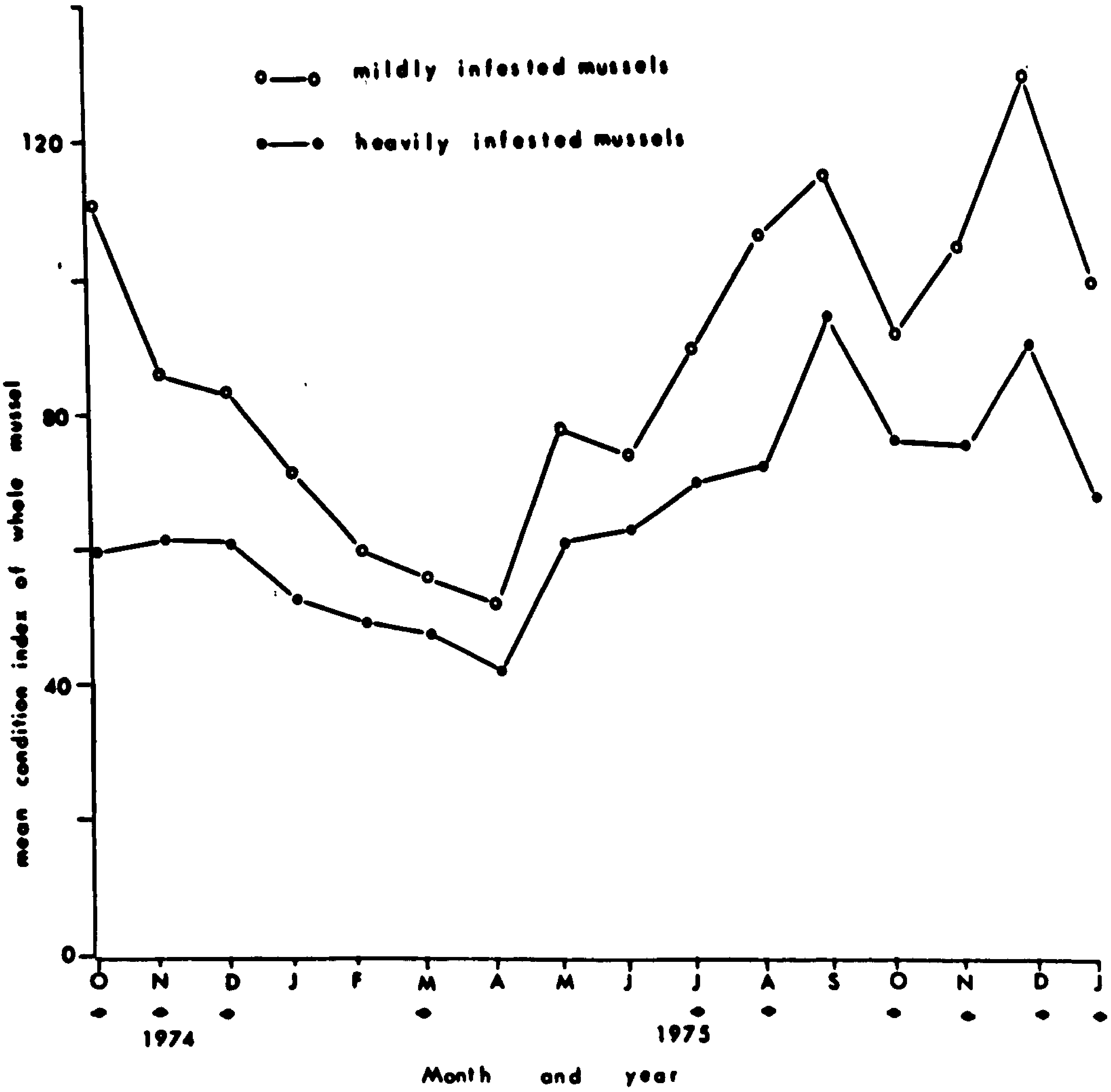
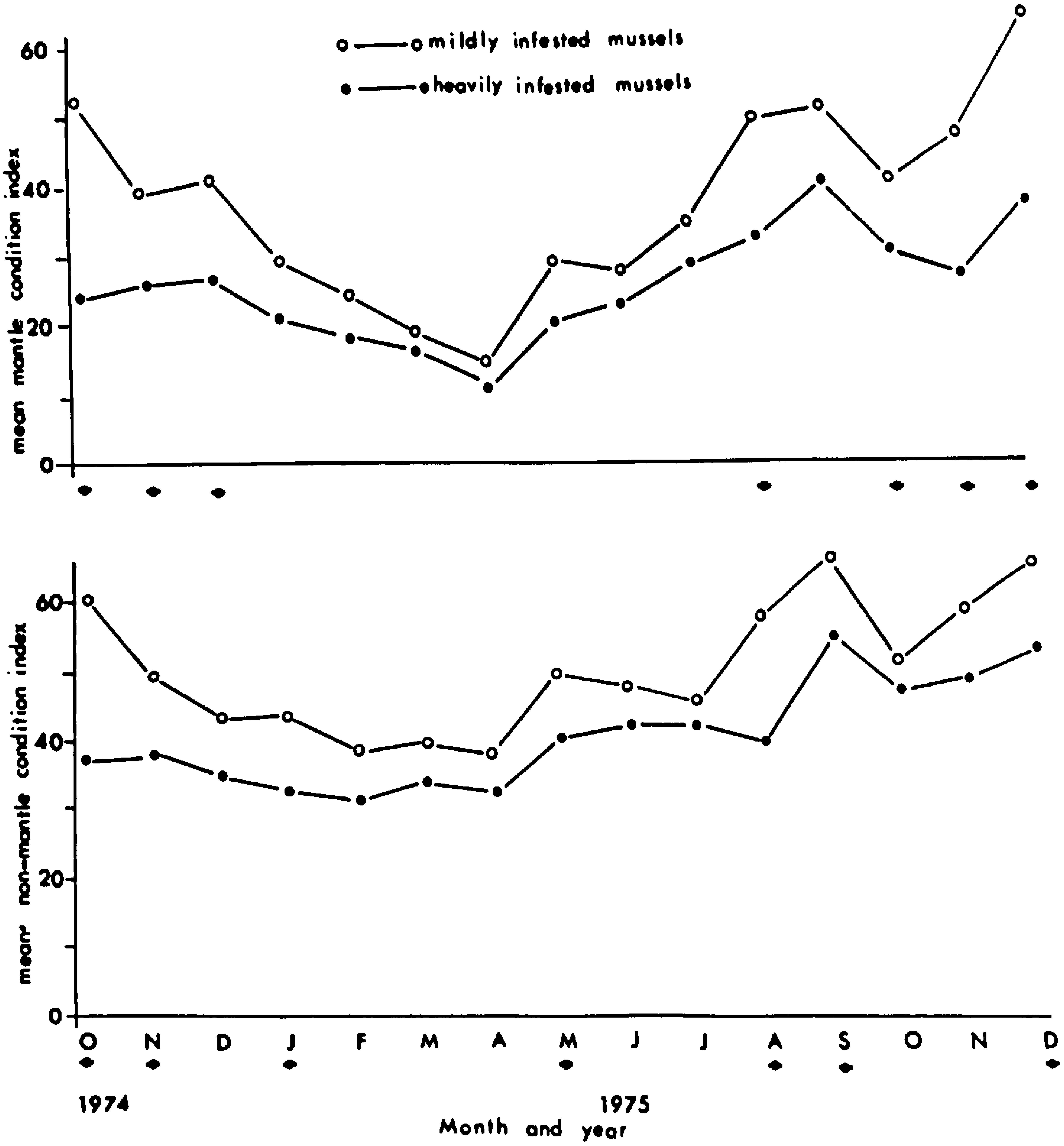

mildly infested mussels
heavily infested mussels
mean condition index of whole mussel
120
80
40
0
O
N
D
J
F
M
A
M
J
J
A
S
O
N
D
J
1974
1975
Month and year

Figure 31 .

Graphs shewing monthly changes in the condition of the mantle and non-mantle tissue of mussels. A significant difference (at the 5% level) between the means of heavily infested and mildly infested mussels is indicated by ◆ .



○——○ mildly infested mussels
●——● heavily infested mussels
mean mantle condition index
60
40
20
0
mean non-mantle condition index
60
40
20
0
O
N
D
J
F
M
A
M
J
J
A
S
O
N
D
1974
1975
Month and year

The mantle is the main repository of energy reserves for the developing gonad, and is also the main storage site for the gametes. Therefore, mantle size is indicative of the relative fecundity of the mussels. The low mantle condition of heavily infested limpets suggests that fecundity is reduced by polydorid infestation. It is very likely that as the condition of the mussel improves, it can commit a greater proportion of its tissue to gamete production. Since the heavily infested mussels are usually in poor condition, this also would indicate an adverse effect of P. ciliata infestation on mussel fecundity. There is no evidence to suggest that infestation affects the development of the gonad.

Figure 32 shows that the water content of heavily infested mussels was significantly higher than that of mildly infested mussels in the spring and summer of 1975. A comparison of Figures 10 and 13 shows that the water content and condition of the mussels is generally inversely related, but this relationship is by no means exact. Nevertheless, the results do support the view that heavy infestations of P. ciliata impair the condition of mussels.

Figure 33 shows that heavy infestations of polydorids result in the secretion of more shell material, and therefore a greater shell volume of the mussels. I thought that this increase in shell deposition, induced by P. ciliata borings, might contribute to the loss of condition of heavily infested mussels. Therefore, I simulated the P. ciliata borings by drilling holes into the extra-pallial cavity of mussels. The condition of these mussels was compared with those of mussels with holes drilled only partly into the shell, and with mussels collected

Figure 32 .

Graph showing monthly changes in the water content of mussels. A significant difference (at the 5% level) between the means of heavily infested and mildly infested mussels is indicated by ◆ .

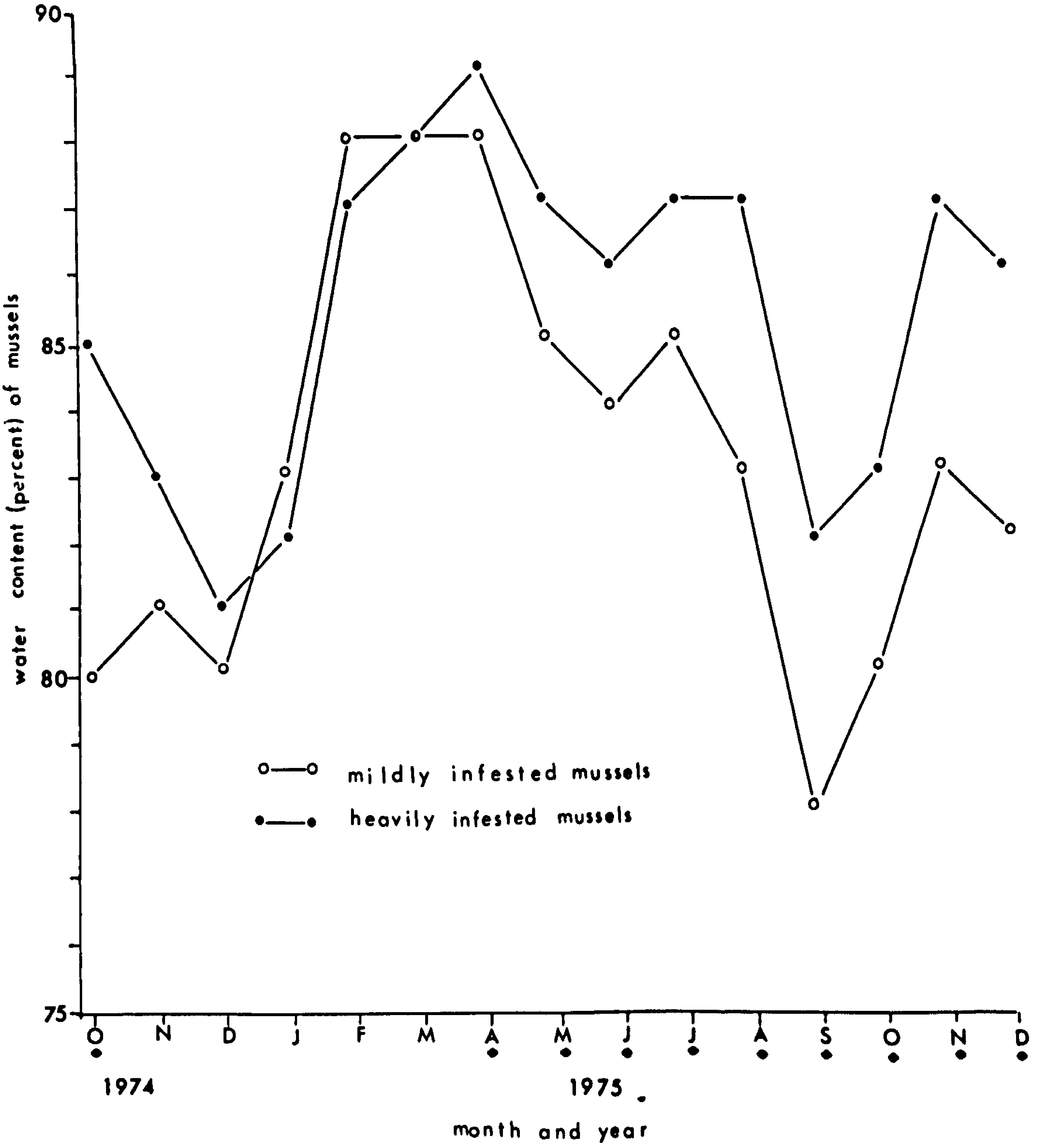

90
85
80
75
water content (percent) of mussels
○—○ mildly infested mussels
●—● heavily infested mussels
O
N
D
J
F
M
A
M
J
J
A
S
O
N
D
1974
1975
month and year

Figure 33

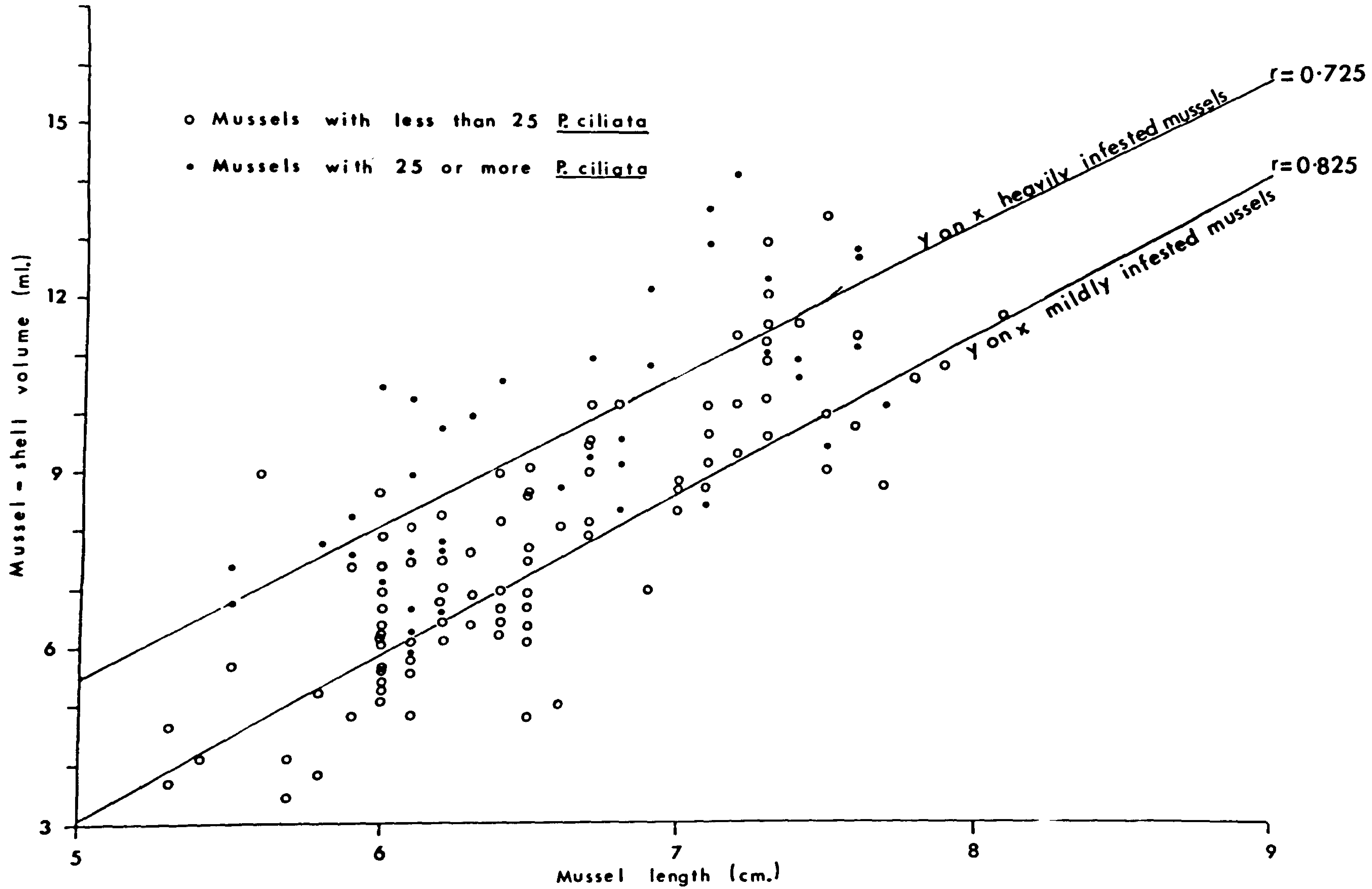
Scatter diagram and regression lines showing the relationship between length and volume of mildly and heavily infested mussels.

For mildly infested mussels:

$r = 0.825$; $n = 93$; $Y = -11.392 + 2.931X$; $p = \angle\, 0.001$

For heavily infested mussels:

$r = 0.725$; $n = 40$; $Y = -6.868 + 2.484X$; $p = \angle\, 0.001$


○ Mussels with less than 25 P. ciliata
• Mussels with 25 or more P. ciliata
Y on x heavily infested mussels
r = 0·725
Y on x mildly infested mussels
r = 0·825
Mussel - shell volume (ml.)
3
6
9
12
15
Mussel length (cm.)
5
6
7
8
9

from the natural habitat. The experimental mussels were kept in conditions of starvation so that any loss of condition was due to the metabolism of the mussel rather than its consumption or competition with P. ciliata. The results are shown in Table 3. They indicate that boring through the shell into the shell cavity does result in a greater loss of condition, suggesting that there are extra demands on the metabolism of bored mussels. This conchyolin was so small that it could not be accurately weighed. It seems unlikely that the material has any great calorific value. The loss of condition may be due to the mobilisation of haemocytes which are involved in the laying down of shell material (Narain,1973) rather than the energetic cost of the material itself.

Figure 34 shows that there was no clear affect of P. ciliata infestation on the condition of Crassostrea gigas, on the three occassions they were analysed.

Table 3.

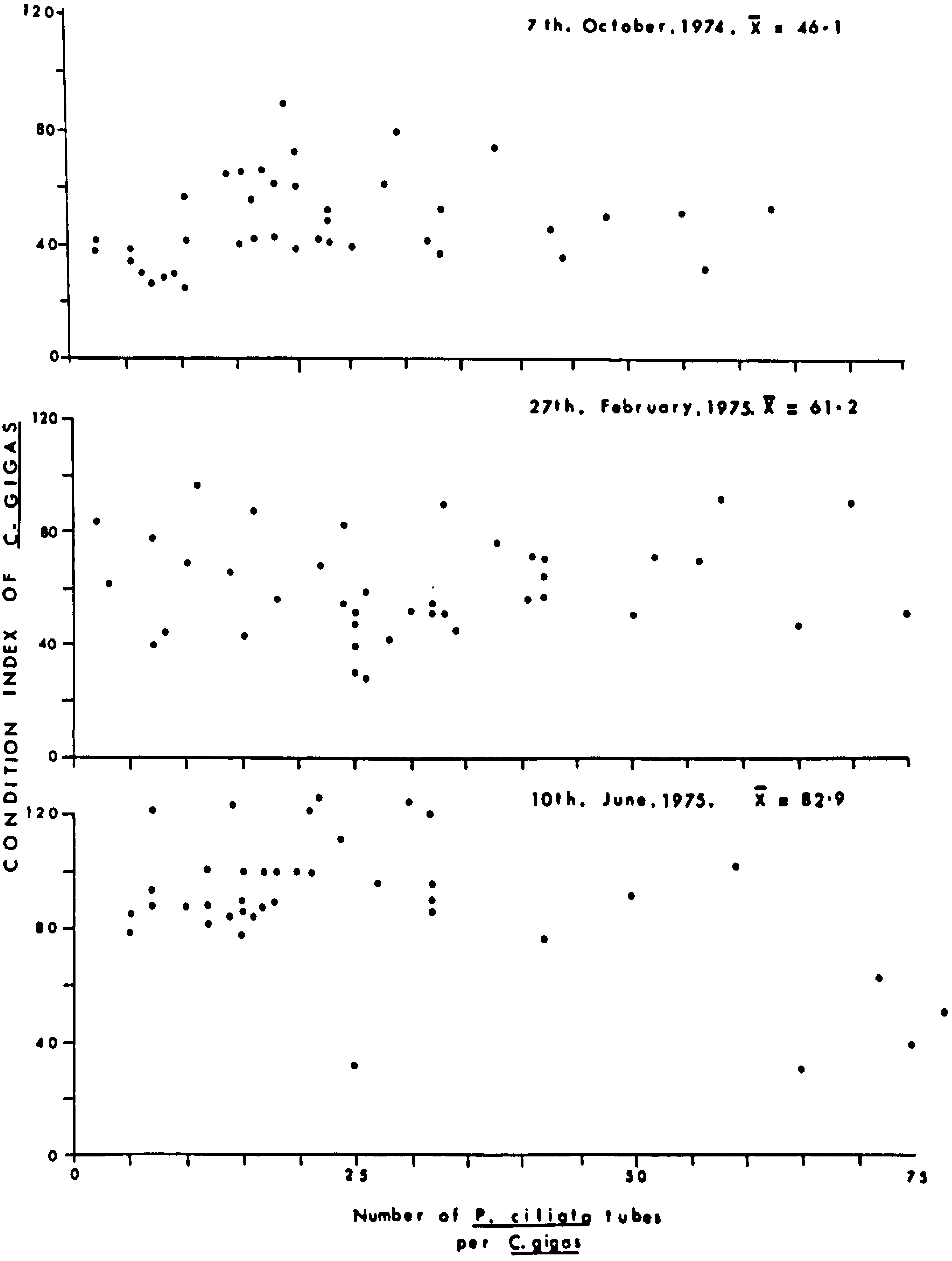
ANALYSIS OF THE CONDITION INDEX OF MUSSELS WITH AND WITHOUT DRILL HOLES IN THE SHELL

	Mean	S.D.	n
April, 21st. Start of the experiment.			
Natural mussels (natural feeding)	58.04	9.94	30
May, 15th. End of the experiment.			
Natural mussels (natural feeding)	74.60	7.64	30
Partly drilled mussels (starved)	47.31	12.28	30
Completely drilled mussels	30.43	8.17	30

A Student's 't' test was undertaken to find the significance of the difference between the means of the partly drilled and completely drilled mussels at the end of the experiment: 't' = 3.89
p = less than 0.001

Figure 34 .

Scatter diagrams of the condition of oysters (Crassostrea gigas) with different degrees of infestation. There was no detectable effect of Polydora ciliata on the condition.


7th. October, 1974. $\bar{X}$ = 46·1
27th. February, 1975. $\bar{X}$ = 61·2
10th. June, 1975. $\bar{X}$ = 82·9
CONDITION INDEX OF C. GIGAS
120
80
40
0
0
25
50
75
Number of P. ciliata tubes per C. gigas

DISCUSSION

The results indicate that heavy infestations of P. ciliata do harm limpets and mussels, although light infestations may be harmless. A major disadvantage of using condition indices and water content as estimates of molluscan condition, is that the specific causes of changes in condition are not revealed. It is likely that the fundamental mechanisms that bring about the reduction in condition index and increase the water content of limpets and mussels with heavy polydorid infestations, are complex and have no single cause. If we accept the assumption that a lowering of condition index indicates a reduction in tissue size, then this lowering may be caused by a disruption of the mollusc's energy budget. This is described by Crisp (1971) and can be summarised by the equation:

Consumption = Production + Respiration + Excretion + Faecal production.

A lowering of tissue size may indicate a decrease in production by the mollusc. This could result from a decrease in consumption, a decrease in assimilation, or an increase in metabolism (represented in the equation by respiration).

Reduction of consumption may be caused, in heavily infested limpets, by the heavy shell impeding the limpet in its feeding excursions. Consumption of heavily infested mussels may be reduced by competition with P. ciliata for food; or it could be due to the blisters on the interior of the shell reducing the feeding efficiency of the mussel.

Extra metabolic demands may be imposed on heavily infested limpets and mussels by the polydorids enforcing shell secretion by their hosts. Davis and Hillman (1971) suggested that regeneration of shell material may act as a drain on the energy reserves of oysters. This could result from the extra production of calcareous and organic material, which constitute the shell, or it could be due to the production of extra haemocytes, which are involved in the transport of calcareous material (Narain, 1973). However, the increase in haemocyte count associated with shell regeneration (Malek and Cheng, 1974; Moore, pers. comm; Narain, 1973) may be due to the diversion of haemocytes from other functions, to that of shell secretion. But, since little is known about haemopoesis, this problem cannot be resolved.

Haemocytes are involved in digestion and excretion of ingested material (Narain, 1973). If there is a diversion of haemocytes from these functions to that of shell secretion, assimilation may be impaired with the result that the condition is lowered.

Another possible cause of the lowering of condition caused by P. ciliata, may be the intrusion of pathological microbes through bore holes, created by P. ciliata, into the extrapallial cavity of mussels.

The drilling experiment showed that, in mussels at least, the damage caused by actual bore holes can result in a reduction of the condition. This reduction of the mussels' condition was due to the extra demands on their metabolism, rather than an impairment of consumption or assimilation, since the mussels were starved.

It seems likely that the major cause of the lowering of limpet and mussel condition is the extra demands on the metabolism imposed by the bore holes resulting from the heavy infestations of *P. ciliata*. This hypothesis is supported by the results of the condition analyses of *C. gigas*; some oysters had very heavy infestations of *P. ciliata*, but did not exhibit a clear reduction of condition. The *P. ciliata* were in a position to compete for food with the oysters, but very few entered the extra-pallial cavity to induce shell secretion; the polydorids tended to lodge between the many shell layers of the oyster, without boring into the shell. The results suggest that *P. ciliata* which do not enter the extra-pallial cavity are relatively harmless; but polydorids which do enter the extra-pallial cavity may upset the energy balance and act as a drain on the energy reserves of their hosts.

Heavy infestations of *P. ciliata* seem to reduce the fecundity of both limpets and mussels. Vance (1973) developed a model to examine the advantages of a species, such as limpets and mussels, which have planktotrophic larvae, He stated that such species are at a maximum energetic advantage when the subdivision of energy available for reproduction is maximal; that is, when fecundity is greatest and the energy content of each egg is small. Thus, the reduction of fecundity associated with heavy infestations, is likely to be a disadvantage to the species.

There is no evidence in my results to suggest that the development of limpet or mussel gametes is impaired by *P. ciliata* infestations. Bayne (1973) suggests that mussels under stress can continue with gameto~~n~~genesis as long as the gametes are not ripe. This supports Field's (1922) opinion that mussels in poor condition can still spawn. However, there is some evidence to suggest that mussel embryos from stressed adults show abnormalities during development, and the vitality and vigour of the larvae produced by stressed adults is impaired to some degree (Bayne,1972;1973; Bayne et.al.,1975).

The seasonal changes in the condition of mussels and limpets, result from storage and utilization of food reserves in relation to the complex interaction of food availability and temperature, with growth, respiration and reproductive processes.

The seasonal pattern of condition changes for the Fowey mussels seems to conform with those of other mussels. (Baird,1966; Dare and Edwards,1975; Dethlefsen,1975; Williams,1968; Zwann and Zandee,1972). The mussels' condition was highest in late summer and early autumn,when they accumulate glycogen reserves (Williams,1968; Bayne,1975; Zwann and Zandee,1972); then they lose condition through the winter, when consumption cannot compensate for metabolic losses of the energy reserves; and the condition reaches a minimum in early spring, possibly coinciding with a spawning period.

The seasonal changes of gonad condition of Porthpean limpets seems to conform to the pattern of limpets from other areas (Ballantine, 1961b; Blackmore,1969a; Lewis and Bowman,1975; Orton et. al.,1956), although the details differ. The changes can be separated into three stages: gonad maturation in late summer; gonad spawning and regression in late autumn and early winter; and gonad resting from winter to mid-summer. My results suggest that there was a prolonged spawning period for limpets at Porthpean in 1975; but it is not possible to pinpoint the exact dates of spawning. Prolonged spawning of limpets has been reported by Blackmore (1969a), Choquet (1968), and Orton et. al.,(1956); but Ballantine (1961b) suggested that limpets in Plymouth Sound spawned synchronously over a short period. The length of the spawning period possibly depends on the intensity of the spawning stimulus, which seems to be heavy wave action (Ballantine,1961b; Orton et. al., 1956); the greater the wave action the greater the spawning, and the shorter the spawning period.

Changes in the body component indices may be explained by the accumulation and utilization of energy reserves, which may take place at different months in the different conponents. (Barry and Munday, 1959; Blackmore,1969b). The growth of the visceral mass seems to precede that of the foot, and they both decline when the gonad is developing. Glycogen is first stored in the hepatopancreas, in the visceral mass, and then in the foot; the glycogen reserves are then utilised by the gonad (Barry and Munday,1959).

The commercial implications of polydorid infestation are difficult to unravel. Disease or stress are usually recognized as significant factors in the culture of molluscs only on ~~occassions~~ occasions of disastrous losses. This seems an unlikely possibility when we consider the effect of <u>P</u>. <u>ciliata</u> on Fowey mussels. However, it is clear the heavy infestations of <u>P</u>. <u>ciliata</u> may reduce the condition and commercial value of mussels; but it may not be practicable to eliminate this pest because of its prolonged planktonic stages. <u>M</u>. <u>edulis</u> supports a large fishery in England and Wales, with gross landings of 3,000 - 5,000 tonnes, and it is likely to increase (Dare and Edwards,1975; Mason, 1972). No matter how marginal the effect of <u>P</u>. <u>ciliata</u>, it can be of considerable value in the development of mussel cultivation to be aware of the presence of this pest, and anticipate the potential damage it may cause.

THE EFFECT OF *P. CILIATA* ON THE STRENGTH OF MUSSEL SHELLS

A number of authors have noted that molluscan shells infested with *P. ciliata* are friable (Dollfus,1932; Forbes,1966; Korringa, 1952; Leloup,1937), but no one has attempted to quantify the relationship between shell strength and polydorid infestation. Therefore, I madecompression tests on *Mytilus edulis* shells to determine to what extent different degrees of infestation reduce~~s~~ the compression strength of the shells.

Associated with these tests, were observations of the predation of mussels by the crab, *Cancer pagurus*, to see if polydorid infestation of the shells increases the mussels' vulnerability to predation.

The mussels were collected from the river Fowey mussel bed at the level of mean low water spring tides. It was important that all the mussels came from the same tidal level, since Baird and Drinnan (1957) stated that shell weight of mussels increases with increased exposure to air, and it is possible that shell strength follows a similar relationship.

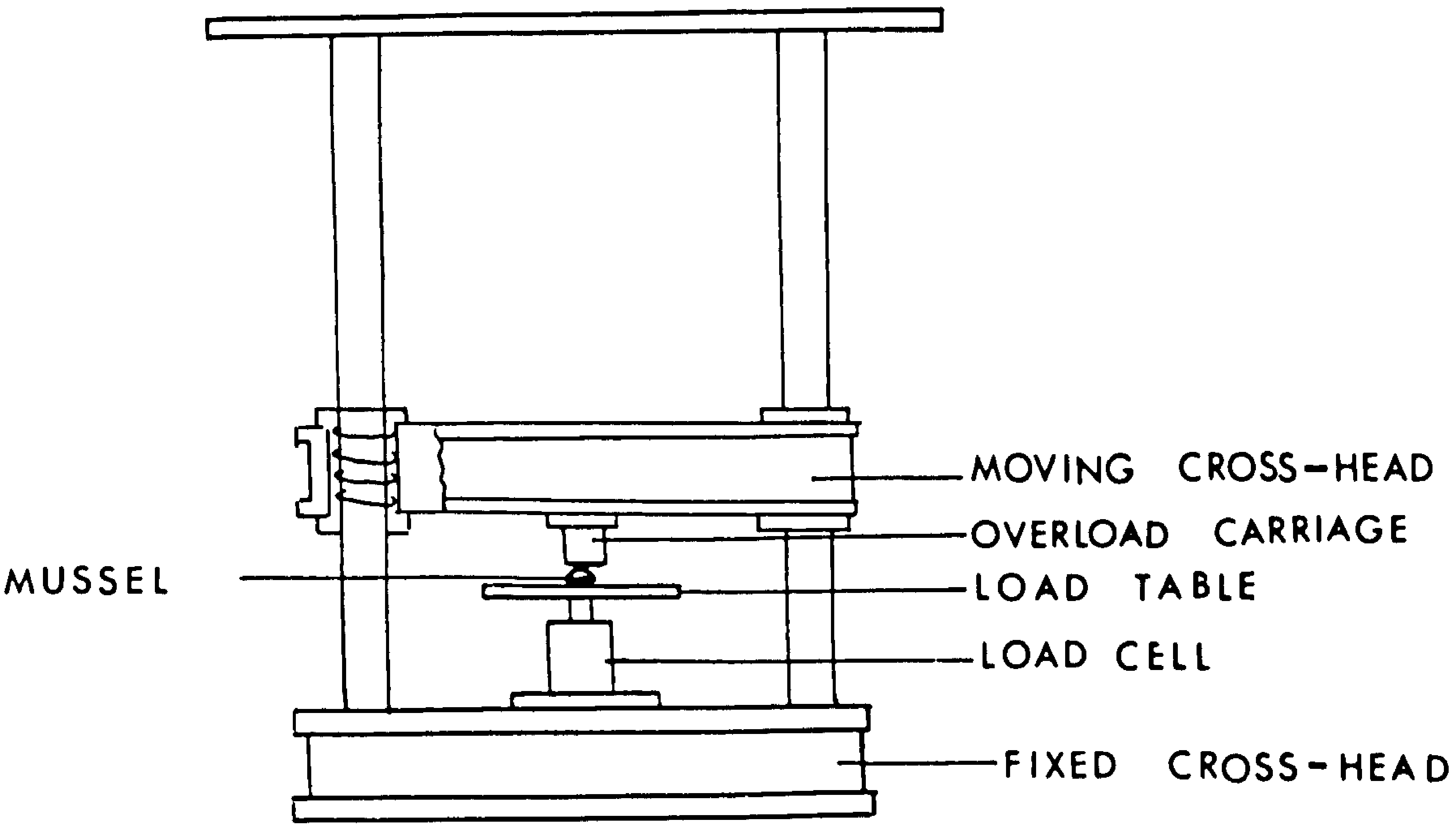
After collection, the shells were transported to the laboratory in plastic bags, and cleaned of all epifauna. They were then placed in aerated seawater for at least three hours prior to testing. The mussels were prodded to make them close their valves before removing them from the seawater and placing them on the compression testing apparatus. All gaping mussels were rejected. Therefore, all the mussels had their mantle cavities full of seawater during the compression tests.

Compression tests were made on shells exposed to air, using an Instron Universal Testing Instrument. Full details of the operating instructions are provided by the manufacturer's manual (Instron,1967). Figure 35 shows, diagrammatiacally, a mussels shell being compression tested; the recording equipment is not shown. The Instron incorporates a highly sensitive electronic weighing system, with load cells that are stretch guages for detecting and recording compression loads. The end of the spindle of the compression load cells supported a load table on which the mussels were placed. The crosshead was lowered,to increase the compression load on the shells, by two vertical screws, and a positional servo mechanism facilitated accurate and flexible control over the crosshead motion. The change in load on the mussel shells was monitored by a chart recorder which was driven synchronously with respect to the crosshead. A load cell provided a full-scale sensitivity of 200 kg. The load weighing system was electronically calibrated before the compression tests. The rate of increase of the compression load was controlled by the speed of the crosshead , which was 0.5 cm / sec. for each test. Figure 36 show three compression tests. Fracture of the shells is indicated by a sharp downward deflection of the tracing. The tests were completed within 24 hours of collecting the mussels from the shore.

Tests were made of the relationship between shell length and shell strength, and also between shell volume and shell strength. Shell length was measured with vernier callipers; and shell volume was measured by weighing the shells first in air then in water, as previously described.

Figure 35 .

Diagram of the Instron Universal Testing Instrument, showing a mussel being compressed. The recording apparatus is not shown. The lower figure shows the point at which the compression load was applied.


MOVING CROSS-HEAD
OVERLOAD CARRIAGE
MUSSEL
LOAD TABLE
LOAD CELL
FIXED CROSS-HEAD

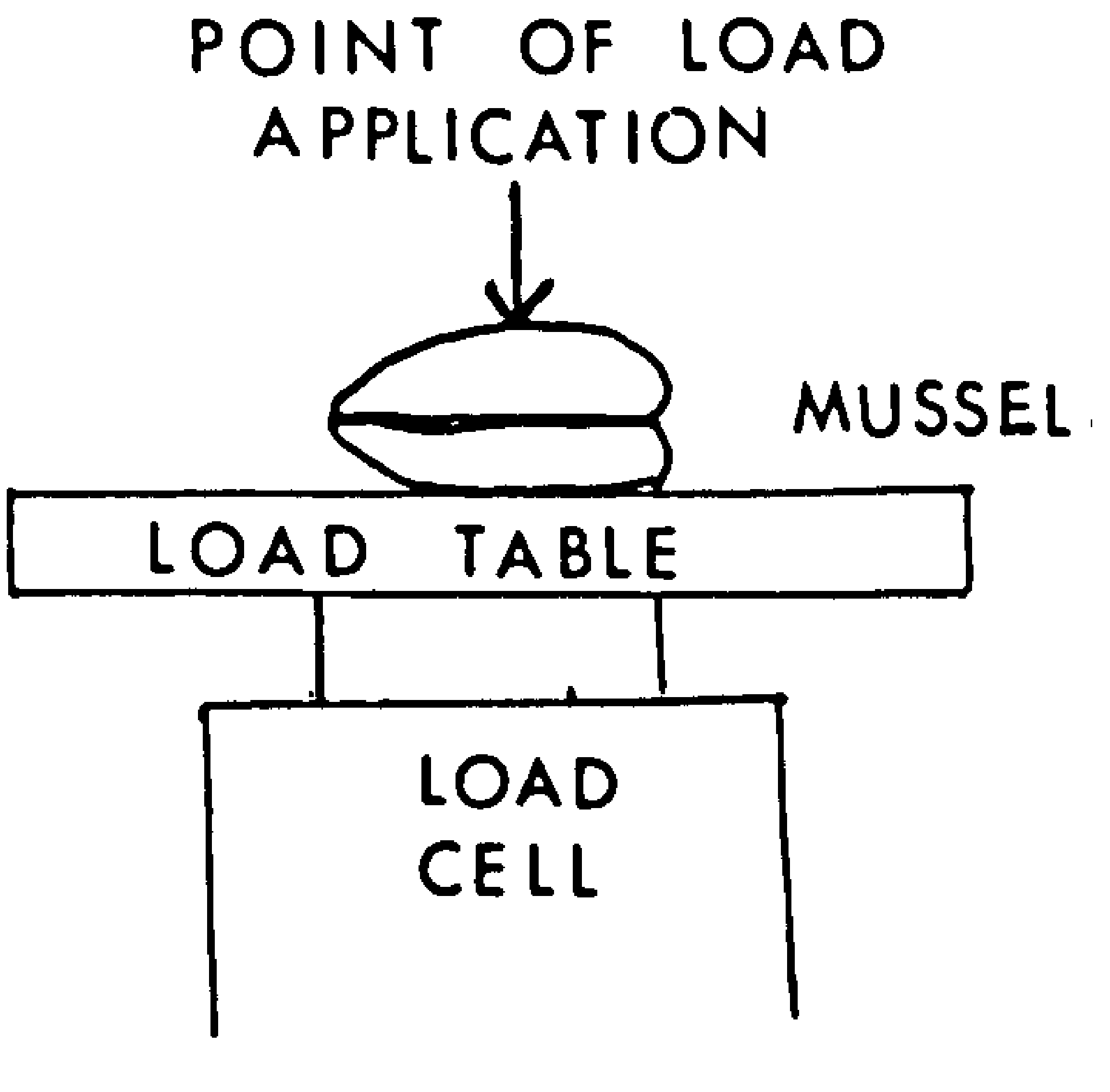

POINT OF LOAD APPLICATION
MUSSEL
LOAD TABLE
LOAD CELL

Figure 36

Actual records of three compression tests on mussels.


full scale 200 kg
77 kg
86 kg
87 kg
NO. 19
NO. 18
NO. 17

The degree of polydorid infestation of the mussels was established by X-radiography.

The effect of polydorid infestation on the predation of mussels by the crab, Cancer pagurus, was determined using cage experiments. A random sample of 120 mussels, all between 6.3 and 6.7 centimetres in length, was collected from the river Fowey mussel bed at the level of mean low water spring tides. The mussels were cleaned of epifauna and then placed in plastic cages with the crabs. Four cages were used, each measuring 1 metre wide, by 1 metre long, by 0.5 metres high. 30 mussels and one male crab, of carapace width 150 - 170 mm., were put into each cage.

The mussels were randomly allocated to the cages. The degree of infestation of the mussels was not known until the mussels were removed from the cages. To have established the degree of infestation of the mussels prior to the experiment, would have necessitated the removal of the mussels from seawater for a considerable time, during which some of them might have become debilitated and more susceptible to predation.

The experiment was conducted under natural conditions. The cages were anchored down by weighted ropes 1 metre below the level of extreme low water spring tides, off a beach near to Porthpean. This beach was chosen because it was secluded. The Fowey mussel bed was frequented by divers and pleasure craft which might have disturbed the experiment.

The cages were checked daily during a SCUBA dive, and the experiment was terminated when approximately 50% of the mussels were crushed by the crabs. The degree of infestation of the crushed and surviving mussels was established by X-radiography.

The cage experiments were complemented by aquarium observations of the crabs' feeding beaviour.

RESULTS AND DISCUSSION

The results indicated that heavy infestation of mussels weakens their shells. Figure 37 shows that there was a significant ($p = \angle 0.001$) negative linear correlation between compression strength and infestation of mussels of the restricted size range. Figure 38 is a scatter diagram of the compression strengths of mussels of different lengths. Uninfested and infested mussels have been differentiated, but there was no clear difference between the compression strengths of the two groups. However, if, as in figure 39 , the compression strengths of heavily infested mussels (ie. with more than 25 P. ciliata per mussel) are compared with those of uninfested mussels, the adverse affects of of polydorid infestation become clear. Figure 39 also shows that the compression strength of uninfested mussel shells followed a strong positive linear correlation with mussel length, and that this correlation is disturbed by heavy polydorid infestation.

Figure 37 shows that polydorid infestation tends to weaken the mussel shells despite the tendency for heavily infested shells to have a greater volume of shell material, and the positive linear correlation (at least for uninfested shells) between shell volume and compression strength (figures 40 & 41) is also shewn.

Figure 42 shows that the percentage of mussels crushed by the crabs, tended to increase with increased polydorid infestation. If there was no effect of polydorid infestation, the same proportion mussels should have been crushed at each level of infestation. However,

Figure 37 .

Scatter diagrams and regression lines showing the relation between polydorid infestation and the compression strength of mussel shells .

For mussels 76 - 80 mm. long :

$r = -0.718$; $n = 19$; $Y = 94.125 + (-0.772)X$.

For mussels 71 - 75 mm. long :

$r = -0.473$; $n = 47$; $Y = 91.414 + (-0.573)X$.

For mussels 66 - 70 mm. long :

$r = -0.474$; $n = 57$; $Y = 85.752 + (-0.588)X$.

For mussels 61 - 65 mm long :

$r = -0.397$; $n = 85$; $Y = 78.430 + (-0.558)X$.

In each case, $p = \angle 0.001$.

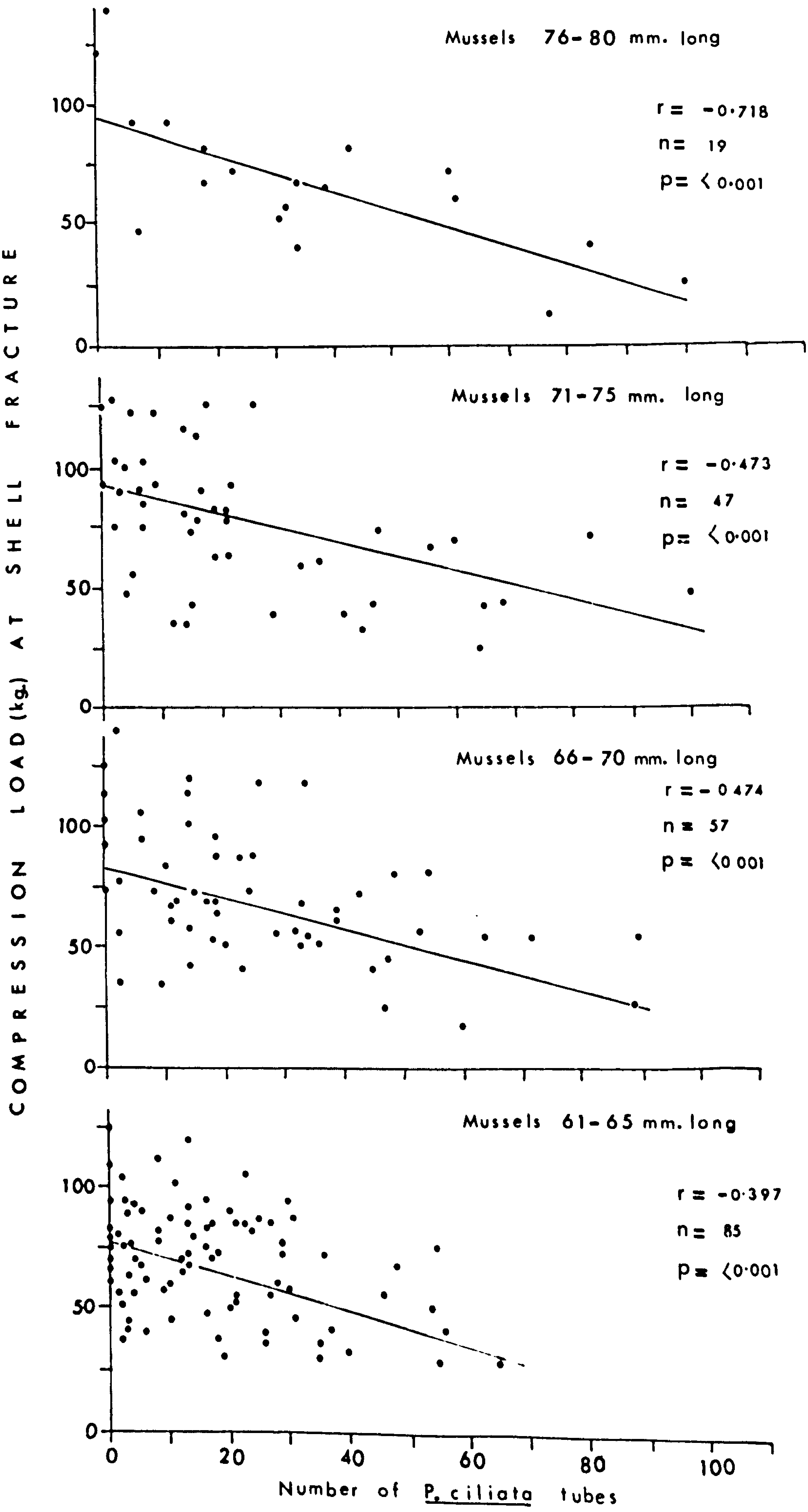

Mussels 76-80 mm. long
r = -0·718
n = 19
p = < 0·001
Mussels 71-75 mm. long
r = -0·473
n = 47
p = < 0·001
Mussels 66-70 mm. long
r = - 0 474
n = 57
p = < 0 001
Mussels 61-65 mm. long
r = -0·397
n = 85
p = < 0·001
COMPRESSION LOAD (kg.) AT SHELL FRACTURE
0
50
100
0
20
40
60
80
100
Number of P. ciliata tubes

Figure 38

Scatter diagram showing the relationship between length and strength of uninfested and infested mussel shells.

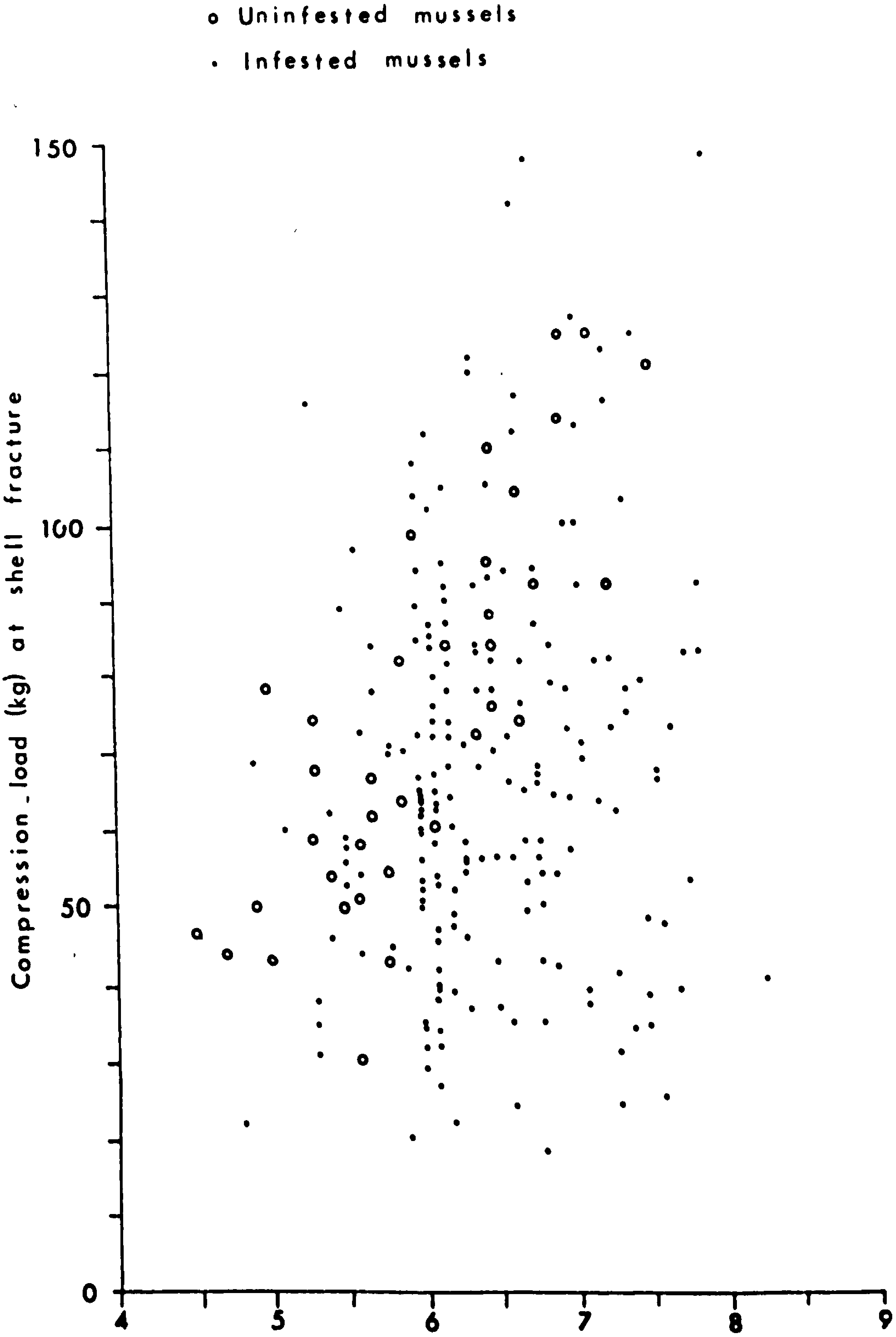

o Uninfested mussels
. Infested mussels
150
100
50
0
Compression - load (kg) at shell fracture
4
5
6
7
8
9
Mussel length (cm.)

Figure 39

Scatter diagram of the relationship between length and shell strength of uninfested and heavily infested mussels. The regression line is drawn for the uninfested mussels.

$r = 0.810$; $n = 34$; $Y = -83.977 + 2.631X$: $p = \leq 0.001$

The linear regression coefficient for the heavily infested mussels was 0.135, and was not significant at the 0.05 level.

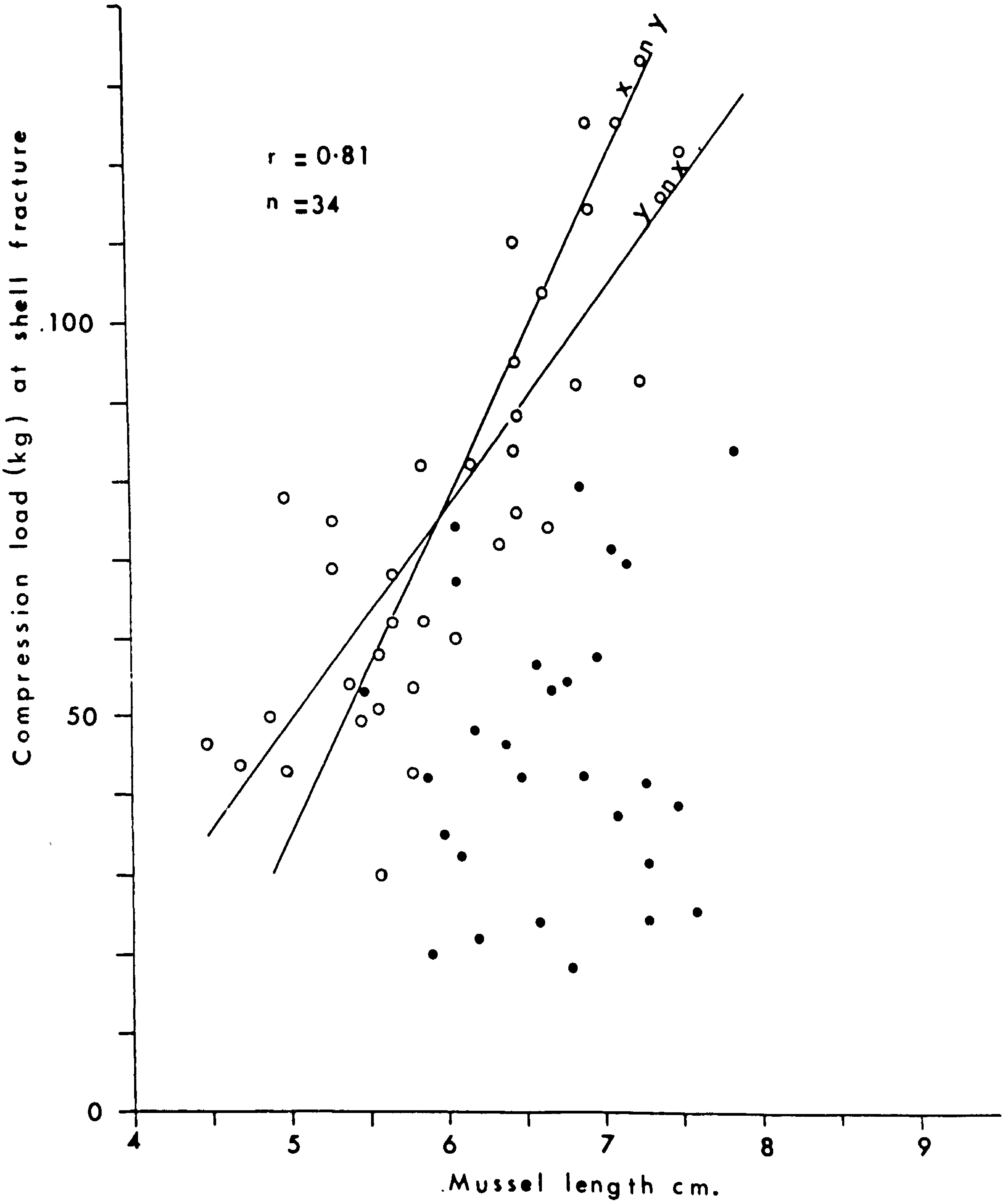
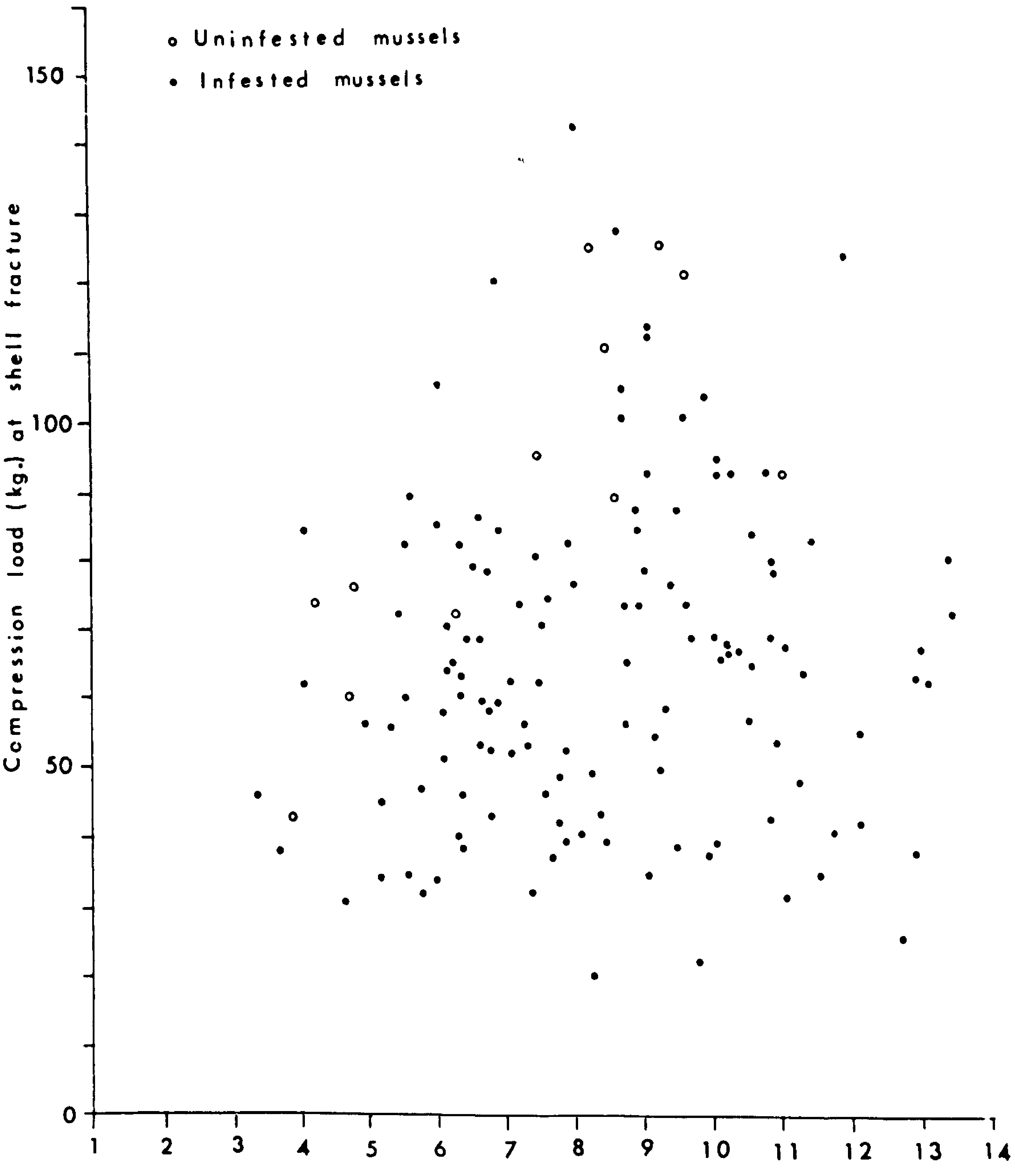

r = 0·81
n = 34
x on y
y on x
Compression load (kg) at shell fracture
100
50
0
4
5
6
7
8
9
Mussel length cm.

Figure 40

Scatter diagram showing the relationship between shell volume and shell strength of uninfested and infested mussels.



○ Uninfested mussels
• Infested mussels
Compression load (kg.) at shell fracture
150
100
50
0
Mussel-shell volume (ml.)
1
2
3
4
5
6
7
8
9
10
11
12
13
14

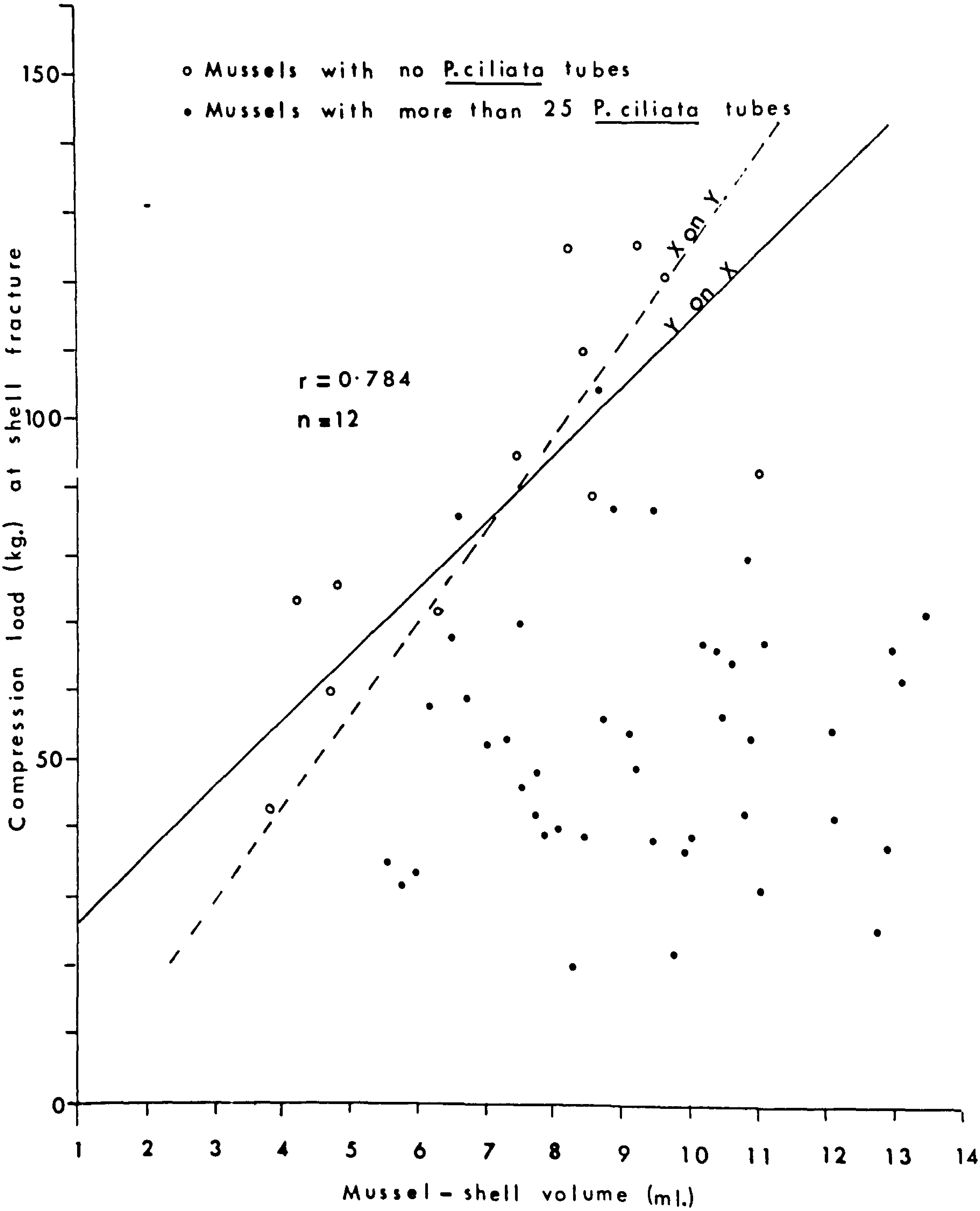
Figure 41

Scatter diagram of mussel shell volume and shell strength of uninfested and heavily infested mussels. The regression lines are drawn only for the uninfested mussels.

$r = 0.784$; $n = 12$; $Y = 26.898 + 8.630 X$; $p = \angle 0.001$

The linear regression coefficient for heavily infested mussels was not significant.

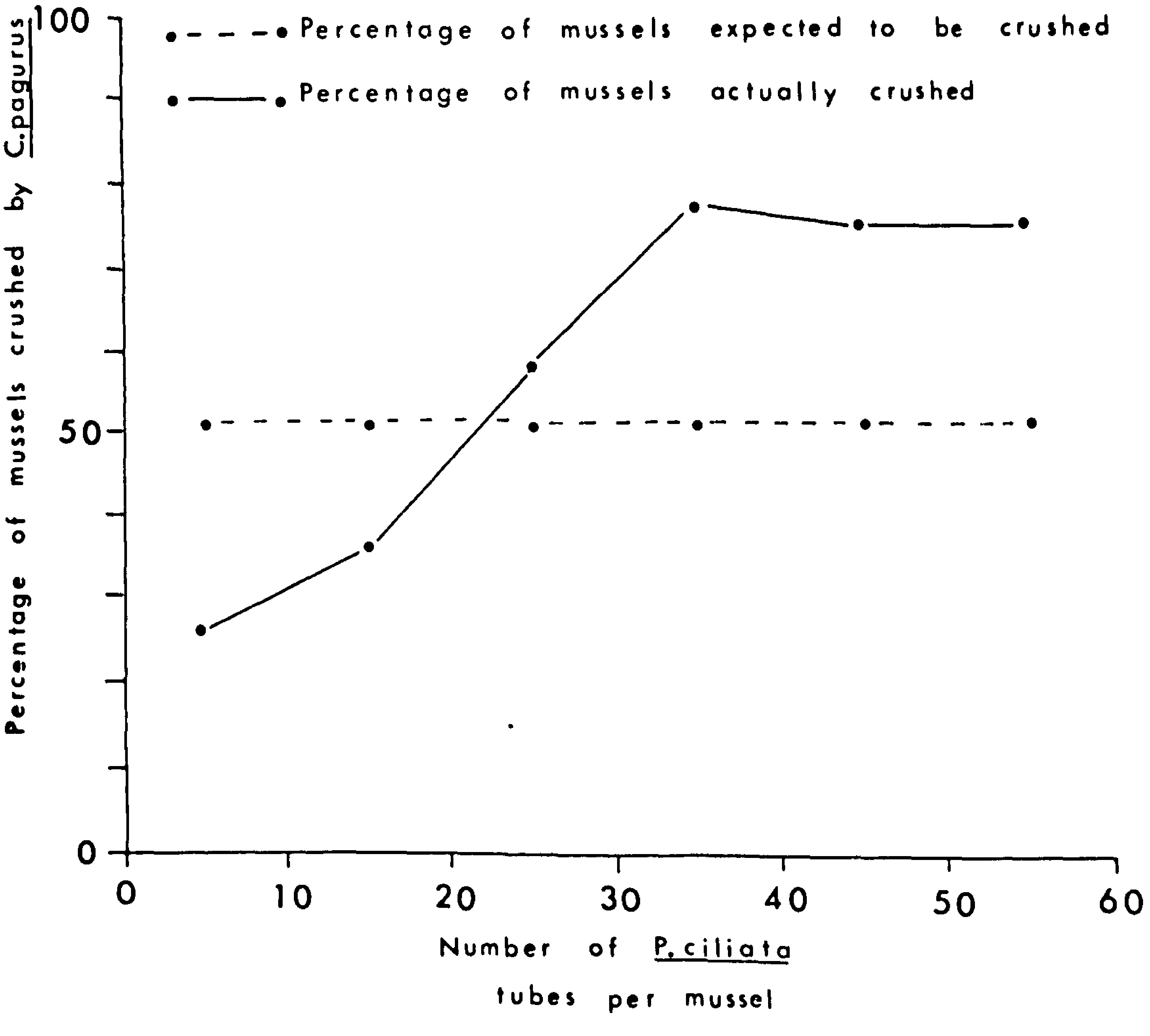
$r = 0.138$; $p \not\angle 0.05$.



o Mussels with no P. ciliata tubes
• Mussels with more than 25 P. ciliata tubes
X on Y
Y on X
r = 0·784
n = 12
150
100
50
0
Compression load (kg.) at shell fracture
1
2
3
4
5
6
7
8
9
10
11
12
13
14
Mussel - shell volume (ml.)

Figure 42

Graph showing that the percentage of mussels crushed by <u>Cancer pagurus</u> in sublittoral cages tended to increase with increased polydorid infestation.



●- - - -● Percentage of mussels expected to be crushed
●——● Percentage of mussels actually crushed
Percentage of mussels crushed by C.pagurus
100
50
0
0
10
20
30
40
50
60
Number of P.ciliata tubes per mussel

table 4 shows that the results deviated significantly from what would have been expected if there was no effect of polydorid infestation on the mussels' chances of being crushed by the crabs. Not all of the mussels crushed by the crabs had their tissues removed, therefore it is not known how many of the mussels were consumed by the crabs.

The results suggest that the crabs preferentially crushed the heavily infested mussels. However, this does not imply an ability on the part of the crab to distinguish between mussels with different degrees of infestation. Aquarium observations showed that if a mussel did not yield to the first few attacks, the crab would go on to another mussel; up to four attacks were made by one crab on a mussel before it rejected the mussel.

Other observations of the feeding behaviour of the crabs in the aquarium comply with those recorded by Seed (1969b). C. pagurus has a relatively simple feeding behaviour pattern on mussels, and relies solely on its ability to use its two massive, molar, crushing claws to crack open shells. The mussels are manipulated and held by the maxillipeds and anterior walking legs. The crab raises itself over the mussel shell, and both maxillipeds, held more or less vertically, apply pressure to the mussel shell. Once the shell is fractured, the chelipeds are inserted and pieces of shell and tissue are broken off and conveyed to the mouth where the flesh is removed by the mandibles and sorted by the mouth parts for ingestion.

The reduction of the compression strength of mussel shells by polydorid infestation, may explain why more of the heavily infested mussels were crushed than the mildly infested mussels.

Table 4

The results of the cage experiment. The mussels and crabs were placed in the cages on July 15 th. 1976, and removed after four days.

No. of <u>P. ciliata</u> per mussel	No. of mussels crushed	No. of mussels surviving	Total	% crushed
0 - 9	8 (14.56)	20	28	28
10 - 19	9 (13.00)	14	23	36
20 - 29	7 (6.24)	5	12	58
30 - 39	7 (4.28)	2	9	77
40 - 49	6 (4.16)	2	8	75
50 - 59	15 (10.40)	5	5 x	75
TOTALS	52	50	102 x	51

Number of mussels lost from cages, or dead without being crushed = 18

The number of mussels expected to be crushed, if there was no effect of polydorid infestation, is in parenthesis. A chi-squared test showed that the actual results deviated significantly from the expected results:

Chi squared = 8.279; degrees of freedom = 3; $p = < 0.05$.

The crab/mussel, predator/prey relationship is usually described in terms of the relationship between the sizes of the predators and prey. But the above results highlight the fact that similarly sized mussels vary considerably in their ability to resist compression loads and that this may affect the ability of the crabs to feed on the mussels.

It is not possible, from the above results, to state to what extent P. ciliata infestation increases the predation of mussels by crabs in the natural habitat. However, mussels are heavily predated upon by crabs, and the absence of mussels in some sublittoral areas has been attributed to crab predation (Ebling et. al.,1964; Kitching, 1959; Seed,1969b). Also, I have observed crabs of up to 160 mm. carapace width, in the mouth of the river Fowey. It is possible that these crabs feed on the mussels at high tide. Therefore, the weakening of the mussel shell by polydorid infestation potentially increases the mussels' vulnerability to crab predation.

The main crab predator of mussels is Carcinus maenas, rather than C.pagurus. Carcinus maenas has a more complicated feeding behaviour than C.pagurus (Seed,1969b), but it still relies to some extent on its ability to fracture the shells. Therefore, it is possible that polydorid infestation increases the vulnerability of mussels to this predator. Indeed, it is likely that infestation increases the vulnerability of mussels to any predator which needs to crack open the mussel's shell to get at its tissue.

Polydorid infestation may also increase the mortality of mussels during mechanical harvesting, since Dare (1974) showed that up to 5% of mussels whch had passed through a rotary sorting machine, may have died because of shell fracture.

THE EFFECT OF POLYDORA CILIATA ON THE VALVE CLOSURE OF MYTILUS EDULIS.

The ability of mussels to close their valves provides them with some protection against predators and adverse physico-chemical conditions, such as reduced salinity and desiccation. Valve closure of *Mytilus edulis* depends on the posterior adductor muscle bringing the two valves firmly together to form a hermetic seal. *P. ciliata* may affect the valve closure by weakening and/or diminishing the adductor muscle; or it may induce the formation of blisters which distort the posterior margin of the shells so that adduction of the valves does not form a seal.

Despite qualitative reports of the adverse effects of *P. ciliata* on the musculature of *M. edulis* (eg.Crowley,1972; Lebour,1907), there have been no quantitative reports of the effects of infestation on the strength of the adductor muscle. Therefore, I tested the valve closure of mussels in two ways: firstly, by hanging a constant load on one valve and noting when the mussels started to gape; secondly, by steadily increasing the load on one valve until the valves started to open.

The mussels were collected from the level of mean low water neap tides on the river Fowey mussel bed. Prior to testing, the mussels were cleaned of epifauna and kept in aerated seawater. All the mussels had a shell length of 6.5 - 6.7 centimetres. They were all tested within 24 hours of collection. The tests were conducted in the same month (August,1976), because condition of the mussels is seasonally variable, and, therefore, the strength of shell adduction may also undergo seasonal variations.

The resistance of mussels to a constant load was tested by hanging weights totalling 2.55 kg. from one valve while the other valve was held firm. Figure 43 shows a mussel being tested. Copper clips were bonded to the valves with Isopon, a fiber-glass adhesive which dries within one hour of application. Weights were attached by nylon line to one of these clips. A weight of 2.55 kg. was chosen to simulate the pull of a starfish, such as Asterias rubens, which is thought to be capable of opening a mussel by force alone (Burnett, 1961: Hancock,1965,1974). The Asteroidea are reputed to be able to exert a pull on bivalves' shells of between 2 - 5 kg. (Burnett,1961; Feder,1955; Lavoie,1956). A starfish may prise the shells apart so that it can evert its stomach and then insert it between the mussel's valves and externally devour the mussel's tissue. Apparently, a starfish may require a gap of only 0.1 mm before it can insert its highly elastic stomach into a mussel shell (Lavoie,1956). Therefore, a gap of 0.1mm. was regarded as the critical gape of the mussels under test,

Table 5 shows that the gapers suffered from a significantly higher degree of infestation than the non-gapers. This indicates an adverse affect of infestation on the endurance of the shell closure of mussels.

The strength of valve closure was tested by increasing the load on one valve. The increasing load was applied by the Instron Universal Testing Instrument, already described. Figure 44 shows a mussel being tested. The copper clips, which were bonded onto the shell with Isopon, were clasped by two pairs of jaws. One pair of jaws was attached to a moving crosshead which was lowered to exert an increasing load on the valve. The rate of increase of the load was

Figure 43 .

Diagram showing the attachment of a 2.55 kg. weight to one valve of a mussel, which is being tested to see how long it can withstand the load before it gapes 0.1 mm.

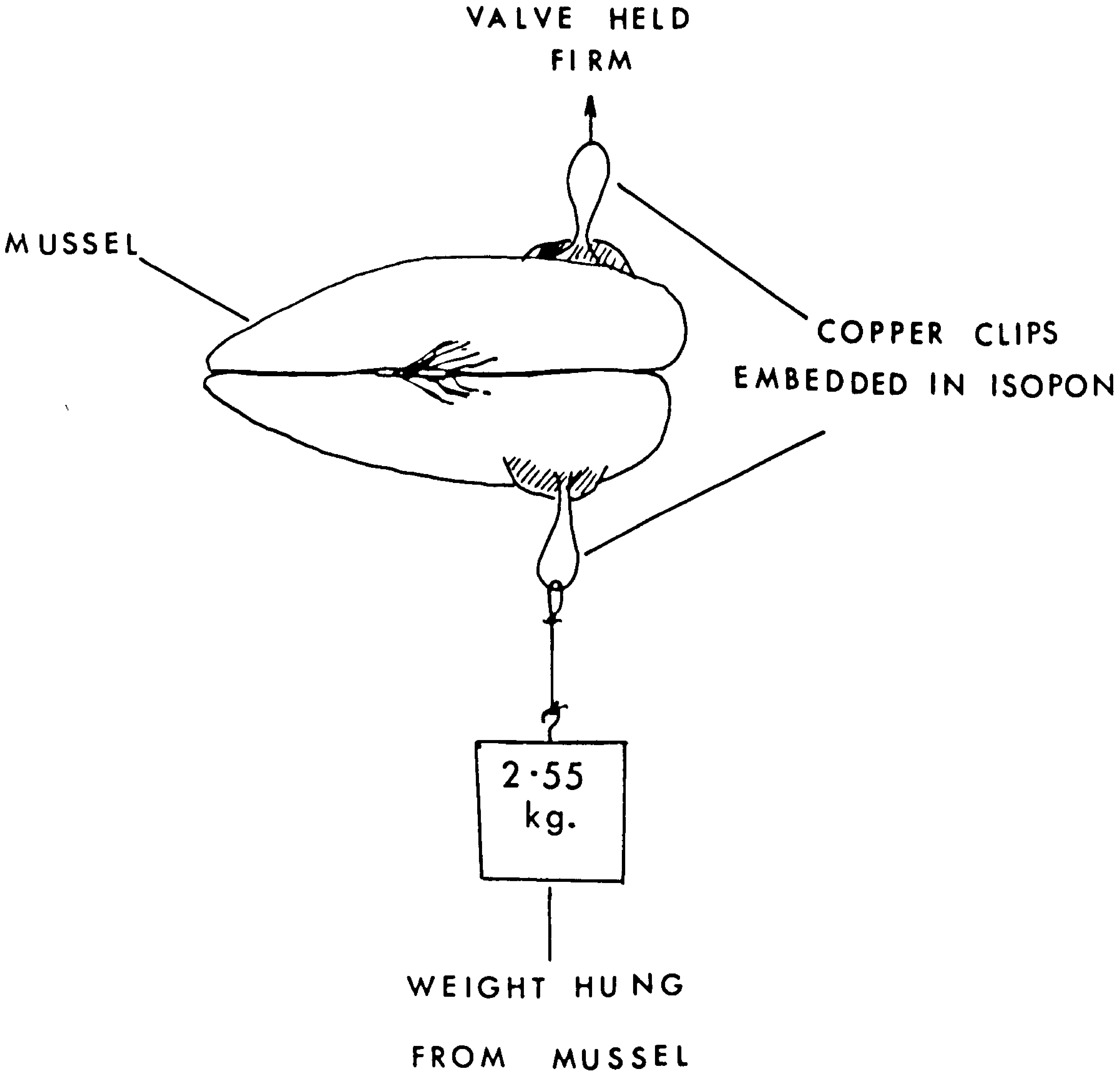

VALVE HELD FIRM
MUSSEL
COPPER CLIPS EMBEDDED IN ISOPON
2·55 kg.
WEIGHT HUNG FROM MUSSEL

Table 5

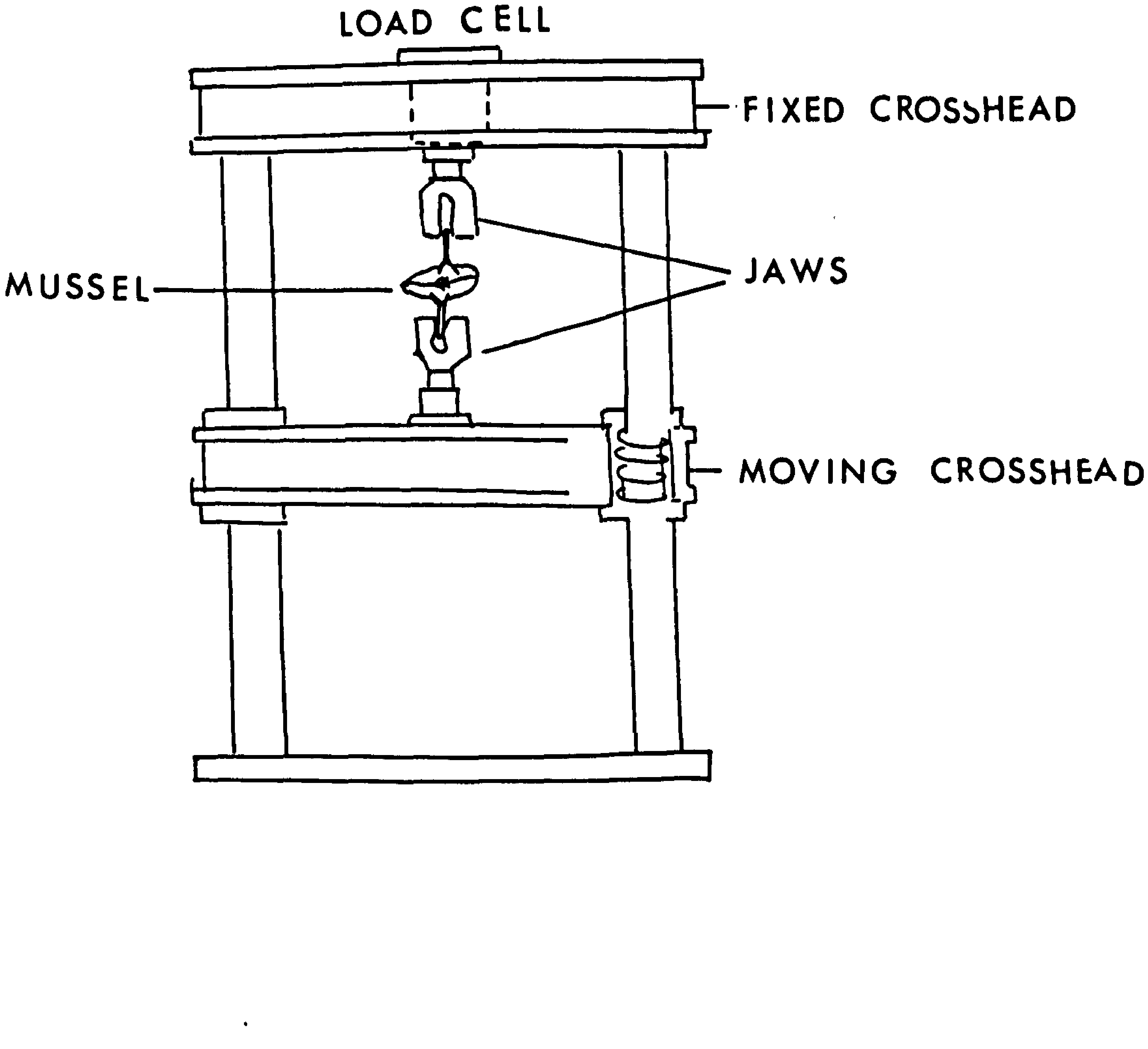
The mussels were grouped into two categories : those which were gaping, and those which were not gaping more than 0.1mm. after having a load of 2.55 kg. hung from one valve. The experiment was undertaken on emersed mussels. All the mussels were between 65 and 70 mm. long. The temperature throughout the experiment was 19°C ± 1°C.

	Mean number of *P. ciliata* per mussel	S.D.	N.
Gaping mussels	48.22	25.96	18
Non-gaping mussels	26.72	27.62	29

$t = 2.65$; $p = \angle 0.05$

Figure 44 .

Diagram of the Instron Universal Testing Instrument, showing the valves of a mussel being pulled apart. The recording apparatus is not shown.


LOAD CELL
FIXED CROSSHEAD
MUSSEL
JAWS
MOVING CROSSHEAD

controlled by the speed of the moving crosshead, which was kept constant at 0.5 cm./sec. The load exerted on the shell was monitored by a chart recorder, and the load at which a 0.5 mm. gape occurred was recorded. (These experiments were done before I became aware of Lavoie's (1956) suggestion that starfish may be able to insert their stomach into a much smaller gap). The degree of infestation of the mussels was analysed. Also, the condition of the posterior adductor muscle was measured, since Hancock (1965) suggested that Danish mussels, which had large posterior adductor muscles, were able to resist starfish predation better than English mussels, which had small adductors. There might therefore be a positive correlation between size and strength of adductor muscles. The condition of the posterior adductor muscle (= dry weight of adductor/between shell volume of mussel X 1000) was used in preference to the diameter of the muscle, since the muscle's dimensions are difficult to measure because of the muscle's elasticity.

The results show that polydorid infestation reduces the strength of valve closure, possibly because of a reduction in the relative size of the adductor muscles. Figure 45 shows that as polydorid infestation increases, the resistance of the valves to increasing loads tends to be reduced. Figure 46 shows a positive correlation between the strength of adduction and size of adductor muscle; while figure 47 shows that as the mussels become more infested, their adductor muscles tend to be reduced in size. The results suggest that this reduction in the size of the adductors, associated with increased polydorid infestation, may be the cause of the weakening of valve closure in heavily infested mussels. However, another possible cause is the mussel's inability to seal off perforations, caused by P. ciliata, in the region of the

Figure 45 .

The relation between polydorid infestation of mussels and the relative strength of valve closure, represented by the pull required to make the shells gape 0.5 mm.

$r = -0{\cdot}462$; $Y = 53.454 - 4.77X$; $p = \angle\, 0.001$

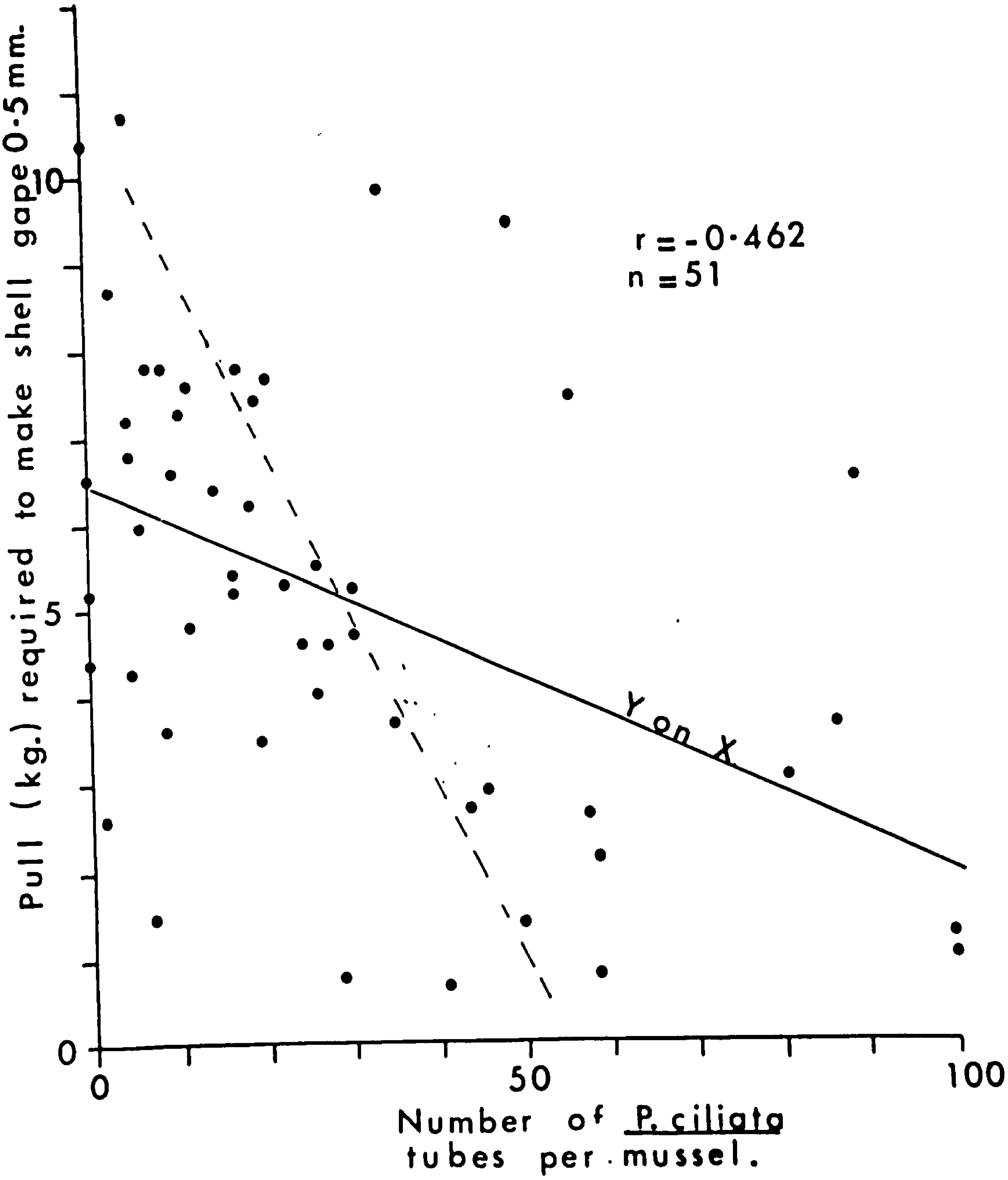

Pull (kg.) required to make shell gape 0·5 mm.
10
5
0
0
50
100
Number of P. ciliata tubes per mussel.
r = -0·462
n = 51
Y on X

Figure 46 .

Relation between condition and strength of the posterior adductor muscles.

$r = 0.426$; $n = 47$; $Y = 6.656 + 0.453X$; $p < 0.001$

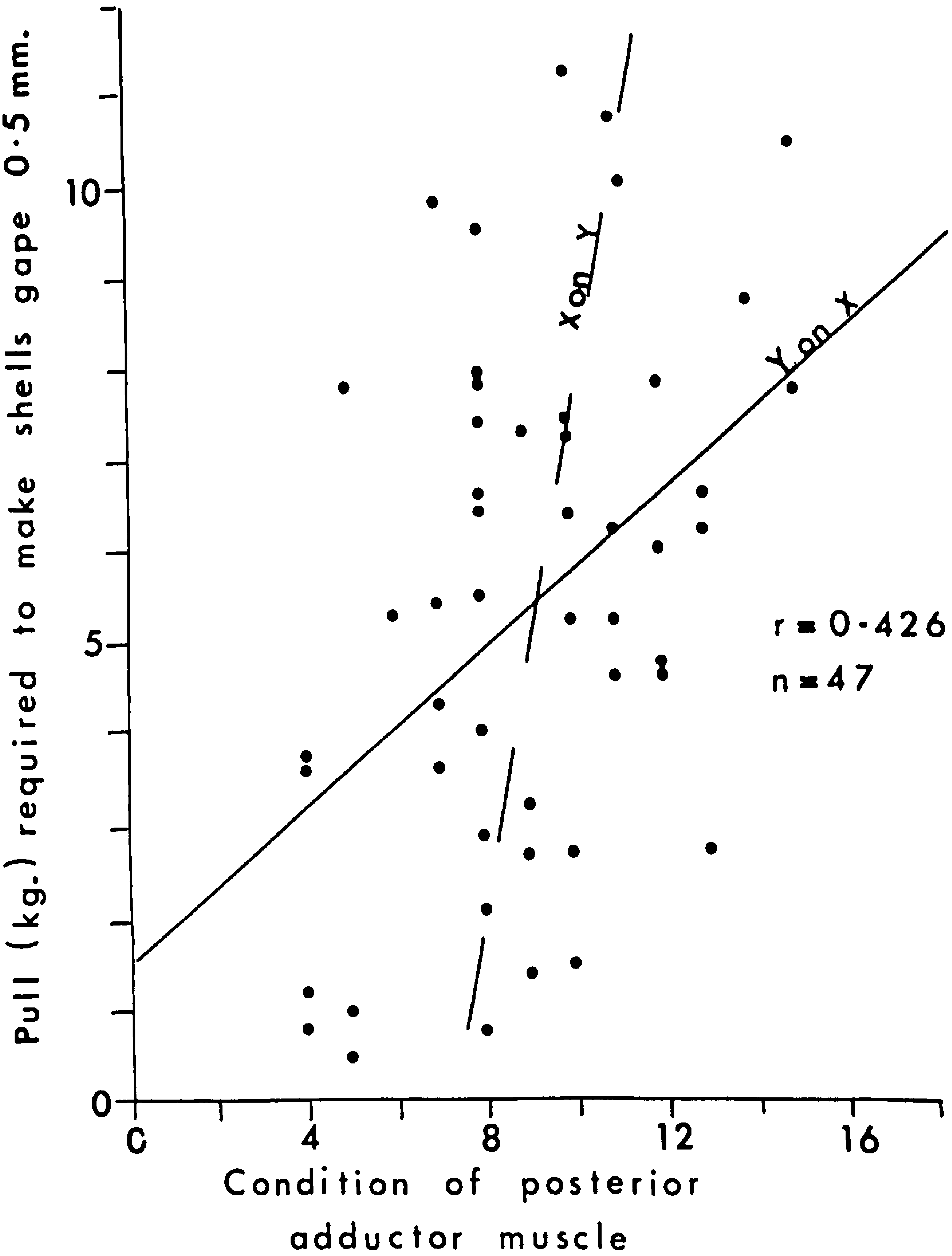
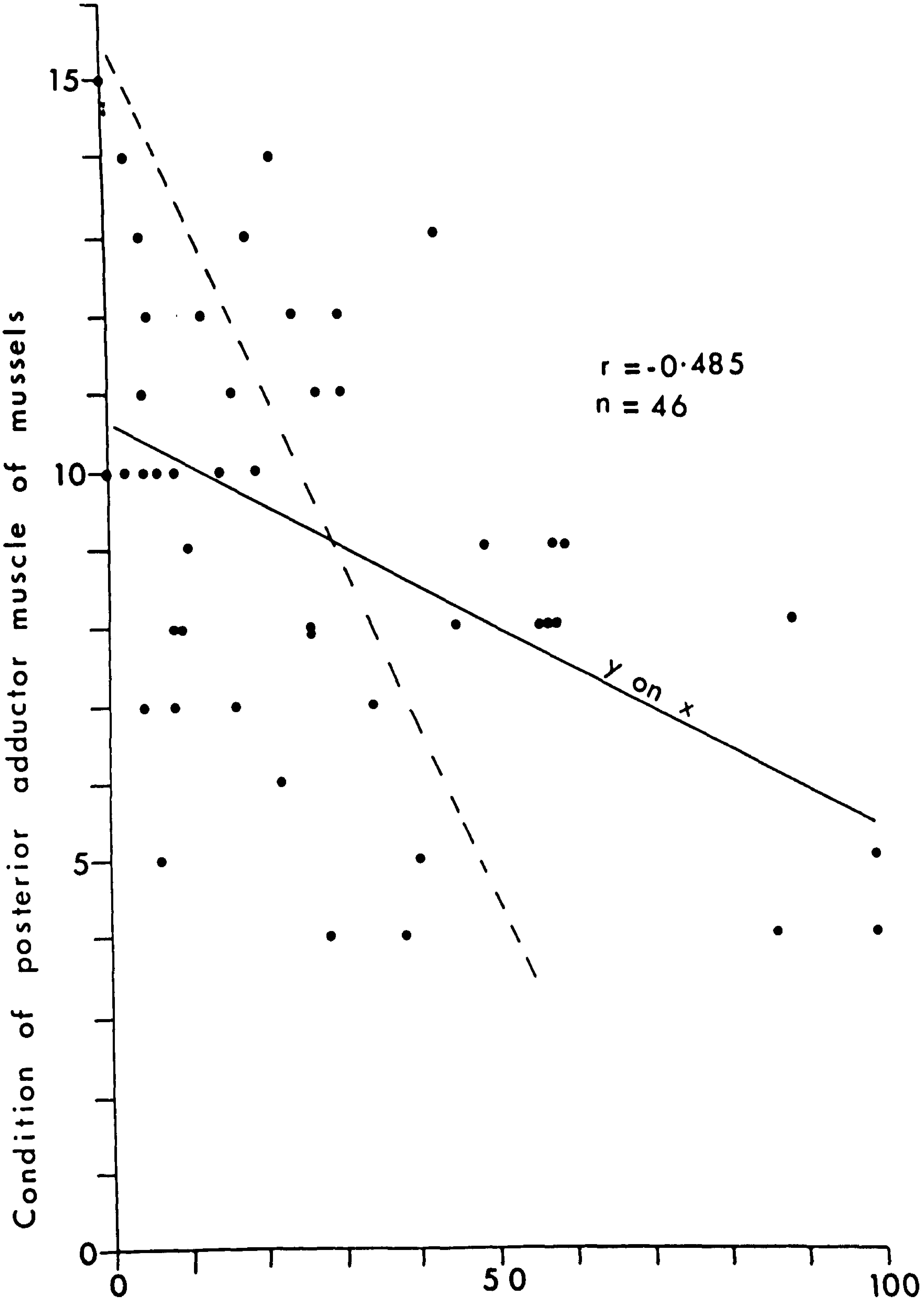

Pull (kg.) required to make shells gape 0·5 mm.
10
5
0
0
4
8
12
16
Condition of posterior adductor muscle
X on Y
Y on X
r = 0·426
n = 47

Figure 47 .

The relationship between polydorid infestation and the condition of the posterior adductor muscle .

$r = -0.485$; $n = 46$; $Y = 10.616 - 0.052X$; $p = \angle 0.001$.


15
10
5
0
0
50
100
Condition of posterior adductor muscle of mussels
Number of P. ciliata tubes per mussel
r = -0·485
n = 46
y on x

adductor muscle; these perforations may weaken the adductor muscle's attachment to the shell, and therefore impair valve closure.

Whatever the cause, heavy polydorid infestation seems to be associated with an impairment of valve closure in mussels, which may increase the mussels' vulnerability to starfish predation, and it may decrease the mussels' tolerance to adverse physicochemical conditions.

THE EFFECT OF POLYDORA CILIATA ON THE ADHESION OF LIMPETS.

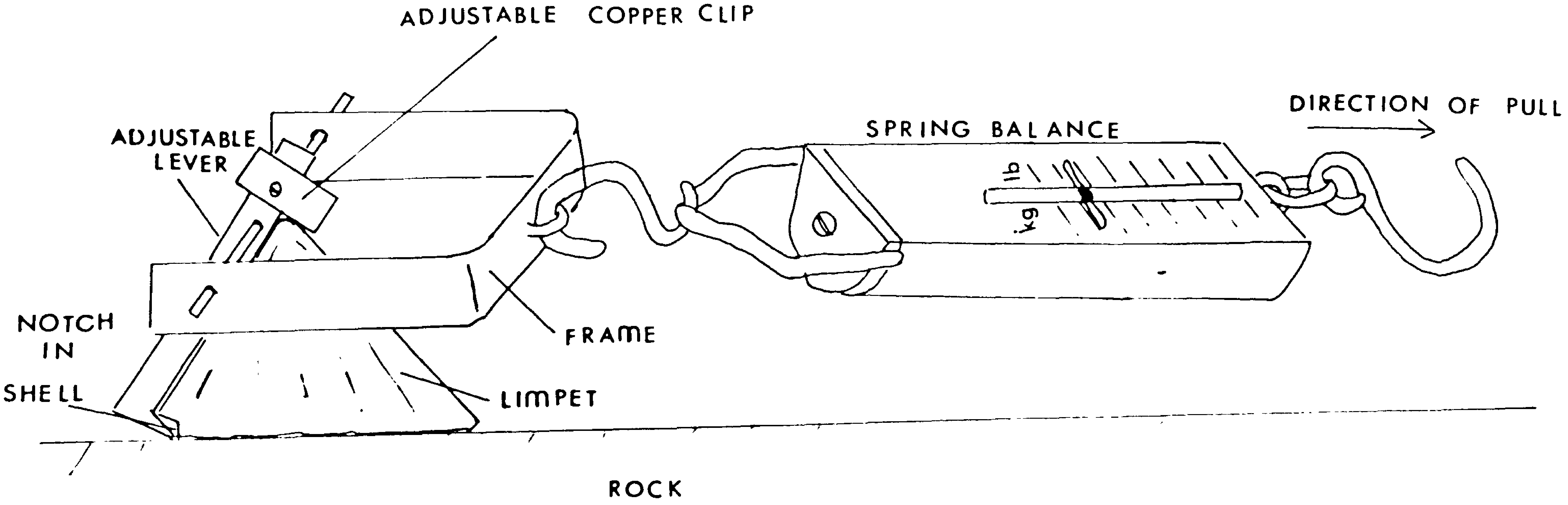
The tenacity with which limpets cling onto rocks is proverbial. The limpets require great powers of adhesion to withstand the physical forces of surf and currents, and to withstand the attempts of predators to dislodge them. Once the limpet is dislodged, the predator can get at its soft tissues which would otherwise be protected by the shell. Limpets also need to cling onto rocks during emersion to avoid being desiccated.

The possibility that polydorid infestation affects the limpet's powers of adhesion, was tested because body-component analyses (see figure 27) indicated that foot condition may be reduced by polydorid infestation, and the foot is generally regarded as being of paramount importance in limpet adhesion (Fretter and Graham,1962; Miller,1974). A number of other workers have measured the tenacity of limpets (Abee, 1931; Aubin,1892; Lawrence-Hamilton,1892; Loppens,1922; Menke,1911; Wells,1917; Woodward,1875), in most cases, with a spring balance. But this is the first report of the effect of P. ciliata on limpet adhesion.

Figure 48 shows the adhesion of a limpet being measured with a simple dynamometer. A notch, measuring 1 cm. wide and 1 mm. high, was cut out of the anterior margin of the limpet shell with a sharp chisel. I pressed the top of the shell firmly onto the substrate while making the notch, so that the limpet was not disturbed. After the notch was made, the dynamometer frame was placed over the shell and the lever pressed against the anterior of the shell, with the sharp protruding edge of the lever inserted into the notch. At no

Figure 48 .

A simple dynamometer used for testing the adhesion of Patella vulgata on rocks. The adjustable copper clip was locked down onto the apex of the shell, to prevent the lever from swinging away from the limpet as the dynamometer was pulled.


ADJUSTABLE COPPER CLIP
ADJUSTABLE LEVER
SPRING BALANCE
DIRECTION OF PULL
lb
kg
NOTCH IN SHELL
FRAME
LIMPET
ROCK

time was the foot directly touched by the dynamometer during the test. The limpet was left for 15 minutes before testing its adhesion. Any shells which had their margins raised above the substrate surface were not tested. The spring balance was pulled parallel to the substrate, so that the direction of the pull was backward on each limpet. The pull was increased steadily at the rate of 1 kg. every 10 seconds until the shearing force removed the limpet from the rock. The limpets were tested, while emersed, within half an hour either side of low water spring tides. They were all on granite rocks at the level of mean low water neap tides on Porthpean beach. All the limpets had a shell length of between 45 and 50 mm.

Figure 49 shows that the adhesion of limpets tended to be reduced by heavy polydorid infestation. The limpets were analysed to see if the poor foot condition of heavily infested limpets could account for their reduced powers of adhesion. But there was no significant ($r= 0.183$; $p \not< 0.05$) linear correlation between limpet adhesion and foot condition. The foot condition is only a relative estimate of foot size. It is possible that limpet adhesion is more dependant on the absolute size of the foot, therefore, foot size was estimated in other ways. Measurements of foot area were found to be inadequate because the foot area of individuals was so variable, and probably depended upon to what extent the blood spaces of the foot were filled. This variability may have been the reason for Menke (1911) finding no clear correlation between foot area and adhesion. The dry weight of the foot was used as the most suitable estimate of foot size.

Figure 50 shows that the limpet adhesion tends to increase

Figure 49 .

The relationship between polydorid infestation and adhesion in limpets. Adhesion is less in the heavily infested limpets.

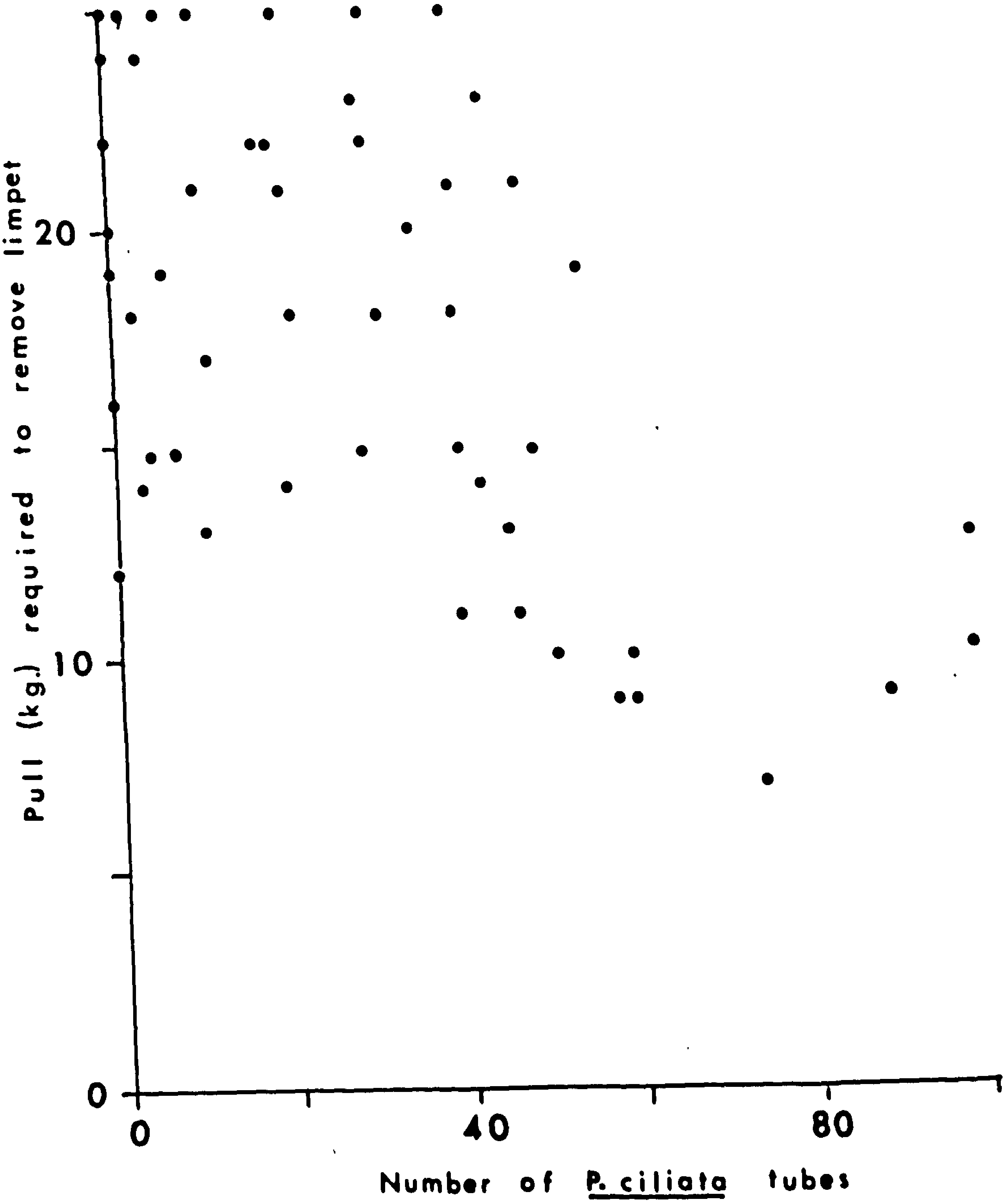
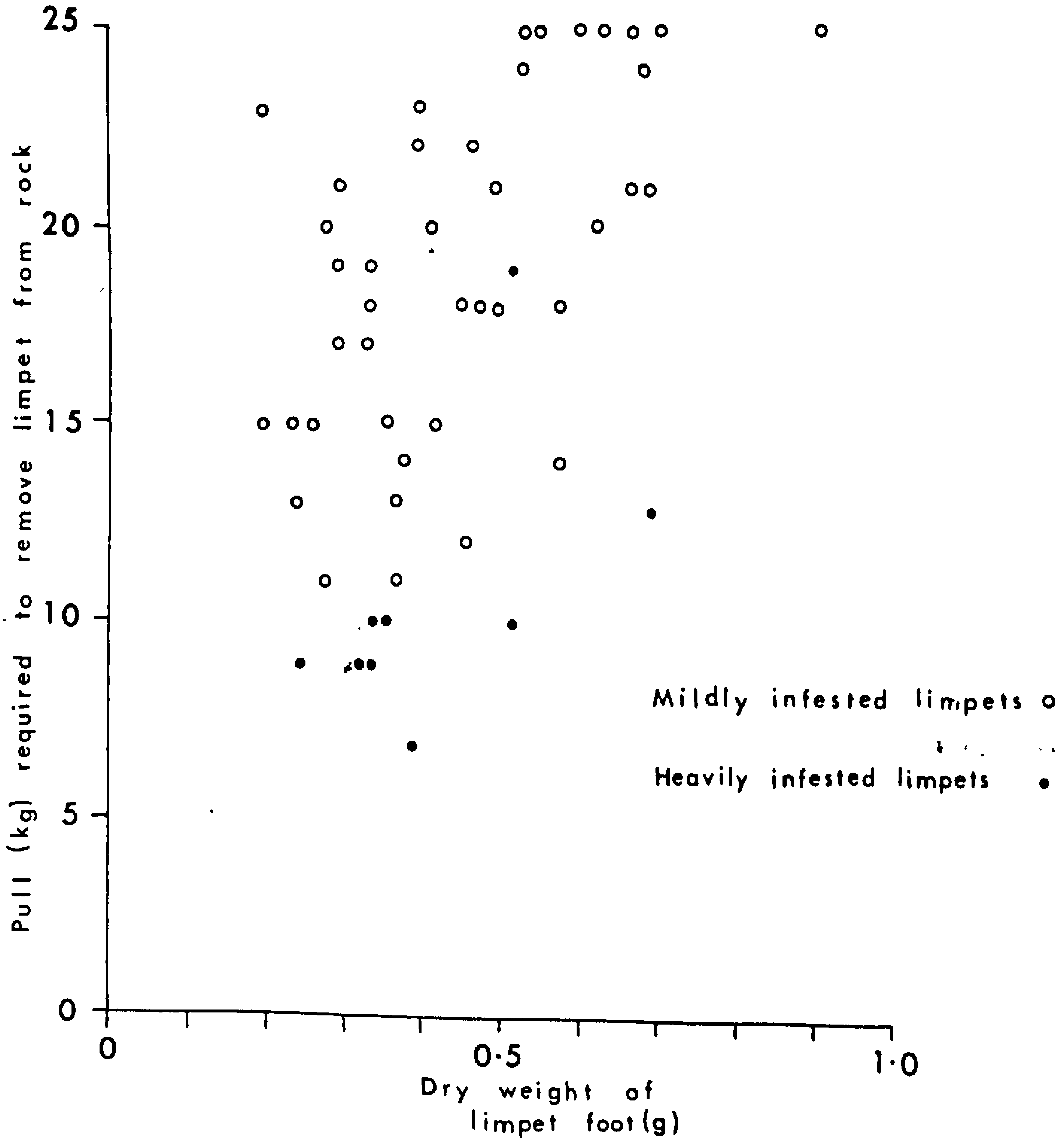

Pull (kg.) required to remove limpet
20
10
0
0
40
80
Number of P. ciliata tubes per limpet

Figure 50 .

The relationship between size of foot and adhesion in limpets. The adhesion seems to increase with an increase in size of foot of both heavily and mildly infested limpets.


25
20
15
10
5
0
Pull (kg) required to remove limpet from rock
0
0·5
1·0
Dry weight of limpet foot (g)
Mildly infested limpets o
Heavily infested limpets •

with an increase in the size of the limpet foot. But table 6 shows thot the adhesion of heavily infested limpets is still lower than that of mildly infested limpets of comparable foot size. Therefore, the smaller size of the foot of heavily infested limpets can not be the only explanation of their reduced powers of adhesion.

Two main theories have been proposed to explain limpet adhesion: the suction theory and the adhesion theory. Woodward (1875) forwarded the suction theory, by which he meant that an actual space forms under the foot, creating a negative pressure as a pull is exerted. This theory was ruled out by Aubin (1892) and Menke (1911) who found that the tenacity of limpets far exceeded the theoretical limits of suction (= 1,031 g/cm^2). Advocates of the adhesion theory, by which is meant the forces holding together two closely applied surfaces with a layer of liquid between them, include Aubin (1892), Davis and Fleure (1903) and Menke (1911). Davis and Fleure (1903) describe the adhesion as "...like that between two smooth pieces of glass brought together. The muscular foot is, so to speak, rolled on the rock with which it is brought into very close contact." It is possible that the mucus glands of the foot actually produce an adhesive (Thomas, 1948).

Both the suction and adhesion theories fail to explain how P. ciliata affects limpet adhesion. Miller (1974), who discussed the adhesion of gastropods in general, suggests that the tenacity is not simply due to passive adhesion, but is an active process which can be greatly enhanced by muscular contractions. She states that the maximum adhesion of most prosobranchs occurs when the individual stops moving and clamps the shell tightly against the substratum by

Table 6 .

The adhesion of limpets with similar foot weights.

Degree of infestation of the limpets	Mean pull required to dislodge the limpets from the rock	S.D.	N
Mild infestation (∠ 50 *P.ciliata*)	17.4 kg.	3.7	12
Heavy infestation (> 50 *P. ciliata*)	9.0 kg.	1.2	5

$t = 4.920$; $p = \angle\, 0.001$

contractions of the columella muscle, and the adhesion to the substrate breaks when the columella muscle has been stretched some distance by a pull on the shell. The limpet has a horseshoe-shaped shell musculature which is ideally placed to pull the shell tightly down onto the substrate (Davis and Fleure, 1903).

Limpet adhesion may also be affected by the conformity of the shell and substrate. The margin of the limpet shell can grow to conform with the exact irregularities of the rock surface. As Fretter and Graham (1962) state, the elliptical edges of the conical shell fit the particular patch of rock so accurately that each ridge is covered by an exactly fitting indentation of the shell. The shell is then able to lock onto the substrate. Table 7 illustrates how effective the locking can be. The limpets tested on the smooth slate were less than 1 metre from those tested on the granite steps at Charlestown Harbour. The harbour is very sheltered and the limpets occurred on north facing rocks, consequently, the limpets did not form scars on the rocks. The granite surface is very irregular and the shells were able to lock onto it, hence the limpets' greater powers of adhesion on granite than on slate.

It would seem that any factor which weakens the shell musculature or disrupts the conformity of the shell margin with the substrate, may reduce the limpets' resistance to a lateral pull. P. ciliata infestation may adversely affect both of these. It may weaken the attachment of the shell musculature to the shell, by inducing the formation of blisters in and around the attachment area. Indeed, some shells of heavily infested limpets were pulled off before the limpets were dislodged from the rocks. Blister formation may also disrupt

Table 7

The effect of rock type on limpet adhesion.

Type of rock	Mean pull required to remove limpet from rock	S.D.
Granite	19.00 kg	4.24
Slate	8.00 kg	2.80

$t = 5.00$; $p = \angle\, 0.05$; degrees of freedom $= 16$

All the limpets were between 4.5 and 5.0 cms. shell length and were all uninfested.

the conformity of the shell margin with the substrate.

It seems that limpet adhesion depends on a number of factors : the ability of the foot to adhere to the substrate, possibly with the aid of mucus secretions; the intensity with which the limpet can pull its shell down onto the substrate, which will depend on the strength of the shell muscle and the security of its attachment to the shell; and the ability to lock the shell onto the substrate surface. Polydora ciliata may affect any of these factors and reduce the limpet's ability to adhere to the substrate.

SECTION IV

GENERAL CONCLUSIONS

GENERAL CONCLUSIONS

In this section I shall make some tentative conclusions concerning the distribution of *P. ciliata*, and how *P. ciliata* affects its hosts, particularly *Mytilus edulis* and *Patella vulgata*.

P. ciliata has an opportunistic life style (Grassle and Grassle, 1974); it can produce vast quantities of larvae which allow it to infest a wide variety of substrates (tables 1 and 2). Despite the relative non-specificity of its choice of substrate, *P. ciliata* does not merely settle passively , but it is able to actively seek out suitable substrates (Daro and Polk,1973; Dorsett,1961b; Kiselva, 1967; Wilson,1928). Table 8 shows some of the characteristics of shores and molluscan substrates which are associated with high levels of *P. ciliata* settlement. But it must be emphasized that the eurytopic nature of *P. ciliata* enables it to infest different substrates in a wide variety of localities, even in areas of low salinity, low oxygen tensions, and heavy organic pollution (Bakker and Pauw,1975; Cognetti, 1972; Percival,1928; Schram ,1968,1970; Wass,1967). *P. ciliata* has a prolonged settlement period, but maximum settlement, at least in British waters, occurs in the late spring. This prolonged settlement period would make it difficult to eradicate the pest from cultivated molluscs; to be effective, removal of polydorids from the molluscs,would have to be an almost continuous process.

Figures 51 and 52 show some of the deleterious effects of heavy infestations of *P. ciliata* on limpets and mussels, at the whole-organism level; it is a matter of conjecture as to how these effects manifest themselves at other levels, such as the population level.

Figure 51

The possible ways in which Polydora ciliata may affect Patella vulgata.

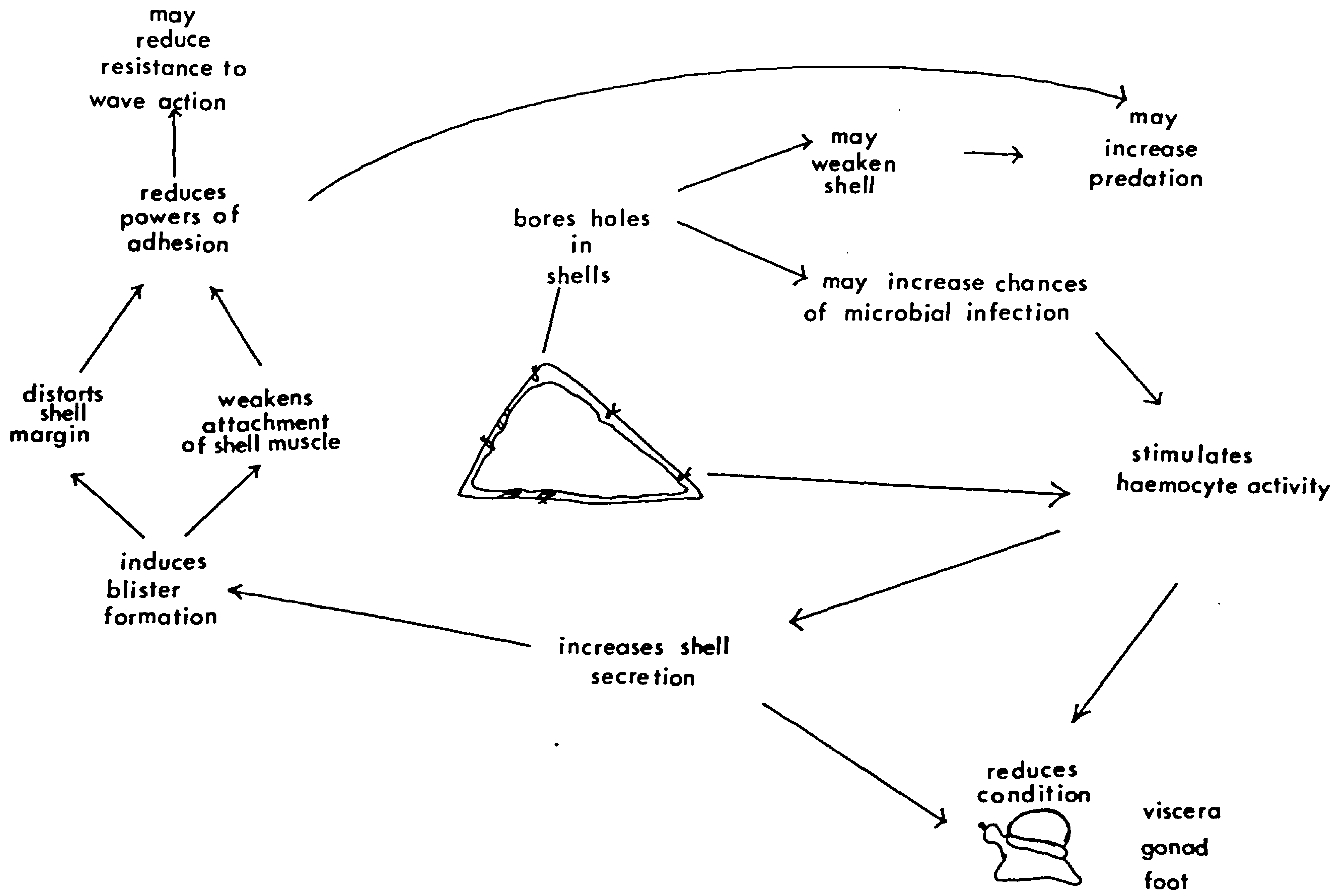

may reduce resistance to wave action
reduces powers of adhesion
distorts shell margin
weakens attachment of shell muscle
induces blister formation
bores holes in shells
may weaken shell
may increase predation
may increase chances of microbial infection
stimulates haemocyte activity
increases shell secretion
reduces condition
viscera
gonad
foot

Figure 52

The possible ways in which Polydora ciliata may affect Mytilus edulis.

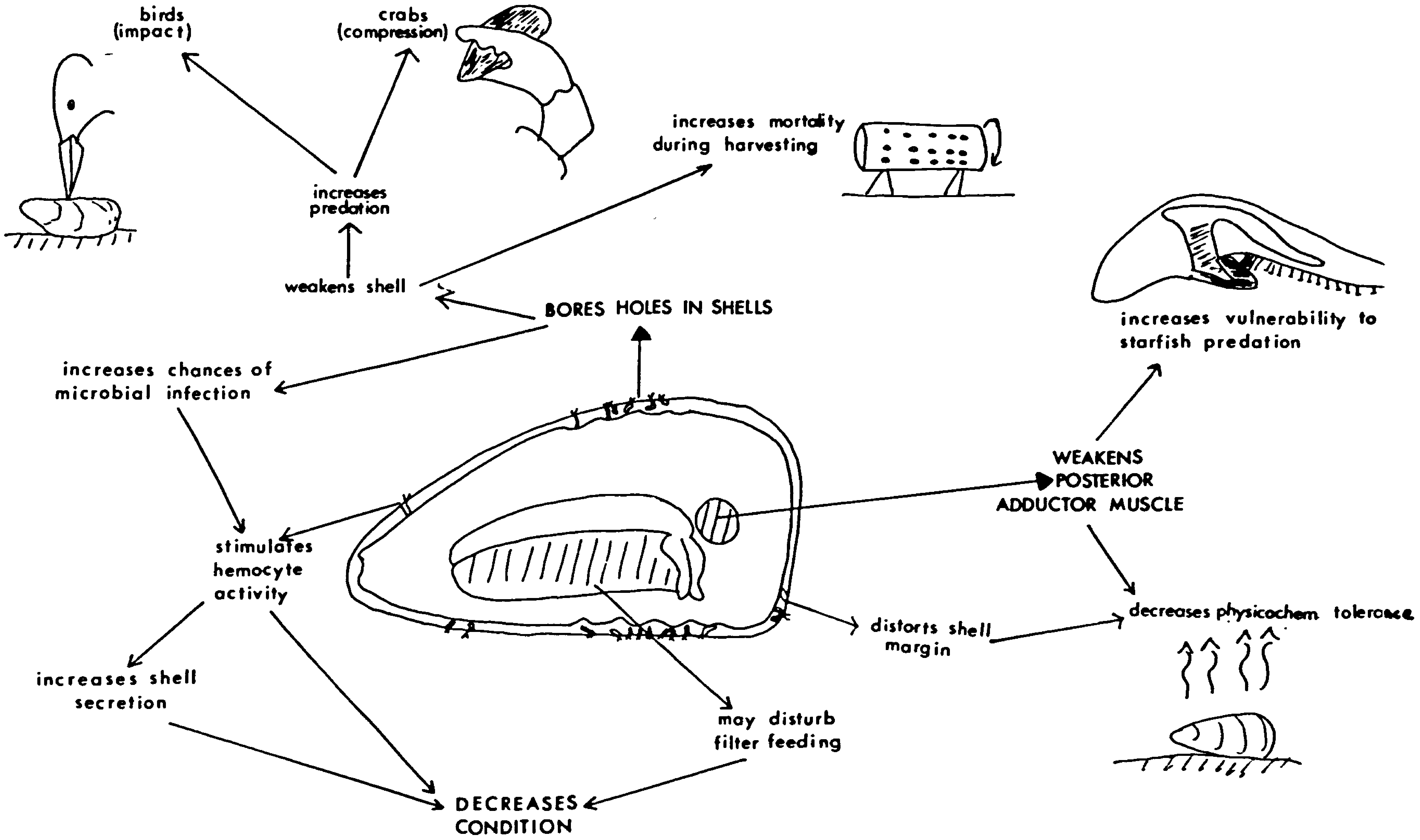

birds
(impact)
crabs
(compression)
increases predation
weakens shell
increases mortality during harvesting
BORES HOLES IN SHELLS
increases chances of microbial infection
increases vulnerability to starfish predation
WEAKENS POSTERIOR ADDUCTOR MUSCLE
stimulates hemocyte activity
increases shell secretion
distorts shell margin
decreases physicochem tolerance
may disturb filter feeding
DECREASES CONDITION

TABLE 8

FACTORS FAVOURING POLYDORA CILIATA SETTLEMENT

SHORE CHARACTERISTICS ASSOCIATED WITH HIGH LEVELS OF *POLYDORA CILIATA* SETTLEMENT	REFERENCES
Low tidal level	Present study
Shelter against wave action	Present study
Water rich in organic material	Schram ,1968,1970.

MOLLUSCAN CHARACTERISTICS ASSOCIATED WITH HIGH LEVELS OF *POLYDORA CILIATA* SETTLEMENT	REFERENCES
Large shells	Present study
Cracks and crevices in shells	Daro and Polk,1973; Orrhage,1969; Wilson, 1928.
Shells living on sediment surface	Present study; Hempel, 1957.
Bacterial film on shells	Bourget and Lacroix, 1973; Daro and Polk, 1973.
Presence of *P. ciliata* adults on the shells	Present study; Blake, 1969b; Kiselva,1967.

It must be emphasized that these figures are partly speculative. For instance, no tests were made on the relationship between polydorid infestation and vulnerability to predation of limpets; this relationship is expected to occur as a consequence of an established relationship; that is, between polydorid infestation and adhesion of limpets. Predators, such as birds and crabs, get at the limpet's tissue by knocking the shells off the rock or by cracking the shells open. Since polydorid infestation is associated with reduced powers of adhesion, it seems reasonable to conjecture that heavily infested limpets will be more easily knocked off the rocks by predators. Also, since infestation weakens mussel shells, it seems likely that it will weaken limpet shells and make them more vulnerable to predators which crack the shells open.

A few words of explanation are necessary concerning the possible adverse effects of P. ciliata on the physico-chemical tolerance of mussels and limpets. Limpets tightly clamp their shells to rocks during adverse environmental conditions, to protect their tissues; while mussels close their valves in response to adverse conditions (Davenport,1977). Therefore, the impairment of limpet adhesion and valve closure of mussels, associated with heavy polydorid infestation, may reduce the tolerance of these molluscs to adverse physico-chemical conditions.

A number of the factors in figures 51 and 52 are linked with the haemocyte activity of the molluscs. Haemocyte activity probably plays a central role in the response of molluscs to polydorid infestation. Narain (1973) described the many different types of molluscan haemocytes. Their classification seems to be confused, but it is clear that haemocytes are multifunctional, and one of their main roles is in shell secretion. They are probably also important in the molluscs' defence against invading foreign bodies, such as microbes (Cheng, 1967).

It is interesting to speculate about the possible effects of P. ciliata on commercial molluscs, specially since much of the future cultivation of molluscs, particularly M. edulis, will be in sublittoral areas where the risk of polydorid infestation is high. Table 9 shows the possible ways in which P. ciliata may reduce the commercial value of molluscs. Whether or not P. ciliata infestation will warrant control measures, will depend on each individual situation. It is likely that, because P. ciliata tends to settle on molluscs in areas conducive to the molluscs' growth, and because P. ciliata is so difficult to eradicate, only very high degrees of infestaion will provoke control measures.

TABLE 9

WAYS IN WHICH <u>P. CILIATA</u> MAY REDUCE THE COMMERCIAL VALUE OF MOLLUSCS .

Increased mortality due to :

a) Increased predation;

b) Increased shell fracture during harvesting;

c) Reduction of physicochemical tolerance.

Reduction of meat content.

Production of unsightly blisters (a particular disadvantage in the oyster half-shell trade).

Accumulation of malodorous sediment.

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APPENDIX

The statistical analyses of mussels (Mytilus edulis) from the river Fowey, and limpets (Patella vulgata) from Porthpean Beach.

ANALYSIS OF LIMPETS FROM PORTHPEAN BEACH

(1) WHOLE LIMPET CONDITION

	Mildly infested limpets			Heavily infested limpets				
DATE	MEAN	S.D.	N	MEAN	S.D.	N	't'	p
1974								
October	117.10	15.51	30	100.10	17.58	10	2.90	0.050
November	75.68	20.75	31	65.43	16.99	7	1.25	0.100
December	96.00	20.58	19	79.00	19.82	23	2.72	0.010
1975								
January	88.13	12.11	12	70.23	11.31	14	3.89	0.001
February	79.30	15.21	27	61.31	8.79	13	3.94	0.001
March	100.54	17.28	26	89.50	24.63	8	1.46	0.100
April	103.38	23.14	21	86.17	22.61	12	2.07	0.050
May	108.93	22.13	20	88.11	23.64	20	2.87	0.010
June	117.18	17.99	17	90.75	11.62	12	4.46	0.001
July	123.23	20.89	24	104.10	12.46	15	3.21	0.010
August	125.80	21.94	25	109.00	9.81	7	1.95	0.100
September	117.43	14.04	35	94.26	19.40	23	5.28	0.001
October	101.86	17.69	29	75.82	15.15	11	4.31	0.001
November	98.82	15.46	28	84.35	11.95	16	3.23	0.010
December	103.11	13.92	27	75.33	15.29	12	5.58	0.001

ANALYSIS OF LIMPETS FROM PORTHPEAN BEACH

(2) FOOT CONDITION

	Mildly infested limpets			Heavily infested limpets				
DATE	MEAN	S.D.	N	MEAN	S.D.	N	't'	P
1974								
October	63.83	7.16	30	53.80	6.46	10	3.93	0.001
November	37.81	9.39	31	31.00	5.35	7	1.84	0.100
December	52.79	13.27	19	50.26	12.71	23	0.63	0.100
1975								
January	47.00	7.27	12	35.71	6.72	14	4.11	0.001
February	44.63	9.53	27	36.31	6.02	13	2.88	0.010
March	51.27	10.18	26	46.00	12.76	8	1.21	0.100
April	58.38	11.91	21	47.25	12.56	12	2.53	0.020
May	62.09	8.92	20	50.22	9.36	20	4.10	0.001
June	65.82	14.33	17	50.75	12.65	12	2.92	0.010
July	70.00	11.90	24	56.90	10.99	15	4.14	0.001
August	74.32	11.20	25	60.71	7.39	7	3.02	0.010
September	56.23	8.21	35	43.39	9.67	23	4.58	0.001
October	44.21	7.74	29	34.63	6.34	11	3.65	0.001
November	37.36	4.48	28	35.25	5.82	16	1.34	0.100
December	43.11	7.10	27	33.50	6.67	12	3.97	0.001

ANALYSIS OF LIMPETS FROM PORTHPEAN BEACH

(3) VISCERAL CONDITION

	Mildly infested limpets			Heavily infested limpets				
DATE	MEAN	S.D.	N	MEAN	S.D.	N	't'	p
1974								
October	38.90	6.19	30	36.30	6.70	10	1.127	0.100
November	24.71	7.49	31	21.57	7.46	7	1.001	0.100
December	26.10	7.78	19	19.30	5.31	23	3.354	0.010
1975								
January	24.00	3.67	12	18.00	4.96	14	4.961	0.001
February	31.44.	6.37	27	25.00	4.93	13	4.932	0.001
March	46.35	12.42	26	43.50	14.59	8	0.544	0.100
April	42.81	12.78	21	38.92	12.30	12	0.853	0.100
May	46.84	10.12	20	37.84	11.24	20	2.660	0.020
June	48.47	8.48	17	39.00	4.61	12	3.511	0.010
July	49.20	11.98	24	43.10	12.02	15	1.545	0.100
August	49.16	12.76	25	47.28	5.15	7	0.376	0.100
September	44.20	7.05	35	35.26	6.91	23	4.760	0.001
October	35.72	7.63	29	29.91	8.00	11	2.124	0.050
November	26.11	4.39	28	24.25	6.89	16	1.093	0.100
December	37.96	6.49	27	27.08	5.11	12	5.107	0.001

ANALYSIS OF LIMPETS FROM PORTHPEAN BEACH

(4) GONAD CONDITION

	Mildly infested limpets			Heavily infested limpets				
DATE	MEAN	S.D.	N	MEAN	S.D.	N	't'	P
1974								
October	14.30	6.64	30	10.40	6.52	10	1.61	0.100
November	13.32	8.07	31	12.71	7.61	7	0.18	0.100
December	16.68	11.02	19	9.39	5.60	23	2.77	0.010
1975								
January	17.17	8.35	12	16.14	10.76	14	0.26	0.100
February	3.26	9.23	27	0	0	13	1.27	0.100
March	2.54	7.38	26	0	0	8	0.96	0.100
April	1.71	5.45	21	0	0	12	1.08	0.100
May	0	0	20	0	0	20	-	-
June	2.88	6.83	17	1.00	3.48	12	0.85	0.100
July	2,78	7.40	24	0.98	2.93	15	0.90	0.100
August	2.32	3.41	25	1.00	2.645	7	0.94	0.100
September	16.92	6.58	35	13.65	6.28	23	1.91	0.100
October	21.59	9.98	29	11.09	6.41	11	3.23	0.001
November	14.00	4.77	28	10.50	4.12	16	2.46	0.020
December	21.89	5.67	27	14.83	7.06	12	3.33	0.010

ANALYSIS OF LIMPETS FROM PORTHPEAN

(5) Percent FOOT

	Mildly infested limpets			Heavily infested limpets				
DATE	MEAN	S.D.	N	MEAN	S.D.	N	't'	p
1974 October	47.74	2.05	30	47.43	1.92	10	0.419	0.100
November	45.52	3.96	31	44.51	5.33	7	0.573	0.100
December	48.09	5.68	19	53.02	3.13	23	3.564	0.001
1975 January	46.97	4.51	12	45.57	5.55	14	0.70	0.100
February	48.83	4.59	27	50.45	3.19	13	1.14	0.100
March	45.68	4.06	26	45.88	4.66	8	0.96	0.100
April	49.46	2.94	21	47.69	2.99	12	1.66	0.100
May	49.00	3.67	20	49.11	3.35	20	-0.10	0.100
June	48.49	5.71	17	48.05	3.00	12	0.24	0.100
July	49.45	3.25	24	48.10	4.55	15	1.08	0.100
August	50.52	3.15	25	48.30	1.94	7	1.76	0.100
September	43.94	9.17	35	43.97	2.58	23	0.03	0.100
October	41.31	3.86	29	42.73	2.87	11	1.10	0.100
November	43.82	2.82	28	45.33	2.74	16	1.73	0.100
December	40.35	2.64	27	42.04	2.91	12	1.79	0.100

Mean and standard deviations (S.D.) are arcsin tranformations.

ANALYSIS OF LIMPETS FROM PORTHPEAN BEACH

(6) Percent VISCERA.

	Mildly infested limpets			Heavily infested limpets				
DATE	MEAN	S.D.	N	MEAN	S.D.	N	't'	P
1974 October	35.20	2.00	30	37.00	1.56	10	2.39	0.050
November	35.12	2.79	31	44.51	5.33	7	0.57	0.100
December	31.31	3.55	19	29.22	3.84	23	1.97	0.100
1975 January	31.42	2.71	12	30.85	4.56	14	0.68	0.100
February	39.23	4.00	27	39.55	3.19	13	0.25	0.100
March	43.77	5.66	26	44.12	4.67	8	0.16	0.100
April	40.28	3.02	21	42.32	3.01	11	1.87	0.100
May	40.03	3.45	20	40.89	3.41	20	0.81	0.100
June	40.16	2.87	17	40.95	3.10	12	0.70	0.100
July	40.20	3.20	24	39.32	4.87	15	0.68	0.100
August	38.11	3.18	25	41.21	2.37	7	2.39	0.050
September	37.82	2.35	35	32.84	2.53	23	0.01	0.100
October	36.55	2.74	29	38.84	3.47	11	2.20	0.050
November	35.34	2.32	28	35.68	2.49	16	0.44	0.100
December	37.35	2.42	27	37.08	3.95	12	0.26	0.100

The means and standard deviations (S.D.) are arcsin transformations.

ANALYSIS OF LIMPETS FROM PORTHPEAN BEACH

(7) Percent GONAD.

	Mildly infested limpets			Heavily infested limpets				
DATE	MEAN	S.D.	N	MEAN	S.D.	N	't'	p
1974								
October	19.95	4.04	30	17.95	4.65	10	0.62	0.100
November	23.55	5.48	31	24.16	8.16	7	0.24	0.100
December	23.58	6.97	19	19.46	4.59	23	2.30	0.050
1975								
January	25.56	6.65	12	27.18	11.52	14	0.43	0.100
February	4.08	10.34	27	0	0	13	1.42	0.100
March	3.12	8.94	26	0	0	8	0.98	0.100
April	2.21	6.98	21	0	0	12	1.55	0.100
May	0	0	20	0	0	20	-	-
June	4.23	7.50	17	1.69	9.03	17	0.81	0.100
July	3.58	8.39	24	2.20	4.98	15	0.58	0.100
August	5.23	7.27	25	2.03	5.37	7	1.08	0.100
September	21.97	3.69	35	21.74	4.32	23	0.22	0.100
October	26.64	5.54	29	21.82	5.75	11	2.44	0.050
November	25.12	3.29	28	22.46	4.13	16	2.35	0.050

The means and standard deviations (S.D.) are arcsin transformations.

ANALYSIS OF MUSSELS FROM THE RIVER FOWEY

(1) DRY-WEIGHT CONDITION INDEX

	MILDLY INFESTED MUSSELS			HEAVILY INFESTED MUSSELS				
DATE	MEAN	S.D.	N	MEAN	S.D.	N.	't'	p
1974								
October	112.31;	24.70;	32.	60.60;	20.09;	10.	6.01	0.001.
November	87.91;	25.35;	22.	63.56;	19.12;	16.	3.23	0.01
December	84.16;	21.97;	25;	62.87;	30.12;	16.	2.62	0.01
1975								
January	72.56;	28.63;	17.	54.04;	26.52;	17.	1.96	0.10
February	60.67;	24.06;	24.	50.06;	12.35;	16.	1.62	0.10
March	57.39;	20.42;	19.	49.85;	13.33;	13.	1.17	0.10
April	52.13;	12.79;	24.	43.76;	14.99;	17.	1.92	0.10
May	79.33;	26.29;	15.	60.76;	12.69;	17.	2.59	0.02
June	74.57;	17.01;	23.	63.80;	17.44;	15.	1.89	0.10
July	90.04;	24.06;	20.	70.17;	25.17;	20.	2.55	0.02
August	107.33;	21.73;	12.	72.21;	31.25;	14.	3.27	0.01
September	115.87;	26.99;	16.	94.71;	35.42;	21.	1.99	0.10
October	92.21;	20.88;	19.	76.38;	22.92;	21.	2.27	0.05
November	104.68;	34.86;	34.	75.92;	28.69;	13.	2.64	0.02
December	129.20;	30.92;	20.	90.07;	26.17;	14.	3.86	0.001

ANALYSIS OF MUSSELS FROM THE RIVER FOWEY

(2) PERCENT MANTLE

	Mildly infested mussels			Heavily infested mussels				
DATE	MEAN	S.D.	N	MEAN	S.D.	N	't'	p
1974								
October	42.61	4.46	32.	39.15	4.69	10.	2.12	0.05
November	41.43	3.07	22	38.83	3.07	16	2.58	0.02
December	43.82	7.76	25	40.15	7.81	16	1.47	0.10
1975								
January	39.37	3.97	17	38.64	4.33	17	0.51	0.10
February	37.59	5.65	24	37.12	4.04	16	0.28	0.10
March	36.32	3.36	19	33.20	4.46	13	2.26	0.02
April	31.46	4.84	24	30.43	3.87	17	0.72	0.10
May	36.53	5.06	15	36.06	5.62	17	0.24	0.10
June	37.52	4.04	23	37.51	2.60	15	0.01	0.10
July	38.60	2.35	20	39.79	4.51	20	1.05	0.10
August	42.53	4.58	12	41.09	4.96	14	0.76	0.10
September	40.75	4.29	16	40.67	5.45	21	1.03	0.10
October	41.56	4.88	19	38.48	3.46	21	2.32	0.05
November	40.94	5.71	34	36.14	5.63	13	2.59	0.02
December	43.80	2,84	20	39.12	5.14	14	3.41	0.01

The analysis is based on arcsin transformations of the percentages; only the transformations are included in the table.

ANALYSIS OF MUSSELS FROM THE RIVER FOWEY

NON-MANTLE CONDITION INDEX

	Mildly infested mussels			Heavily infested mussels				
DATE	MEAN	S.D.	N	MEAN	S.D.	N	't'	p
1974								
October	59.94	11.57	32	36.50	13.19	10	5.41	0.001
November	48.73	12.19	22	37.87	9.52	16	2.95	0.020
December	13.31	13.31	25	35.81	17.89	16	1.47	0.100
1975								
January	43.36	11.32	17	32.59	9.00	17	3.07	0.010
February	36.83	10.79	24	31.75	8.48	16	1.58	0.100
March	39.18	9.59	19	33.30	8.84	13	1.76	0.100
April	37.25	7.54	24	32.06	9.69	17	1.92	0.100
May	49.47	10.16	15	39.59	8.68	17	2.96	0.010
June	46.96	11.87	23	40.40	11.04	15	1.71	0.100
July	44.85	11.64	20	41.47	10.67	20	0.96	0.100
August	57.32	9.11	12	39.79	15.96	14	3.36	0.010
September	65.13	10.93	16	54.05	17.61	21	2.21	0.100
October	50.84	8.32	19	46.14	12.07	21	1.42	0.100
November	57.12	16.26	34	48.54	17.66	13	1.58	0.100
December	64.05	14.39	20	52.57	12.74	14	2.40	0.050

ANALYSIS OF MUSSELS FROM THE RIVER FOWEY

MANTLE CONDITION INDEX

	Mildly infested mussels			Heavily infested mussels				
DATE	MEAN	S.D.	N	MEAN	S.D.	N	't'	p
1974								
October	52.38	17.04	32	24.10	3.38	10	5.06	0.001
November	39.18	15.20	22	25.69	10.14	16	3.07	0.010
December	41.16	17.87	25	27.06	15.49	16	2.59	0.020
1975								
January	29.20	16.34	17	21.45	10.43	17	1.66	0.100
February	23.83	14.87	24	18.31	5.72	16	1.41	0.100
March	18.21	7.78	19	16.56	8.49	13	0.57	0.100
April	14.88	6.53	24	11.70	6.12	17	1.57	0.100
May	29.87	18.43	15	21.18	7.40	17	1.79	0.100
June	27.61	6.21	23	23.40	6.40	15	2.02	0.100
July	35.19	16.02	20	28.70	19.44	20	1.15	0.100
August	50.00	16.66	12	32.43	18.27	14	2.54	0.020
September	50.75	18.59	16	40.67	20.14	21	1.56	0.100
October	41.37	15.02	19	30.24	12.05	21	2.60	0.020
November	47.56	21.53	34	27.38	14.14	13	3.12	0.010
December	65.15	20.98	20	37.50	16.58	14	4.11	0.001

ANALYSIS OF MUSSELS FROM THE RIVER FOWEY

PERCENT WATER

DATE	Mildly infested mussels MEAN	S.D.	N	Heavily infested mussels MEAN	S.D.	N	't'	P
1974 October	63.19	2.40	32	67.47	3.37	10	4.45	0.001
November	64.12	1.99	22	65.46	2.36	16	1.86	0.100
December	62.97	2.98	25	64.05	4.19	16	0.96	0.100
1975 January	65.78	3.60	17	65.10	2.60	17	0.62	0.100
February	70.11	3.23	24	69.39	2.85	16	0.72	0.100
March	69.79	1.87	19	69.88	1.32	13	0.15	0.100
April	69.35	1.68	24	70.80	2.41	17	2.80	0.010
May	66.85	2.24	15	68.58	1.99	17	2.30	0.050
June	66.356	1.41	23	67.74	1.78	15	2.66	0.020
July	67.26	1.42	20	68.74	1.58	20	3.11	0.001
August	65.64	2.21	12	68.48	3.00	14	2.70	0.020
September	61.98	2.10	16	64.65	4.07	21	2.39	0.050
October	63.44	2.15	19	65.46	2.67	21	2.61	0.020
November	65.46	3.54	34	68.98	3.12	17	3.11	0.010
December	64.94	2.21	20	67.76	4.13	14	2.59	0.050

/ The means and standard deviations are arcsin [illegible] transformations of the percentages.