THE ECOLOGY OF *PATELLA*.

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INTRODUCTION

Marine biological research in South Africa is divisible into three historical phases. Initial work was completed largely by visiting or overseas scientists, and was principally of a taxonomic nature. Early research centred around exploration of the fishing banks. It was only in the 1930's that Prof. T.A. Stephenson launched an extensive analysis of the distribution of intertidal marine animals and plants. This work has since been expanded and refined, largely under the direction of Prof. J.H. Day of the University of Cape Town, to include estuaries, sandy beaches and benthic fauna. Other institutes have subsequently taken up facets of this work. This fundamental research has laid an invaluable foundation, and we now have a sound knowledge of our marine faunal distribution. The exhaustive work of Dr. K.H. Barnard is basic to our present taxonomic knowledge.

What is needed now is a detailed ecological analysis of individual species so that these distribution patterns can be explained in terms of biological and physical factors. In particular, quantitative work is required to serve as a baseline for further work, and to monitor the effects of environmental changes. Work of this nature has been completed on some commercial species, principally by the Department of Sea Fisheries. Work on the sandy beach gastropod Bullia has been undertaken by Prof. A.C. Brown and on various decapods by Dr. B. Hill and Dr. A. Heydorn. Apart from these examples, work has tended to be fragmentary, or concerned only with certain facets of a species biology. The intertidal rocky shore fauna has been surprisingly neglected.

In many ways the genus Patella is ideal for such a study, constituting the major intertidal herbivorous group and having considerable influence on algal growth. The genus includes eleven South African species, up to ten of which may be coexistent on one shore. This raises interesting problems of competition, coexistence, and species diversity. Some of these species have a restricted distribution, and all are differentially zoned on the shore and make ideal comparitive material. Comparison of congeneric species obviates many of the problems encountered when dealing with different genera.

The scope of "ecology" is enormous, and as the ecologist A. MacFadyen eloquently writes: ".....It must be admitted that the ecologist is something of a chartered libertine. He roams at will over the legitimate preserves of the plant and animal biologist, the taxonomist, the physiologist, the behavourist, the meteorologist, the geologist, the physicist, the chemist and even the sociologist and he poaches from these and other established and respected disciplines. It is indeed a major problem for the ecologist, in his own interests, to set bounds on his divagations." [Animal Ecology : Aims and Methods, 1957].

The present thesis is aimed principally at the population dynamics and biological interactions of Patella species. Most of the work is based on all eleven of the South African species, although volume of work necessitated the omission of the less common species from parts of the work. The research has been centred around the juveniles and adults, although it is realised that larval biology is logically the next field which needs to be explored.

The thesis is presented as a series of separate papers, the first in published form and the remainder in manuscript, and is concluded by a resume. A single supporting paper is also included. The entire thesis is based on original work by the candidate, except where acknowledged in the text. The more important conclusions are summarised at the end of each section.

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ACKNOWLEDGEMENTS:

Many people have helped with facets of this work, and are acknowledged under the relevant sections. There are however two people to whom more general acknowledgement is due. The constant assistance and encouragement of my wife Margo have been a great pleasure. She has acted as scribe in the field, and her company has removed the tedium from routine recordings. She has also conserved my sanity by helping with the monotonous task of stencilling the labels on many illustrations.

Considerable thanks are also due to my supervisor, Prof. J.H. Day, whose constructive criticisms of my text is very much appreciated. My thanks to him extend beyond the bounds of this thesis, for his continual advice and interest throughout my career.

Financial aid towards the cost of travel and equipment has been received from the University of Cape Town.

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SECTION I:

ZONATION, MOVEMENTS AND FEEDING.

THE ECOLOGY OF *PATELLA* LINNAEUS FROM THE CAPE PENINSULA, SOUTH AFRICA

I. ZONATION, MOVEMENTS AND FEEDING

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INTRODUCTION

The genus *Patella* comprises intertidal and infratidal animals, which are important not only because of their relative abundance on most shores, but because of the marked effect they may have on the ecology of these shores. Despite this, little is known about their detailed ecology in South Africa. The present paper is an introduction to their ecology: principally their zonation, relative movements and feeding habits. The paper includes information drawn from various sources, particularly from the unpublished projects of Mr. D. Pollock on the feeding habits of limpets, and of Mr. R. Day on the behaviour of *Patella compressa* Linn. Information drawn directly from these projects is acknowledged in the text.

The South African coast is particularly well endowed with members of the family Patellidae. Koch (1949) has reviewed the genus *Patella* Linn., and recognises eleven species: *P. argenvillei* Krauss, *P. barbara* Linn., *P. cochlear* Born., *P. compressa* Linn., *P. granatina* Linn., *P. granularis* Linn., *P. longicosta* Lamarck, *P. miniata* Born., *P. oculus* Born., *P. tabularis* Krauss, and *P. variabilis* Krauss. In addition there are three species of *Helcion* Montfort and two of *Cellana* H. Adams, and two acmaeids (Barnard 1963).

This contrasts with other coasts, for example Britain with three species of *Patella* (Evans 1947, Das and Sesheppa 1948 and Lewis 1964) and New Zealand with two species of *Cellana* (Morton and Miller 1968). The coast of America is lacking in Patellidae, but their niche is filled by 17 species of *Acmaea* (Acmaeidae) (Test 1945).

All members of the genus *Patella* are slow-moving browsing animals, which feed on algae, lichens and diatoms. They are predominantly intertidal or infratidal, and are zoned fairly rigidly both vertically and geographically. Thus overlap between the habitats of the different species is relatively restricted.

Most of the species occupy fixed positions on the shore. The individuals become so established in one position that they form well defined scars on the substrate. From these they undertake feeding excursions, returning to their own particular "home scar" subsequently. This habit has long been noted by previous workers (Morgan 1894, Russell 1907, Orton 1946 and Beckett 1968) but little is known about the factors controlling this behaviour. In different species of limpet the habit is developed to variable degrees: in some, no scar is formed at all, while in others the animal orientates itself exactly with the scar.

Most of our knowledge of the distribution of South African limpets is due to the classical series of papers on intertidal ecology by Stephenson and his co-workers (Stephenson 1936, 1939, 1944, 1947). This knowledge has been extended by a series of surveys conducted by the University of Cape Town Zoology Department, from Jangamo in Moçambique to Luderitz in South West Africa. Many of the distribution records discussed in the text are drawn from this source, and are cited below as U.C.T. records.

The distribution of limpets around the South African coast is summarised in Figure 1.

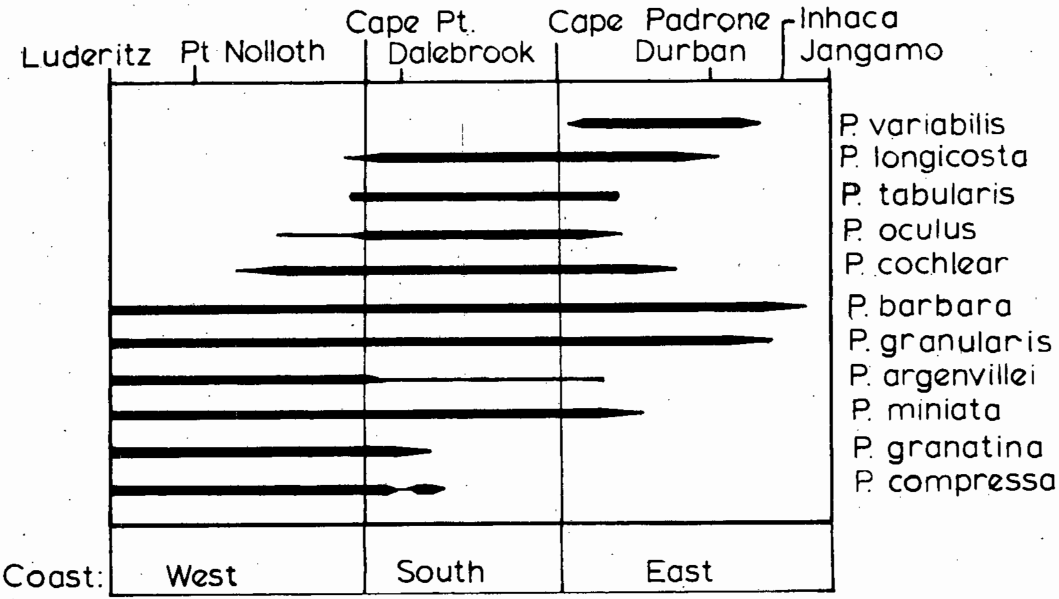

FIGURE 1A
Distribution of *Patella* spp. around the coast of southern Africa.

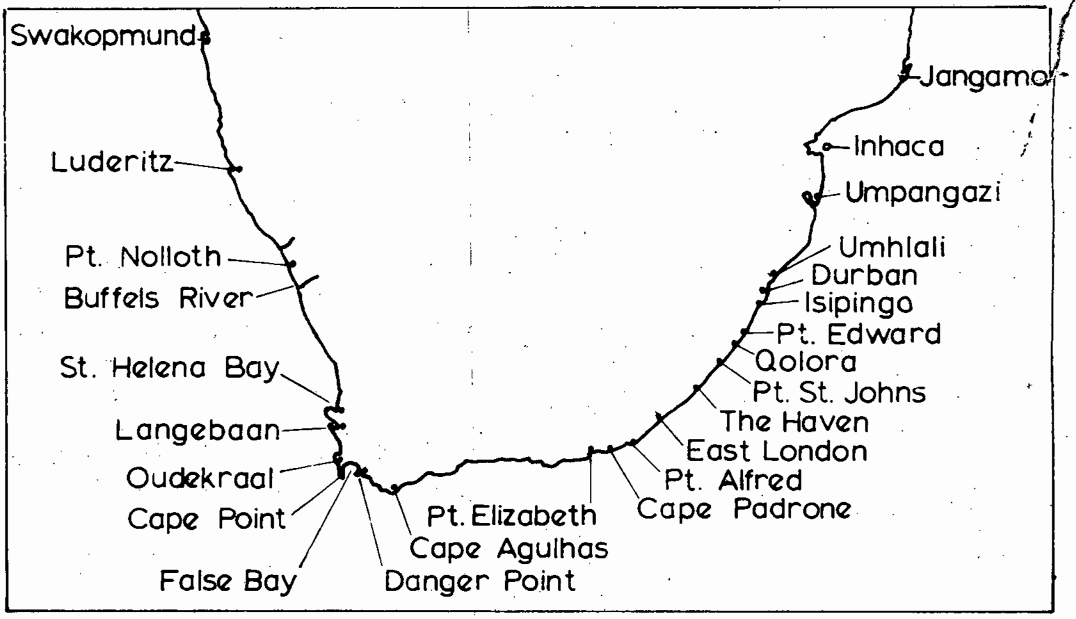

FIGURE 1B
Localities in southern Africa referred to in the text.

Stephenson (1939) has shown that some species occur throughout the area, while others are limited to the cold west coast or the warmer south and east coasts. In several cases where the species extend around the entire coast-line, individuals from the west coast are markedly larger than those from the warmer coasts.

The biology of British limpets, particularly *P. vulgata* L., has been analysed fairly extensively by various authors (Orton 1928a, 1928b, 1929, 1946; Moore 1934; Evans 1947, 1953; Das and Sesheppa 1948; and Lewis 1954). Test (1945) and Shotwell (1950) have both described the zonation and feeding habits of *Acmaea* from the Pacific Coast of N. America.

By contrast, almost nothing has been published on the biology of South African limpets. Allanson (1958) has dealt with the ecology of the genus *Siphonaria*, and shown how three of the species, *S. capensis* Quoy and Gaimard, *S. deflexa* (Hebling), and *S. aspersa* Krauss, are zoned intertidally according to their tolerance to salinity, temperature and desiccation. Cohen (1948 unpublished) has analysed the breeding season of *P. granatina*, *P. oculus*, *P. granularis* and *P. cochlear*, and shown that they breed between March and May.

Various commensal relationships exist between *Patella* and other animals. *Notoplana patellarum* (Stimpson) is commonly found under the shells of *P. oculus*, but is also associated to a less marked degree with *P. barbara*, *P. longicosta*, *P. cochlear*, *P. granatina*, *P. argenvillei* and *P. granularis*.

The amphipod *Calliopiella michaelseni* Schell occurs between the foot and mantle of all species of *Patella*, and its colour varies according to the colour of the limpet.

Dynamenella australis Rich., an isopod, is associated mainly with *P. argenvillei*, but also occurs under *P. cochlear* and occasionally *P. barbara*, and is apparently confined to the Cochlear zone of colder water. In addition, *P. argenvillei* frequently harbours large numbers of small unidentified copepods.

It is hoped that the relationship between these animals and *Patella* will be described in a future paper.

The present work is restricted to those species of *Patella* which occur in the Cape Peninsula. This geographical limitation excludes only one South African species, *P. variabilis*, which occurs only as far south as Cape Padrone (Fig. 1).

MATERIAL AND METHODS

The vertical zonation of the different species was examined at the following places: Hangklip, Strandfontein, Muizenberg, Dalebrook, Seaforth, Oatland Point, Miller's Point, Buffels Bay, Camps Bay and Sea Point (Fig. 2). In each case a line transect was taken from spring high tide to spring low tide, and to a depth of 15 feet, using the method described by Day (1969). These transects include zonation and relative abundance of *Patella* spp., and the relative distribution of foodplants. The transects of Dalebrook and Camps Bay are generally representative of the zonation on warm and cold shores respectively (Figs. 3 and 4). General observations were also made at various other sites.

Gut contents were examined from at least ten individuals of each species. Particles present were generally fragmentary and often unidentifiable due to the rasping of the radula and subsequent digestion. Comparison with macerations of whole algae proved

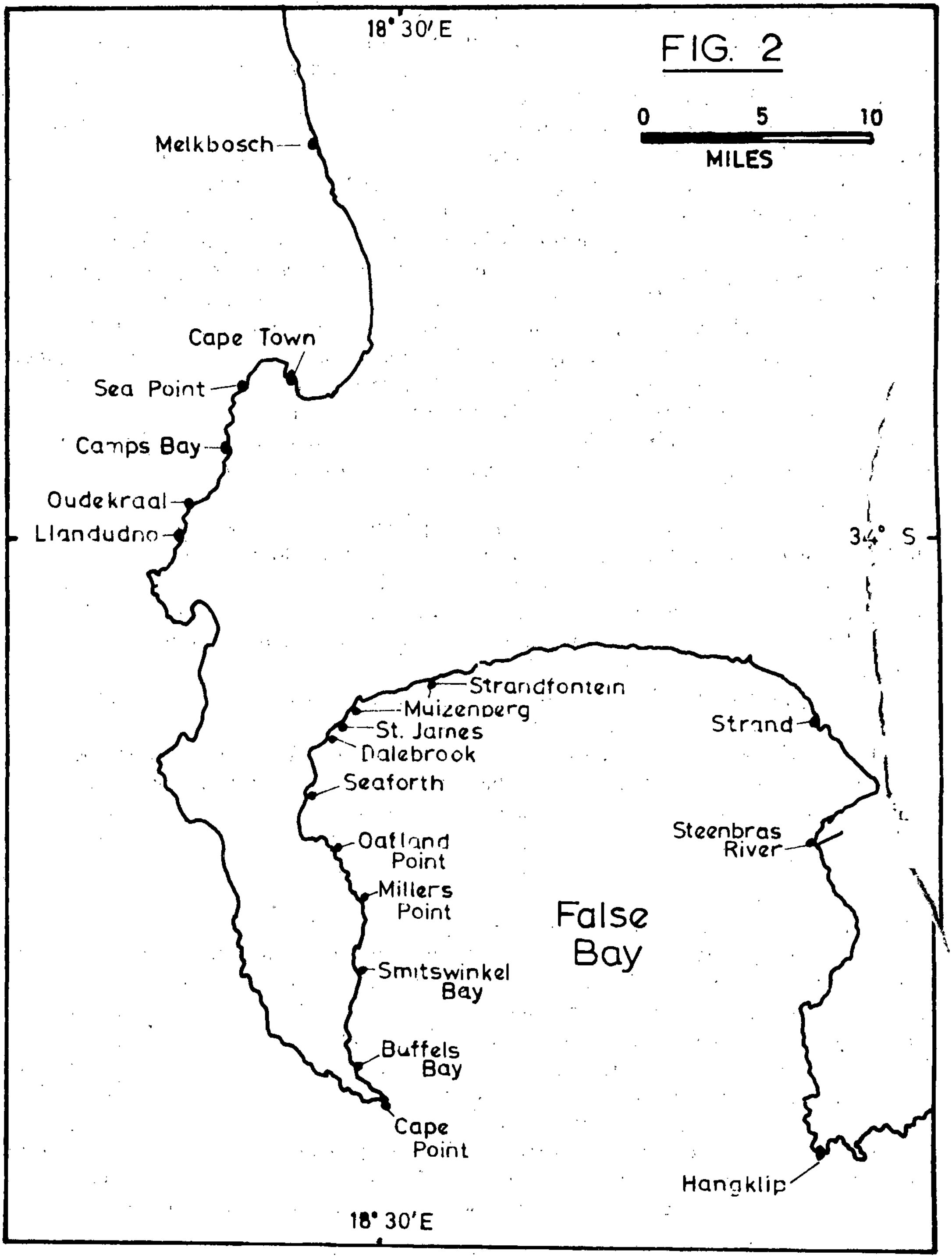

FIGURE 2
Map of the Cape Peninsula, showing areas surveyed and referred to in the text.

FIG. 3

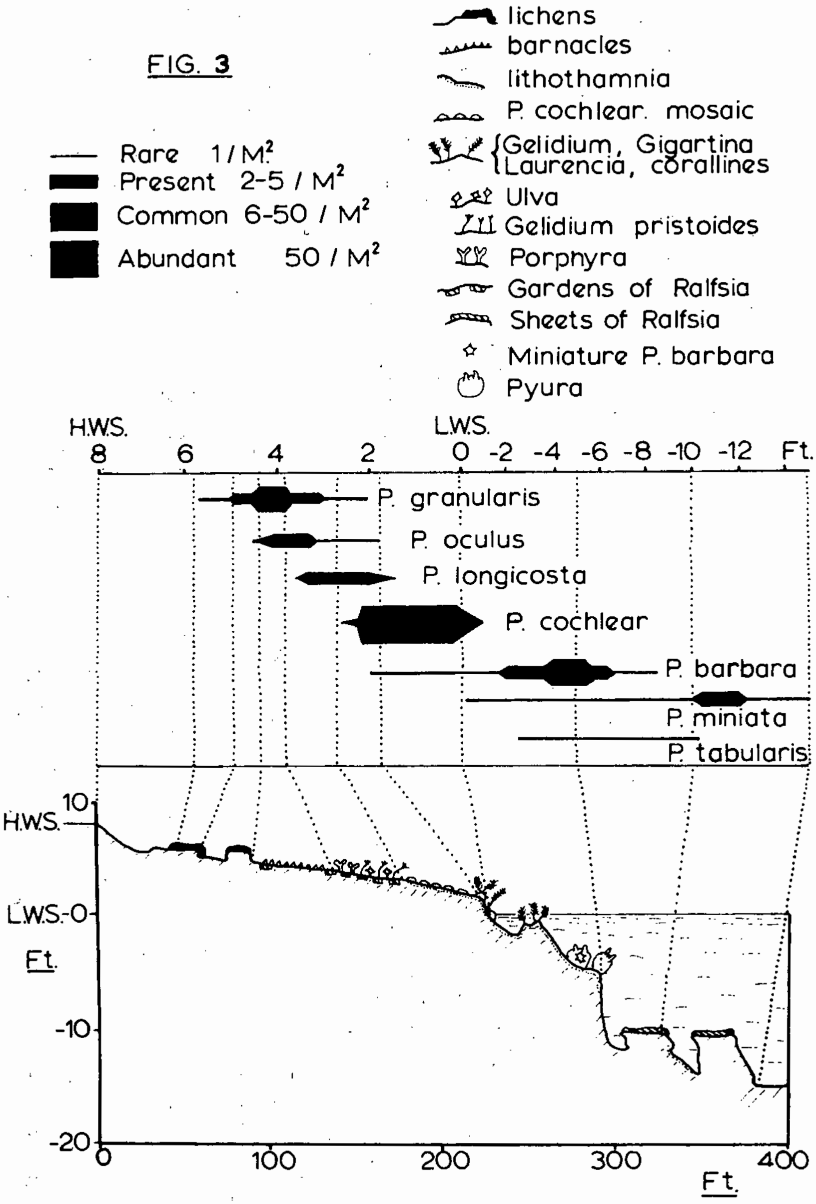

FIGURE 3

Transect at Dalebrook, False Bay, showing zonation of *Patella* spp. typical of warm coasts. Abbreviations of species: Gelidium: *G. pristoides*; Gigartina: *G. stiriata*; Laurencia: *L. glomerata*; Porphyra: *P. capensis*; Ralfsia: *R. expansa*; Pyura: *P. stolonifera.*

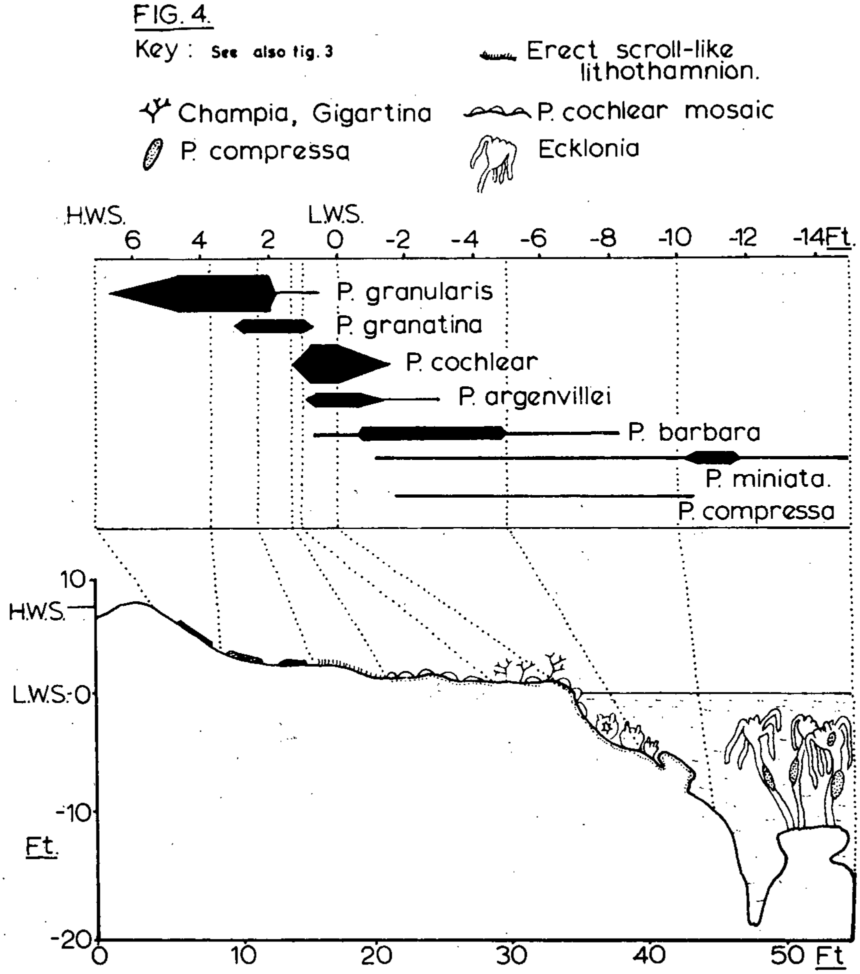

FIGURE 4

Transect at Camps Bay, showing zonation of *Patella* spp. as typically found on the southern parts of the West Coast. Abbreviations of species: Champia: *C. lumbricalis*; Gigartina: *G. stiriata*; Ecklonia: *E. maxima*.

the most accurate method of identification. In a few cases the colour of the gut contents could be correlated with the colour of a dominant food plant, but such diagnoses must be regarded with caution due to the digestion of pigments. The encrusting Corallines, referred collectively to as lithothamnia in this paper, form an important part of the diet in several species, and constitute a white amorphous mass in the gut. This is often identifiable only by its effervescent reaction with hydrochloric acid.

Most of the experimental work described below was conducted on the shore at Dalebrook. Movement of animals was recorded photographically. In addition, nail varnish was used to mark individual animals. Skin diving proved a useful tool in the observation of submerged animals.

Measurements of the shell were taken along the longitudinal axis (L) transversely across the widest point (W) and vertically to give the maximum height (H). The "relative height ratio" referred to in the text is taken as $\frac{H}{L+W}$. All differences between populations were statistically analysed using the students t test.

ZONATION FEEDING AND MOVEMENT

P. granularis

This species is probably the most widespread as regards vertical and horizontal distribution. It is recorded around the entire South African coast, from Rocky Point, S.W.A. (Penrith and Kensley 1970) to Umpangazi (U.C.T. records). Stephenson (1939) has shown that there is a marked increase in the size of the animals on the west coast. This effect is probably due to temperature differences between the different coasts, but in addition the Benguella current which wells up off the west coast is richly loaded with organic matter. Moore (1958) has described how *P. vulgata* thrives in water with a high organic content, and this may explain the greater size of *P. granularis* on the west coast.

P. granularis extends from the upper Balanoid zone, fringing on the Littorina zone, to the Cochlear zone. As *P. cochlear* is limited to rocks covered with lithothamnion, while *P. granularis* never occurs on lithothamnion, the two species meet but do not overlap. Most individuals of *P. granularis* occur in the upper Balanoid and the numbers decrease progressively down the shore to the Cochlear zone where only scattered individuals are found. No specimens are found infratidally.

Stephenson (1936) records *P. granularis* feeding at low water during the night, and making excursions from the scar, to which the return route may or may not follow the outward route. In fact feeding movements occur both during the day and at night; and at high and low water. Very little movement occurs if the rocks are hot or dry, but even spray from wave action is adequate to initiate movement. Feeding movements are thus more extensive lower down the shore. On the west coast – particularly the northern west coast – the mornings are often misty and the rocks damp. *P. granularis* feeds and moves actively at this time (J. H. Day, *pers. comm.*). This pattern of movements is similar to that of *P. vulgata* (Orton 1929).

In the higher regions of the shore the animals have fixed home scars and return to these after feeding forays. Orientation to the scar is so exact that the shell becomes moulded to the rock. In the lower Balanoid and Cochlear zones many individuals lack a fixed scar and movement is far more random. When the rock is dry, large numbers accumulate in crevices, climbing on top of one another. This explains the lack of algae on the backs of most individuals, relative to other *Patella* species. After wetting, these animals roam extensively across the rock, and although tending to return to the same place subsequently, do not settle in exactly the same position.

The difference of behaviour between individuals from high and low areas on the shore is in keeping with the degree of desiccation each group will experience.

Even at night, movement occurs far more at low levels, which indicates that relative humidity is probably the factor initiating and curtailing movement, and not temperature alone.

Orton (1928b) has shown that the shell shape of *P. vulgata* varies with degree of exposure, and that those individuals higher up the shore have proportionally higher shells. This is true also of *P. granularis*, although to a lesser degree. (Table 1.)

TABLE 1

AVERAGE DIMENSIONS OF 20 INDIVIDUALS OF *P. granularis*, RESPECTIVELY FROM LOW AND HIGH POPULATIONS, CAMPS BAY

	Height (H.) mm	*Length (L.) mm*	*Width (W.) mm*	$\frac{H}{W+L}$	*Significance of Difference of means. Probability, p.*
Low level ..	9·7	34·9	25·2	·152	significant. p=0·05
High level ..	10·3	32·3	25·3	·173	

Orton suggests that high level individuals of *P. vulgata* are exposed to a greater degree of desiccation and tend to maintain a more contracted posture while exposed. Thus the shell will be secreted in the form of a more acute cone on the contracted body. As Davies (1969) has pointed out, shells which are proportionally higher will have a relatively smaller open circumference, hence presenting a smaller surface area of tissue from which evaporation may occur.

In *P. granularis* those individuals from low levels have their shells eroded by various organisms. This effect, aided by the greater wave action sustained at lower levels, explains why these individuals have proportionally lower shells, as the apex will be the first part of the shell eroded away.

The diet of *P. granularis* is varied. The majority of those which occur in the Upper Balanoid inhabit almost bare rock, which is covered only by black lichen. Here they may feed only on this lichen and any particulate matter deposited on the rocks. The gut contents of these animals consist of an unidentifiable black paste, consistent with the black lichen present. Individuals from the lower Balanoid eat any available prostrate or creeping algae in addition to this lichen, and particles of *Porphyra capensis* Kütz., *Ulva* sp. and *Gelidium* sp. have been identified in the gut.

P. oculus

P. oculus occurs throughout the Balanoid zone, although predominantly in the lower Balanoid. It is abundant along the entire south coast, its numbers decreasing towards East London, and its range ceasing at The Haven on the east coast. On the west coast it occurs as far as St. Helena Bay, but its numbers are limited on this coast and it is usually common only in sheltered bays such as Langebaan where local warming of the water occurs.

The home scars consist of marked impressions on the rock, but the rock is not eroded

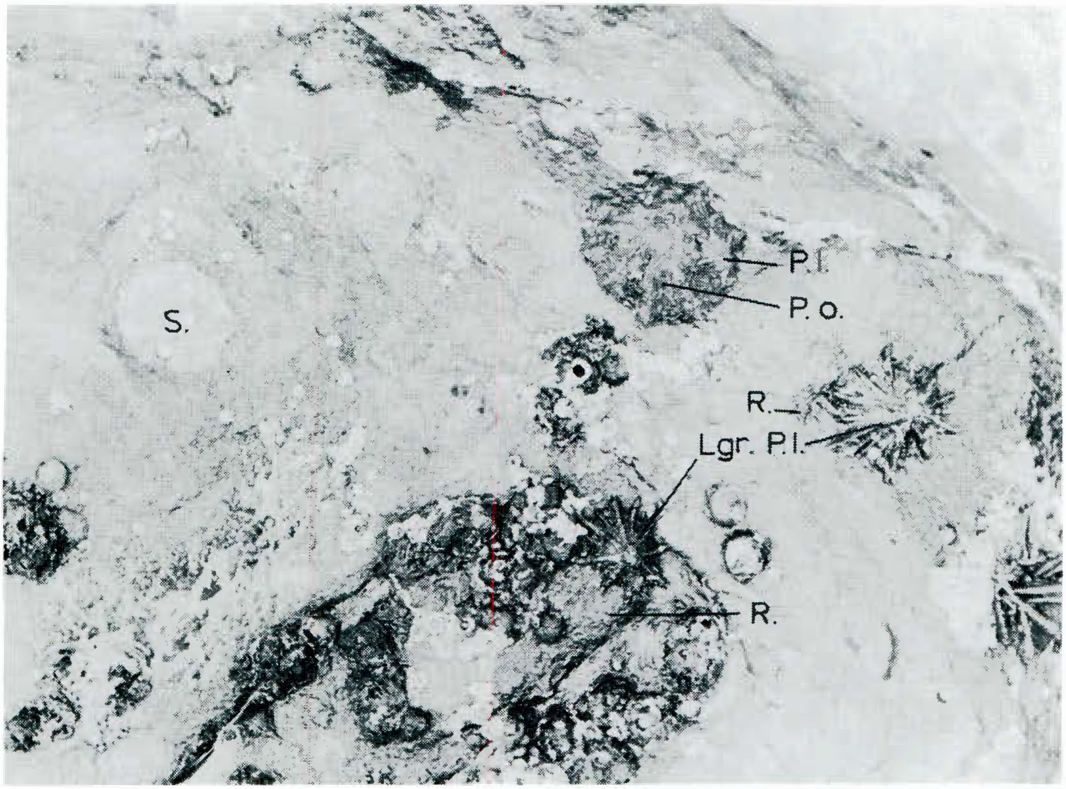

PLATE 1
Movement of *P. oculus* from scar. P.l.: Small *P. longicosta* situated on shell of *P. oculus*. Lgr. P.l.: Larger *P. longicosta* on *Ralfsia*. P.O.: *P. oculus*. R.: *Ralfsia expansa*. S.: *P. oculus* scar.

away to form a sunken pit as it may be with *P. granularis*. Movement away from these scars occurs only when the incoming tide wets the animals, and takes place during both day and night, distances of up to 150 cm being covered. The return route to the scar usually does not follow the outward route, or may only partially do so (Plate 1).

Examination of the gut contents from animals living in the lower Balanoid reveals a wide variety of algal types. These include *Ralfsia expansa* (J. Ag.), *Ulva* sp., black lichens, and occasionally lithothamnia. In addition large amounts of unidentifiable algal fragments occur in the gut, and a certain number of diatoms. This indicates a wide range of diet, coincident with the zone in which these animals are living. The absence of *Gelidium pristoides* (Turn.) Kütz. from the diet is unexpected considering the abundance of this alga in the lower Balanoid. Probably it can be explained by the bushy, upright habit of the plant as *P. oculus* normally browses on encrusting or prostrate forms.

In the upper Balanoid the available food is more limited and gut contents contain only black lichens and *Ralfsia*.

A small percentage of these limpets occur in the extreme upper Balanoid and even

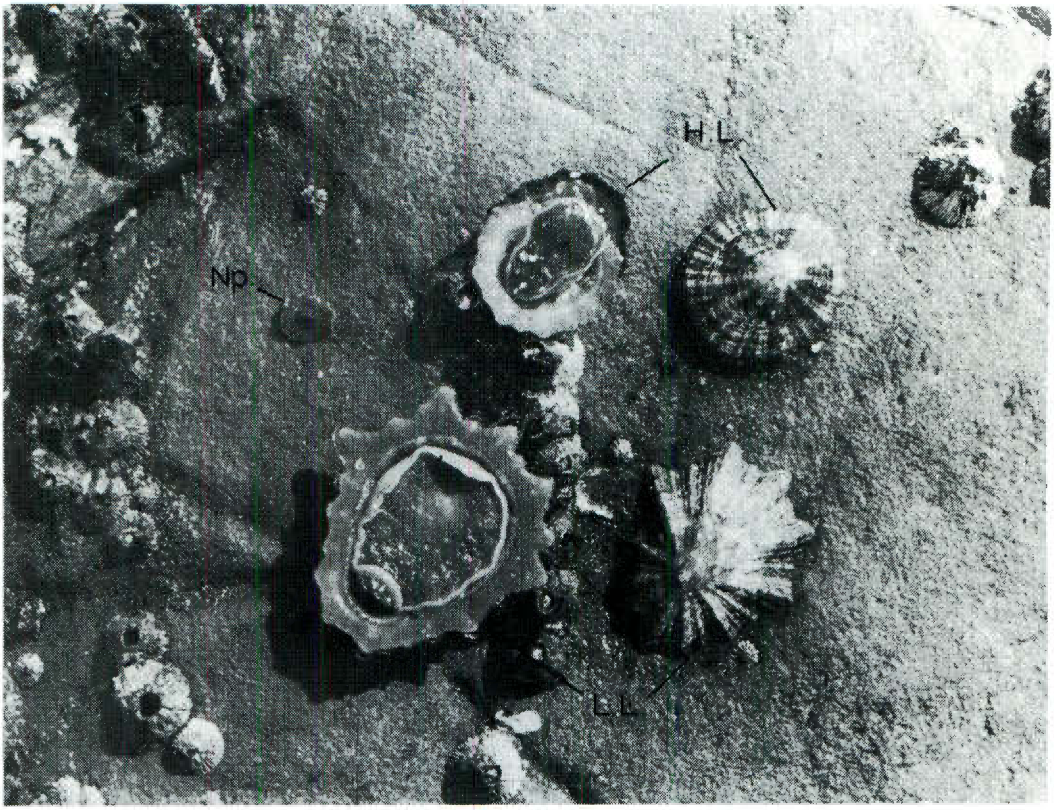

PLATE 2
P. oculus. H.L.: High level specimens. L.L.: Low level specimens. Np.: *Notoplana*—commensal with *P. oculus.*

penetrate into the Littorina zone. These individuals are markedly different from those lower down but examination of their radulae proved them to be *P. oculus.* The shell is oval in shape, the margin being unbroken by costae, and the animals are noticeably paler (Plate 2). The relative proportions of the shell also differ (Table 2).

It is evident from Table 2 that these extreme high level specimens are significantly smaller in size and weight, and that the shell is proportionally higher, in comparison with specimens from the lower and more normal habitat.

The smaller over-all dimensions and paler colour can be explained by the relative lack of food high up on the shore. Here the rocks are almost barren, and bear only encrusting lichens. The gut contents of animals from this zone contain only black lichen, fine particulate matter, including isolated diatoms, and large quantities of sand. This suggests that particles deposited on the rock are also eaten.

The oval outline and relatively greater height of the shell are more difficult to explain. Rao (1953) has shown in pelecypods that the shell weight is proportionally greater in animals which occur lowest on the shore. In the present case the ratio of shell weight to total weight

TABLE 2

AVERAGE DIMENSIONS OF *P. oculus* FROM A RANDOM SAMPLE OF 16 INDIVIDUALS EACH FROM HIGH AND LOW LEVEL POPULATIONS AT DALEBROOK

Average Dimensions	*Low Level Population*	*High Level Population*	*Significance of Difference of means. Probability, p.*
Length (L) mm	63·4	48·3	Highly signif. p = ·01
Width (W) mm	56·6	42·4	Not signif. p = ·1
Height (H) mm	12·8	11·4	Not signif. p = ·2
$\frac{H}{W + L}$	0·104	0·124	Highly signif. p = ·001
Weight gm	16·20	9·47	Highly signif. p = ·01
Shell weight/Total weight	0·678	0·626	Highly signif. p = ·001

is statistically less in the higher population, and shell secretion is probably being relatively retarded due to the paucity of food.

The increased relative height of the shells may be correlated with the greater degree of desiccation at higher levels, as suggested by Orton (1928b) for *P. vulgata* (see above, p. 8). The need for a closer fit to the rock to avoid loss of water, may also explain the oval shape of these shells.

These extreme high level specimens are found only on rocks which are surrounded by sand. This implies that the larvae of *P. oculus* settled randomly in the Balanoid zone, but that those individuals at the extreme upper limits subsequently move downwards to a more equable situation. This is supported by the fact that stunted individuals are found only on isolated rocks where the animals will be confined to the extreme high level, where their growth and shell deposition will be impeded due to lack of food. Lewis (1954) has shown that high level populations of *P. vulgata* move downwards during summer when conditions are unsuitable at a higher level.

P. granatina

This limpet occurs in essentially the same zone as *P. oculus*, but is predominantly a cold water species, extending from Rocky Point (Penrith et al. 1970) to Cape Point, with local outcroppings in False Bay, at Hangklip and at Danger Point. Where the two species do occur together, *P. oculus* tends to inhabit drier rocks than *P. granatina*.

The distribution of *P. granatina* in False Bay is significant. From Cape Point to Smitswinkel Bay it occurs in relatively large numbers. From here to the mouth of the Steenbras River only isolated specimens are found, while on the eastern coast of the bay increased numbers are again found. This distribution pattern is coincident with temperatures within the bay, most of the animals occurring on the west and east shores of the bay, where the water is generally colder than on the northern shore (Day 1970). The distribution is thus closely correlated with temperature.

In False Bay and at Hangklip *P. granatina* is more restricted in habitat than on the west coast, and is largely limited to intertidal pools in the lower Balanoid. This supports Stephenson's (1944) contention that when a species nears the end of its geographical range, it becomes restricted in habitat, whereas in regions of abundance it spreads into a greater variety of habitats.

The animals occupy home scars and only move from these when submerged by the incoming tide. The distances covered are less extensive than in *P. oculus*, the maximum recorded being 75 cm.

Most west coast specimens contain only diatoms in their gut. Small particles of lithothamnia also occur but in such a small proportion as to suggest that they have been rasped up together with the diatoms. Of the diatoms, ? *Nitschia* sp. accounts for about 90 per cent. This is a littoral species and probably forms the staple diet of *P. granatina*. The remaining diatoms include *Melosira* sp., *Biddulphia aurita*, *Licmophora* sp., and *Achnanthes* sp., all of which are predominantly benthic and have probably been deposited by the receding tide. Other west coast specimens contain algae as well as diatoms in their gut, including *Gigartina radula*, ? *Caulacanthus* sp. and *Zonaria* sp.

West coast water is known to be rich in planktonic organisms and organic matter, and scrapings of intertidal rocks reveal that these are deposited on the shore by the receding tide. In addition, it is probable that spume also contains organic matter which will be left on the shore when the spume dries. These depositions provide food for *P. granatina* and enable it to extend on to bare rocks.

South coast specimens contain a variety of algae in their guts: *Ulva* sp., *Ralfsia expansa*, *Cladophora* sp., a few diatoms, and spores. Pollock (1966, unpublished) also records the presence of lithothamnia and other corallines, lichen and *Gelidium* sp. The relative absence of diatoms and deposited organic matter may explain the limitation of south coast specimens to intertidal pools where algal growth is profuse. However, this is more likely due to the cooler temperature of the pools in comparison with the surrounding bare rock.

P. longicosta

Recorded from Isipingo on the east coast to Oudekraal on the west coast, this is characteristically a warm water species. At Isipingo it is reduced in size and has curtailed ribs (Stephenson 1939). Similar specimens have been collected from Jangamo (U.C.T. records) but examination of their radulae indicate that they are not *P. longicosta*.

Within False Bay, *P. longicosta* is far more abundant on the northern coastline than either the east or west coastline. Atkins (1970) has shown that the average surface water temperature varies seasonally between 14·2°C and 20·6°C at the northern coastline, and that this temperature is consistently about 2°C higher than that of the western and eastern coastlines, for most of the year.

Thus even within False Bay the distribution of *P. longicosta* coincides with the warmer waters.

P. longicosta occurs in the lower Balanoid, below the main concentration of *P. oculus*.

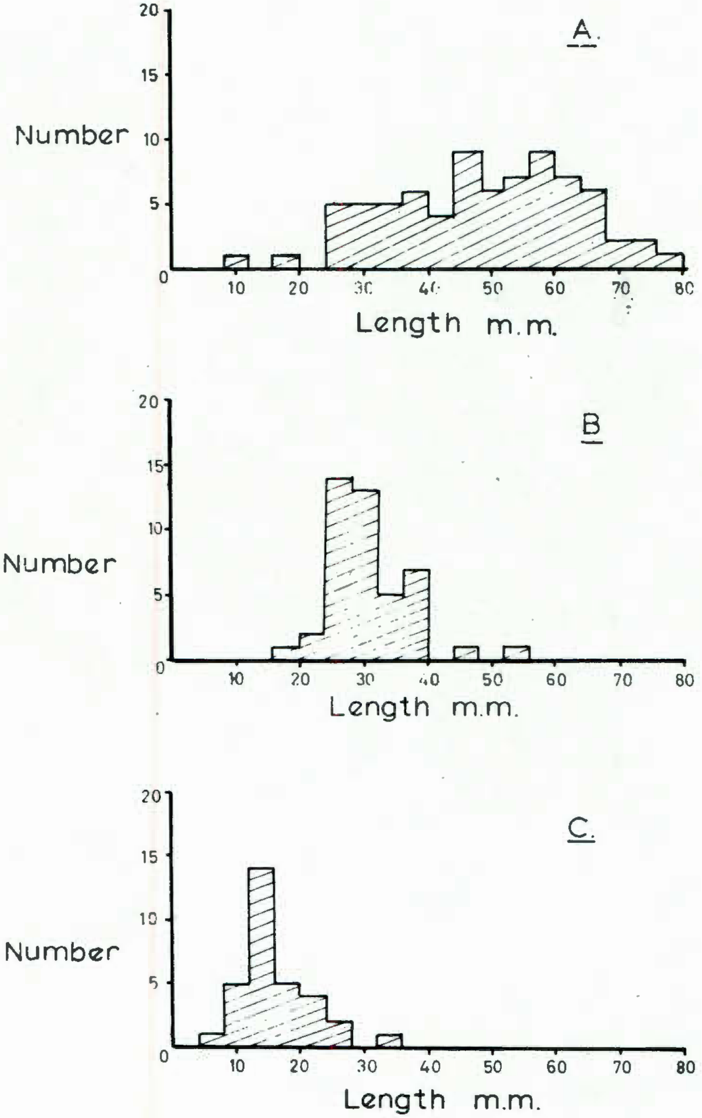

FIGURE 5
Size of *P. longicosta* in relation to substrate. A. On *Ralfsia* gardens. B. On lithothamnion. C. With *Ralfsia* on shells of other molluscs.

Small numbers extend into the Cochlear zone or even into the sublittoral fringe.

As Stephenson (1936) has noted, a high percentage of the adults are found on patches of the alga *Ralfsia expansa* while smaller individuals are more variable in food and habitat. In fact there is a fairly rigid association between the size of the animal and the type of habitat and food (Fig. 5 and Table 3).

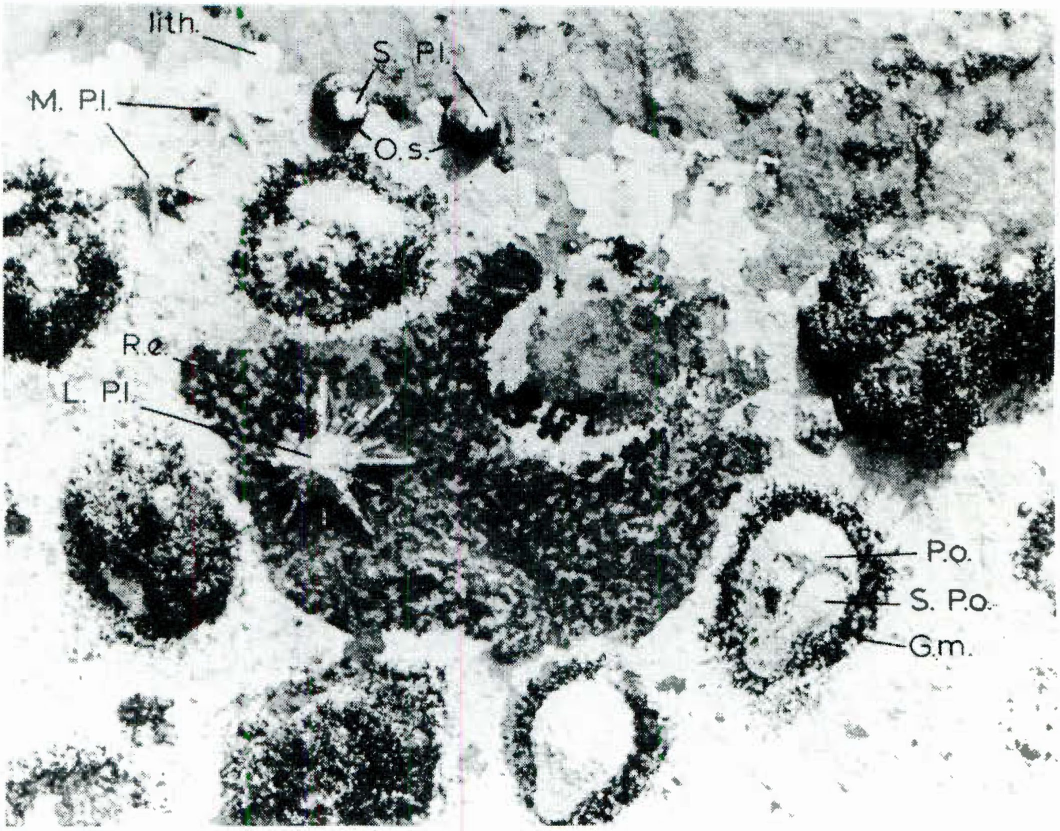

PLATE 3

P. longicosta and P. cochlear. S. P.l.: Small *P. longicosta* on *Oxystele sinensis* shells (*O.S.*). M. P.l.: Medium *P. longicosta* on lithothamnion. (lith.). L. P.l.: Large *P. longicosta* on *Ralfsia expansa* (R.e.). P.o.: *P. cochlear* with garden of *Gelidium micropterum* (G.m.). S. P.o.: Small *P. cochlear* on shell of larger individual.

TABLE 3

SUBSTRATE AND FOOD RELATED TO SIZE IN A RANDOM SAMPLE OF 153 *P. longicosta*.

Habitat	*Food in gut*	*No.*	*Length mm*			*Significance of Difference of means. Probability, p.*
			Max.	*Min.*	*Average*	
Ralfsia garden	*Ralfsia*	77	78	28	48·8	Highly signif. p = ·001
Lithothamnion	Lithothamnion	44	55	18	30·8	„ „
Other shells ..	*Ralfsia*	32	35	8	16·5	

A high percentage of mature individuals over 4·0 cm in length are found on small "gardens" of *Ralfsia expansa*, the animal occupying a scar in the centre of the garden. The alga is extensively grazed in an irregular manner, but never eaten back to the stage where it disappears (Plate 3).

The gut contents of these animals consist almost entirely of *Ralfsia*, although traces of other surrounding algae are usually present, notably lithothamnia. The *Ralfsia* is grazed in such a way that it is scraped completely off the rock. Thus both the curled margin and the prostrate centre are eaten. The latter contains a hard reddish-brown deposition which is indigestible and readily recognisable in the gut.

These animals usually make short feeding forays of about 20 cm from the scar and feed on the *Ralfsia*. Occasionally they move off the garden and feed on the surrounding algae. All movements occur only when the animals are immersed.

Maturing animals of approximately 2·5 cm to 4·5 cm usually occur on lithothamnion, on which their scars are also situated (Plate 3). Their gut contents consist almost solely of this alga, although *Ralfsia* may also occur in smaller quantities if it is found in the vicinity of the animal.

Small specimens of under 2·5 cm are almost invariably found on the shells of other animals. More specifically, nearly all are found on the shells of other *P. longicosta*, on *P. oculus* and on *Oxystele sinensis* (Table 4).

TABLE 4

SUBSTRATE SELECTION BY *P. longicosta* OF SIZE RANGE 6 MM TO 25 MM. RANDOM SAMPLE OF 100 SPECIMENS

Substrate	*Number of* P. longicosta
Other *P. longicosta* shells	43
P. oculus shells	19
P. cochlear shells	1
Oxystele sinensis shells	31
Other shells	2
Bare rock	1
Rock with *Ralfsia*	3

The high percentage of these small *P. longicosta* occurring on other shells is explicable in a number of ways. All the shells they are found on are covered with *Ralfsia*, and the guts of the small limpets are filled with this alga. This suggests that the larvae or perhaps the newly metamorphosed individuals, are restricted to *Ralfsia* in the early stages of settling. Thus either the larvae may specifically select *Ralfsia* as a substrate or they may not initially be able to survive without it once they have metamorphosed. Furthermore, those settling on existing *Ralfsia* gardens will be destroyed by the browsing of larger limpets already inhabiting the gardens. Thus only those individuals settling on top of shells with *Ralfsia* will survive. Lewis (1954) has similarly described how *P. vulgata* decimates the population of settling barnacles by grazing the area in which the spat settle.

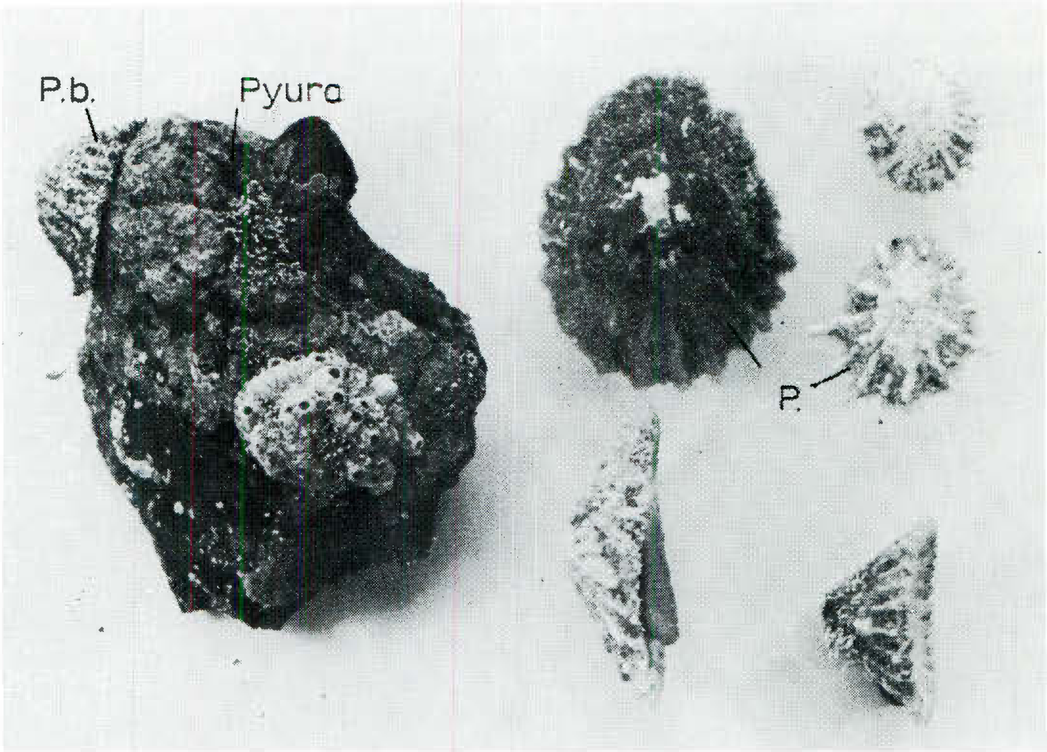

PLATE 4

P. barbara. Pyura with *P. barbara* (P.b.); Normal *P. barbara* in centre and miniature concave specimens on right. Note growth of ?*Pantoneura* (P.) on all.

This hypothesis also explains why such a high percentage of small *P. longicosta* are found specifically on shells of their own kind, or on *P. oculus* and *Oxystele sinensis:* these are the only animals consistently bearing *Ralfsia* on their shells. In this connection it is significant that only one *P. longicosta* was found on the shells of *P. cochlear*, *P. barbara* and *P. granularis*, all of which occur within the range of *P. longicosta* but lack a covering of *Ralfsia*.

In areas where *P. longicosta* is particularly common, up to 39 per cent of the larger *P. longicosta* and 36 per cent of *O. sinensis* bear smaller limpets of this species on their shells. It is of interest that these two molluscs have the same vertical and geographical distribution.

The three different size groups of *P. longicosta* – small, medium and large – are very different in their substrate selection and feeding habits.

At Dalebrook an area of 5 square metres was cleared of the 27 large *P. longicosta* present on gardens of *Ralfsia*. Within a single tide, three medium sized *P. longicosta*, originally situated on lithothamnion, had occupied the vacant areas. Twenty-four hours later, five were present on these scars; after 48 hours a further one, and 72 hours later a total of eight. After two weeks 10 medium sized individuals had occupied old scars and the remaining scars were overgrown by *Ralfsia*. Some of the invading animals had moved up to 2·5 m to occupy their new position.

This reveals that the medium sized *P. longicosta* prefer *Ralfsia* gardens although they are largely restricted to lithothamnia. Furthermore they do not settle on existing *Ralfsia* patches unless there is a vacant scar available. This suggests that the scar acts as a releaser, and that the animal will not settle on top of an algal growth but only on a scar where the smooth rock is bared. In addition, the scar may bear traces of a chemical exuded by the previous occupant.

The small individuals situated on shells move relatively little and feeding is confined to the algal incrustation on the shell. Some do however occasionally move off the shell to feed on surrounding *Ralfsia*, subsequently returning to their scar on the shell. In one observed instance of this, the host animal moved from its scar while the small individual was off the shell. The small individual returned to the vicinity of the host's scar and settled on the scar. When the larger animal returned it forced the smaller specimen off the scar. After indecisive turning movements, the small animal climbed on to the host shell again.

The maximum size these animals on the host shells can reach is obviously limited by the shape and size of the host shell, and the amount of food available there. When this maximum size is reached, the animal must move off the shell on to the rocky substratum.

If the suggestion put forward above is correct – that bare smooth rock will act as a releaser – then these animals will not settle on an algal turf but on smooth patches of rock or lithothamnion. Settling in one position will soon establish a new scar as the lithothamnion will die and be dissolved away from under the foot. From here long feeding forays will take place, the animal eating largely lithothamnia and surrounding algae. *Ralfsia* may also be eaten, but settling on this alga will not take place due to the lack of a scar. Repeated movements and feeding will eradicate the lithothamnion in the immediate vicinity of the scar.

Ralfsia is never found growing on top of lithothamnion, only on bare rock. Thus it is possible that as the limpet grazes away the encrusting coralline, so the *Ralfsia* may become established on the bare rock. The relatively rapid growth of *Ralfsia* would prevent it from being obliterated by the grazing activities of the limpet. In addition, *P. longicosta* can be seen cropping back the surrounding algal turf so that the encrusting *Ralfsia* is not overgrown by more bushy algae (Plate 5).

Large *P. longicosta* seldom leave their gardens and feed almost solely on these. Smaller individuals roam more extensively from their scars – up to 2 m. Their feeding activities are subsequently not centred around the scar, and the lithothamnion is not cleared sufficiently to allow the establishment of *Ralfsia*. Movements become more restricted as the animal matures and the grazing of lithothamnion visibly clears this alga from the vicinity of the scar. Small amounts of *Ralfsia* soon appear on the bare rock. This explains why only larger individuals are associated with *Ralfsia* gardens.

Ralfsia is physiologically independent of the *Patella*, and grows far more vigorously when not grazed. Similarly the limpet can survive without this alga, except possibly when very small.

P. cochlear

Stephenson (1939) has defined the different zones in the intertidal area of South African shores. Of these the Cochlear zone is the lowest on Cape shores, and is typified by a mosaic

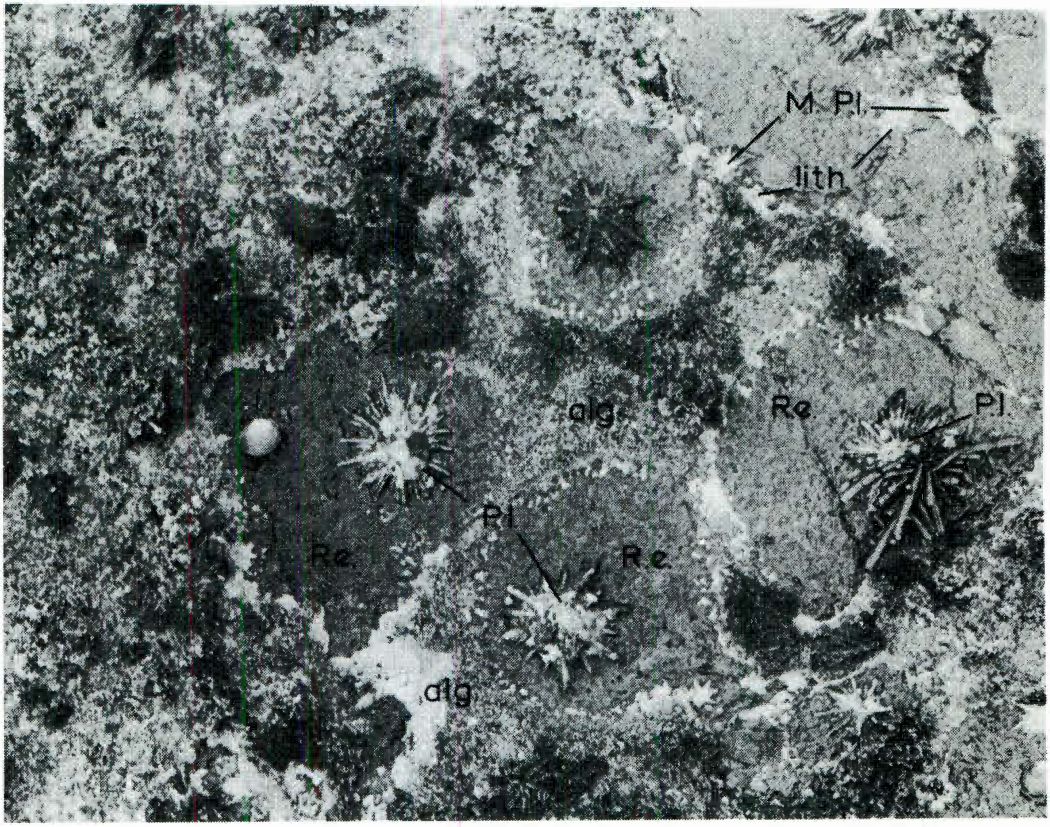

PLATE 5
P. longicosta (P.l.) on gardens of *Ralfsia expansa* (R.e.). The surrounding algal turf (Alg.) is cropped back. Medium *P. longicosta* (M.P.l.) situated on the peripheral lithothamnion (lith.).

of the limpet *P.cochlear*. The communities of this animal form a sharply defined and narrow fringe just above the infratidal zone. Here they are usually associated with lithothamnia, which forms a heavy incrustation on the rocks and normally covers the limpet shells as well.

Such communities of *P. cochlear* are distributed from Buffels River on the west coast to Port Edward on the east coast. (Bright 1938, Stephenson 1939 and Koch 1949.) The concentration of animals within these communities varies from 25 per square metre to over 1,400 per square metre. The number of animals present and the height to which they may extend up the shore depends on the wave action at any particular site. The community is normally associated with "parts of any reef in which wave action is strong or moderate" (Stephenson 1944, p. 501). The animals are typically absent from the landward side of rocks (Bright 1938) and from shores which are not reasonably washed (Morgans 1958). These observations have been verified by the present surveys, which show a striking absence of *P. cochlear* from sheltered bays (where they tend to be replaced by an algal carpet), and maximum concentration on fairly exposed prominences. Furthermore, in areas of strong wave action, the effective tidal level is higher, and the populations extend higher up the shore. However, in the case of extreme wave action the Cochlear mosaic tends to disappear and is replaced by mussels and barnacles (Stephenson 1944).

A notable feature of *P. cochlear* is that larger individuals very often bear smaller ones on their shells (Plate 3). This habit is accentuated under very crowded conditions, and Stephenson (1939) has recorded up to 40 smaller individuals on the shell of a single large animal.

Within a population, almost all of the smaller individuals are situated on larger specimens, unless the population is sparse, in which case they are fixed to the lithothamnion covered rock. This latter fact makes it improbable that settling larvae are selecting the shells of other individuals. Furthermore, the shells and surrounding rock are normally covered with lithothamnia, which would make selective detection difficult. It is more likely that larvae settled randomly on lithothamnion covered objects within the Cochlear zone, but that most will be eradicated by the browsing of established limpets. Only those settling on the backs of other limpets will survive.

P. cochlear is characteristically associated with lithothamnia of the genus *Lithophyllum* which forms the dominant algal encrustation at this level of the shore. The limpets possess well defined scars which are frequently sunken into the *Lithophyllum* so that the latter forms a crater-like perimeter. This is probably due in part to death and erosion of the alga from under the foot, and partly to continued growth of the surrounding alga.

In most cases the spaces between the limpets are devoid of any other algae, except in the infratidal fringe. The tops of the shells however frequently bear a luxuriant growth of algae, notably *Gelidium pristoides* (Turn.) Kütz., *Gigartina radula* (Esp.) J. Ag., *Laurencia glomerata* Kütz., *Cheilosporium cultratum* (Harv.) Aresch. and other corallines. This again suggests that algal spores settling on the surrounding lithothamnion are consumed by the browsing limpets.

A characteristic feature of the Cochlear mosaic is the presence of a fringing "garden" of algae which grows around a high percentage of *P. cochlear*. This fringe may consist of one or two species, *Herposiphonia heringii* (Harv.) Falk. and *Gelidium* sp. The latter has been described by different authors as *G. pristoides*, *G. reptans* and *G. micropterum*, and in fact is probably *G. micropterum* (det. R. H. Simons) (Plate 3).

Herposiphonia is a common constituent of moss-like turfs on the Natal coast (Stephenson 1947) but is considerably reduced in size around *P. cochlear*. *G. micropterum* is normally an upright branching alga, but when in association with the limpet, grows only as a dwarf prostrate form.

In addition to these two species, an isolated garden of the *Antithamnion* group was found around one *P. cochlear*.

The relationship between *P. cochlear* and its garden is complex. The gut contents comprise largely lithothamnion, fragments of *Ralfsia*, a number of diatoms (notably *Rhabdonema* sp.) in west coast specimens, and a certain amount of *Herposiphonia* if this is present in the garden. Very little *G. micropterum* occurs in the gut, even though this is almost invariably present in the gardens. Examination of the *Gelidium* gardens shows that although prostrate and small, the fronds are intact and seldom cropped.

It is surprising that lithothamnion constitutes the bulk of the limpets' diet, as *Gelidium* has previously been regarded as the main food source. However, *Acmaea* is also known to feed on *Lithothamnion* (Sneli 1958).

It is also significant that although large quantities of *G. pristoides* occur on the shells of *P. cochlear*, and sometimes on the rocks of this zone, none was ever found in the guts of animals examined.

At Dalebrook, two areas in the Cochlear zone, of one square metre each, were cleared of all the limpets present (areas I and II), and in two comparable areas, half the limpets were removed, leaving alternate animals in place (areas III and IV). (January, 1968.)

In area I the limpets were surrounded by gardens of *Gelidium* only. Within two weeks of removing the limpets, the *Gelidium* began to diminish, and after four weeks had disappeared completely. However, a few of the scars left vacant were reoccupied by other *P. cochlear*, and in each case the *Gelidium* did not disappear, but remained in the same state. The disappearance of the remaining gardens is not in accordance with the findings of Bokenham (1938). After clearing a comparable patch at Saint James, she found that the *Gelidium* spread after the removal of limpets, and continued spreading for five months, when the alga developed upright shoots. Subsequently, however, the alga disappeared. As the patch had not been reinvaded by other *P. cochlear*, this disappearance was not due to the browsing of limpets.

Patches comparable to area I were cleared at five different places in the Peninsula (Hangklip, St. James, Dalebrook, Miller's Point and Camps Bay) and in each case the fate of the gardens repeated that of area I at Dalebrook.

In area II the gardens consisted of both *Herposiphonia* and *Gelidium*. The latter again died within four weeks of removing the limpets, unless the scars were reinvaded. Conversely the *Herposiphonia* rapidly developed, and within four weeks had completely overrun the area to become the dominant, and reaching an average height of 5·2 cm. Subsequently other *P. cochlear* invaded the area, and the amount of *Herposiphonia* diminished due to grazing. This is in agreement with the results of recolonisation experiments by Bokenham (1938) in the Cochlear zone at Sea Point, except that at Dalebrook the *Herposiphonia* developed far faster.

Herposiphonia gardens disappear at irregular intervals from different areas. After five months this alga disappeared not only from area II, but from the surrounding limpets. This suggests that the grazing of limpets is not the only factor controlling algal growth, but that there may be local seasonal fluctuations.

Areas III and IV, in which alternate limpets were removed, contained gardens of respectively *Gelidium* and *Gelidium* plus *Herposiphonia*. In both areas the vacant scars were reoccupied within two weeks by smaller limpets from the shells of larger limpets and the gardens remained unchanged. After three months the gardens had decreased in size to lie around the perimeter of each new occupant.

The results of clearing in areas II and IV suggest that *Herposiphonia* is continually being grazed down by the limpet, and exists only immediately around the foot of the animal.

When feeding, the limpets either move completely off their scars, or they rotate symmetrically on their scars and feed on the edge of the garden and the underlying lithothamnion. In both cases the *Herposiphonia* growing close to the foot is left untouched as the head of the animal projects beyond the garden as the animal rotates. While feeding, the limpets move apart if they come in contact, so that the garden of a stationary limpet will be protected.

The possibility also exists that *P. cochlear* provides moisture to the garden during exposure. However, this is not the factor limiting the gardens to the vicinity of the limpets, as comparable gardens exist around *P. cochlear* which are continually submerged.

In the case of *Gelidium*, the association is more complex, and the results in areas I to IV suggest some dependency of the alga on *P. cochlear*.

At Dalebrook 20 *P. cochlear* were removed from their *Gelidium* gardens, stripped from their shells, and each shell screwed back on to the rock in its original position. Two weeks later the *Gelidium* had diminished or disappeared, and after four weeks had completely vanished. Thus the possibility that the shell is providing only mechanical protection, against water movement or other limpets can be discounted.

Stephenson (1936) has suggested that *P. cochlear* takes in the spores of *Gelidium* while feeding, and that the garden is continually replaced by spores passed out with the faeces.

At Dalebrook 20 individuals of *P. cochlear* were transplanted from one area in the Cochlear zone to an area which was comparable, but lacked other specimens of *P. cochlear*. Ten of these originally possessed *Gelidium* gardens while the remainder lacked gardens. After three months neither lot had developed gardens. Thus it is unlikely that *Gelidium* spores are being passed on in the faeces.

The sizes of *P. cochlear* in relation to presence or absence of a garden are significant in this context (Table 5, Fig. 6).

TABLE 5

SIZES OF A RANDOM SAMPLE OF *P. cochlear* FROM DALEBROOK, IN RELATION TO SUBSTRATE AND ALGAL GARDENS

Substrate	*Gelidium garden*	*Number*	*Length mm*			*Significance of difference of means Probability, p.*
			Max	*Min*	*Avr.*	
Rock	Present	23	56	20	37·8	Signif. p = ·05
Rock	Absent	15	46	12	21·0	Not signif. p = ·31
P. cochlear shell . .	Present	13	25	16	20·2	
P. cochlear shell . .	Absent	15	18	4	12·5	Highly signif. p = ·001

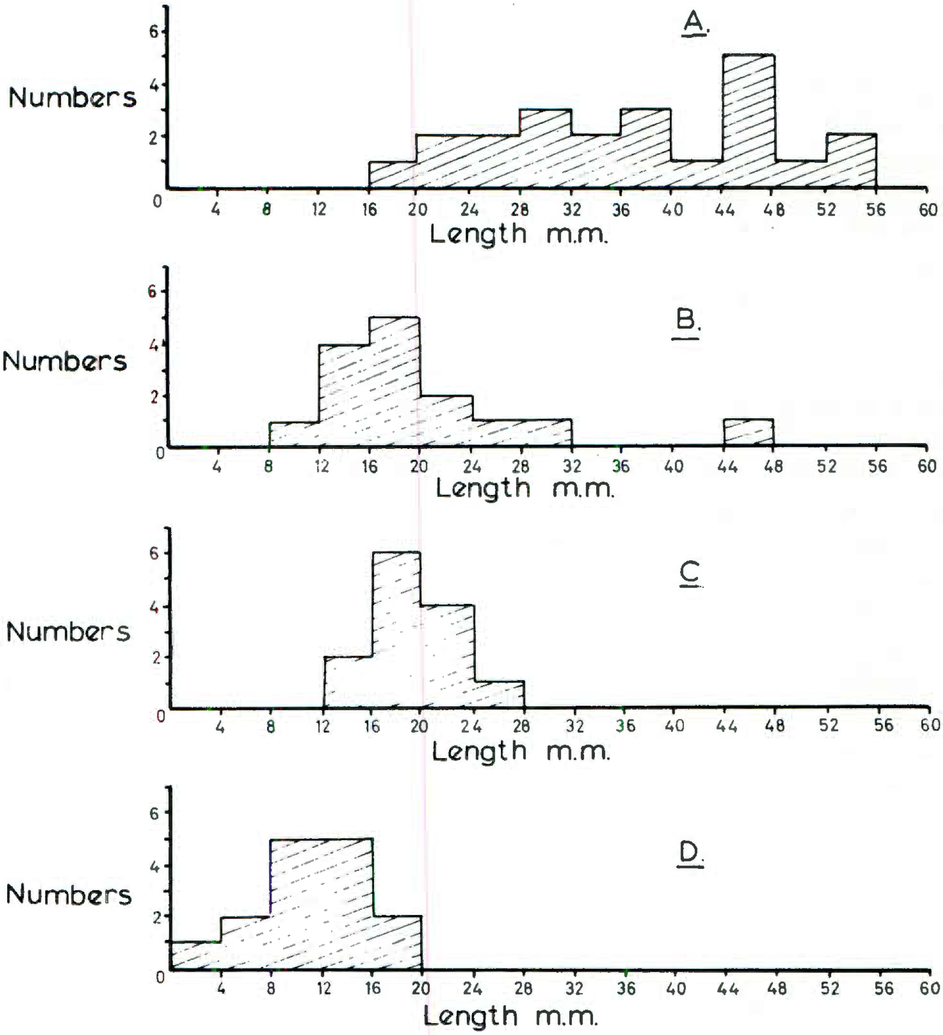

FIGURE 6
Size of *P. cochlear* in relation to substrate and algal gardens. A. On rock, with garden. B. On rock, but lacking garden. C. on shells of other *P. cochlear*, with garden. D. on shells of other *P. cochlear*, and lacking garden.

The pattern revealed indicates that the limpets develop for some time on the shells of other limpets before they acquire gardens. The change of home scar from host shell to rock occurs when the limpets are about half grown, and the algal garden is of necessity deserted in the transition. There is a statistically significant difference in size between those animals on rock which lack algal gardens and those which possess them. This is important because it again indicates a fairly lengthy period before a garden is redeveloped. This is further evidence that a garden is not simply regenerated from spores in the faeces.

Gelidium micropterum cannot coexist with more bushy algae as it becomes overgrown. *P. cochlear* shells are frequently covered by a luxuriant growth of other algae, and in all such cases the animals lack a garden. When such an algal covering is lacking, browsing clears the spaces between the limpets of all other algae, thus allowing continued growth of *Gelidium* gardens. Unlike the case of *P. longicosta* and *Ralfsia* (see above, p. 17) the *Gelidium* garden grows on top of the lithothamnion, and is not dependent on the limpet to graze away the lithothamnion before developing. Nor does the garden depend upon the limpet for moisture while exposed: some *P. cochlear* which occur in the sublittoral zone and never emerge still have well developed gardens.

Gelidium gardens are highly specific in their association with *P. cochlear*. Despite the fact that *P. longicosta*, *P. oculus*, *P. barbara*, and especially *P. argenvillei* all occur in the Cochlear zone, they have never been found with regular gardens of *G. micropterum* during the present survey. Stephenson (1939) records that gardens are occasionally found around *P. barbara*. This has only been observed twice in the present work, in both instances the *P. barbara* simply occupying a vacant *P. cochlear* scar with the remnants of a garden still present. *G. micropterum* was also found once on *Pyura* in association with *P. barbara*, but no distinct garden was present. Stephenson also records this dwarf *Gelidium* growing on the shells of *Vermetus corallinaceous* Tomlin. I have on isolated occasions found it associated with *Perna perna* (Linn.), on the shell of *P. longicosta*, and on *Gunnarea capensis* (Schm.) tubes.

Thus it appears that *G. micropterum* occurs in a reduced and prostrate form when associated with *P. cochlear*, and that in this form it is dependent on the limpet. This dependency is specific and possibly physiological in nature. The closeness of the association is indicated by the fact that this alga grows only around the immediate periphery of the foot, whereas *Herposiphonia* spreads irregularly outwards from the foot and is cropped back continually.

P. cochlear begins to feed only when the incoming tide is washing strongly across the animals. Feeding movements decrease once the tide has risen sufficiently for the wash to decline, and there is little feeding when the animals are again washed by the outgoing tide. No feeding occurs during exposure. Thus feeding is correlated with the tidal rhythm. Not all the individuals feed every tide, and up to 60 per cent of the population may remain stationary throughout a particular tidal cycle (Fig. 7). In the case of animals which are perpetually submerged, this feeding pattern is less obvious or even absent.

Koch (1949, p. 499) states that "the species hardly moves about at all. The foot merely rotates on the same spot so that the head can move in a circle, and crop the algae within this area. The alga on which it feeds is usually, but not invariably, *Gelidium pristoides*, and a cropped garden is found around every *P. cochlear*, even around those which are attached to the shells of other specimens".

In fact at least 10 per cent of any *P. cochlear* population lacks gardens. Most of the mature individuals do feed as Koch describes, but their main diet comprises lithothamnia and not

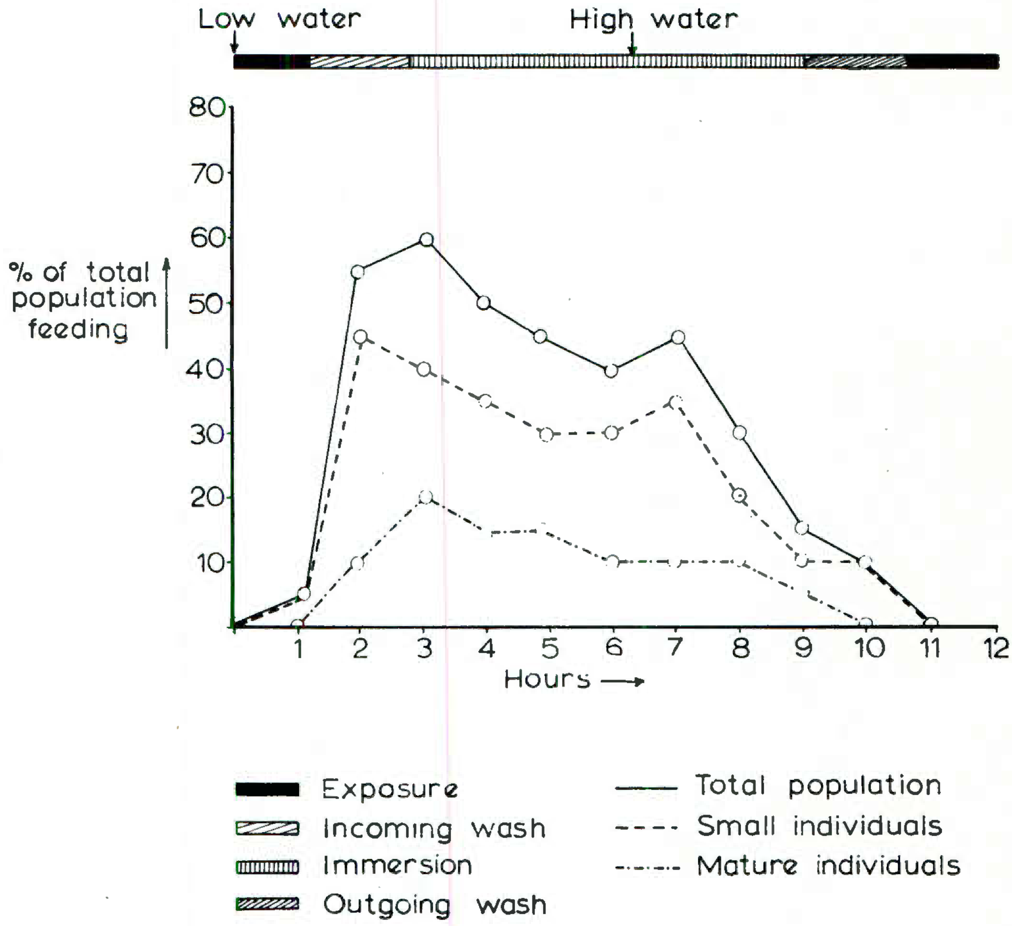

FIGURE 7

Feeding in *P. cochlear* relative to tidal rhythm. Counts taken at hourly intervals of the population in a fixed square metre at Dalebrook. Figures expressed to the nearest 5%.

Gelidium. However, it is noticeable that mature individuals with gardens are usually confined to their scars while feeding, whereas those without gardens roam more widely. Small individuals, on the shells of other *P. cochlear*, move far more than the adults. Almost all leave their host shell with the incoming tide and cover considerable distances of up to one metre before returning to the scar. Adults cover a maximum of 30 cm while feeding.

Removal of all the limpets from area I (see above, p. 20) indicated the extent of movement. Area I was reinvaded by 10 mature and 5 small individuals over a period of 14 days. Thus although the majority of adults remain on their scars, a certain number still migrate around while feeding. These invading limpets moved up to one metre to occupy their new positions, and it is significant that in each case they settled on vacant scars.

This latter phenomenon was even more marked in area III where alternate animals were removed from the rock. Within 14 days all the vacant scars had been occupied. Most of the scars were taken over by smaller individuals originally situated on other shells. Some individuals moved from their own scars on the rock, to vacant scars. A number of smaller limpets living on host shells moved to other scars on the same shell, left vacant by migrating animals. Thus there was a general exchange of scars. However, the significant point is that in every case, the animals moved to a scar which was larger than their original scar.

This supports the suggestion put forward above (p. 17) that the scar acts as a releaser inducing settling, as releasers are generally considered to be cumulative in their effect. Thus the larger the scar, the more likely it is to induce settling.

In a stable population, each individual returns to its particular scar, and there is almost no exchange of scars. This can be explained by the relative movements of the animals. Mature specimens seldom leave their scars, and when they do, they return to them after a short space of time. Smaller specimens cover greater distances and remain away from their scars longer (Fig. 7). Thus after the incoming tide has induced feeding, the larger scars will be reoccupied first, leaving the smallest scars to be reoccupied by the smallest individuals.

The degree of movement is a function of the age of any individual. Smaller individuals have their home scars situated on the shells of larger specimens and undertake extensive feeding forays from their scars. These animals return to their own specific scars subsequent to feeding, but if larger vacant scars exist on the rocks, these are more likely to induce settling. As larger individuals seldom vacate their scars to feed, and return to them soon if they do, this will seldom occur in a stable population.

On isolated occasions, medium sized specimens were observed to abandon their scars on host shells and settle on the lithothamnion, ultimately establishing a new scar.

To a certain extent movement is determined by the availability of food. Two samples of 14 animals each were transplanted to two areas of 30 cm squared, in the Cochlear zone, which were respectively encrusted with lithothamnia and lacking in this alga. In the former case only eight animals survived, and after four days were still situated in the original area. A certain amount of movement had occurred, presumably a random search for a scar. In the latter area, lacking in lithothamnion, 10 animals survived, and after four days were distributed over an area 100 cm by 60 cm. Of these animals, seven had settled on lithothamnion within four days; after 10 days all 10 had settled on this alga.

In some cases *P. cochlear* may settle above the normal Cochlear zone, where conditions are more severe than usual. Such limpets are almost invariably surrounded by a ring of lithothamnion, which under these conditions evidently depends on the limpet for moisture.

When a large *P. cochlear* is removed from the rock, smaller individuals living on its shell respond by elevating their own shells, moving around, and even dropping off the host shells. This behaviour occurs even when the smaller limpets are not touched during the removal of the host animal. Subsequent to removal, inversion of the large individual causes all the smaller specimens to drop off within 20 seconds. When the small limpets are touched prior to inversion, they clamp down initially, but still drop off within 60 seconds.

All *Patellas* possess statocysts in their feet (Hyman 1967) which enable them to detect changes in vertical orientation. Inversion of a *P. cochlear* will thus be detected and induces the animal to drop off its substratum. Subsequently the animal clings immediately to the first object it contacts.

Such behaviour must be of survival value. Death or dislodging of a host animal in the wave-swept Cochlear zone would otherwise be fatal to all smaller limpets living on that host.

P. argenvillei

This species is abundant on the west coast, at least as far as Lüderitz (U.C.T. records), but its numbers decrease markedly on the south coast and it extends only as far as Qolora on the east coast. Apart from decreasing numerically on the warmer coasts, the average size is also less (Stephenson 1939, Koch 1949).

In the more northern extremes of the west coast, *P. argenvillei* replaces *P. cochlear* completely, and as it occupies the same position on the shore, this is termed the *Argenvillei* zone in this region. Extending southwards from Buffels Bay on the west coast, the *P. argenvillei* are interspaced by increasing numbers of *P. cochlear* and the two species are co-existent in this area. In the more southern extremes of this coast and on the warmer coasts, only isolated patches of *P. argenvillei* are found in the Cochlear zone.

On the west coast *P. argenvillei* extends in small numbers slightly above the zone normally occupied by *P. cochlear*, but the majority occur in a belt immediately below the Cochlear zone. Thus on this coast *P. argenvillei* penetrates both the infratidal and the lower Balanoid, whereas on the south and east coasts it is limited more strictly to the Cochlear zone. This again is in agreement with Stephenson's (1944) concept that a species is more restricted in habitat near the end of its geographical range.

The distribution of *P. argenvillei* in False Bay is of interest. The species is largely restricted to the colder east and west coasts of the Bay. This is similar to its distribution on a wider scale as the animal is predominantly a cold water species. The distribution in False Bay lends weight to the concept that water temperature rather than availability of food, is the limiting factor.

Large specimens of *P. argenvillei* frequently bear smaller individuals on their shells, similar to *P. cochlear*. When the two species are co-existent, small *P. cochlear* are found on the shells of *P. argenvillei*, although the reverse seldom occurs.

Almost invariably *P. argenvillei* is found on lithothamnia and has a well developed scar. Isolated specimens have been found on *Pyura stolonifera* (Heller) which is itself covered by lithothamnia.

The limpets move off their scars when the incoming tide washes over them, and remain off their scars while immersed. Feeding movements usually cover less than 60 cm.

While the tide is sluicing over the animals, *P. argenvillei* frequently remains stationary with its shell well elevated so that the water flows over the animal. This may mean that they are trapping detritus or plankton (J. H. Day pers. com.) or it may simply be a means of rapidly replenishing oxygen in the blood following an oxygen debt during exposure.

The gut contents of *P. argenvillei* consist of a certain amount of lithothamnia, large numbers of diatoms, *Cladophora capensis* (Ag.) Kütz., *Centroceras clavulatum* (Ag.) Mont., *Ralfsia expansa* (J. Ag.) J. Ag., *Bifurcaria brassicaeformis* (Kütz.) Barton, ? *Gigartina* sp. ? *Aeodes* sp., and a few unidentified algal fragments.

P. barbara

This species occurs around the entire coastline at least as far as Lüderitz on the west coast (U.C.T. records), and Inhaca on the Moçambique coast (Macnae and Kalk 1958). Its size becomes progressively less on the south and east coasts (Stephenson 1939).

Vertically it is distributed from the infratidal zone to the lower Balanoid, but the majority are infratidal or situated in intertidal pools where they are perpetually submerged. Macnae and Kalk (1958) describe it as occurring in the "lower midlittoral" at Inhaca.

P. barbara is almost invariably associated with lithothamnion. It is thus broadly comparable with *P. aspera* which is characteristic of *Lithothamnion* lined pools on British shores (Lewis 1964).

On the lithothamnia the limpet forms a rough and poorly defined scar. Marked specimens returned regularly to their scars after feeding, but orientation to the scars was often random. This was particularly noticeable in infratidal individuals. Feeding occurs at all phases of the tide, but specimens in intertidal pools feed more when the pools are flushed by tidal waters.

The gut contents comprise a wide variety of algae: *Ralfsia expansa*, lithothamnia, corallines, *Ulva* sp., ? *Gelidium* sp., and *Cladophora* sp. Pollock (1966, unpublished) also records *Ceramium tenerrimum* (Mart.) Okam., and *Lophosiphonia subadunea* (Kütz.) Falk. The inclusion of copious quantities of sand in the gut, as well as many diatoms, foraminiferan shells, sponge spicules and spores, suggests a random rasping of the substrate until food is encountered.

A reduced form of *P. barbara* occurs on the tests of *Pyura stolonifera*. Koch (1949) records this variety from False Bay and the Atlantic side of the Peninsula. On an average this form is about half the normal size, and the shell is markedly misshapen to fit the curvature of the *Pyura*. The resultant shell is shorter and proportionally higher than normal (Plate 4). The modified shape of the shell is due entirely to the site this variety inhabits, as normal individuals are found on the rocks in close proximity. The relatively small size is probably a reflection of the limited amount of food available on *Pyura*: lithothamnia and corallines predominate on the tests, and must contain a low percentage of nutriment.

These modified individuals form marked scars on the lithothamnia which encrust *Pyura*. From the scars they move over the *Pyura*, but are restricted to it by the curvature of the shell.

The gut contents consist almost entirely of lithothamnia and fragments of corallines, although one specimen was filled with *Cladophora capensis* (Ag.) Kütz. The predominance of lithothamnia and corallines is due to the limited variety of algae present on *Pyura* tests.

Of 50 limpets collected randomly from *Pyura* at Dalebrook, all were *P. barbara* except for single specimens of *P. tabularis* and *P. miniata*. A comparable collection from Camps Bay revealed a similar preponderance of *P. barbara*, but five *P. cochlear* and four *P. argenvillei* were also found on *Pyura*. The preponderance of *P. barbara* is partially explicable by its zonation, and by its apparent preference for lithothamnia. Although predominantly infratidal, *P. barbara* usually occurs in shallow water. As *Pyura* occurs mainly in the infratidal fringe and is covered by lithothamnia, beds of this ascidian form a logical settling place for *P. barbara*.

Specimens on *Pyura* readily abandon their host if the latter is cut free from the substrate. As in the case of *P. cochlear*, this is induced by inversion. If the *Pyura* is cut free and brought to the surface in an upright position, the limpets may raise themselves up and move around, but do not drop off. This eliminates the possibilities that a change in pressure, or the presence of tissue fluid from the damaged *Pyura* are inducing the reaction. However, almost immediately the ascidian is inverted the limpets drop off. Subsequently they cling very readily to any object with which they come in contact.

This behaviour sequence is of obvious survival value, as *Pyura* is often torn free in violent storms.

P. barbara shells are almost invariably covered with algae. The species present vary greatly, but many of the limpets are covered by a moss-like alga which is described as *Gelidium reptans* by Eyre and Stephenson (1938), but is possibly ? *Pantoneura* sp. (det. R. H. Simons).

Macnae and Kalk (1958) describe *P. barbara* as having gardens of *Gelidium reptans* on the exposed rock of the "lower midlittoral" at Inhaca.

P. miniata

P. miniata extends around the entire west coast from Rocky Point (Penrith et al. 1970), to Umhlali on the east coast (U.C.T. records). In general, specimens are larger on the west coast (Stephenson 1939) although the form originally known as *P. sanguinans* (and now included in *P. miniata*) reaches considerable size on the east coast. It is seldom found on dry rock, and most individuals occur infratidally or in tidal pools. The vertical distribution extends from pools in the lower Balanoid to eleven metres below spring low tide. In this latter respect *P. miniata* is thus found deeper than any other limpet.

The animals are usually found associated with lithothamnia, on which a poorly defined scar may be formed. In most cases no fixed scar is formed at all. This is an indication of how widely they roam while feeding. Frequently they do not return to their original position after feeding. Time of movement is apparently random, and specimens may be seen feeding at day and night, and independent of the tide.

In contrast to *P. barbara*, only a single *P. miniata* was found on *Pyura.* This individual also had a modified shell to fit the convex *Pyura*. The lack of *P. miniata* on beds of this ascidian is probably due to the lack of a fixed scar and the relatively extensive movements of this limpet.

The gut contents consist almost solely of lithothamnia, with traces of algae and spores. The single specimen from *Pyura* also contained much lithothamnia in its gut.

P. tabularis

The largest member of the genus, *P. tabularis*, is distributed from the Cape Peninsula to Port St. Johns on the east coast, and is thus predominantly a south coast species (Stephenson 1944, Koch 1949). It is seldom found intertidally, but is fairly common in the infratidal fringe extending down to about four metres.

Almost invariably the larger individuals of over six cm are found on patches of *Ralfsia expansa* which covers many of the rocks subtidally. In this respect the limpet is comparable with *P. longicosta. P. tabularis* has also been reported on patches of *Hildenbrandtia* (Day 1969).

P. tabularis possesses a marked scar and undertakes short feeding excursions of up to 50 cm to graze mainly on *Ralfsia*. The gut contents consist almost entirely of this alga. The area around a large specimen of *P. tabularis* which is free from other algae suggests a feeding area of about 0·25 sq. m.

Smaller specimens are not rigidly associated with *Ralfsia* and cover greater distances of up to three metres from their scars while feeding. Nevertheless their guts are filled with *Ralfsia*. This applied even to a small specimen found on *Pyura*. This specimen was also of interest because the shell shape was unmodified, and when the *Pyura* was inverted the limpet did not react by dropping off as is the case with *P. barbara*.

Most large individuals are overgrown by a dense covering of algae, notably corallines, but no specific association with any of these algae is evident.

P. compressa

P. compressa is a west coast species, distributed from Lüderitz (U.C.T. records) to Cape Point (Stephenson 1939), with local outcroppings as far as Port Alfred on the south coast. Of all the members of the genus, *P. compressa* is most restricted in habitat, being confined almost entirely to the stipes and fronds of kelps, mainly *Ecklonia maxima* (Osbeck) Papenf. but also to a much lesser extent on *Laminaria pallida* Grev. ex J. Ag. (mainly in South West Africa). The distribution of these kelps is from Port Nolloth to respectively Cape Agulhas and Cape Point, and is thus coincident with the distribution of *P. compressa*. However, it is unlikely that this is the only factor limiting the distribution of the limpet, as *Ecklonia biruncinata* (Bory) Papenf. occurs on the south coast and is abundant from Port Elizabeth northwards: this alga would presumably provide a suitable substrate.

The behaviour of *P. compressa* on kelp has been analysed by R. Day of this department and much of his work is included below.

P. compressa normally occupies a scar on the stipe, but smaller individuals are usually found on the "hand" and fronds of the kelp, and at this stage the shell is flat and coincides with the shape of the hand. More mature animals shift down the stipe and the mouth of the shell becomes curved to fit the cylindrical stipe. At this stage the scar is between one and three metres from the surface of the water, but the position of the scar is periodically changed with growth of the animal.

Occasional specimens of *P. compressa* are found on rocks, and in these the shell is flattened to fit the rock.

The limpets always orientate along the axis of the stipe, with their anterior end upwards. This position allows maximal adherence, and minimal resistance to water movements. Specimens which are removed from kelp and kept in aquaria, rapidly orientate themselves so that they are vertical and the head is uppermost.

Feeding movements are extensive and may cover the entire kelp including the fronds. In most cases the limpets rasp away the cortex of the kelp and feed on it, leaving a characteristic trail of radula marks. In these animals the gut is filled solely with particles of kelp. In some cases the kelp is covered by epiphytic algae, notably *Suhria vittata* (L.) J. Ag., *Carpoblepharus flaccida* (Turn.) Kütz., ? *Polysiphonia* sp., *Bangia* sp., *Antithamnion* sp., and an unidentified green alga. In such cases both kelp cortex and epiphytes are eaten.

Ecklonia stipes are hollow and gas-filled so that they stand upright and are swayed from side to side by water movements. Consequently when the alga is torn free from the substrate, the whole plant rises to the surface in a horizontal position. When this occurs, *P. compressa* readily abandons the kelp, normally within 30 seconds. Once it has fallen off, the limpet clings rapidly to the first object it contacts. This behaviour is comparable with that of *P. cochlear* and *P. barbara*, and has the same survival value.

The factor inducing this response is not as definite as in *P. cochlear* or *P. barbara*. Change in orientation as the kelp swings up into a horizontal position may cause the limpets to drop off, as is the case with the above two limpets. However, wave action frequently swings kelp horizontally without inducing this behaviour, and kelp may be experimentally bent and fixed in a horizontal position, again with negative results (R. Day, pers. comm.).

Alternatively the different motion experienced at the surface may be important in initiating the behaviour.

Finally the pressure change as the kelp rises through the water may release the response.

The majority of *P. compressa* will drop off kelp immediately it rises to the surface, but some individuals persist in clinging to the alga. These are ultimately washed up on the shore and perish, and Smith (1890) records an instance of *P. compressa* reaching the shores of St. Helena on weed drifting from the Cape.

DISCUSSION

Rocky shores are known to be areas of high speciation. This is primarily due to the diversity of habitats which is present. Within a short distance ecological variables may change entirely. Among these the most important are probably the external temperature and humidity, for these affect directly the desiccation an animal is subjected to while exposed. In addition, water temperature, wave action, salinity, substrate structure, and availability of food also vary a great deal intertidally, and will encourage speciation and zonation.

In this connection the limpets are obvious examples; all the South African Patellidae are intertidal or infratidal in their distribution.

Limpets are well adapted to an intertidal existence. The conical shell covers the animal completely and may be closely applied to the substratum to prevent loss of water during exposure. Normally the space between the shell and the animal retains water: this not only prevents desiccation, but allows slow evaporation to cool the animal. The shell also protects against abrasion and predators, and provides minimal resistance to water movements. It is interesting that such a shell has been evolved by such diverse families as the Patellidae, Acmaeidae, and Siphonariidae, all of which occupy the intertidal zone and have the same browsing habit.

The mantle cavity of *Patella* is richly lined with blood vessels and may act as a respiratory organ in air (Davis and Fleure 1903).

The eleven species of *Patella* are fairly rigidly zoned both vertically and horizontally. Thus there is relatively little overlap between their habitats, and competition is reduced. A comparable situation exists on the Pacific coast of North America, where Test (1945) has shown that the 17 species of *Acmaea* are restricted either in habitat or food requirements, so that with the exception of three species, no interspecific competition occurs.

In the case of *Patella*, zonation and distribution is such that overlap occurs only between *P. argenvillei* and *P. cochlear;* and between *P. miniata*, *P. barbara* and *P. tabularis*. It is significant that the food requirements of each species are very different. *P. cochlear* feeds predominantly on lithothamnia, and *P. argenvillei* on a wide variety of algae. This reflects their different feeding habits: *P. cochlear* remains closely applied to the rock and feeds on encrusting algae, while *P. argenvillei* readily climbs on to more bushy algae. In the second case, *P. tabularis* and *P. miniata* are restricted to respectively *Ralfsia* and lithothamnia while *P. barbara* feeds on a variety of algae.

This supports the Gause principle that species which co-exist may not have the same ecological requirements.

FACTORS EFFECTING ZONATION

The fairly rigid zonation of limpets is probably due to a multiplicity of factors, acting either on the larva or the adult:

Food

The availability of food is unlikely to be a limiting factor in most cases. With the exception of four species, *P. longicosta*, *P. cochlear*, *P. miniata* and *P. tabularis*, the limpets feed on a wide variety of algae and are probably unrestricted in diet. The distribution of *P. longicosta* does not coincide with lithothamnion or *Ralfsia*, the two principal foodplants. *Ralfsia* occurs around the entire South African coastline (Stephenson 1947) from the upper Balanoid to a depth of six metres. Similarly different species of the lithothamnion group extend around the entire coast although mainly restricted to the infratidal and Cochlear zones. Isolated patches of lithothamnion species occur further up the shore, and it is on these that smaller *P. longicosta* are found.

The case for *P. tabularis* is similar, and there is no correlation between its distribution and zonation and that of *Ralfsia*, on which it is usually found.

P. miniata is more closely associated with lithothamnion, but the latter extends into the intertidal zone whereas the former is largely infratidal.

In the Cochlear zone there is a marked association between *P. cochlear* and lithothamnia, and the zonation of the limpet coincides with the upper limit of lithothamnia. Furthermore, the experiments described above (p. 25) indicate that adult *P. cochlear* will not settle if lithothamnion is lacking. Thus in the case of this limpet the upper limit of zonation may be correlated with the foodplant. However, the lower limits of these two are entirely different. Furthermore *P. cochlear* is restricted in its distribution to the south coast and the more southern aspects of the east and west coasts while the lithothamnion group is virtually ubiquitous.

The upper limit of *P. oculus* may also be related to availability of food, as animals isolated high on the shore are small and misshapen when food is not adequate (p. 10). This may also be related to the greater desiccation experienced here.

Thus although some limpets are specific to their foodplants, this is unlikely to be a limiting factor in zonation and distribution. This is in agreement with Orton's (1929) findings, that food often occurs well above the upper limit for *P. vulgata*. Contrary to this, Das and Seshappa (1948) consider food to be most important in determining the upper extremes of zonation in the same species. More critical observations by Lewis (1954) support the contentions of Orton.

Pollock (1966, unpublished) has discussed how the shape of the radula teeth differs between the species and how this is related to habitat. *P. granularis*, *P. oculus* and *P. granatina* all inhabit the upper portion of the shore and possess heavily chitinised strong pointed teeth, associated with the desiccated algae and lichens which occur in this area. *P. longicosta*, *P. cochlear* and *P. argenvillei* occupy the lower part of the shore where algae are more available and less desiccated. Their teeth are less heavily chitinised, smaller, but still pointed. The predominantly infratidal species, *P. tabularis*, *P. miniata* and *P. barbara*, have rounded or square teeth. *P. compressa* has markedly truncate or even concave cutting surfaces to its teeth, associated with the soft, smooth surface of the kelp stipe.

Salinity

Broekhuysen (1940) has shown for six species of prosobranch molluscs that tolerance to extreme salinities is related to their zonation: those inhabiting the upper shore having the greatest tolerance. Allanson (1958) has shown a similar correlation with four species of *Siphonaria*. In the case of *Patella*, tolerance to extremes of salinity is unlikely to be a limiting factor in zonation, as only *P. barbara* and *P. miniata* regularly inhabit intertidal pools, and these are low on the shore where salinity changes will be minimal due to frequent tidal flushing. Furthermore, Arnold (1957) describes how *P. vulgata* reacts negatively to splashing with freshwater and positively to sea water, so that rainwater pools will be avoided.

Desiccation

Using the same animals described above, Broekhuysen and Allanson have produced evidence that zonation is closely associated with resistance to desiccation and temperature. Their conclusions have been verified by the more critical work of Brown (1960).

On British shores, *P. aspera* is confined to the lowest part of the shore, while *P. vulgata* extends from low water spring tide to high water neap tide. Using three groups of animals, *P. aspera*, low level *P. vulgata* and high level *P. vulgata*, Davies (1969) has shown that when desiccated, *P. aspera* loses water faster than low level *P. vulgata*, while rate of water loss is least in high level *P. vulgata*. Furthermore, the lethal thermal limit is highest in high level *P. vulgata*, intermediate in low level specimens and lowest in *P. aspera*. Davies has also proved that water loss and temperatures normally experienced in the field never approach lethal limits, so that as isolated factors they are not limiting. He suggests that the upper limit of distribution is set by a combination of water loss and tolerance during exposure, and the rate water is recovered during immersion.

Desiccation is probably the most important single factor limiting the vertical distribution of limpets although no quantitative data are available for South African species. It has already been mentioned that the limpet shell is an ideal shape to reduce loss of water. The habit of returning to a fixed home scar enhances this asset, as the shell becomes moulded to the substrate. This habit varies not only from one species to another, but within one species. Thus high level specimens of *P. granularis* have marked scars while those lower down the shore may lack scars. *P. barbara* possesses a scar, but orientation to the scar is limited, and *P. miniata* often lacks a scar. These two species are predominantly sublittoral so that a rigid homing behaviour is not essential. *P. compressa*, although sublittoral, has a well defined scar on the kelp, presumably because of the considerable and often violent water movements that may occur in kelp beds. Even in sublittoral species a scar may be of survival value as predators will have greater difficulty in removing a limpet if it fits the contour of its substrate. *P. cochlear* has the most pronounced scars and a rigid homing behaviour. This is in keeping with the fact that it occupies areas of fairly strong wave action and abrasion. In addition the Cochlear zone, being low on the shore, is subjected to wave action and water movement for greater lengths of time than areas higher on the shore.

Feeding excursions in intertidal species are correlated with the tides, and movement away from the scar occurs only when the animals are wet by the incoming tide. *P. granularis*, which is presumably more resistant to desiccation than other *Patella* spp., feeds when the rock is moist. *P. oculus* and *P. granatina* must be wave washed before they will move, while *P. longicosta* is normally immersed completely. *P. argenvillei* and *P. cochlear* are induced to move from their scars when water movement occurs over them, with the incoming tide.

In contrast, the infratidal species (*P. barbara*, *P. miniata*, *P. tabularis* and *P. compressa*), leave their scars at irregular periods, unconnected with the tides.

P. barbara, *P. cochlear*, *P. compressa* and to a lesser extent *P. argenvillei*, all abandon their substrate when disturbed, particularly when they are inverted. This habit is either lacking or poorly developed in other limpets. This is related to the stability of the substrate which the different species normally inhabit. Large numbers of *P. cochlear* and *P. argenvillei* live on the shells of larger individuals, and are subjected to strong wave action where the host shell may be wrenched off the rock. *P. barbara* and *P. compressa* may occur respectively on *Pyura* and kelp, which may be torn free in violent seas. The substrate of the remaining species is relatively stable.

Wave Action

P. cochlear is associated with shores where moderate to strong wave action occurs (Stephenson 1944), and the absence of this animal from sheltered regions is so marked that wave action may be a limiting factor in its distribution.

Light

Light evidently plays little part in habitat selection, as all the species concerned occur where they are exposed to direct sunlight. The lower limit of infratidal limpets may be affected by the penetration of light, which will determine the depth to which algal food will occur.

Substrate

The nature of the substrate influences limpet distribution considerably. The relative absence of limpets from Strandfontein is attributable to the crumbly and jagged rock. A smooth and gradually sloping rocky substrate generally bears maximal numbers of limpets.

Temperature

Temperature obviously plays a major part in the geographical distribution of the species, as is reflected by the precise restriction of several species to either the cold west or warmer south and east coasts. Water off the west coast is known to be rich in organic matter, and this may explain the relatively greater size of several species of limpet on this coast.

Even on a local scale, the distribution of limpets in False Bay reflects the importance of temperature. Cold water species are restricted to the west and east shores of the bay, and warm water species are more abundant on the north shores. In a relatively restricted area such as this, the amount of nutrient matter is unlikely to affect the distribution, so that the effect of temperature is more obvious.

Larval Behaviour

Zonation of the different species will also be affected by the tolerance of larvae to physical conditions. Nothing is known about the larval behaviour of South African limpets.

Settlement of *P. vulgata* larvae and young is known to be greater in moderate wave action than in shelter (Fischer-Piette 1948) and exposure of the young is essential (Hatton 1936).

Acclimation

Ability to tolerate physical extremes is not an absolute measure of the conditions under which a species may exist, as acclimation may occur. Arnold (1957) has shown that high level populations of *P. vulgata* react to and avoid salinity extremes far more than low level populations, in keeping with the conditions they respectively experience. This ability to acclimate will also affect zonation of the species.

Davies (1966, 1967) describes how high level *P. vulgata* are able to acclimate, and have a lower respiratory rate during summer when compared with low level specimens. Furthermore, they have a relatively lower Q_{10}, so that increased temperature will affect metabolic rate relatively little. Davies suggests that *P. aspera* lacks the ability to acclimate in these ways, so that it is restricted to the lower shore where extreme temperatures are not experienced.

BIOTIC RELATIONSHIPS

Limpets have a profound influence on algal growth. Clearing of areas in the present work, and comparable work by Bokenham (1938) and Jones (1946), has shown that algal growth may increase tremendously in the absence of limpets. The Cochlear zone, for example, normally has a limited algal growth on the rocks, except for lithothamnia and limpet gardens. After removing all limpets from various areas in the Cochlear zone, between nine and fifteen species of algae appeared within four months. Furthermore, the amount of alga present had increased enormously. Browsing of limpets accounts for large quantities of alga, but more important than this, it eradicates all algal spores settling on the substrate, thus preventing the establishment of several species. This accounts for the barren state of rocks surrounding limpets in comparison with the heavy algal growth on limpet shells. Moore (1938) has analysed the food requirements of *P. vulgata* in relation to algal production.

Limpets house a wide variety of animals under their shells, including amphipods, isopods, copepods, turbellarians and polychaetes. Most of these are casually associated with the limpets and are afforded protection from desiccation when the shore is exposed. This habit has led to more intimate relationships so that a few species are now commensal with limpets in general, or even with specific limpets. (As discussed above, p. 3.)

Predators of *Patella* are largely unknown, but the suckerfish, *Chorisochismus dentex* (Pallas) frequently contains whole limpet shells in its gut. Other fish probably also feed on limpets. Test (1945) lists Oyster Catchers, rodents, raccoons, fish and probably crabs as being predators of *Acmaea*. As *Acmaea* spp. are generally smaller and more fragile than *Patella* spp. the latter are less likely to fall prey to comparable animals.

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SUMMARY

1. A description is given of the relative movement and feeding habits of the ten species of *Patella* occurring in the Cape Peninsula, South Africa, correlated with their zonation.

2. The species are zoned fairly rigidly in the following sequence:

P. granularis
P. oculus and *P. granatina*
P. longicosta } Intertidal
P. cochlear and *P. argenvillei*
P. barbara
P. miniata
} Infratidal
P. tabularis
P. compressa

3. Of these species, only 5 are restricted in diet: *P. cochlear* and *P. miniata* feed on lithothamnia, *P. longicosta* and *P. tabularis* on *Ralfsia* and *P. compressa* on *Ecklonia*. The remaining species feed on any available algae, lichens, diatoms and spores. Where species are co-existent, their diets differ. *P. longicosta* changes its diet at different stages and occupies *Ralfsia* gardens at maturity. This association is in no way obligatory.

4. *P. cochlear* has algal "gardens" of *Herposiphonia* and *Gelidium*. The former is cropped back by the limpets and is protected only in the immediate vicinity of the scar. The latter is apparently physiologically dependent on the limpet.

5. Most species of *Patella* inhabit "home scars". This habit is best developed in intertidal species. Movement from the scar is correlated with tidal rhythms in intertidal species. The suggestion is put forward that the scar acts as a releaser inducing adult settling.

6. Species inhabiting unstable substrates readily abandon a shifting substrate. The factor inducing this is a change of vertical orientation.

REFERENCES

ALLANSON, B. R. 1958. Some aspects of the ecology of the molluscan genus *Siphonaria* in South Africa. *Portug. Acta Biol.* (B) 6 (2): 179–212.

ARNOLD, D. C. 1957. The response of the limpet *P. vulgata* to waters of different salinities. *J. mar. Biol. Assoc. U.K.* 36: 121–128.

ATKINS, G. R. 1970. Thermal structure and salinity of False Bay. *Trans roy. Soc. S. Afr.* 39 (2): 117–128.

BARNARD, K. H. 1963. Contributions to the knowledge of South African marine Mollusca. Pt. IV. Gasteropoda: Prosobranchiata: Rhipidoglossa Docoglossa. Tectibranchiata. Polyplacophora. Solenogastres. Scaphopoda. *Ann. S. Afr. Mus.* 47: 201–360.

BECKETT, T. W. 1968. Limpet movements – an investigation into some aspects of limpet movements, especially the homing behaviour. *Tane* 14: 43–63.

BOKENHAM, N. A. H. 1938. The colonisation of denuded rock surfaces in the intertidal region of the Cape Peninsula. *Ann. Natal Mus.* 9 (1): 47–81.

BRIGHT, K. M. F. 1938. The South African intertidal zone and its relation to ocean currents. III. An area on the northern part of the west coast. *Trans. roy. Soc. S. Afr.* 24 (1): 67–88.

BROEKHUYSEN, G. J. 1940. A preliminary investigation of the importance of desiccation, temperature, and salinity as factors controlling the vertical distribution of certain intertidal marine gasteropods in False Bay, South Africa. *Trans. roy. Soc. S. Afr.* 27 (3): 255–292.

BROWN, A. C. 1960. Desiccation as a factor influencing the vertical distribution of some South African Gasteropoda from intertidal rocky shores. *Portug. Acta Biol.* (B) 7 (1), 11–23.

COHEN, C. 1948. The breeding seasons of *Patella.* University of Cape Town. Unpublished thesis.

DAS, S. M. and SESHAPPA, G. 1948. A contribution to the biology of Patella: on population distribution and sex proportions in *Patella vulgata* Linnaeus at Cullercoats, England. *Proc. zool. Soc. London.* 117: 411–423.

DAVIES, P. S. 1966. Physiological ecology of *Patella.* I. The effect of body size and temperature on metabolism. *J. mar. Biol. Assoc. U.K.* 46: 647–658.

DAVIES, P. S. 1967. II. Effect of environmental acclimation on the metabolic rate. *Ibid* 47: 61–74.

DAVIES, P. S. 1969. III. Desiccation effects. *Ibid.* 49: 291–304.

DAVIS, J. R. A. and FLEURE, H. J. 1903. *Patella* (The Common Limpet) L.M.B.C. Memoirs X. Williams & Norgate, Liverpool.

DAY, J. H. 1969. *A Guide to Marine Life on South African Shores.* Balkema, Cape Town.

DAY, J. H. 1970. The general biology of False Bay. *Trans. roy. Soc. S. Afr.* 39 (2): 211–221.

EVANS, R. G. 1947. Studies on the biology of British limpets. *Proc. zool. Lond.* 117: 411–423.

EVANS, R. G. 1953. Pt. II. *Ibid.* 123: 357–376.

FISCHER-PIETTE, E. 1948. Sur les elemente de prospérité des Patelles et sur leur spécificité. *J. Conchyliol.* 88: 45–96.

HATTON, H. 1936. Observations sur l'habitat et sur la croissance de *Patella vulgata.* L. *Bull. lab. maritime Dinard.* 15: 17–20.

HYMAN, L. H. 1967. The Invertebrates Vol. VI. Mollusca I. McGraw-Hill, New York.

JONES, N. S. 1946. Browsing of *Patella. Nature* 158: 557.

KOCH, H. J. 1949. A review of the South African representatives of the genus *Patella* Linnaeus. *Ann. Natal Mus.* 11 (3): 487–517.

LEWIS, J. R. 1954. Observations on a high-level population of limpets. *J. Anim. Ecol.* 23: 85–100.

LEWIS, J. R. 1964. *The Ecology of Rocky Shores.* English Universities Press, London.

MACNAE, W. and KALK, M. 1958. *The Natural History of Inhaca Island, Mocambique.* Witwatersrand University Press, Johannesburg.

MOORE, H. B. 1934. The relation of shell growth to environment in *Patella vulgata. Proc. malacol. Soc. London.* 21 (3): 217–222.

MOORE, H. B. 1938. Algal production and food requirements of a limpet. *Proc. malacol. Soc. Lond.* 23 (3): 117–118.

MOORE, H. B. 1958. *Marine Ecology.* John Wiley & Sons, New York.

MORGAN, C. L. 1894. The homing of limpets. *Nature* 51: 127.

MORGANS, J. 1958. The benthic ecology of False Bay. Pt. I. The infratidal zone observed by diving, related to infratidal rocks. *Trans. roy. Soc. S. Afr.* 35 (5): 381–441.

MORTON, J. and MILLER, M. 1968. *The New Zealand Sea Shore.* Collins, London.

ORTON, J. H. 1928a. Observations on *Patella vulgata* Pt. I. Sex phenomena breeding and shell growth. *J. mar. Biol. Assoc. U.K.* 15: 851–862.

ORTON, J. H. 1928b. Pt. II. Rate of growth of shell. *Ibid.* 15: 863–874.

ORTON, J. H. 1929. Pt. III. Habitat and habits. *Ibid.* 16: 277–288.

ORTON, J. H. 1946. Biology of *Patella* in Great Britain. *Nature* 158: 173.

PENRITH, M.-L. and KENSLEY, B. 1970. The constitution of the fauna of rocky intertidal shores of South West Africa. Part II. Rocky Point. *Cimbebasia* (ser. A) 1 (10): 243–268.

POLLOCK, D. E. 1966. The feeding habits of the Cape limpets of the genus *Patella* Linnaeus. Unpublished project. University of Cape Town.

RAO, K. P. 1953. Shell weight as a function of intertidal height in a littoral population of pelecypods. *Experientia* 9 (12): 465.

RUSSELL, E. S. 1907. Environmental studies on the limpet. *Proc. zool. Soc. Lond.* 1907: 856–870.

SHOTWELL, J. A. 1950. The vertical zonation of *Acmaea*, the limpet. *Ecol.* 31 (4): 647–649.

SMITH, E. A. 1890. Report on the marine molluscan fauna of the island of St. Helena. *Proc. zool. Soc. Lond.* 1890: 247-317.

SNELI, J. A. 1968. The Lithothamnion community in Nord Möre Norway. With notes on the epi fauna of *Desmarestia viridis* (Müller) *Sarsia* 31: 69–74.

STEPHENSON, T. A. 1936. The marine ecology of the South African coasts, with special reference to the habits of limpets. *Proc. Linn. Soc. Lond.* 148: 74–79.

STEPHENSON, T. A. 1939. The constitution of the intertidal fauna and flora of South Africa. Pt. I. *Journ. Linn. Soc.* (*Zool.*) 40: 487–536.

STEPHENSON, T. A. 1944. Pt II. *Ann. Natal Mus.* 10 (3): 261–358.

STEPHENSON, T. A. 1947. Pt III. *Ibid.* 11 (2): 207–324.

TEST, A. R. 1945. Ecology of California *Acmaea. Ecol.* 26: 395–405.

ADDENDUM

Since going to press, the work of Mr. B. Kemsley and Dr. M.-L. Penrith of the South African Museum has extended the distribution records in South West Africa and Angola. Of the South African species of *Patella*, only *P. granularis* extends into Angola, where *P. safiana* is the dominant species.

SECTION II:

PATELLA CONCOLOR: ZONATION, FEEDING AND MOVEMENTS, WITH A NOTE ON THE EFFECTS OF HUMAN CONSUMPTION.

THE ECOLOGY OF PATELLA CONCOLOR: ZONATION, FEEDING & MOVEMENTS.

The intertidal rocky shores of South Africa are divisable into three faunistic regions. In general the cold west coast fauna is distinct from the warmer south coast element, and the subtropical east coast species (Stephenson, 1939). Most of the *Patella* spp. extend into either the west or the south coast regions and have been described in a previous paper (Branch, 1971). Only *P. concolor* is restricted to the East coast.

Krauss (1848) recognised several subspecific colour variations of *P. variabilis* including *P. variabilis concolor*. Justification for these subspecies is tenuous, as the colour variations are numerous and show no constancy with respect to distribution or zonation. The following colour variations are common: yellow with brown rays, black, russet, yellow with brown spots, and white with black rays.

Krauss' subspecific name *concolor* has now been proposed as a specific name to replace the preoccupied *P. variabilis* (Kilburn, in press).

The present paper deals with the zonation, feeding and movements of *P. concolor*. Mention is also made of the biology of *Cellana capensis* as a possible competitor with *P. concolor*. Details of the interaction between these two limpets will be considered in a subsequent section.

Material & Methods.

Collections of both *P. concolor* and *C. capensis* were made at various sites including East London, Port St. Johns, Cintza, Bulugha, Lwandile, Bashee River Mouth, St. Lucia and Xai Xai. Quantitative transects were made at Lwandile (31° 53'S, 29° 15'E) and at Cintza (32° 53'S, 28° 6'E), and 0.25m^2 quadrats used to assess densities. Gut contents were examined from 50 specimens of each species, covering a wide range of sizes. Daily photographs were taken for 2 weeks at fixed sites to determine the amount of movement taking place.

I am most grateful to Mrs. Giles of Cape Town for access to her collection of P. concolor, which has been made systematically over the past five years in the Transkei. This has enabled assessment of the effects of human consumption on the populations of P. concolor.

Gonads were dissected out whole and weighed wet. Smears of each gonad were microscopically examined and the ovaries graded according to whether they were mature (containing only mature ova), immature (with a mixture of ova and oocytes), or spent (filled with interstitial tissue and obviously deflated).

ECOLOGY:

Patella concolor

P. concolor has been recorded from Richmond (near Port Elizabeth) to Cape Vidal (Day, 1969), but a single specimen recorded from Xai Xai in Mocambique now extends its northern limits. Typically it occurs in the balanoid zone. Intertidal pools may extend the upper limits (Fig. 1). In areas of relatively strong wave action, such as Lwandile, the zonation is extended considerably up the shore (fig. 1) in comparison with more sheltered areas such as Cintza (fig. 2).

Fig 1 Transect at Lwandile

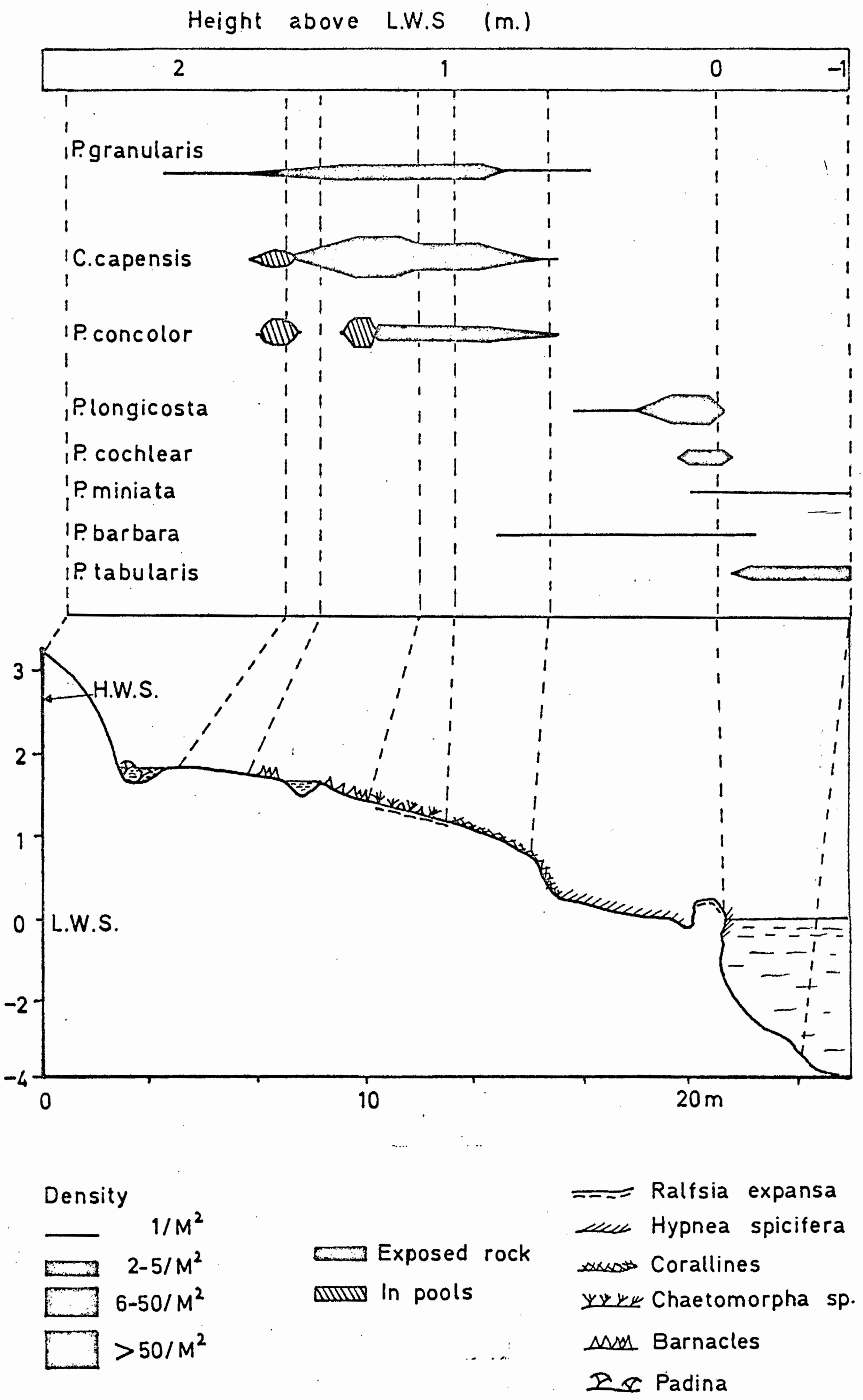
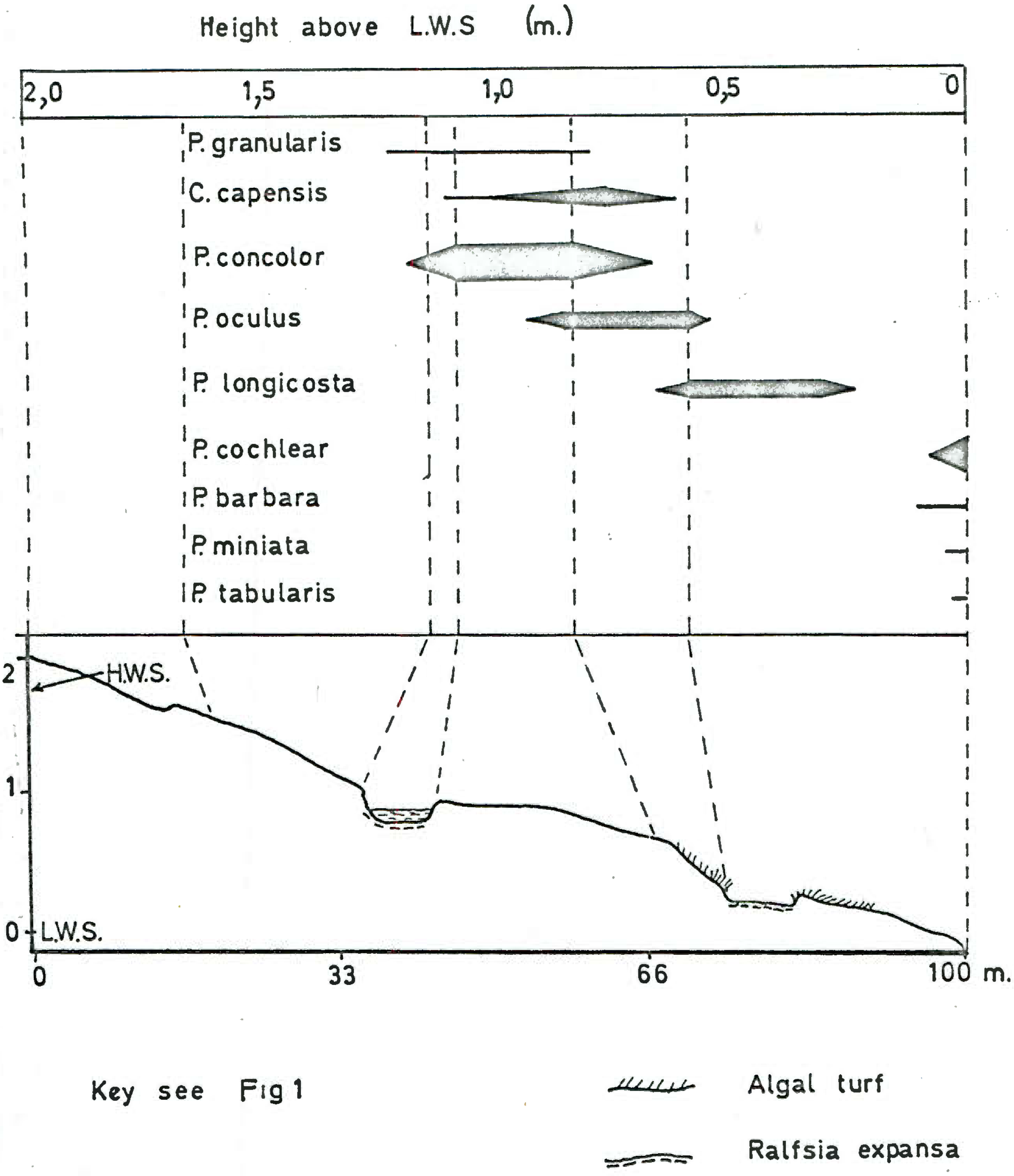
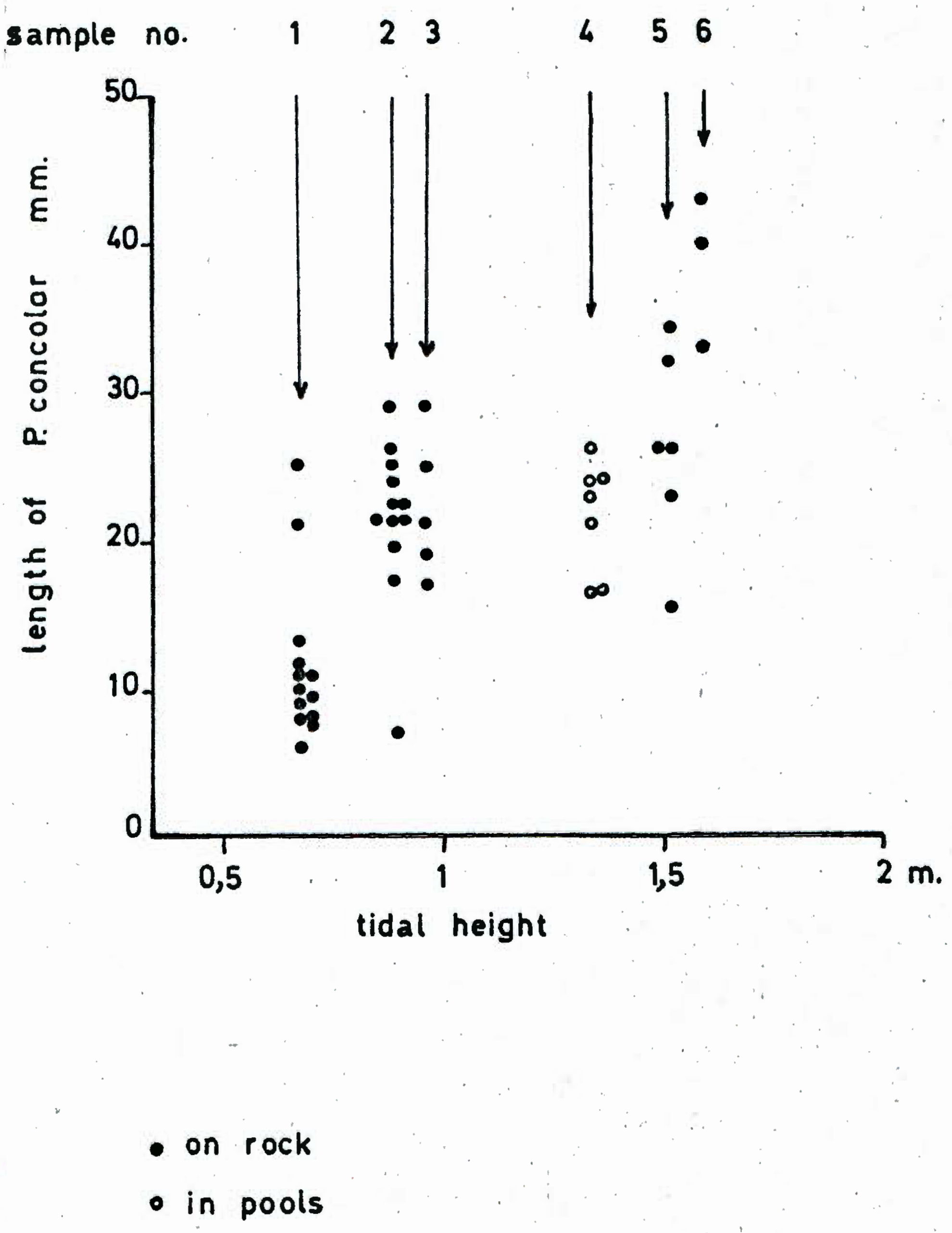


Fig. 2 Transect at Cintza



Key see Fig 1

Fig. 3


sample no.
1
2
3
4
5
6
length of P. concolar mm.
50
40
30
20
10
0
0,5
1
1,5
2 m.
tidal height
● on rock
○ in pools

Examination of gut contents reveals a great variety of food substances. About 60% contained large quantities of sand, comprising roughly 80% of the gut contents, and small amounts of diatoms, sponge spicules and algal fragments. 32% of the specimens contained a mixture of algae, lichens and detritus, while a few animals had eaten only a single species of alga. Most of the algal fragments were unidentifiable, but the following could be recognised: ? Polysiphonia sp., Ralfsia expansa, Chaetomorpha sp., Enteromorpha sp., "lithothamnion" and jointed corallines. In general the diet is that of a generalised grazer, and P. concolor appears to rasp almost randomly over the substrate, devouring all particles in its path. Organic detritus blown ashore in spume is also eaten. Even the unusually large amounts of sand in the gut of many specimens must yield a certain amount of nutriment as they are often coated with dried spume and probably bear bacterial populations.

The radula teeth terminate in sharply pointed cusps (Koch, 1949), in common with all other limpets living fairly high up the shore: presumably an adaptation to rasping desiccated and hard food.

There is a marked tendency for small specimens to be found low on the shore, in crevices, or even covered completely by sand. Specimens left exposed on dry rock by the receding tide were observed migrating a few centimetres down a rock and forcing their shells under damp sand. Juveniles clearly prefer moist situations and are intolerant of dry hot conditions. Larger specimens are found higher up the shore: the majority still occur on moist rocks or in pools, but very large individuals may occur on bare rock (fig. 3).

A similar relationship between zonation and size has been found in P. vulgata in Britain (Jones,1948; Das & Sesheppa,1948; Lewis,1954), and also in Acmaea digitalis in California. In the latter case, an upward winter migration and a lesser downward spring migration have been shown by Frank (1965) and by Breen (1973).

There is thus probably a general tendency for many limpets to migrate up the shore, so that older and larger individuals are found in the upper regions. This is certainly true of P. concolor at both Lwandile and Cintza. Such a zonation according to size is logical in terms of physical stresses, as smaller individuals lose water faster (Davies, 1969) and are presumably less tolerant to desiccation.

Most large P. concolor (over 35mm) possess a home scar to which they return after feeding. Photographic records at daily intervals show that this behaviour is variable. Of 50 specimens, 36 remained on (or returned to) their scars for the complete 10 days of observation at Lwandile. Seven remained for part of the time, and seven moved every few days.

Small individuals (under 20mm) do not possess fixed scars, but have a tendency to return to the same general area after feeding. Frequently they may retreat into crevices in small groups, or force their way under moist sand.

Some species of upper-shore limpets form aggregates or clusters. Lewis (1954) has described this in high level P. vulgata, and Breen (1973) in A. digitalis. Willoughby (1973) has shown that a high proportion of A. digitalis are in contact with one another, and suggests that this contact is necessary before an animal will settle. Juveniles of P. concolor may form small groups in crevices, but this is probably simply a reaction to moisture and not due to contact. Adult P. concolor space themselves and are seldom in contact.

Cellana capensis

Extending from Port Alfred to Northern Mocambique (Kalk, 1959) the distribution of C. capensis overlaps with that of P. concolor. In addition, it also predominates in the balanoid zone, thus increasing the overlap in habitats. At Lwandile C. capensis extends higher up the shore than P. concolor (fig. 1) while at Cintza the reverse is true (fig. 2).

Examination of gut contents indicated a diet essentially similar to that of P. concolor. A small number contain quantities of sand in their intestine, but most had a mixture of algal fragments, diatoms, sponge spicules, unidentifiable organic debris, and even occasional copepod exoskeletons. Algae which could be identified were Ralfsia expansa, lithothamnion, and Padina sp. As in P. concolor the diet is typical of a generalised browser, feeding on any available material, and rasping up quantities of indigestible substances in the process.

Although the homing behaviour of Cellana was not examined in detail, they appear to return to a fixed scar more frequently than P. concolor, and even relatively small individuals may possess scars. Unlike P. concolor there was no obvious correlation between zonation and size at either Lwandile or Cintza.

P. concolor changes its position frequently and appears to migrate up the shore, while C. capensis has a more rigid homing behaviour and does not migrate. This is similar to the situation

Fig 4

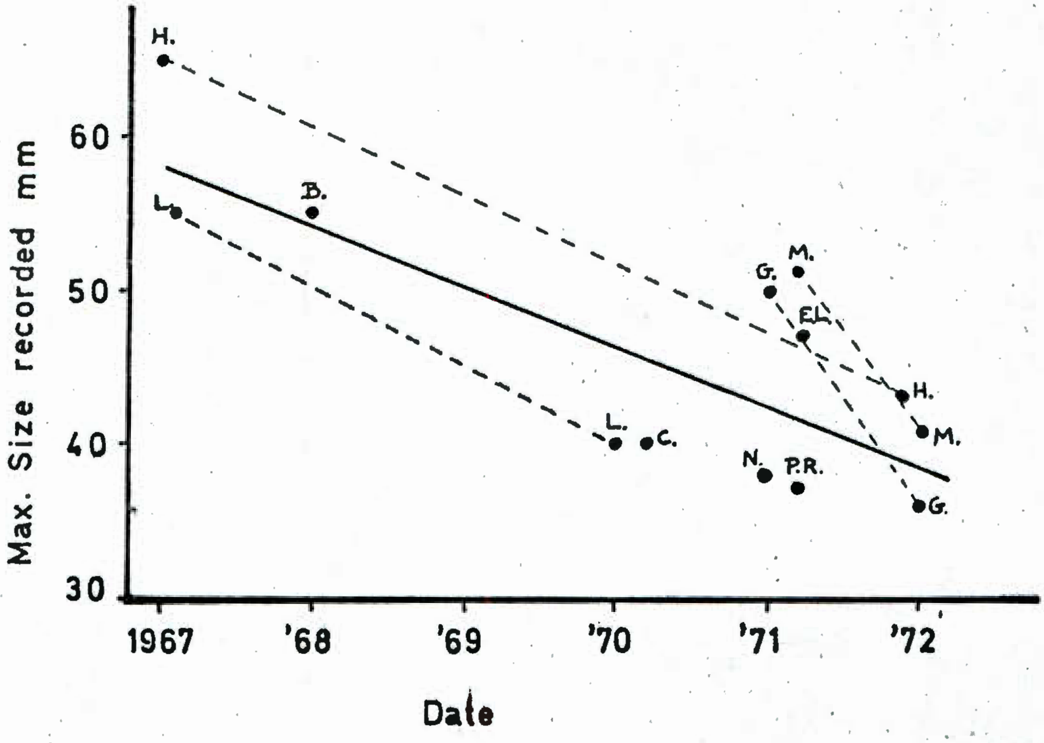


FIG. 4. SIZE OF P. CONCOLOR

Isolated records have been included to show the overall reduction in size. The regression gives an approximation of the average reduction.

H. Haga Haga
B. Bulugha Mouth
C. Coffee Bay
G. Gonubie
E.L. East London.
M. Mboyti
P.R. Park Rynie
N. Nthlonyane
L. Lwandile.

described by Haven (1971) in which Acmaea digitalis moves up the shore and forms loose clusters, while A. scabra is solitary, has a fixed homing behaviour, and does not migrate seasonally.

Human consumption of P. concolor

For many years the Bantu of the Transkei have supplemented their diet by collecting intertidal molluscs. Over the past five years, with crop failure and droughts coinciding, the collecting of molluscs has been intensified. This has led to a dramatic reduction in densities and average sizes of some molluscs. P. concolor and C. capensis are particularly susceptible, as they predominate in the balanoid zone and are thus accessible at all low tides: in addition they are favoured because they yield a reasonable quantity of meat, and the flesh is easily removed. The entire animal is eaten, after removal of the radula from larger specimens.

An obvious change in the populations of P. concolor has been noted at the following sites: Haga Haga, Lusikisiki, Lwandile, Mboyti (near Lusikisiki), Qolora and Gonubie. No monitoring of this effect has been attempted, but Giles (pers. comm.) has systematically collected specimens of P. concolor from various sites on the East coast over the past five years. Measurements of the largest specimens from this collection indicate the progressive reduction in maximum size (fig. 4). In most areas a reduction of about 15 to 20mm has occurred in the maximum size, over the last three to five years.

DISCUSSION:

P. concolor and C. capensis are both generalised browsers, feeding on any available food material. This is similar to the diet of P. granularis, P. oculus, and P. granatina in the Cape Peninsula (Branch, 1971), P. vulgata in Britain (Moore, 1938; Southward, 1964), and Acmaea digitalis and A. scabra in California (Test, 1945). Thus it appears a general principle that high level species of limpet are generalised in their feeding habits, while low level and subtidal species may be very specialised. Examples of the latter group are P. longicosta, P. miniata, P. cochlear, P. tabularis and P. compressa (Branch, 1971); Patina pellucida on Laminaria (Graham and Fretter, 1947); and Acmaea paleacea on the blades of Phyllospadix torreyi (Yonge, 1962).

This differentiation is logical, as the upper shore supports little macroscopic algal life, and limpets in this region must feed on any available material, including washed up debris and spume. Lower on the shore, and subtidally, algae are abundant and specialised feeding is not only possible, but preferable in terms of reduced competition.

Clearly P. concolor and C. capensis are possible competitors for food: their interspecific relationship will be described in greater detail in a later section.

P. oculus normally occupies the upper balanoid. It is distributed principally on the South coast, extending as far north as The Haven on the East coast. The potential overlap between P. oculus and P. concolor is avoided, because towards the extremes of its distribution on the East coast, P. oculus is restricted to a much narrower band lower on the shore, and is limited to the lower balanoid (fig. 2). This is a general principle applicable to most intertidal organisms: that zonation and choice of habitat

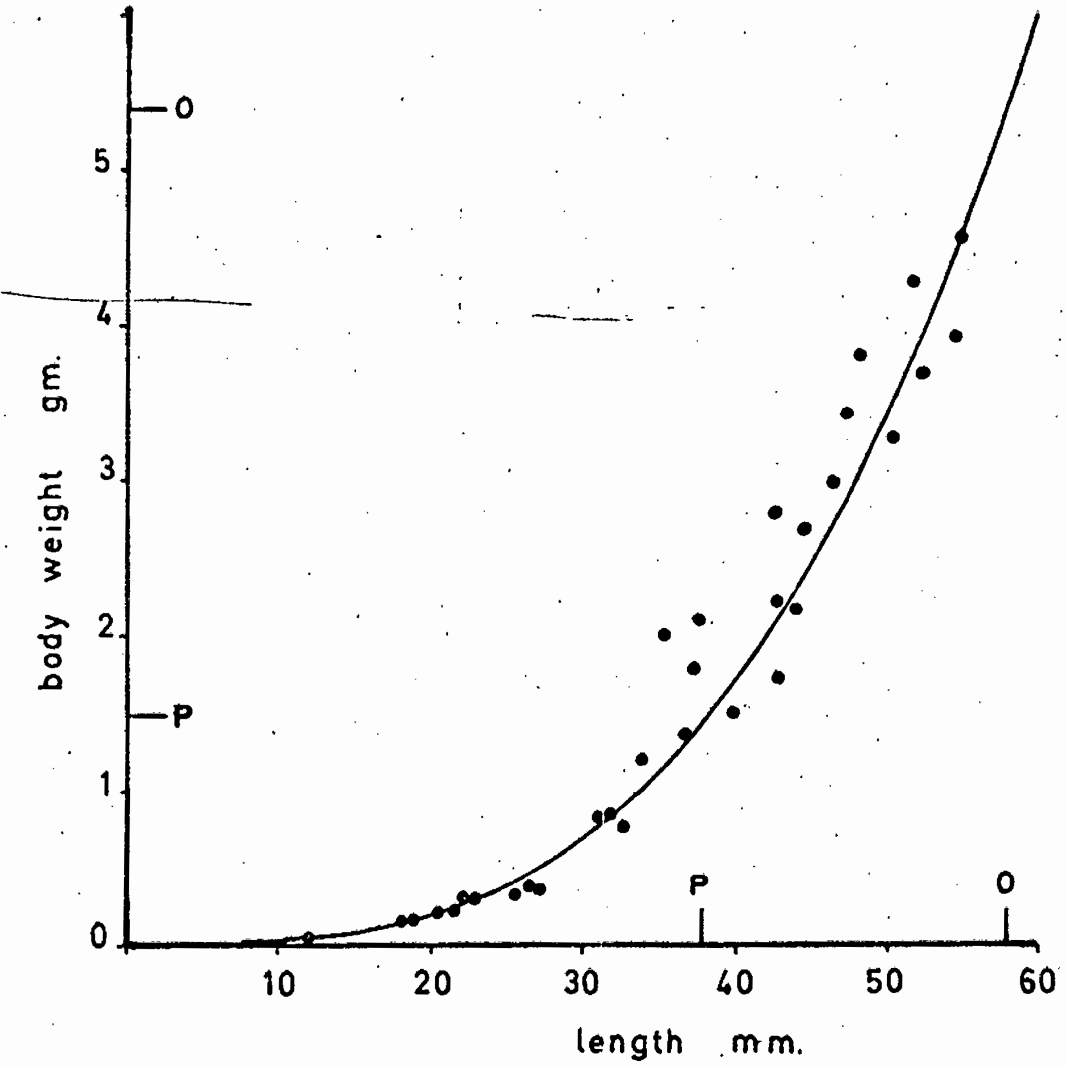


FIG. 5. LENGTH-WEIGHT RELATIONSHIP IN P. CONCOLOR

O and P indicate the original and present maximum lengths and weights, as deduced from the regression in figure 4.

become restricted at the extremities of distribution. An instance of this had already been described for P. granatina (Branch, 1971).

The consumption of shellfish on the Transkei coast has clearly had an effect on the populations of P. concolor, reducing the maximum size of specimens considerably. This reduction is more dramatic when consideration is given to the wet body weight and to gonad output. Figure 5 shows the exponential relationship between shell length and wet flesh weight. This is expressed by the function:

$$w = cl^{b}$$

where l = length

c = intercept of y axis

w = wet flesh weight

b = exponential relationship

Logarithmic transformation yields a linear relationship from which c and b can be calculated to yield the relationship:

$$w = 0.000\,0229\ l^{3.05}$$

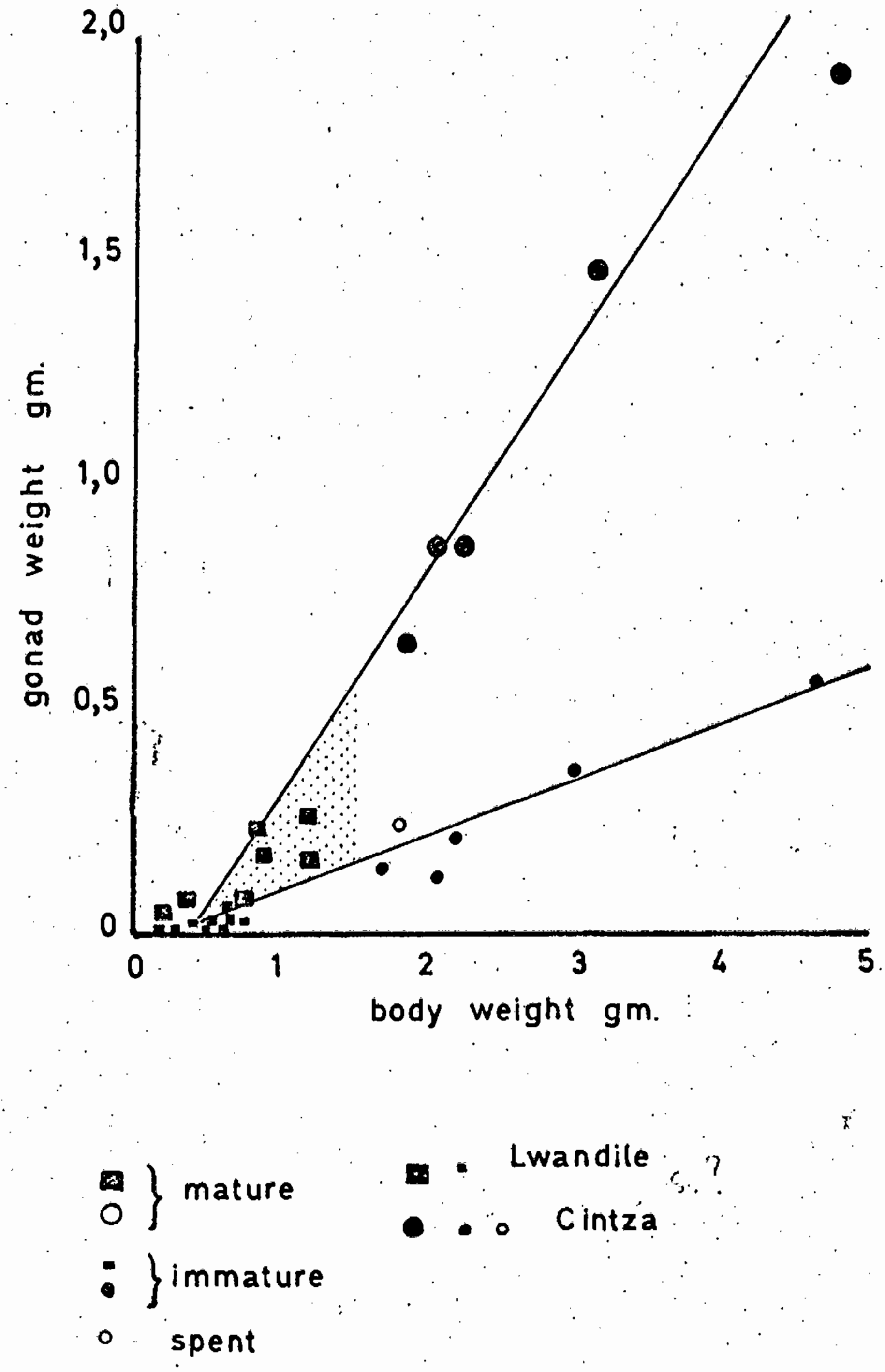
Clearly a decrease in maximum length will have a dramatic effect on the biomass. A regression line through all the points in Figure 4 gives an estimate of the "average" decrease in length throughout the region (i.e. from Gonubie to Lusikisiki) in five years. This yields a reduction of 20mm in the maximum length, which on transformation is equivalent to diminishing the maximum body weight from 5.4 gm to 1.5 gm.

The available biomass must have been sharply reduced, thus increasing the need to collect far larger numbers of animals for a comparable amount of meat.

The effect on gamete output is more difficult to predict, as

FIG. 6. GONAD WEIGHT IN *P. CONCOLOR*

The shaded area indicates the estimated output in depleted areas, and the total area between the two regression lines is an estimate of the original output.



the gonad cycle and quantitative output are not known. An approximation can be gained from a single sample of 40 animals collected from Lwandile and Cintza in January 1969, in which mature, immature and a single spent animal were present. No collecting of molluscs for consumption had occurred at Cintza by that date so that an assessment of an unaltered population was possible.

Figure 6 shows the relationship between body weight and mature gonad weight, and also between body weight and immature or spent gonad weight. The difference between these two relationships gives an estimate of gamete output. Statistical analysis of the slopes and intercepts (Table 1) indicate that the slopes of mature and immature gonads are significantly different ($p < .001$). Samples from Lwandile and Cintza were not significantly different and were grouped together.

Table 1 Statistical analysis of the relationship between body weight and gonad weight.

		Signif.of difference	
Samples	Regression	Slopes	Intercepts
Cintza (mature)	$y = -0.176 + 0.468x$	$p > .1$	$p > .1$
Lwandile (mature)	$y = -0.013 + 0.216x$		
Cintza (immature)	$y = -0.242 + 0.075x$	$p > .1$	$p > .1$
Lwandile (immature)	$y = -0.021 + 0.125x$		
Total Mature	$y = -0.191 + 0.472x$	$p < .001$	$p > .1$
Total Immature	$y = -0.011 + 0.158x$		

If the maximum body weight is being reduced from approximately 5.4 gm to 1.5 gm (fig. 5), the equivalent gonad output will be reduced by roughly 90% or more (fig. 6).

Even if these estimates are only accurate to within twenty percent, the reductions in maximum size, biomass and gamete output are dramatic, and the populations are being reduced considerably.

SUMMARY:

1. *Patella concolor* occurs on the East coast of South Africa and predominates in the balanoid zone. It is a generalised browser, feeding on any available material.

2. *Cellana capensis* has a similar distribution, zonation and feeding habits and is a probable competitor with *P. concolor*.

3. Large specimens of *P. concolor* occur in the upper regions of the shore and possess home scars, but homing is eratic. Smaller specimens occur in the lower balanoid and lack scars. This pattern suggests an upward migration.

4. Recent excessive human consumption of *P. concolor* has reduced the average size considerably. The implications of this in terms of biomass and gonad output are considered.

REFERENCES:

BRANCH, G.M. 1971. The ecology of *Patella* Linnaeus from the Cape Peninsula, South Africa. Pt.I. Zonation, movements and feeding. *Zool. Afr.* *6* : 1-38.

BREEN, P.A. 1973. Seasonal migration and population regulation in the limpet Acmaea (*Collisella*) *digitalis*. *Veliger 15* (2) : 133-141.

/ A DAS, S.M. and SESHEPPA, G. 1948. A contribution to the biology of *Patella* : on population distribution and sex proportions

?

in Patella vulgata Linnaeus at Cullercoats, England. Proc. Zool. Soc. Lond. 117 : 653-662.

DAVIES, P.S. 1969. Physiological ecology of Patella III. Desiccation effects. J. mar. biol. Ass. U.K. 49 : 291-304.

DAY, J.H. 1969. A Guide to Marine Life on South African Shores. Balkema, Cape Town.

FRANK, P.W. 1965. The biodemography of an intertidal snail population. Ecology 46 : 831-844.

GRAHAM, A. and FRETTER, V. 1947. The life history of Patina pellucida (L). J. mar. biol. Ass. U.K. 26 : 590-601.

HAVEN, S.B. 1971. Niche differences in the intertidal limpets Acmaea scabra and Acmaea digitalis (Gastropoda) in Central California. Veliger 13 (3) : 231-248.

JONES, N.S. 1948. Observations and experiments on the biology of Patella vulgata at Port St.Mary, Isle of Man. Proc. Lvpool. biol. Soc. 56 : 60-77.

KALK, M. 1959. A general ecological survey of some shores in Northern Mocambique. Revista de Biologia 2 (1) : 1-24.

KILBURN, R.

KOCH, H.J. 1949. A review of the South African representatives of the genus Patella Linnaeus. Ann. Natal. Mus. 11 (3) : 487-517.

KRAUSS, F. 1848. Die Sudafrikanischen Mollusken. Ebner & Siebert. Stuttgart.

LEWIS, J.R. 1954. Observations on a high level population of limpets. J. anim. Ecol. 23 : 85-100.

MOORE, H.B. 1938. Algal production and food requirements of a limpet. Proc. Malacol. Soc. Lond. 23 (3) : 117-118.

SOUTHWARD, J. 1964. Limpet grazing. J. mar. biol. Ass. U.K. 45 : 561.

STEPHENSON, T.A. 1939. The constitution of the intertidal fauna and flora of South Africa. Pt.I. J.Linn. Soc. Zool. 40 : 487-536.

TEST, A.R. 1945. Ecology of California *Acmaea*. Ecology 26 : 395-405.

WILLOUGHBY, J.W. 1973. A field study of the clustering and movement behaviour of the limpet *Acmaea digitalis*. Veliger 15 (3) : 223-230.

YONGE, C.M. 1962. Ciliary currents in the mantle of species of *Acmaea*. Veliger 4 (3) : 119-123.

SECTION III:

GONADIAL CYCLES.

PART III REPRODUCTIVE CYCLES

Data on the gonadial cycles of South African molluscs are limited. Stephenson and his co-workers investigated the breeding seasons of *Patella*, but his work was never published, except for a preliminary note in 1936: "All eleven species breed in April - May, but the exact duration of the breeding season has been determined only for *P. granularis*, which is fertile from about November to the subsequent August." (Stephenson, 1936 p.76).

Subsequent to this work, Cohen (1948, unpublished) undertook a more detailed analysis of *P. granularis* and *P. granatina* from Sea Point, and of *P. cochlear* and *P. oculus* from St. James. She concluded that all spawned mainly between March and May.

Newman (1967) has given a critical and detailed analysis of the cycle in *Haliotis midae*, in which he used the cross-sectional area of the gonad as a quantitative index of its maturity.

In Europe, *P. vulgata* and *P. depressa* have been extensively analysed in the classical papers of Orton and his co-workers (Orton, 1920, 1928; Orton et al, 1956; Orton & Southward, 1961). Many others have verified and extended this work, (Das and Sesheppa, 1948; Ballantine, 1961; Blackmore, 1969). *P. vulgata* is a consecutive hermaphrodite which spawns once a year in October or November. Orton et al (1956) have shown that the spawning was consistent for four consecutive years, throughout Britain. *P. depressa* spawns in midsummer and shows no signs of undergoing sex change as it ages (Orton and Southward, 1961).

Fritchman (1961a, 1961b, 1961c, 1962) has analysed the breeding seasons of several Californian acmaeid limpets, and his final paper summarises the results and relates them to distribution patterns.

The present work includes an analysis of seven Patella spp. from Kommetjie and Kalk Bay, respectively on the cold and warm coasts of the Cape Peninsula. Previous analyses of limpet gonadial cycles have been based on the methods of Orton et al (1956), who graded the gonads according to their size and maturity, and derived a gonadial index from this arbitrary grading. Such methods are easy to apply and they give an accurate assessment of spawning time. They do not allow quantitative comparisons to be made of the gonad output or mean size, under differing environmental conditions. To overcome this limitation, a gravimetric assessment was used in the present work, thus allowing a quantitative evaluation of the gonadial cycle. The resultant data can therefore be used as a base-line to measure or predict the effect of variables such as density, competition, temperature or pollution. Changes in gonadial output can be quantitatively evaluated and statistically compared. The disadvantage of a gravimetric method is the time involved in dissection and weighing. In addition, it can be applied only to species in which the gonad is separable from the visceral mass.

MATERIAL AND METHODS:

Monthly samples were collected from Kommetjie and Kalk Bay. Samples comprised 30 specimens of each species, except for P. cochlear which displayed greater variability, so that 90 specimens were collected. Because of their relative scarcity in warm waters, *P. granatina*, *P. argenvillei* and *P. barbara* were only collected at Kommetjie, and for the converse reason collection of *P. oculus* and *P. longicosta* was restricted to Kalk Bay. *P. cochlear* and *P. granularis* were sampled at both sites. Collecting was limited to the habitats typical of each species, and successive collections were made close together to reduce environmental variables. Samples encompassed a wide range of sizes.

Four techniques were used to assess gonadial maturity: 1. Gravimetric; 2. Egg counts; 3. Subjective grading of ovaries; 4. Histological. Subjective grading was introduced to establish the accuracy of this method, gauged against the quantitative gravimetric technique.

All specimens were preserved in 5% formalin for at least two months to harden the gonad into a compact mass. Preliminary experiments indicated that this treatment decreased the wet body weight by only 0.5% to 1.1%, and probably effected the visceral and gonadial weights to a similar extent; the effect has accordingly been ignored.

1. Gravimetric Determinations

Specimens were removed from their shells, blotted dry and weighed. The gonad was then dissected out, blotted and weighed. Wet weights were used in preference to the more accurate dry weights because this enabled subsequent histological examination. The "somatic weight" was calculated by subtraction of gonad weight from total flesh weight. For each sampling date, species and sex, the gonadial weight was plotted against somatic weight. This yielded a linear relationship (provided the very small individuals with minute gonads were excluded). Seapy (1966) has described a similar relationship in *Acmaea limatula*. An example of such a plot is given in fig.1a.

Newman (1967) has shown a sigmoidal relationship in Haliotis midae, but in Patella the older individuals continue to produce a proportionally large amount of gonad, and do not decrease their output.

For each plot of gonadial and somatic weight, a regression line was calculated by method of least squares, linearity tested, 95% confidence limits calculated, the correlation coefficient calculated, and the significance of the correlation coefficient obtained by a t test. Any relationships based on inadequate numbers, or which were not statistically significant, are indicated by a query on the graphs of annual cycles. With the exception of P. cochlear, all the species conformed closely to a linear relationship. In P. cochlear females there was considerable scatter about the regression line, but as larger numbers were analysed (80 to 90 per sample) the results were still significant. However, predictions about egg output in P. cochlear must perforce be less reliable than they are in the other species.

Two samples (P. granularis from Kommetjie, 22.4.1970., and P. granatina from Kommetjie, 23.3.1970.) yielded a biased or inaccurate reflection of gonad to somatic weight because only small individuals were sampled on these occasions. These have been included in the analyses, but their wide confidence limits make it obvious that their accuracy is limited.

Within each species and sex, the regression for each monthly sample was tested against the subsequent monthly sample to see if any significant difference existed with respect to slopes or intercepts. In this way the statistical significance of changes

FIG. I AN EXAMPLE OF THE PROCESSING OF GONAD DATA.

Fig. 1a

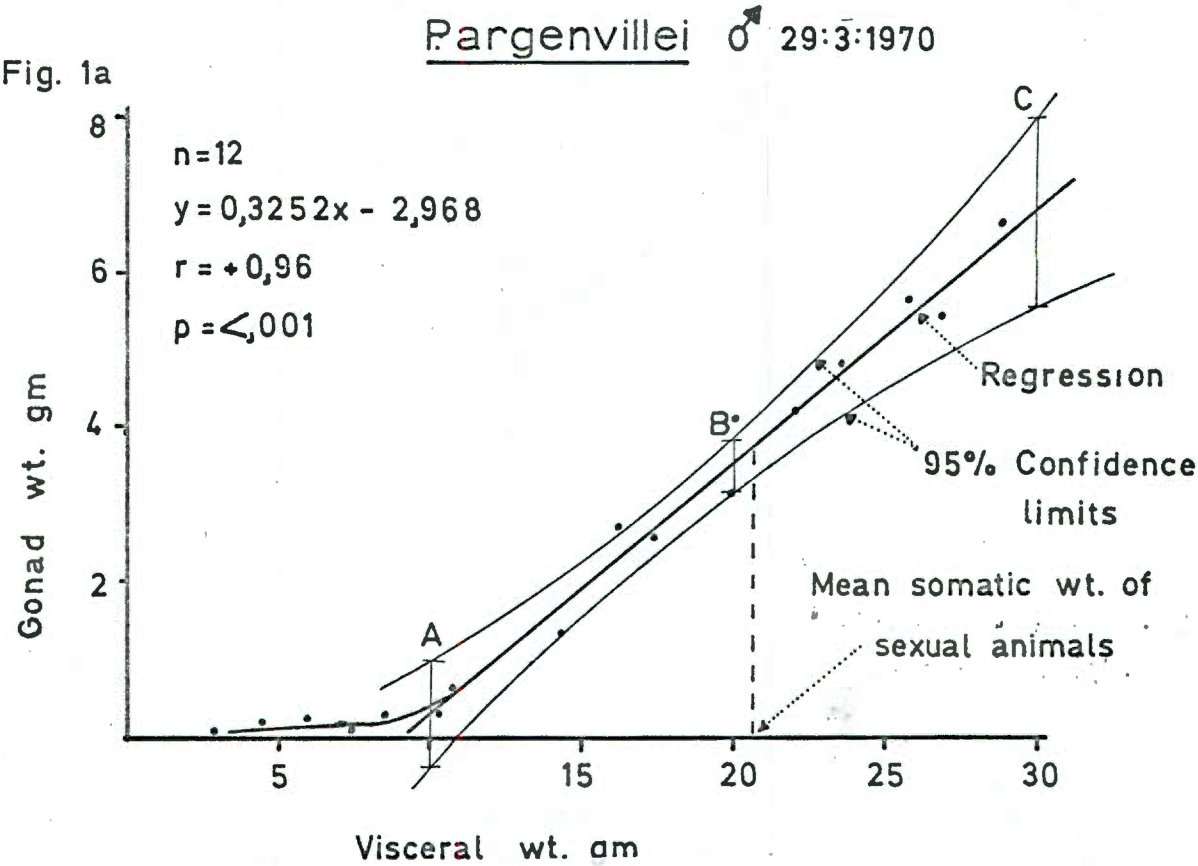
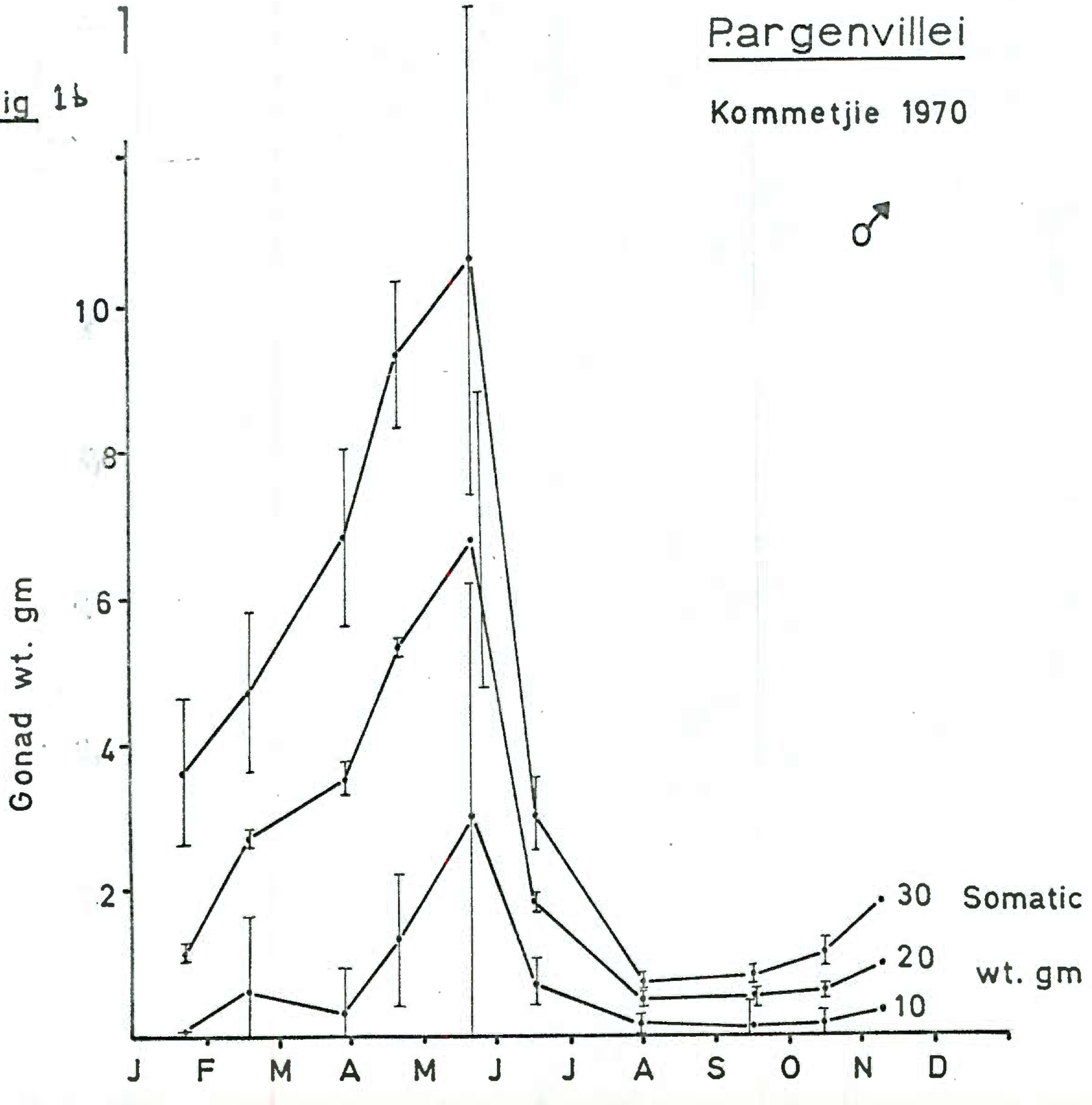


Fig 1b



from month to month could be assessed. Details of the statistical results are included in appendix I.

As the amount of statistical calculation was formidable, a Fortran V program was developed to compute the calculations on an Univac 1106 computer.

To condense this volume of data into a meaningful and comprehensible annual analysis, three somatic weights were selected for each species, representing approximately the maximum, mean and minimum gonad producing somatic weights. The corresponding gonad weights were plotted against the time of collection to obtain an annual cycle (figs. 1a and 1b).

To compare the gamete output of different species and sexes, the term "mean gonadial output" has been used. This is defined as the gonad output corresponding to the mean somatic weight of sexual individuals, and can be expressed in grams or as a percentage of the mean somatic weight.

2. Egg Counts

Three squashes were prepared from each ovary, respectively from the anterior, middle and posterior. From these, counts were made of the number of previtellogenic oocytes, immature oocytes and mature oocytes, present in one microscope field at 100X magnification. The numbers of each category were then totalled for the monthly sample and expressed as a percentage of the total number of oocytes. Underwood (1972) used a similar method, but utilised histological sections.

The size frequency of eggs was determined for P. cochlear at various stages of development, by subsampling and measuring all the eggs in each subsample.

Fecundity was determined by counting all the mature eggs

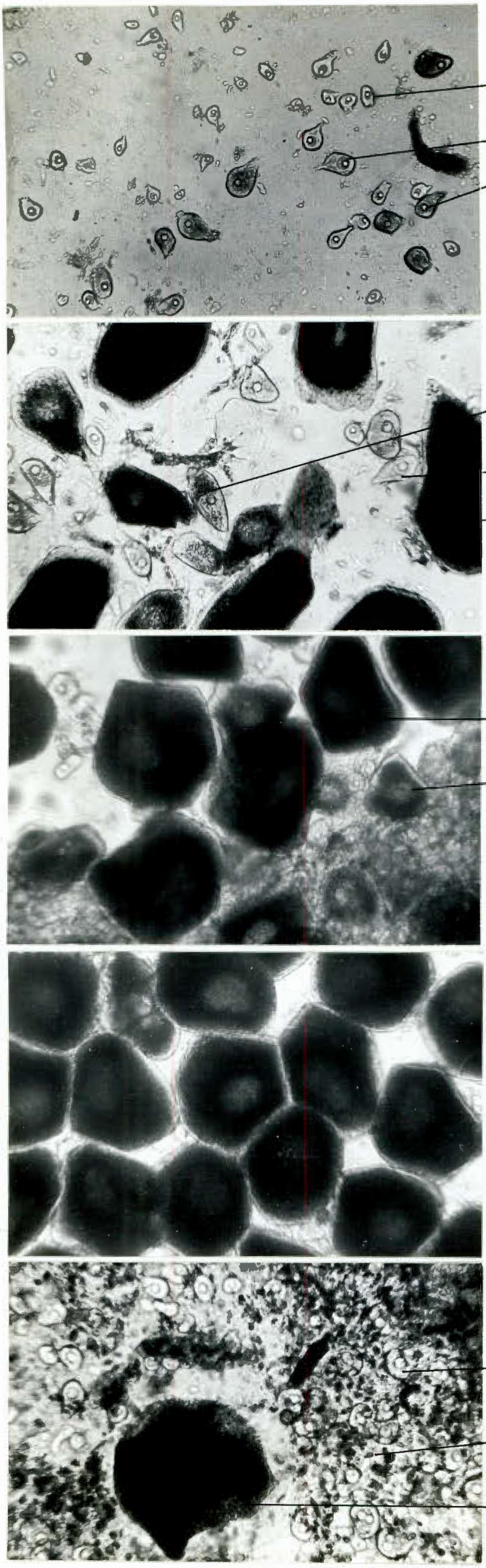


PLATE I
SMEARS OF OVARY

a. Grade I.

b. Grade II.

c. Grade III.

d. Grade IV.

e. Grade SII (Spent).

present in subsamples of ovary of known weight. At least three determinations were made on each species, from mature and spent ovaries.

3. Subjective Grading of Ovaries

Every ovary was subjectively rated according to its size and the composition of its eggs. The following arbitrary classification was used:

I Ovary small to minute, only Previtellogenic oocytes present (plate 1 a).

II Ovary size intermediate, Previtellogenic and immature oocytes present (plate 1 b).

III Ovary large; Previtellogenic, immature and mature oocytes present (plate 1 c).

IV Ovary swollen and turgid, predominantly mature oocytes present (plate 1 d).

SI Ovary collapsed, spent, often wrinkled. Filled with interstitial cells and a few oocytes, or empty (plate 1 e).

SII Ovary slightly expanded. Abundant Previtellogenic oocytes regenerated.

For the purpose of obtaining "average" values for a monthly sample, these six grades were respectively assigned the following arbitrary units:

1, 2, 3, 4, -1, 0.

Averages could then be obtained to yield an ovarian index. The results are presented in figures 7c to 15c.

4. Histology

Representative examples of each sample were sectioned at 4 to 10 and stained with haemotoxylin and erythrosin.

STRUCTURE OF THE GONADS

The gross structure and histology of the gonad is similar in all of the species examined. The sexes are separate and in both

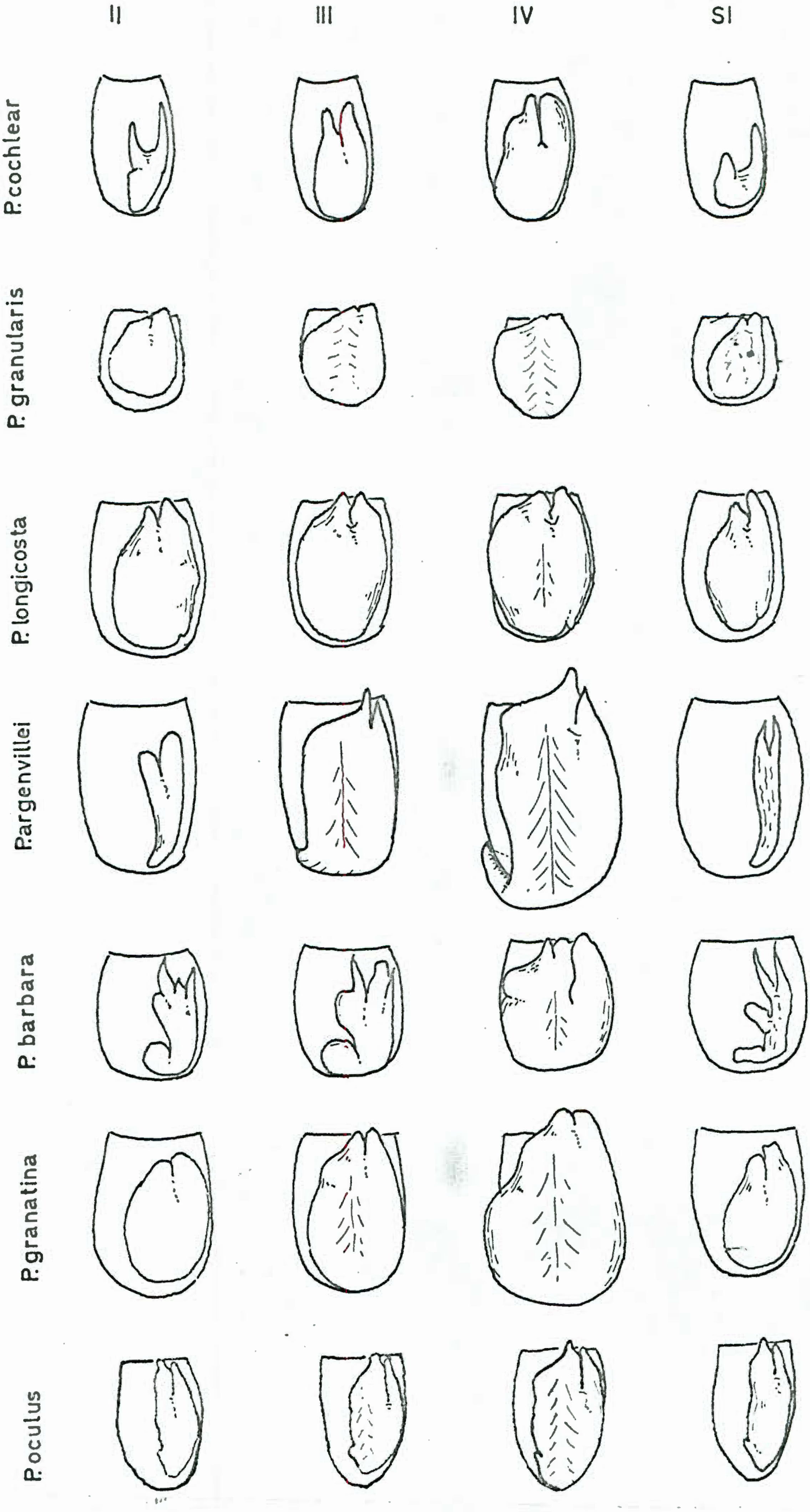


FIG. 2. Gonad shape and maturation (relative to the visceral mass). Ventral view.

sexes the gonad forms a discrete solid body lying dorsal to the foot and below the visceral mass, its uppermost surface interdigitating slightly with the digestive gland (Plate 2). The gonad is easily revealed by cutting peripherally through the visceral membrane and deflecting the viscera forwards from the foot. In most of the species the gonad is similar in shape in both sexes: roughly oval, larger on the left, and narrowing to two horns anteriorly. The shape and dimensions vary with the species and are summarised in fig 2. With maturation the gonad expands to approximately ten times its initial volume.

Internally there is a single lumen, partitioned to variable degrees and bounded by a membrane containing collagen-like fibres.

Testis

In the male, numerous tubular lacunae extend inwards, particularly from the ventral surface of the gonad, and ramify throughout the lumen in a vertical direction. These lacunae are made up of connective tissue and contain only small numbers of cells, particularly in mature gonads. Inside the gonadial lumen, these tubules are lined by germinal epithelium. The lacunae originate as broad honey-comb-like interstices on the surface of the gonad (Plate 3a), but rapidly extend into the gonadial lumen, and narrow as spermatocytes are produced and begin to fill the lumen (Plate 3b). Spermatocytes are spherical and about 4 μ in diameter. Maturation proceeds rapidly with the formation of smaller spermatids (2.5μ in diameter) and sperm. The latter have narrow heads about 5 to 8μ in length, and long flagella. Active sperm can be extracted from almost all stages of the male gonads, even shortly after they have discharged. Sperm are active throughout the year, but appear to be temperature sensitive.

PLATE II :

Transverse section of <u>P.granularis</u>.

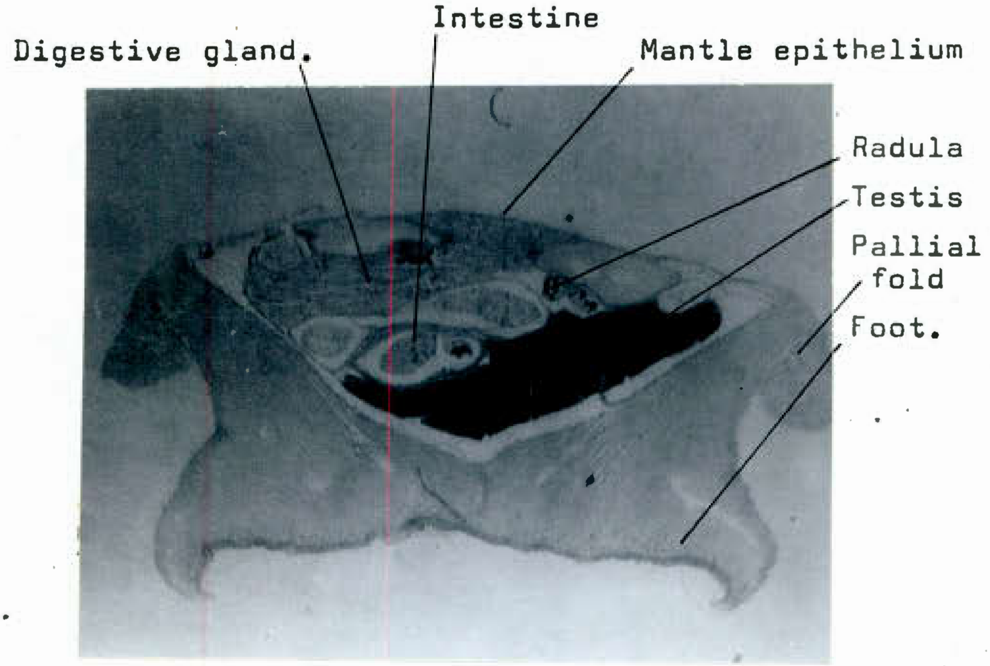
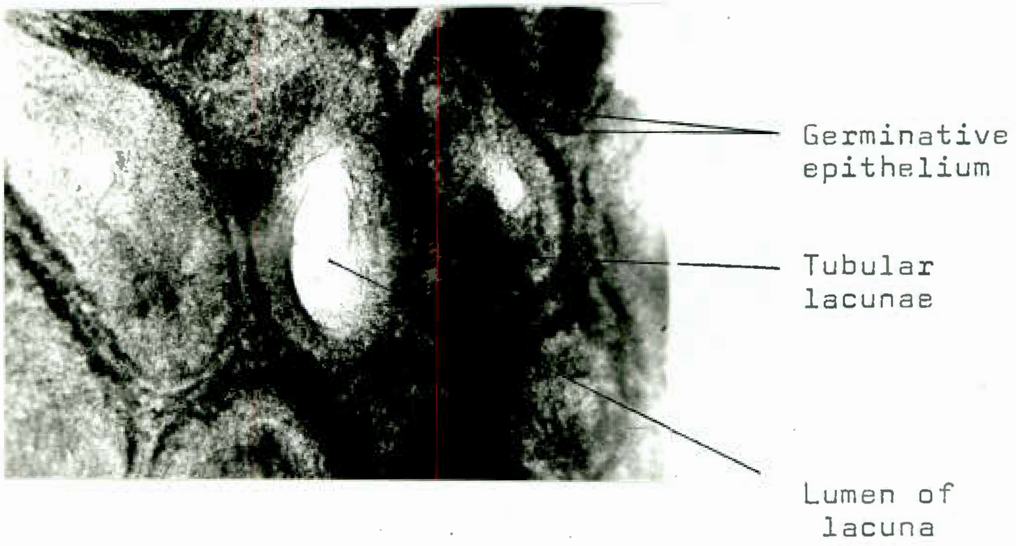


PLATE III :
STRUCTURE OF TESTIS

A. Surface view of immature testis.



B. Horizontal section of developing testis.

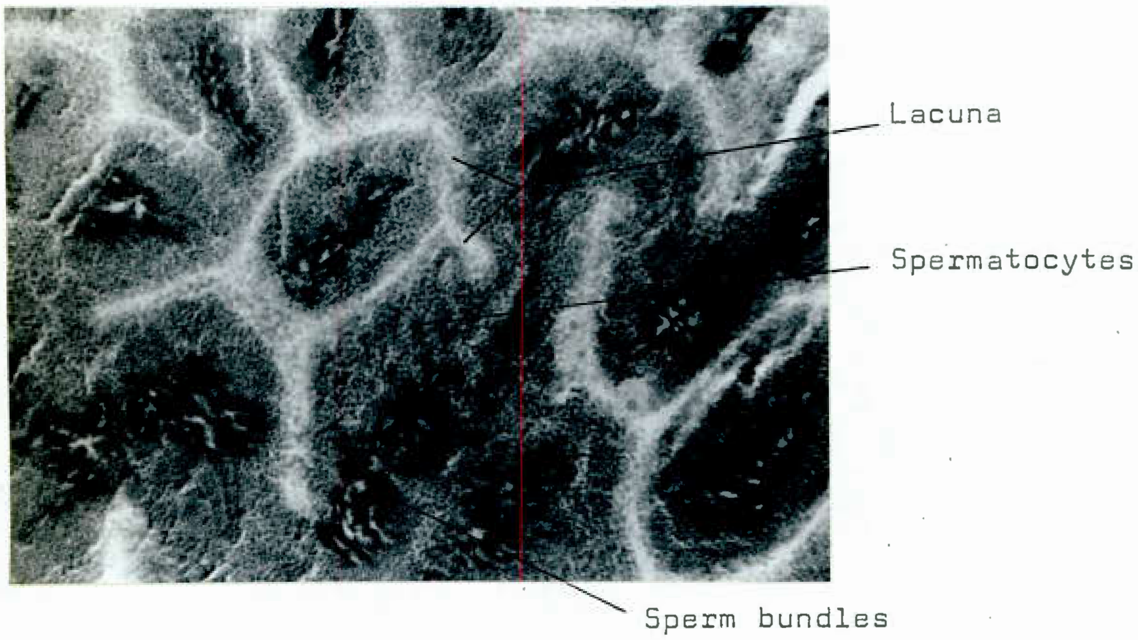
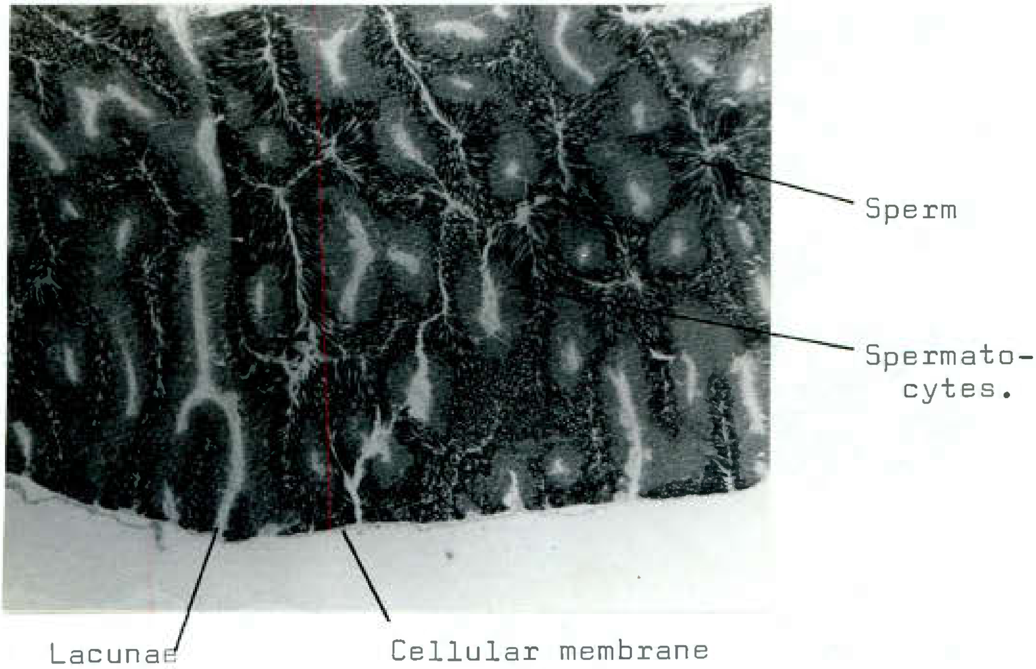


PLATE III

C. T/S. Relatively mature testis.



D. Detail of Testis.

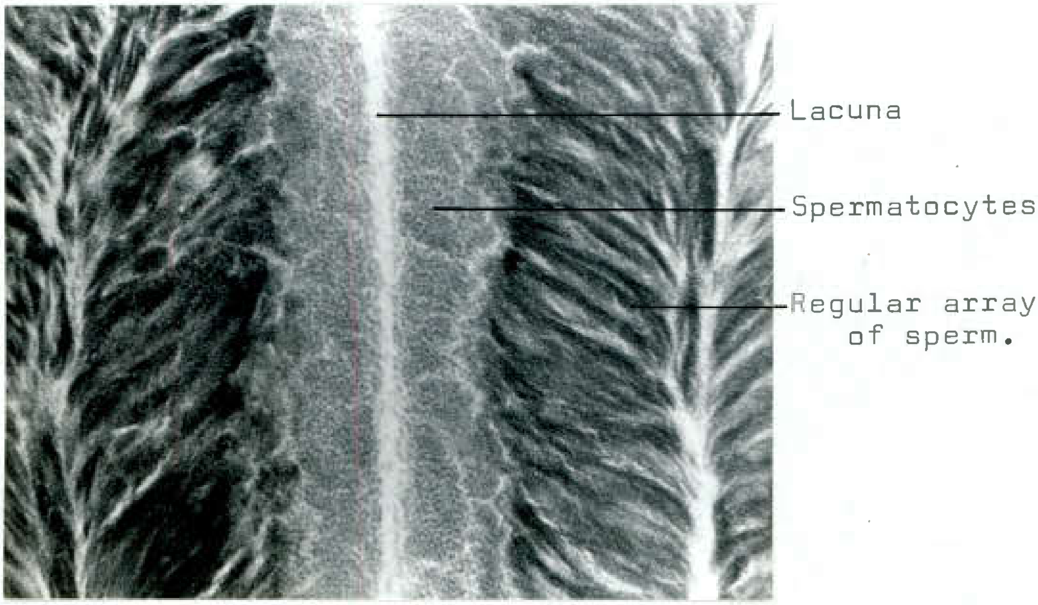
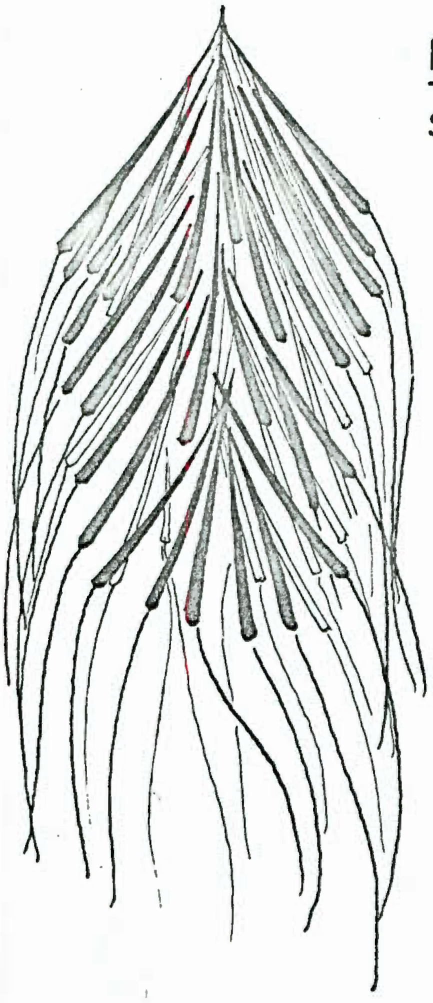
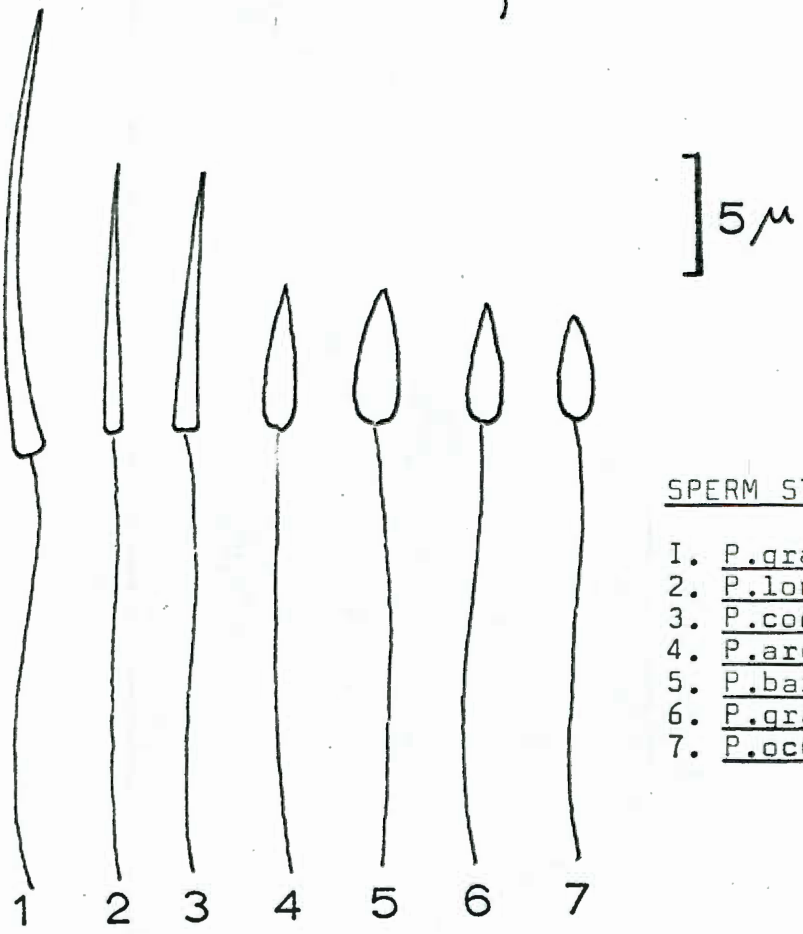


Fig. 3



P.granularis sperm bundle

Fig. 4



SPERM STRUCTURE:

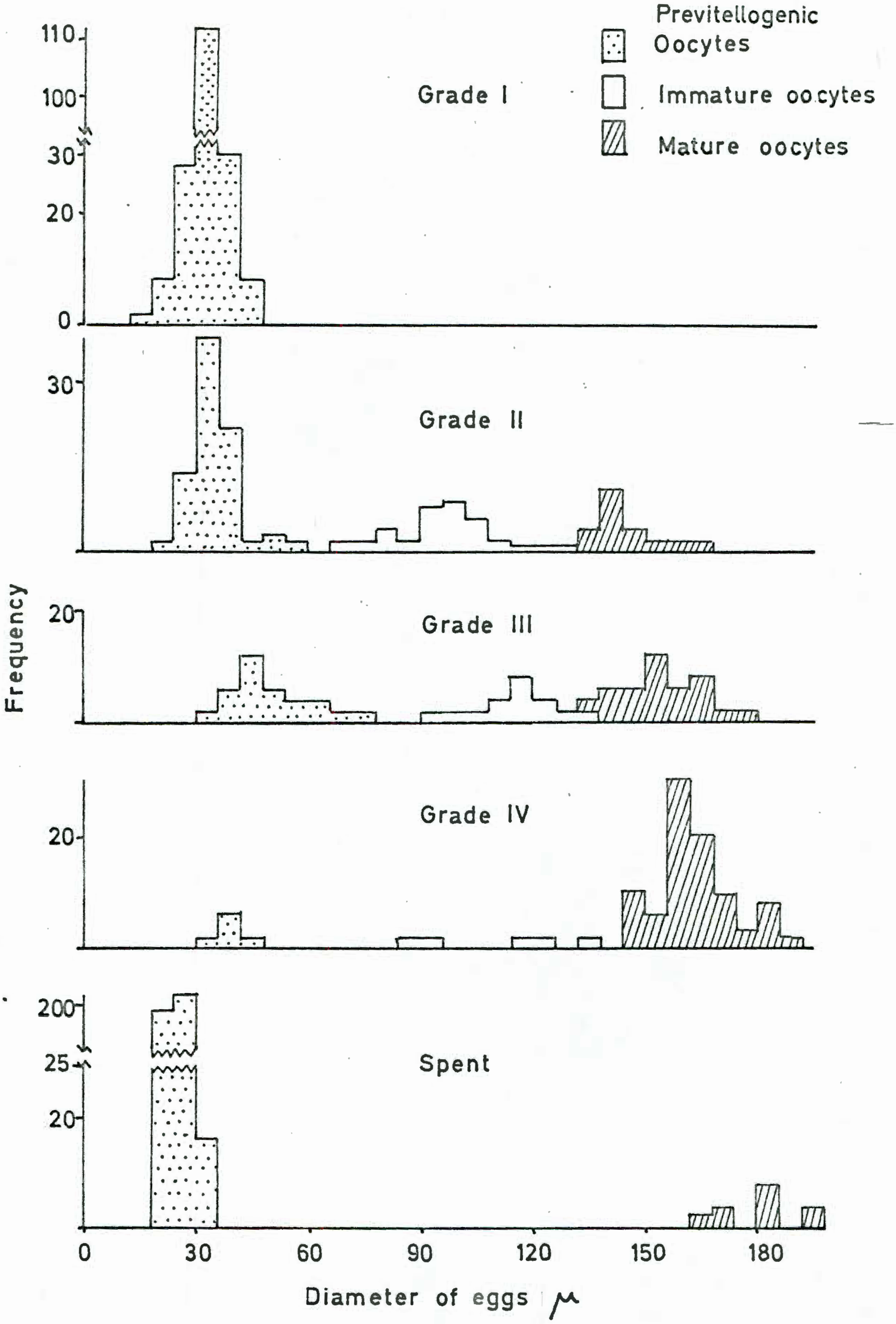
1. P.granularis
2. P.longicosta
3. P.cochlear
4. P.argenvillei
5. P.barbara
6. P.granatina
7. P.oculus

Spermatocytes and spermatids form a wide lining to the lacunae. The sperm are oriented in a regular manner, so that sperm produced from adjacent lacunae are formed into a compact cylindrical array with the sperm heads pointing in one direction (Plate 3c,d). Dorsally there is a fairly large longitudinal space in the lumen, through which the sperm presumably pass during spawning. A high proportion of the sperm are shed at spawning and the gonad collapses : nevertheless, a certain amount of sperm is retained, and in most species almost immediate regeneration occurs.

In some species the sperm are bound together into regular bundles and these collectively make up the cylindrical structures described above. In P. granularis these are particularly well developed (Plate 1). Within each bundle the sperm heads are arranged regularly so that they point towards the centre of the bundle at an angle of about 15°. The sperm heads are firmly united while their tails trail behind, forming a sheath around the heads (fig. 3).

In P. cochlear and P. longicosta similar bundles are present, but are not as striking. P. argenvillei possesses bundles, but they are poorly defined. P. oculus and P. granatina have bundles only when immature and lose them as the gonad matures and fills with sperm. P. barbara lacks bundles and the sperm lies loose in the tubules. This graded series is probably due to the structure of the sperm head which is long and slender in P. granularis and progressively shorter and squatter as one passes down the series (fig. 4). The functional significance of this is obscure. There is no obvious correlation with gonad output, sperm activity or zonation.

Fig. 5 Size Distribution of Eggs



Ovary

The ovary is similar to the testis in gross structure, being a compact body under the visceral mass. It is encased by a thin cellular membrane containing collagen-like fibres. As the ovary matures, this membrane is stretched and the fibres dispersed, so that the membrane becomes extremely thin.

The ovary is repeatedly divided by thin sheet-like trabeculae, which extend from the ventral surface up through the lumen. These trabeculae support the germinal epithelium (Plate 4).

Large numbers of oocytes are produced and remain attached to the trabeculae until they mature, and are often associated with minute interstitial cells (Plate 4). Maturation occurs progressively throughout the season and expands the ovary. Mature oocytes lie loose in the lumen and pass into the dorsal region of the ovary where the trabeculae are interrupted and the lumen continuous. When completely gravid, the ovary is taut and the eggs compacted against one another (Plate 4).

Analysis of the size of eggs reveals a trimodal distribution, corresponding to previtellogenic oocytes, immature oocytes and mature oocytes (fig. 5). Immature ovaries possess only previtellogenic oocytes, but as maturation progresses, larger numbers of mature eggs appear and eventually dominate the grade IV ovaries (fig. 5). P. granularis, P. barbara and P. argenvillei have slightly larger mature eggs than the other species, but this is not statistically significant.

Previtellogenic oocytes are small (33μ), with an irregular shape and a clear cytoplasm. The nucleus is large and clear and contains an obvious nucleolus which may be paired (fig. 6). Immature oocytes are about three to four times the size, again

Fig. 6 Egg Types (*P. cochlear*)

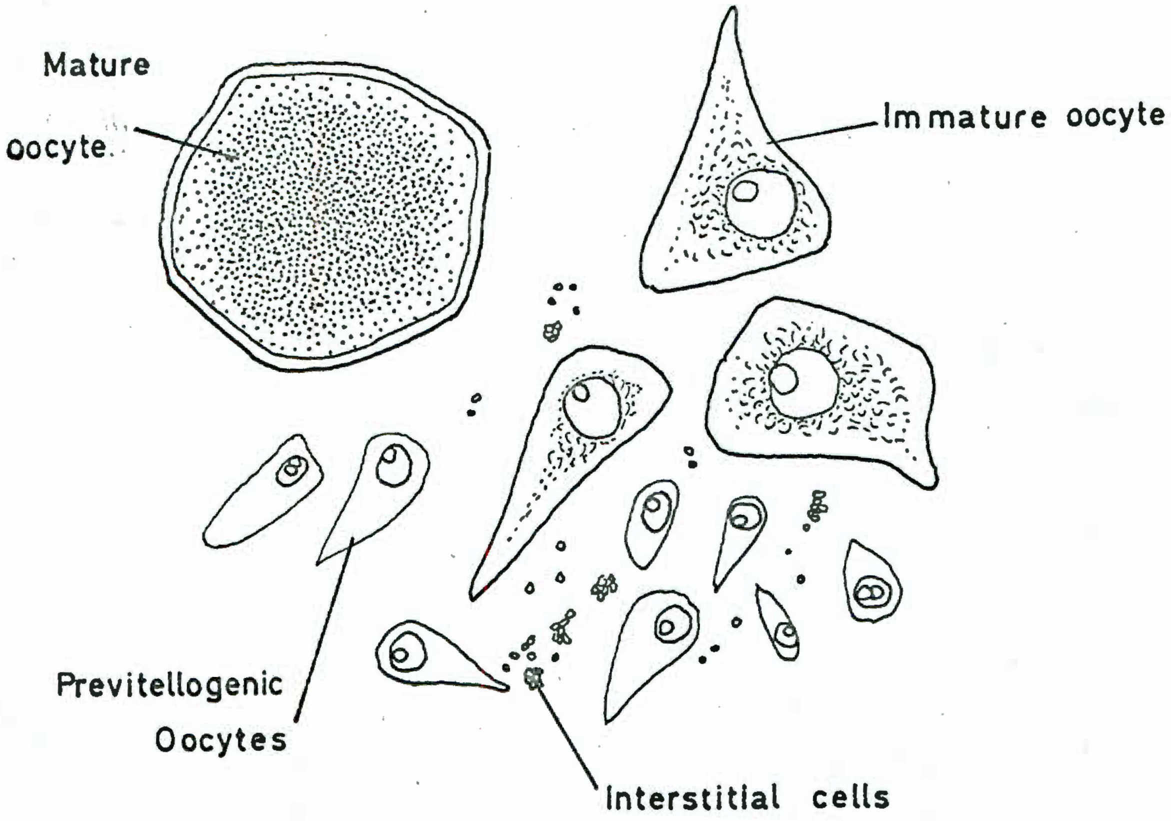
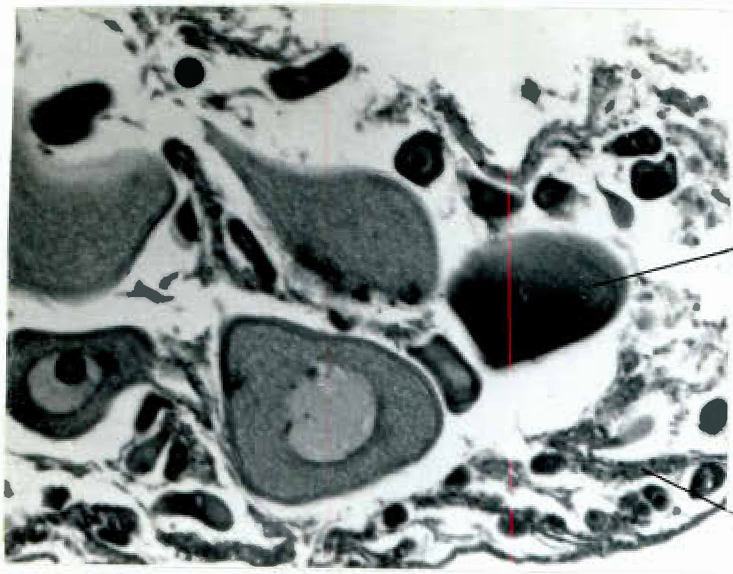
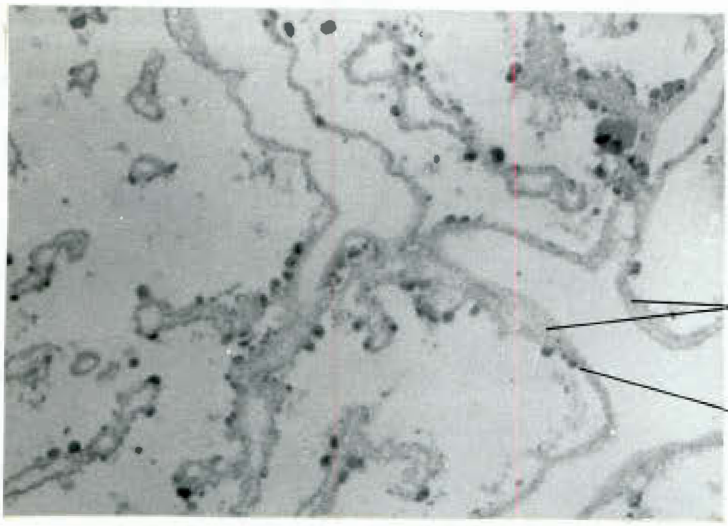


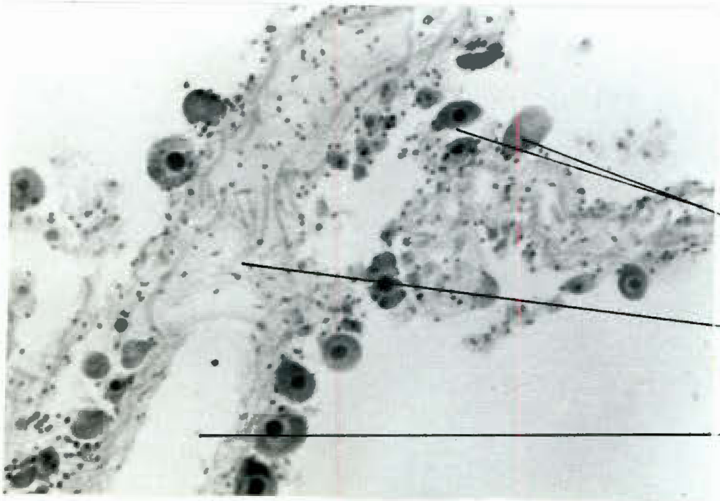
PLATE IV (Cont.)



d. Spent.



E. Completely Spent.



F. Detail of above.

irregular in shape, but with a granular cytoplasm due to vitellogenesis. The nucleus is prominent and the nucleolus dark. Mature oocytes are spherical in shape and 160μ in diameter, but may be distorted by compression against the other eggs. The cytoplasm is very dark and granular, particularly in the centre, and obscures the nucleus completely (unless the eggs are stained). A hyaline chorion surrounds the egg. This disappears when the mature eggs are placed in sea water. With slightly immature eggs the membrane remains intact in sea water, and appears to inhibit penetration by sperm.

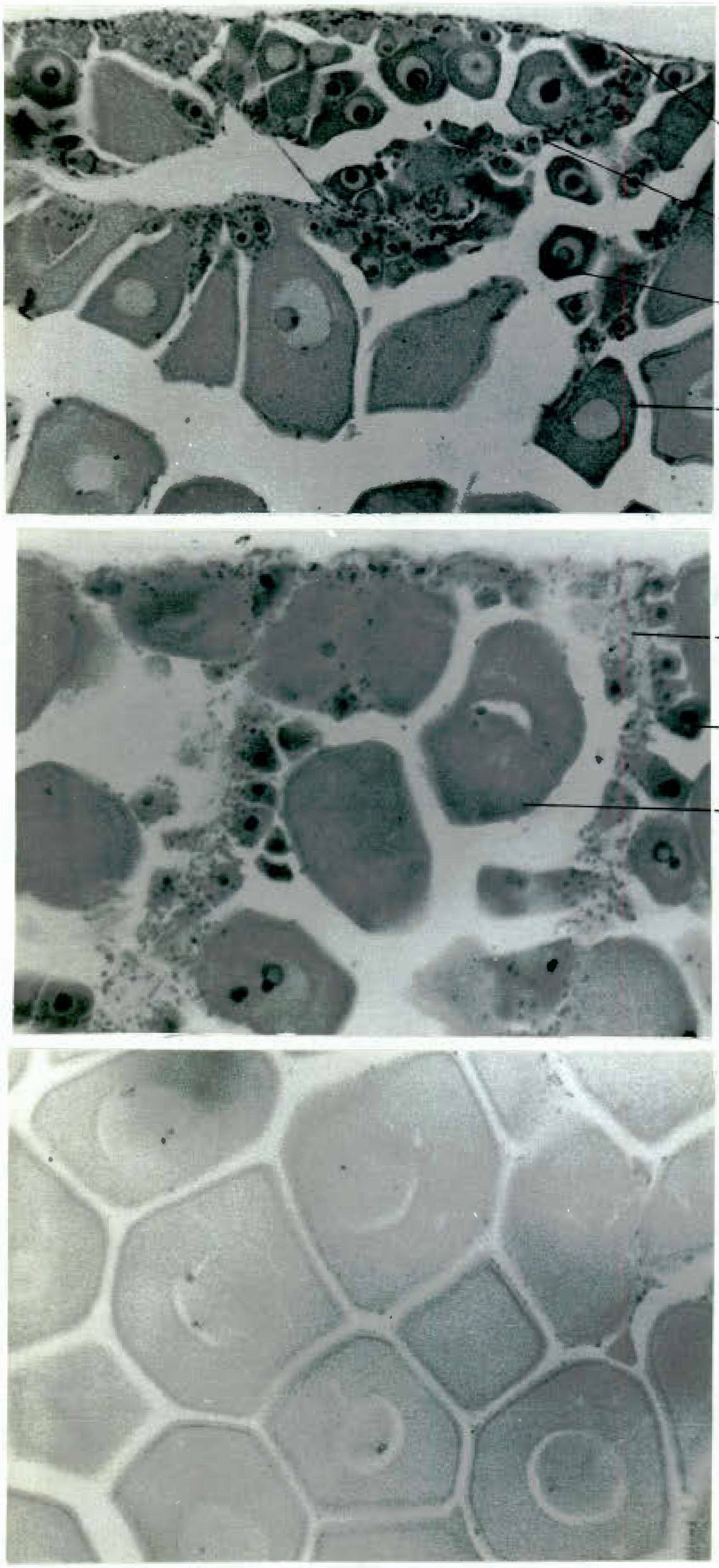
During spawning most of the mature eggs are shed and the ovary collapses (Plate 4 d). The peripheral membrane contracts, and within it and the trabeculae, collagen-like fibres are concentrated and very obvious (Plate 4 e). Shortly after spawning large numbers of tiny interstitial cells invade the ovary (Plate 1 e), and in some species degeneration of the remaining eggs occurs. A resting period follows varying from two weeks to three months. In most species oogenesis occurs shortly after spawning, and large numbers of oocytes are generated.

In Haliotis midae (Newman, 1967) oocytes are retained at spawning and give rise to mature eggs the following season. This is probably not true for Patella, for although oocytes are always present, their numbers dwindle with maturity and large numbers are produced after spawning.

REPRODUCTIVE CYCLES

As described above, gonadial cycles were assessed by gravimetric determination, egg counts and grading of ovaries. The

PLATE IV :
STRUCTURE OF THE OVARY .



A. Immature

B. Grade III.

C. Compacted Oocytes.

results are presented in figures 7a, b, c and d to 15a, b, c and d.

In all the species investigated the gravimetric method gives an unequivocal indication of when spawning occurs, particularly when used in conjunction with the egg counts. Most of the limpets have a single spawning each year, and this occurs simultaneously in males and females. After spawning the gonads do not regress completely, and regeneration begins shortly afterwards. Except for P. granularis, motile sperm could be found throughout the year in all the species. P. granularis has a particularly long resting period after spawning, lasting about four months. Mature eggs appear in small numbers fairly soon after spawning, and are progressively added to during maturation. Consequently artificial fertilisation can be achieved in most months of the year except for a post-spawning and resting period. The success of artificial fertilisation is unpredictable, but appears to be very temperature sensitive.

P. argenvillei: This species reached maximum maturity late in May and a rapid spawning followed in June and to a lesser extent July. Gonad regression was completed by August. Males (fig. 7a) began to mature again almost immediately, while the females (fig. 7b) remained in a resting state until the end of the year.

Egg counts (fig. 7d) follow this trend fairly closely. The proportion of mature eggs increases rapidly until spawning, when it drops sharply in June. Conversely the number of pre-vitellogenic oocytes increases sharply after spawning.

P. barbara: In P. barbara the cycle was very similar to that

Fig 7a

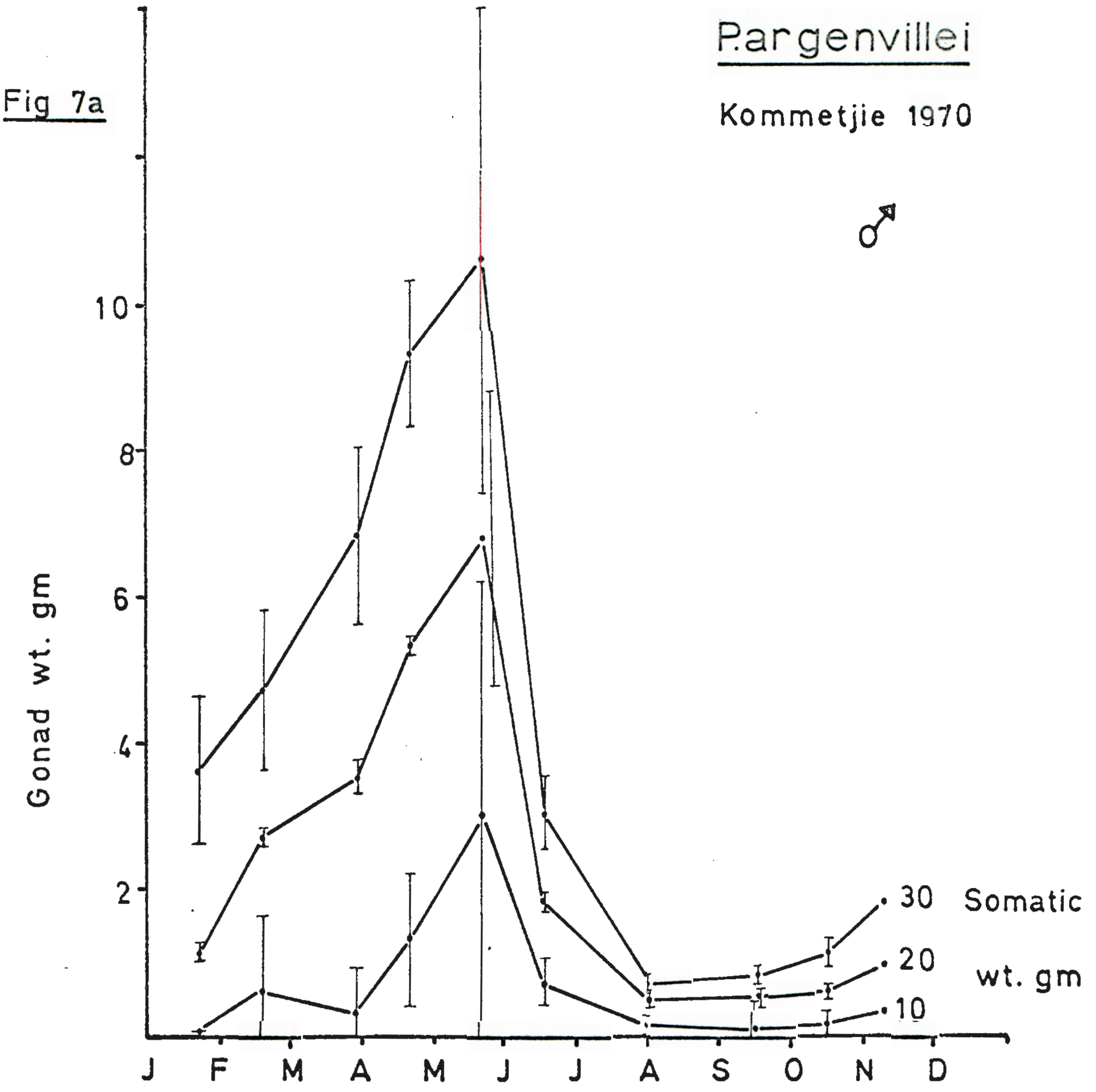
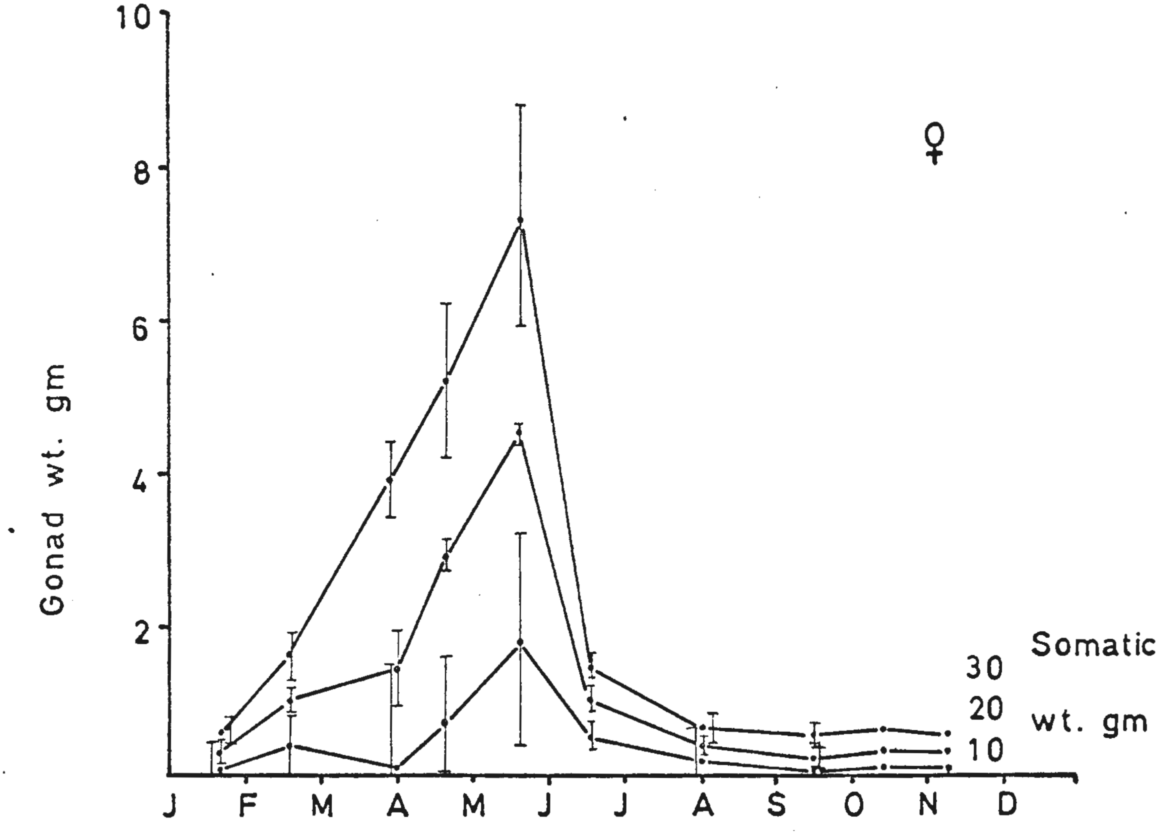

P.argenvillei
Kommetjie 1970
♂
Gonad wt. gm
10
8
6
4
2
30
20
10
Somatic
wt. gm
J
F
M
A
M
J
J
A
S
O
N
D

Fig 7b


♀
Gonad wt. gm
10
8
6
4
2
Somatic
30
20
10
wt. gm
J
F
M
A
M
J
J
A
S
O
N
D

P. argenvillei

Kommetjie 1970

Fig 7c Subjective grading

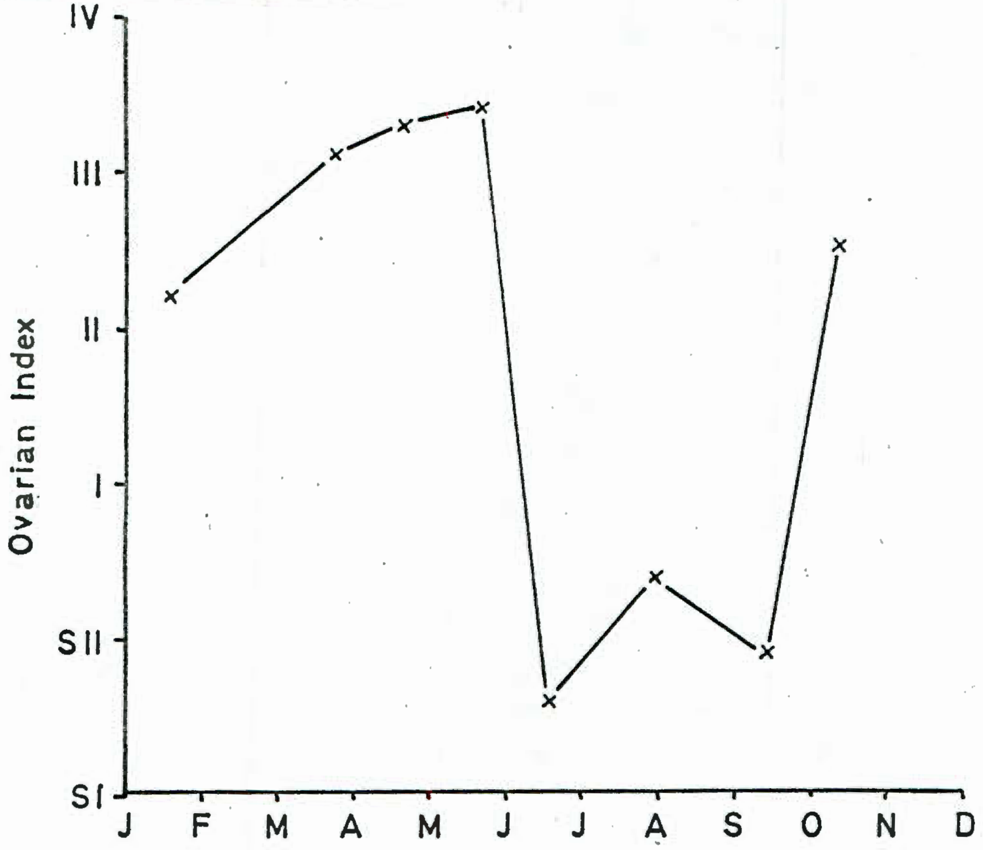
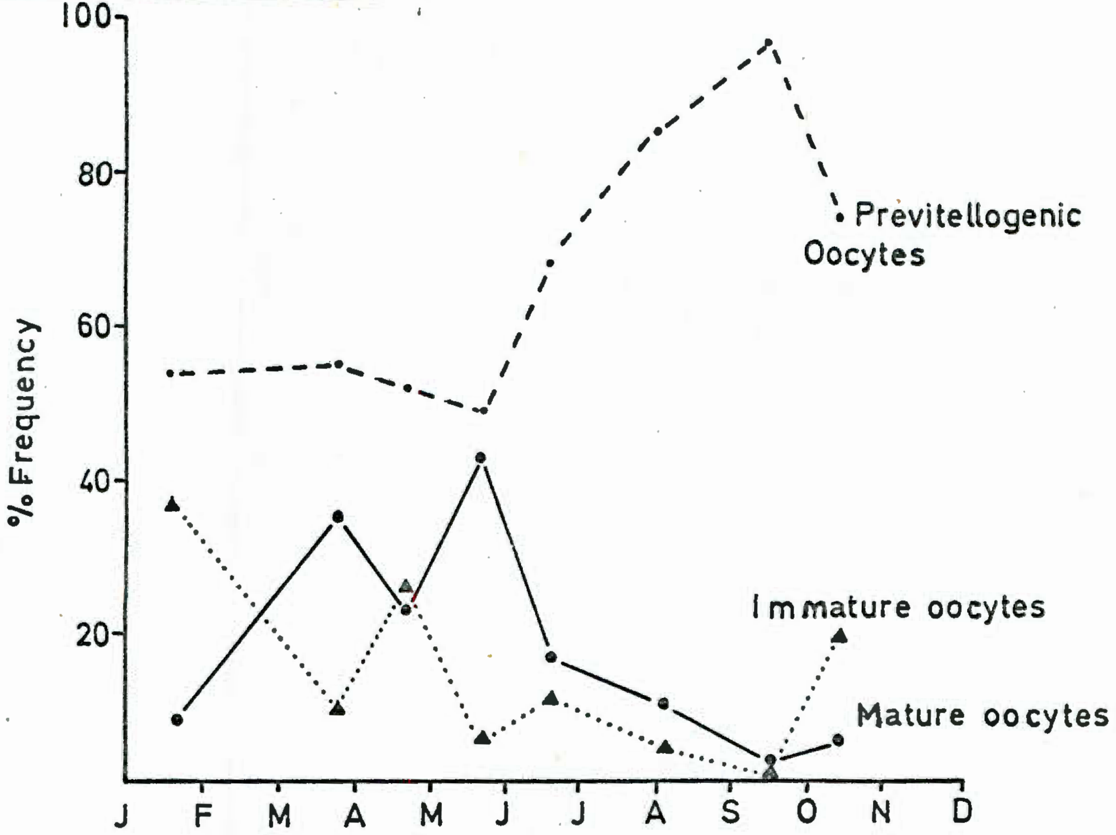


Fig 7d Egg counts



of P. argenvillei, except that the maximum peak was reached earlier in April in the males (fig. 8a). Release of gametes in both sexes again occurred in late May to June (figs. 8a, b). Redevelopment followed almost immediately after regression was complete. Egg counts (fig. 8d) show the rapid production of new oocytes immediately after spawning, reaching a peak about August. Progressive increase in the proportion of mature eggs then follows, reaching a pre-spawning peak: a concurrent decrease occurs in the numbers of oocytes. As in all the subsequent species, the relative number of immature oocytes remains low and relatively constant throughout the year. This probably indicates that they represent a transient and short-lived stage of maturation between oocytes and mature eggs.

P. cochlear: Samples from Kommetjie (figs. 9a, b) have an almost identical spawning cycle to that of P. argenvillei with a maximum peak in May, rapid spawning in June, and a progressive recovery during the following months. One point of interest is the slight reduction in gonad size in April, just before the attainment of maximum size. Large numbers of animals were collected in this sample and statistical analysis (Appendix) reveals no reason for considering the sample inadequate or insignificant: sampling error is thus improbable. More probably this represents a preliminary or partial spawning. In support of this, the egg counts (fig. 9d) and the ovarian index (fig. 9c) reveal a drop in the percentage of mature eggs in April, accompanied by a related rise in the number of immature eggs. This effect was transient, and the mature eggs rapidly increased to a peak in May, before the anticipated sharp drop in June associated with spawning. Again, oocytes dominate the ovary shortly after spawning and their progressive maturation occurs in subsequent months.

P. barbara

Kommetjie 1970

Fig 8a

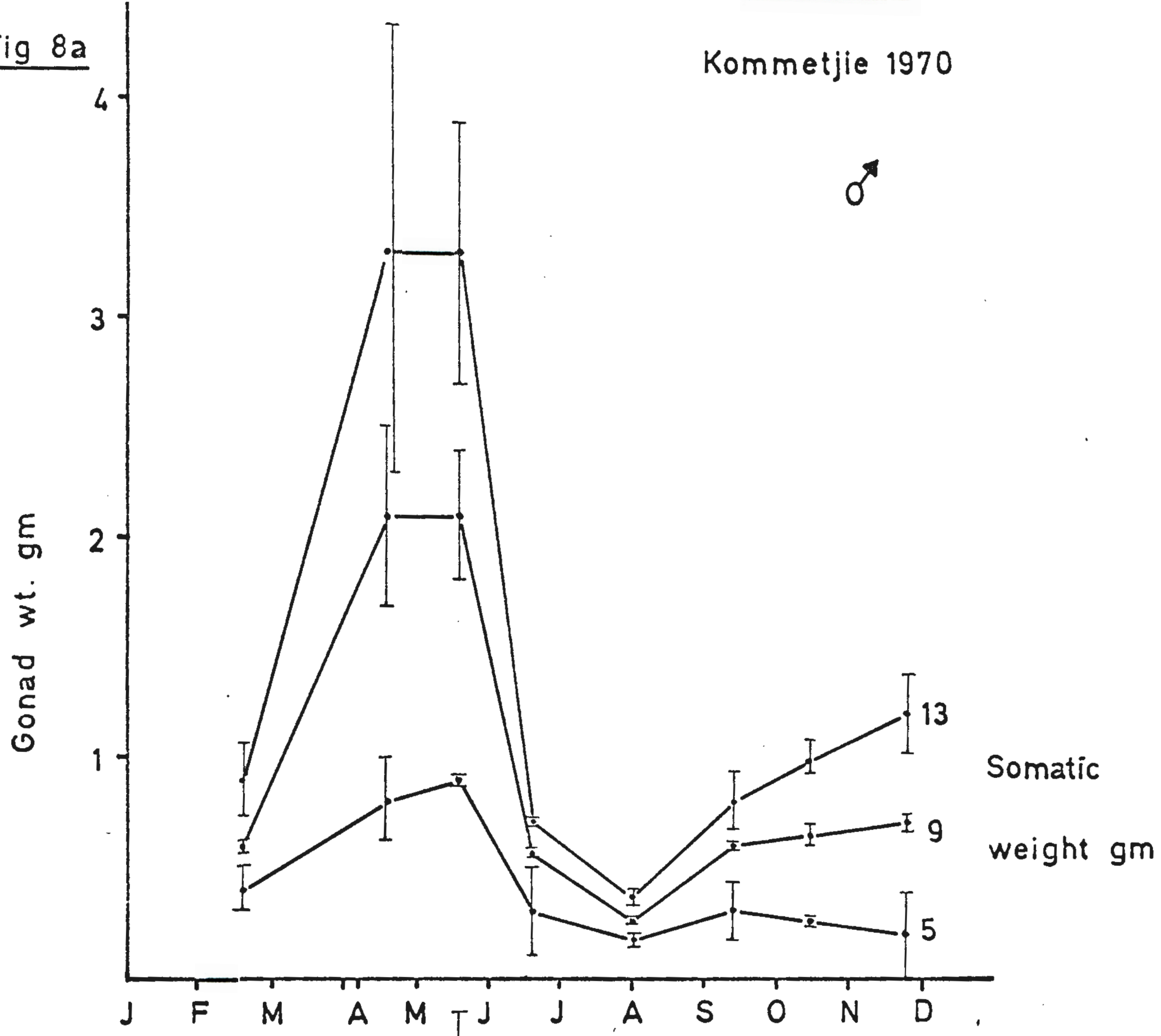
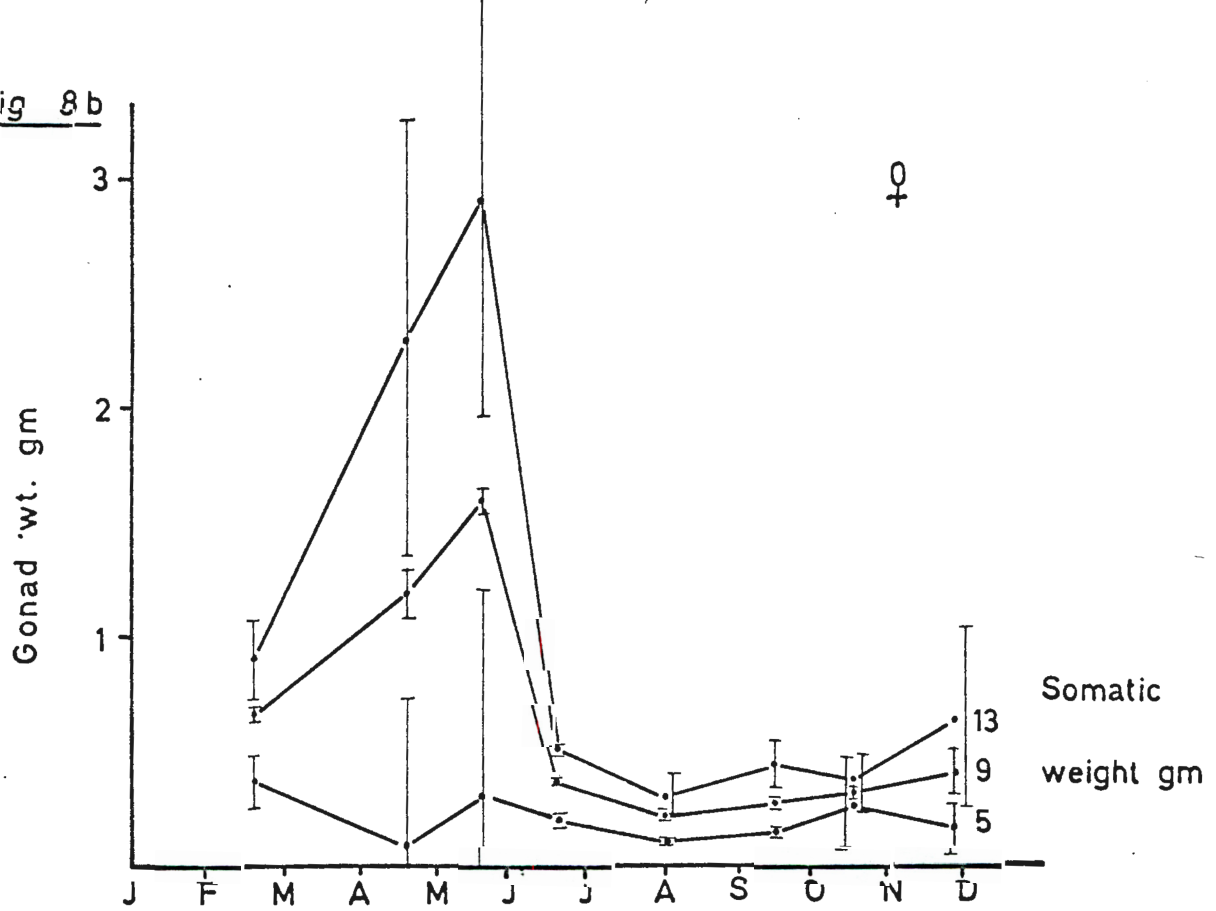


Fig 8b



P. barbara

Kommetjie 1970

Fig 8c Subjective grading

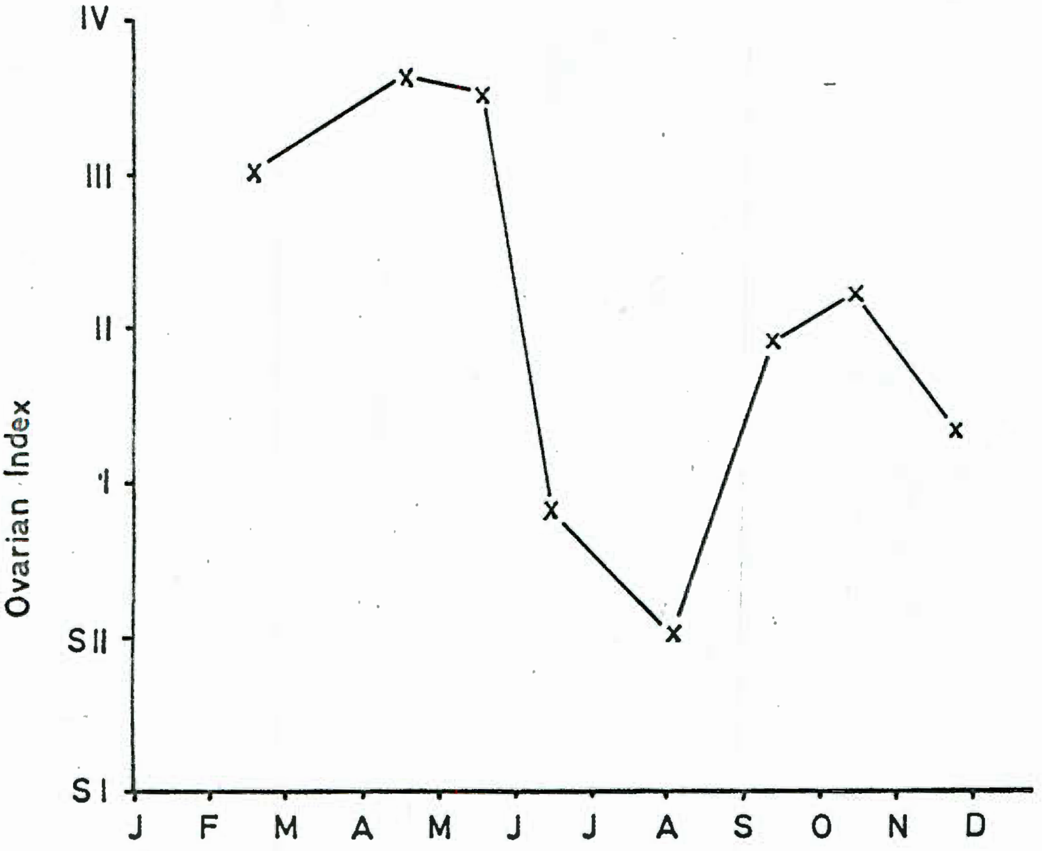


Fig 8d Egg counts

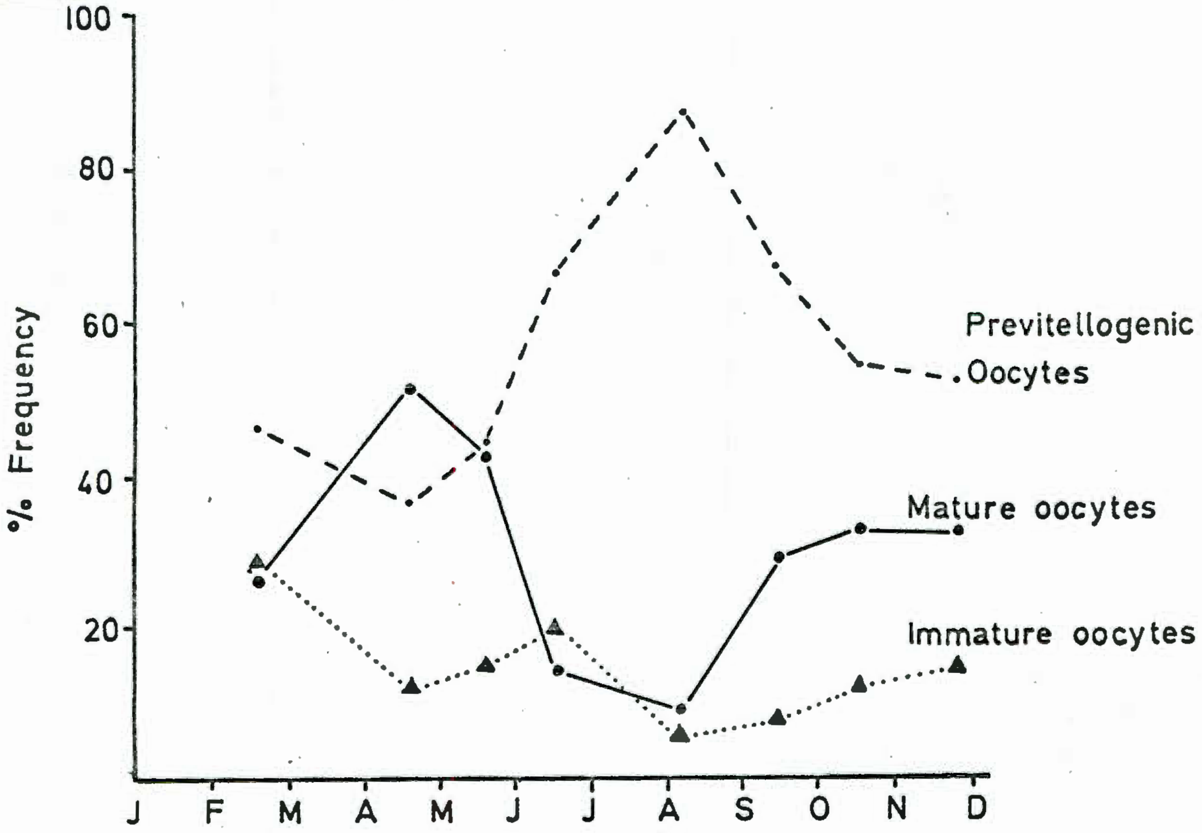
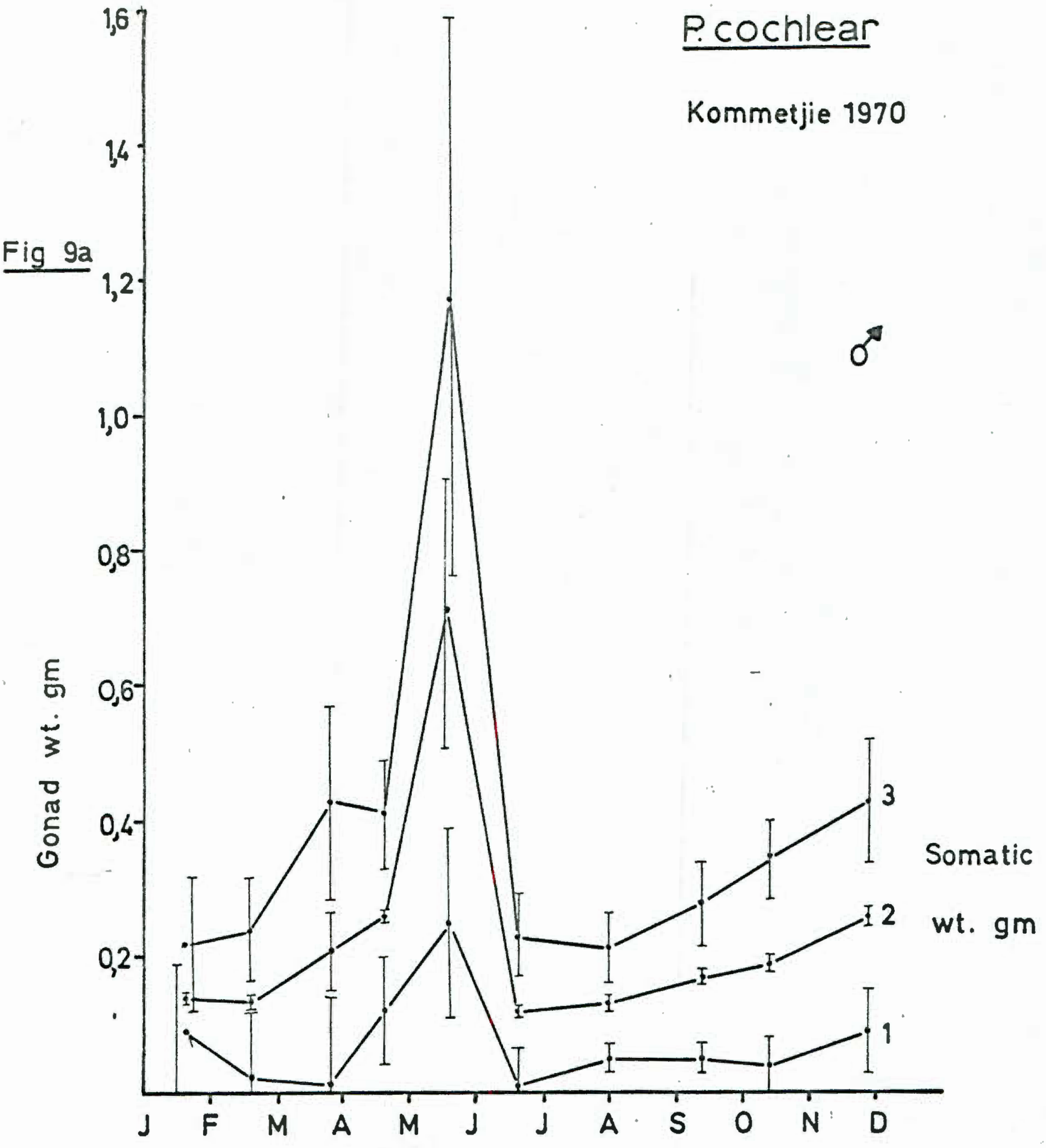
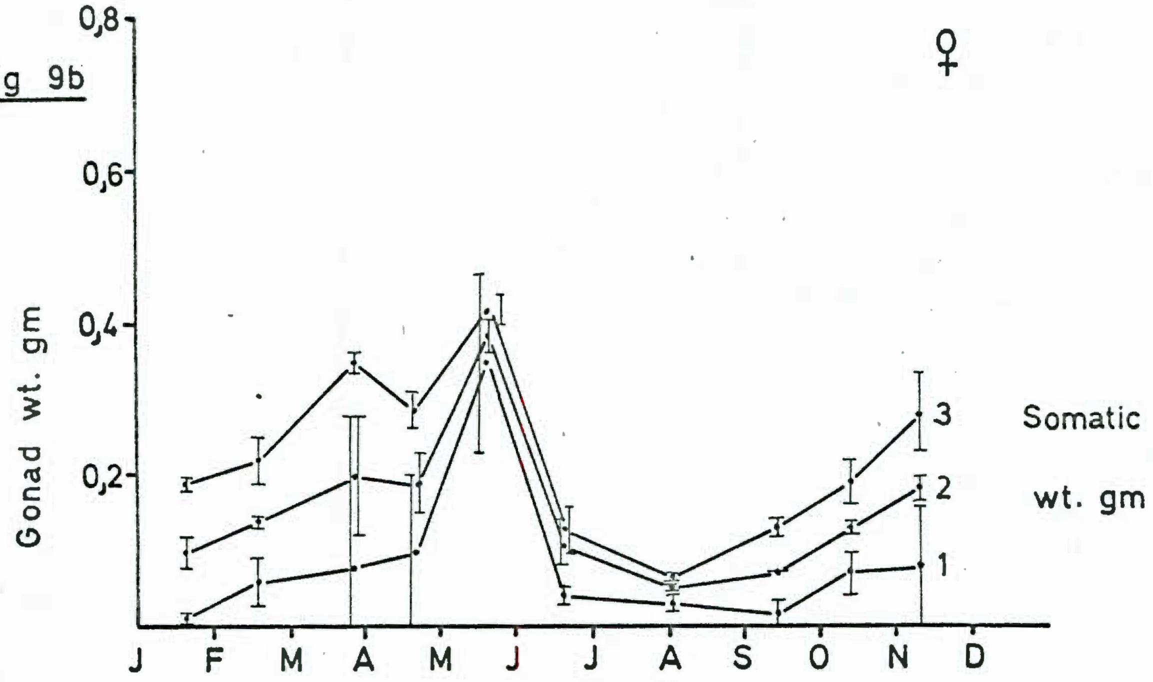


Fig 9a



P. cochlear
Kommetjie 1970
♂
1,6
1,4
1,2
1,0
0,8
0,6
0,4
0,2
Gonad wt. gm
3
2
1
Somatic
wt. gm
J
F
M
A
M
J
J
A
S
O
N
D

Fig 9b



♀
0,8
0,6
0,4
0,2
Gonad wt. gm
3
2
1
Somatic
wt. gm
J
F
M
A
M
J
J
A
S
O
N
D

P.cochlear

Kommetjie 1970

Fig 9c Subjective grading

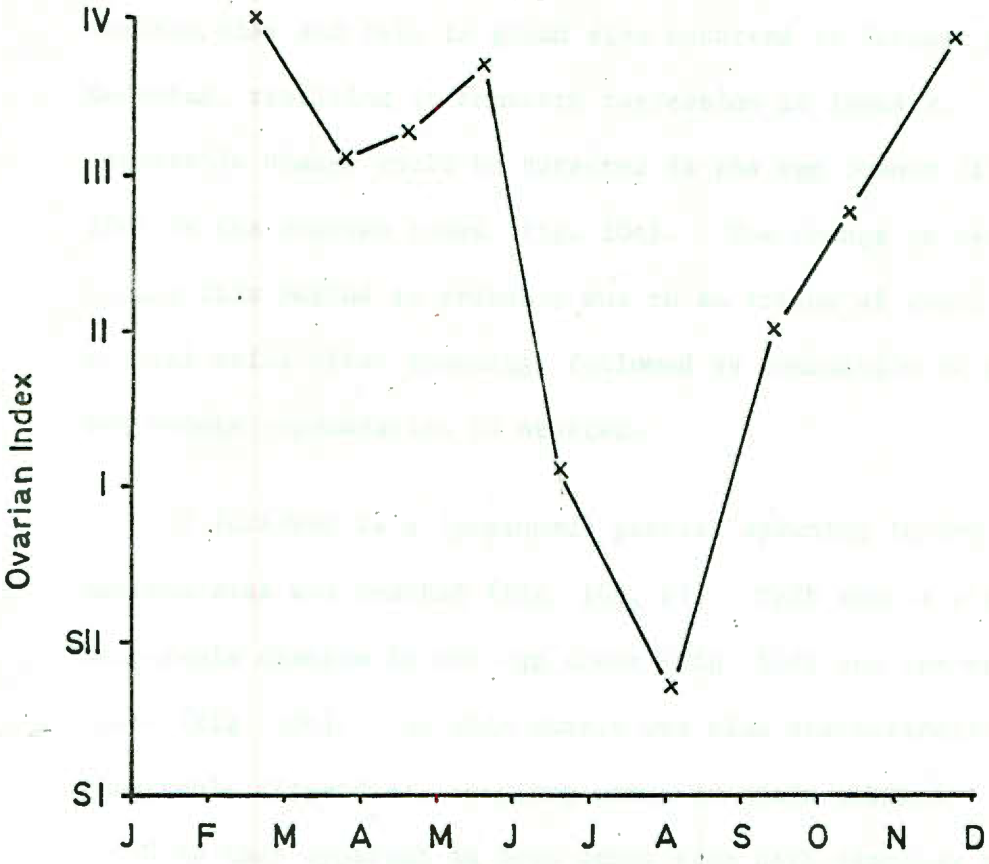
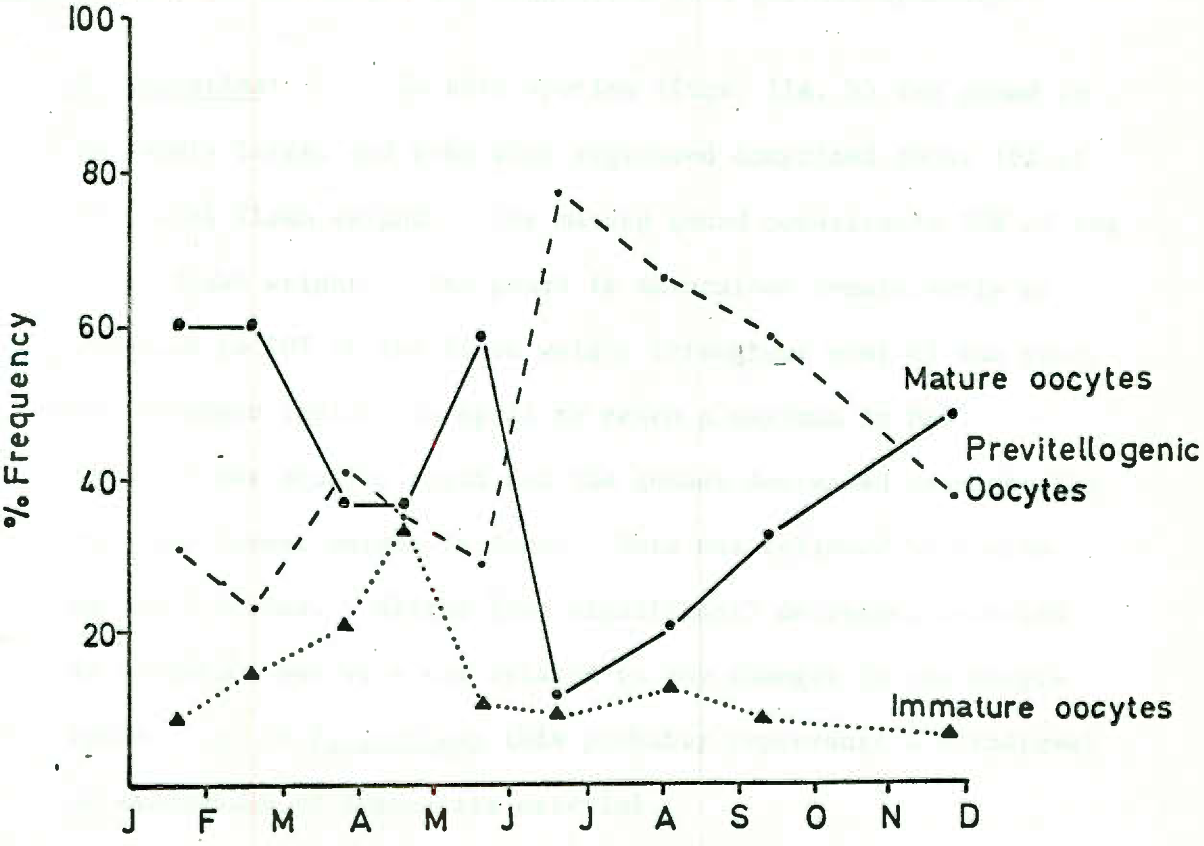


Fig 9d Egg counts



P.cochlear

Kalk Bay 1970

Fig 10a

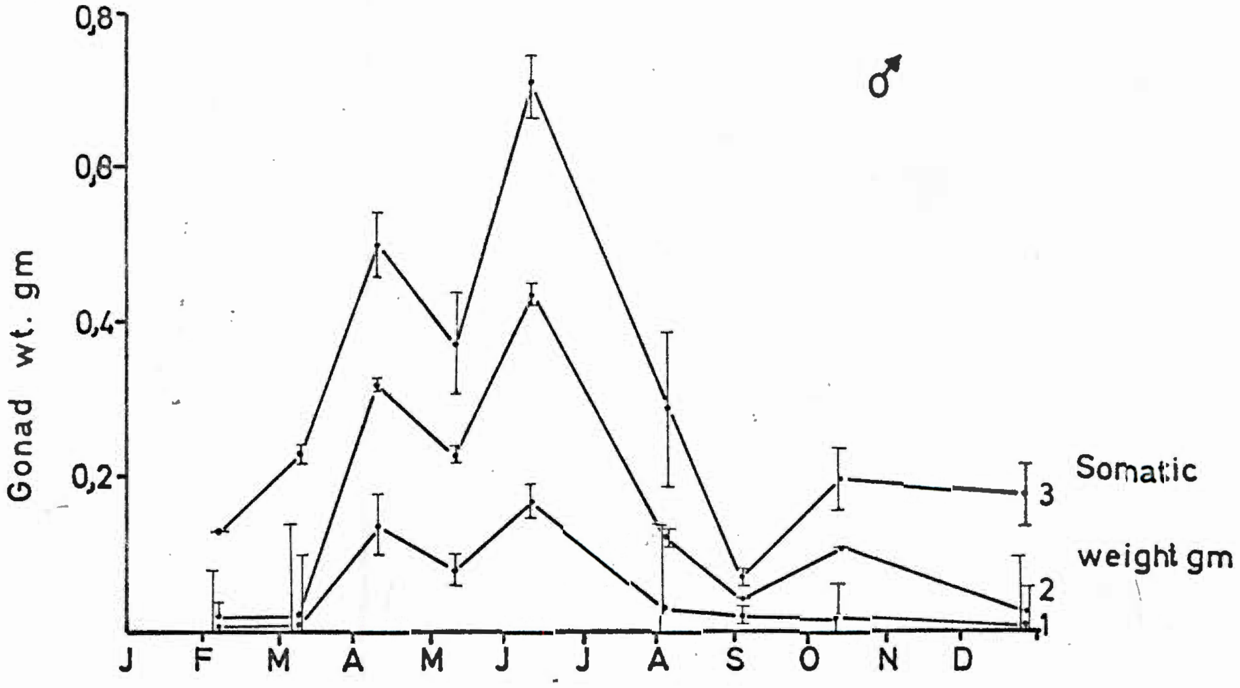
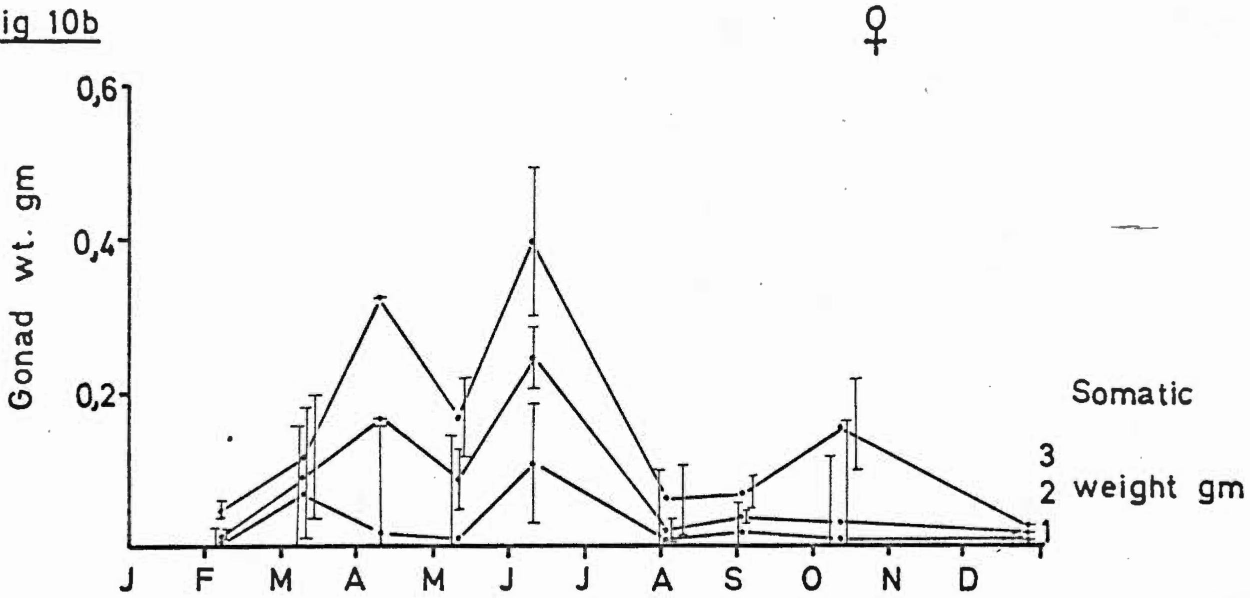


Fig 10b



P. cochlear

Kalk Bay 1970

Fig 10c Subjective grading

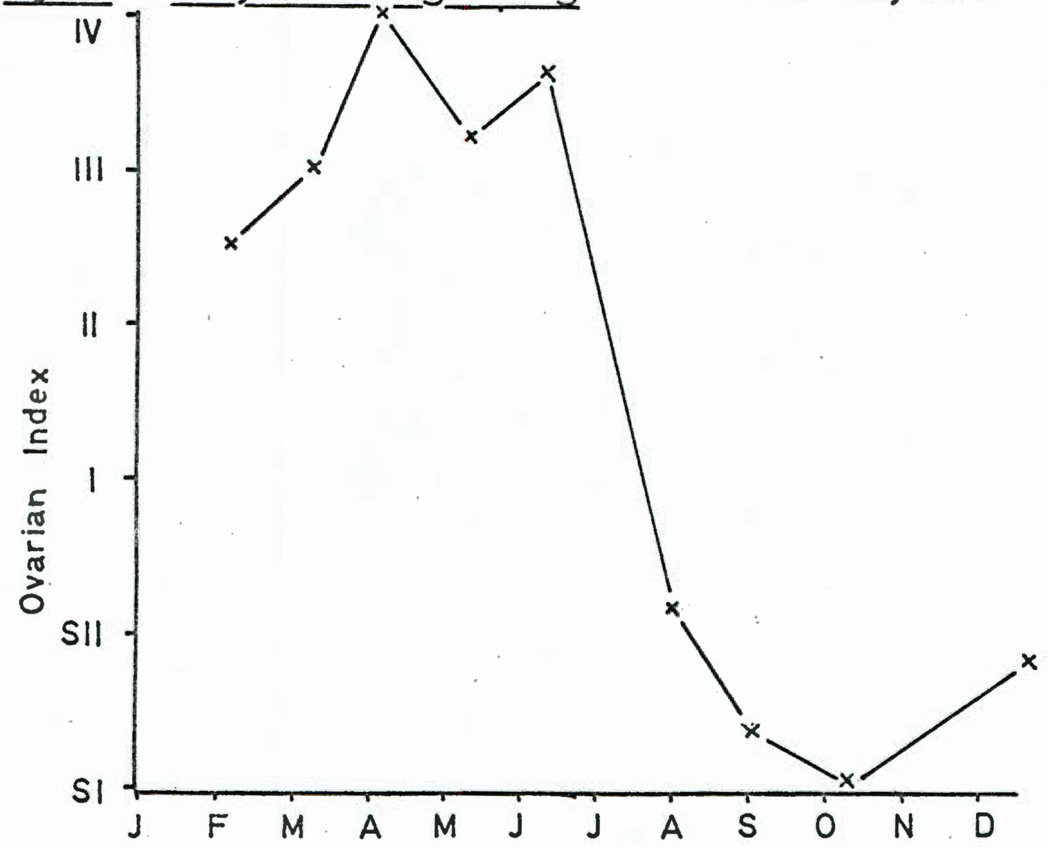


Fig 10d Egg counts

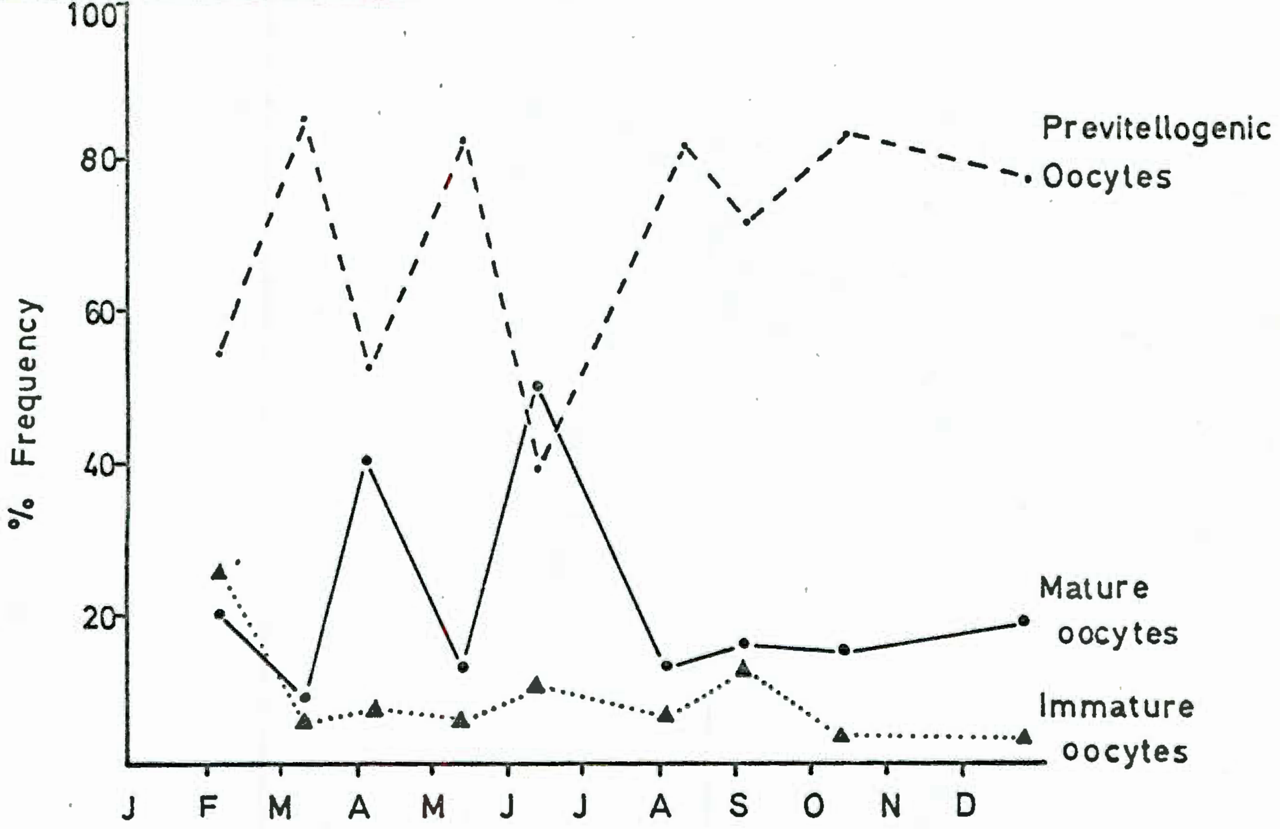


Fig 11a

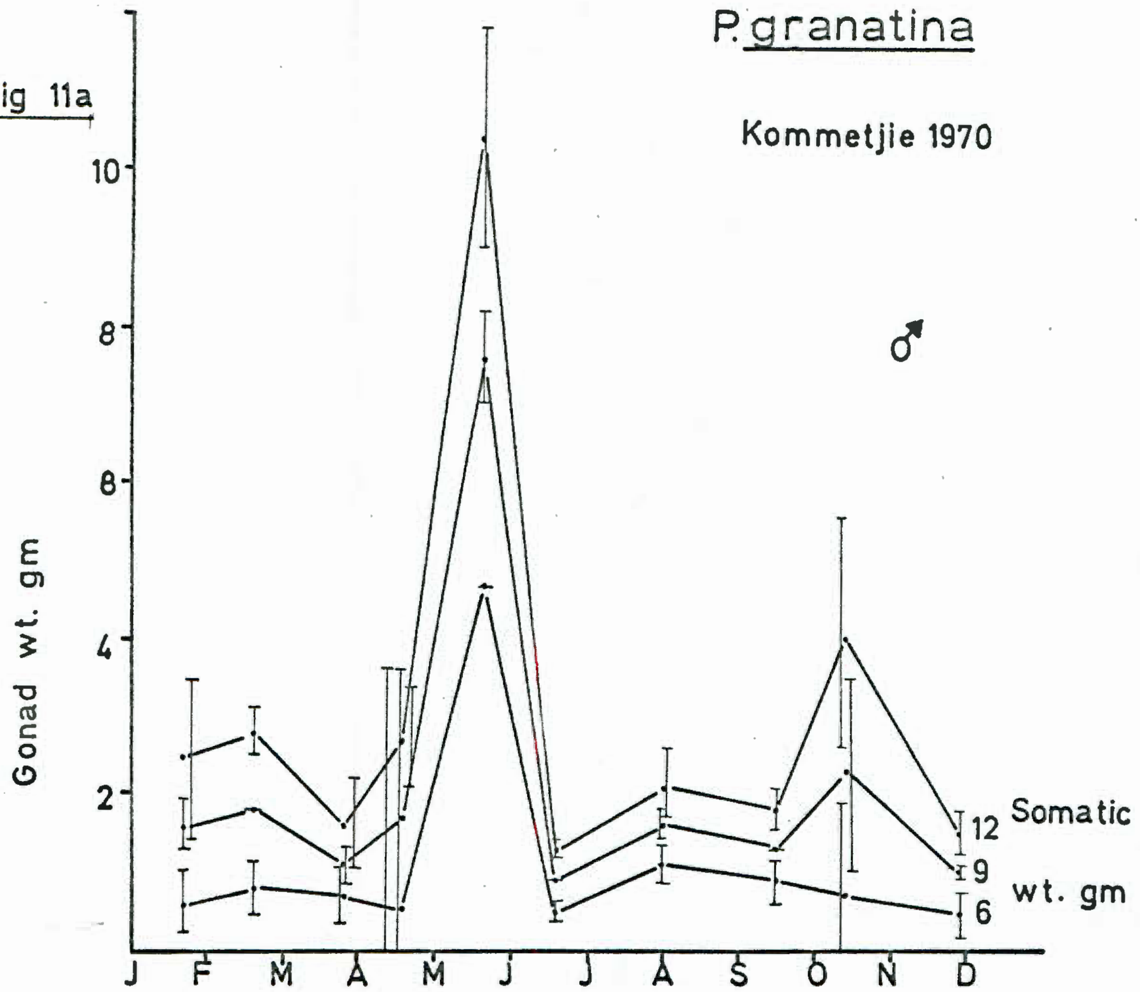
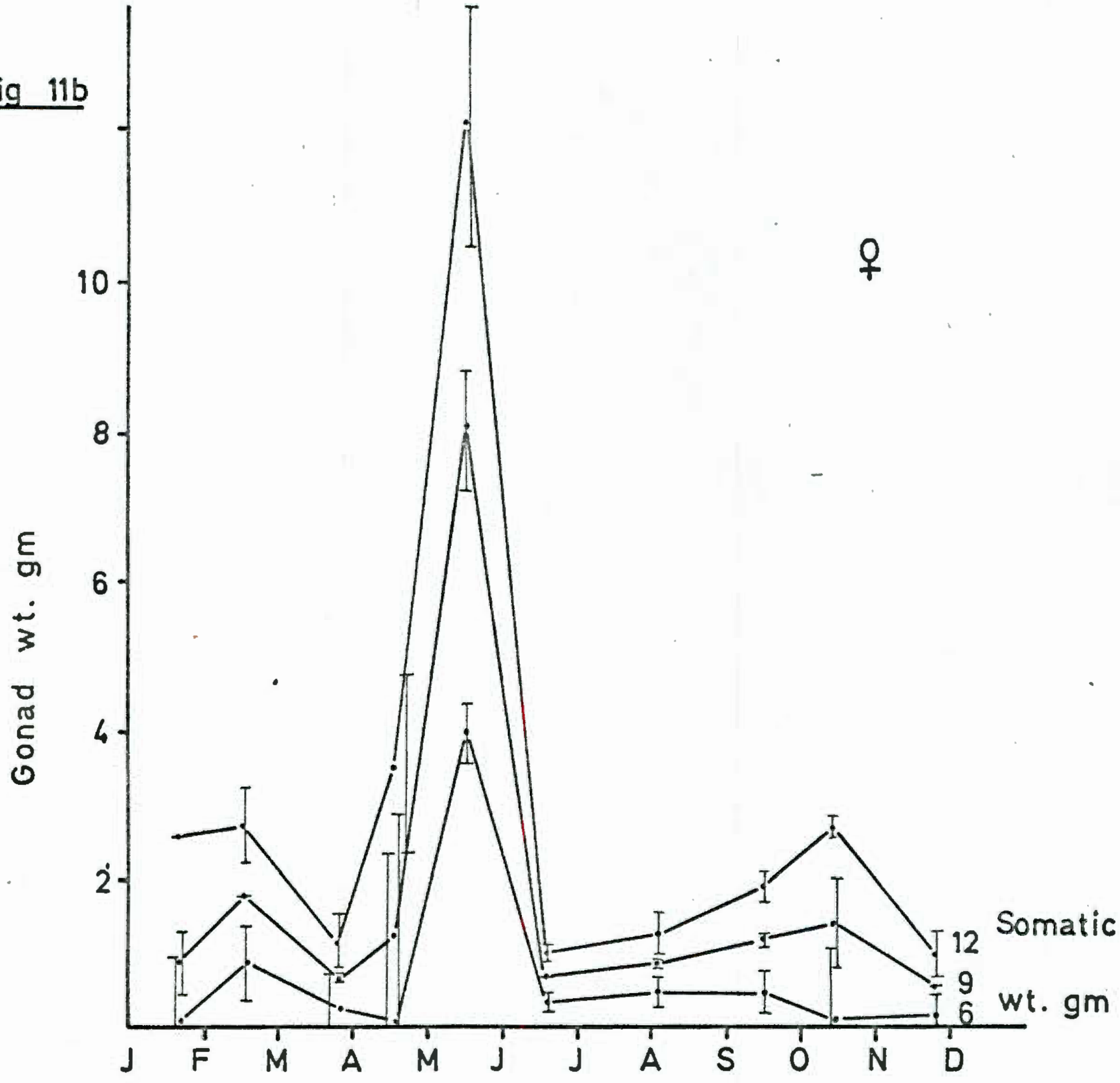


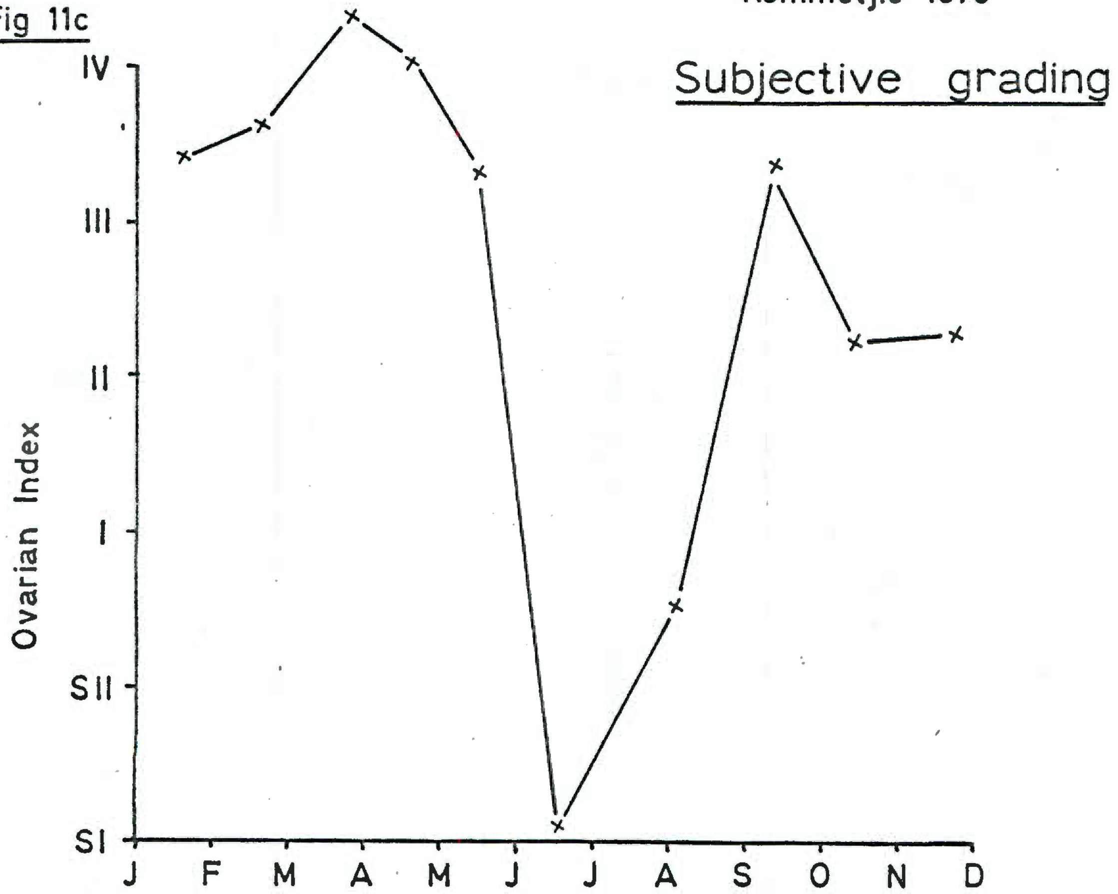
Fig 11b



P. granatina

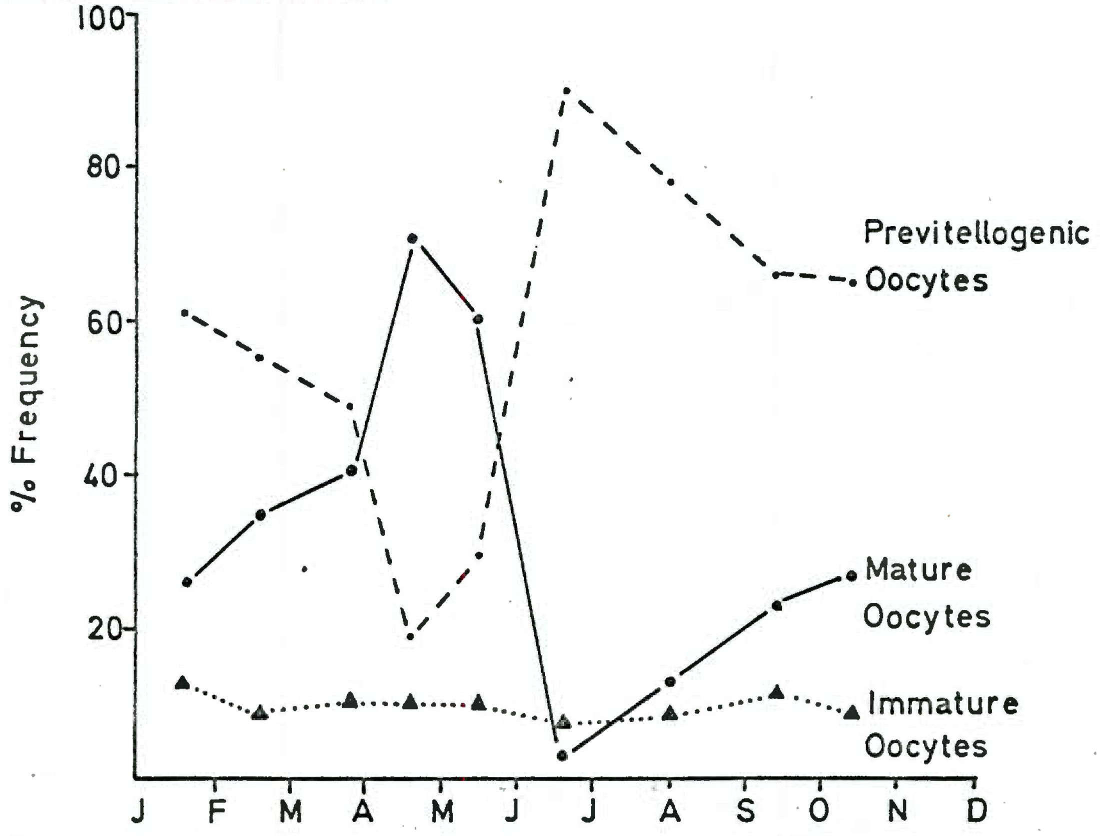
Kommetjie 1970

Fig 11c



Subjective grading

Fig 11d Egg counts



is an artificial depression caused by sampling only small animals on that date.

P. granularis: Samples from Kommetjie (figs. 12a, b) displayed a gradual increase in gonad size to a maximum in late May. Rapid spawning followed in June and July and the gonads remained resting for the remainder of the year. During this latter period the incidence of mature eggs remained low (fig. 12d) and artificial fertilisation could not be achieved. This agrees with Stephenson's (1936) statement that fertilisation could only be induced from November to the subsequent August. Cohen (1948, unpublished) found that sperm were not active during this period either.

The sample taken in April was unfortunately based only on small animals and yielded an artificially low gonad size. This was due to inadequate sampling and the confidence limits are correspondingly wide. The subsequent increase in May makes it very unlikely that spawning had occurred in April. Nevertheless, a slight decrease in the proportion of mature eggs was recorded for this month (fig. 12d) and the ovarian index decreased slightly (fig. 12c): thus the possibility of a partial and incomplete spawning in April cannot be discounted.

The mean size of P. granularis decreases markedly on the warm coast (Stephenson, 1939) and the gonad size was therefore correspondingly lower in samples from Kalk Bay (figs. 13a, b). Maturation and spawning occurred slightly later in the year than at Kommetjie, but again the gonads remained regressed for the rest of the year after spawning. There was no sign of a partial spawning before maturation was complete. Egg counts (fig. 13d) followed the gonad cycle closely. In December there was a decrease of ovary size at both Kommetjie (fig. 12b) and Kalk Bay

Fig 12a

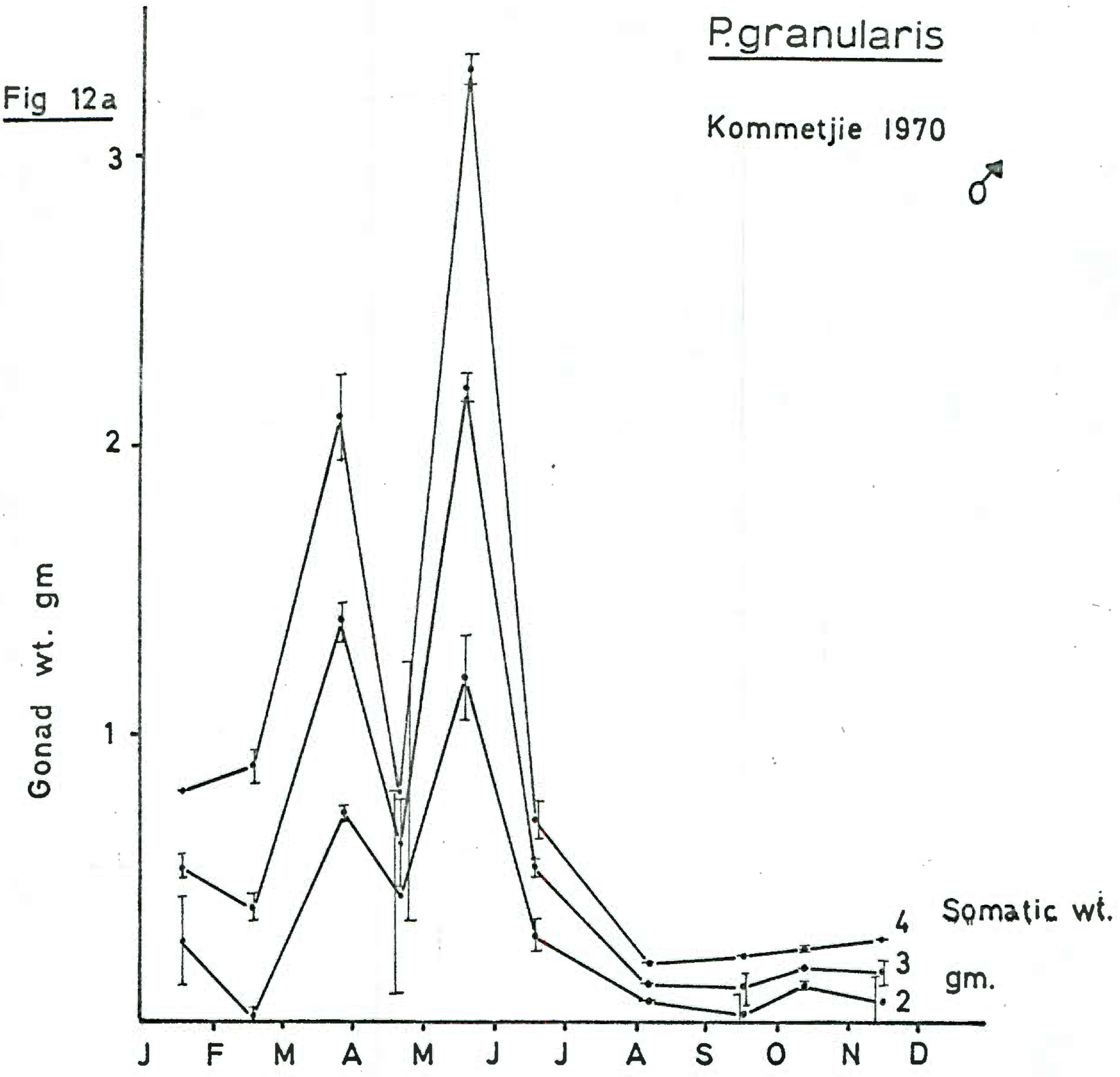
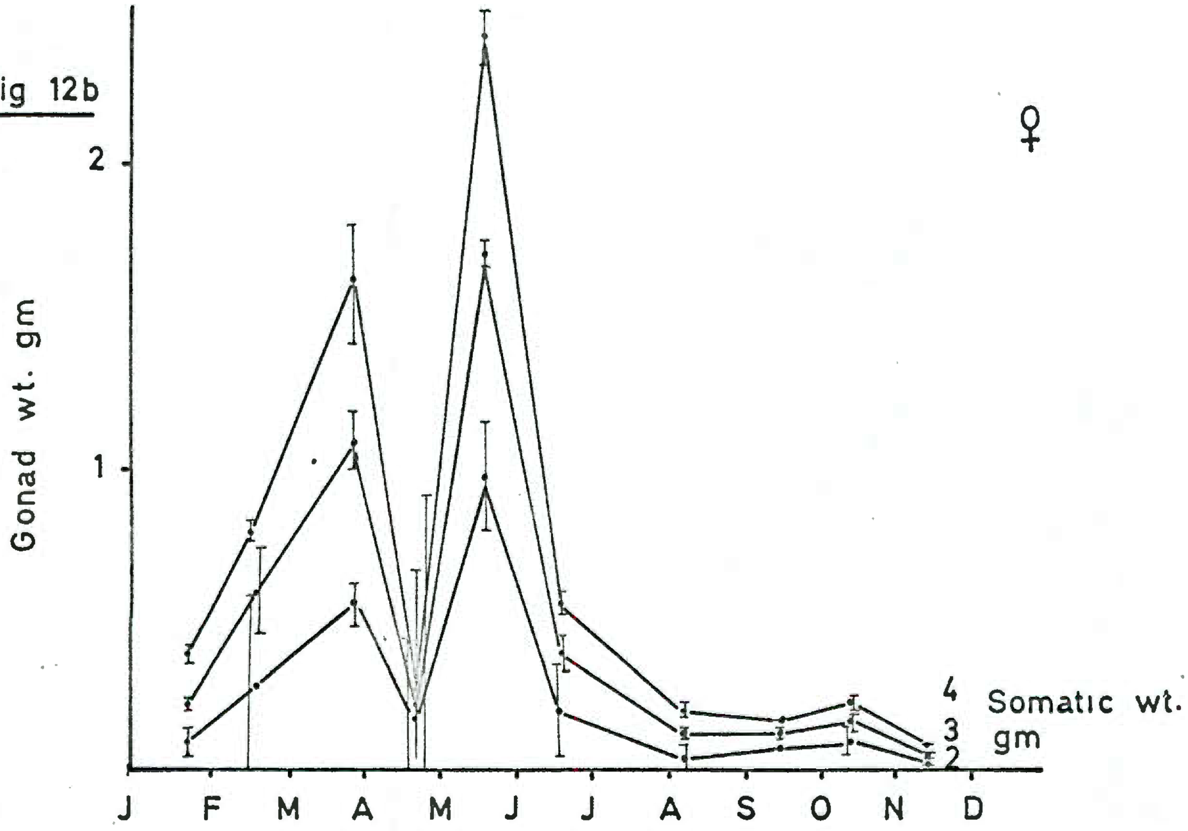


Fig 12b



P granularis

Kommetjie 1970

Fig 12c Subjective grading

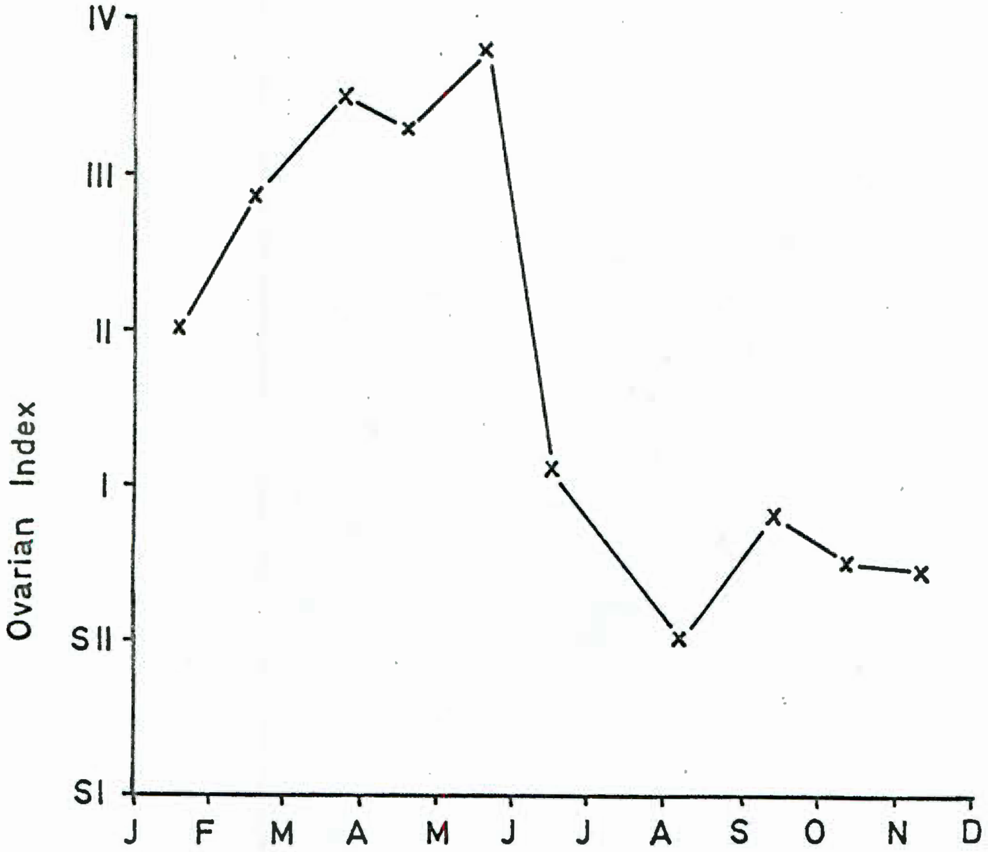
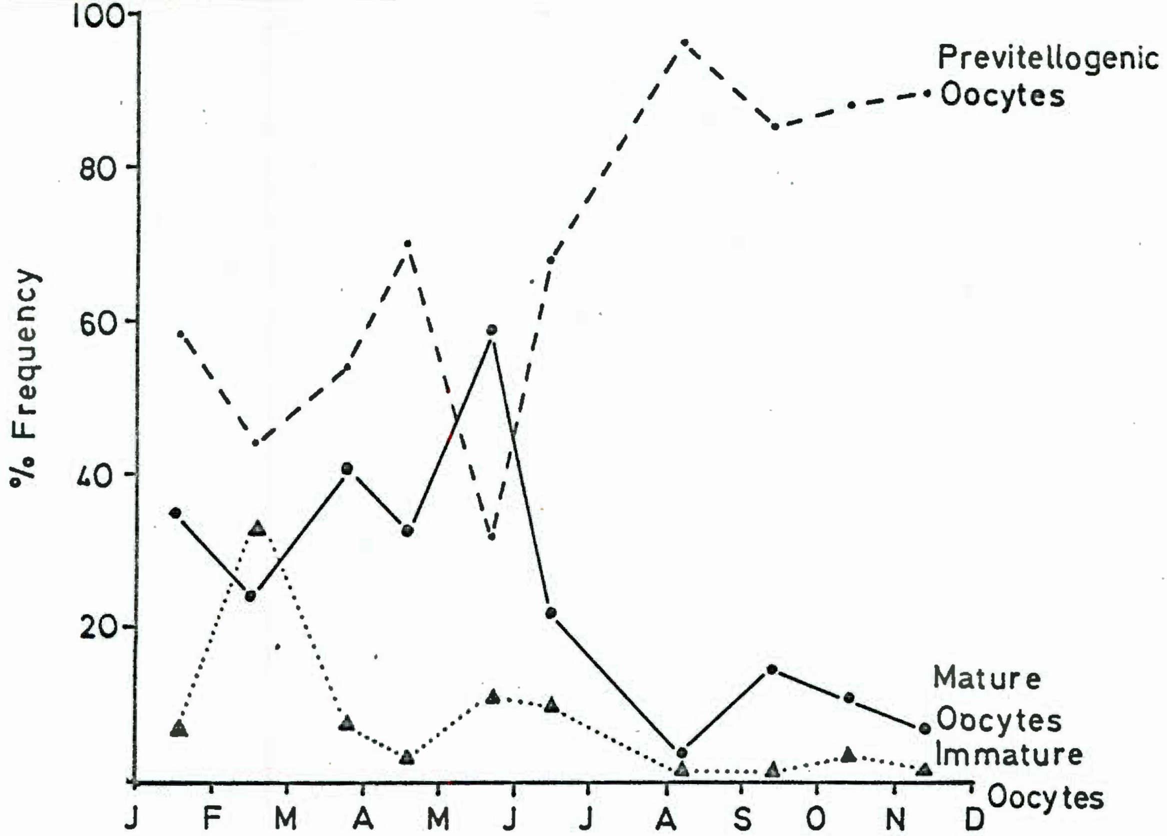


Fig 12d Egg counts



P.granularis

Kalk Bay 1970

Fig 13a

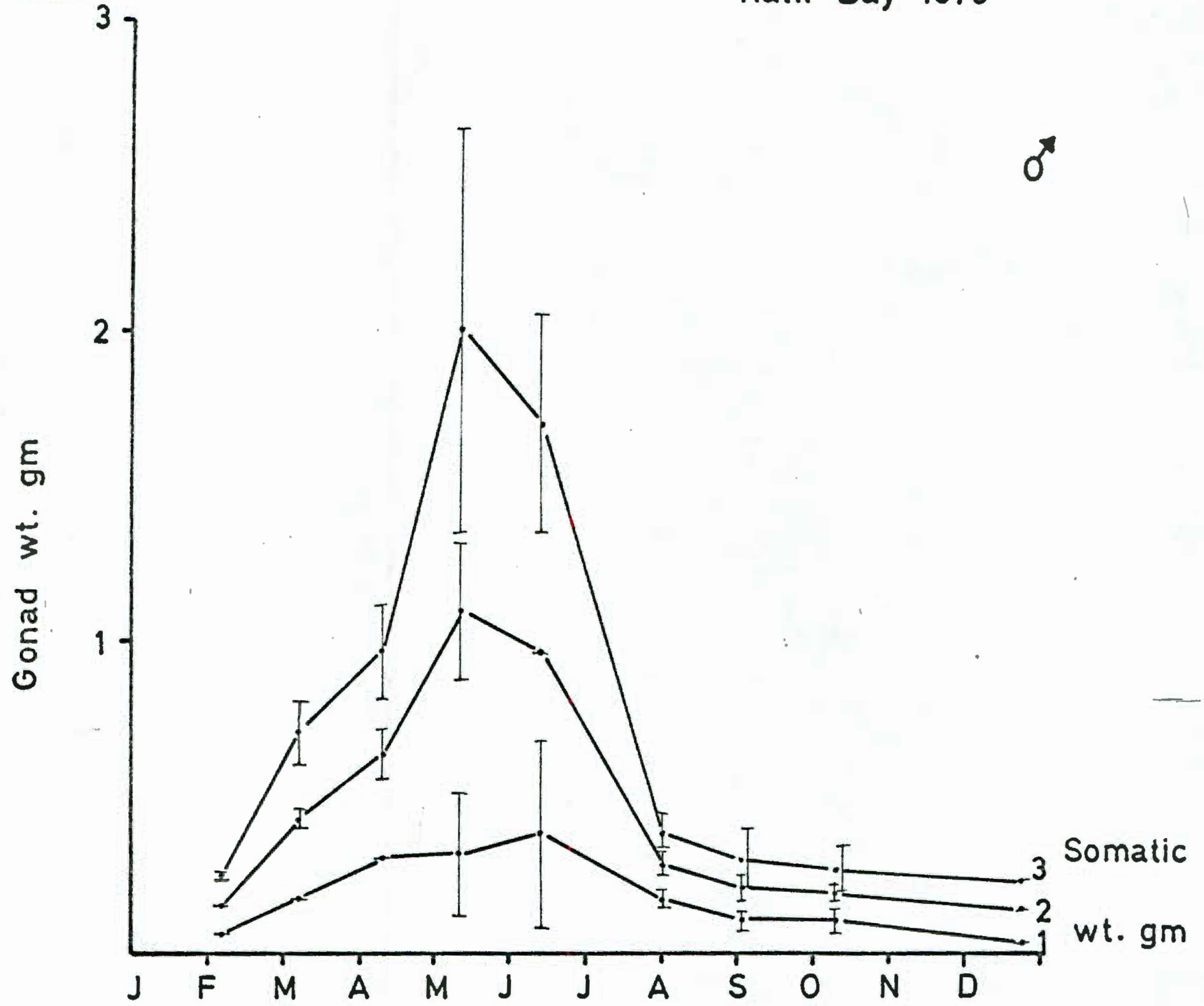
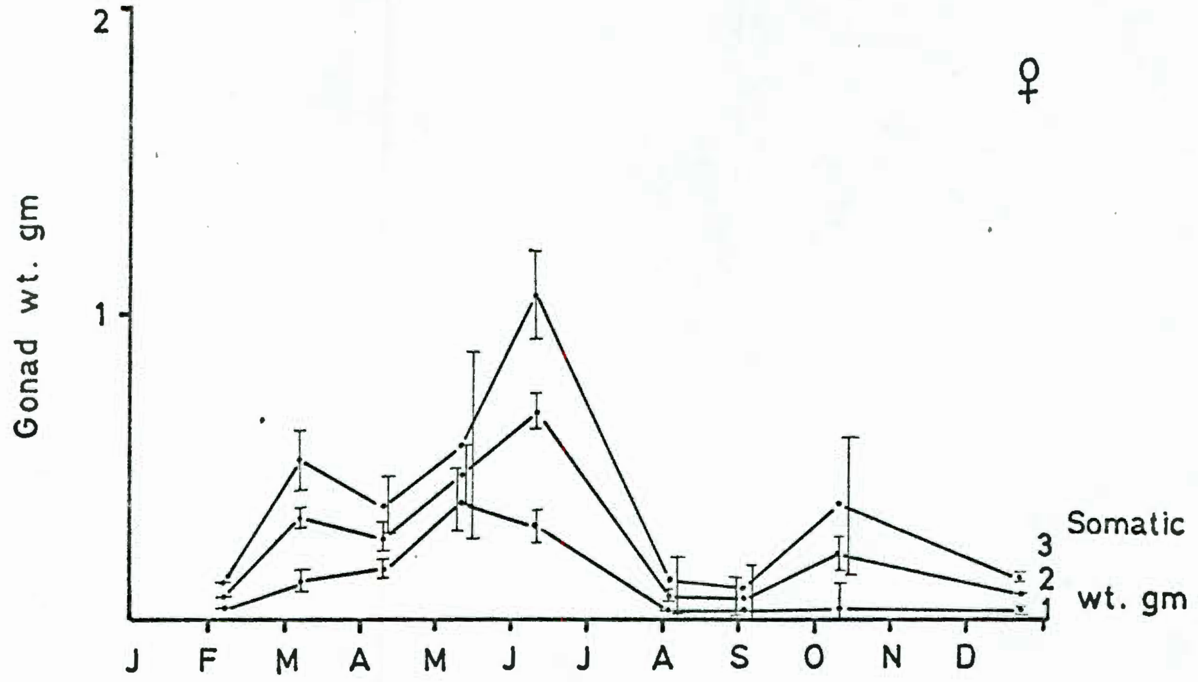


Fig 13b



P.granularis

Kalk Bay 1970

Fig 13c Subjective grading

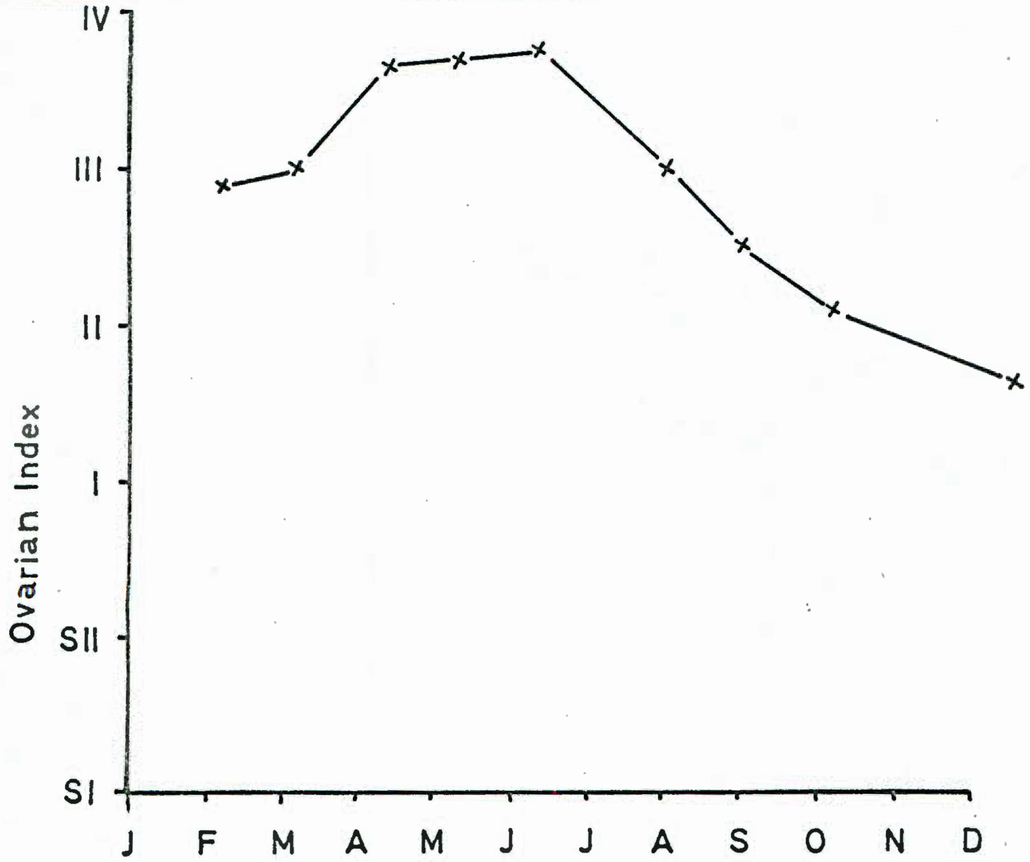
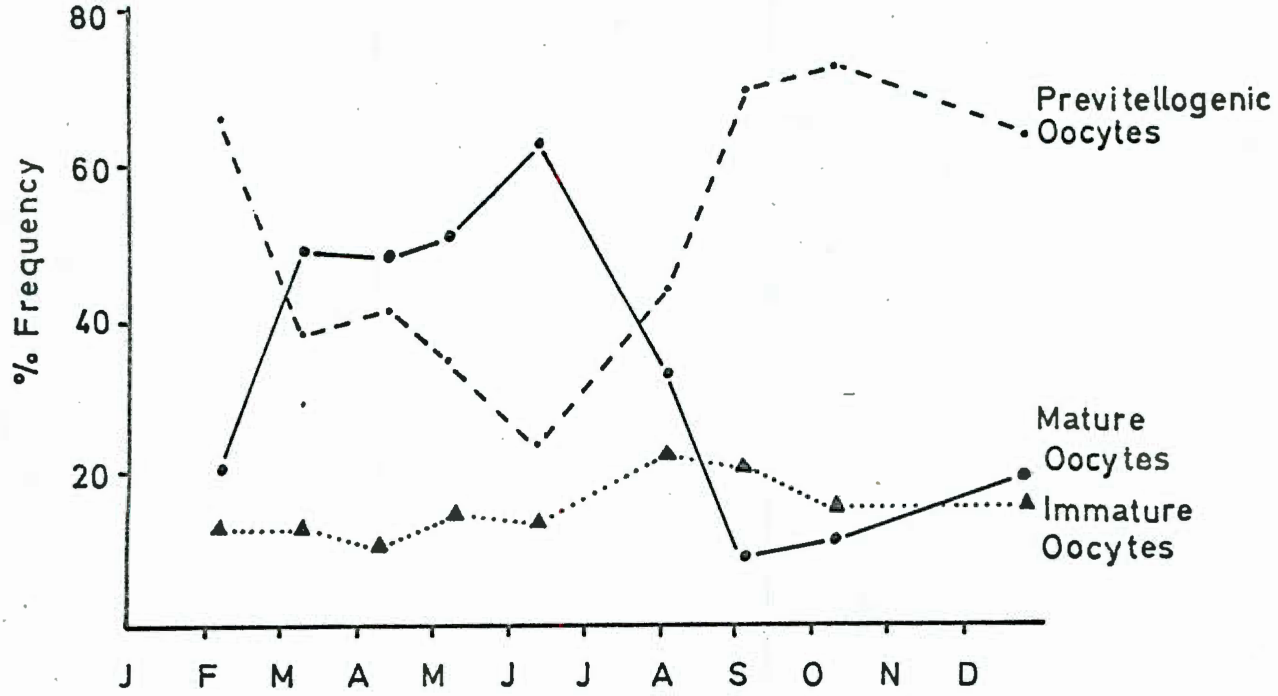


Fig 13d Egg counts



(fig. 13b), representing the removal of interstitial cells and degenerate eggs prior to redevelopment.

P. longicosta: A gradual increase in gonad size occurred from January to September, except for a slight, statistically insignificant decrease in May (figs. 14a, b). Spawning occurred progressively from late September to December, and was sporadic: some individuals spawned early in October while others remained mature until late November. In each individual spawning was rapid once initiated, and specimens tended to be either very mature or completely spent. This is reflected in the eratic egg counts obtained during this period (fig. 14d).

P. oculus: P. oculus presents a rather unusual case in that the females are very much larger than the males, and very much less common - as will be discussed below (p. 21). As a result, females were inadequately represented in several samples due to their scarcity, and could not be statistically analysed in these samples. Less reliance can thus be placed on the female cycle, but as it followed the male cycle closely, it is at least qualitatively accurate.

In both sexes there was a progressive build up in gonad weight until August, when a sharp but not very pronounced spawning occurred (figs. 15a, b). The testes then regressed slowly, a minimum size being recorded in February. The females recovered more quickly (fig. 15b).

In the May sample, a few spent females were recorded, constituting 18% of the total sample. These were treated separately in processing the data (fig. 15b), but contributed substantially to lowering the percentage of mature eggs (fig. 15d) and the ovarian index (fig. 15c). This may have been a partial

P. longicosta

Kalk Bay 1970

Fig 14a

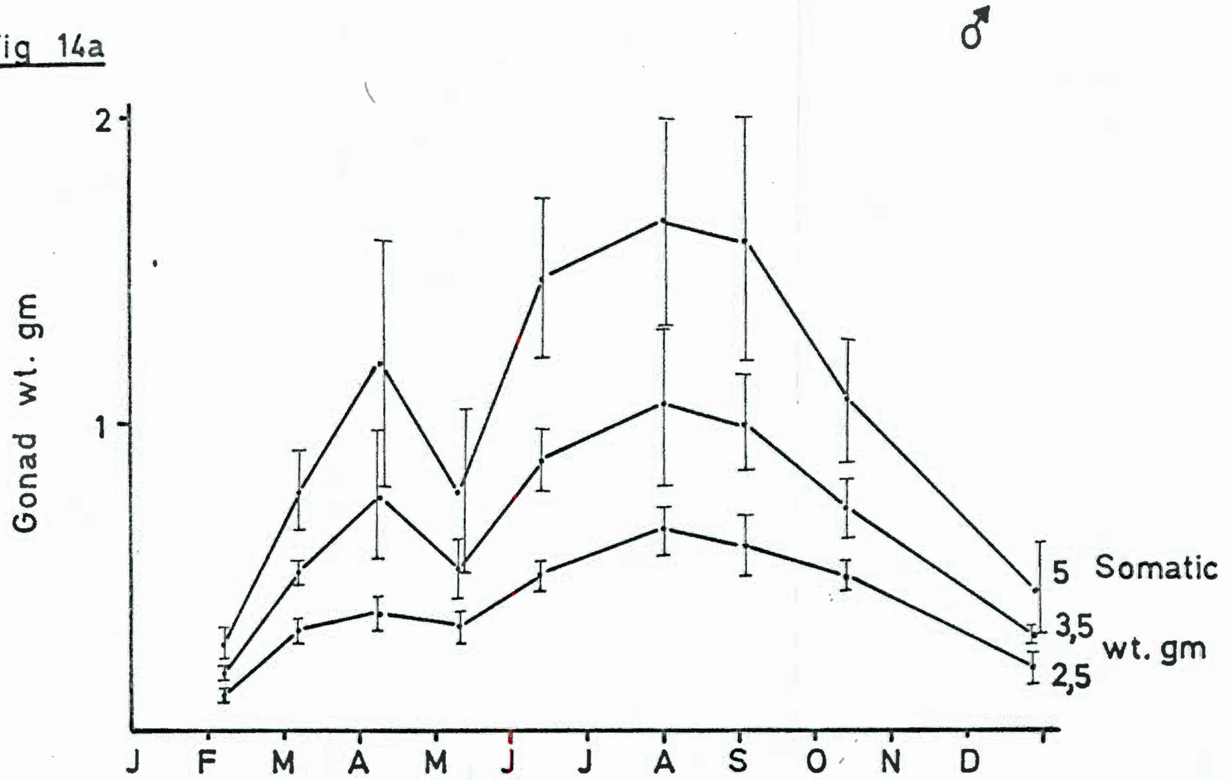
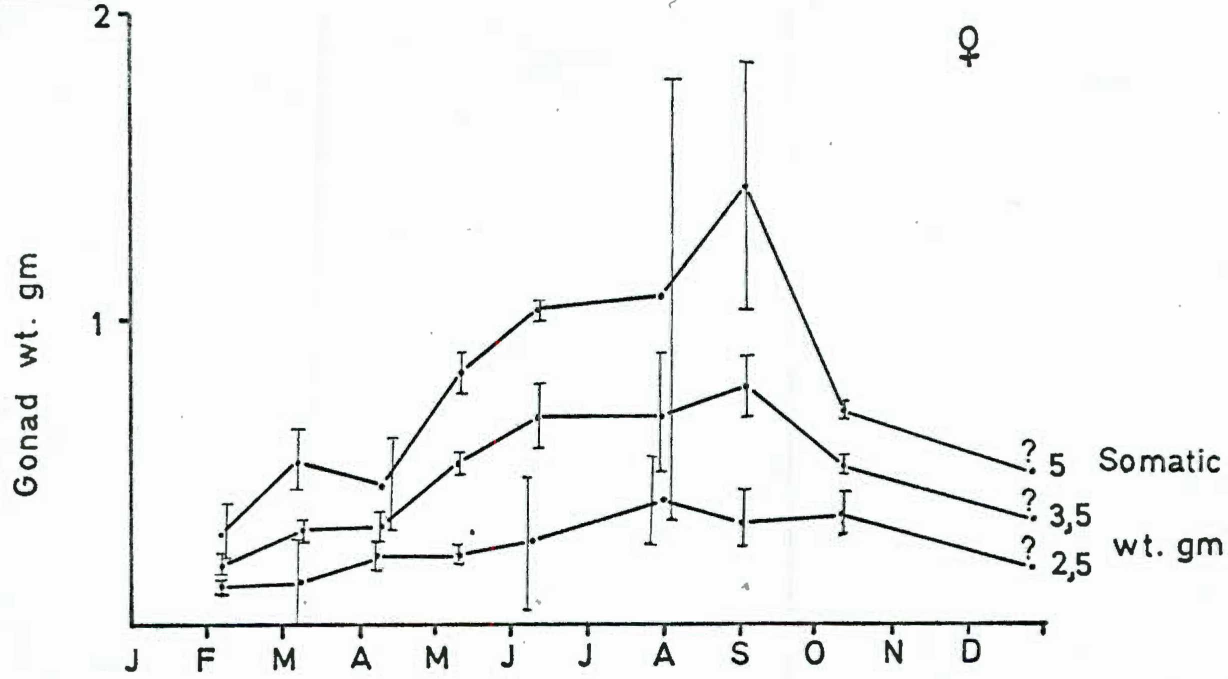


Fig 14b



P.longicosta

Kalk Bay 1970

Fig. 14c Subjective grading

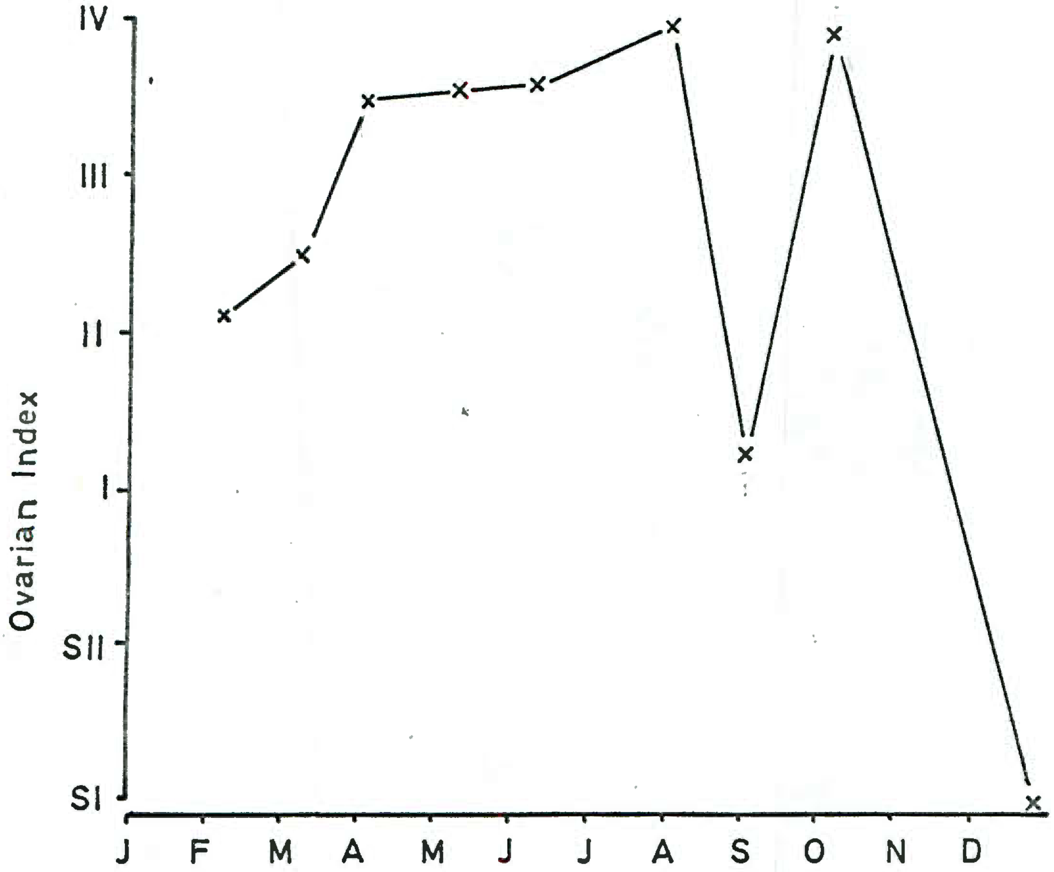
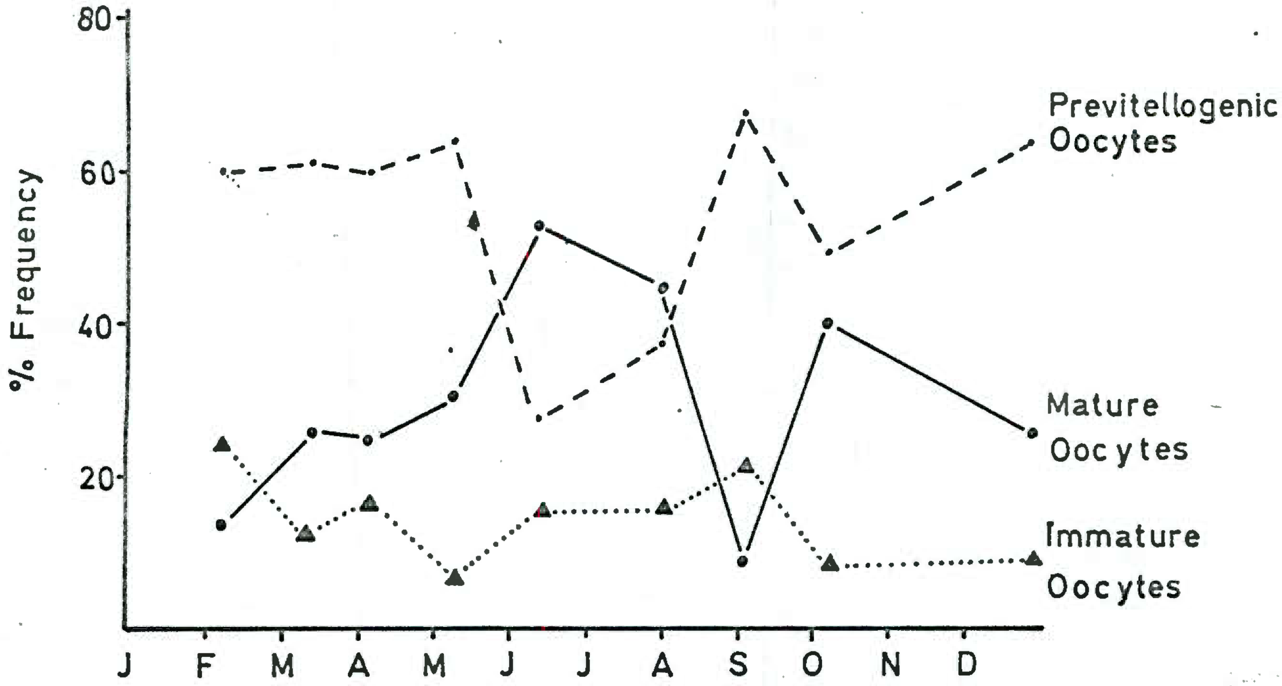


Fig. 14d Egg counts



Poculus

Kalk Bay 1970

Fig 15a

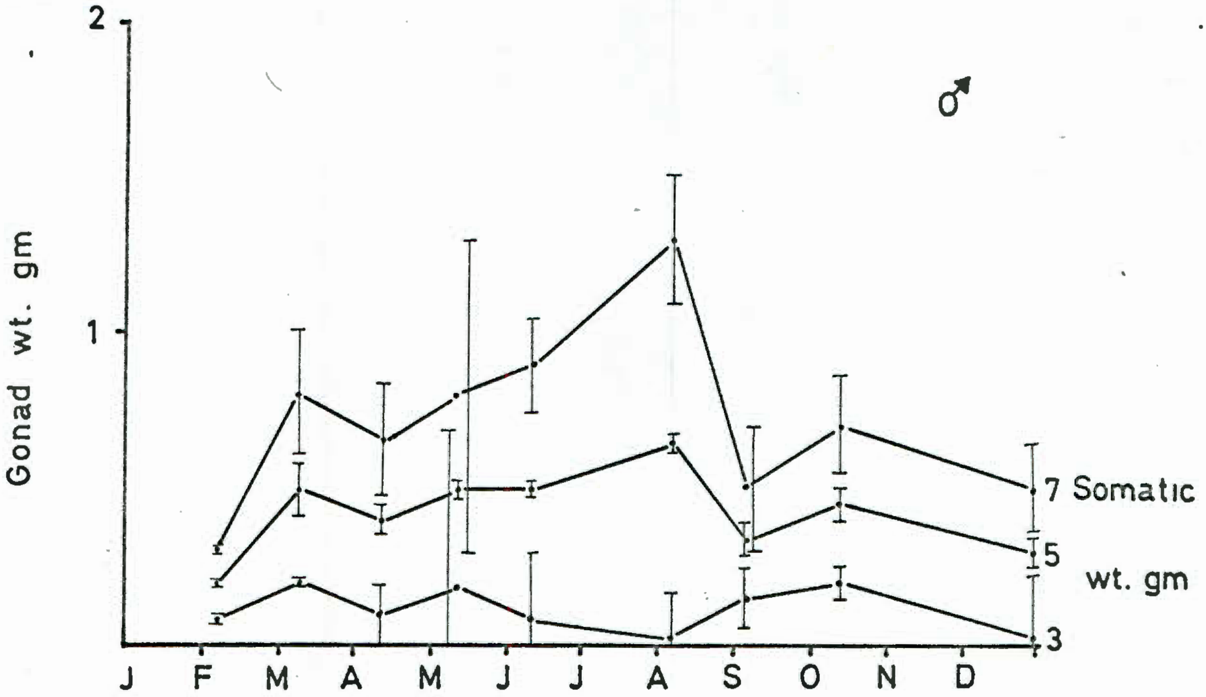
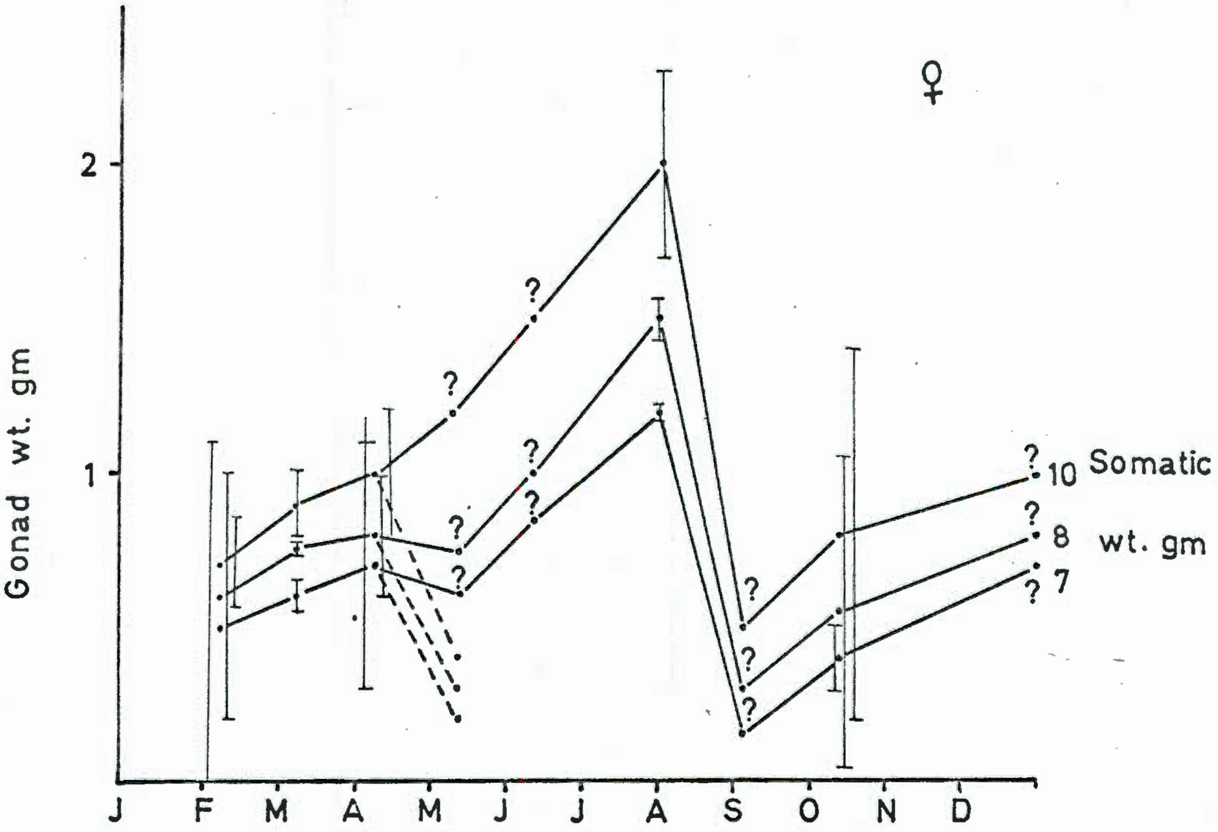


Fig 15b



P.oculus

Kalk Bay 1970

Fig 15c Subjective grading

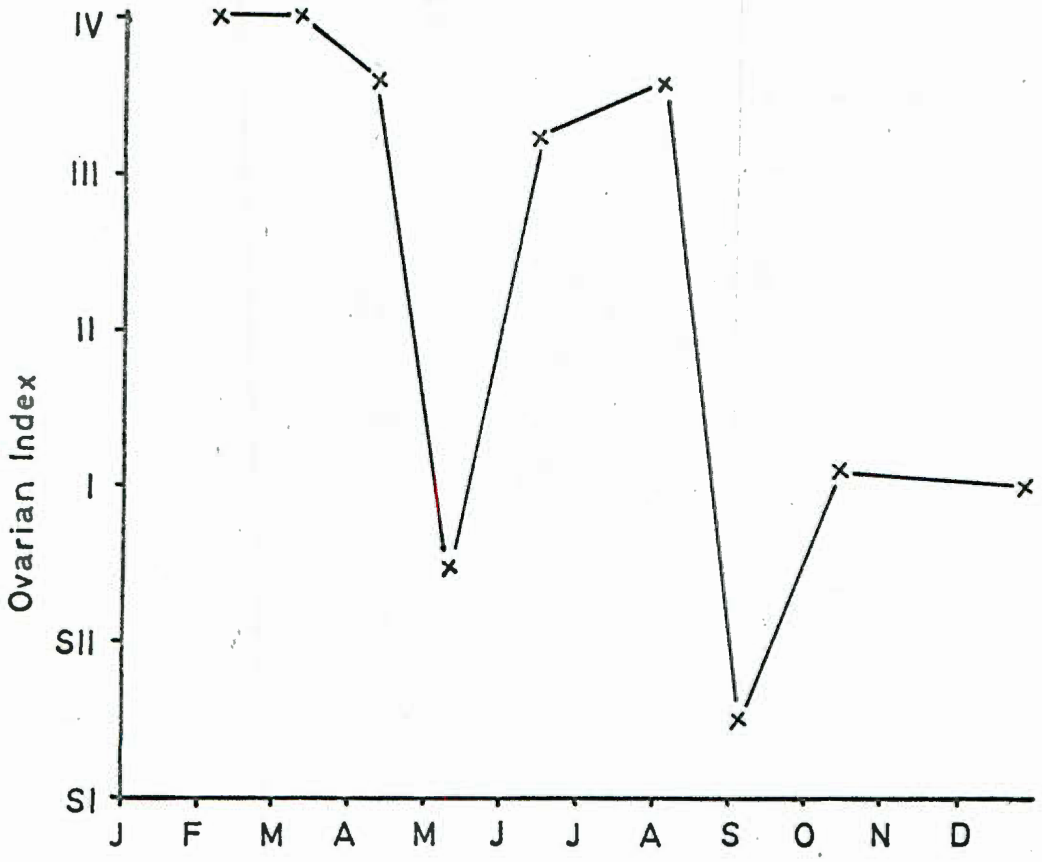
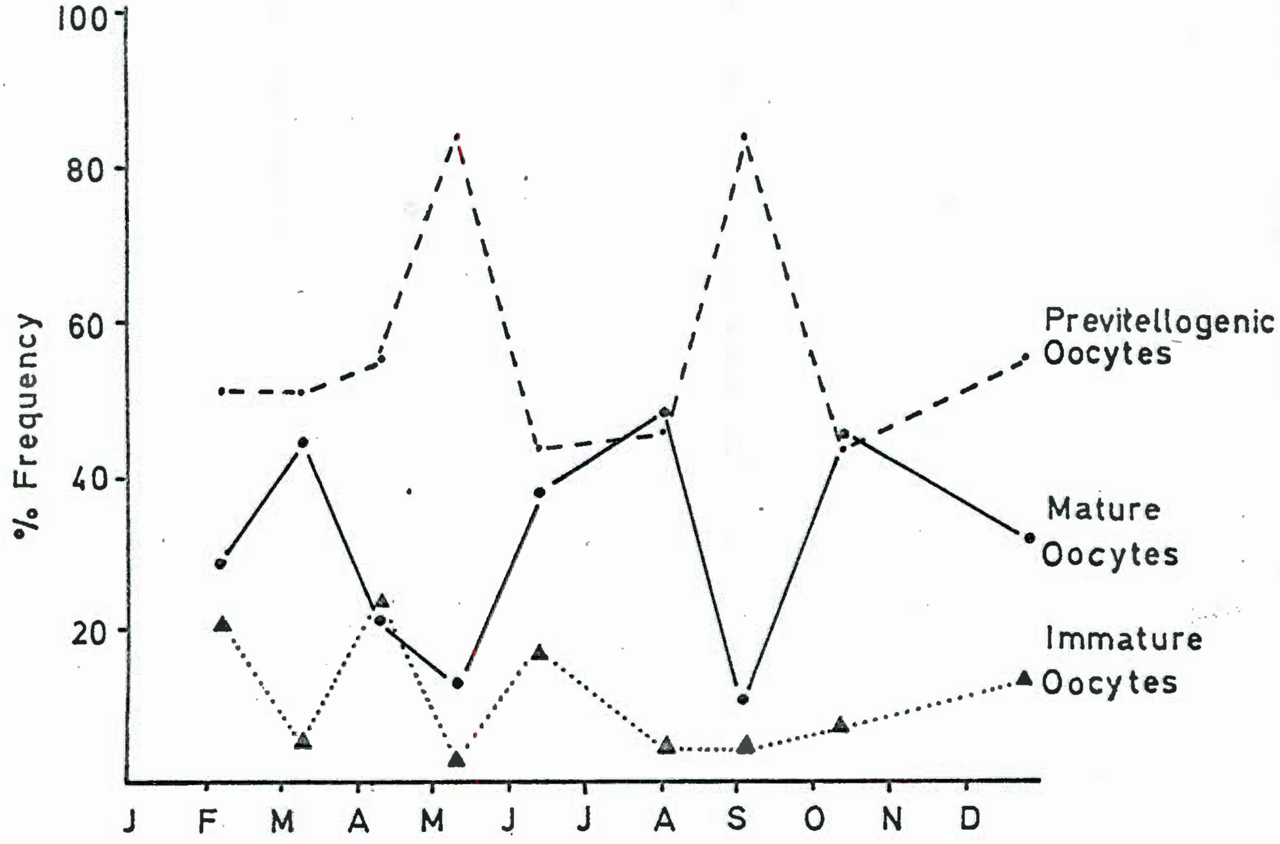


Fig 15d Egg counts



(or false) spawning, as there was no significant corresponding spawning in the males. The subsequent samples of June and August included no spent specimens and the population as a whole contained progressively more mature animals.

As in P. longicosta, spawning was not well defined, and was more irregular than in the other species.

P. miniata, P. compressa and P. concolor: No detailed analysis of these species was made. Small samples of P. miniata were collected throughout the year, and they appeared to spawn between May and July. P. compressa were sampled in April (when they were mature) and in June and August (when most were spent). Spawning probably occurred in May. Only one sample of P. concolor was available, collected in January 1971. This contained a mixture of immature and very mature, and one spent specimen (See Section II, p. 9). This suggests that spawning would have occurred later in January. This does not of course preclude the possibility that spawning occurs at other periods, or continuously throughout the year.

In these three species, evidence for spawning is scant and further analysis is required before confidence can be placed in the results.

Ovarian Index

Ovaries were graded on the basis of size and maturity of eggs, as described above. The technique is easily applied and quick: it was undertaken primarily to assess its accuracy relative to the gravimetric quantitative method. The average ovarian indices are summarised in figures 7c - 15c. Comparison with the gravimetric results (figs. 7a, b to 15a, b) and the egg counts (figs. 7d to 15d) shows that grading gives a relatively accurate, non-quantitative reflection of the spawning period. This is particularly true for P. argenvillei, P. barbara, P. cochlear, P. granatina and P. granularis.

In P. longicosta, spawning of the population is protracted and grading tends to over-emphasize the eratic distribution of mature and spent specimens (fig. 14c). Similarly, in the case of P. oculus the false spawning in May only involved a minority of the population, and the grading technique over-emphasizes the importance of these animals and gives the impression that a major spawning has occurred (fig. 15c).

Nevertheless, in most Patella spp. this technique can be used confidently in future studies which are required only to pinpoint the period of spawning.

FECUNDITY

Fecundity was assessed in terms of the number of eggs per gram of ovary and total eggs per ovary and comparison made between mature and spent gonads. In mature ovaries the fecundity was very variable, and an analysis of variance indicated that the interspecific differences did not contribute significantly to the total variation, as compared with the random (intraspecific) differences. In P. cochlear, P. longicosta and P. oculus fairly large numbers of eggs are retained after spawning, while the other species (particularly P. argenvillei) tended to evacuate almost all their mature eggs. The average fecundity in mature ovaries was 516 ova per gram. This is much higher than the equivalent figure for Haliotis midae (Newman, 1967).

Table I summarises the data.

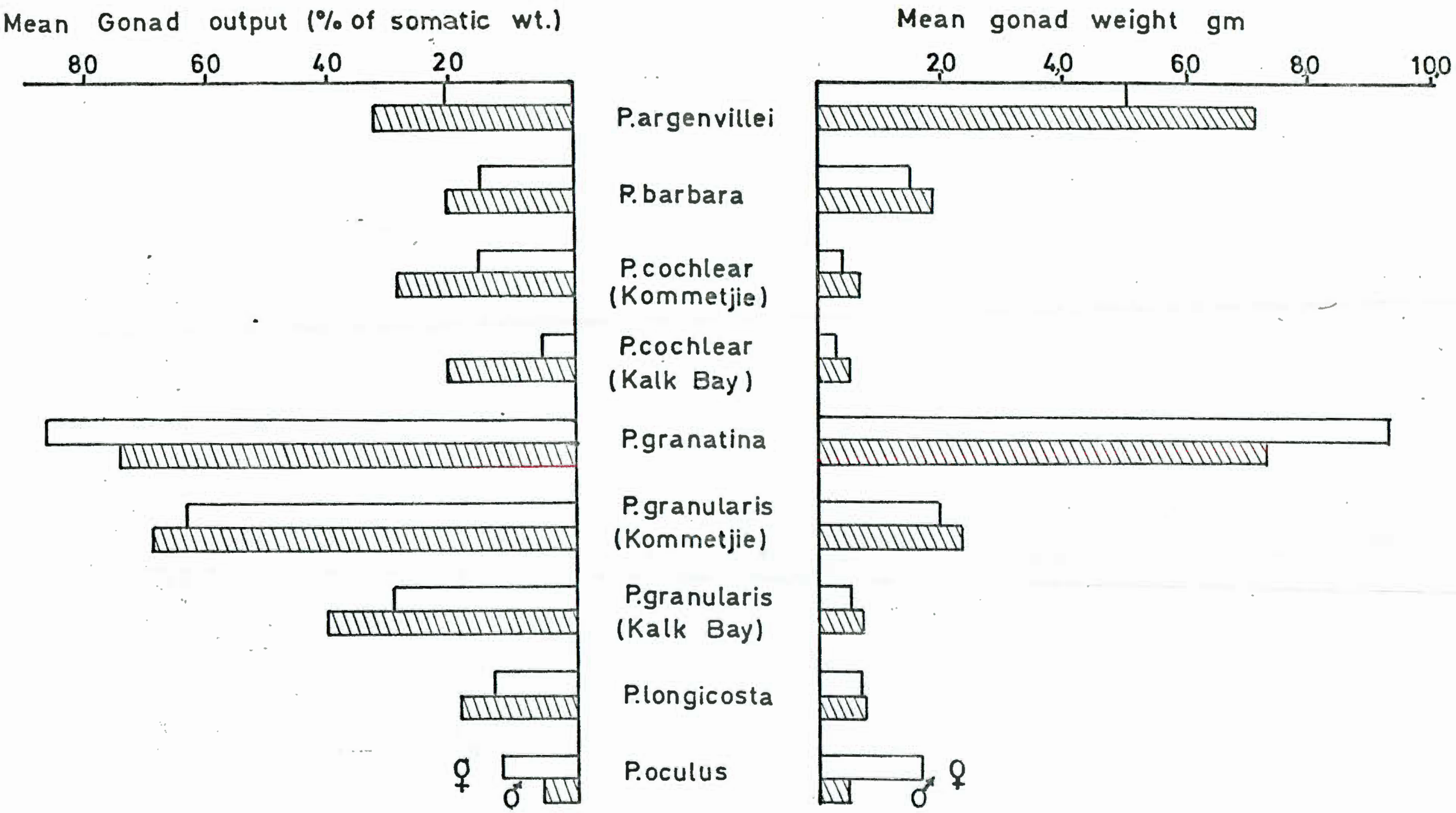


Fig 16 Gonad Output

TABLE I. Fecundity in Patella spp.

Species	Mature Ovary		Spent Ovary	
	Eggs/gm. x 10^3	Total No. of eggs x 10^3	Eggs/gm. x 10^3	Total No. of eggs x 10^3
P. argenvillei	580	3920	0,4	0,2
	520	3080	1,5	0,9
	390	3220		
P. barbara	447	1331	1,7	0,6
	520	1490		
	390	1140		
P. cochlear	372	120	126	12,6
	456	212	114	9,2
	398	161	27	1,9
P. granatina	392	4212	72	68
	420	4100		
	550	5420		
P. granularis	840	1700	2,9	0,31
	876	1322		
	641	690		
	367	422		
P. longicosta	701	821	34	9
	505	611		
	536	482		
P. oculus	433	872	41	16
	507	1020		

As a linear relationship exists between gonad weight and body weight, it can be assumed that the total number of eggs per animal will be similarly related to body weight. Newman (1967) has shown this to be true for Haliotis midae.

While output of mature eggs is the true gauge of fecundity, the relative output of males and females and interspecific differences are of interest. These are summarised in Table II and figure 16.

TABLE II. Gonad output relative to body weight, in Patella spp. from Kommetjie (Kom) and Kalk Bay (K/B).

Species	Locality	Mean somatic weight of sexual individuals gm.		Mean wt. of mature gonads. gm.		Mean gonad output gm.		Mean gonad output(% of somatic weight.)	
		♀	♂	♀	♂	♀	♂	♀	♂
P. argenvillei	Kom.	22.2	20.7	5.02	7.08	4.61	6.64	20.7	32.1
P. barbara	Kom.	8.6	8.1	1.48	1.86	1.28	1.63	14.8	20.1
P. cochlear	Kom.	2.3	1.9	0.40	0.67	0.35	0.54	15.4	28.6
P. cochlear	K/B	2.8	2.1	0.19	0.47	0.13	0.43	4.7	20.2
P. granatina	Kom.	9.8	8.7	9.33	7.32	8.31	6.46	86.8	74.3
P. granularis	Kom.	3.3	3.1	1.95	2.36	1.80	2.14	63.6	68.9
P. granularis	K/B	1.5	1.5	0.51	0.74	0.44	0.60	29.7	40.0
P. longicosta	K/B	3.2	2.5	0.65	0.66	0.41	0.46	12.9	18.3
P. oculus	K/B	8.5	4.5	1.65	0.48	1.02	0.21	12.0	4.6

With the exception of P. granatina and P. oculus, all the males have larger gonads than the females and a higher output.

SEX PROPORTIONS

Fretter & Graham (1964) have observed that in most dioecious molluscs females predominate, and that this tendency is particularly true for older populations. However, there are many exceptions to this. Newman (1967) and Sinclair (1963) working with Haliotis midae and H. iris respectively, showed that males were more common than females. In Fissurella barbadensis, Acanthopleura granulata and Chiton tuberculatus a similar relationship occurs (Ward, 1966;

Glynn, 1970). Males of *P. depressa* are also predominant (Orton and Southward, 1961). In the present work almost all the species possessed more males than females, and the ratio was significantly different from 1:1 in most cases (Table III).

TABLE III. Sex Ratios in *Patella* spp.

Species	Locality	No.of males	No.of females	Ratio ♀ : ♂	Significance
P. argenvillei	Kommetjie	168	147	0.87	$p > .05$
P. barbara	Kommetjie	171	198	1.18	$p > .05$
P. cochlear	Kommetjie	348	340	0.97	$p > .05$
P. cochlear	Kalk Bay	339	168	0.50	$p < .001$
P. granatina	Kommetjie	279	228	0.82	$p < .05$
P. granularis	Kommetjie	366	252	0.66	$p < .001$
P. granularis	Kalk Bay	252	198	0.72	$p < .02$
P. longicosta	Kalk Bay	363	282	0.77	$p < .001$
P. oculus	Kalk Bay	742	320	0.43	$p < .001$

What is more interesting than the sex proportions, is the distribution of sexes with reference to size. In *P. barbara*, *P. argenvillei*, *P. granularis* and *P. cochlear* (at Kommetjie) there is little difference between the sexes. However, in *P. cochlear* (from Kalk Bay), *P. longicosta* and to a lesser extent *P. granatina*, small individuals are predominantly male, while females reach a greater maximum weight and make up the majority of larger animals (fig. 17). As the size range of the two sexes overlaps completely in each case, and very few hermaphrodites have been found in these species, it is unlikely that the size differences can be attributed to a state of consecutive hermaphroditism as has been described

Fig 17 Size Distribution and Relative Abundance of Sexes

(Curves have been visually smoothed)

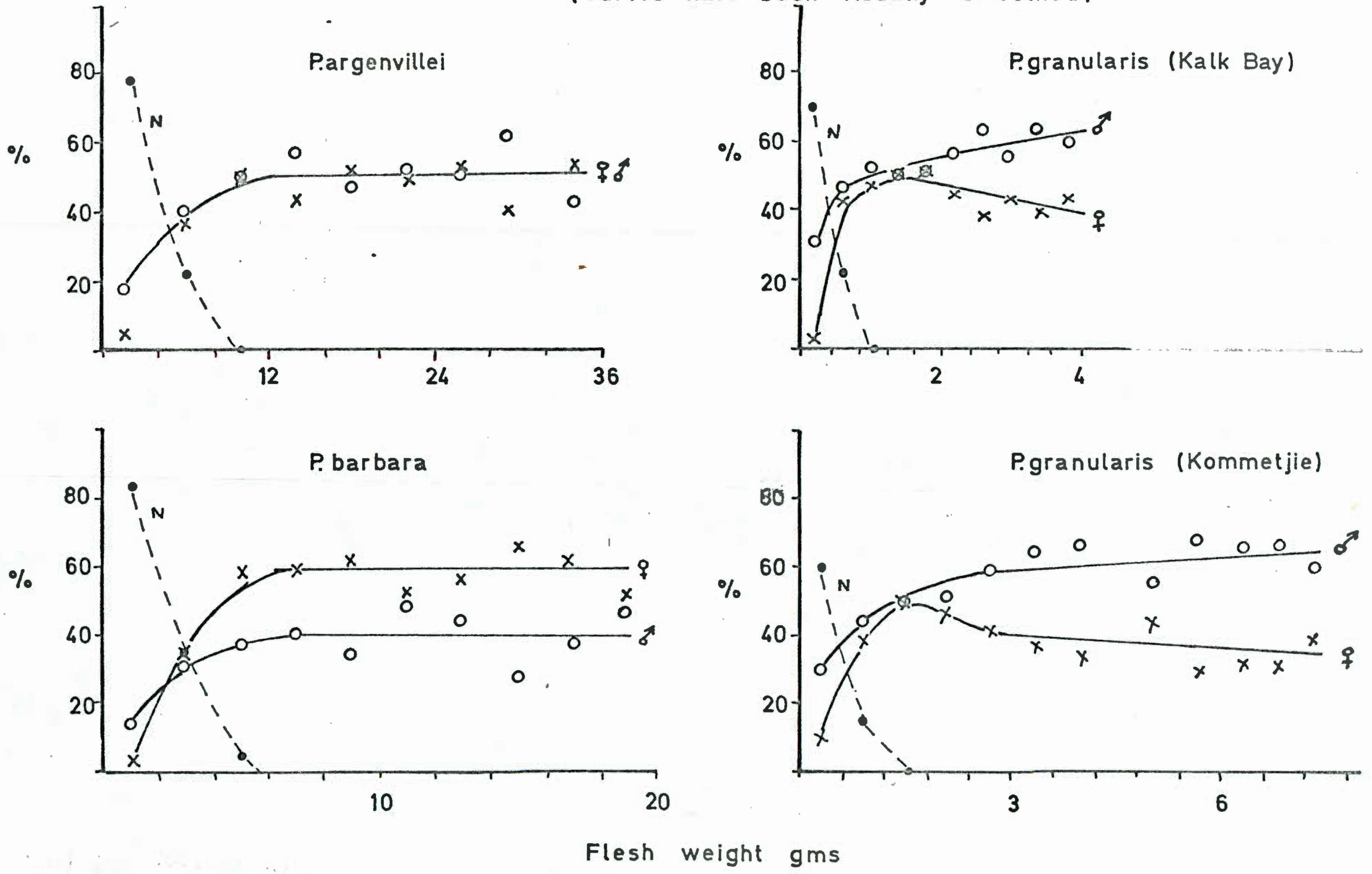
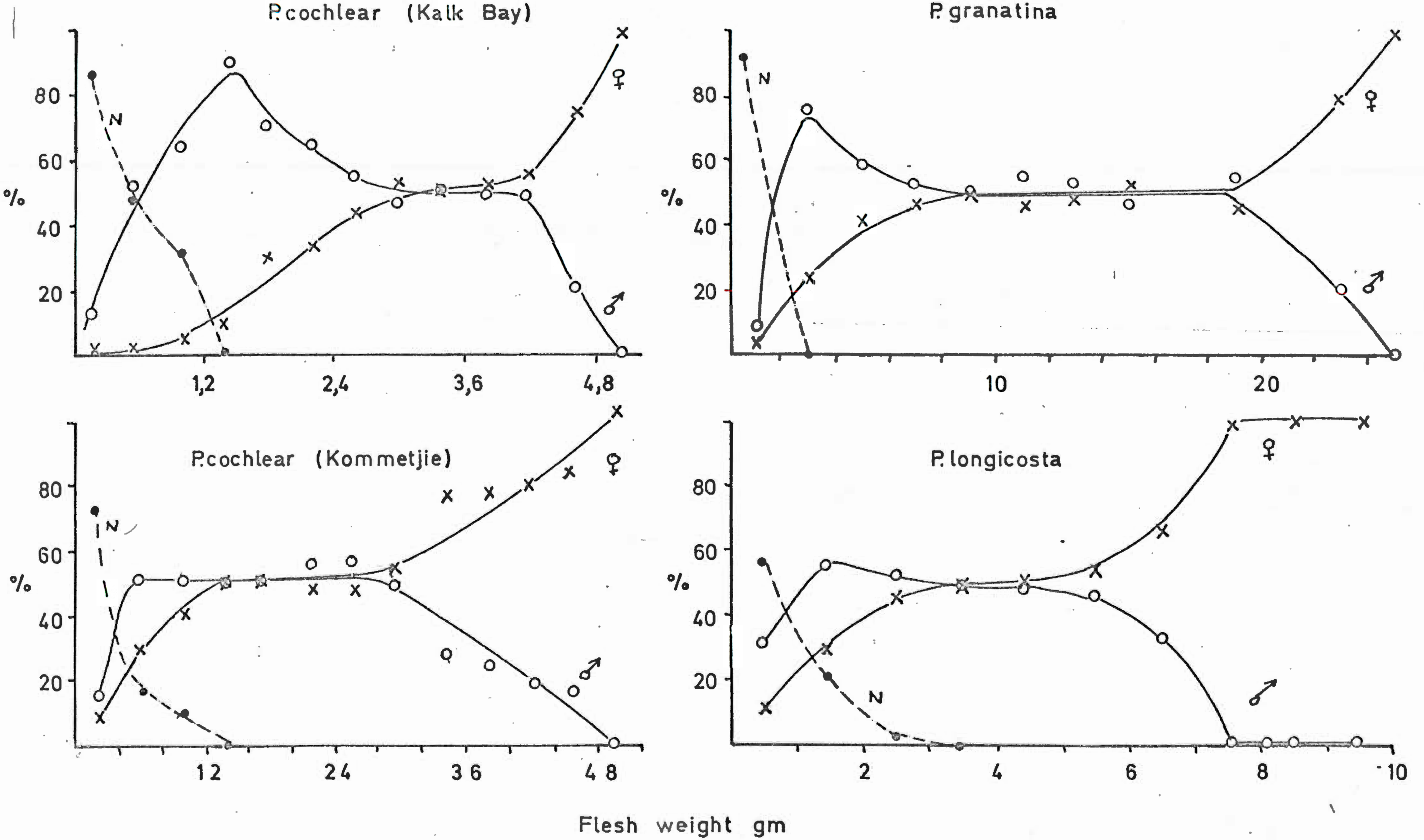


Fig. 17 (continued)



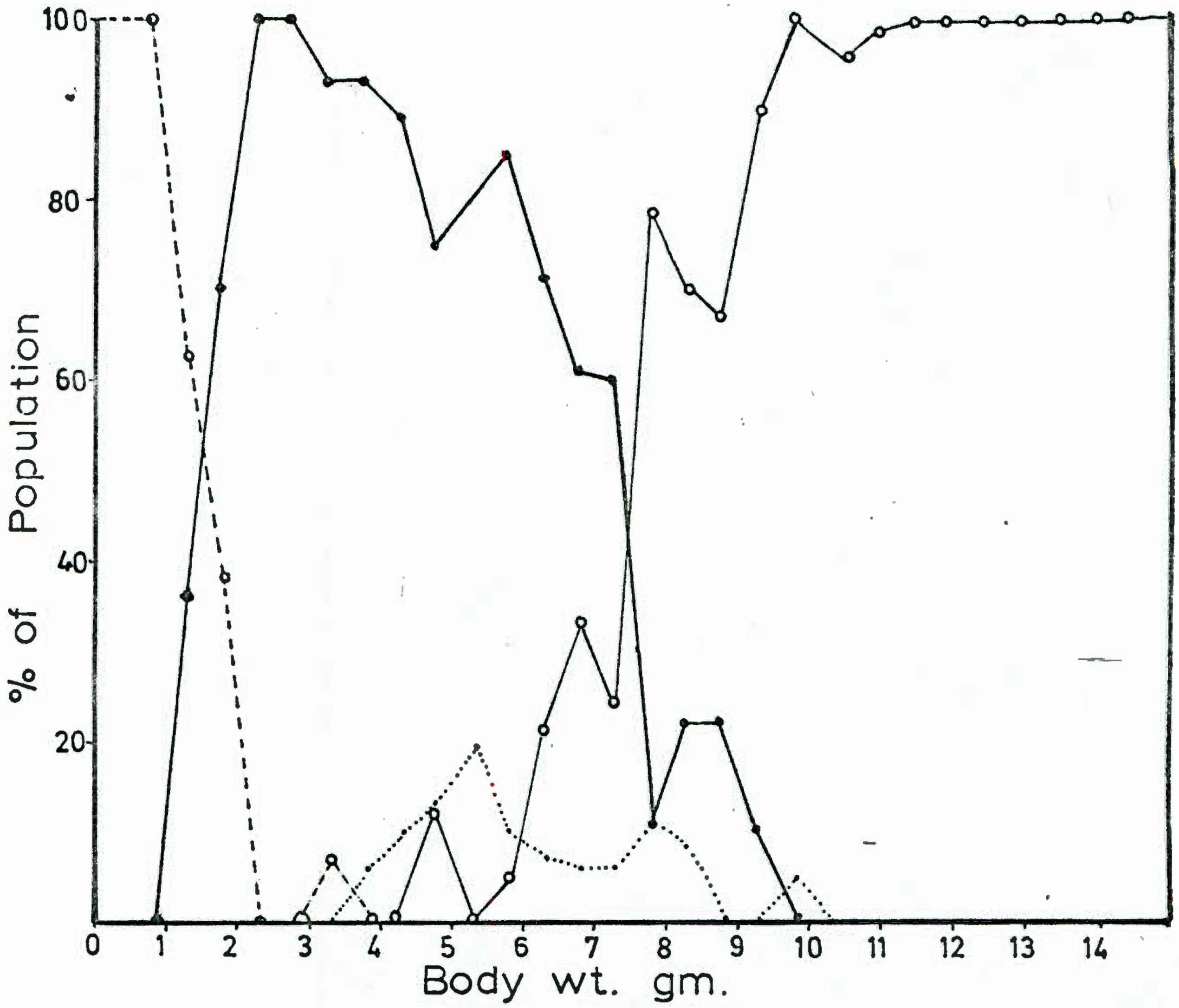


Fig. 18. Size distribution of P.oculus, related to sex. o- - - -o Neuter, •———• male, o———o female, • ····· hermaphrodites.

for some British and Mediterranean species. It is more likely that differential growth rates occur, the females growing slightly faster than the males, and possibly living longer. However, such a differentiation could not be statistically demonstrated in growth rate studies. Earlier maturation and higher mortality of males are also possible.

The special case of P. oculus requires more detailed consideration.

P. oculus is the only South African species which undergoes a definite sex change. The size distribution of males, females and neuter specimens (from Dalebrook, Cape Town) is strongly suggestive of a protandric development (fig. 18). A similar occurrence has been described for P. vulgata (Orton, 1920; 1928) and for P. coerulea (Bacci, 1947). The possibility that the size distribution in P. oculus was due to differential growth rates, was dismissed after a growth rate analysis of marked animals which were subsequently sexed: no sexual differences in growth rate could be detected.

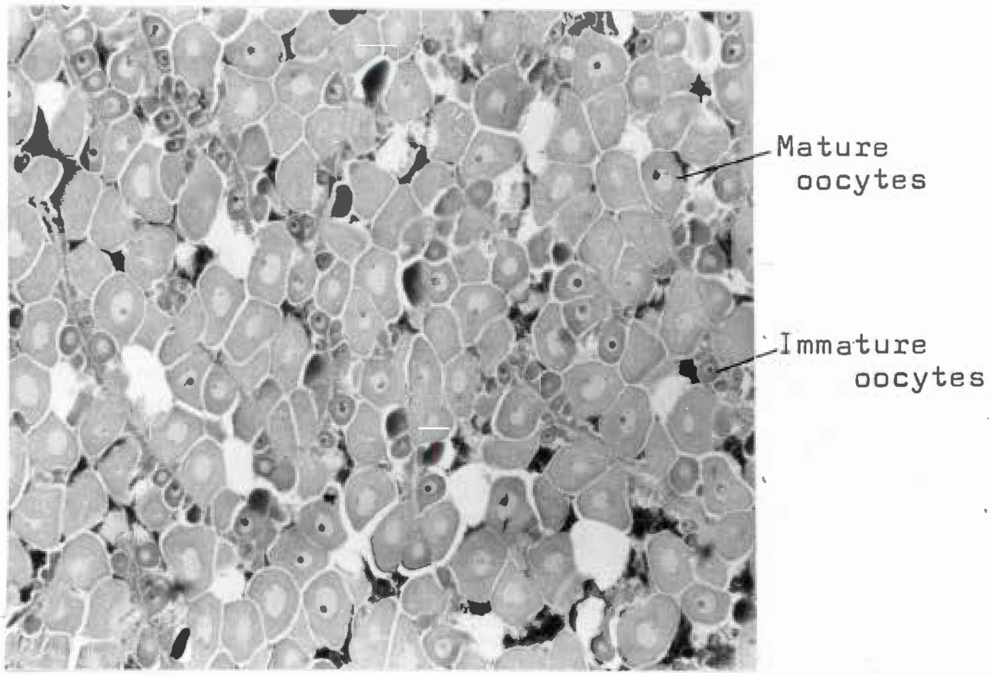
There is a low incidence of hermaphroditism in all South African Patella spp. and in European species too (Dodd, 1956), but in P. oculus the incidence is higher, and two types can be distinguished. The first has been termed "mosaic hermaphroditism", in which discrete patches of the gonad are functionally female and contain eggs at all stages of development, while other patches contain mature sperm (Plate 5a, b). This is comparable to the condition in P. vulgata and has a similar incidence of 0.2% to 4.0%.

The second type, or "transitional hermaphroditism" is characterised by a morphologically uniform gonad, comprising an essentially male gonad with small oocytes scattered throughout the

PLATE V :

MOSAIC HERMAPHRODITE GONAD .

a. ♀ section.



b. Mixed section.

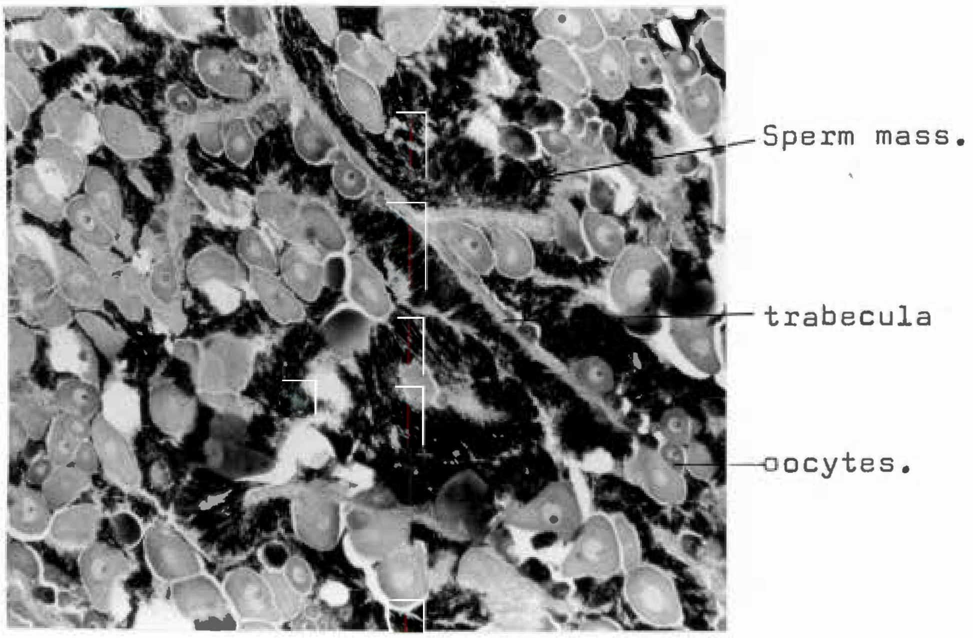
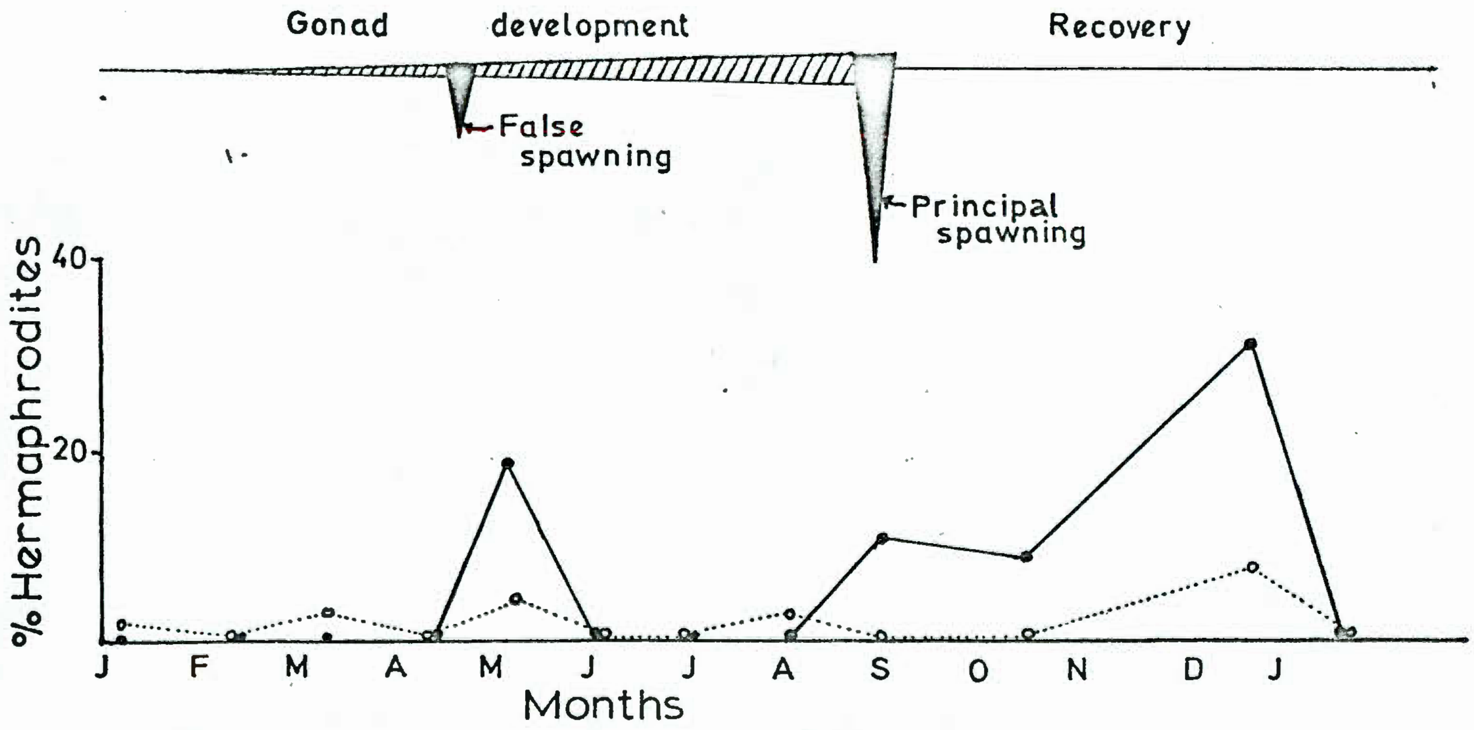


Fig. 19. Incidence of hermaphroditism in P. oculus, related to spawning. ●——● Transitional hermaphroditism, ○- - - -○ Mosaic hermaphroditism.



organ and proliferated from the germinal epithelium. This is equivalent to the condition in P. coerulea (Bacci, 1947).

Relating the incidence of hermaphroditism to the spawning cycle, it is obvious that mosaic hermaphrodites occur sporadically throughout the year, and are unrelated to spawning (fig. 19). This too is similar to P. vulgata (Dodd, 1956).

Transitional hermaphroditism is clearly linked with spawning, and up to 40% of the population undergoes transition (fig. 19). The size distribution of these hermaphrodites and their link with spawning make it probable that this represents a transitional phase during sex change.

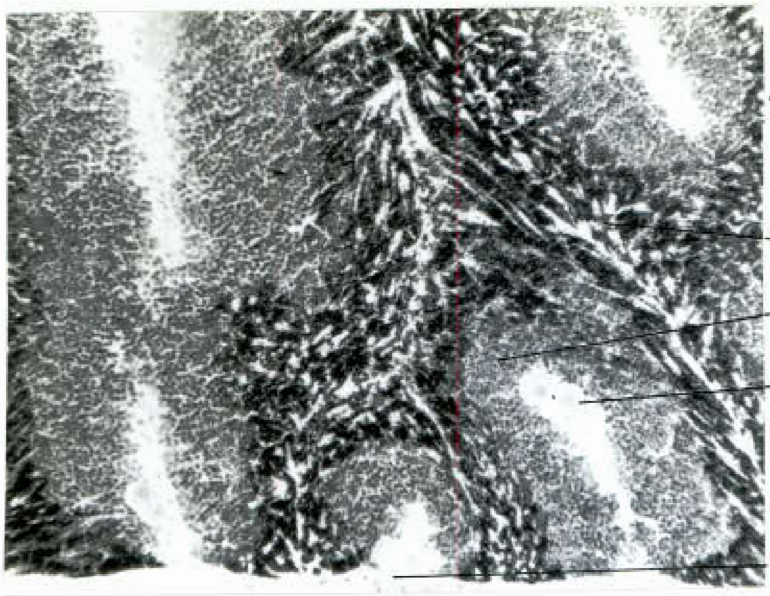
Histological examination reveals the course of transitional hermaphroditism. At spawning the males release approximately half their sperm. Almost immediately, the germinal epithelium on the trabeculae produces new spermatocytes and small quantities of tiny oocytes (Plate 6a). These oocytes rapidly increase in number and size (Plate 6b) and progressively reduce the number of spermatocytes being generated. Within about four weeks, spermatogenesis ceases, leaving quantities of mature sperm in a tubule-like arrangement between the newly formed oocytes (Plate 6d).

Growth rate studies indicate that P. oculus is neuter for the first 6 to 12 months of growth and then becomes male in the first or second year. Small (and presumably first year) males may regenerate only sperm after spawning, and appear to remain male for the subsequent cycle. The majority of males (including all of the larger specimens) undergo transition after spawning.

Three months after spawning (in November) no transitional individuals could be found in a sample of 43 animals, suggesting

PLATE VI :

TRANSITIONAL HERMAPHRODITISM IN P.OCULUS.


A. Early transition.


B. Later transition.

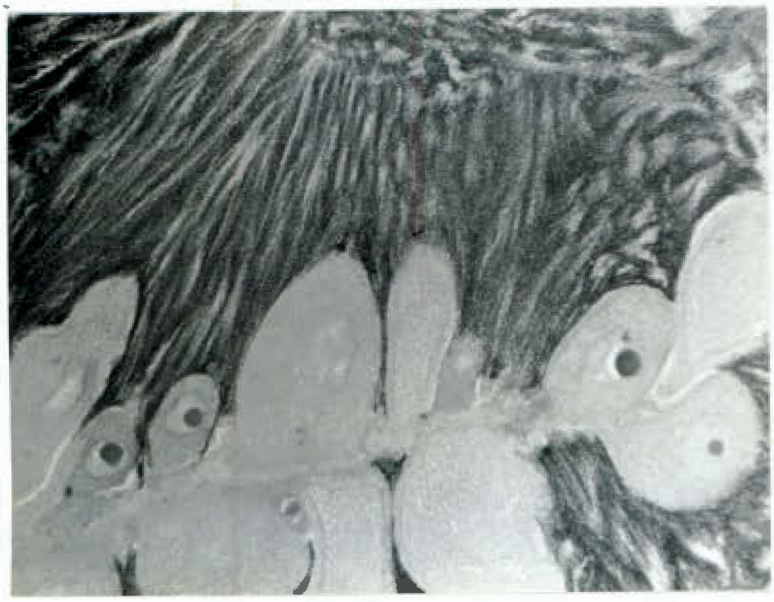

C. T/S. of transitional gonad.

Reduction of spermatocytes.

PLATE VI.

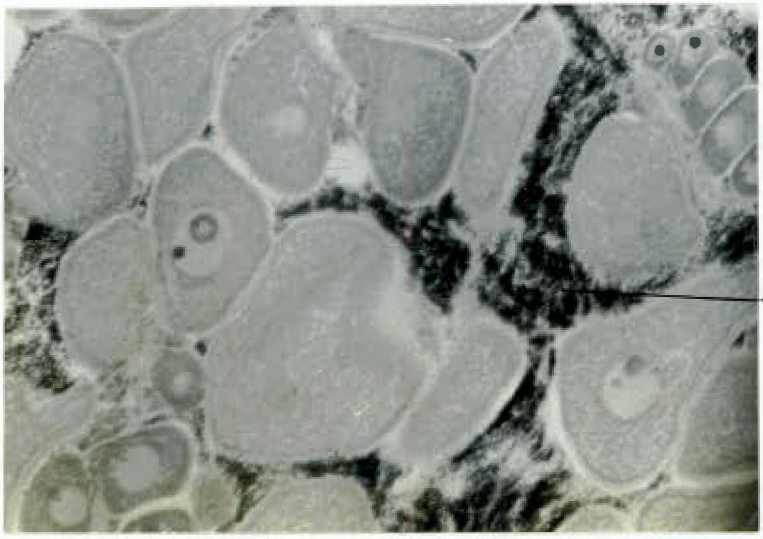
D. Mid transition.

Increased oogenesis.



E. Detail of above.

Spermatogenesis has ceased.



F. Late transition.

SUMMARY OF SPAWNING PERIODS

Species	Method of Assessment			Remarks
	Gonad Index	Egg counts	Subjective Grading	
P. argenvillei	June	?April; June.	June	Resting period Aug. to Jan.
P. barbara	June	May to June	June	Resting period Aug. to Dec.
P. cochlear (Kommetjie)	June (major) April (partial)	June (major) April (partial)	June (major) March-April (partial)	Partial spawning prior to major spawning.
P. cochlear (Kalk Bay)	July-Aug. (major) May (partial)	July-Aug. (major) May (partial)	July-August	Partial spawning prior to major spawning
P. granatina	June	June	June	Rapid build-up in April-May
P. granularis (Kommetjie)	June	June	June	Resting period Aug. to Dec.
P. granularis (Kalk Bay)	June to August	June to September	June to September	Resting period Sept.to Dec.
P. longicosta	Oct. to December	September	Sept. to December	Egg counts and subjective grading not reliable.
P. oculus	Sept. (major) April (?♀ only, false spawning)	Sept. (major) Apr.-May (?♀ only, false spawning)	Sept. (major) April-May (?♀ only, false spawning)	Possibly spawns in April-May as well as September; only a false spawning recorded in April 1970.

that sperm (or oocyte) resorption occurs.

The size distribution of females suggests that they make up the majority of three year old specimens, so that sperm resorption (or evacuation) is more probable. Most females generate only oocytes after spawning, although traces of sperm were found in a few smaller (and presumably younger) females.

The mosaic condition may of course represent a post-transitional state in which resorption of the sperm was not achieved, and a hermaphrodite condition established.

Subsequent to the false spawning of females in April (fig. 14b), a small percentage of the population were found to be transitional (fig. 19), but this trend had disappeared in the subsequent sample in May. Of greater interest is the fact that some of the transitional individuals were ripe, suggesting that spawning itself is not the trigger inducing transition, but that spawning of other individuals may initiate the transition.

DISCUSSION

1. Gonadial Cycles

The species analysed in this work fall into two broad categories: those which are spring or summer breeders, and those which are autumn or winter breeders. In the first category belong P. oculus, P. longicosta (and possibly P. concolor ?). P. oculus may spawn in April as well as September. Among the winter breeders are P. cochlear, P. granatina, P. granularis, P. argenvillei and P. barbara (and possibly P. compressa and P. miniata). Winter breeding has the advantage that larval settlement occurs when temperatures are low, humidity high and desiccation therefore limited.

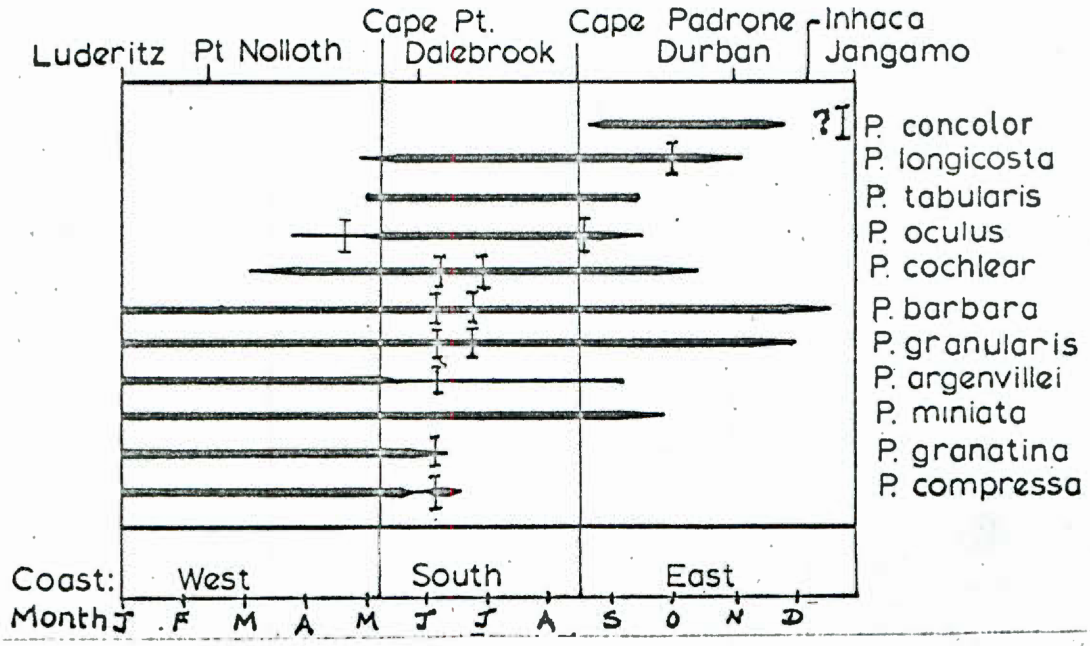


FIG. 20. DISTRIBUTION AND BREEDING IN PATELLA

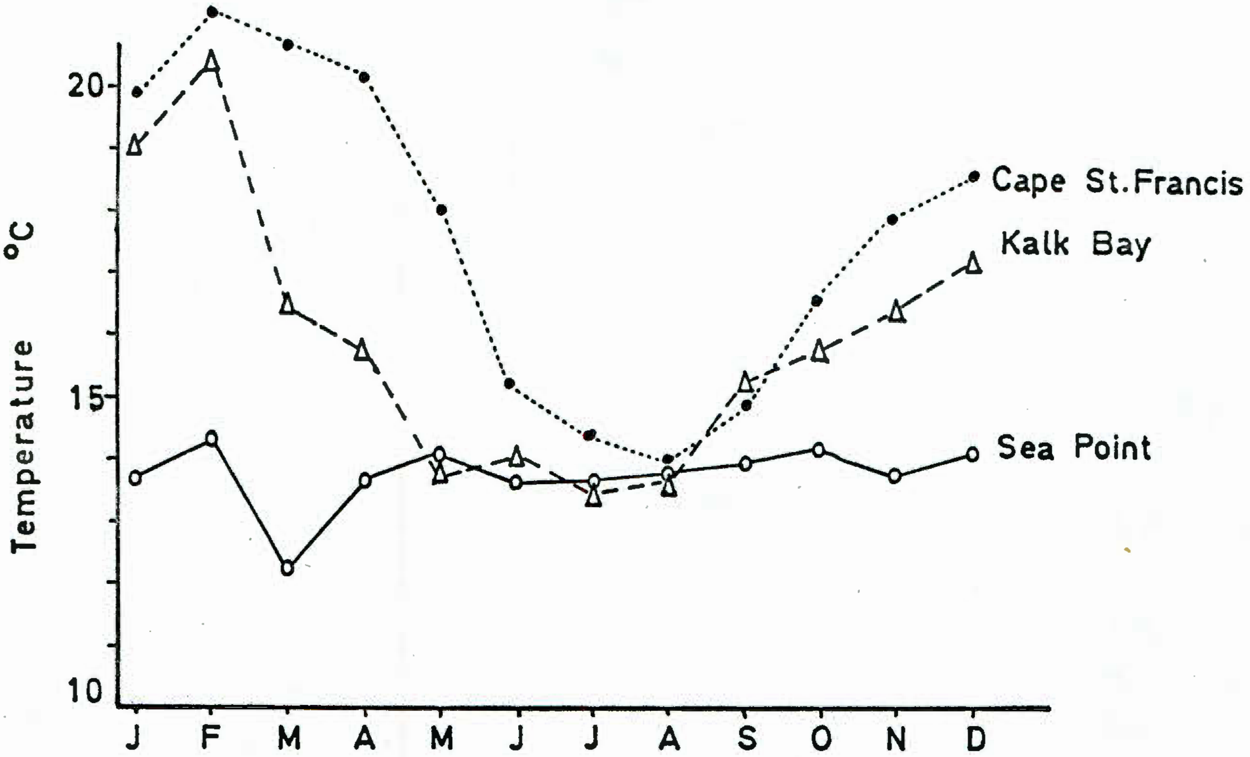
The horizontal kites indicate distribution, and the vertical bars time of spawning.

This seasonal division coincides with a geographic distinction: the spring and summer breeding group are restricted to warm waters and predominate on the South and East coasts, while the winter breeders all occur in the cold waters of the West coast, or on all three coasts (see Section I, p. 2). In figure 20 the geographic distribution has been superimposed on the spawning periods. It is clear from this that warm water species breed in the warmer months of the year, while cold water species and ubiquitous species breed in winter. Significantly, the spawning of *P. cochlear* (figs. 9a, b and 10a, b) and *P. granularis* (figs. 12a, b and 13a, b) occurred slightly later in the year at Kalk Bay than at the cold water site at Kommetjie.

A similar relationship between distribution and spawning period has been shown for *Acmaea* on the Californian coast (Fritchman, 1961a; 1961b; 1961c). The northern cold water species breed in winter, and their southern counterparts in spring or summer. The excellent review of Moore (1972) summarises two tendencies: firstly, in warmer waters spawning tends to be more protracted; secondly, at a given locality, the species ranging into colder waters or warmer waters tend to be winter and summer breeders respectively. In the present work it was noticeable that in warm water samples spawning was less defined and more protracted than at Kommetjie (particularly in warm water species).

The season distinction described above must reinforce the geographic barriers restricting the distribution of some species: in spring and summer the temperature difference between False Bay and the West coast is maximal (fig. 21), and larvae of animals breeding in this period are unlikely to tolerate the sharp changes in temperature between the two coasts. In this connection it is interesting that the warm water *P. oculus* occurs in isolated pockets on the West coast, such as Langebaan Lagoon and St. Helena

Fig. 21 Mean Monthly Temperatures



Sea Point temperaturea after Newman (1967).
Kalk Bay temperatures fromthe Naval Hydrographer.
Cape St. Francis temperatures from Shackleton (1973).

Bay, where the water is locally warmer. The warm Agulhas current sometimes sweeps around Cape Point, driven by South East winds in early spring, and may merge with warm Atlantic water to form a continuous tongue of warm water parallel to the West coast. This tongue sometimes swings close to the shore opposite Saldanha and St. Helena Bay. Significantly, such isotherms occur mainly in October, just after the main spawning of P. oculus, and may allow dispersal of larvae to the localised pockets of warm inshore water, where settlement and maturation may occur.

Bang (1973) has recorded how the boundary between the warm South East Trade Wind Drift and the cold upwelling close to the West coast break down in late winter and spring. This allows the Agulhas current to extend around Cape Point and up the West coast, forming a shallow tongue. Pools of this water may travel up the West coast but are readily mixed with deeper water by turbulence. Shannon (1966) has also described the movement of mixed Agulhas and Atlantic waters being swept up the West coast, and in one instance demonstrated penetration as far as 32°S (about the lattitude of Lamberts Bay).

P. oculus probably also spawns in March to April (see below, p. 31), although only a false or partial spawning of females was recorded in 1970. During these months the Agulhas swings south, away from the South coast, and cannot possibly aid in the distribution of larvae up the West coast. Temperature differences between False Bay and the West coast are still relatively great during this period (fig. 21). More importantly, Shannon (1966) and more recently Duncan and Nell (1969), have recorded a persistent inshore countercurrent running southwards from Lamberts Bay to Cape Point; which is most marked in winter. Such a current will probably prevent dispersion of warm water larvae up the West coast unless they are transmitted by a northerly offshore warm water current, (in spring) as suggested above.

The distribution of P. longicosta stops abruptly at Cape Point. This is probably due to a greater sensitivity to cold water, but it is also true that spawning occurs in late spring to early summer, too late for the northerly movements of Agulhas water described above.

In winter temperature differences between False Bay, the South coast and the West coast are minimal (fig. 21) and it is interesting that only one species occurring on the West coast (and breeding in late autumn to winter) does not extend at least on to the South coast. Such dispersal will be aided by the southerly inshore current which reaches its height in winter and may intrude past Cape Point (Duncan and Nell, 1969).

The evidence of spawning can very speculatively be used to discuss the possible geographic origins of the species under consideration. P. granatina and P. argenvillei are clearly of cold water origin. P. barbara and P. granularis occur on all three coasts, but spawn in winter, and decrease markedly in size on the warmer coasts: P. granularis also grows faster on the West coast (see Section IV). This suggests a cold water origin and suboptimal survival and encroachment into the warmer waters. P. granularis is probably less affected by water temperatures than P. barbara as it occurs high on the shore and is exposed for much of the time, but its juveniles occur lower on the shore.

P. longicosta and P. oculus are definitely of warm water origin. The general similarity between P. oculus and P. granatina in body form and zonation suggests they are closely related, and they may have diverged from a common species. Their present reproductive cycles will tend to keep them isolated, and only one hybrid was recorded in this work. Stephenson (1936) noted that artificial fertilisation could yield hybrid larvae, but hybrids are rare in nature.

Only P. cochlear is predominantly South coast in its distribution, decreasing in the northern parts of the East and West coasts. Its mean size is unaffected by distribution, but this may be because high density crowding obscures this effect.

P. cochlear may have originated on the South coast and been able to tolerate both warmer and colder coasts by virtue of breeding in winter when temperature differences between the coasts are minimal.

Newman (1967) has described how Haliotis midae spawns more effectively at Stony Point than at Sea Point, and ascribes this to the continually low and constant temperatures at Sea Point. No evidence of this was found in the present work: in fact in both P. cochlear and P. granularis, output was higher at Kommetjie than Kalk Bay (even allowing for size differences).

The sample of P. cochlear from Kommetjie in June is of interest, because while most of the specimens were completely spent, a few were still maximally mature. No intermediate specimens were present, and this suggests that once spawning commences in an individual, it is total and rapid. It also suggests that while spawning is simultaneous in most of the population, at least some individuals spawn out of phase with the rest of the population. Simultaneous spawning has obvious advantages, but is liable to catastrophic destruction of the entire output. If a few individuals spawn later, recruitment may recover from such catastrophic events.

2. Stimulation of spawning and gonad growth

In many molluscs changes in temperature are known to trigger spawning, particularly with captive material subjected to experimentally controlled temperatures. It is difficult to relate this to field data unless temperature and spawning are simultaneously and continuously monitored. In the present case no reliable temperature data is available for either site. Temperature records have been made for False Bay (Stephenson, 1947) and Sea Point (Newman, 1967) and these are the nearest records comparable to Kalk Bay and Kommetjie. At Sea Point temperatures are relatively constant and low throughout the year, while in False Bay temperatures drop from a February maximum of about 19°C to about 13°C in July, and then rise again (fig. 21). At Kalk Bay a February maximum of 20.5°C was recorded in 1972 (Naval Maritime weather records). Temperatures are reasonably predictable on the northern shore of False Bay, but on the West coast temperatures may fluctuate dramatically from day to day due to upwelling.

Despite the very different temperature conditions on the two coasts of the Cape Peninsula, it is striking that P. granularis and P. cochlear spawned almost simultaneously at both sites. This makes it unlikely that temperature changes actually trigger spawning, although the gonad cycle is almost certainly geared to the temperature conditions. All the species considered in this work are intertidal and experience considerable diurnal changes in temperature in relation to exposure and immersion at day and night. This also suggests that temperature changes per se will not be suitable as a trigger for spawning.

Air temperatures are fairly similar on the two coasts of the Peninsula, and may in themselves be related to the gonad cycles.

All the autumn and winter breeders spawned at a time when water and air temperatures had dropped to a minimum, while P. oculus and P. longicosta did so when temperatures were beginning to increase in spring.

Orton et al (1956, 1961) suggest that spawning in P. vulgata and P. depressa is triggered by prevalent local storms. Certainly in many of the South African species the gonad is so large and swollen at maturity that violent mechanical stimulation might well induce spawning, but experimental attempts to simulate this all failed.

Cohen (1948, unpublished) concluded that P. granatina spawned in April and to a lesser extent May and June, P. granularis in April and May, and P. cochlear in March to May (June and July). These results are similar to those of the present work, except that in Cohen's analysis all three spawned slightly earlier in the year. Of interest is the fact that Cohen's P. cochlear reached their maximum spawning at the period when mine exhibited a partial spawning.

These comparisons suggest that maturation in winter breeders occurs progressively as sea or air temperatures drop, and will be relatively constant from year to year. Spawning may depend on a different trigger, which will induce only mature gonads to spawn: spawning may be slightly different each year dependent on the timing of this stimulus. Partial spawning may result from a subthreshold stimulus, or incomplete maturity.

Even in the warm water P. longicosta and P. oculus, gonad maturation occurs while temperatures are dropping, while spawning occurs progressively as temperatures rise again. Increasing temperatures may in these cases promote spawning, but no conclusive evidence is available to support this.

Cohen (1948, unpublished) states that *P. oculus* spawns in February to May. However she did not detect sex change and may consequently have confused the state of transitional gonads. Furthermore, she records a minimum gonad length in September, as in the present work. Nevertheless, a false spawning was recorded in April 1970, in addition to the main spawning in September. This suggests that a biannual spawning is possible. In relation to the growth rate, the population structure also suggests biannual settlement. This will be described in greater detail in Section IV, p.11.

3. *Size distribution relative to sex*:

In *P. longicosta*, *P. cochlear* from Kalk Bay, and to a lesser extent *P. granatina*, the size distribution is related to sex, and males predominate over the lower size range. Even in the other species where this is not so obviously true, the females are consistently larger than the males (Table II). This may be due to earlier maturation of males or a differential growth rate between the sexes, although the latter could not be statistically detected in growth rate experiments (Section IV). Fotheringham (1971) has noted a similar paucity of males in the larger size classes of two muricid gastropods and ascribes this to differential growth rates or mortality. As the males of *Patella* almost all have a higher gonad output than females relative to size (Table II), proportionally more energy may be channelled into gamete production, thus reducing somatic growth proportionally. If this is true, then the effect should be greatest in populations where competition for food is high. *P. cochlear* and *P. longicosta* are the two species in which intraspecific competition for food is greatest (as will be described below in Section V), and it is probable that in these two species greatest stress will be placed on food reserves. In support of this, the density of *P. cochlear* in the Kommetjie sampling area was 200/m^2; well below the density at which intraspecific competition becomes significant (see Section V below). In this population much less differentiation occurs in the sizes of males and females (fig. 17).

Conversely, at the Kalk Bay sampling area, densities of between 650 and 800/m^2 were recorded, and differentiation of male and female sizes was obvious (fig. 17).

4. Gamete output:

In almost all the South African Patellas the gonad size and gamete output is greatest in males (Table II, fig. 16). This is unexpected, for by virtue of their smaller size, vast numbers of sperm must be contained in a testis, in comparison with the number of eggs in a comparable sized ovary. In addition, in all the species except P. barbara, males are numerically dominant (Table III).

The balance between numbers of male and female, and output of sperm and eggs must ultimately reside in the relative success of fertilisation.

In the laboratory sperm remains active for relatively short periods of time, while eggs are viable for much longer. This is no doubt a reflection of their relative activity and storage of metabolites, and will mean that vast numbers of sperm will be required for fertilisation of relatively few eggs.

The ratio of female to male gamete output is less than one in all the species except P. granatina and P. oculus (which is exceptional because it undergoes sex change). A negative correlation exists between the ratio of females to males and the "average" density of the species at each sampling site. This is summarised in Table IV.

TABLE IV. Reproductive potential of *Patella* spp.

Species	Locality	Density (Ranked)	Ratio of ♀ : ♂ (ranked)	Growth rate (ranked) (see Section IV)	Gonad weight (ranked)	Generation time (years.)
P. cochlear	Kalk Bay	1	8	8	8	5 - 8
P. granularis	Kommetjie	2	7	3	3	1
P. cochlear	Kommetjie	3	2	7	7	4 - 5
P. granularis	Kalk Bay	4	5	4	6	1 - 2
P. granatina	Kommetjie	5	4	1	1	1
P. longicosta	Kalk Bay	6	6	6	5	2 - 3 ?
P. argenvillei	Kommetjie	7	3	?5	2	?1
P. oculus	Kalk Bay	omitted	omitted	2	4	2
P. barbara	Kommetjie	8	1	?	omitted	?1

In both P. granularis and P. cochlear (for which two areas were sampled), the lower density samples were associated with proportionally more females.

At an interspecific level this association also occurs. Any speculation as to the significance of this must be very tentative in view of the many variables involved, but it is possible that a population control mechanism operates at this level: many molluscs are sexually labile while juvenile, and sex may be influenced by such variables as density, availability of food or the presence of other sexual individuals.

The output of gametes is markedly different in the various species considered, ranging from P. granatina (in which the gonad weight is almost half the total body weight), to P. cochlear, where the gonad makes up only 10% of the body weight (fig. 16).

There is no relationship between gamete output and vertical zonation or relative density of the species, but as a generalisation species with high growth rates (see Section IV) have large gonads (Table IV). Species which experience intense intraspecific competition (P. cochlear, P. longicosta and P. granularis from Kalk Bay) have relatively small gonads. (See Section V below for details of competition.)

Evans and Smith (1952) have suggested that reproductive capacity is inversely related to the time involved in completing a generation, and to size, in different species. In Patella generation time is related to the regular spawning once a year, and to the age at which sexual maturity is reached. In most of the species sexual maturity is attained at an age of one year (as described in Section IV) (although one year old individuals may contribute a limited amount to the population output). In these cases generation time is potentially one year. In P. cochlear sexual maturity is reached after two to six years growth (depending on the effect of density on growth rate). *P. longicosta* matures in the second, third or even fourth year. *P. oculus* produces sperm after one year and then becomes female in the second year. Generation time is thus two years in reality.

Table IV shows the striking correlation between generation time and reproductive potential (gonad output) as Evans and Smith (1952) postulated.

If the principle is extended to include longevity, a negative correlation exists between gonad size and longevity. A balance must exist between long lived species with small gonads, which can spawn over several years, and short lived species which compensate by having larger gonads. *P. oculus* is the only obvious exception to this rule; its growth is rapid, longevity low, and gonad size small. Clearly these generalisations must be tempered by other variables such as the success of fertilisation, survival of larvae and percentage mortality to maturity.

No relationship between body size and gonad size is evident in *Patella*, but this in no way invalidates Evans' and Smith's concept : their work was based on, and intended as, a generalisation for animals of widely differing groups and not on intrageneric analysis.

5. Sex Change:

Orton (1920, 1928) first pointed out that the size distribution of *P. vulgata* suggests protandric consecutive hermaphroditism. Since then Bacci (1947) and Pellegrini (1948) have shown a similar effect in the Mediterranean *P. coerulea*. Orton's findings have since been verified and amplified by a number of other workers

(Das and Sesheppa, 1948; Dodd, 1956; Orton et al, 1956; Blackmore, 1968).

Dodd (1956) analysed the incidence of simultaneous hermaphrodites in *P. vulgata*, and concluded that their appearance was not related to spawning, and their incidence too low to associate them with sex change. Conversely, Bacci (1947) found that in *P. coerulea* oocytes were generated in spawned males, and he showed this condition to be the start of sex change.

Among the South African limpets, only *P. oculus* undergoes a protandric sex change. As described above, transitional hermaphrodites represent an intermediate and transitory stage in this sex change, comparable to the condition of *P. coerulea*. Mosaic hermaphrodites on the other hand are not related to spawning or sex change and probably represent abnormal individuals comparable to those in *P. vulgata*.

In *P. vulgata* there is a complete regression of the gonad after spawning, and a resting period of at least three months (Orton et al, 1956). Presumably this explains why few hermaphrodites are found: complete regression of the testis may be followed by development of an ovary. In *P. oculus* (and presumably *P. coerulea*) the testes never regress completely, and oocytes progressively displace the spermatocytes at the germinal epithelium, during sex change.

Tentatively it can be suggested that development of the gonad (and regeneration after spawning) is controlled by hormones, and that an interplay between male and female factors determines the sex. Presumably the female influence becomes progressively dominant with age. The fact that small males regenerate only sperm, while larger specimens enter a transitional state, supports this idea.

The elegant work of Choquet (1965, 1967, 1969; summarised by Streiff, 1971) has demonstrated the presence of male and female factors in P. vulgata. Choquet cultured rudiments from juvenile animals containing both egg and sperm primordia. He was able to show that gametogenesis is induced by a hormone from the cerebral ganglion, produced and released at gametogenesis. This cerebral factor acts antagonistically to, and dominates, a continuously produced spermatogenic inhibitor from the ocular tentacles. The latter hormone therefore inhibits spermatogenesis during the resting phase.

A second cerebral factor, the vitellogenic hormone, is released after oogenesis starts, and triggers vitellogenesis. Both spermatogonia and oogonia must reach a receptive state before they will respond to these hormones.

The survival value of consecutive hermaphroditism in Patella is obscure. On the shore, males and females of P. oculus are randomly distributed and there is no association of the sexes as there is in Crepidula.

Sex is labile in many molluscs. In the remaining species analysed in this paper, sex appeared to be fixed throughout life, and yet in P. longicosta and P. argenvillei, about 10% of the population displayed a transitional condition after spawning. This serves to emphasize the lability of sex in the group.

In P. oculus the relative disadvantage of having fewer females (due to progressively greater mortality with age) is counteracted by their greater output of gonads. The ratio of females to males (0.43) is lower than in any other Patella, but this is balanced by the mean gonad output being five times higher in the female than in the male.

Thus it may be that the labile sexual condition has been specialised in P. oculus into a protandric condition in which advantages balance disadvantages. As the gonad rudiment has both male and female elements, such a specialisation could be brought about simply by changing the relative proportions of gonad stimulating (or inhibiting) hormones.

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SUMMARY

The gonad structure and cycles of seven Patella spp. are described. Most spawn once a year. P. cochlear, P. argenvillei, P. barbara, P. granatina and P. granularis are autumn to winter breeders spawning in May - June. P. oculus spawns in September and P. longicosta in October - November. Partial spawning was

recorded for P. cochlear, prior to the attainment of maximum maturity. In P. oculus a false spawning of a small percentage of females occurred in May and biannual spawning is possible.

Spawning time is related to distribution. Autumn and winter breeders occur on the cold West coast and may also occur on the warmer coasts. Spring and summer breeders are restricted to warm waters. The role of sea temperatures in limiting larval dispersal is discussed.

Gonad maturation is related to decreasing temperatures, but spawning may be stimulated by a different factor.

The output of eggs in all species was in the region of 500 x 10^3 eggs per gram of ovary. With the exception of P. granatina and P. oculus, the weight of gamete output was greater in males. Males were also numerically predominant in all species except P. barbara, and the sex ratio may be correlated with the mean density of populations. The mean size of males is less than females, and they mature sexually at a smaller size. This may be because more energy is channelled into gonad growth in the males, at the expense of somatic growth. High gamete output occurs in species with high growth rates and low generation time.

P. oculus is the only South African species displaying protandric hermaphroditism.

REFERENCES

Bacci, G. 1947. L'inversione del sesso ed il ciclo stagionale della gonade in Patella coerulea L. Pubbl. Staz. Zool. Napoli 21 : 183-217.

Bang, N.D. 1973. The Southern Benguela system : bathythermography and related air/sea interactions. M.Sc. thesis, University of Cape Town.

Ballantine, W.J. 1961. The population dynamics of *Patella vulgata* and other limpets. Ph.D. thesis, Queen Mary College, London University.

Blackmore, D.T. 1969. Studies of *Patella vulgata* L. I. Growth, reproduction and zonal distribution. *J. exp. mar. Biol. Ecol. 3* : 200-213.

Branch, G.M. 1971. The ecology of *Patella* Linnaeus from the Cape Peninsula, South Africa. I. Zonation, movements and feeding. *Zool. Afr. 6* : 1-38.

Choquet, M. 1965. Recherches en culture organotypique, sur la spermatogenese chez *Patella vulgata* L. (Mollusca Gasteropode). Role des ganglions cerebroides et des tentacules. *C.R. Acad. Sci. Paris 261* : 4521-4524.

——————— 1967. Gametogenese *in vitro* au cours du cycle annuel chez *Patella vulgata* L. en phase male. *Ibid 265* : 333-335.

——————— 1969. Contribution a' l'etude du cycle biologique et de l'inversion du sexe chez *Patella vulgata* L. (Mollusca Gasteropode Prosobranche). *These doct.Sc.Nat.Lille 185* : 1-234, 19 pl.

Cohen, C. 1948. The breeding seasons of *Patella*. Unpublished M.Sc. thesis, University of Cape Town.

/a Das, S.M. and Sesheppa, G. 1948. A contribution to the biology of *Patella* : on population distribution and sex proportions in *Patella vulgata* Linnaeus at Cullercoats, England. *Proc. Zool. Soc. Lond. 117* : 653-662.

Dodd, J.M. 1956. Studies on the biology of limpets III Hermaphroditism in the three British species of *Patella*. *J. mar. biol. Ass. U.K. 35* : 327-340.

Duncan, C.P. and Nell, J.H. 1969. Surface currents off the Cape coast. Investl. Rep. Div. Sea Fish. S.Afr. 63 : 1-38.

Evans, F.C. and Smith, F.E. 1952. The intrinsic rate of natural increase for the human louse, Pediculus humanis L. Am. Nat. 86 : 299-310.

Fotheringham, N. 1971. Life history patterns of the littoral gastropods Shaskyus festivus (Hinds) and Ocenebra poulsoni Carpenter. (Prosobranchia, Muricidae). Ecol. 52 : 742-757.

Fretter, V. and Graham, A. 1964. Reproduction. In "Physiology of Mullusca" (Ed. Wilber, K.M. & Yonge, C.M.). Academic Press, N.Y.

Fritchman, H.K. 1961a. A study on the reproductive cycle in the Californian Acmaeidae. (Gastropoda) Pt. I. Veliger 3 : 57-63.

———— 1961b. Pt. II ibid. 3 : 95-100.

———— 1961b. Pt.III ibid. 4 : 41-46.

———— 1962 Pt. IV ibid. 4 : 134-140.

Glynn, P.W. 1970. On the ecology of the Caribbean Chitons Acanthopleura granulata, Gmelin & Chiton tuberculatus Linne : Density, mortality, feeding, reproduction, growth. Smithsonian Contrib. Zool. No.66 : 1-21.

Moore, H.B. 19 . Aspects of stress in the tropical marine environment. Adv. Mar. Biol. 10 : 217-269.

Newman, G.G. 1967. Reproduction of the South African Abalone Haliotis midae. Investl. Rep. Div. Sea Fish. S. Afr. 64 : 1-24.

Orton, J.H. 1920. Sex phenomena in the common limpet (Patella vulgata). Nature 104 : 373.

———— 1928. Observations on Patella vulgata, Pt. I. Sex phenomena, breeding and shell growth. J.mar.biol.Ass.U.K. 15 : 851-862.

————, Southward, A.J. and Dodd, J.M. 1956. Studies on the biology of limpets II. The breeding of Patella vulgata L. in Britain. Ibid. 35 : 149-176.

———— and Southward, A.J. 1961. Studies on the biology of limpets IV. The breeding of Patella depressa Pennant on the North Cornish Coast. Ibid. 41 : 653-662.

Pellegrini, O. 1948. Ricerche statistiche sulla sessualita di Patella coerulea L. Boll.Zool. 15 : 115-121.

Seapy, R.P. 1966. Reproduction and growth in the File Limpet, Acmaea Limatula Carpenter 1864 (Mollusca, Gasteropoda). Veliger 8 : 300-311.

Shackleton, N.J. 1973. Oxygen isotope analysis as a means of determining season of occupation of prehistoric midden sites. Archeometry 15 : 133-141.

Shannon, L.V. 1966. Hydrology of the South and West Coasts of South Africa. Investl. Rep. Div. Sea Fish. S. Afr. 58 : 1-22.

Sinclair, M. 1963. Studies on the Pana, Haliotis iris martyn in the Wellington district, 1945-1946. Zoology Publs. Vict. Univ. College 35 : 16pp.

Streiff, W. 1971. Analyse experimentale de la differenciation sexuelle chez les mollusques gasteropodes. In "Hormones et differenciation sexuelle chez le Invertebres" (Ed. Wolff, E.). Gordon & Breach. 266pp.

Stephenson, T.A. 1936. The marine ecology of South African coasts, with special reference to the habits of limpets. Proc. Linn. Soc. Lond. 148 : 74-79.

———— 1939. The constitution of the intertidal fauna and flora of South Africa. Pt. I. Linn. Soc. Journ. Zool. 40 : 487-536.

———— 1947. Ibid. Pt.III. Ann.Natal Mus. 11 : 207-324.

Ward, J. 1966. The breeding cycle of the Keyhole limpet, Fissurella barbadensis Gmelin. Bull.mar.Sci.Gulf.Caribb.16 : 685-695.

Underwood, A.J. 1972. Observations on the reproductive cycles of Monodonta liniata, Gibbula umbilicalis and G. cineraria. Mar.Biol. 17 : 333-340.

APPENDIX I

For each sample, species and sex, regression lines were calculated between gonad weight (y) and visceral weight (x); the correlation coefficient (r) calculated and its significance tested; and the slopes and intercepts of each sample tested for significant differences against the subsequent sample. Samples too small to analyse have been omitted.

P. argenvillei

	Sample Date	N	Regression equation y = mx + c	r	t test of r (probability)	Probability of difference between regressions	
						Slope	Intercept
♀	23.1.70.	7	y=0,025x-0,199	0,82	<,05	<,05	>,05
	22.2.70.	6	y=0,062x-0,260	0,98	<,02	<,01	<,001
	29.3.70.	8	y=0,250x-3,614	0,95	<,001	>,05	>,05
	22.4.70.	9	y=0,222x-1,494	0,93	<,01	>,05	>,05
	21.5.70.	8	y=0,275x-0,972	0,93	<,01	<,001	>,05
	19.6.70.	9	y=0,043x+0,087	0,81	<,02	>,05	>,05
	17.8.70.	9	y=0,019x-0,006	0,58	>,05	>,05	>,05
	16.9.70.	8	y=0,035x-0,550	0,89	<,01		
♂	23.1.70.	7	y=0,252x-3,928	0,96	<,001	>,05	>,05
	22.2.70.	13	y=0,208x-1,488	0,83	<,001	>,05	>,05
	29.3.70.	7	y=0,325x-2,968	0,99	<,001	>,05	>,05
	22.4.70.	10	y=0,401x-2,704	0,97	<,001	>,05	>,05
	21.5.70.	8	y=0,376x-0,699	0,40	>,05	>,05	>,05
	19.6.70.	10	y=0,117x-0,460	0,94	<,001	<,001	>,05
	17.8.70.	8	y=0,028x-0,139	1,00	<,001	>,05	>,05
	16.9.70.	9	y=0,033x-0,215	0,78	<,05	>,05	>,05
	16.10.70.	9	y=0,047x-0,306	0,90	<,001		

Patella barbara

	Sample Date	N	Regression equation y = mx + c	r	t test of r (probability)	Probability of difference between regressions	
						Slope	Intercept
♀	22.2.70.	11	y=0,068x+0,025	0,80	< ,001		
						< ,001	< ,05
	22.4.70.	7	y=0,283x-1,305	0,93	< ,02		
						> ,05	> ,05
	21.5.70.	8	y=0,325x-1,309	0,89	< ,02		
						< ,001	> ,05
	19.6.70.	10	y=0,043x-0,019	0,88	< ,001		
						> ,05	> ,05
	3.8.70.	7	y=0,021x+0,021	0,84	< ,05		
						> ,05	> ,05
	16.9.70.	13	y=0,036x-0,040	0,79	< ,001		
						> ,05	> ,05
	16.10.70.	10	y=0,010x+0,209	0,20	> ,05		
						> ,05	> ,05
	30.11.70.	12	y=0,061x-0,057	0,67	> ,05		
♂	22.2.70.	13	y=0,068x+0,025	0,80	< ,001		
						< ,001	> ,05
	22.4.70.	9	y=0,309x-0,667	0,90	< ,001		
						> ,05	> ,05
	21.5.70.	12	y=0,297x-0,545	0,94	< ,001		
						< ,001	> ,05
	19.6.70.	11	y=0,049x+0,049	0,71	< ,05		
						> ,05	> ,05
	3.8.70.	9	y=0,025x+0,032	0,88	< ,001		
						< ,05	> ,05
	16.9.70.	9	y=0,062x+0,012	0,90	< ,001		
						< ,05	> ,05
	16.10.70.	8	y=0,102x-0,289	0,99	< ,001		
						> ,05	> ,05
	30.11.70.	7	y=0,124x-0,420	0,98	< ,001		

Patella cochlear (Kommetjie)

	Sample Date	N	Regression equation y = mx + c	r	t test of r (probability)	Probability of difference between regressions	
						Slope	Intercept
♀	23.1.70.	13	y=0,094x-0,087	0,93	< ,001	> ,05	> ,05
	22.2.70.	11	y=0,081x-0,019	0,91	< ,001	> ,05	> ,05
	29.3.70.	11	y=0,126x-0,044	0,77	< ,05	> ,05	> ,05
	22.4.70.	17	y=0,090x+0,016	0,63	< ,02	> ,05	> ,05
	21.5.70.	22	y=0,036x+0,320	0,17	> ,05	> ,05	> ,05
	19.6.70.[a]	7	y=0,136x+0,114	0,79	< ,05	< ,05	> ,05
	19.6.70.[b]	11	y=0,043x+0,004	0,87	< ,001	< ,05	> ,05
	3.8.70.	9	y=0,012x+0,026	0,75	< ,05	< ,001	> ,05
	16.9.70.	13	y=0,058x-0,041	0,92	< ,001	> ,05	> ,05
	16.10.70.	16	y=0,057x+0,022	0,74	< ,001	> ,05	> ,05
	30.11.70.	13	y=0,097x-0,009	0,72	< ,02		
♂	23.1.70.	10	y=0,064x+0,035	0,49	> ,05	> ,05	> ,05
	22.2.70.	8	y=0,110x-0,088	0,82	< ,05	> ,05	> ,05
	29.3.70.	13	y=0,219x-0,226	0,45	> ,05	> ,05	> ,05
	22.4.70.	14	y=0,149x-0,024	0,71	< ,01	< ,02	> ,05
	21.5.70.	15	y=0,461x-0,217	0,84	< ,02	< ,02	> ,05
	19.6.70.	15	y=0,117x-0,113	0,85	< ,001	> ,05	> ,05
	3.8.70.	16	y=0,082x-0,031	0,80	< ,001	> ,05	> ,05
	16.9.70.	14	y=0,113x-0,053	0,85	< ,001	> ,05	> ,05
	16.10.70.	12	y=0,157x-0,116	0,90	< ,001	> ,05	> ,05
	30.11.70.	18	y=0,167x-0,068	0,87	< ,001		

a = ripe females

b = spent females

Patella cochlear (Kalk Bay)

	Sample Date	N	Regression equation y = mx + c	r	t test of r (probability)	Probability of difference between regressions	
						Slope	Intercept
♀	5.2.70.	16	y=0,041x-0,071	0,97	< ,001	> ,05	> .05
	9.3.70.	14	y=0,027x+0,044	0,25	>,05	< ,05	>,05
	8.4.70.	17	y=0,151x-0,123	0,91	<,001	>,05	>,05
	5.5.70.	19	y=0,077x-0,063	0,60	<,05	>,05	>,05
	6.6.70.	8	y=0,174x-0,290	0,74	>,05	>,05	>,05
	2.8.70.	10	y=0,036x-0,044	0,42	>,05	>,05	>,05
	2.9.70.	12	y=0,024x-0,003	0,49	>,05	>,05	> ,05
	16.10.70.	8	y=0,127x-0,219	0,65	>,05	> ,05	>,05
	27.12.70.	9	y=0,009x-0,009	0,41	>,05		
♂	5.2.70.	8	y=0,148x-0,308	0,47	<,001	> ,05	> ,05
	9.3.70.	10	y=0,215x-0,419	0,91	<,001	>,05	>,05
	8.4.70.	13	y=0,179x-0,037	0,92	<,001	> ,05	>,05
	5.5.70.	14	y=0,145x-0,057	0,87	<,001	<,02	> ,05
	6.6.70.	23	y=0,274x-0,102	0,96	<,001	>,05	>,05
	2.8.70.	14	y=0,162x-0,198	0,72	<,001	< ,001	>,05
	2.9.70.	14	y=0,026x-0,005	0,76	<,001	<,02	>,05
	16.10.70.	15	y=0,087x-0,059	0,77	<,001	>,05	>,05
	27.12.70.	9	y=0,159x-0,290	0,92	<,001		

Patella granatina

	Sample Date	N	Regression equation $y = mx + c$	r	t test of r (probability)	Probability of difference between regressions.	
						Slope	Intercept
♀	23.1.70.	6	$y=0,563x-4,140$	0,99	< ,001	> ,05	> ,05
	22.2.70.	15	$y=0,312x-0,983$	0,78	< ,001	> ,05	> ,05
	23.3.70.	8	$y=0,135x-0,436$	0,80	> ,05	> ,05	> ,05
	22.4.70.	9	$y=0,713x-5,049$	0,76	< ,05	> ,05	> ,05
	21.5.70.	5	$y=1,035x-4,062$	0,96	< ,001	< ,001	> ,05
	19.6.70.	11	$y=0,115x-0,326$	0,91	< ,001	> ,05	> ,05
	3.8.70.	14	$y=0,132x-0,281$	0,72	< ,01	> ,05	> ,05
	19.9.70.	9	$y=0,240x-0,967$	0,94	< ,001	< ,02	< ,05
	16.10.70.	5	$y=0,437x-2,545$	1,00	< ,001	< ,001	< ,001
	30.11.70.	7	$y=0,134x-0,618$	0,92	< ,001		
♂	23.1.70.	14	$y=0,322x-1,277$	0,69	< ,02	> ,05	> ,05
	22.2.70.	17	$y=0,334x-1,202$	0.88	< ,001	> ,05	> ,05
	23.3.70.	11	$y=0,157x-0,284$	0,68	< ,05	> ,05	> ,05
	22.4.70.	10	$y=0,333x-1,252$	0,69	< ,05	< ,001	> ,05
	21.5.70.	17	$y=0,949x-0,933$	0,92	< ,001	< ,001	> ,05
	19.6.70.	11	$y=0,141x-0,369$	0,96	< ,001	> ,05	> ,05
	3.8.70.	10	$y=0,164x+0,163$	0,69	< ,05	> ,05	> ,05
	19.9.70.	10	$y=0,162x-0,062$	0,81	< ,01	> ,05	> ,05
	16.10.70.	9	$y=0,558x-2,664$	0,57	> ,05	> ,05	> ,05
	30.11.70.	9	$y=0,186x-0,689$	0,88	< ,001		

Patella granularis (Kommetjie)

Sample Date	N	Regression equation y = mx + c	r	t test of r (probability)	Probability of difference between regressions	
					Slope	Intercept
♀ 23.1.70.	15	y=0,115x-0,112	0,91	< ,001	< ,05	> ,05
22.2.70.	11	y=0,251x-0,213	0,81	< ,001	< ,02	> ,05
29.3.70.	13	y=0,527x-0,488	0,91	< ,001	> ,05	> ,05
22.4.70.	7	y=0,036x+0,101	0,26	> ,05	< ,05	> ,05
21.5.70.	10	y=0,748x-0,519	0,98	< ,001	< ,001	> ,05
19.6.70.	13	y=0,175x-0,149	0,91	< ,001	> ,05	> ,05
3.8.70.	9	y=0,077x-0,109	0,94	< ,001	< ,02	> ,05
16.9.70.	8	y=0,031x+0,015	0,87	< ,02	> ,05	> ,05
16.10.70.	6	y=0,055x-0,004	0,99	< ,01	< ,02	> ,05
3.11.70.	10	y=0,028x-0,038	0,90	< ,001		
♂ 23.1.70.	13	y=0,265x-0,263	0,92	< ,001	< ,02	> ,05
22.2.70.	21	y=0,046x-0,968	0,85	< ,001	< ,02	> ,05
29.3.70.	11	y=0,697x-0,657	0,99	< ,001	< ,001	> ,05
22.4.70.	11	y=0,173x+0,106	0,74	< ,05	< ,001	> ,05
21.5.70.	14	y=1,035x-0,839	0,99	< ,001	< ,001	> ,05
19.6.70.	13	y=0,234x-0,169	0,95	< ,001	< ,001	> ,05
3.8.70.	8	y=0,072x-0,082	0,99	< ,001	> ,05	> ,05
16.9.70.	14	y=0,112x-0,215	0,85	< ,001	< ,05	> ,05
16.10.70.	17	y=0,068x-0,018	0,96	< ,001	> ,05	> ,05
30.11.70.	12	y=0,111x-0,157	0,82	< ,001		

Patella granularis (Kalk Bay)

	Sample Date	N	Regression equation y = mx + c	r	t test of r (probability)	Probability of difference between regressions	
						Slope	Intercept
♀	5.2.70.	9	y=0,042x+0,001	0,94	<,001	<,001	>,05
	9.3.70.	18	y=0,192x-0,050	0,83	<,001	>,05	>,05
	8.4.70.	9	y=0,098x+0,080	0,71	>,05	>,05	>,05
	5.5.70.	13	y=0,087x+0,320	0,25	>,05	<,05	>,05
	6.6.70.	11	y=0,376x-0,054	0,96	<,001	<,001	>,05
	8.8.70.	8	y=0,034x-0,014	0,78	<,05	>,05	>,05
	2.9.70.	8	y=0,032x+0,008	0,68	>,05	>,05	>,05
	15.10.70.	8	y=0,174x-0,129	0,80	<,05	<,05	>,05
	27.12.70.	9	y=0,051x-0,006	0,92	<,001		
♂	5.2.70.	9	y=0,097x-0,034	1,00	<,001	<,001	>,05
	9.3.70.	12	y=0,270x-0,093	0,96	<,001	>,05	>,05
	8.4.70.	12	y=0,333x-0,031	0,95	<,001	<,02	>,05
	5.5.70.	11	y=0,841x-0,521	0,84	<,001	>,05	>,05
	6.6.70.	13	y=0,564x-0,168	0,75	<,001	<,001	>,05
	8.8.70.	17	y=0,111x+0,062	0,77	<,001	>,05	>,05
	2.9.70.	12	y=0,098x+0,007	0,73	<,02	>,05	>,05
	15.10.70.	15	y=0,079x+0,023	0,60	<,05	>,05	>,05
	27.12.70.	13	y=0,096x-0,048	0,97	<,001		

Patella longicosta

	Sample Date	N	Regression equation y = mx + c	r	t test of r (probability)	Probability of differences between regressions	
						Slope	Intercept
♀	5.2.70.	8	y=0,066x-0,029	0,90	< ,001	> ,05	> ,05
	9.3.70.	8	y=0,157x-0,236	0,81	< ,02	> ,05	> ,05
	8.4.70.	10	y=0,092x-0,007	0,65	< ,05	< ,05	> ,05
	5.5.70.	7	y=0,200x-0,167	0,99	< ,001	< ,001	> ,05
	6.6.70.	7	y=0,400x-0,705	0,98	< ,001	> ,05	> ,05
	2.8.70.	14	y=0,259x-0,221	0,55	> ,05	> ,05	> ,05
	2.9.70.	6	y=0,441x-0,759	0,95	< ,001	< ,001	> ,05
	16.10.70.	8	y=0,118x+0,099	0,89	< ,001		
♂	5.2.70.	9	y=0,060x-0,017	0,92	< ,001	< ,001	> ,05
	9.3.70.	10	y=0,180x-0,110	0,93	< ,001	> ,05	> ,05
	8.4.70.	9	y=0,293x-0,252	0,88	< ,001	> ,05	> ,05
	5.5.70.	11	y=0,173x-0,088	0,77	< ,001	< ,02	> ,05
	6.6.70.	8	y=0,391x-0,481	0,97	< ,001	> ,05	> ,05
	2.8.70.	13	y=0,404x-0,347	0,86	< ,001	> ,05	> ,05
	2.9.70.	7	y=0,417x-0,440	0,92	< ,001	> ,05	> ,05
	16.10.70.	13	y=0,230x-0,070	0,88	< ,001	< ,05	> ,05
	27.12.70.	6	y=0,095x-0,031	0,85	< ,05		

Patella oculus

	Sample Date	N	Regression equation y = mx + c	r	t test of r (probability)	Probability of difference between regressions	
						Slope	Intercept
♀	5.2.70.	5	y=0,059x+0,148	0,62	>,05	>,05	>,05
	9.3.70.	7	y=0,069x+0,205	0,91	<,02	>,05	>,05
	8.4.70.	6	y=0,097x+0,006	0,71	<,05	>,05	>,05
	2.8.70.	7	y=0,279x-0,718	0,91	<,001	>,05	>,05
	16.10.70.	5	y=0,132x-0,493	0,56	>,05		
♂	5.2.70.	20	y=0,049x-0,062	0,74	<,001	<,001	>,05
	9.3.70.	23	y=0,159x-0,290	0,79	<,001	>,05	>,05
	8.4.70.	15	y=0,136x-0,300	0,75	<,001	>,05	>,05
	5.5.70.	9	y=0,164x-0,315	0,57	>,05	>,05	>,05
	6.6.70.	11	y=0,206x-0,529	0,84	<,001	>,05	>,05
	2.8.70.	20	y=0,322x-0,969	0,78	<,001	<,05	>,05
	2.9.70.	10	y=0,094x-0,152	0,72	<,05	>,05	>,05
	16.10.70.	17	y=0,135x-0,218	0,80	<,001	>,05	>,05
	27.12.70.	9	y=0,127x-0,353	0,80	<,05		

GROWTH RATES

The population structure and productivity of any species can only be determined with a knowledge of growth rates, age structure, longevity and mortality rates. In the case of Patella, no obvious growth rings occur in the shell, so that growth and age cannot be obtained directly. Growth of younger animals can be deduced if the size distribution of a population is monitored, but older age groups merge too much to be distinguished. Thus periodic measurement of labelled specimens is necessary.

The present work was aimed at determining the "typical" growth rates of five Patella spp., from Kommetjie, Kalk Bay and Dalebrook in the Cape Peninsula. Comparisons were also made at Elands Bay on the West Coast. Growth rates are characteristically variable, and the present analysis was deliberately restricted to specimens in typical habitats, so that interspecific rather than environmental differences could be determined. The work therefore serves primarily as a base-line study on which predictions can be based and comparisons made. In addition it allows analysis of population age structure.

No previous assessment has been made of growth in South African limpets, and indeed Newman's (1968) analysis of Haliotis midae is the only work of its kind on South African marine molluscs. Hamai (1937) has given a generalised mathematical description of allometry and growth in limpets and Orton (1928), Fischer-Piette (1941, 1948), Hatton (1936), Ballantine (1965) and Blackmore (1969a) have all analysed the growth of Patella vulgata. Recently Shackleton (1973) has used the ratio of the isotopes ^{16}O and ^{18}O in the shell of P. tabularis to determine the temperature at which the shell was deposited. By sampling from the shell edge toward the apex, he was able to detect seasonal variations and hence deduce the rate of growth. Shackleton's aim was to assess the temperature at which death occurred, in sub-fossil shells found in middens. However, he did analyse a single living animal from Plettenberg Bay, and concluded that it grew from a length of 45mm to 90mm in a period of two years.

MATERIAL AND METHODS:

Detailed analyses were made of growth in P. cochlear, P. granatina and P. granularis at Kommetjie and P. cochlear, P. granularis, P. oculus and P. longicosta at Kalk Bay or Dalebrook. More superficial comparisons were made with P. granularis and P. granatina at Elands Bay.

Growth rates can be determined in various ways: arithmetic, geometric or total (Simpson, Roe and Lewontin, 1960), or as mean specific growth (Wilbur and Owen, 1964). In the case of limpets, shell dimensions are the only parameters which can be periodically measured without damaging the animal. Arithmetic changes in shell length were used as the most convenient measure, and determined at monthly intervals for one year.

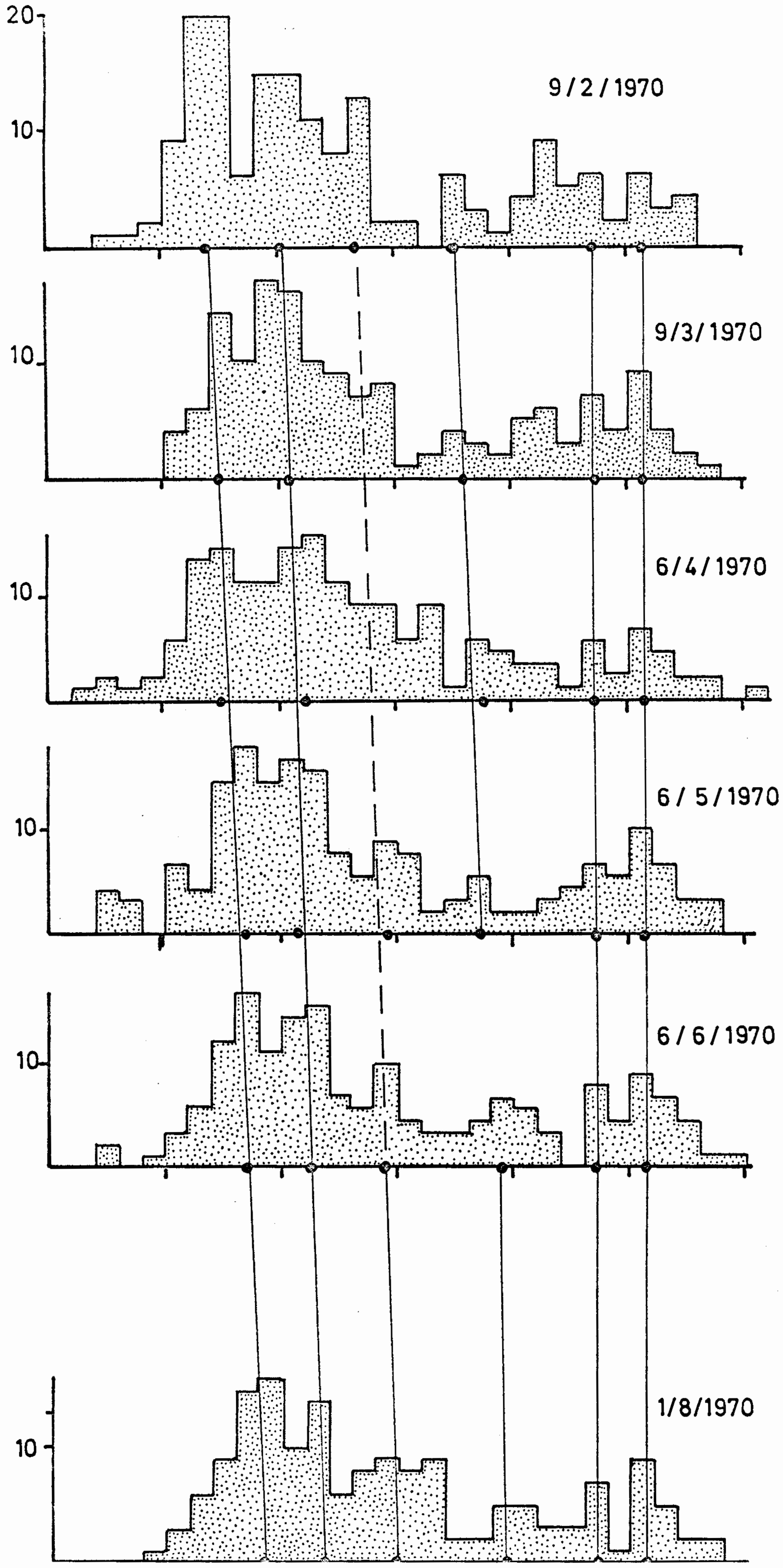
All specimens were measured to an accuracy of 0,01 mm using vernier calipers, and then labelled with numbered Petersen discs supplied by Floy Tagging Co., Seattle, Washington; Biofast dental cement was used to attach the labels and proved a quick setting very strong adhesive provided it was applied to dry shells. Approximately 150 of each species were labelled at each site except Elands Bay where 25 were labelled. Animals were selected so that the complete size range of each species was represented. All animals were measured at monthly intervals except at Elands Bay where only three-monthly intervals were possible.

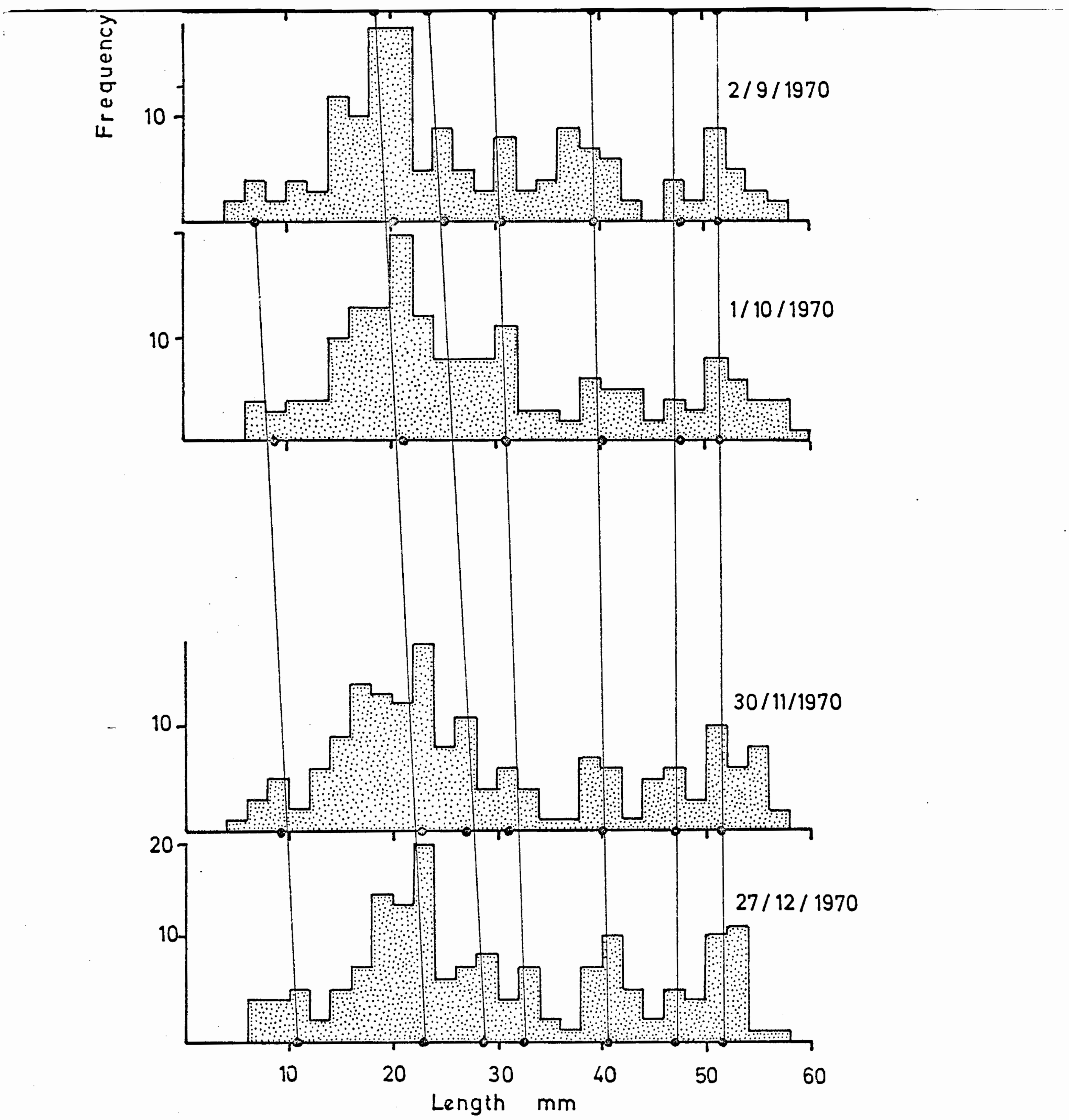
In the case of P. cochlear an additional technique was used: the lengths of all individuals in a preselected area of 0,6 m^2 were measured at monthly intervals for 12 months, and the changes in size frequency taken as an indication of growth. This method is not recommended in future as it is more time consuming and less precise than measurement of labelled animals. However, it is useful for species which are difficult to tag, or with low recovery rates.

The irregular costae of P. longicostae made measurement in the field difficult to replicate, so monthly photographs were taken of labelled animals, and growth determined from these.

Mean growth rate was quantified by plotting initial length against the increment per year. In all cases this proved to be a linear negative correlation and regression lines were calculated and lower and upper limits drawn. Regression had the effect of slightly underestimating growth in very large animals, as these may continue to grow at a slow (and often immeasurable) rate. However, as the intercept on the X axis (predicted maximum size) was close to the actual size recorded in each case, the inaccuracy incurred was probably slight, and has been ignored. 95% confidence limits were calculated for each regression. Statistics are given in Appendix I.

FIG.I. Growth rate of P.cochlear at Kalk Bay (site I), deduced from monthly changes in size-frequency peaks.




Frequency
10
2/9/1970
10
1/10/1970
10
30/11/1970
20
10
27/12/1970
10
20
30
40
50
60
Length mm

was determined in the same area as growth, by measuring all the animals present (using a minimum sample of 150). With P. granatina and P. cochlear it was difficult to assess the first year group because the specimens were small and cryptic. To overcome this, a mark and recapture technique was used for P. granatina. All specimens in a given area were marked with nail varnish. On the following day the ratio of marked to unmarked animals was determined, and immigration of unmarked animals taken to equal emigration of marked animals. From the ratio, and a known migration rate, the total first year group could then be assessed.

Juveniles of P. cochlear are almost all found on the shells of larger specimens (Branch, 1971). The population was determined by removing all the animals from an area and then examining the shells microscopically to locate the smaller specimens.

SHELL GROWTH:

P. cochlear: The growth of P. cochlear was determined at two sites at Kommetjie and two at Kalk Bay. In the latter locality growth in site I was obtained by periodic measurement of all animals in a given area (fig. 1), while at site II measurement of labelled animals was used.

For all four sites, the results are expressed as the relationship between initial shell length and increment per year (figs. 2a and b). These results were then converted to an annual growth rate by extrapolation from a known length of 1mm at metamorphosis and a known settling period of about July. Annual growth is summarised in figs. 3a and b for

FIG. 2. P.cochlear: Increments in shell length. (Minimum, maximum, and mean increments are given. Vertical bars indicate 95% confidence limits)

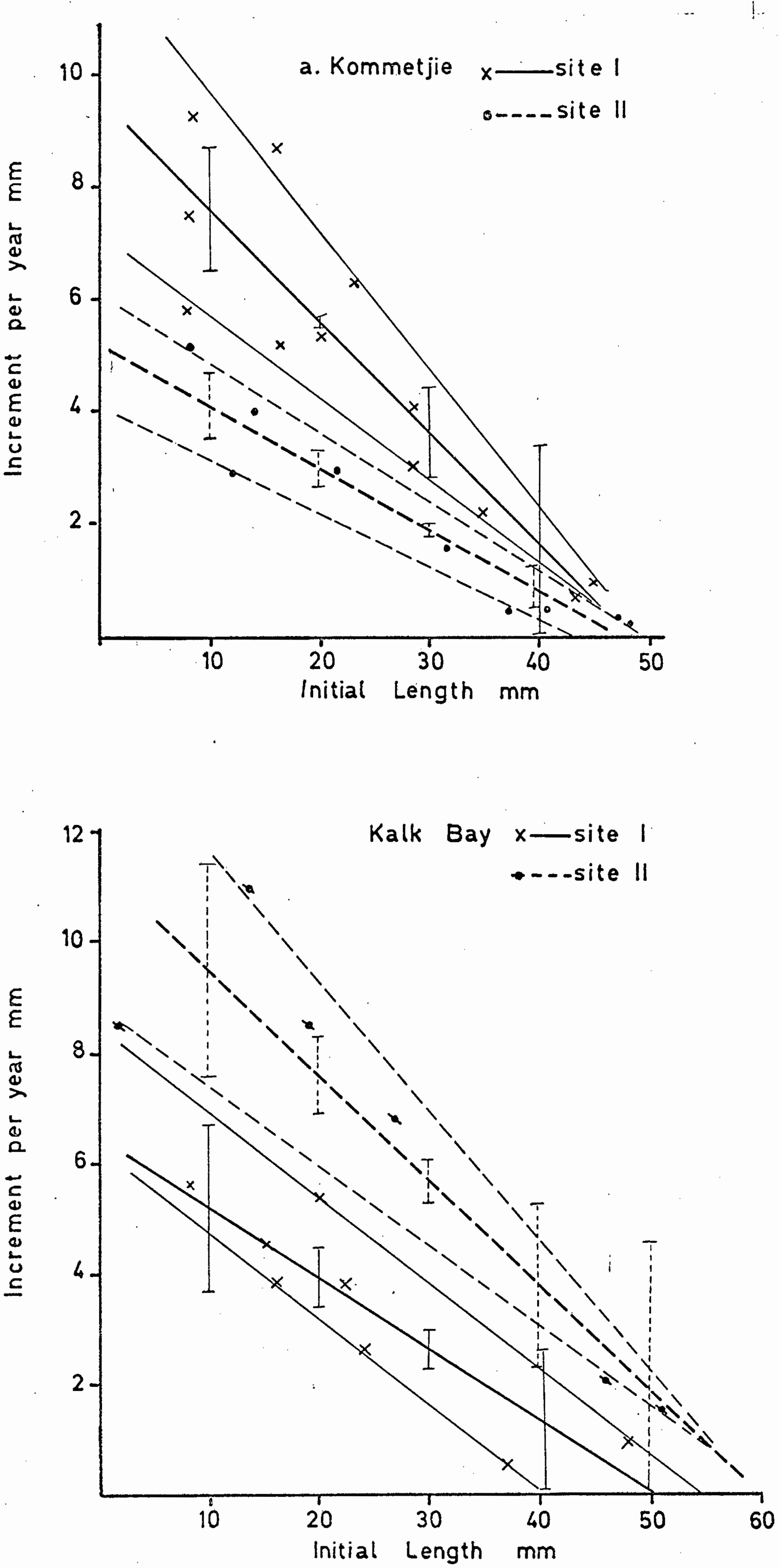
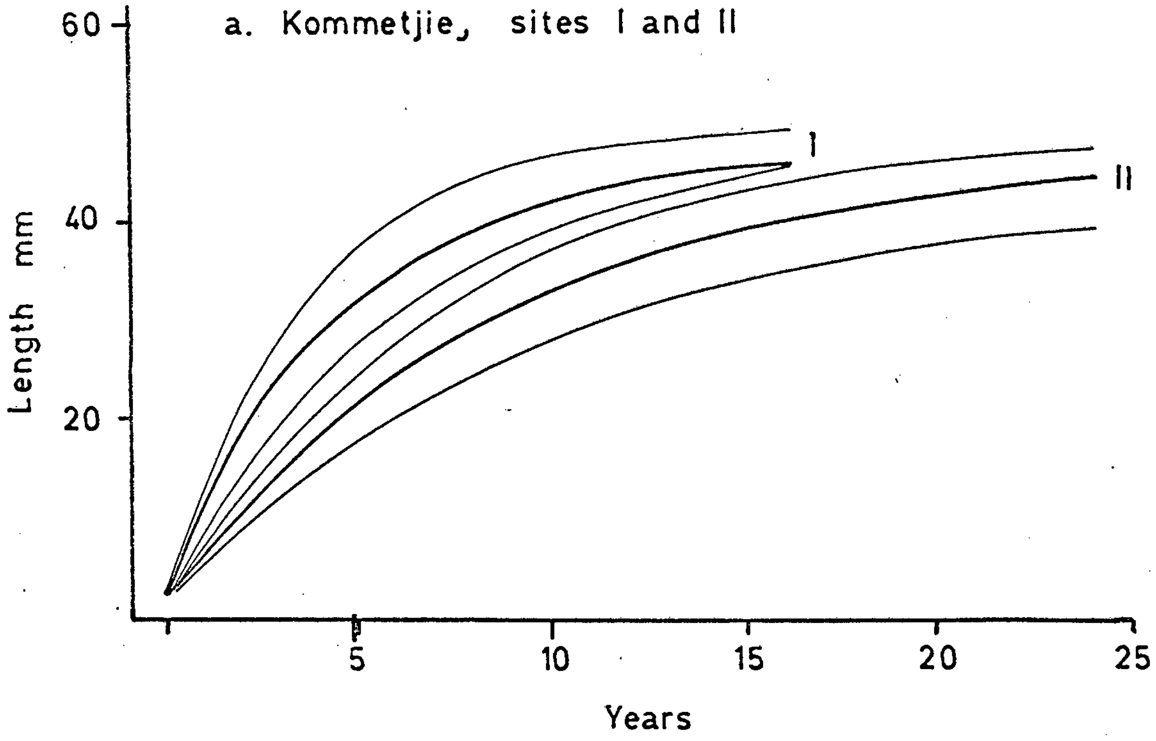
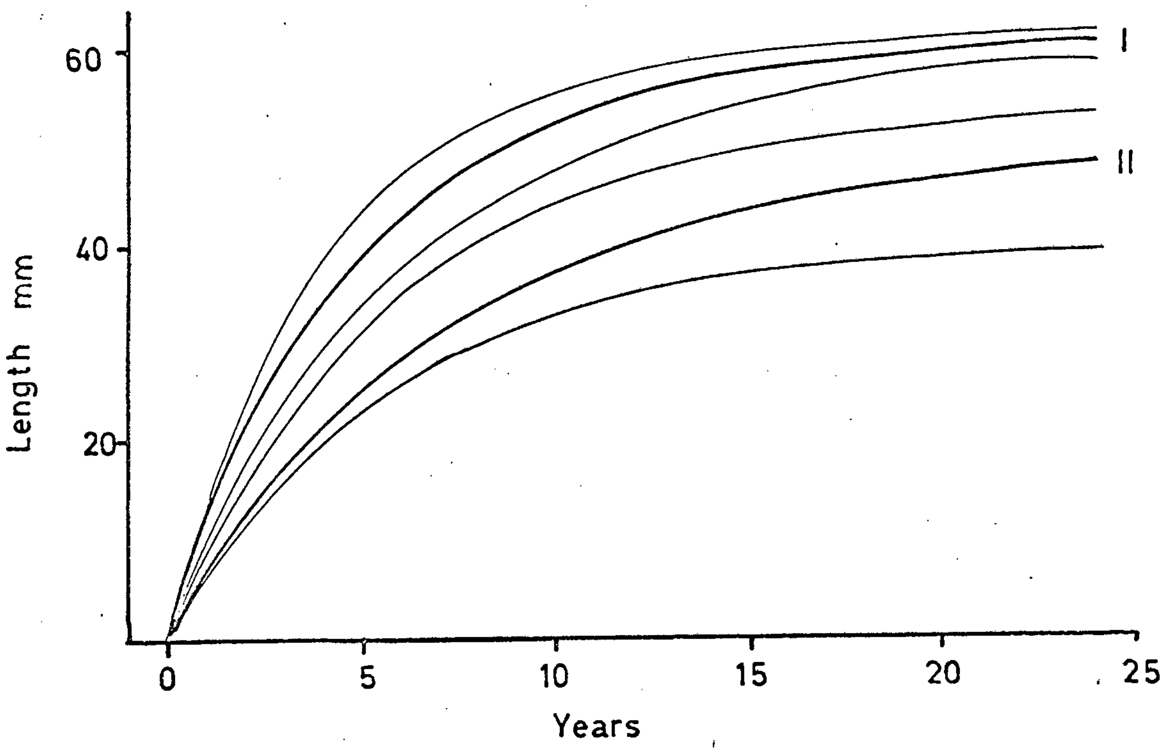


Fig. 3 P. cochlear: Maximum, Mean and Minimum Shell Growth

a. Kommetjie, sites I and II



b. Kalk Bay, sites I and II



for all four sites.

At each locality growth was relatively rapid at one site and slower at the other. The initial regressions were analysed for difference in slopes and intercepts. The analysis is presented in Table I and shows that the two sites with rapid growth are not statistically different, and nor are the two slower growing populations.

TABLE I. Statistical analysis of growth increments in *P. cochlear* (significance of difference in intercepts above diagonal and slopes below. N.S. = Not significant).

			A	B	C	D
A.	Kommetjie I	(fast)		$<.001$	N.S.	$<.01$
B.	Kommetjie II	(slow)	$<.05$		$<.001$	N.S.
C.	Kalk Bay I	(fast)	N.S.	N.S.		$<.001$
D.	Kalk Bay II	(slow)	N.S.	N.S.	N.S.	

This indicates that the difference between sites at one locality was greater than between localities.

P. cochlear obviously grows very slowly. Growth is highest in the first five years, a length of between 22 and 40 mm being attained. Subsequently the growth rate slows and after 15 years increments of about 1 mm per year can be expected. Implied in this low growth rate is a longevity of 15 to 25 years - greater than any of the remaining *Patella* spp.

The calculated annual growth rates agree well with peaks in the size frequency of each population, in the younger age groups, but older groups merge and are indistinguishable (fig. 13). Predictions of maximum size can be made from the

Fig. 4a P. granatina: Increments in Shell Length

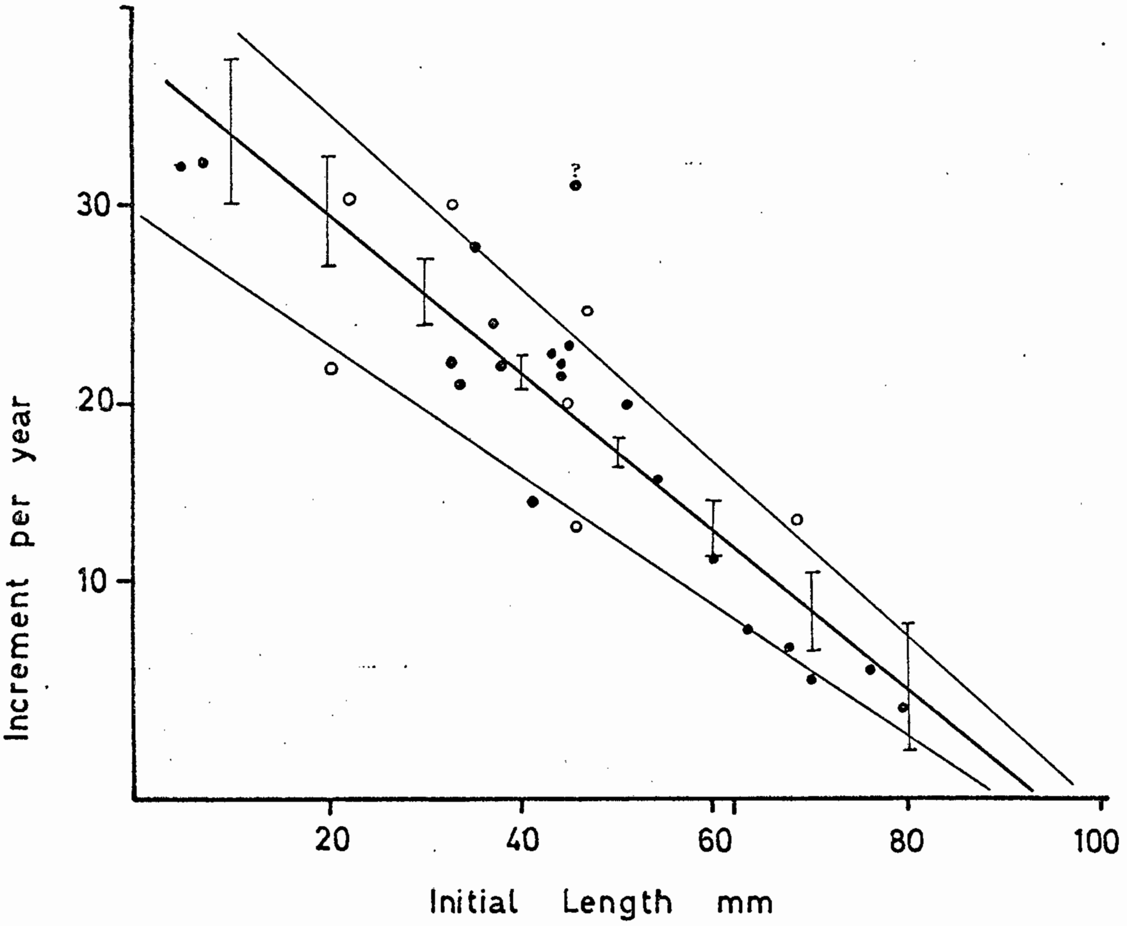
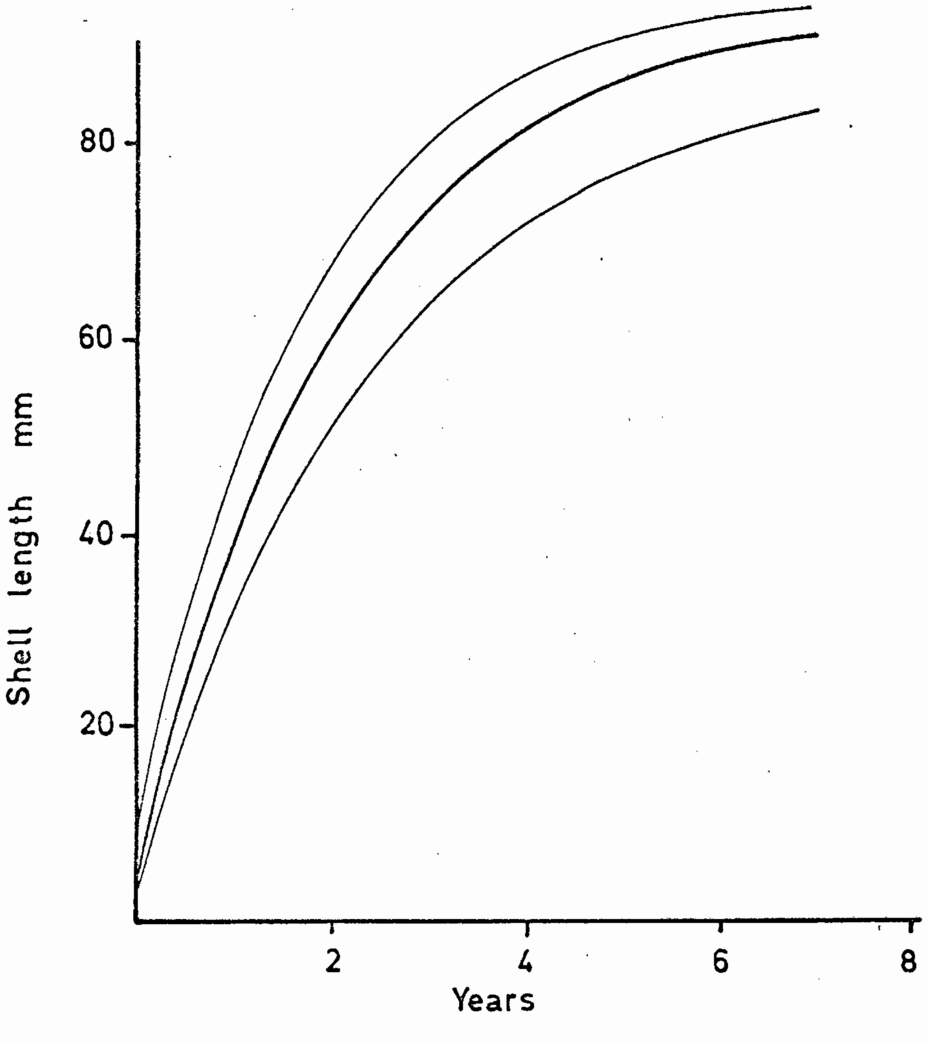


Fig. 4b P. granatina: Growth of Shell (maximum, mean and minimum)



regressions, and these too are close to the actual maximum recorded at each site. This is corroborative evidence indicating that the calculation of mean growth rate is fairly accurate.

P. granatina: Shell deposition in P. granatina is rapid and an increment of about 35mm occurs in the first year. Subsequently there is a linear decrease in the amount of growth each year, until increase in length ceases in the seventh or eighth year (figs. 4a, b). The maximum size predicted from the growth regression (fig. 4a) is 93mm, which almost coincides with the largest specimen of 95mm recorded at Kommetjie. Longevity is about seven to eight years. The assessment of growth coincides almost exactly with peaks in the size distribution of the population, which are taken as year - groups (fig. 14).

A small sample was labelled at Elands Bay, and the growth rate of these animals fell within the range of the Kommetjie sample (fig. 4a). The mean rate was slightly (but not significantly) higher than at Kommetjie, but as the sample was small, construction of an annual curve is not justified. Much larger specimens were found at Elands Bay, particularly in gulleys where spume is deposited, and in intertidal pools. This is probably related to the higher nutritive content in these sites, due to deposition of spume, and growth of algae in pools. Almost certainly growth would have been higher in these animals.

P. granularis: Growth of this species was determined at Elands Bay, Kommetjie and Kalk Bay. In the latter area, several sites were used to measure the effect of barnacles on

Fig. 5 P. granularis : Increment in Shell Length

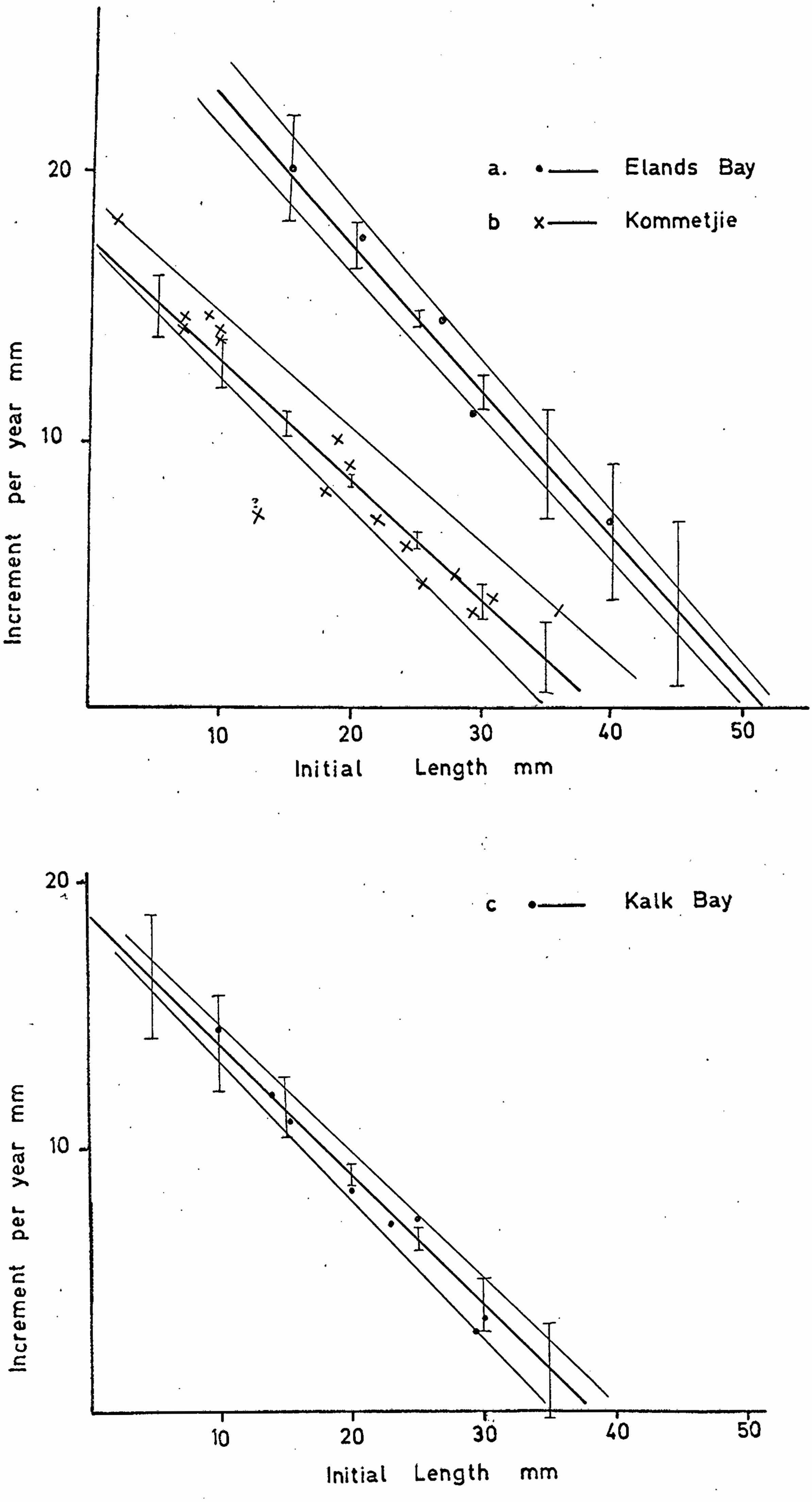


Fig. 7a P.longicosta: Shell Shape relative to Habitat

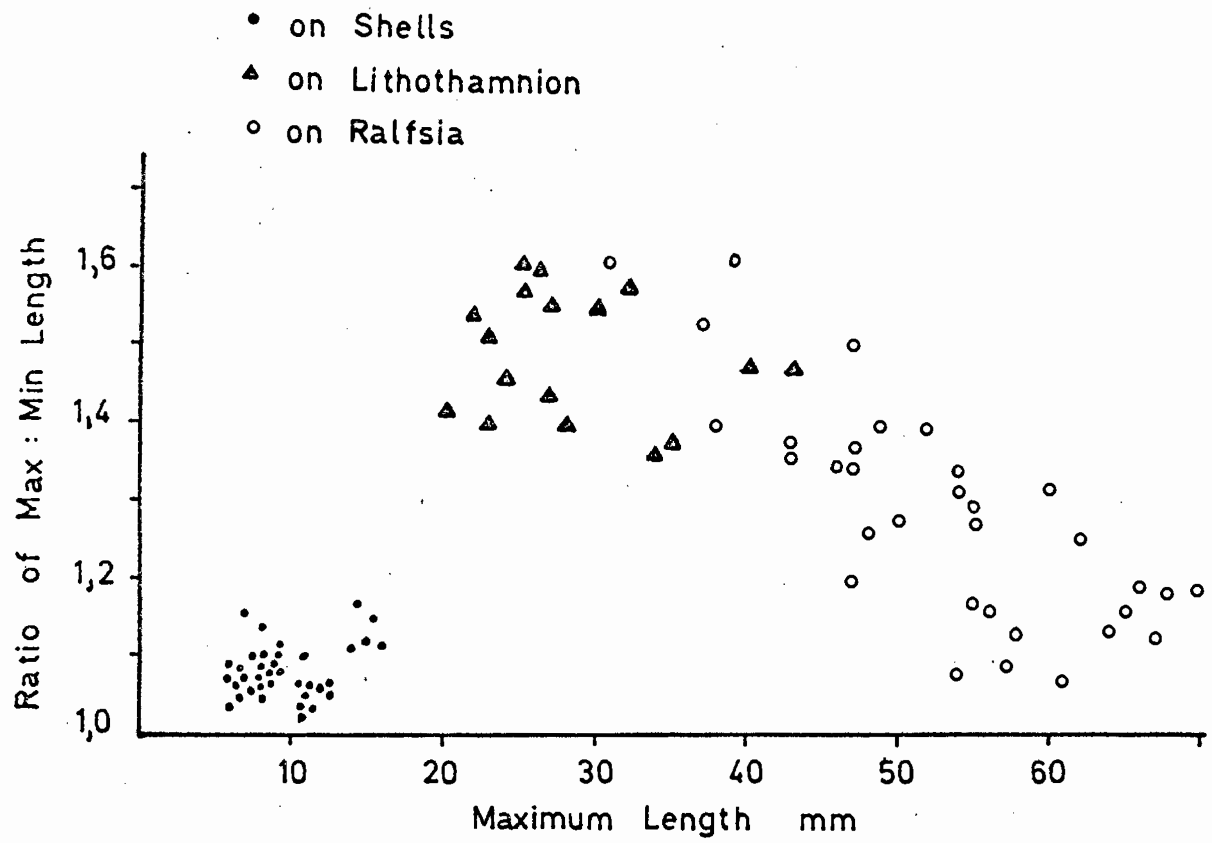
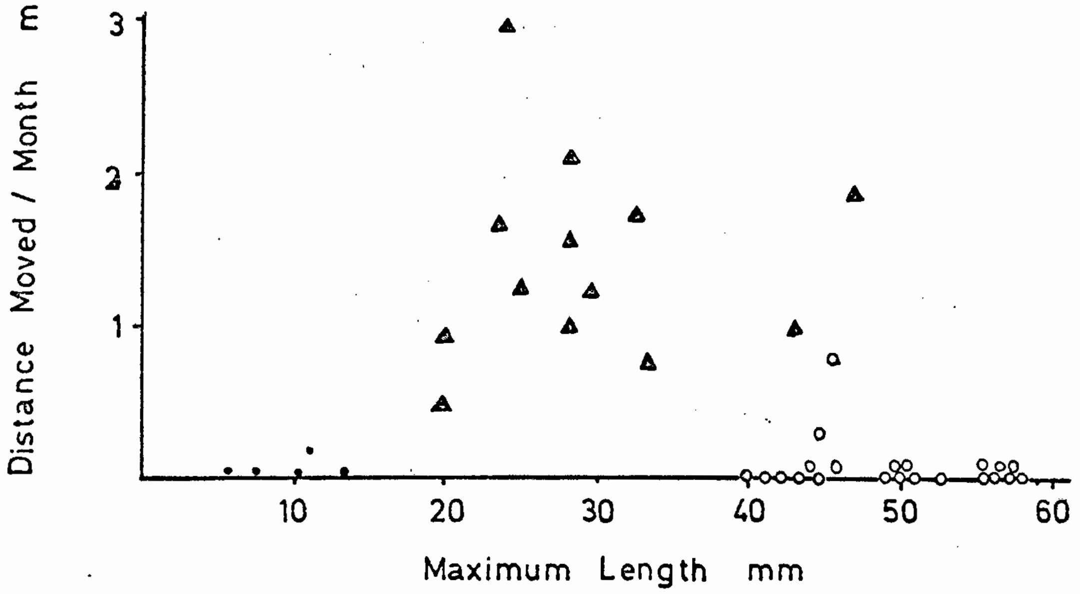


Fig. 7b P.longicosta: Movement relative to substrate



actual maximum values were 40mm (fig. 5b): less than at Kommetjie. Size frequency peaks could not be detected because of the sparcity of the population. The similarity between Kalk Bay and Kommetjie may be more apparent than real, for various reasons. The density of the Kalk Bay population (26 per m^2) was much less than the sample at Kommetjie (192 per m^2). The Kommetjie sample comprised animals with a maximum size less than that recorded elsewhere at Kommetjie, and growth was probably also less. Growth at Kalk Bay is probably, in general, less than at Kommetjie.

P. longicosta: In P. longicosta the shell shape makes replication by measurements difficult. In addition, shell proportions change during life. Juveniles are found on other shells, particularly Oxystele sinensis, and have short stubby costae and relatively high shells. As growth occurs, the P. longicosta shift to lithothamnion on a rocky substrate, and migrate a considerable amount. During movement the mantle is extended and the shell deposited in a flatter shape with long costae. Finally specimens develop algal gardens of Ralfsia expansa and migration ceases. Fortnightly photographs were taken of an area of $9m^2$, using a grid of 50 x 50 cm. From this the average monthly movements were recorded in relation to size and substrate. Juveniles on Oxystele were considered not to have moved if they remained on the same winkle. The results (fig. 7b) show the increase of movement when the animals are on lithothamnion. With the reduction in movement, the mantle is more often in a contracted state and deposition of the shell changes, causing a relative reduction in the length of the costae. Moore (1934a) and Orton (1933) have shown comparable changes of shell shape in

P. vulgata in relation to mantle contraction or expansion. They associate this with the amount of desiccation experienced, but this is not the case in P. longicosta.

Changes in the shell shape of P. longicosta are summarised in figure 7a. As a consequence of changing shell shape, growth is difficult to assess in terms of a single shell dimension. Maximum shell length (including costae) has been used because it is the easiest dimension to measure.

In addition to the problem of shell shape, the shells of larger animals may decrease in length from November to March, when shell growth ceases, and the shells (particularly the costae) are worn away. During the remaining months shell deposition is resumed and length increases again. Figure 11 shows examples of this phenomenon.

Because of these difficulties, growth may not have been accurately measured. Despite this, a close agreement occurs between the predicted growth rates and population size frequency peaks, so that the growth rate determinations are probably reliable.

Growth in P. longicosta follows the pattern shown for previous species and is summarised in figures 8a, b. The rate of growth is relatively slow and roughly equivalent to that of slow growing populations of P. granularis.

P. oculus: Due to loss of labels and a high mortality, growth was determined in two samples covering six months each. As there was no significant difference between these periods, the results were pooled to give the mean increment per six

Fig.8a P. longicosta: Increments in Shell Length

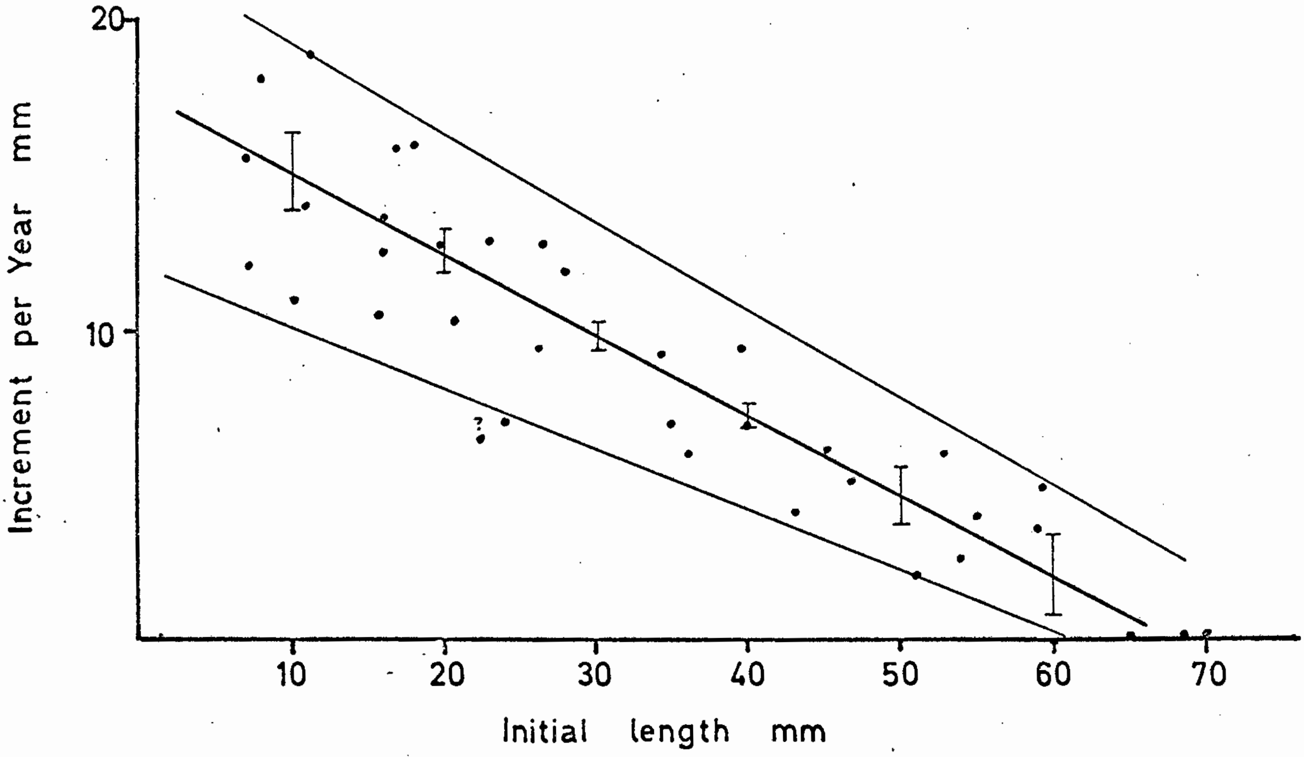


Fig 8b P. longicosta: Maximum, Mean and Minimum Shell growth

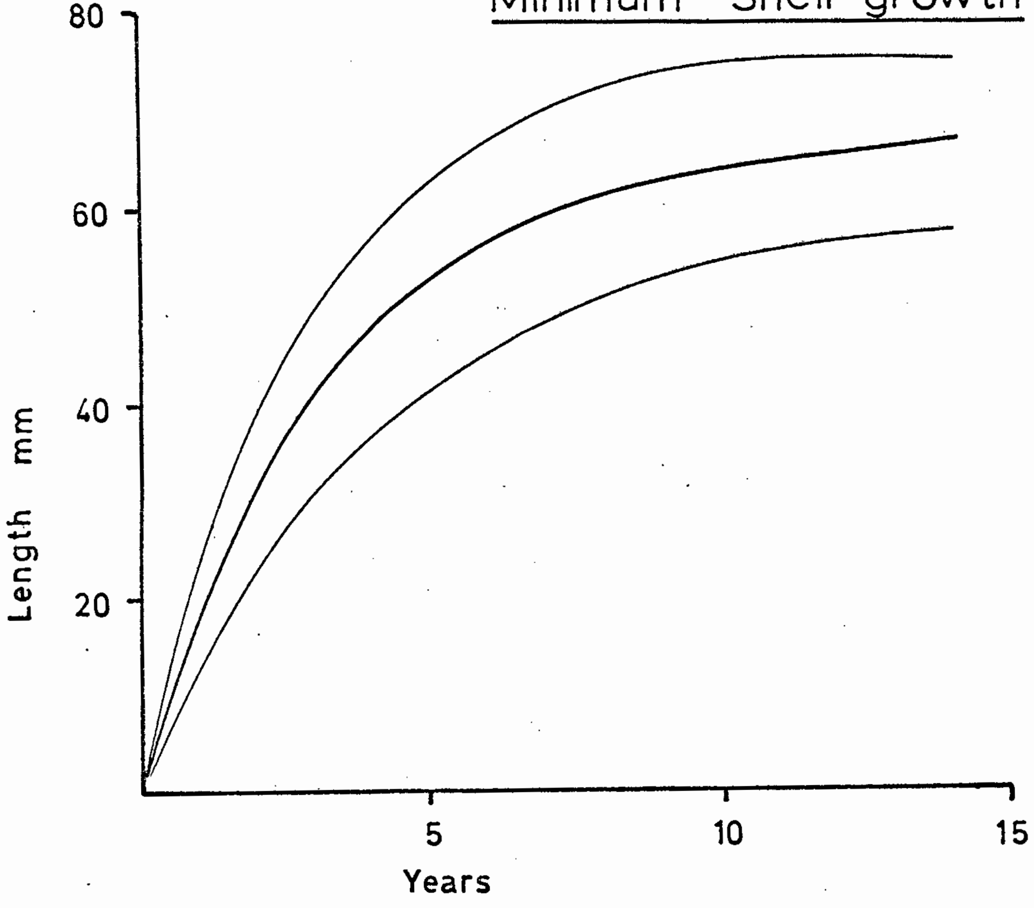


Fig 9a P.oculus: Increments in Shell Length

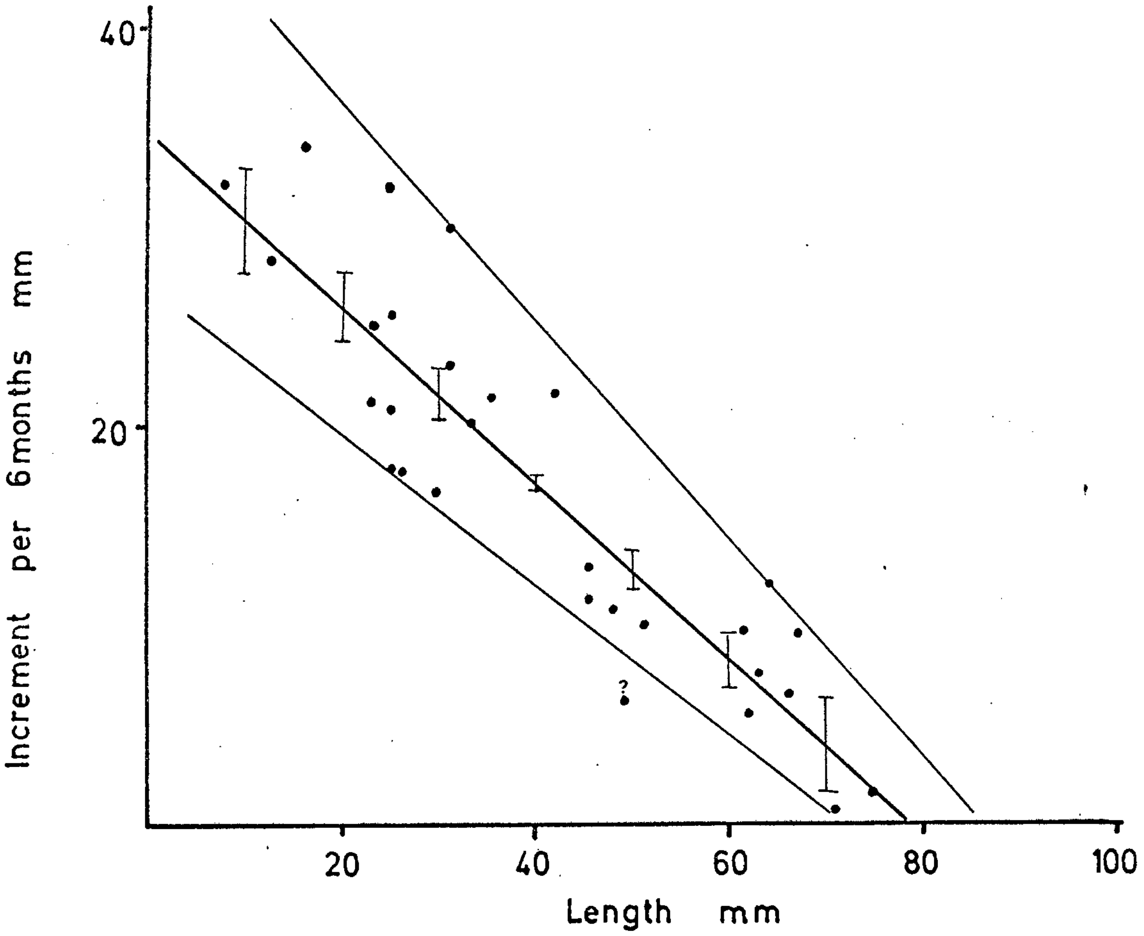
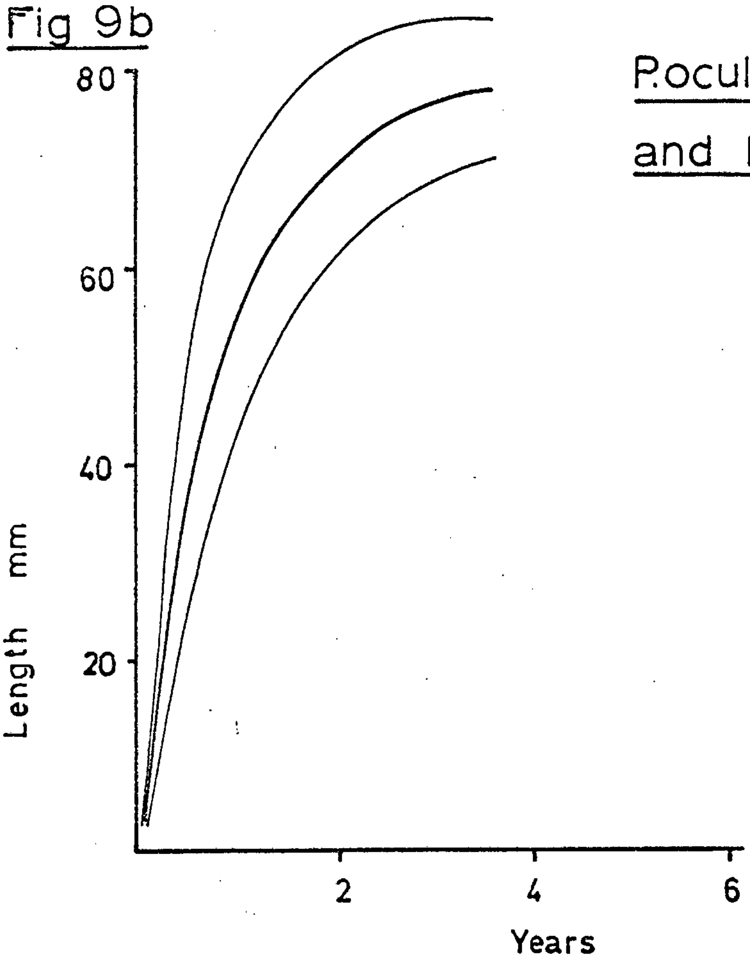


Fig 9b

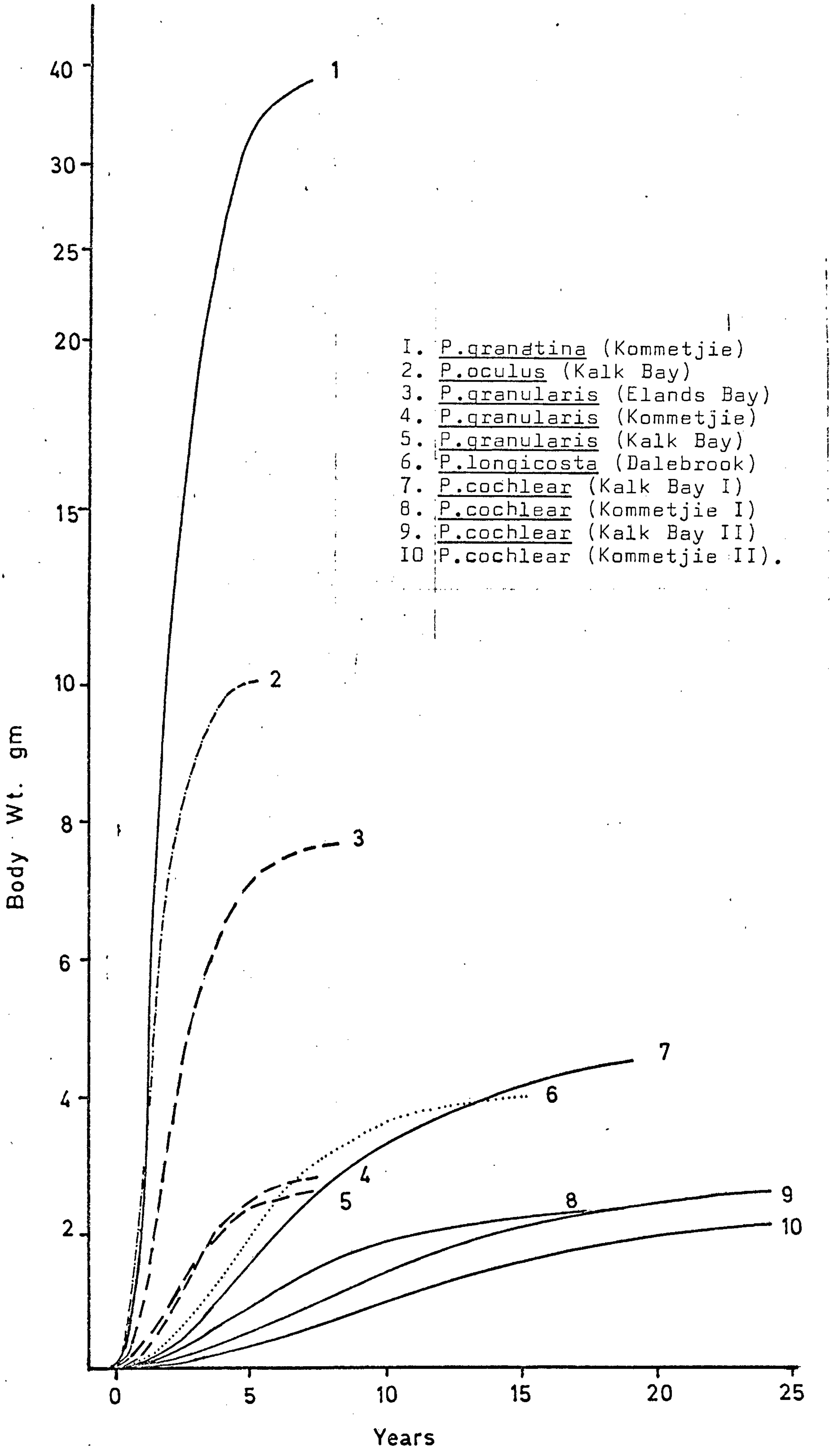


P.oculus: Maximum, Mean and Minimum Shell Growth months (fig. 9a). Growth of the shell is remarkably rapid. With a mean growth rate, a length of 56mm is achieved in the first year, and 70mm in the second (fig. 9b). Very few animals survive beyond this age, but the largest animal recorded at Kalk Bay was 79mm, and about 3.5 years old. This compares well with the calculated maximum value of 78mm. Occasional specimens are found with the shell worn back considerably. These animals have thick shells and very large bodies and are probably older than 3.5 years. The worn shells prevent estimates of age based on shell length, but extrapolation of the body growth curve (fig. 10) produces an estimate of 5 years. Such animals are however exceptional.

Comparison of the growth rate with the population structure (fig. 17) reveals the apparent anomaly that there are two obvious size frequency peaks during the equivalent of each years growth. In describing the gonad cycle of P. oculus for 1970 (Section III, p. 15) the main spawning was recorded in September, with a partial or false spawning in April. Cohen (1948, unpublished) considered that P. oculus spawned in March (although her data for this species is ambiguous). In view of the biannual peaks in the population size frequency, it seems very probable that P. oculus may spawn twice a year. This is supported by the (intermittent) records kept of the appearance of juveniles each year (about two months after spawning): December 1970, December 1971 (no records January - August), May 1972, January 1973, June 1973.

There is thus fairly strong evidence of a biannual spawning. Judging by the size frequency distribution and

Fig. 10 Growth in Body Weight



the gonadial index (Section III) the major spawning occurs about September and a minor spawning in about April.

On the basis of biannual settlement, the size frequency peaks coincide with the predicted growth rates (fig. 17).

GROWTH OF BODY WEIGHT

While shell length is the easiest parameter to measure when analysing growth, flesh weight is of equal importance. As body weight is exponentially related to shell length (Appendix II), growth of body weight can be calculated from known growth of the shell.

The mean body growth for the five species is shown in figure 10. In all cases the growth is sinusoidal, maximum absolute growth rate being reached within the first quarter of the life span and then progressively decreasing. Growth is fast in *P. granatina*, *P. oculus* and *P. granularis* from Elands Bay, intermediate for Kalk Bay and Kommetjie samples of *P. granularis*, and slow in *P. longicosta* and *P. cochlear*.

These rates correlate with the rates of shell deposition, except that in *P. granatina* body growth is faster than in *P. oculus*, while the reverse is true for shell growth. This is because the body weight of *P. granatina* is much greater in relation to shell length than in *P. oculus*.

DISCUSSION

1. Factors effecting growth rates:

Age: In most molluscs shell deposition decreases with age, while body growth rises to a maximum in early life and then decreases progressively. This is true of the five species considered here. Decrease and cessation of shell deposition is probably of great importance in determining longevity. In *P. oculus* and *P. longicosta* some specimens were recorded with negative shell increments because the shell was being worn away. In both, the shell wears unevenly and does not fit the substrate exactly. In extreme cases the mantle extends beyond the shell and is vulnerable. Predation is high in these individuals and on five occasions *Burnupena delalandii* were seen feeding on specimens in which the mantle was damaged and the shell no longer fitted the substrate. These scavengers were never seen feeding on younger animals with intact shells.

Decrease in the rate of shell deposition may be due to a number of factors. Metabolism decreases with age and size (Davies, 1966). More significantly, the activity of carbonic anhydrase (associated with shell deposition) decreases with age, as Kawai (1955) has shown for the oyster *Pinctada martensii*. However, shell deposition is complex and a single cause and effect relationship is unlikely to explain its decrease with age.

At the mantle edge, the periostracum and prismatic layers are formed, while the central mantle epithelium lines these internally with nacreous layers. In *Patella* the latter function is never lost, and thickening of the shell continues throughout life, even after increments in shell length have ceased. Mechanical damage or the action of boring organisms is compensated for by increased deposition of nacreous layers, thickening the shell as it is eroded. Parasites or commensals may be encased by the deposition of nacreous layers, forming structures comparable to the well known "blisters" in oysters.

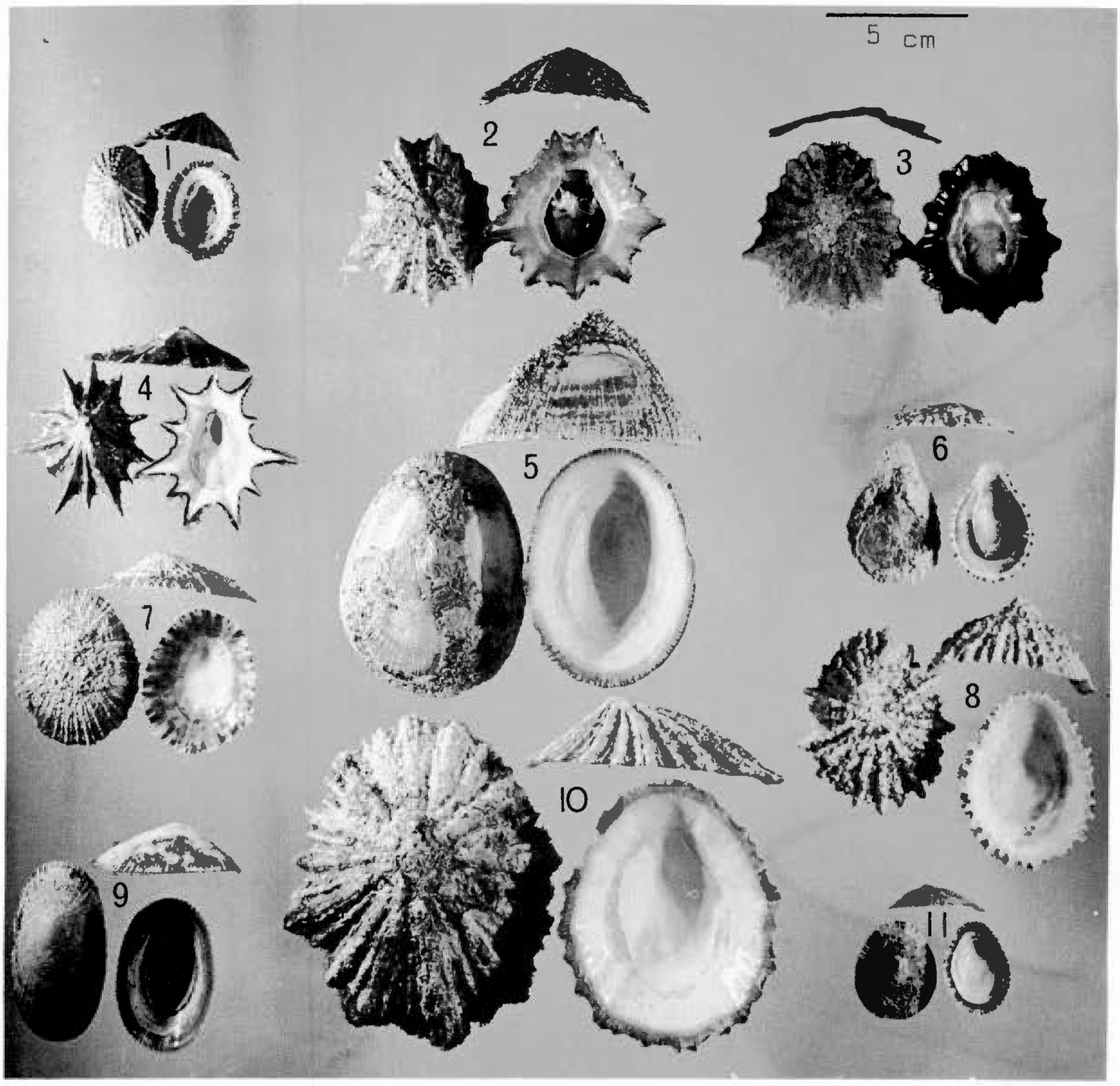
Seasonal temperatures and gonad cycles: Tests were made of the differences in growth rate between winter (June to August), spring (September to November), summer (December to February) and autumn (March to May).

In False Bay, *P. oculus*, *P. granularis* (in barnacle-free sites) and *P. cochlear* showed no seasonal differences in growth rate. In these cases gonad development is initiated when temperatures are high, during late summer and early autumn, and possibly the higher growth anticipated with high temperatures is being offset by gonad growth. Conversely, the gonads of *P. granularis* and *P. cochlear* spawn or are in a resting state while temperatures are low. Thus growth may appear uniform because gonad growth and low temperatures alternate in False Bay.

At Kommetjie, seasonal effects could not be detected in *P. granatina*, *P. granularis* or *P. cochlear*. Sea temperatures on the West Coast are relatively constant throughout the year, although dramatic short-term fluctuations may occur.

Gonad size in *P. cochlear* is very small (see Section III) and probably has little influence on growth rate. In *P. granatina* the gonad may comprise 55% of the flesh weight, and gonad development occurs in a short period of about six weeks in April, May and June. It is therefore surprising that no significant decrease in growth accompanied this. Possibly reserves are stored before gonad growth starts, as Blackmore (1969b) has shown for *P. vulgata*.

P. granularis occurs high on the shore, and air temperatures may influence growth. However, gonad development from January to May again coincides with the highest temperatures, so that the anticipated increase of growth may be channelled



FRONTISPIECE:

SOUTH AFRICAN *PATELLA* SPECIES

1. *P. granularis*
2. *P. granatina*
3. *P. oculus*
4. *P. longicosta*
5. *P. argenvillei*
6. *P. cochlear*
7. *P. miniata*
8. *P. barbara*.
9. *P. compressa*
10. *P. tabularis*
11. *P. concolor*

into gonad production. Newell and others have shown that many intertidal animals enter a state of basal metabolism when exposed, and are temperature independent in this state (see Newell, 1970 for a review). Whether this means that growth is also minimal during this state is not known.

P. longicosta from Dalebrook, in False Bay, displayed differential patterns of growth dependent on the size of the animal. Animals less than about 45mm long grew significantly faster from November to March than during the rest of the year. Gonad development is associated with the latter period, developing from March and spawning in October or November. The period of slower growth also coincides with the colder months of the year.

In larger animals a curious situation exists in which shell deposition ceases (or is very low) from about November to March, and the shell may be worn away to yield negative increments. During the remainder of the year shell deposition is resumed and the annual increment is usually positive. Cessation of shell deposition does not occur in all animals, but about 82% of the larger individuals displayed the phenomenon.

This reduction or cessation of shell growth occurs when sea temperatures are highest, and when the gonad is regressed or just beginning to redevelop.

Growth of the foodplant Ralfsia expansa was assessed by measuring the percentage cover of this alga on the shells of large P. longicosta (which occupy gardens of this alga). The mean results show that Ralfsia growth is related to temperature (fig. 11), and it is apparent that decrease in shell growth occurs when Ralfsia is most abundant. Lack of food is clearly not implicated. Both the maximum growth of smaller animals and the major growth of the gonad occur when the alga is growing fast (fig. 11).

The cause of reduced shell growth in larger P. longicosta is thus something of an enigma, and appears unrelated to temperature, gonad growth or availability of food.

Sutherland (1970) has shown an interesting situation in Acmaea scabra, where growth is maximal in summer low on the shore, but maximal in winter high on the shore. He relates this to summer mortality of algae high on the shore, and seasonal temperature differences lower down.

In Britain, Blackmore (1969a) has shown that growth of P. vulgata is lowest when air and sea temperatures are low and that maximum growth coincides with gonad maturation. Russell (1909) and Orton (1928) also recorded greatest growth in summer, but Fischer-Piette (1948) could not detect any winter depression of growth in the same species, working on the northern coast of France.

Newman (1968) has shown that shell growth in Haliotis midae is lowest in late spring and autumn, and that this is probably due to gonad maturation.

Of the South African limpets analysed, only P. longicosta shows marked seasonal patterns of growth, as described above. The general trend is that South African Patella spp. are not as effected by winter as their British counterparts. This may be related to the severity of winter conditions.

Food: Some Patella spp. are highly specific in their food requirements while others are generalised browsers (Branch, 1971, and Section II). Of the species concerned here, P. longicosta feeds specifically on Ralfsia expansa, although smaller animals may be limited to lithothamnion until they establish Ralfsia gardens. P. cochlear feeds largely on lithothamnion. P. granatina, P. granularis and P. oculus feed on any available algae, lichens, diatoms or spume.

The nutritive values of South African algae are not known, but the calorific values given by Paine and Vadas (1969) for algae in Western Washington State, are instructive. Lithothamnion sp. has an extremely low calorific value (0.67 Kcal/gm dry weight) and even the ash free dry weight yields a value of only 3.94 kcal/gm. The latter value was the fourth lowest value obtained by Paine and Vadas in an examination of 39 rhodophytes. Lithothamnion has a very high ash content of 83%. It is thus not surprising that P. cochlear has a growth rate lower than any of the other species.

Ralfsia sp. had higher calorific values (3.12 kcal/gm. dry weight and 4.16 kcal/gm ash-free dry weight), but the latter value was still the lowest recorded for 25 species of Phaeophyta (Paine and Vadas, 1969). In relation to this, the growth of P. longicosta is also slow.

Paine and Vadas have suggested that low nutritive value and high ash content may be an adaptation in these two algae, compensating for their low encrusting habit which makes them readily available to rasping herbivores.

Paine and Vadas quote the work of Fuji (1962), Leighton and Boolootian (1963) and Leighton (1966) on food preferences in 13 herbivorous invertebrates. Of the algae examined, the nine preferred by these animals had ash-free dry weight calorific values of between 4.32 and 4.67. The values of Lithothamnion and Ralfsia fall well below this range.

The food value of algae eaten by generalised browsers is difficult to assess. P. granularis feeds largely on a black encrusting lichen and organic detritus: few algae are present in the upper balanoid. The nutritive value is probably usually low but variable, depending on the content of the detritus. The growth of this limpet is intermediate in rate, and variable within each locality: this may be related to fluctuations in the availability of organic detritus.

P. oculus and P. granatina occupy the lower balanoid where they are diverse and profuse. As would be anticipated, growth of these animals is very rapid.

Distribution: Stephenson (1939) has described the effect of distribution on size, and shown that P. granularis in particular decreases in size as the mean sea temperature increases. This is also true of P. barbara, P. tabularis and P. longicosta, and to a lesser extent P. argenvillei. This conforms with Bergman's rule that smaller sized individuals of a species are associated with the warmer parts of its distributional range.

Growth of P. granularis was much faster at Elands Bay than at Kommetjie. Although similar growth rates were recorded at Kommetjie and Kalk Bay, growth is probably generally less at the latter locality. As will be described below (Section VI), barnacles in False Bay inhibit limpet growth and depress it below that of the barnacle-free site considered here.

The growth rate of P. granatina is similar at Elands Bay and Kommetjie, although larger specimens recorded at Elands Bay suggest a faster growth may occur there.

In these two species growth in colder waters appears faster than in warm waters. This may not be a simple relationship however. Relative densities, competition from barnacles and deposition of upwelled nutrients by West Coast storms may all modify growth.

The growth of P. cochlear is modified more by local conditions than by differences between the coasts. At both Kommetjie and Kalk Bay two sites were analysed. As described above (p. 6) there was more difference between sites than between localities. This may be due to a number of variables, such as growth of food plants, density of limpets, wave action, temperature, or any combination of these factors. Of these, only density could be determined on an absolute basis. Relative wave action was estimated (and ranked) at the four sites, and the mean annual temperature taken from figures for Sea Point and Kalk Bay. The data is summarised in table 2.

TABLE 2. Growth of P. cochlear relative to physical variables.

Site	Growth (ranked)	Density /m^2	Wave action (ranked)	Mean sea temp. °c
Kommetjie I	2	250	2	13.8
Kommetjie II	4	420	4	13.8
Kalk Bay I	1	660	1	16.2
Kalk Bay II	3	800	3	16.2

While all these factors act in concert and cannot be separated, two points emerge. Firstly, there is a correlation between growth rate and wave action. P. cochlear are always found in areas of moderate to strong wave action and disappear in sheltered areas (Branch, 1971). Wave action may also effect growth, but due to the interaction of factors and the small number of sites, this must remain a possibility only. Secondly, growth at Kalk Bay was higher on average than at Kommetjie, despite the higher densities of the populations. Evidence will be presented below (Section V) that growth is markedly reduced by high density. This paradox may be explained by the higher temperatures at Kalk Bay.

In most populations the densities of P. cochlear are so high that they will obscure the effect of other variables. This is probably why P. cochlear is the only species showing no change of mean size in relation to sea temperatures.

Dehnel (1956), working on Mytilus californianus, has shown that submergence increases growth rate. This is logical in a filter-feeder which can only feed when submerged. He also showed that samples in Alaska grew more slowly than samples at an equivalent level in Southern California. Although temperature is probably the main factor influencing the different growth rates, the degree of submergence must have exerted some effect.

Moore (1934) showed that Balanus balanoides in colder water grows more rapidly than specimens in warmer waters, and Barnes (1959) has demonstrated that the availability of food may override the importance of temperature in relation to growth rate.

Newman (1969) concluded that Haliotis midae grows faster in the warmer waters off Port Elizabeth (mean annual temperature 17.4°c) than at Stony Point (15.8°c) and he deduced that growth is probably even slower on the cold West Coast (where maximum size is recorded).

This is certainly not the case in P. granularis where growth rate (and size) are maximal on the West Coast. P. granatina grows slightly faster at Elands Bay than Kommetjie. In P. cochlear distributional effects are obscured by high density. Clearly there is no simple relationship between mean temperature and growth rate, and availability of food may override any temperature effect.

Longevity: Fischer-Piette (1948) recorded that in P. vulgata, growth rate is inversely related to longevity. Working on the same animal, Ballantine (1965, unpublished) verified this and extended the principle to show that rapid growth is also associated with high mean body weight, and high gonad output. Frank (1965) found a similar effect in Acmaea digitalis, although the relationship does not hold for A. scabra (Sutherland, 1970).

The present work shows that this principle may also be true on an intrageneric level. Table 3 shows that those Patella spp. with a rapid growth rate also have relatively short lives. The inverse relationship between longevity and gonadial output has already been discussed (Section III).

TABLE 3. Relationship between growth, longevity and gonad output in Patella.

Species	Shell growth rate (ranked)	Approximate longevity yrs.	Mean Ovarian output gm.
P. oculus	1	2-3	1,900
P. granatina	2	5-6	9,200
P. granularis	3	6-8	0,600 - 2,100
P. longicosta	4	12-17	0,700
P. cochlear	5	15-25	0,400

The "rate of living" concept has been suggested for this relationship: high metabolic rate and nutrient requirements are associated with early mortality. The metabolic rates of local Patella spp. are not yet known, but high growth rates are probably related to a high metabolism. Furthermore, almost all the males have a higher gonadial output (which must entail metabolic expenditure) and in many, their longevity is lower (see Section III).

2. Life Tables:

Deevey (1947) has described the methods of construction and advantages of life tables; and the three types of data from which they can be constructed. Briefly these are as follows: (1) Known age at death, (2) Survival of a known cohort throughout its existence, (3) Estimation of mortality from the relative sizes of successive age classes.

In the case of Patella only the third source of data is available, because age must be assessed from growth rates and distinct age groups. This source of data is the least satisfactory, because it necessitates the assumption that the population is stable in time (or at least from year to

Fig. 12

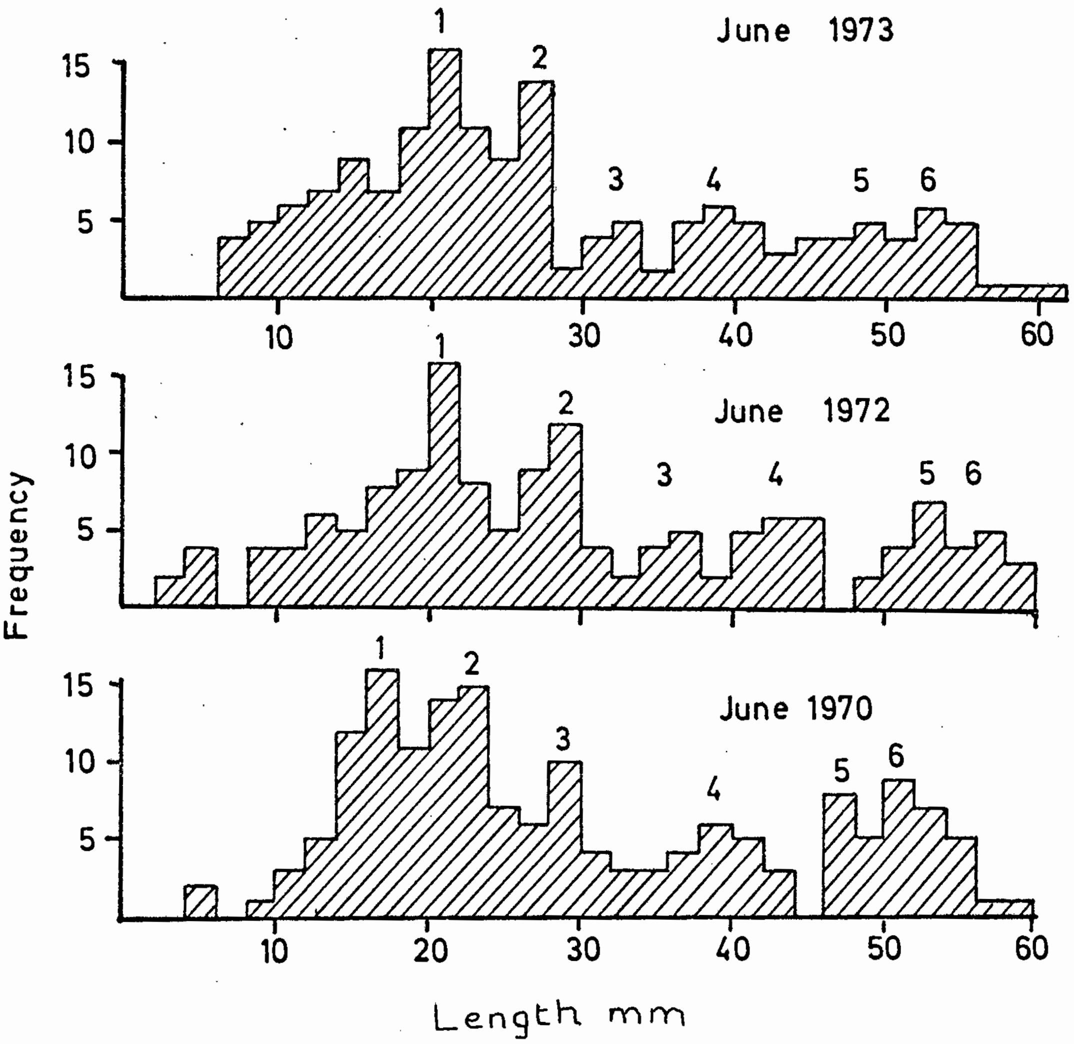


FIG. I2 POPULATION STABILITY IN P.COCHLEAR: Size frequency analysis at the same site, over a three year period. Numbers indicate recognisable peaks which recur.

year). One population of P. cochlear was assessed for four years and found to be very stable (fig. 12), although the position of peaks shifted slightly from year to year. In the remaining species stability has been assumed.

First year groups were often difficult to assess accurately and inaccuracies are most likely to have occurred at this level. With the limitations of the data source, the life tables must be accepted with caution. Nevertheless they are certainly valid for the intrageneric comparison for which they are intended.

Life tables for P. cochlear (Kalk Bay), P. granatina (Kommetjie), P. granularis (Kommetjie) and P. longicosta (Dalebrook) are presented in tables 4 to 7. The population structure and growth rates on which each is based are given in figures 13 to 16.

From the life tables, survivorship curves can be constructed. Three types of survivorship curves can be recognised: (1) Negatively skew rectangular, in which mortality is low until late in life, when most individuals die at a similar age; (2) Diagonal, where mortality rates are relatively constant in all age groups; (3) Positively skew rectangular, where mortality is very high in early life, but low in older age groups. (Deevey, 1947; Kormondy, 1969).

All of the species considered here can be included in the Diagonal category (although if larval mortality could be included, this would modify the survivorship curves considerably). P. granularis and P. granatina are particularly typical of diagonal survivorship, although the former deviates slightly because mortality rates decrease with age,

FIG. 13. Population structure and growth rates of *P.cochlear*. (Arrows indicate year-groups).

Fig. 13 P.cochlear

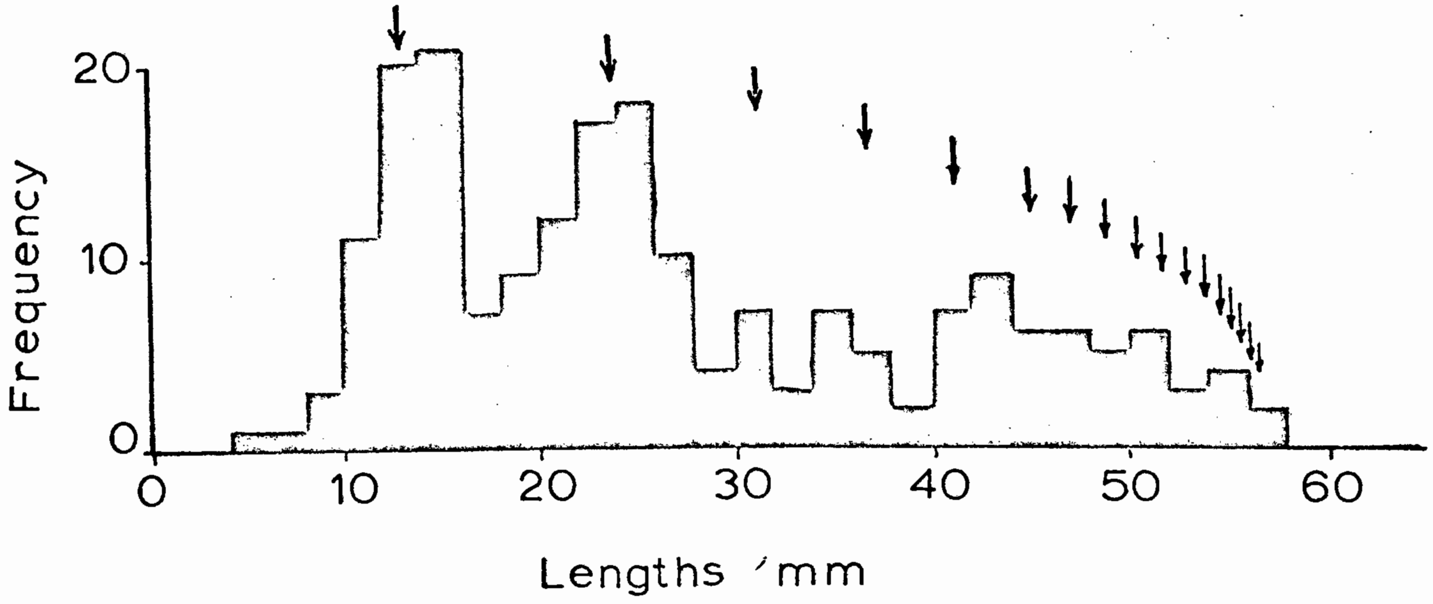


Fig. 14 P. granatina: Population Structure and Growth Rates (arrows)

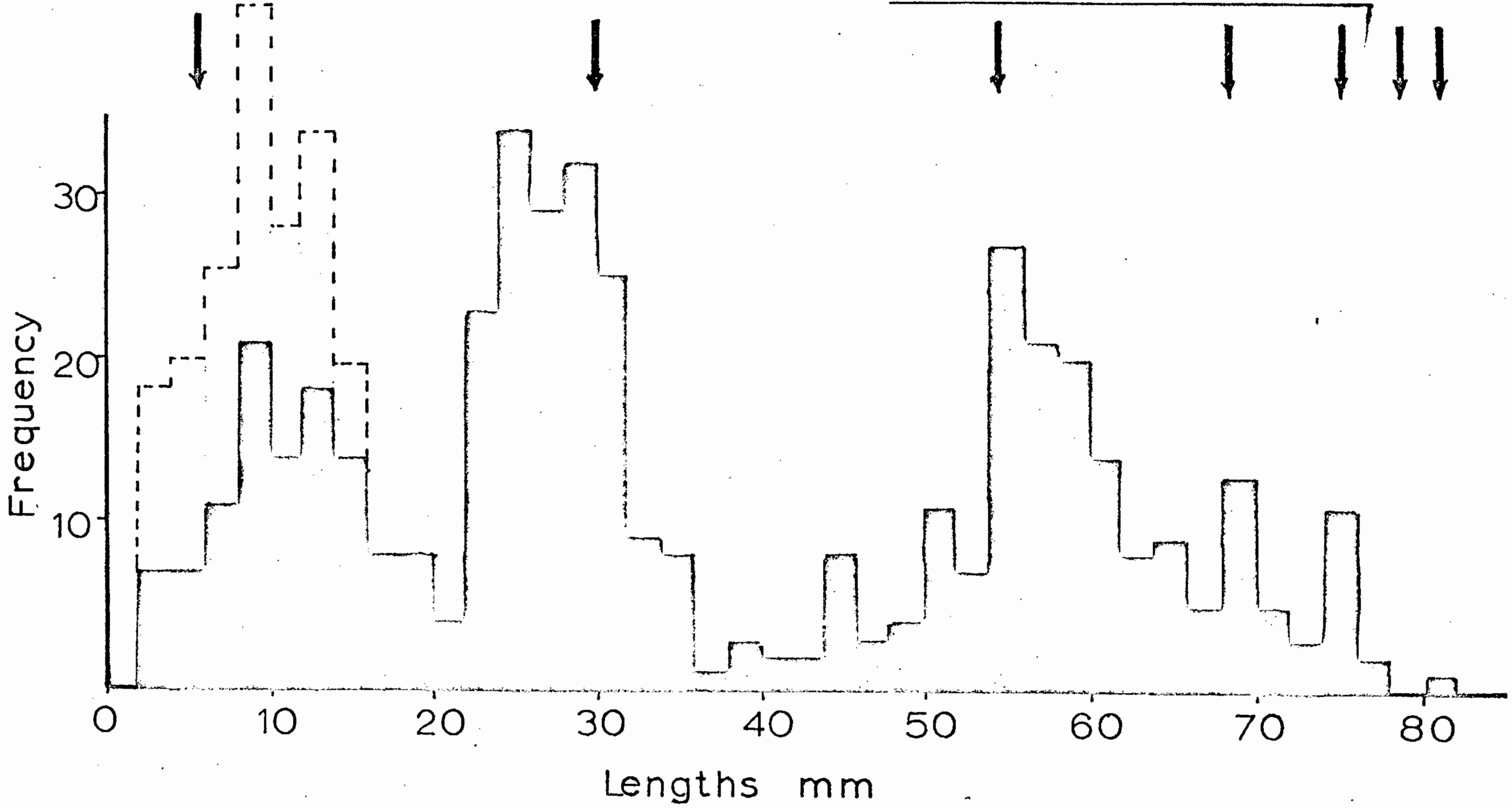


Fig.15 P. granularis : Population Structure and Growth rates (arrows)

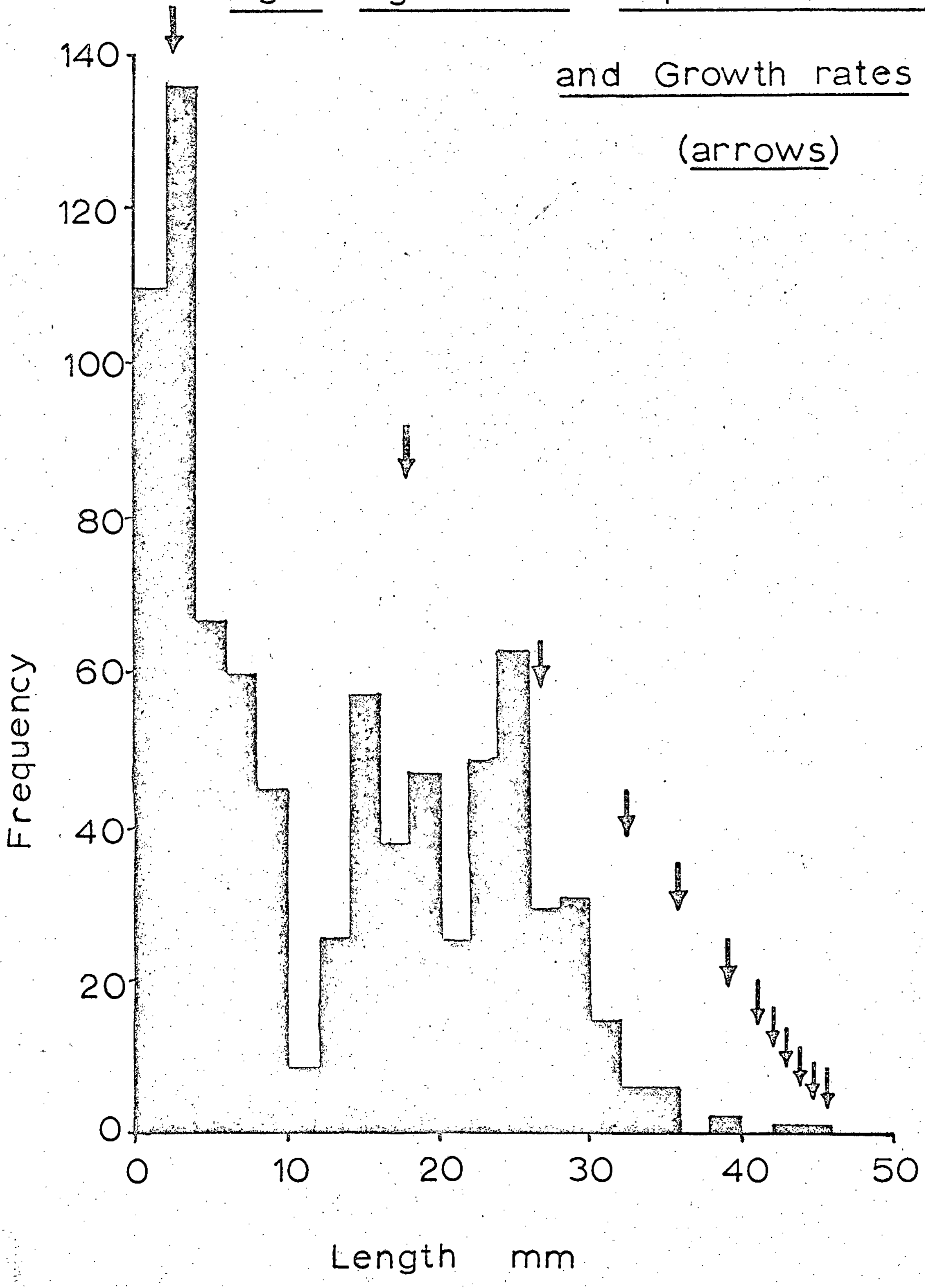
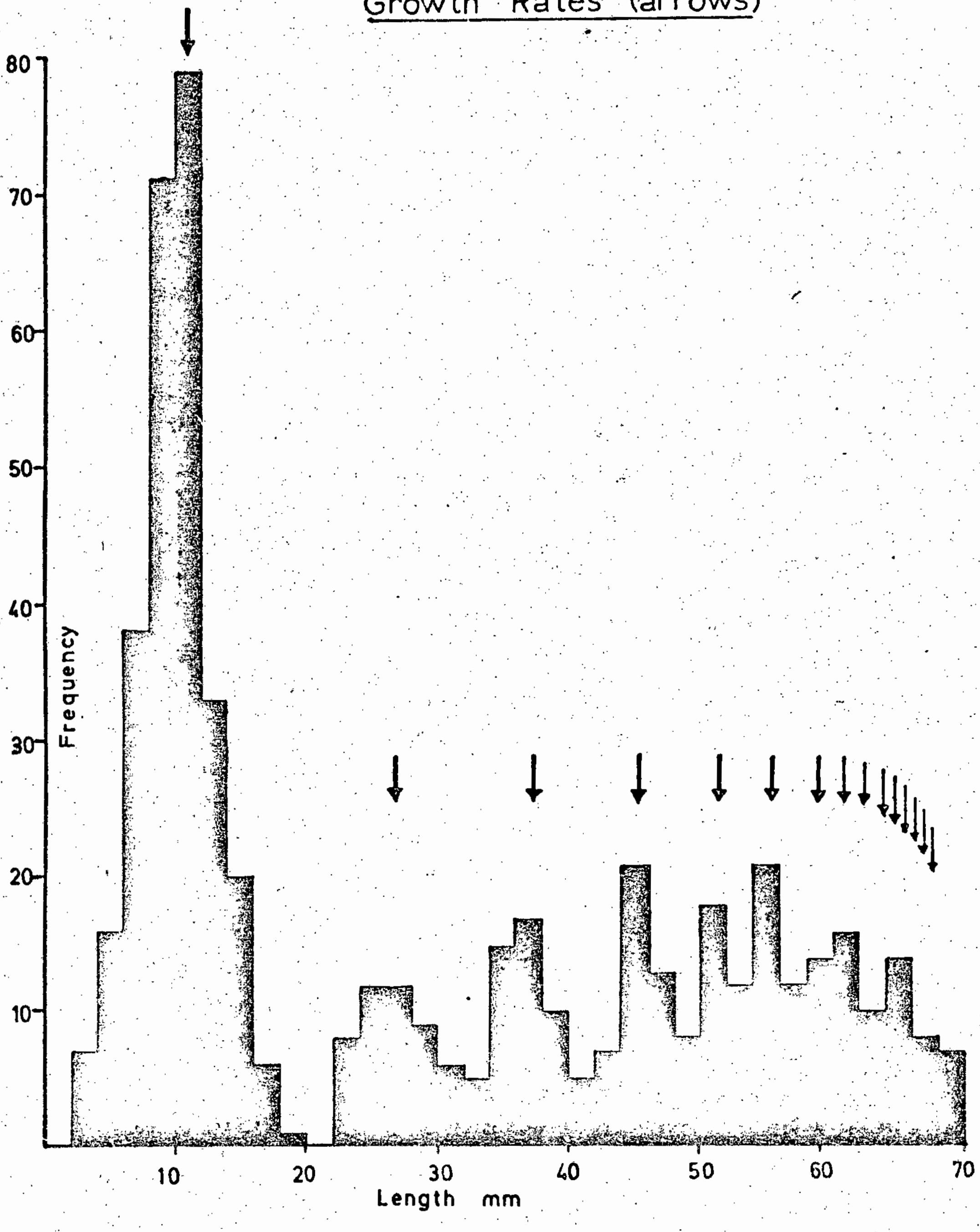


Fig. 16 P. longicosta: Population Structure and Growth Rates (arrows)



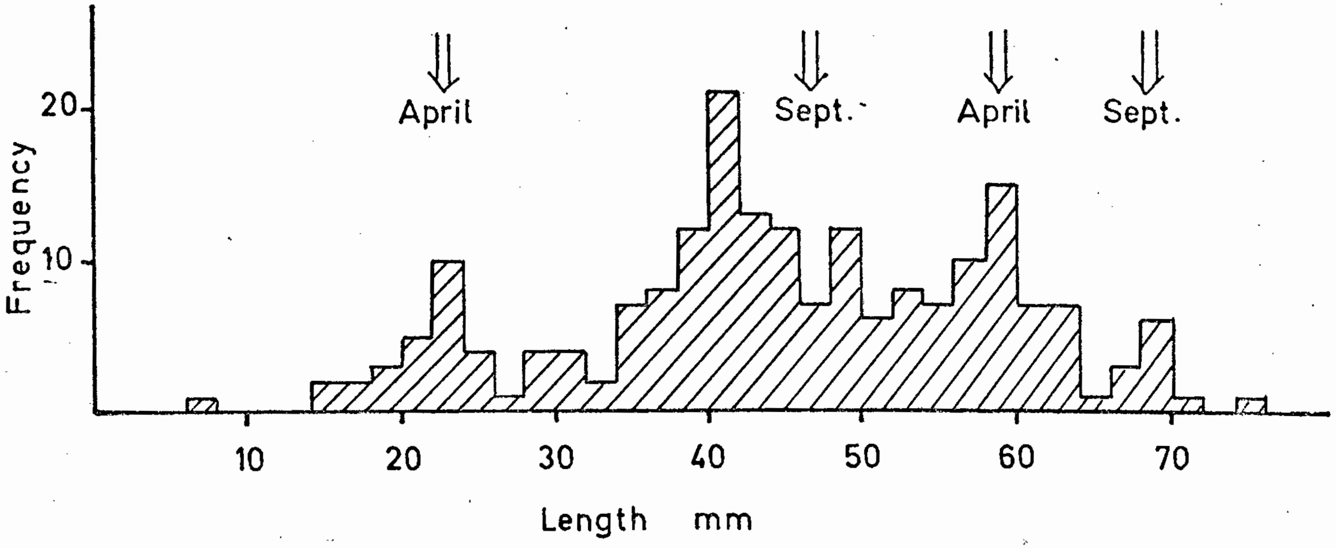
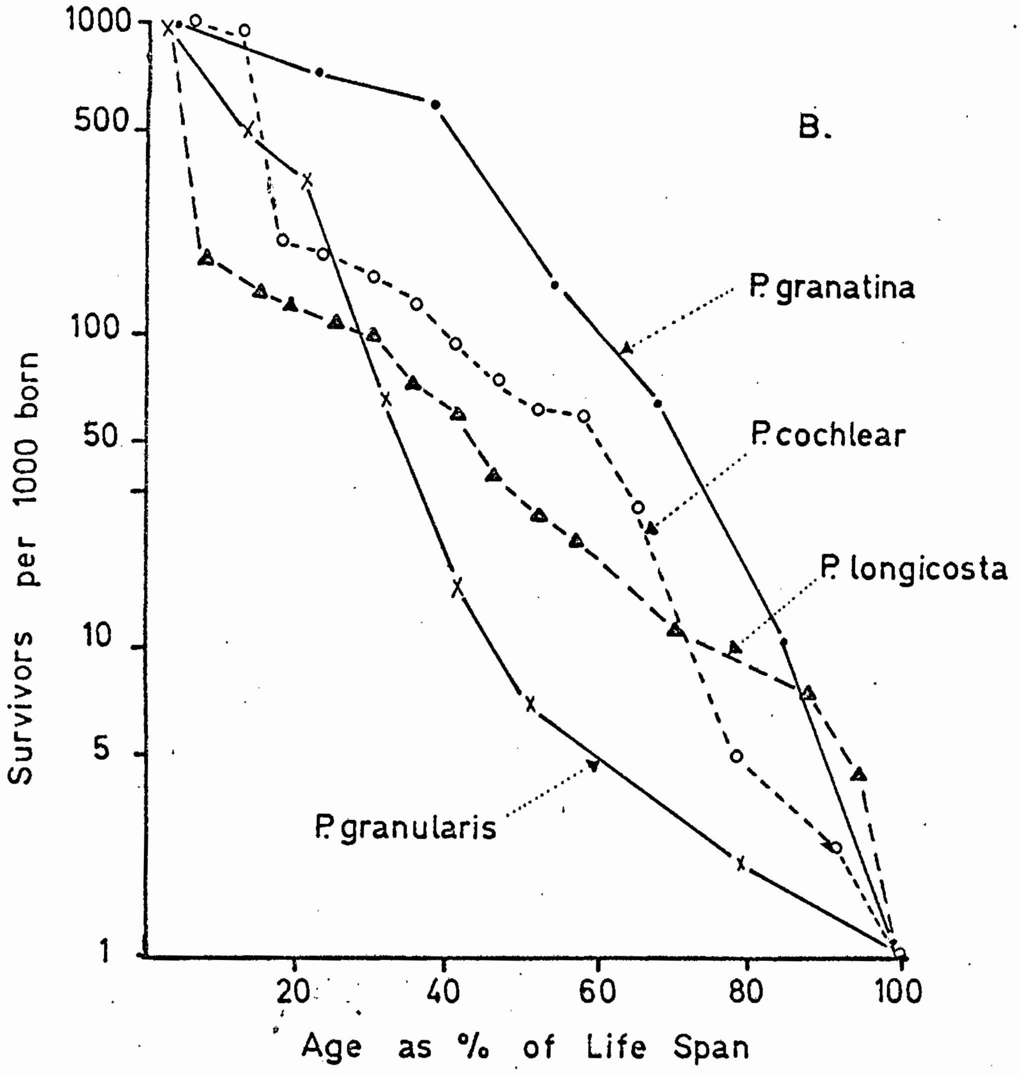


FIG. I7. SIZE FREQUENCY DISTRIBUTION OF P.OCULUS.
(Arrows indicate year groups).

Fig. 18 Survivorship Curves for Patella spp.



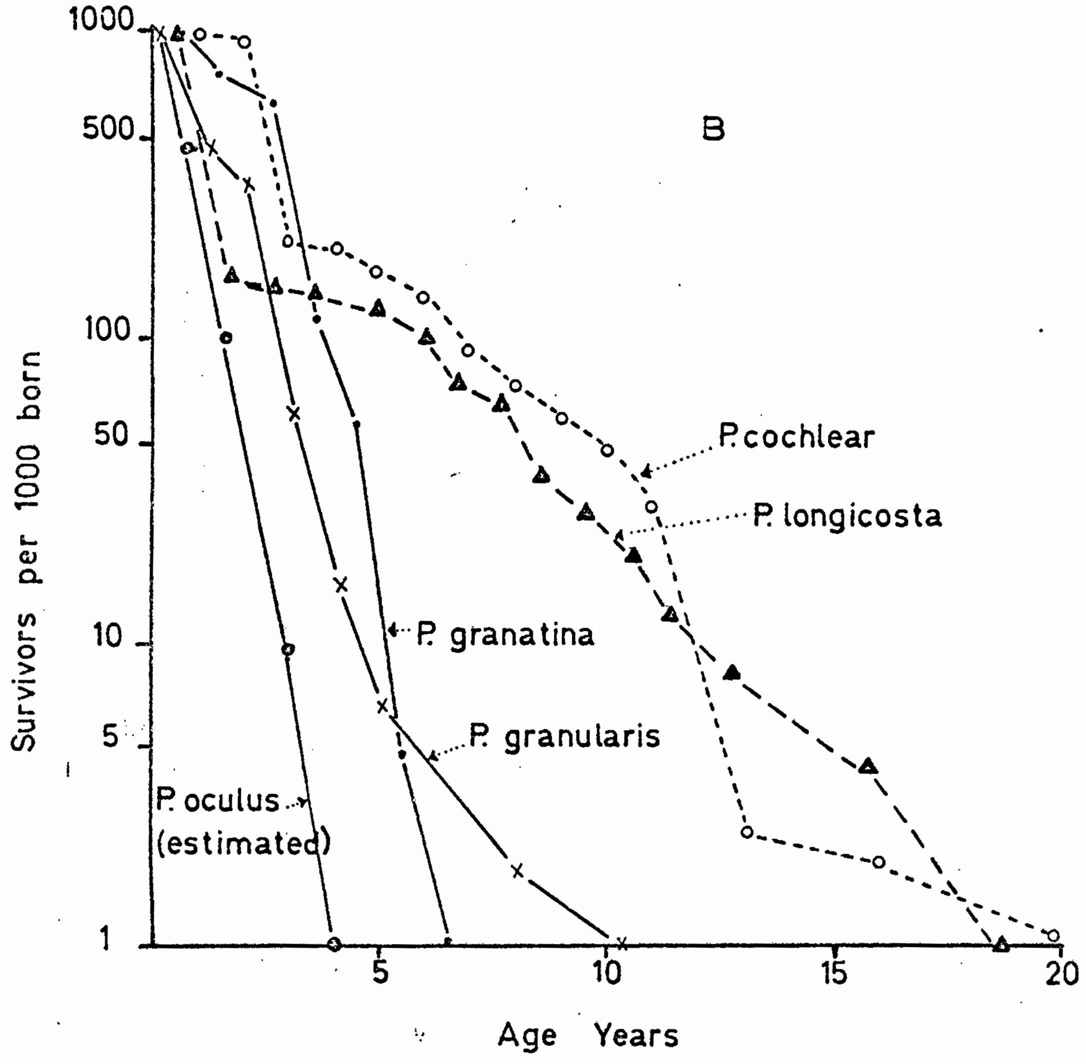


TABLE 4. Life Table of *P. cochlear* (based on a sample of 209).

x	x^1	dx	lx	1000 qx
Age yrs.	Age as % of Max.	No.dying in each age interval out of 1000	No.surviving at start of age interval per 1000 born.	Mortality rate per 1000 alive at start of each age interval.
0.7 - 1.7	5.8	30	1000	30
1.7 - 2.7	11.7	727	970	749
2.7 - 3.7	17.6	30	243	123
3.7 - 4.7	23.5	30	213	140
4.7 - 5.7	29.4	30	183	163
5.7 - 6.7	35.3	45	153	294
6.7 - 7.7	41.9	15	108	138
7.7 - 8.7	47.1	15	93	160
8.7 - 9.7	53.0	15	78	192
9.7 - 10.7	58.9	30	63	476
10.7 - 11.7	65.8	10	33	303
11.7 - 14.7	76.6	10	23	434
14.7 - 18.7	94.3	6	17	352
18.7	100.0	7	11	636

TABLE 5. Life Table of *P. granatina* (based on a sample of 550).

x	x^1	dx	lx	1000 qx
0.5 - 1.5	3.9	209	1000	209
1.5 - 2.5	23.1	165	791	208
2.5 - 3.5	38.4	439	626	701
3.5 - 4.5	53.8	117	187	625
4.5 - 5.5	69.2	58	70	803
5.5 - 6.5	84.6	5	12	416
6.5	100.0	7	7	1000

TABLE 6. Life Table of _P. granularis_ (based on a sample of 818).

x	x^1	dx	lx	1000 qx
0.2 - 1.2	1.9	540	1000	540
1.2 - 2.2	11.7	47	460	102
2.2 - 3.2	21.5	351	413	849
3.2 - 4.2	31.2	45	62	725
4.2 - 5.2	40.9	7	17	411
5.2 - 6.2	50.8	2	7	285
6.2 - 10.2	79.9	2	5	400
10.2	97.0	3	3	1000

TABLE 7. Life Table of _P. longicosta_ (based on a sample of 554).

x	x^1	dx	lx	1000 qx
0.5 - 1.5	2.7	808	1000	808
1.5 - 2.5	8.1	18	192	94
2.5 - 3.5	15.8	3	174	17
3.5 - 4.5	18.9	48	171	280
4.5 - 5.5	25.6	18	123	148
5.5 - 6.5	29.7	29	105	276
6.5 - 7.5	35.1	15	76	197
7.5 - 8.5	41.5	22	61	360
8.5 - 9.5	45.9	7	39	179
9.5 - 10.5	52.6	4	32	125
10.5 - 11.5	56.7	15	28	535
11.5 - 14.5	70.0	?3	13	230
14.5 - 18.5	89.0	?3	10	300
18.5	97.0	?7	7	1000

while in *P. granatina* they increase by a constant amount (figs. 18a, b). Such deviations are well within the group of curves considered to be diagonal.

Life tables could not be calculated for *P. oculus*, although an estimated survivorship curve has been included in figure 18b. With a life span of about two years, estimation of mortality from age groups is difficult. In addition, each year group is confused by the probable bi-annual pattern of settling. Juveniles are cryptically coloured and difficult to find, and low density and high migration rate preclude a mark-and-recapture technique to assess the juvenile population. Survival of *P. oculus* appears to be of the diagonal type, but with a higher juvenile mortality and almost total mortality after two years. Figure 17 shows the population structure of *P. oculus*. In the light of the very rapid growth recorded, the size frequency peaks of the population can only be interpretted as the result of biannual spawning and settling.

In the case of *P. cochlear* (figs. 18a, b) the survival pattern is also basically diagonal. However, the otherwise smooth curve is interrupted by a massive mortality after the second year of growth. This corresponds to the period when small specimens shift from the shells of other *P. cochlear* to establish scars on the rock surface (Branch, 1971). Obviously the animals are vulnerable during the transition, until they have formed new scars, and heavy mortality occurs. The importance of the scar as a defence against predators will be described below (Section VIII).

P. longicosta undergoes a comparable change of habitat during the life cycle, as has been summarised above (p. 9).

Transition from a substrate of other shells to lithothamnion occurs after one year's growth and is accompanied by heavy mortality. About 70% of the first year population is found on Oxystele sinensis shells and their shells are curved to fit those of their host. The shift to a flat rocky substrate must leave the animals very susceptible to predation and desiccation until their shells grow to fit the new substrate. After this period, a permanent scar is established and mortality becomes relatively constant and low (figs. 18a, b).

SUMMARY:

1. An analysis was undertaken of the growth rates of Patella cochlear, P. granatina, P. granularis, P. longicosta and P. oculus at Kommetjie and Kalk Bay (or Dalebrook) in the Cape Peninsula.

2. Shell growth is rapid in the first year and then decreases. A negative linear relationship exists between initial length and increment per year. Increases of shell length eventually cease and this may be important in determining longevity. Shell thickness increases throughout life.
   Body growth is sigmoidal, maximum absolute growth occurring after about a quarter of the life span is complete.

3. P. oculus and P. granatina grow very rapidly, P. granularis at an intermediate rate, and P. cochlear and P. longicosta very slowly. These relative rates are probably related to the nutritive value of the different food sources.

4. P. granularis grows faster on the cold West Coast than

in warmer waters. This may be due to the relative availability and nutrient value of organic depositions.

5. In P. cochlear high densities probably override the effects of other environmental factors, but temperature and wave action were positively correlated with growth.

6. Only P. longicosta shows significant seasonal patterns in growth. Smaller animals grow slowest in March to November, coincident with gonad maturation and low temperatures. Larger animals decrease growth from November to March, but there is no logical explanation for this. In the other species gonad maturation and low temperatures alternate (Kalk Bay), or sea temperatures are relatively constant (Kommetjie), and this may explain the lack of seasonal patterns in growth.

7. Longevity is inversely related to growth rate on both an interspecific and an intraspecific basis.

8. Life tables and survivorship curves were constructed for P. cochlear, P. granatina, P. granularis and P. longicosta. All have a basically "diagonal" survivorship, although in P. cochlear and P. longicosta this is modified by massive mortality at a specific point in the life cycle. This is related to a transition between habitats.
   The population structure of P. oculus does not lend itself to the construction of life tables, and is strongly suggestive of a biannual settling.

REFERENCES:

BALLANTINE, W.J. 1965. The population dynamics of Patella vulgata. Ph.D. Thesis, Queen Mary College, London University.

BARNES, H. and BARNES M. 1959. A comparison of the annual growth patterns of Balanus balanoides (L.) with particular reference to the effect of food and temperature. Oikos 10 : 1-18.

BLACKMORE, D.T. 1969a. Studies of Patella vulgata L. I Growth, reproduction and zonal distribution. J. exp. mar. Biol. Ecol. 3 : 200-213.

——————— 1969b. Ibid II. Seasonal variation in biochemical composition. Ibid 3 : 231-245.

BRANCH, G.M. 1971. The ecology of Patella Linnaeus from the Cape Peninsula, South Africa. I. Zonation, movements and feeding. Zool. Afr. 6 : 1-38.

COHEN, C. 1948. The breeding seasons of Patella. M.Sc. Thesis, University of Cape Town. Unpublished.

DAVIES, S.D. 1966. Physiological ecology of Patella. I. The effect of body size and temperature on metabolic rate. J. mar. biol. Ass. U.K. 46 : 647-658.

DEEVEY, E.S. 1947. Life tables for natural populations of animals. Quart. Rev. Biol. 22 : 283-314.

DEHNEL, P.A. 1956. Growth rates in latitudinally and vertically separated populations of Mytilus californianus. Biol. Bull. 110 : 43-53.

FISCHER-PIETTE, E. 1941. Croissance taille maxima et longevite possible de quelque animaux intercotidal en fonction de milieu. Annls. Inst. Oceanogr. Monaco. 21 : 1-28.

——————— . 1948. Sur les elements de prosperite de Patelles et sur leur specificite. J. Conchyl. 88 : 45-96.

FRANK, P.W. 1965. The biodemography of an intertidal snail population. Ecol. 46 : 831-844.

FUJI, A. 1962. Studies on the biology of the sea urchin. V. Food consumption of Strongylocentrotus intermedius. Jap. J. Ecol. 12 : 181-186.

HAMAI, I. 1937. Some notes on relative growth, with special reference to the growth of limpets. Sci. Repts. Tohoku Univ. 12 : 71-95.

HATTON, H. 1936. Observations sur l'habitat et sur la croissance de P. vulgata. Bull. Lab. marit. Dinard. 15 : 17-20.

KAWAI, D.K. 1955. Carbonic anhydrase in pearl oyster. II. Changes of the enzyme activity in relation to growth and seasons. Publs. Seto. Marine Biol. Lab. (Kyoto Univ.) 5 : 89-94.

KORMONDY, E.J. 1969. Concepts of Ecology. Prentice Hall.

LEIGHTON, D.L. 1966. Studies on food preference in algivorous invertebrates of Southern California kelp beds. Pacif. Sci. 20 : 104-113.

―――――― and BOOLOTIAN, R.A. 1963. Diet and growth in the black abolone, Haliotis cracherodii. Ecology 44 : 227-238.

MOORE, H.B. 1934a. The relation of shell growth to environment in Patella vulgata. Proc. malacol. Soc. London. 21 : 217-222.

―――――― 1934b. The biology of Balanus balanoides I. Growth rate and its relation to size, season and tidal level. J. mar. biol. Ass. U.K. 19 : 851-868.

NEWELL, R.C. 1970. Biology of intertidal animals. Logos Press.

NEWMAN, G.G. 1968. Growth of the South African Abalone Haliotis midae. Investl. Rep. Div. Sea Fish. S. Afr. 67 : 1-24.

———————— 1969. Distribution of the Abalone (Haliotis midae) and the effect of temperature on productivity. Ibid. 74 : 1-7.

ORTON, J.H. 1928. Observations on Patella vulgata. Part II. Rate of growth of shell. J. mar. biol. Ass. U.K. 15 : 863-874.

———————— 1933. Studies on the relation between organism and environment. Proc. Liverpool Biol. Soc. 46 : 1-16.

PAINE, R.T. and VADAS, R.L. 1969. Calorific values of benthic marine algae and their postulated relation to invertebrate food preference. Mar. Biol. 4 : 79-86.

RUSSELL, E.S. 1909. The growth of the shell of Patella vulgata. Proc. Zool. Soc. Lond. 79 : 235-252.

SHACKLETON, N.J. 1973. Oxygen isotope analysis as a means of determining season of occupation of prehistoric midden sites. Archaeometry 15 : 133-141.

SIMPSON, G.G., ROE, A. and LEWONTIN, R.C. 1960. Quantitative Zoology. Harcourt, Brace & World, Inc. N.Y.

STEPHENSON, T.A. 1939. The constitution of the intertidal fauna and flora of South Africa. Pt. I. J. Linn. Soc. (Zool.) 40 : 487-536.

SUTHERLAND, J.P. 1970. Dynamics of high and low populations of the limpet Acmaea scabra (Gould). Ecol. Monogr. 40 : 169-188.

WILBUR, K.M. and OWEN, G. 1964. Growth. In Physiology of Mollusca. Eds. Wilbur, K.M. and Yonge, C.M. N.Y. Academic Press.

APPENDIX I.

Regression of initial length $^{(x)}$ against increment per year $^{(y)}$ and relevant tests of differences in slopes and intercepts.

Species	Locality	Regression	Signif.of Diffs. Slopes	Intercepts.
P. cochlear	Kalk Bay I	$y=-0.18x+11.30$	$>.05$	$<.001$
	Kalk Bay II	$y=-0.13x+6.42$	$>.05$	$<.001$
	Kommetjie I	$y=-0.20x+9.60$	$<.05$	$<.001$
	Kommetjie II	$y=-0.11x+5.20$		
P. granatina	Kommetjie	$y=-0.40x+37.50$		
P. granularis	Kalk Bay	$y=-0.49x+18.58$	$>.05$	$>.05$
	Kommetjie	$y=-0.44x+17.05$	$>.05$	$<.001$
	Elands Bay	$y=-0.54x+28.06$		
P. longicosta	Dalebrook	$y=-0.26x+17.62$		
P. oculus	Kalk Bay	$y=-0.44x+34.86$		

APPENDIX II.

Exponential relationship between flesh weight $^{(w)}$ and shell length $^{(L)}$. $w=cl^b$

Species	Equation
P. cochlear	$w = 0.0001537\ L^{2.51}$
P. granatina	$w = 0.00001301\ L^{3.30}$
P. granularis (Kalk Bay)	$w = 0.00002620\ L^{3.17}$
P. granularis (Kommetjie)	$w = 0.00001100\ L^{3.42}$
P. longicosta	$w = 0.00002602\ L^{2.83}$
P. oculus	$w = 0.00000902\ L^{3.19}$

SECTION V:

INTRASPECIFIC COMPETITION IN <u>PATELLA</u> <u>COCHLEAR</u>.

V. INTRASPECIFIC COMPETITION IN PATELLA COCHLEAR

Competition is the requirement by two or more individuals of a common resource, which is (or may become) limiting to these individuals. The limitations which may result can effect a variety of functions such as growth, size or mortality, but the most important limit is that placed on reproductive potential.

Closely related species usually have the greatest overlap in the resources they require, and are more likely to compete if they are coexistent. This reaches its highest intensity in intraspecific relationships, where the requirements of the individuals may be identical. In limpets, food and space are the major resources competed for. Obviously the intensity of competition will be density dependent.

The present work is concerned with the quantitative effects of competition on P. cochlear populations. Of all the South African limpets, P. cochlear is the most obvious subject for such an analysis, because the populations vary in density from 90 to 1700 per square metre: no other limpets experience densities of this order. Furthermore, populations of P. cochlear are stable in time, thus enabling estimations of mortality from the composition of the age groups. This stability also increases the accuracy of predictions made from the results. A comparable analysis was also completed on P. granularis, but will be considered in a separate paper in relation to competition with barnacle populations.

MATERIALS AND METHODS:

Most of the analysis was completed at Dalebrook and Kalk Bay in the Cape Peninsula. Zonation and densities were assessed by line transects and random quadrats. Wave action was measured using a turbulometer (Field, 1968a).

Growth rates were obtained by measurement of labelled animals, and the details of this technique have previously been described (Section IV). Reproductive output was determined for subsamples of random populations by calculating gonad indices (between somatic and gonad weights) just prior to and just after spawning. (See Section III for details of the method.) From the results, the output of eggs per square metre could be related to density.

Deductions about mortality are based on the composition of age groups in populations of known growth rate. The technique has previously been described (Section IV) and is based on that of Deevey (1947).

COMPETITION:

Densities of P. cochlear may vary considerably, but numbers up to 1700 per m^2 have been recorded. The numbers are closely related to wave action, highest densities being found in regions of fairly strong wave action. Ebling et al (1947) have shown that Patina pellucida also occurs where water movement is fairly strong, and Atapattu (1972) remarks that in Ceylon Cellana occurs only on wave washed shores. P. argenvillei also occurs predominantly where wave action is fairly strong.

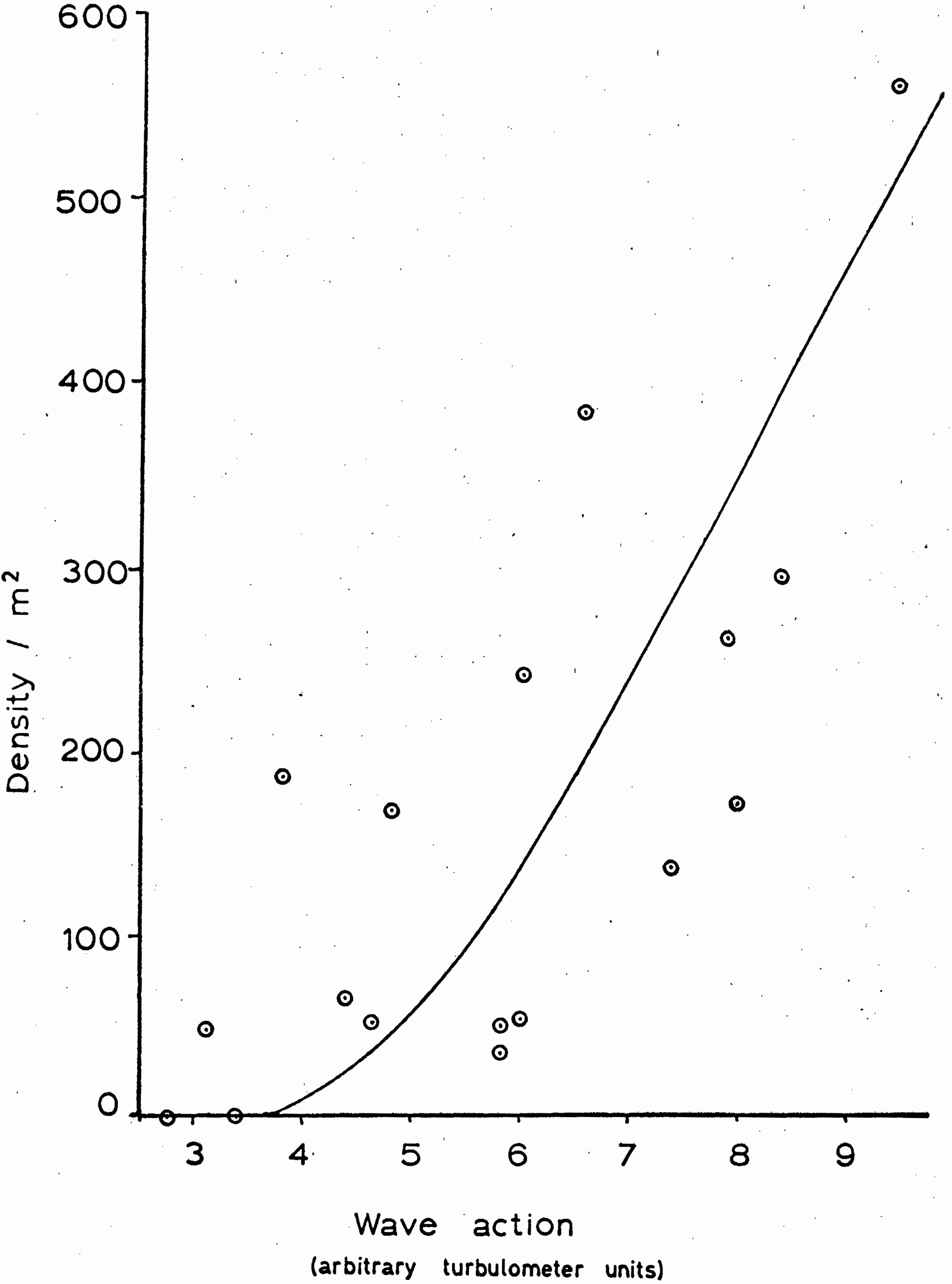


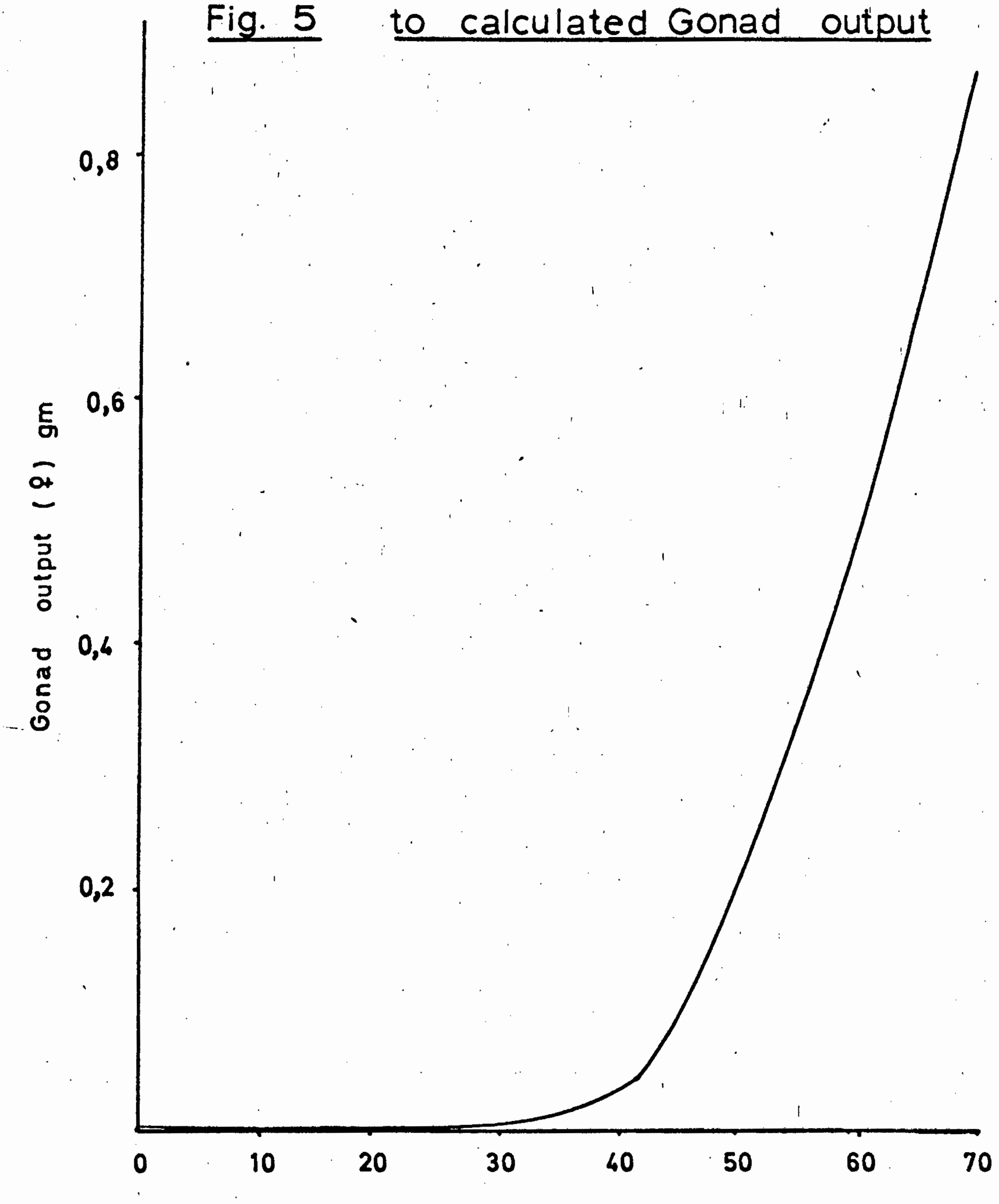
Fig. 1 P. cochlear

As wave action decreases, so do the densities of P. cochlear, and in sheltered waters it is totally lacking. Here, the lower shore may become covered by an algal turf which is normally excluded by limpet browsing. The converse may also be true: that dense algal growth in sheltered areas excludes the limpets. The competition between different algal species under different conditions of wave action may also be important in limiting P. cochlear. The main foodplant of P. cochlear, lithothamnion, is overgrown in sheltered areas and disappears as a result. Experiments will be described below which suggest the limpets are responsible for maintaining the lithothamnion and preventing its overgrowth. In the absence of P. cochlear, P. longicosta may penetrate into these sheltered areas. Under extreme wave action, P. cochlear is replaced by mussel beds, particularly those of Aulacomya ater or by Octomeris angulosus.

As Ballantine (1961) has pointed out, the prevailing wave action of a shore is often most easily and accurately defined in terms of the biological components present, and in this respect P. cochlear is a particularly good indicator species.

Wave action is difficult to quantify, but Field (1968b) has shown a convincing numerical correlation between wave action and numbers of P. cochlear. In the present work a turbulometer (Field, 1968a) was used to measure wave action on a short term basis, and its relationship to P. cochlear densities is shown in figure 1. Although the data are scattered, a significant linear relationship exists over the central range of wave action. Extreme wave action could not be measured.

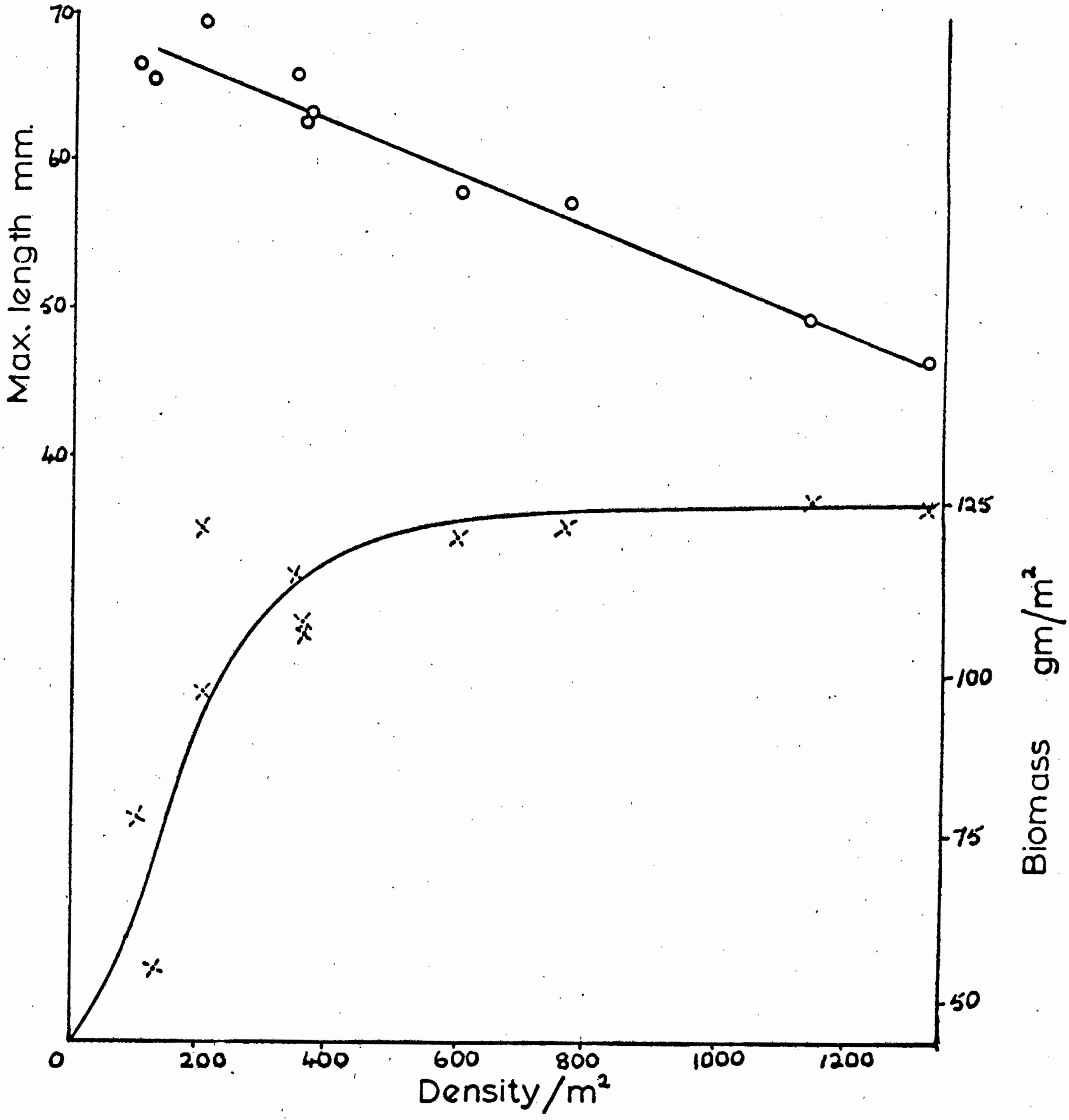
Fig. 5 P.cochlear: Shell length relative to calculated Gonad output



The intensity of intraspecific competition must obviously be related to density. In P. cochlear an unusual condition exists in that increasing numbers of juveniles are found on the shells of adults, as the density rises. Frequently smaller juveniles live on the larger juveniles in a multitiered arrangement. As lithothamnion covers the shells, these provide both substrate and food for the juveniles. However, the juveniles do not restrict their feeding to the shell surface, and crawl down onto the rocky substrate to feed. The result is that competition is almost "two-layered": juveniles compete on the shells, while all size groups compete on the rocky substrate. As the size groups all compete to some extent, it is not practical to separate their interactions. Furthermore, the space occupied by each animal will be devoid of food, so that food available on the shell will merely compensate for that which is lost because of the physical presence of the animal. Thus the amount of food remains constant, but will be shared by increasing numbers of limpets as the density increases. Consequently competition for food has been considered from the standpoint of its effect on all limpets present in a given sample. Clearly a multi-tiered arrangement eliminates competition for space, but it can only reduce the intensity of competition for food, and not eliminate it. Its effect can be measured in terms of mean and maximum size, growth rate, standing crop, mortality rates and gonad output.

As density increases, the mean size of P. cochlear decreases. A plot of length on an accumulative percentage basis shows this clearly (fig. 2). It also shows the preponderance of smaller animals in high density populations.

Fig. 3 Maximum Length (o) and Biomass (x) Relative to Density



Those with moderate densities have approximately equal numbers of juveniles and adults, while low density groups contain a majority of larger, older animals. In general terms this means that mortality of juveniles is greatest in the high density populations. The maximum size (taken as a mean of the five largest animals) is also negatively correlated with density (fig. 3a), and the regression of the relationship is:

$$y = -0{,}017x + 70{,}1$$

(where y = maximum size and x = density).

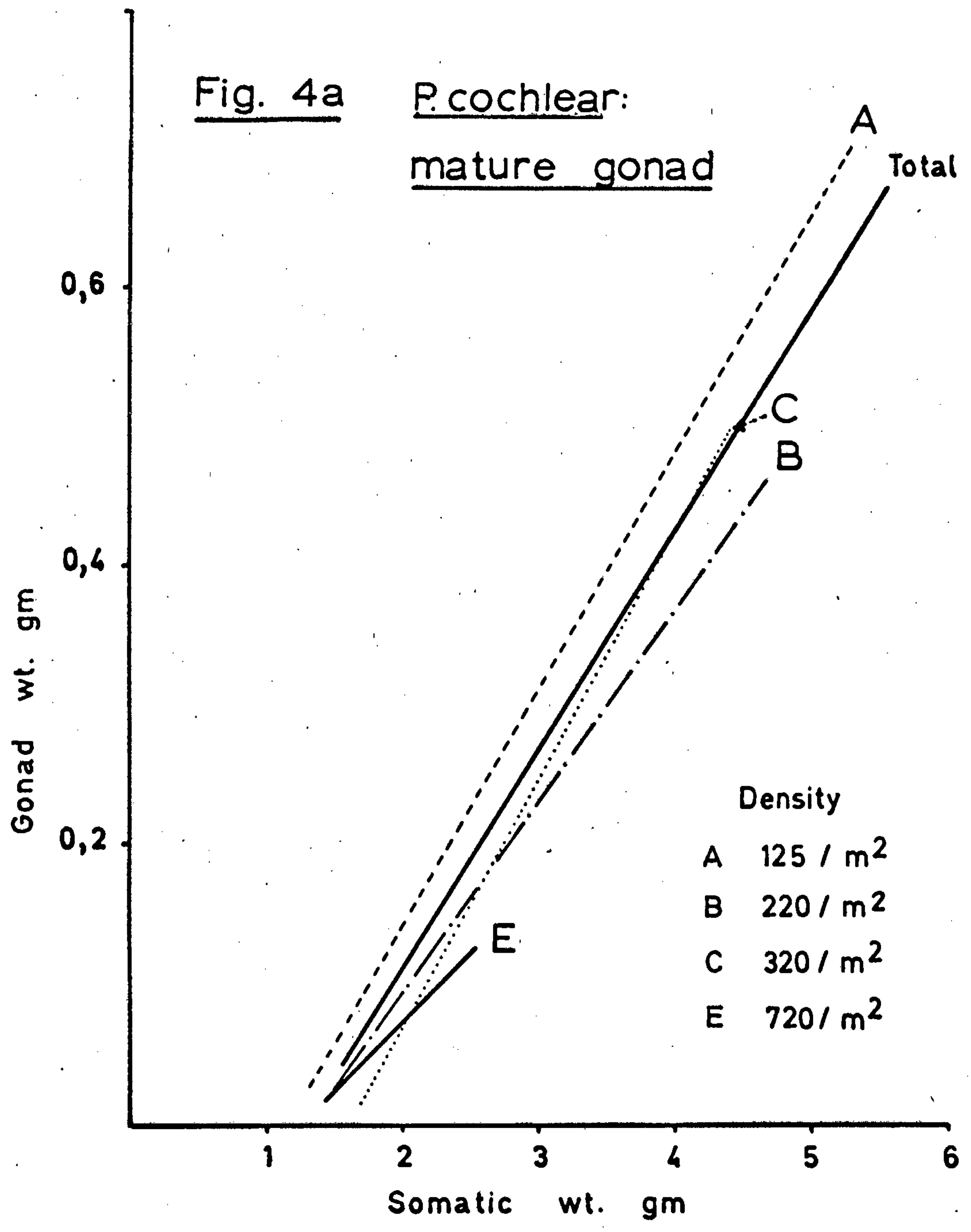
The y intercept (70,1mm) should give an estimate of the maximum size attained by P. cochlear at Dalebrook, and does in fact correspond closely to the largest recorded animal (72,3mm).

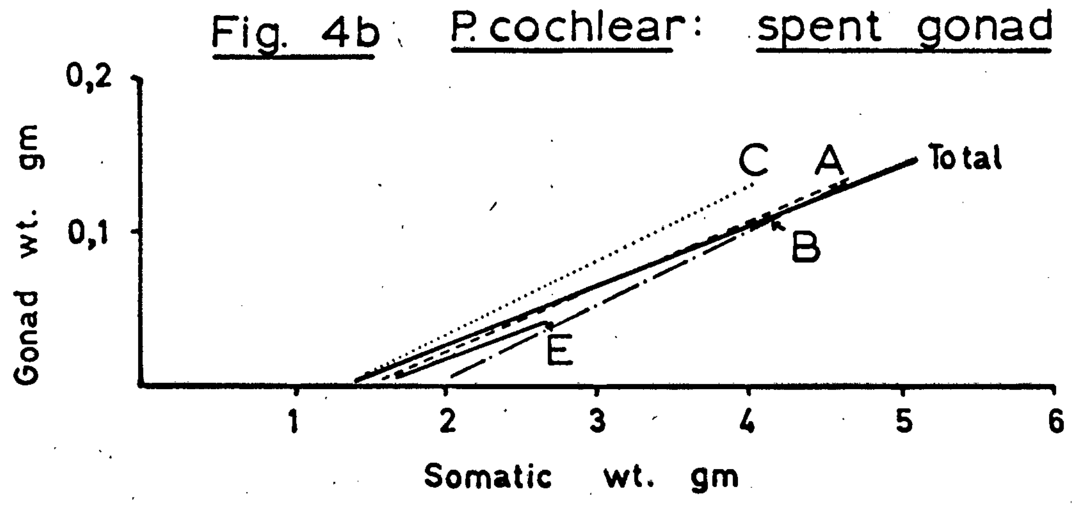
More important than size, is the standing crop which can be supported in relation to density. Figure 3 shows the relationship between biomass (dry flesh weight per m^2) and density. As density increases, so biomass must increase. If competition is lacking the two will be related in a linear fashion and at densities below $250/m^2$ this is the case.

At densities of above $450/m^2$, a limit is reached to the standing crop which can be supported by available resources. The biomass then remains static at about $125gm/m^2$ despite further increases in density. Competition must become progressively more and more intense as the resources are distributed among more and more animals. Between densities of 250 to $450/m^2$ competition must exist, but at a relatively lower intensity.

The most important aspect of competition is its effect

Fig. 4. Reproductive output of *P.cochlear* at four sites (A to E).





on gonadial output, for this has a direct influence on recruitment, and hence the future abundance of the species. This effect may be direct in that the relative size of the gonad is reduced; alternatively (or additionally) it may be indirect and simply reduce the mean size of the sexual individuals. As has been previously demonstrated (Section IV), larger animals produce proportionally more gametes, so that any reduction in size will effectively reduce gamete output.

An analysis of five sites at Dalebrook was undertaken just before and just after spawning (in April and October respectively) to assess gamete output relative to density. At one site the data were too scattered to give significant results and this site is omitted. Results from the remaining sites (A, B, C and E) are summarised in figures 4a, b, and show that density has little direct effect on the output: gamete output relative to body weight was constant in all four sites. A slightly greater output occurred at Site A (density 125/m^2) but was not statistically higher than the other sites. Regressions for this data and statistical comparisons of slopes and intercepts are given in Appendix I. As no significant differences existed, the data was pooled and total regressions calculated for mature ovaries (April) and spent ovaries (October).

The relationships were as follows:

Mature ovaries: $y = 0{,}1600x - 0{,}2147$

Spent ovaries: $y = 0{,}0444x - 0{,}0615$

(y = gonad weight, x = somatic weight).

The assumption was then made that these relationships are true for all the populations subsequently analysed and

Fig. 2

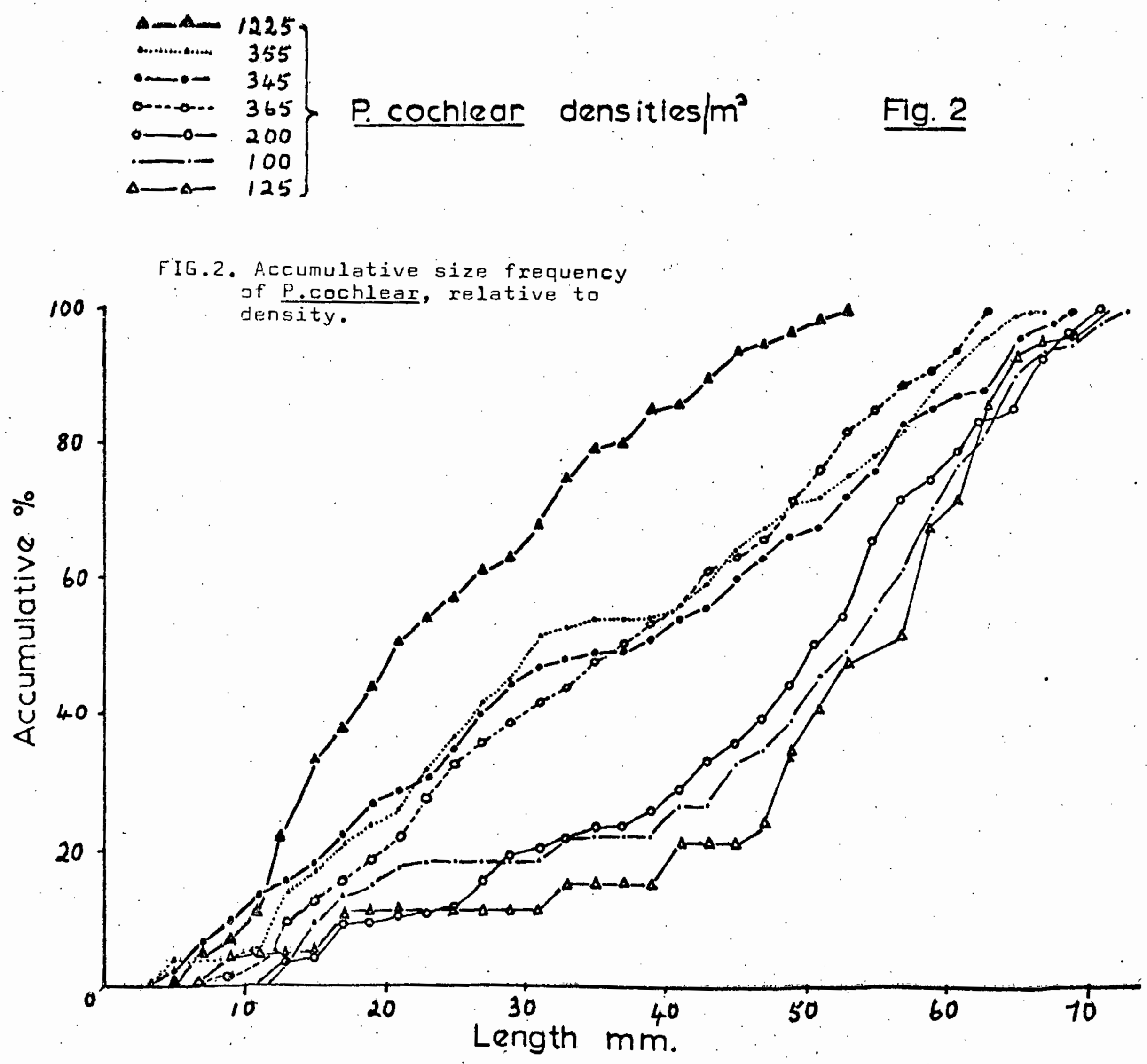


FIG.2. Accumulative size frequency of *P.cochlear*, relative to density.

that the difference between the two regressions is a reflection of average gamete release in relation to somatic weight. Shell length (l) is related to body weight (w) by the exponential function:

$$w = cl^b = 0,0001537\ l^{2.51}$$

From this, shell length was related to gamete output (fig. 5). This relationship allows analysis of numerous large samples, because shell length is the quickest parameter to use in assessing the composition of a population. In addition, the output which was directly measured at sites A, B, C and E has been included and agrees well with the calculated output (fig. 6).

Calculations for nine sites of varying density show that oocyte release (per unit somatic weight) decreases almost linearly as density increases (fig. 6). This is partly because the average size of the sexual individuals is reduced, and partly because there is a greater percentage of juveniles in the population. What is more biologically significant is that the total output (per unit area) initially increases relative to density, reaches a peak at a density of about $430/m^2$, and then progressively decreases despite further increases in density.

Thus increased competition at higher densities not only establishes a maximum standing crop, but sharply decreases the output of eggs.

The effect of competition on growth rates was directly measured at three sites, ranging in density from 90 to $620/m^2$. Figures 7a, b, c show the increment per six months, relative to initial length. Regressions were calculated for each

Fig. 6 Gonad output in *P.cochlear* relative to density.

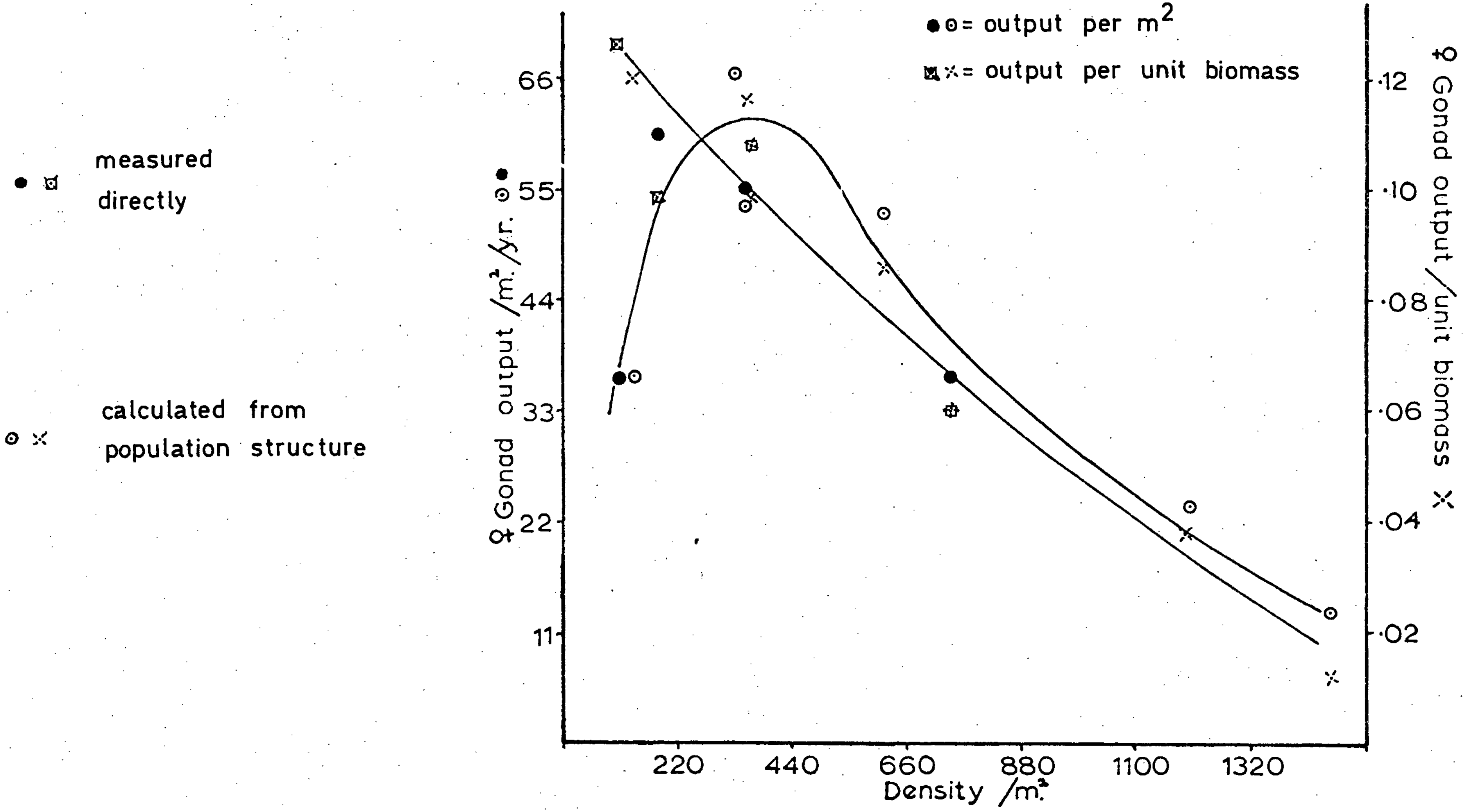


Fig. 7 Effect of Density on Growth

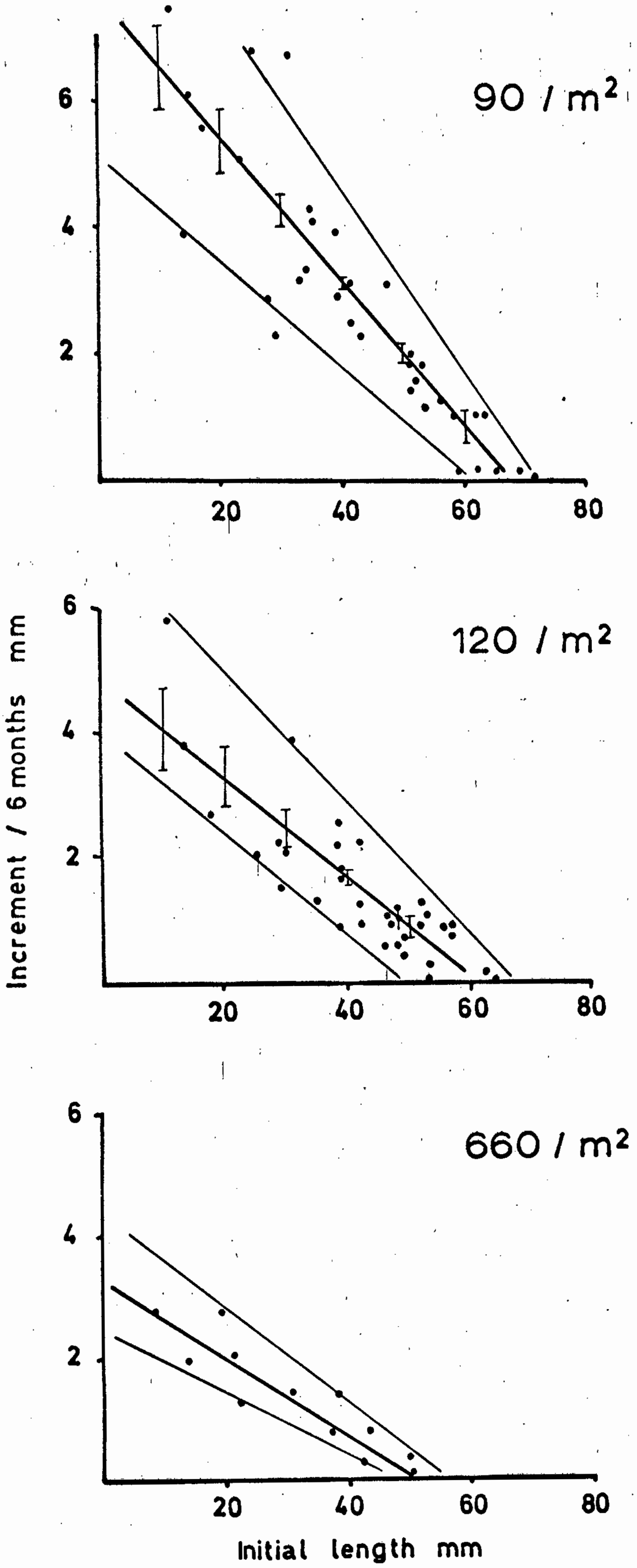
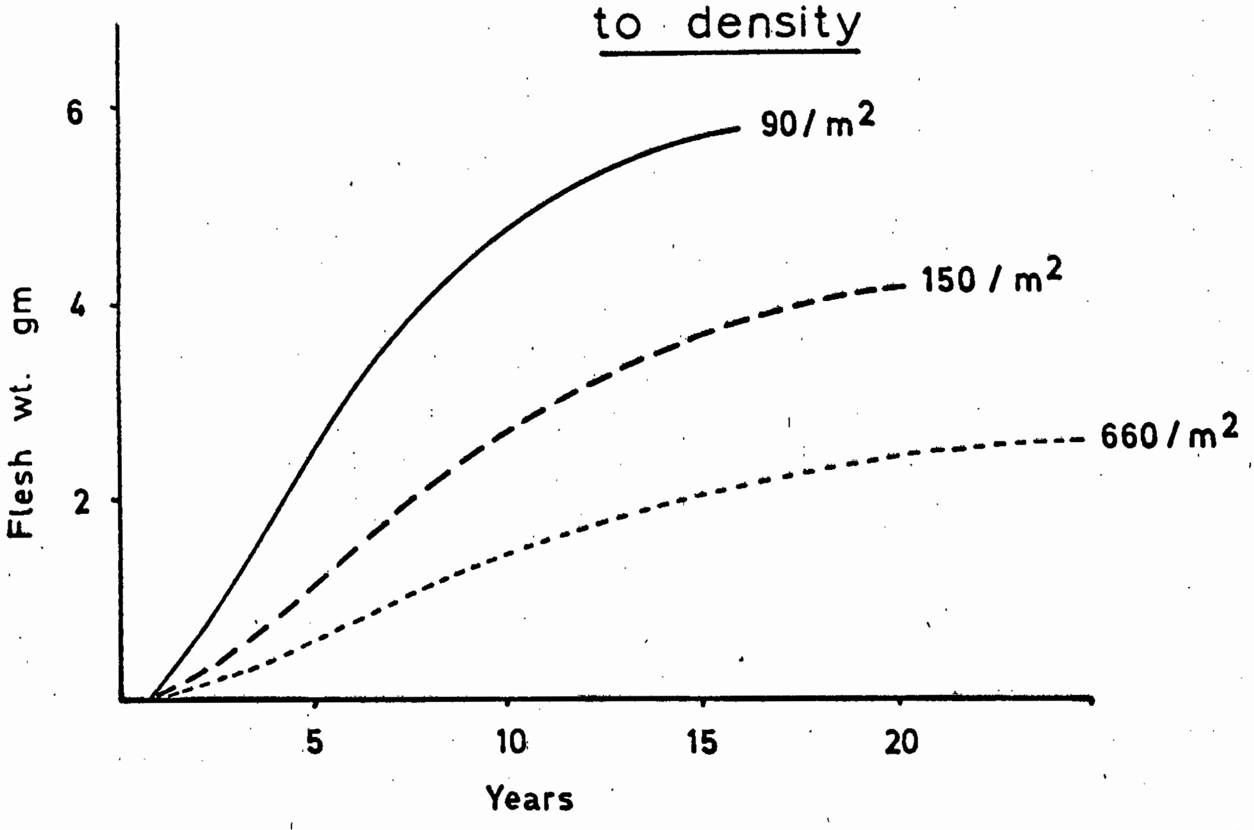
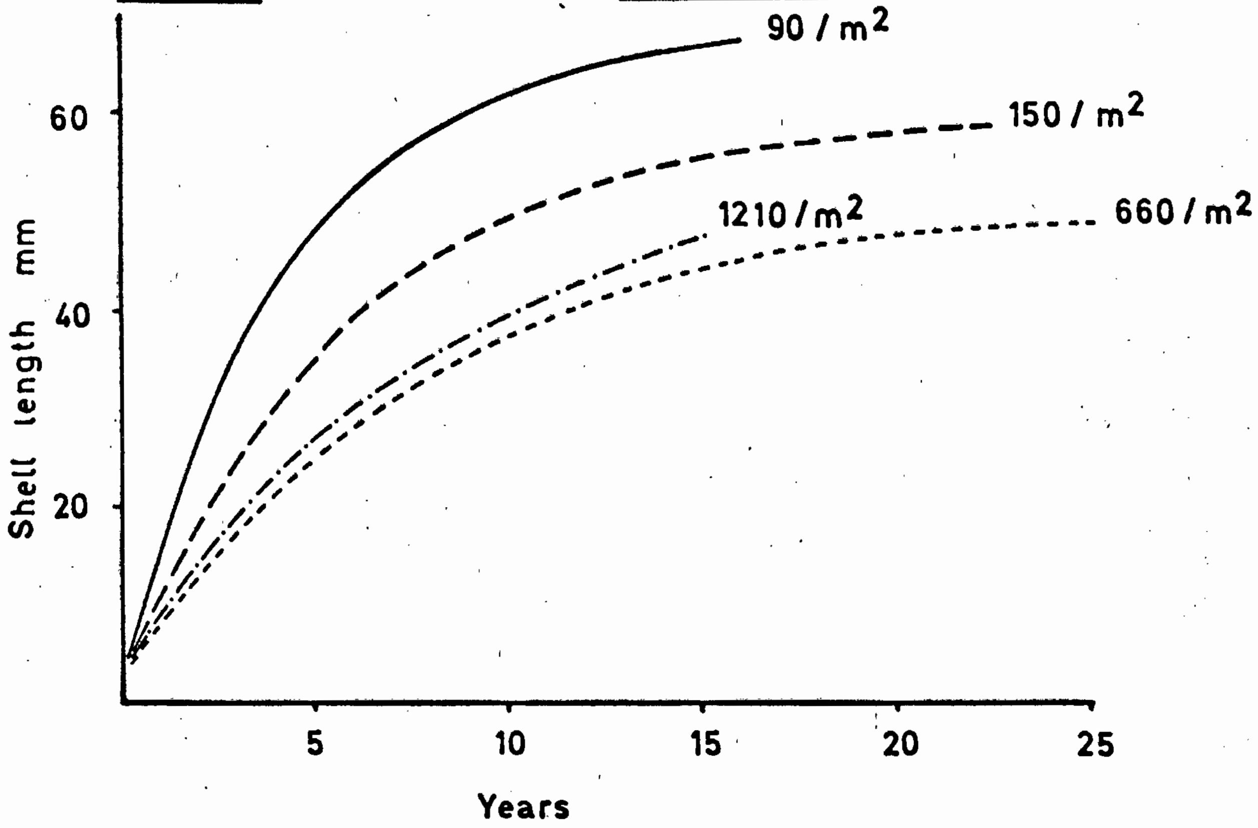


Fig. 8a P. cochlear : Body growth relative to density



P. cochlear : Shell growth relative to density

Fig. 8b



site to give the mean growth (Appendix II). These values could then be used to obtain the shell growth and body growth throughout life (figs. 8a, b). This presumes that the densities remain constant from year to year, as has already been demonstrated in other P. cochlear populations (Section IV, fig. 12). To these curves a fourth has been added from a high density population (1260/m^2). Growth could not be measured directly at this site because of violent wave action, but has been deduced from the spacing of younger age groups and extrapolated. This is reasonable because year groups correspond to measured growth in the other three sites but the results must still be regarded as tentative.

Quite clearly there is a dramatic reduction of growth rate as density increases. This will of course reflect back on the reproductive potential.

A curious effect is however evident. In the highest density population (1260/m^2), growth was comparable to that in the second densest population (620/m^2). This may be because at densities greater than 450/m^2, the standing crop is static and maximal. Possibly the chances of getting food are no longer related to the numbers of limpets, but fixed by the (static) level of biomass which is being supported. To justify and amplify this statement, one needs to consider the population structure and survivorship in various populations.

From the size of different age groups (fig. 9) estimates can be made of mortality between one age group and the next. These estimates are only reliable if the population is stable in time (Deevey, 1947). Stability has been demonstrated in medium density populations (Section IV), but it is possible

Fig. 9

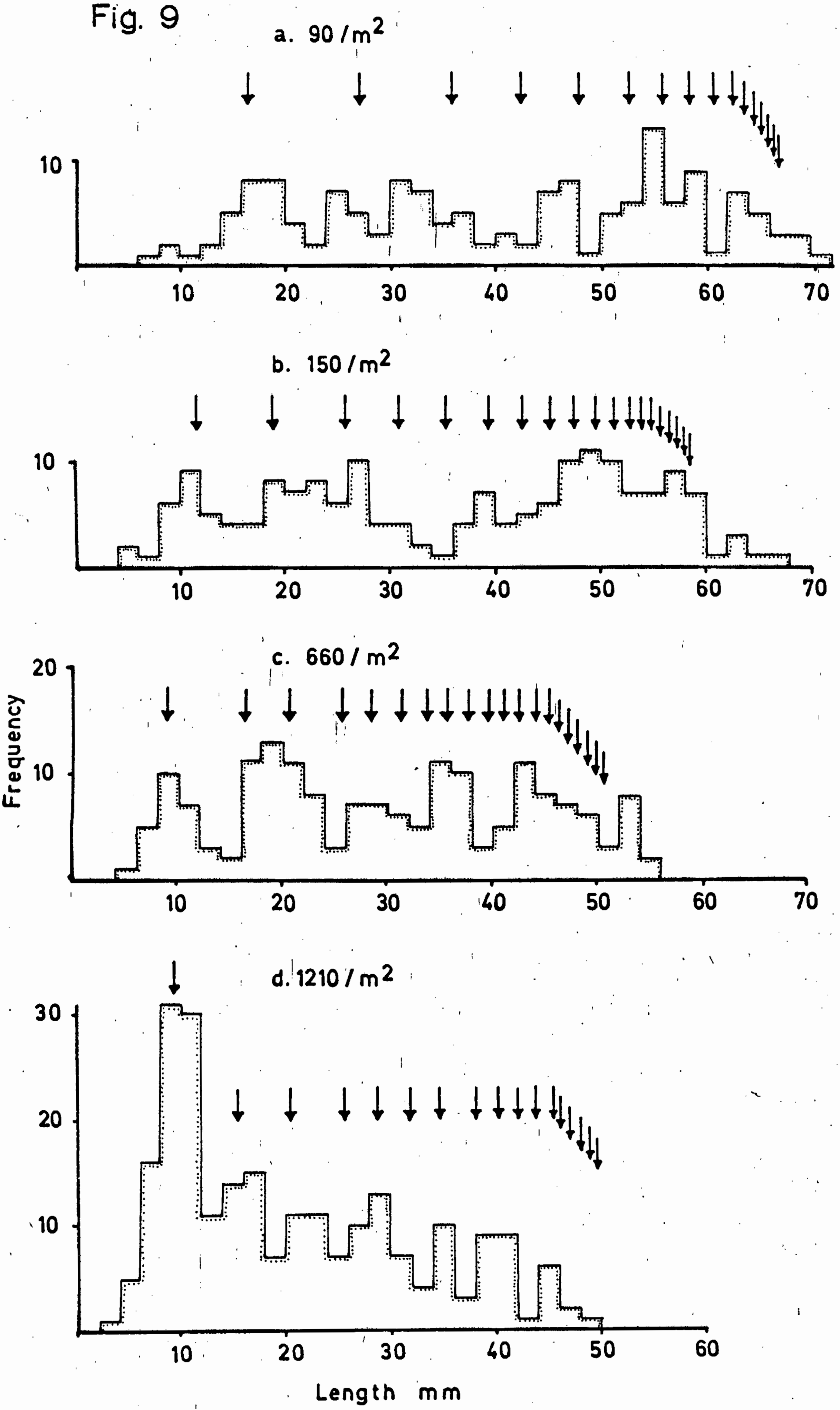


Fig. 9. Size frequency distribution in <u>P.cochlear</u> relative to density per square metre. Arrows indicate calculated year groups, determined from known growth rates.

Fig. 10 Survivorship curves for P. cochlear in relation to density

Fig. 10a

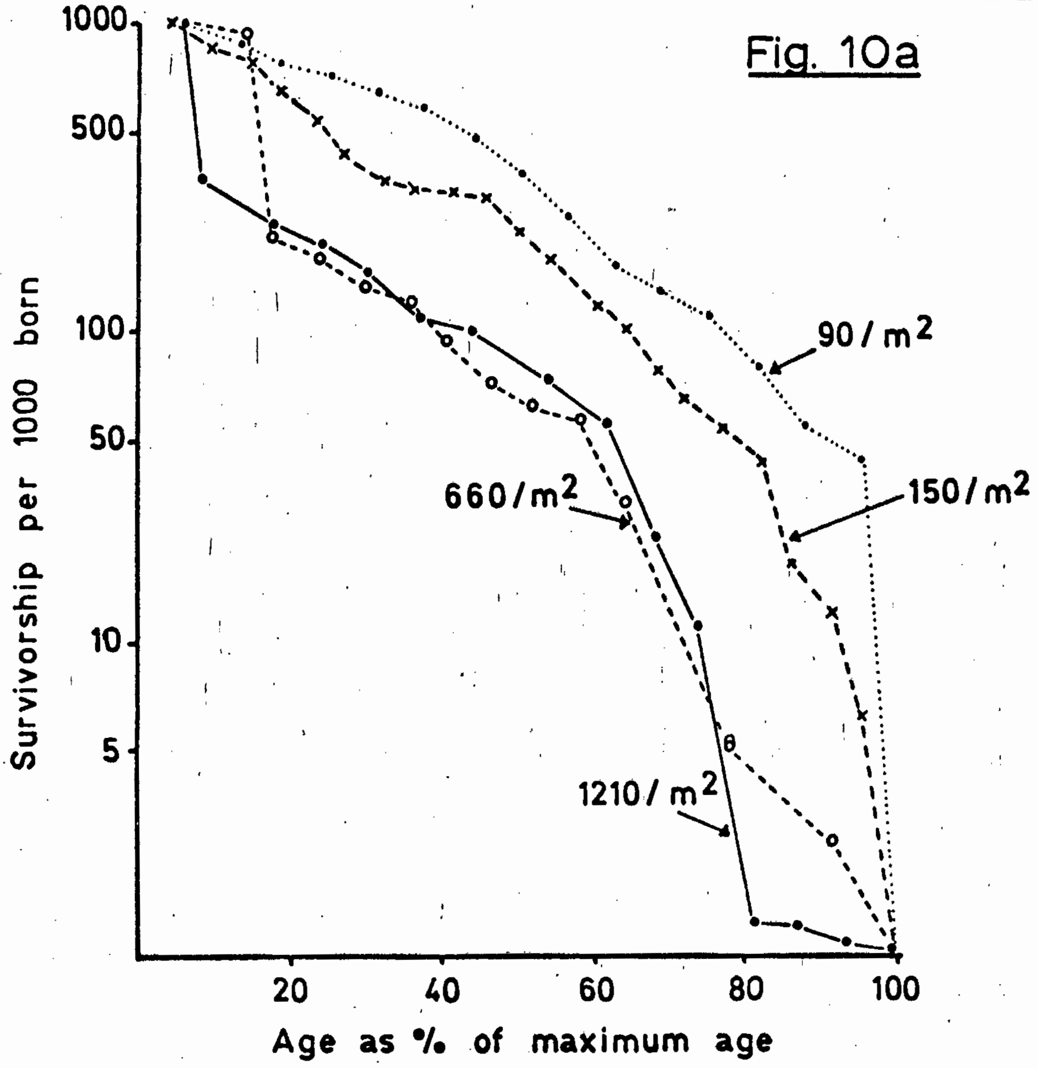
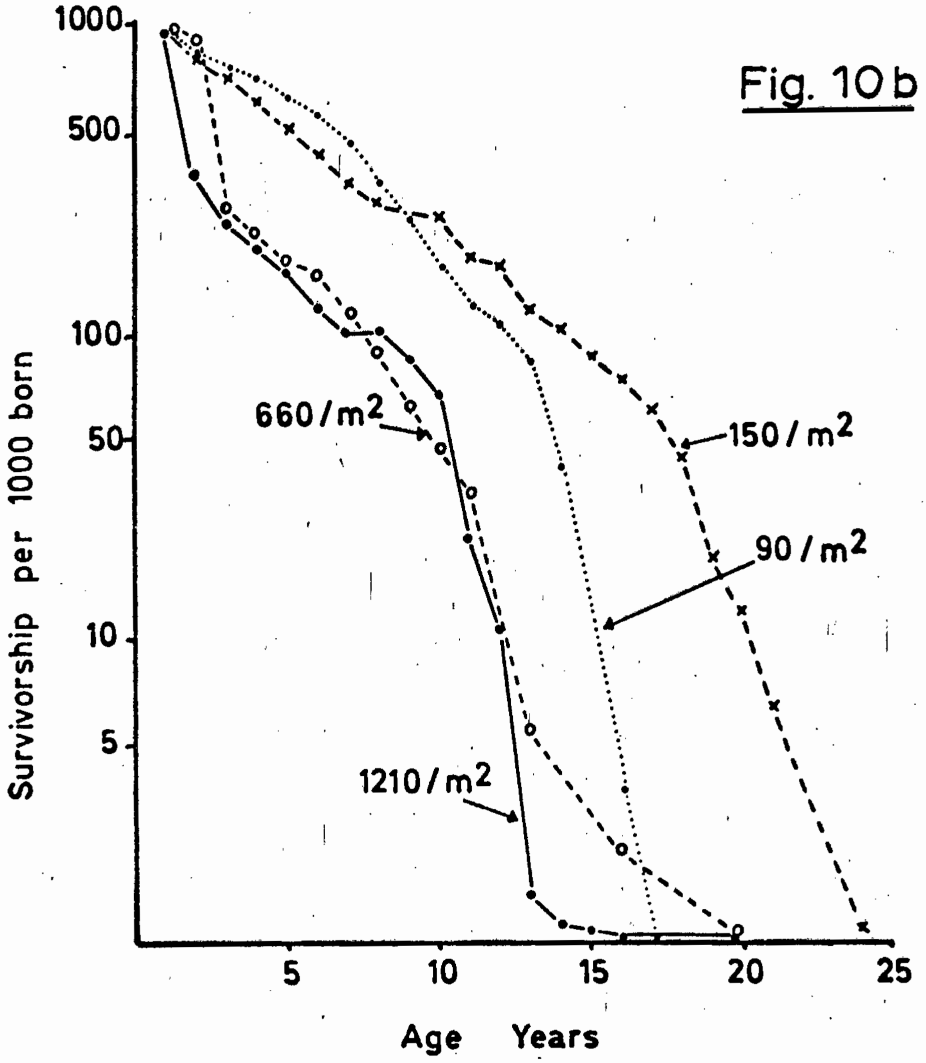


Fig. 10b



that low density populations are more subject to the vagaries of random settlement. For this reason the value of survivorship curves must be comparative and not absolute.

Several features are obvious from the survivorship curves (fig. 10). Firstly, as density increases, there is a proportionally greater mortality of juveniles. If mortality in the first 20% of the life span is ignored, the curves become remarkably similar. Density then effects survival of juveniles rather than adults. This is principally because as density increases, a large percentage of juveniles are found on the shells of other limpets (fig. 11). Previously it was shown that massive mortality occurs during transition from shell to rock (Section IV), so that the population of juveniles settling on shells will radically effect the mortality pattern. In this way mortality of juveniles is density dependent, while once a scar has been established on rock, mortality ceases to be a function of density.

The second trend that is important follows logically from this. High density populations will have proportionally larger numbers of juveniles. Both the population structure (fig. 9) and the accumulative size composition (fig. 2) demonstrate this.

One can now justify the statement made above that at densities above $450/m^2$ growth may be relatively constant because the standing crop is fixed (and by implication, competition is also fixed).

Standing crop can only be static in denser populations if the mean growth is reduced (which does not appear to be the case), or if there is a higher proportion of juveniles and the mean size therefore less. As the latter has been demonstrated, it appears that growth is probably effected by standing crop rather than by density as such.

DISCUSSION:

In the concentrated populations of P. cochlear, considerable intraspecific competition has been demonstrated. Crowding results in reduced growth, lower maximum and mean sizes, higher mortality of juveniles, and more importantly, a reduced output of eggs (per unit area). In populations of less than $250/m^2$ competition is slight, although growth rates may be moderated by density. Competition is most intense in populations of over $450/m^2$, because at this density biomass reaches a ceiling. Above this value, gonad output drops dramatically. Some aspects of these results parallel those of Sutherland (1970), working on Acmaea scabra. Analysing high and low level populations, he showed that high on the shore (at the "edge" of the range), growth is greater, mortality lower and biomass higher.

Density is related directly to wave action. Quantitative values for settlement are impossible to obtain, but the size of the first year group is a reasonable indication of successful settlement. Table 1 summarises this, and shows that high density is always related to high settlement, and that this is consistent and not due to random settlement in a given year. High density is, in other words, due to consistently high settlement in certain areas. Whether this dense settlement is due solely to the wave action experienced, or modified by a gregarious response as well, is not known.

Thus in P. cochlear there exists a feedback mechanism

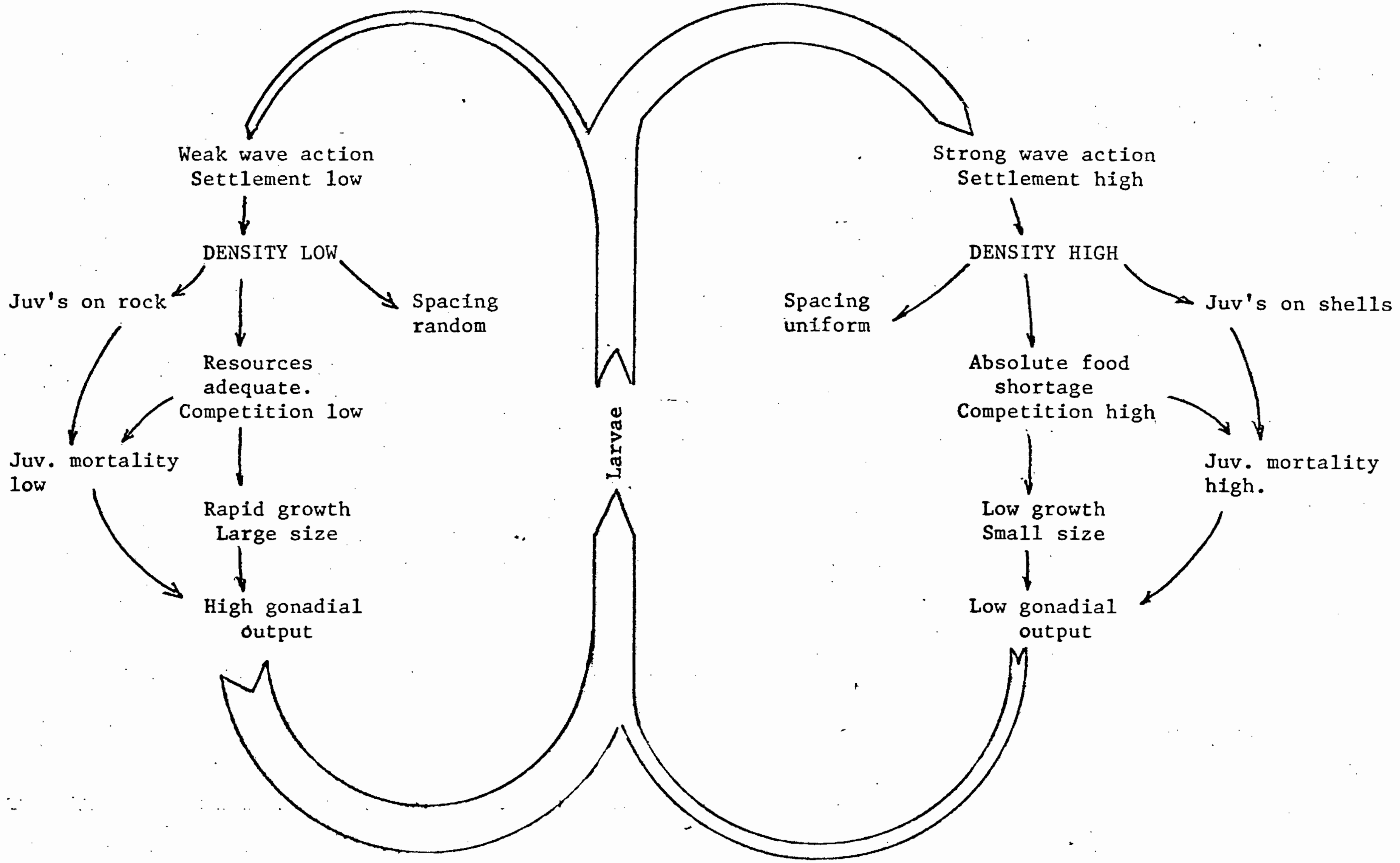


Fig. 12 Gonadial output and recruitment in P. cochlear.

TABLE 1: Size of first year groups in relation to total density.

Total Density /m^2	Density of 1st year group /m^2 (1972)	Density of 1st year group /m^2 (1973)
90	19	7
99	18	29
120	29	31
198	26	36
341	95	90
352	109	120
363	139	131
1210	448	461

controlling overall population levels. Gonad output and survival are highest in low density populations, but settlement is greatest in regions of wave action, resulting in high density populations in which slow growth, small size, high mortality and low gamete output are all features. The problems of density cannot be ameliorated by emigration, because P. cochlear occupies such a narrow zone on the shore.

The numbers of P. cochlear are clearly self-regulated.

Figure 12 represents the balance which exists between sparce and dense populations. In this way a dynamic equilibrium is maintained, and the total population remains stable. Variations in density are local and related to prevailing wave action.

In many ways this is analagous to Chitty's (1967) hypothesis, put forward to explain the "crashes" which occur in vole populations, He argued that as density rises, mutual interference between individuals also increases, resulting in a reduced rate of increase and selection for aggressive animals which are more likely to survive the mutual interference. Obviously this is the start of a vicious circle which intensifies until the population crashes. In the subsequent low density populations, interference is lacking, selection occurs against aggressiveness, and the population again builds up to repeat the cycle.

Chitty's hypothesis is an explanation of temporal variations in populations, while in P. cochlear the variations are spacial while overall constancy is maintained in time. Some limpets react aggressively when they encounter other members of the same species (Section VI), pushing against them until they retreat. In P. cochlear it is difficult to conceive of short-term selection for or against aggressiveness, because with external fertilisation and larval disposal, settlement of a larva will probably occur under different conditions to those experienced by the parents. Selective pressures are likely to change from generation to generation. On a long-term basis, aggressiveness is likely to be selected against because it would lead to energy wastage in crowded populations. This does appear to have happened, for intraspecific reactions are notably mild in P. cochlear, (as will be described in Section VI). In denser populations, interference must occur between individuals; for when feeding they will encounter and react to an increasing number of other animals.

One of the interesting features in P. cochlear is that increasing density does not reduce the gonad size (relative to body size)(fig. 4), while growth is much reduced (figs. 7 and 8). This suggests that gonad growth takes precedence over somatic growth. It has previously been suggested that male limpets grow more slowly because of their proportionally

Fig. 13a

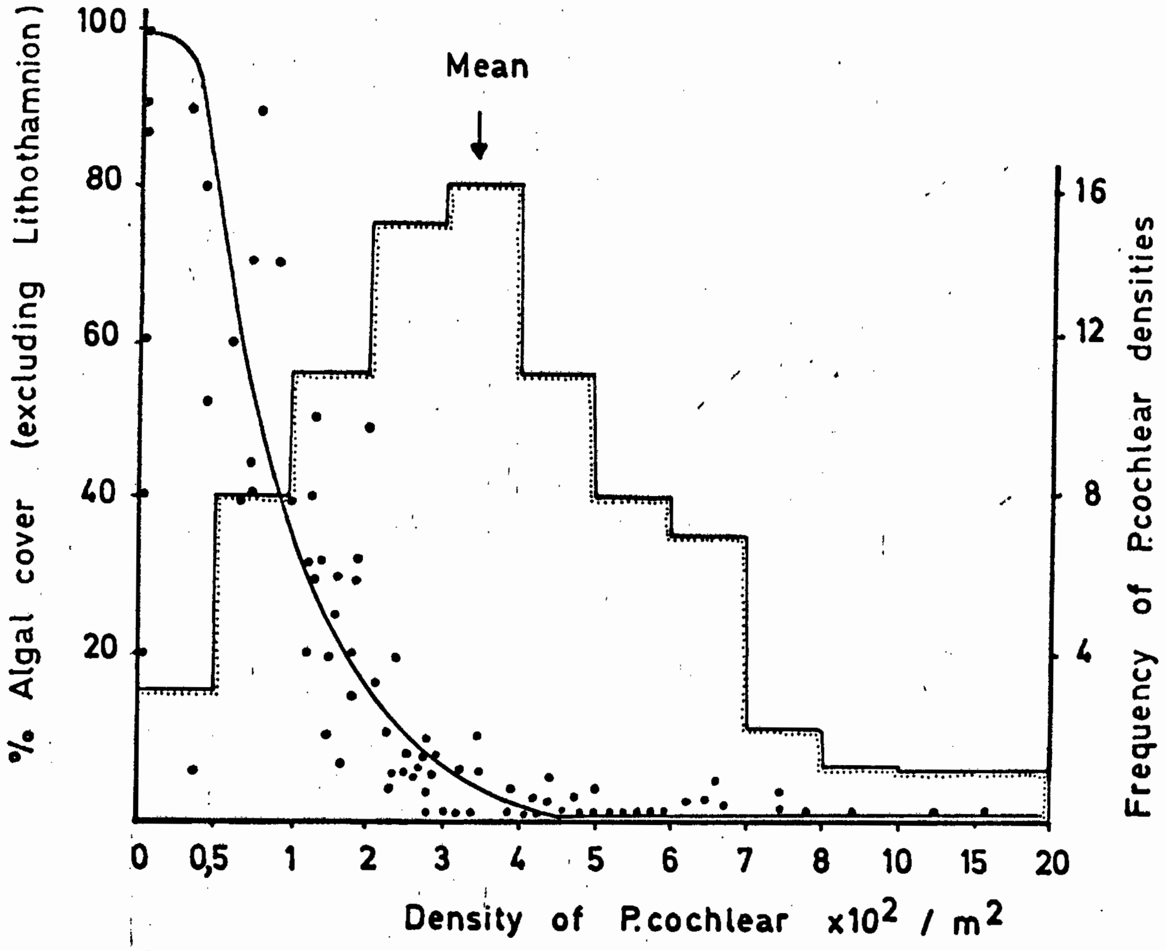
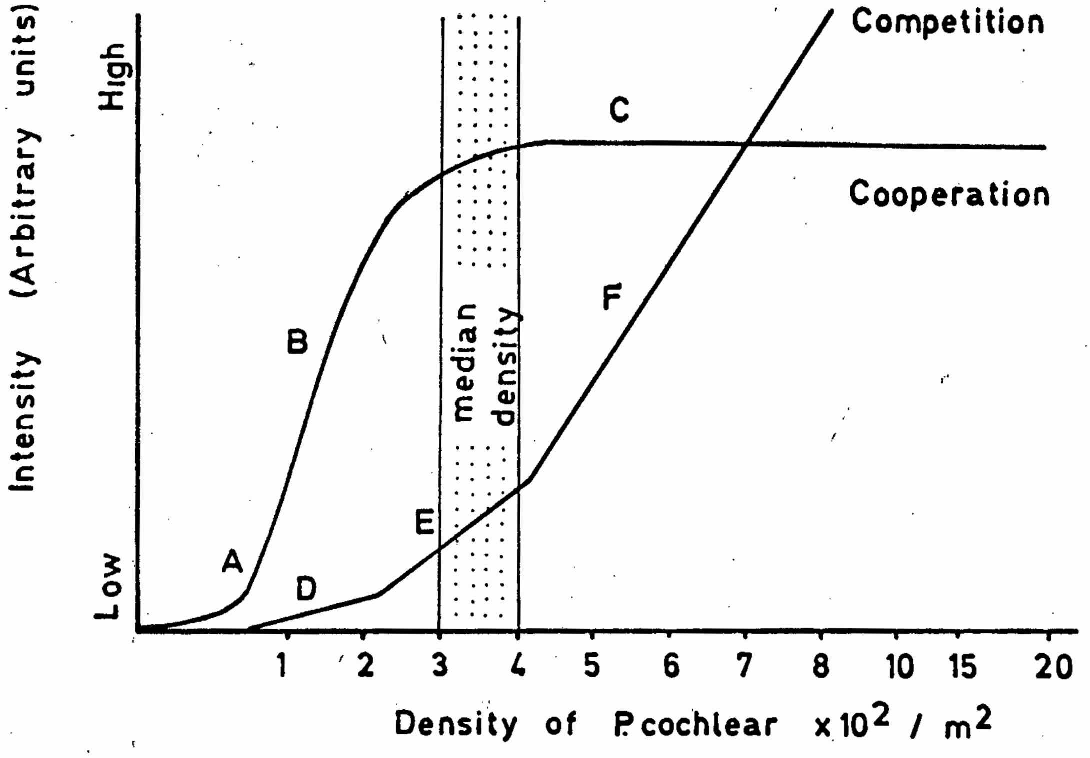


Fig. 13b



A. Limited cooperation: animals too dispersed.
B. Cooperation increases relative to density.
C. Cooperation reaches a maximum.
D. Intraspecific competition limited or absent.
E. Competition increases.
F. Competition most intense: biomass reaches a maximum.

larger gonads (Section IV). Evidence is also available that in P. granularis somatic growth is curtailed if food is short, while gonad development is relatively uneffected. (See below, Section VII).

Figure 14 is a semidiagrammatic three dimensional view of part of the shore at Dalebrook, indicating the zonation and numbers of P. cochlear. The shore shelves gradually to just above low water springs and then drops sharply about one metre before sloping gently again. The outer edge of the shelf acts as a buffer on which the wave force is spent, so that the shelf above is washed but does not receive strong wave action. In relation to this the P. cochlear are densest where wave action is strong, and decrease up the shelf or where the shore is protected by rocky outcrops. The densities of P. cochlear in 83 random quadrats indicate a median density of between 300 and 400/m^2 (fig. 13a), while many of the samples are in the range where competition is intense, the standing crop has reached a ceiling, and gonad output is suboptimal.

At first sight it appears strange that much of the total population exists under "self imposed" competitive stress, and that the self-regulatory mechanism has not been selectively refined until densities are optimal with respect to intraspecific competition.

There are probably three reasons why this has not recurred. Firstly, recruitment occurs from low density populations to offset low gamete release in high density populations, thus enabling the situation to continue.

Secondly, lithothamnion is partly maintained by the activities of the limpets because they graze away other algae

Fig. 14a Three-dimensional of Dalebrook shoreline and the zonation of P.cochlear

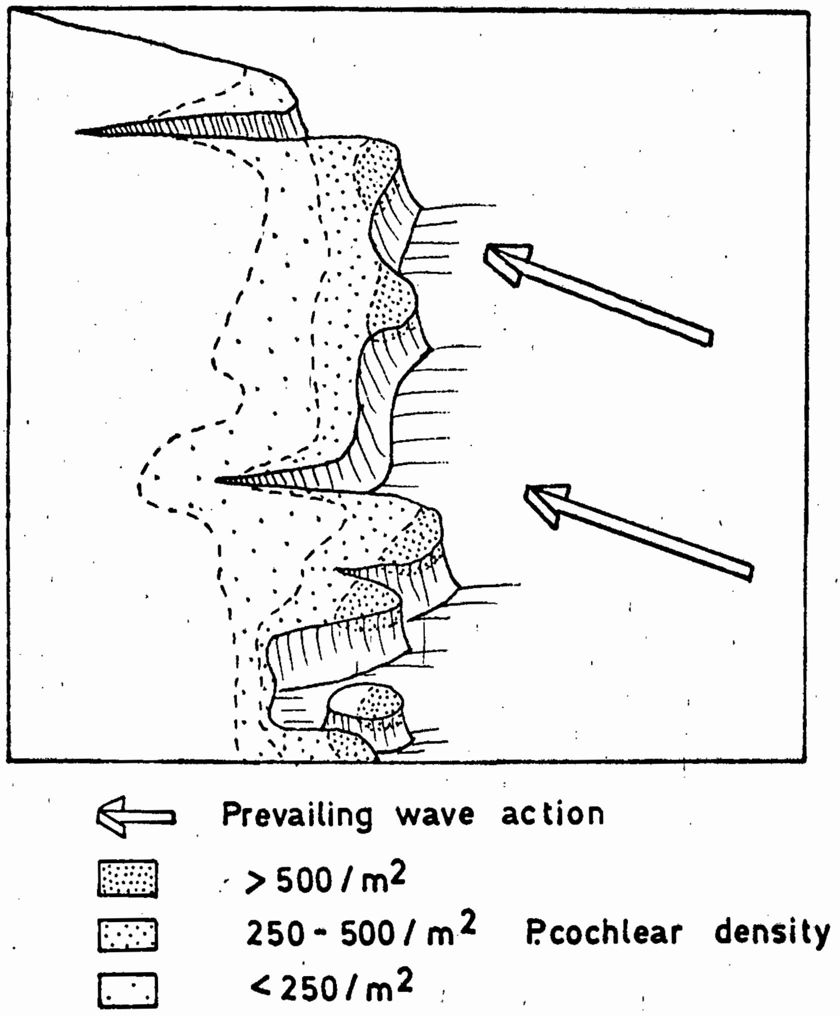
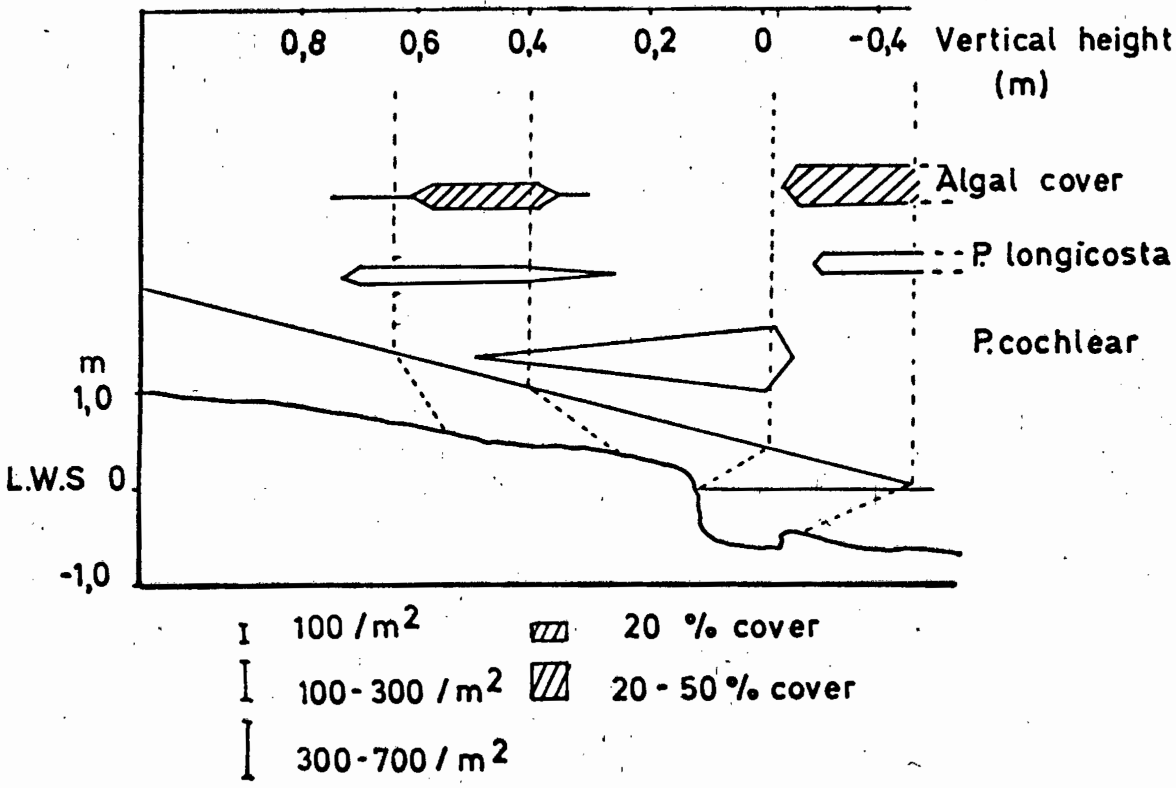


Fig. 14b Transect at Dalebrook



and settling spores preventing overgrowth by other algae. Algal spores are frequently found in the gut contents. At limpet densities of less than 300/m^2, algae begin to develop on the rocks in the Cochlear zone and competitively displace the lithothamnion (fig. 13a). Higher densities prevent this, aided by the greater wave action which tears away the less robust erect algae.

This raises the question of physico-biological interaction: in areas of low wave action, do erect algae flourish and therefore preclude P. cochlear settlement (or the growth of lithothamnion, the foodplant of P. cochlear), or conversely is settlement of the limpet less because of reduced wave action, therefore allowing algal growth? In fact, the two possibilities are probably linked in a dynamic balance, as the unpublished work of Wood (1935) suggests. She cleared areas in the cochlear zone to study recolonisation, and showed how a dense covering of algae (especially Ulva sp.) developed in the absence of P. cochlear. In the subsequent two years, larval settlement was prevented by the algal mat, and lithothamnion disappeared except where stray invading limpets cleared the algal turf away.

Finally, competition for space occurs between P. cochlear and P. longicosta. The details of this interaction will be described in a subsequent section, but briefly, P. longicosta can only establish itself in the cochlear zone if P. cochlear densities are less than about 200/m^2. The transect in figure 14a indicates the relationship between these two limpets and algal cover. Clearly both algae and P. longicosta are displaced by P. cochlear, but compete with the latter when its densities are low enough. Although all the algae have been lumped together, it must be remembered that different species (with different tolerances) may occur above and below P. cochlear.

Nevertheless, in the absence of P. cochlear (or after its experimental removal), algae encroach from both above and below into the cochlear zone: there can be no doubt that the activity of the limpets excludes the algae, and not merely the tolerances of these algae.

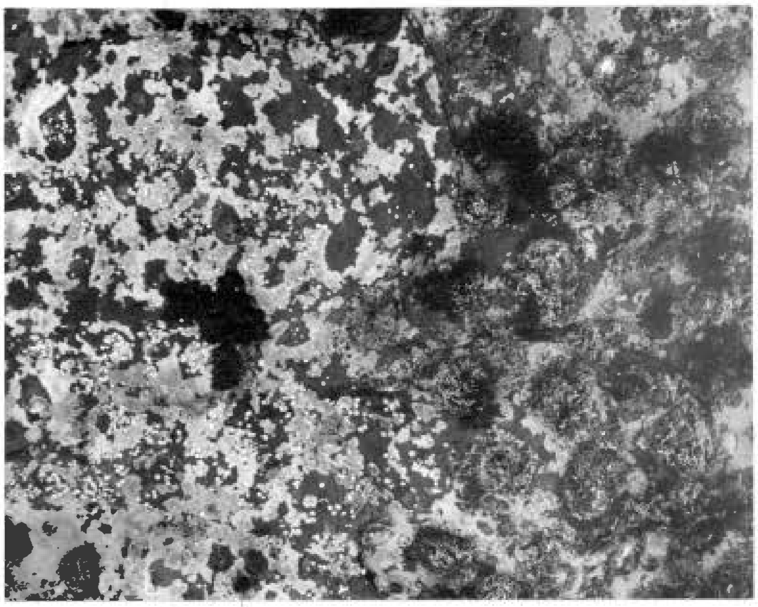
P. cochlear also prevents barnacle settling. Cyprid larvae and small barnacles have been found in the gut, and clearing experiments show that large numbers of Balanus algicola establish themselves in the cochlear zone in the absence of this limpet. (Unpublished notes of M. Wood, 1935) The latter effect has been strikingly demonstrated by White (1973, unpublished), from whose work Plates 1, 2 and 3 are taken.

The density of P. cochlear must therefore be high to prevent competition or invasion of the zone. High densities are maintained by recruitment from low density populations, the latter existing on the fringe of the habitat at the lower limits of wave action which can be tolerated. At the centre of the range (high wave action, high density) the maintenance of the cochlear community is assured unless catastrophic events (such as oil pollution) modify the environment. At the periphery of the range, intraspecific reactions are stronger and more varied, and the numbers of P. cochlear are likely to oscillate, depending on whether local conditions favour one or other of the species in the community.

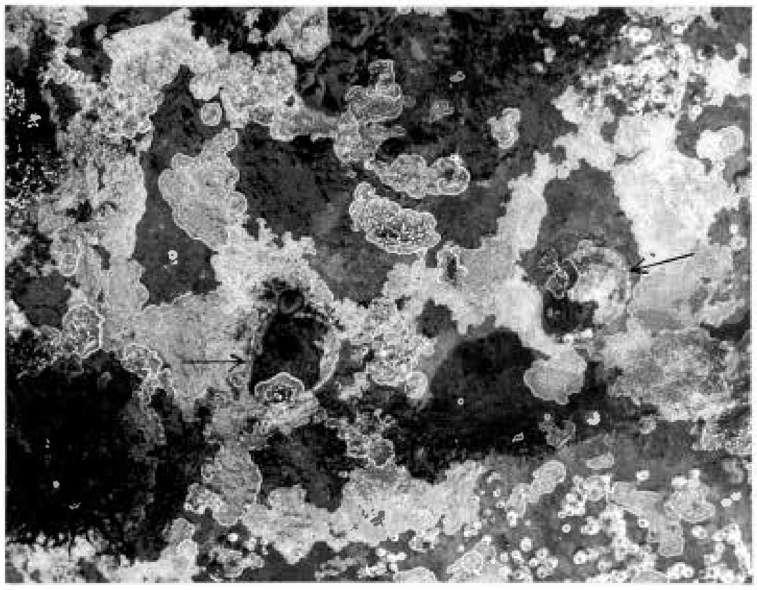
Almost certainly, all other limpets will experience similar, if less intense, intraspecific competition. This is certainly true of P. granularis (see Section VII), P. vulgata (Ballantine, 1965), Acmaea scabra (Sutherland, 1970) and A. digitalis (Breen, 1973). Competition is also indicated

PLATES I,II

Settling of barnacles in areas which have been cleared of Patella cochlear.



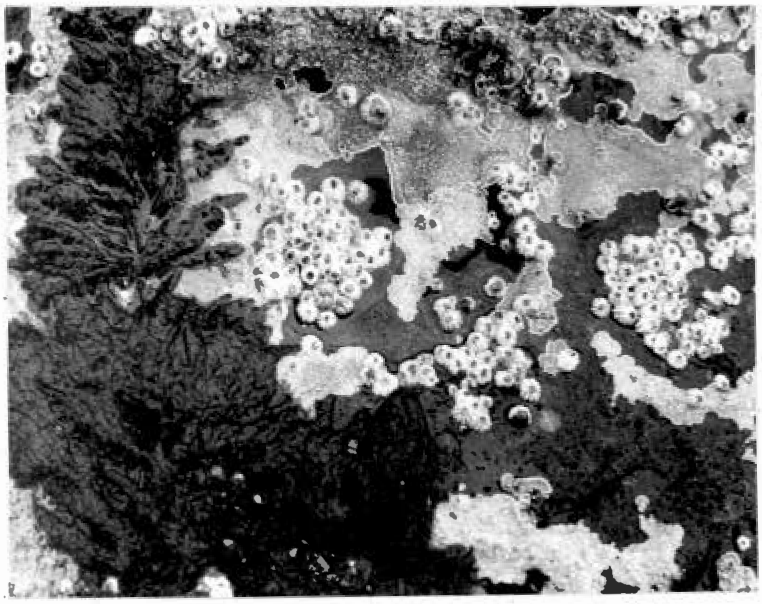
cleared control



Detail of above showing how invading P.cochlear ↑ clear away young barnacles or prevent their settlement.

PLATE III :

Detail of plate I, showing the growth of barnacles which occurs in the absence of P.cochlear. (cf. plate II)



by the interesting remark Forster (1967, p.294) makes about Haliotis tuberculata: "in fished populations the rates of growth are possibly rather higher" (than in unfished areas).

Ballantine (personal communication) has suggested that limpets may simultaneously compete for food while cooperating to maintain their habitat. Groups of P. vulgata collectively prevent overgrowth by Fucus although individually incapable of this - but they may also compete for food.

A comparable situation is true in P. cochlear. Densities of about 200 to 300/m^2 are required to exclude P. longicosta, and of about 350/m^2 to prevent algal growth covering lithothamnion. Thus at levels less than 350/m^2, cooperation will increase with density, while in excess of this, no further advantage is gained by increasing the density. It has also been shown that intraspecific competition is limited if densities are less than 250/m^2, and most intense when these exceed 450/m^2. This relationship is summed up in figures 13a, b. Here it is apparent that the median density of P. cochlear falls in the range where cooperation and competition are balanced. Many populations however exceed this value.

The stimulating work of Paine and others (Paine 1966, 1969, 1971; Dayton 1971) has shown that experimental removal of top predators from food "subwebs" results in a reduction of diversity and often a monopolisation of space by a single species. Predation keeps dominants at a level where other species can still share the habitat. In the case of P. cochlear, its complete domination of the cochlear zone may be due to relative immunity from predation; or its potential population growth may be much higher than in other species, resulting in densities so high that predation is insufficient to prevent monopolisation. The latter possibility might also explain the "unnecessarily" high densities in P. cochlear, which allow the monopoly of space this species enjoys.

In all the limpets mentioned above, density in the centre of the range is such that intraspecific competition is considerable. This in itself raises interesting possibilities - both ecological and commercial. How general is the phenomenon that intraspecific competition is greater than "desired"? And is this effect a necessary corrollary to maintaining the species in the face of interspecific and predatory pressures?

These questions have basic ecological implications for population control mechanisms, but their formulation into general principals must await data from a far wider range of animals.

In his excellent review on competition, Miller (1967, p.4) succinctly raises the problem that "there is still no satisfactory explanation for the tremendous diversity of species... observed in natural systems". The answer is likely to be complex, but one facet is suggested from the present work. For one species to totally exclude another it must saturate the habitat completely. This has been observed in the centre of the cochlear zone: but here intraspecific competition reduces gamete output to the point where the population would crash if recruitment from elsewhere did not occur. If this were true throughout the limpets range, the population could not be maintained, and saturation of the total habitat is thereby prevented. If intraspecific competition cannot rise beyond certain levels without self regulation occurring then it may be impossible to totally exclude other species.

ACKNOWLEDGEMENTS:

Working under my supervision, Miss P. White showed the effects of removing P. cochlear from selected sites; and Plates 1 to 3 were taken at her experimental sites.

SUMMARY:

The density of Patella cochlear varies from 90 to 1700/m^2, and is correlated with wave action. Highest densities occur with moderate to strong wave action. As density increases, mean and maximum sizes decrease, growth rate is lower, and mortality of juveniles is greater. The latter is partly because a greater proportion of juveniles occur on shells of other limpets, and mortality is high during their transition to a rocky substrate.

Standing crop increases with density until the latter reaches about 450/m^2. Above this value, biomass remains static at about 125 gm/m^2 despite further increases in density. This suggests that competition is most intense above this density.

Density has no direct effect on gonad size, but at above 430/m^2 gonadial output per m^2 decreases relative to density because mean size is reduced. Low densities are associated with high gonadial output, high densities with low output. This results in a negative feedback controlling overall numbers. High density populations remain high because of recruitment, settlement being highest where wave action is strong.

Intraspecific competition is slight at densities of less than 250/m^2 and most intense over 450/m^2. The median density at Dalebrook is 300-400/m^2, but many populations have higher densities.

Densities of about 300/m^2 are required to exclude other limpets and to prevent foodplant lithothamnion from being overgrown by other algae. To maintain monopoly of the cochlear zone, high densities of P. cochlear are required. Concomitantly intraspecific competition is high, but it is suggested that this is balanced against cooperation enabling exclusion of other limpets from the community and maintenance of the foodplant.

REFERENCES:

ATAPATTU, D.H. 1972. The distribution of molluscs on littoral rocks in Ceylon, with notes on their ecology. Mar. Biol. 16 : 150-164.

BALLANTINE, W.J. 1961. A biologically-defined exposure scale for the comparative description of rocky shores. Field Stud. 1, 19 pp.

BRANCH, G.M. 1971. The ecology of *Patella* Linnaeus from the Cape Peninsula, South Africa. I. Zonation, movements and feeding. Zool. Afr. 6 (1) : 1-38.

BREEN, P.A. 1971. Homing behaviour and population regulation in the limpet *Acmaea (Collisella) digitalis*. Veliger 14 : 177-183.

—— 1973. Seasonal migration and population regulation in the limpet *Acmaea (Collisella) digitalis*. Ibid. 15 : 133-141.

CHITTY, D. 1967. The natural selection of self-regulatory behaviour in animal populations. Proc. Ecol. Soc. Australia. 2 : 51-78.

DAYTON, P.K. 1971. Competition, disturbance and community organisation : the provision and subsequent utilisation of space in a rocky intertidal community. Ecol. Monogr. 41 : 351-389.

DEEVEY, E.S. 1947. Life tables for natural populations of animals. Q. rev. Biol. 22 : 283-314.

EBLING, F.J., KITCHING, J.A., PURCHON, R.D. and BASSINDALE, R. 1948. The ecology of the Lough Ine Rapids, with special reference to water currents. 2. The fauna of the Saccorhiza canopy. J. anim. Ecol. 17 : 223-244.

FIELD, J. 1968a. The 'turbulometer', an apparatus for measuring relative exposure to wave action on shores. Zool. Afr. 3 : 115-118.

——— 1968 b. Numerical methods in marine ecology. I. A quantitative "similarity" analysis of rocky shore samples in False Bay, S. Africa. Ibid : 119-137.

FOSTER, G.R. 1967. The growth of Haliotis tuberculata : results of tagging experiments in Guernsey. J. mar. biol. Ass. U.K. 47 : 287-300.

MILLER, R.S. 1967. Pattern and process in competition. Adv. ecol. Res. 4 : 1-74.

PAINE, R.T. 1966. Food web complexity and species diversity. Amer. Nat. 100 : 65-75.

——— 1969. The Pisaster-Tegula interaction : prey patches, predator food preference and intertidal community structure. Ecol. 50 : 950-961.

——— 1971. A short term experimental investigation of resource partitioning in a New Zealand rocky intertidal habitat. Ibid 52 : 1096-1106.

SUTHERLAND, J.P. 1970. Dynamics of high and low populations of the limpet Acmaea scabra (Gould). Ecol. Monogr. 40 : 169-188.

WHITE, P. 1973. Recolonisation experiments in the intertidal zone at Dalebrook. Unpublished undergraduate project, University of Cape Town.

WOOD, M. 1935. Unpublished notes. University of Cape Town.

APPENDIX I: Relationship between somatic weight (x) and gonad weight (y) for five sites at Dalebrook from mature and spawned samples.

	Site	Regression	Correl. coeff. r.	p.
Mature (April 1972)	A	y = .173x - .204	.94	<.001
	B	y = .143x - .196	.76	<.02
	C	y = .190x - .308	.97	<.001
	D	y = .070x + .030	.50	>.05
	E	y = .107x - .144	.91	<.02
	Total	y = .160x - .214	.87	<.001
Spent (October 1972)	A	y = .045x - .067	.91	<.001
	B	y = .050x - .094	.77	>.05
	C	y = .053x - .068	.76	<.02
	E	y = .038x - .052	.66	>.05
	Total	y = .044x - .061	.81	<.001

Significance of difference in slopes (above diagonal) and intercepts (below diagonal).

Mature:

	A	B	C	D	E
A		>.05	>.05	<.02	>.05
B	>.05		>.05	>.05	>.05
C	>.05	>.05		>.05	>.05
D	>.05	>.05	>.05		>.05
E	>.05	>.05	>.05	>.05	

Spent:

	A	B	C	E
A		>.05	>.05	>.05
B	>.05		>.05	>.05
C	>.05	>.05		>.05
E	>.05	>.05	>.05	

APPENDIX II: Regressions of increment in shell length (per six months)(y), against initial shell length (x).

Density	Regression	r.	p.
A $150/m^2$	$y = -0.080x + 4.85$	0.79	$<.001$
B $90/m^2$	$y = -0.113x + 7.708$	0.88	$<.001$
C $660/m^2$	$y = -0.070x + 3.21$	0.82	$<.001$

Tests of difference in slopes (above diagonal) and intercepts (below).

	A	B	C
A		$<.05$	$<.05$
B	$<.01$		$>.05$
C	$<.01$	$<.01$	