# THE ECOLOGY OF *PATELLA*

(VOL. II)

G. M. BRANCH.

DEPARTMENT OF ZOOLOGY
UNIVERSITY OF CAPE TOWN

THESIS SUBMITTED
FOR THE DEGREE OF PH.D.
SEPTEMBER 1973.

# SECTION VI:

# MECHANISMS REDUCING INTRASPECIFIC COMPETITION.

FIG.I Size frequency of P.granularis relative to zonation.(Figures in brackets indicate height above low water springs in meters).

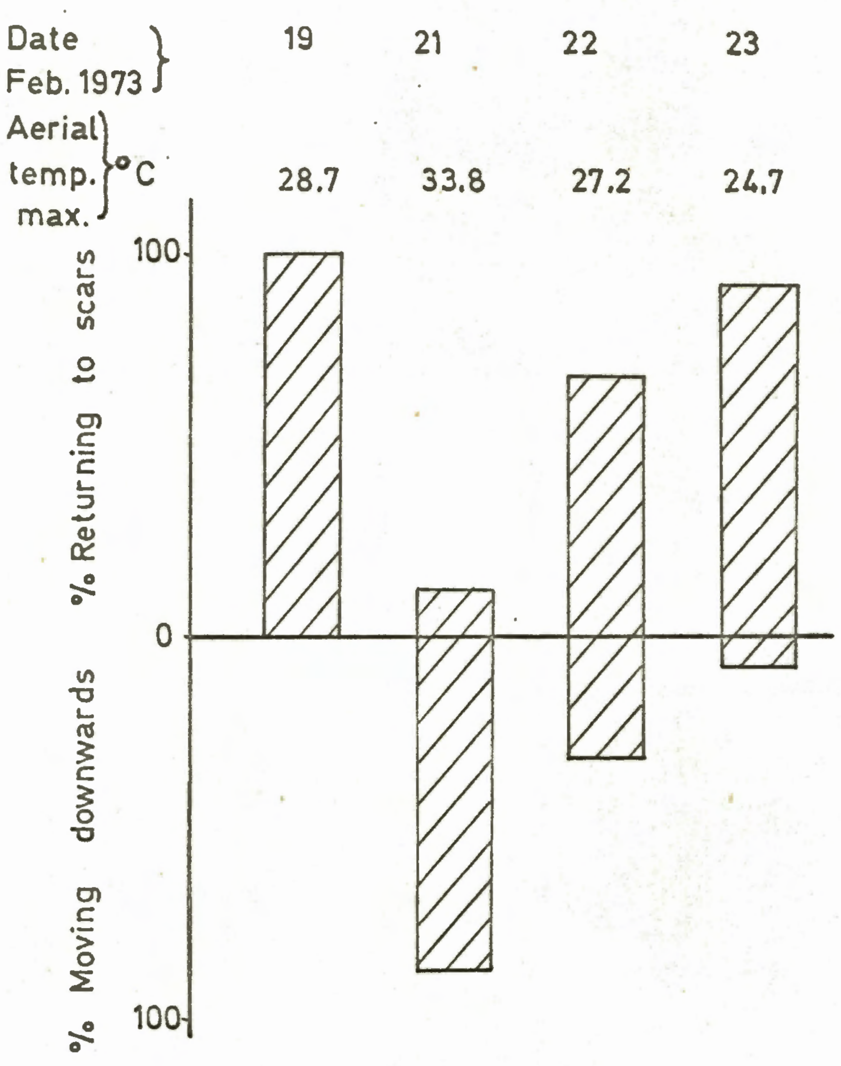


FIG. 2. Movement of P.granularis relative to temperature All records were made at a fixed site at Melkbos Strand, I,2m above L.W.S., over a period of five days in February, 1973. During normal conditions the limpets returned to their scars, but during exceptional heat they abandoned these and moved downwards into moist crevices.(see plate 1)

TABLE 1. Movements of P. granularis at Kommetjie.

| Month in 1970 | % Movement Upward | Downward | None | Total number |
|---|---|---|---|---|
| Feb. | 0 | 26 | 74 | 52 |
| Mar. | 18 | 6 | 76 | 48 |
| Apr. | 42 | 16 | 42 | 40 |
| May | 32 | 8 | 62 | 40 |
| June | 32 | 10 | 58 | 12 |
| Aug. | 48 | 15 | 47 | 15 |
| Sept. | 32 | 2 | 66 | 15 |
| Oct. | 21 | 10 | 69 | 14 |
| Dec. | 26 | 26 | 48 | 14 |

In summer movement was limited, but animals reacted strongly to exceptionally hot days and groups were seen which abandoned their exposed high level scars and retreated downwards to crevices and damp depressions in the rocks. This appeared a short-term response, as many of the animals subsequently returned to their scars when high temperatures abated. An example of this is recorded for a four day period (February, 1973) at Melkbos Strand (fig. 2), when exceptionally hot dry conditions occurred for a single day, followed by cool weather.

No P. granularis ever occupy intertidal pools, and in aquaria may migrate upwards to the water-air interface. This behaviour is probably important in relation to the upward migration of the species.

Thus two mechanisms appear operative in P. granularis: an upward movement which occurs progressively although it may be variable or interrupted in individuals; and a short-term downward retreat in response to high summer temperatures.

In P. granatina analysis of size in relation to zonation

## PLATE I

P. granularis: downward migration in response to exceptionally high summer temperatures.

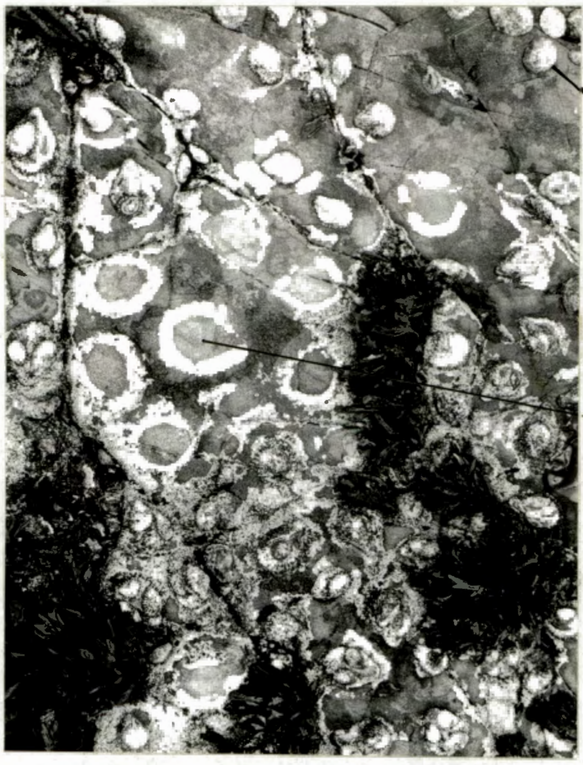
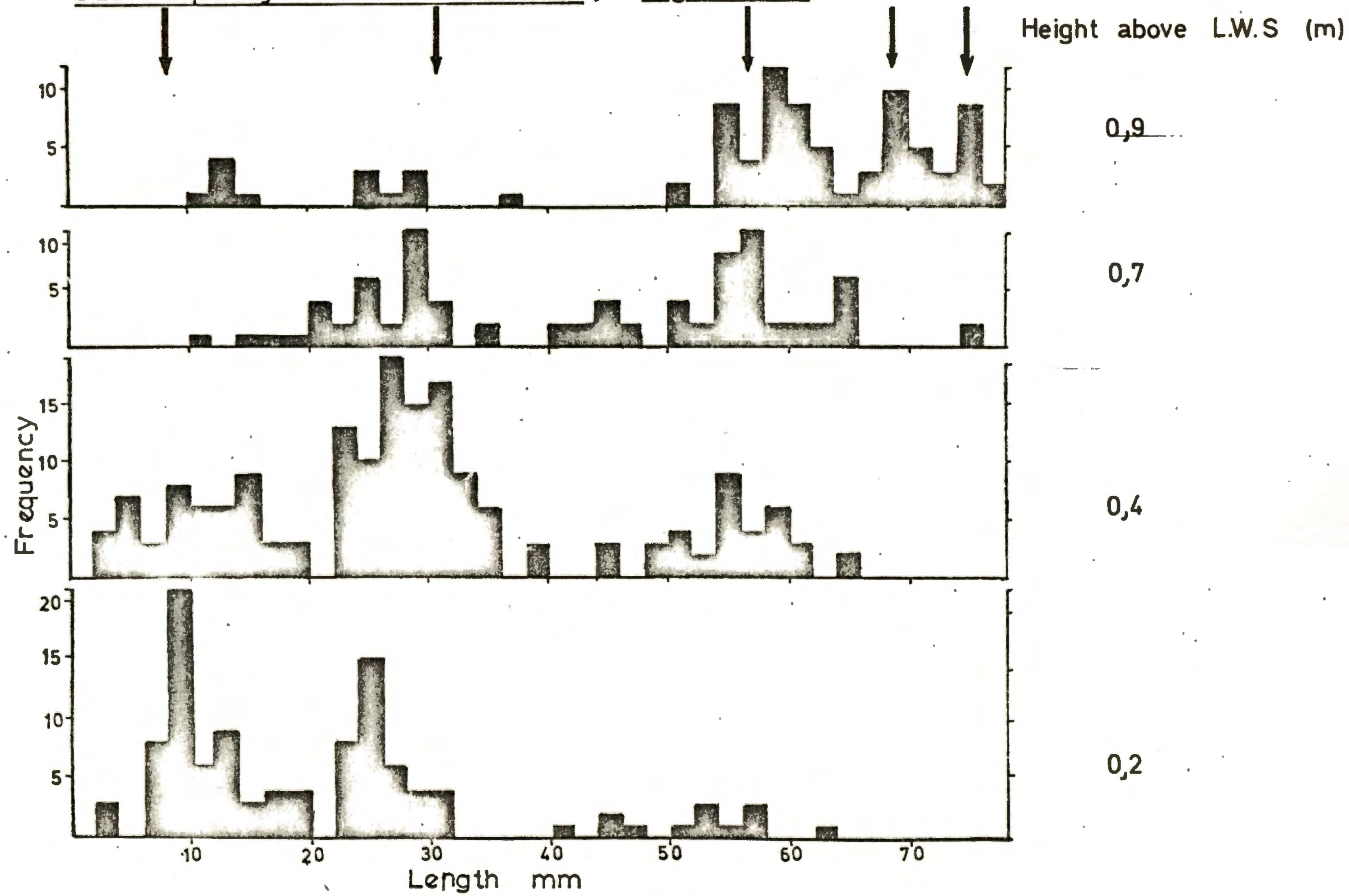


Fig. 3

Size frequency relative to zonation: *P. granatina*



(at Kommetjie) reveals a similar but less obvious trend: smaller animals predominate near low water while larger ones are commoner higher up the shore (fig. 3). Small specimens lack scars and move considerably and apparently at random. Larger animals have variable homing behaviour. Some specimens were recorded on the same scar for three years while others moved quite frequently. More important, the scar behaviour was more rigid higher up the shore. Table II is based on animals over 30mm. (approximately the size at which scars are formed).

TABLE II. Scar formation in P. granatina over 30mm. long (Kommetjie, 16.2.1973.)

| Site | Highest above L.W.S. (m.) | Mean length (mm.) | % with scars. |
|---|---|---|---|
| I | 0,2 | 49 | 15 |
| II | 0.8 | 47 | 20 |
| III | 1,3 | 56 | 90 |
| IV | 1,4 | 60 | 80 |

This clearly indicates the greater percentage of animals higher on the shore which possess scars.

P. oculus displays a similar size distribution on the shore, except that size is more closely linked to distance from water rather than vertical height. All juveniles are found in damp crevices or on encrusting algae which remain moist at low tide. Larger animals occur on bare exposed rocks. This results in a tendency for larger sizes to occur higher on the shore, but intertidal pools and moist depressions allow juveniles to occur relatively high on the shore as well. Settlement probably occurs over the entire shore in moist niches, as P. oculus may occur on isolated rocks (surrounded by sand) high in the upper balanoid (Branch, 1971). As the limpets mature, they disperse onto dry rock.

P. oculus form only temporary scars and seldom remain in one position for more than two weeks. Juveniles lack scars and move continually when covered with water. Although variable, movement generally decreases with age. Daily photographs of selected sites at Dalebrook show the positional changes which may occur, and how this is related to size (fig. 4).

The size distribution of P. concolor is also strongly suggestive of upward migration, as has been previously described (Section II, p.4).

These four species thus fall into a group in which there is a general tendency for larger animals to occur higher up the shore. This is due to upward migration in P. granularis, P. granatina (and possibly P. concolor) or movement away from damp niches in P. oculus. These animals have been grouped as "migratory".

P. cochlear, P. longicosta, P. miniata, P. tabularis and P. compressa all belong to a different category in which the individuals remain within a fixed habitat for their entire life. Dispersion from the site of settlement is lacking or restricted to the habitat of each species. No progressive upward movement occurs, and the term "non-migratory" has been coined to describe the group. P. argenvillei probably also belongs to this group, for although the juveniles move a great deal, they remain within the cochlear zone. P. barbara is impossible to categorise because of its sparcity, but occurs low in the intertidal or subtidally. Specimens are often found on <u>Pyura</u>.

In the migratory group, competition is alleviated by upward migration.

## <u>ADULT-JUVENILE DIFFERENTIATION</u>:

In the migratory group the requirements of adults and juveniles are fairly similar, for despite migration may occupy a similar substrate and eat the same food, and their habits are either similar or intergrade. By contrast, members of the non-migratory group often display sharp differences between adults and juveniles. Well defined transitions may occur in habitat, food or behaviour. Because all age groups share the same restricted zone, these differences may be important in reducing competition.

In medium to high density populations of <u>P. cochlear</u>, juveniles are restricted to the shells of other <u>P. cochlear</u> (Branch, 1971). This is not due to larval preference for this site, but rather because this is the only position where larvae are not destroyed by grazing of the other limpets. In sparse populations most of the juveniles occur on the rock itself. After about two years growth the juveniles on shells shift to the surrounding rock and establish scars there.

Lithothamnion coats the shells of <u>P. cochlear</u>, so that the limpets themselves provide space and a certain amount of food for juveniles. In this way these resources are not density dependent, and competition between adults and juveniles is minimised. Juveniles also descend onto the rock and feed there.

High density <u>P. argenvillei</u> populations are probably similar to those of *P. cochlear*, juveniles also occurring on the backs of adults. Such dense populations occur in the northern regions of the West Coast and were consequently not studied in any detail in the present work.

*P. longicosta* undergoes changes of habitat at different stages of its life. Details have already been given (Branch, 1971; and Section IV, p.9), but can be briefly summarised here as follows: First year animals occur on other shells (particularly *Oxystele sinensis* and other *P. longicosta*) and feed on the Ralfsia growing there. In the second year they move onto rock and feed on lithothamnion until they establish a *Ralfsia* garden (or occupy an empty scar with a garden). These transitions in habitat and food must also reduce competition between these age groups, although the second year group are competitively excluded from occupied *Ralfsia* patches. Movement is greatest in animals which lack gardens (see Section IV, p.9).

In this case, competition is primarily for the foodplant, *Ralfsia*.

*P. tabularis* is similar to *P. longicosta* in many respects. Adults occupy large subtidal patches of *Ralfsia*, clearing these of other algae and establishing a fixed scar roughly in the centre of the patch. Smaller animals are not found on *Ralfsia* patches, lack scars, and move around considerably. Adults feed only on *Ralfsia*, while juveniles browse more generally but still prefer *Ralfsia*.

The sparcity of *P. tabularis* makes it difficult to find them under water, but the discovery of five specimens on a *Turbo sarmaticus* suggests they parallel the life cycle of *P. longicosta*, being initially limited to shells and then

Fig. 4 Movement of P.oculus

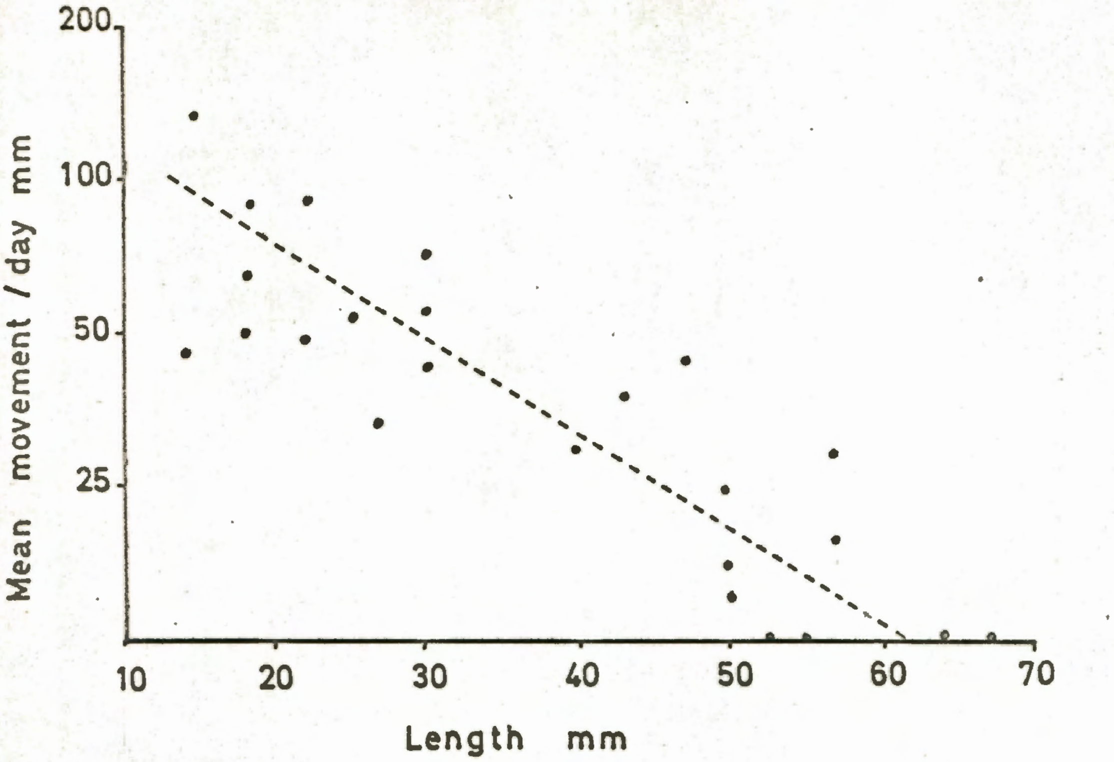
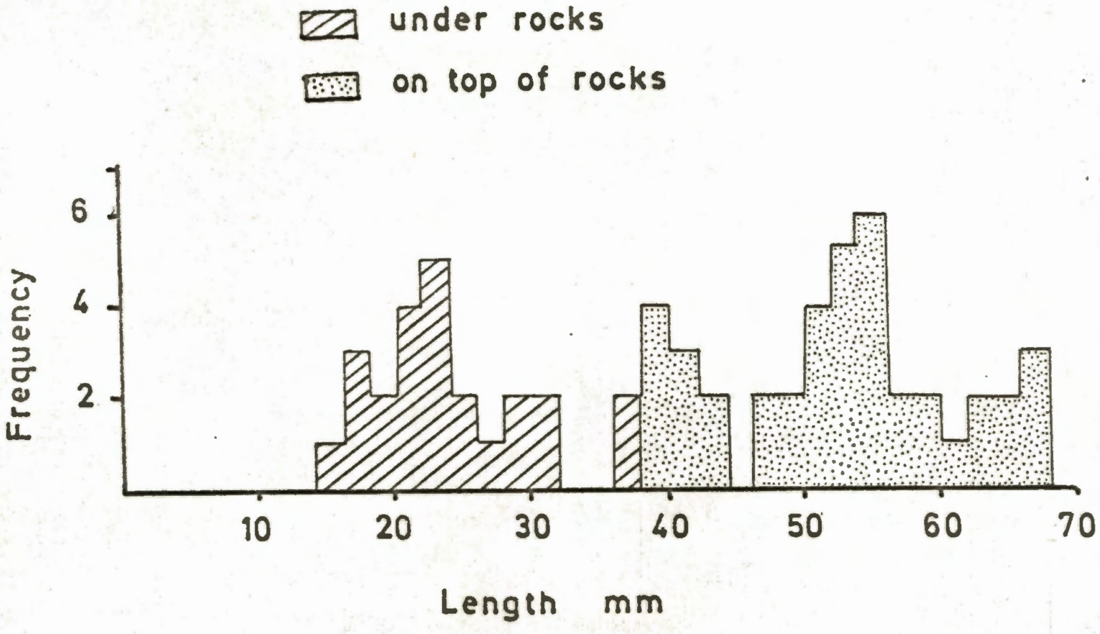


Fig. 5 Habitat differentiation in P. miniata



dispersing until they establish *Ralfsia* gardens. Larger numbers must be analysed before this can be established as certain. Such a differentiation would again reduce competition between adults and juveniles.

*P. miniata* juveniles are found on the lower surfaces of subtidal rocks, while adults occur only on the upper surfaces (fig. 5). In relation to this, they display different geotaxes. Juveniles are strongly geopositive, while adults are not. This can be demonstrated in the field by inverting stones they occupy: juveniles rapidly migrate downwards to the lower surface, while adults remain on the lower surface for variable lengths of time, but usually return to the upper surface within 24 hours.

In aquaria, this behaviour can be induced. Ten juveniles (20 to 25mm) were placed on five rocks in an aquarium and allowed 24 hours to establish themselves. The rocks were inverted and the direction and speed of limpet movement recorded. Nine animals moved under the rock within 15 minutes. The experiment was then repeated in total darkness and with light reflected from beneath. (In the dark speed could only be estimated from initial and final positions.)(Table III)

TABLE III: Geotaxis in *P. miniata*.

| Conditions | N. | Mean speed of movement cm/sec. | No. under rock in 15 mins. | Signif. (p.) |
|---|---|---|---|---|
| Light from above | 10 | 0,3 | 9 | < .001 |
| Total darkness | 10 | ±0,21 | 8 | < .05 |
| Light from below | 10 | 0,18 | 7 | < .05 |

In each case an obvious geopositive response occurs, and

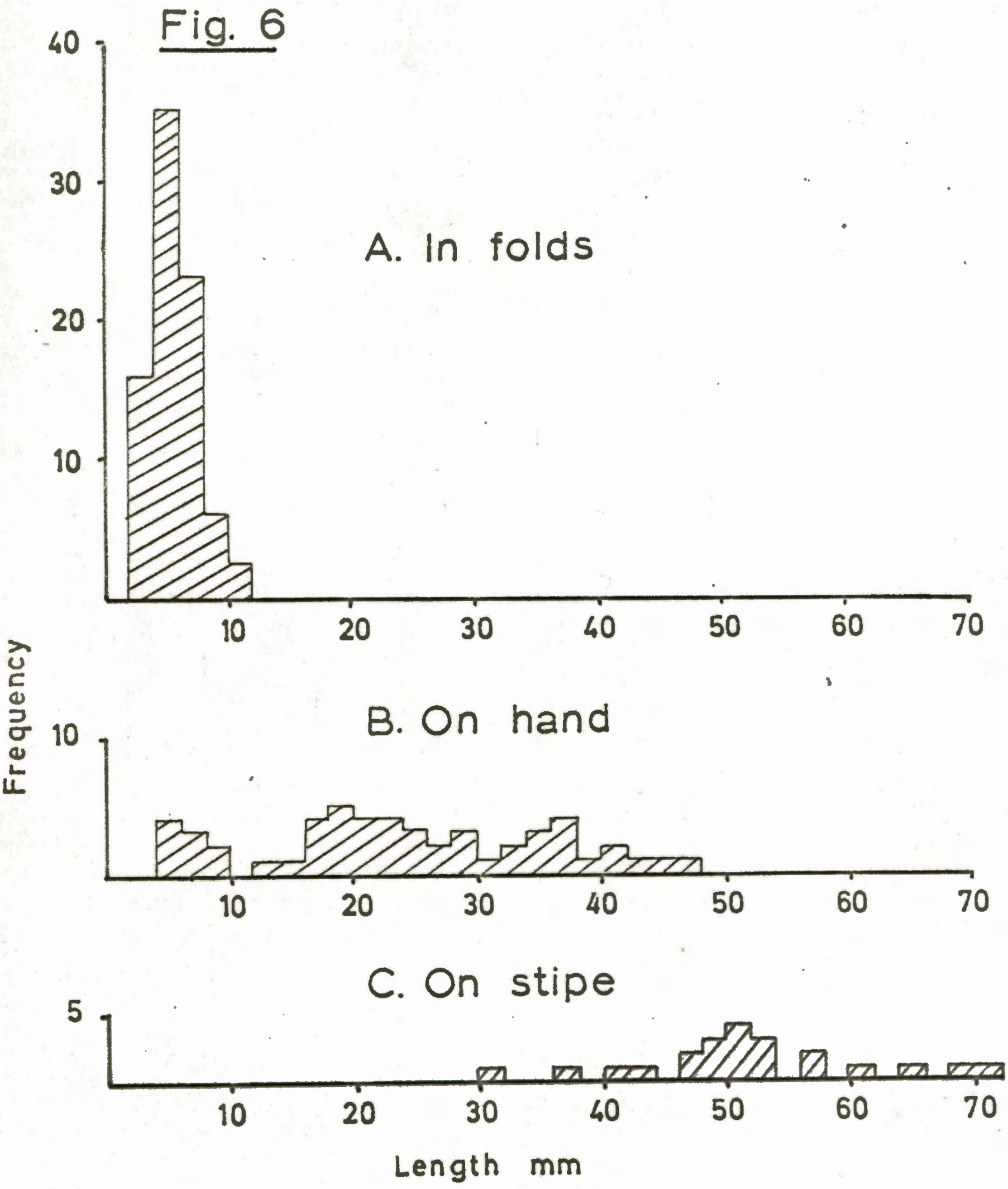


FIG. 6. *P.compressa*: habitat selection on *Ecklonia maxima*. Small animals accumulate in the folds at the base of the fronds, medium sized on the hand, and large on the stipe.

is reinforced by a photo-negative response under natural conditions.

Adults are less responsive because they possess scars, and reaction to the scar is probably dominant. Juveniles lack scars and do not remain in a fixed position. Adults feed almost solely on lithothamnion (Branch, 1971). Juveniles have a more varied diet but still prefer lithothamnion. Of a sample of 25, 80% contained lithothamnion while the others had a mixture of lithothamnion and other algae, bryozoan fragments and pieces of hydroid.

Once again the differentiation between juvenile and adult habitats is well defined and must reduce competition between the two.

<u>P. compressa</u> is almost entirely restricted to the kelp <u>Ecklonia maxima</u>, although small numbers may be found on <u>Laminaria pallida</u>. <u>Ecklonia</u> plants comprise a basal holdfast, with a single long hollow stipe terminating in a broader "hand", bearing lateral strap-shaped fronds. The plants may reach 10 m. in length. Juvenile <u>P. compressa</u> aggregate in folds where the fronds join the hand of the kelp. Animals of about 16 to 40 mm. move onto the hand. Some are found on the fronds but never remain there: dispersal occurs this way, animals moving from one kelp to another, as the fronds touch. Growth rates are unknown, but the size frequency distribution suggests these animals correspond to second and third year groups. Individuals larger than 40mm. are almost all found singly on kelp stipes (fig. 6). Day (1967, unpublished) found a similar relationship in his analysis of the kelp-bed community.

Fig. 7 Shell Shape in P. compressa

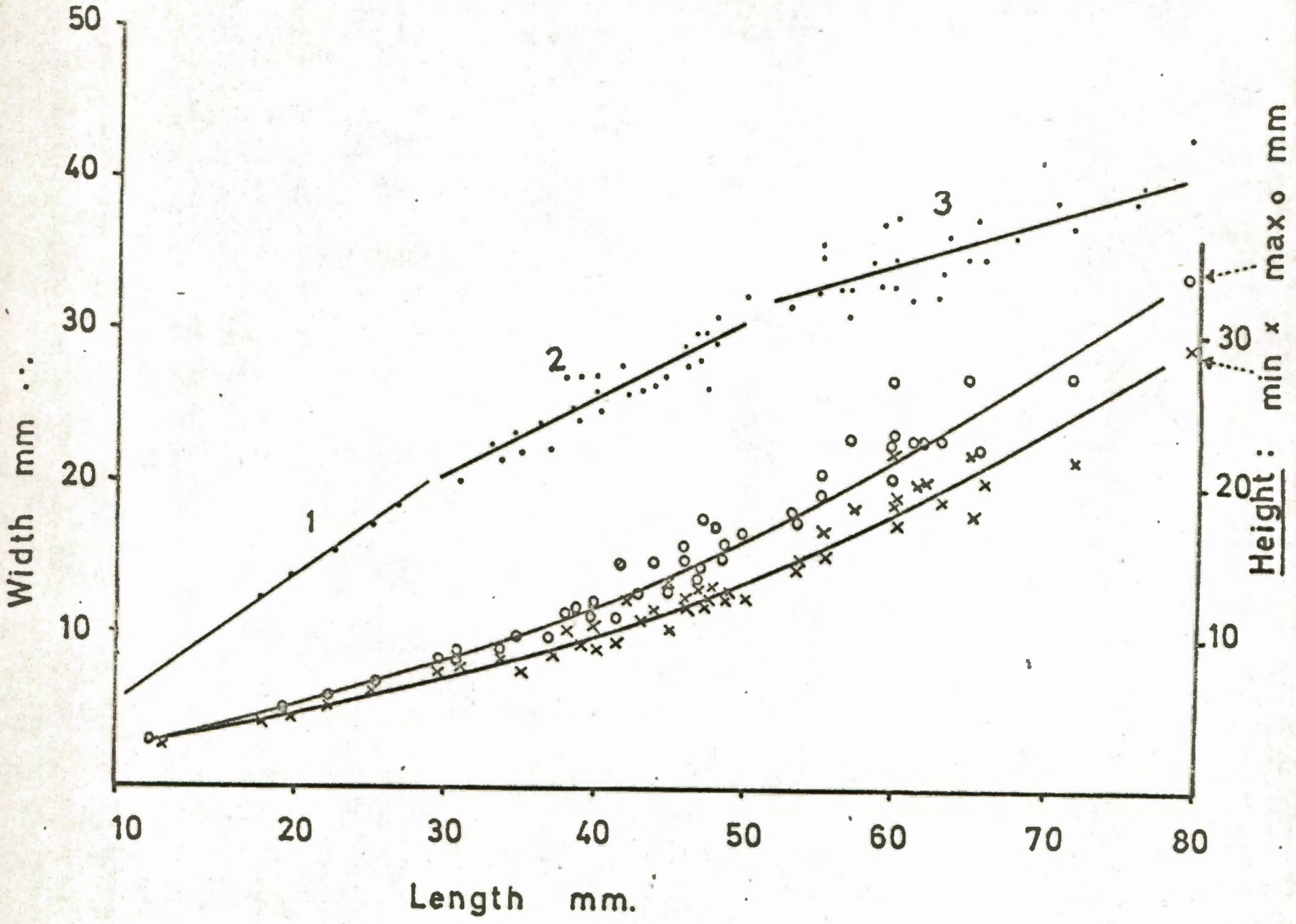
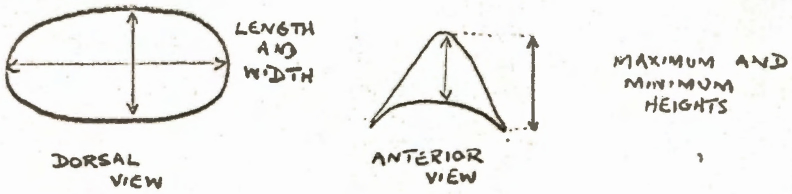


FIG. 7. Shell shape in P.compressa. The numbers I, 2,3, refer to animals on the folds, hand and stipe respectively.

Kain and Svendsen (1969) describe a similar occurrence in Britain, where juvenile *Patina pellucida* occur on the fronds of *Laminaria* spp. and then migrate down the stipe. Older animals form cavities in the holdfast.

In conjunction with positional changes, the shell of *P. compressa* changes shape. The shell becomes progressively concave (across the width) to fit the cylindrical kelp stipe. The ratio of width to length therefore decreases, while the maximum and minimum heights (see text figure) increase relative to length. Figure 7 summarises the proportions of the shell and demonstrates that there are three phases corresponding to the three changes of habitat. Regressions for these and tests of significance are given in Appendix I. Interestingly, the shell is ventrally concave even in juveniles, although they inhabit concave folds in the kelp. Concavity is more marked in larger animals on the kelp stipe.

TEXT FIGURE.



Thus in *P. compressa* the available space and food are again differentially utilised by different age groups, minimising competition.

*P. barbara* has not been studied in any detail, but there is no obvious adult - juvenile differentiation. Their habitats, food and habits are similar. However, small animals (less than 10mm) are commonly found on the shells of *Haliotis midae*, *Turbo sarmaticus* and other *P. barbara*. This is certainly imposed by grazing herbivores, and the habit seems to be short lived. Large numbers of *P. barbara* may also occur on

*Pyura*, and their shells are shaped to fit the *Pyura* test. These specimens remain on *Pyura* throughout their lives (Branch, 1971). The densities of *P. barbara* are very low, and no significant intraspecific competition would be expected.

## TERRITORIAL BEHAVIOUR:

The defence of an algal territory by the limpet *Lottia gigantea* has been described by Stimson (1970), and a similar behaviour recorded for *P. longicosta* (Branch, 1971). Experiments have now shown that the behaviour is widespread in South African limpets, although always restricted to the non-migratory group.

Adult *P. longicosta* occupy gardens of the alga *Ralfsia expansa*. These vary in size according to the size of the limpet, but most are about 150 $cm^2$ in area. The limpets feed almost entirely on this alga, and never move further than the perimeter of the garden. The establishment of gardens has been described earlier (Branch, 1971), but may be briefly summarised here: Most second year *P.longicosta* occur on lithothamnion, which they eventually graze away to the bare rock beneath. *Ralfsia* can only grow on bare rock, and is established in place of lithothamnion. The limpet then forms a scar in the centre of the *Ralfsia* and maintains the alga by grazing back any other alga (Branch 1971, plate 3).

Lithothamnion is not the only alga grazed back to establish *Ralfsia*. Low on the shore (or subtidally) *Colpomenia sinvosa*, *Leathesia diformis*, *Ulva* sp., corallines and other species may be cropped back, leaving *P. longicosta* in a crater surrounded by algal turf, in which it maintains Ralfsia (Branch 1971, plate 5).

Experimental introduction of Ulva sp. and Colpomenia sinvosa into Ralfsia gardens resulted in their complete removal by limpet grazing within two weeks.

Ralfsia is grazed away at about the same rate as it grows. The feeding pattern of P. longicosta is also different from that of other limpets. Most species completely graze all food in their paths, but P. longicosta rasps narrow irregular grooves across the Ralfsia, spaced so that ridges of the alga are left between the grooves (Plate 3b). This allows rapid regeneration of the alga.

More dramatic than the establishment of the gardens is the territorial defence of them against other limpets. This behaviour is evoked most readily when the animals are under water, and particularly with the incoming tide. This coincides with the period when most Patellas are feeding. Territorial behaviour is elicited by both natural and staged encounters with other limpets, and response is strongest to like species.

In a series of experiments, P. longicosta were removed from rocks and placed on the scars or gardens of territorial specimens which had moved off their scars to feed during the incoming tide. In each case the territorial animal thrust out its pallial tentacles as soon as contact was made and tested the invader with these ("Tentacle testing"). Variable periods of time (10 seconds to 9 minutes) then lapsed before the territorial animal slowly but forcibly pushed against the intruder. The latter always retreated slowly until it was pushed off the garden. Pushing then stopped, but the invader usually continued its retreat. In a few unusual cases the reaction was more violent and the territorial limpet rocked back and forward or twisted, banging the other animal forcibly.

Territorial defence can occasionally be induced in exposed animals,but reaction is unpredictable and failed to occur in 35 out of 38 tests.

Such behaviour is not limited to intraspecific contacts, and the gardens are also defended against P. oculus, P. barbara, and (to a lesser extent) P. granularis. Strangely, reaction to P. cochlear was often ambiguous or negative.

Natural territorial clashes are not often seen because they occur under water and usually in the incoming turbulent water when the animals start feeding. The following instances were recorded under water: P. oculus (4), P. granularis (1), P. barbara (3), other P. longicosta (10). A few encounters were seen while animals were exposed: P. barbara (1); other P. longicosta (4). In one interesting case two exposed P. longicosta were found touching one another, apparently contesting a Ralfsia garden. They remained in the same position for 3.5 hours until the incoming tide covered them again, when one started pushing the other away and forced it off the garden. In a further two cases exposed specimens were found locked together, unmoving for two hours, but observations could not be continued to include the effect of tidal submergence. This suggests that territorial defences are postponed if the animals are left exposed by the receeding tide and are resumed with the incoming tide.

If P. longicosta are removed from their gardens, the scars are rapidly occupied by smaller *P. longicosta* which had previously been restricted to lithothamnion (Branch, 1971). If this fails to occur (or is prevented) the gardens flourish initially but are eventually eradicated by other limpets (particularly *P. oculus*), or they are slowly overgrown by other algae. An analysis of 150 random quadrats (50 x 50 cm) at Dalebrook showed that 96.4% of the *Ralfsia* present is being maintained by *P. longicosta*. In this connection, an observation of Dayton's (1971) is interesting. He analysed the effects of competition and disturbance on intertidal populations in Washington State, and at five sites *Ralfsia* sp. was totally excluded unless limpets (*Acmaea* spp.) were removed from the sites. Conversely, almost all of the *Ralfsia* at Dalebrook is being actively maintained and conserved by the territorial behaviour of *P. longicosta*, preventing consumption by other limpets.

Such defence is important in reducing both intraspecific and interspecific competition. Smaller *P. longicosta* are prevented from invading established gardens, and resort to lithothamnion until they form gardens. This is important because each garden can probably only regenerate fast enough to support a single animal. The statement that territorial behaviour reduces competition needs explanation, for at first sight it appears that territorial behaviour is a *compment* of competition and not a factor *reducing* competition. However, it must be remembered that competition, by definition, limits a competitor's access to a necessary resource. The accent is on the word 'necessary', for while young *P. longicosta* clearly prefer *Ralfsia*, they can survive and grow normally without it. In this sense, territorial behaviour is compelling diversification and thus reducing competition.

P. tabularis also possesses large territorial gardens of Ralfsia, and displays a territorial behaviour which parallels that of P. longicosta in many respects. No territorial defence occurs while the animals are exposed, but when submerged they vigorously defend their territory during staged encounters. Ten P. tabularis were removed from their scars and held adjacent to others which were on their scars. In eight cases the scar owner lifted its shell, tested with its pallial tentacles for about two minutes and then violently shoved away the interloper until it was forced off the Ralfsia garden.

The Ralfsia gardens comprise areas of about 1600 to 2500 $cm^2$, kept free of other algae by the limpets. During feeding, only the top layer of Ralfsia is grazed away, allowing regeneration. Growth of this alga is more luxurient subtidally and recovery rapid. Underwater surveys of 50 random quadrats indicate that between 60 and 80% of the Ralfsia present occurs in gardens of P. tabularis and P. longicosta.

Curiously, although only one P. tabularis occurs on each garden, P. longicosta are quite often found on P. tabularis gardens and establish their own smaller territories there. The limited extent of their territory is indicated by their characteristic radular pattern. Neither P. longicosta nor P. tabularis could be induced to react to other herbivorous gastropods such as Oxystele spp. (although only small numbers were tested). This will be discussed further in Section VII.

Large P. compressa occur singly on kelp stipes, where they form an obvious scar. Staged encounters between scar owners and other animals always elicit a territorial defence. Tentacle testing is followed by a steady and strong pushing, forcing the intruder away. No such behaviour occurs in smaller animals which occupy the hand of the kelp and usually lack scars. Up to four such animals were found together on a single hand.

In an analysis of 360 kelp plants (at Buffels Bay, Cape Point), 232 carried a single P. compressa on their stipes, and only 15 had more than one. Of these, in 8 cases two animals were in contact with one another and were pushing against each other. Three of these kelp plants could be marked and relocated the next day when there was only a single animal remaining on the stipe. In the other 7 cases, two widely spaced scars had been formed on the stipe.

Such behaviour will prevent competition and ensure dispersal. Subjectively, this appears excessive, because each stipe must be able to support more than one limpet. Nevertheless, it does ensure that overcrowding never occurs.

P. cochlear populations are much more dense than those of other limpets, and as demonstrated in the previous section, competition can be considerable. With high densities, encounters can be expected frequently. Scars are clearly defined and homing behaviour very rigid. Older animals do not leave their scars at all, but rotate around on the scar to feed. Many scars are surrounded by a narrow fringe of Gelidium micropterum or Herposiphonia heringii, and the details of this relationship have been previously discussed (Branch, 1971). The limpets feed mainly on lithothamnion, although the Gelidium and Herposiphonia are also cropped.

Contact between animals is reduced by the rotatory movement of adults, feeding on lithothamnion in the immediate vicinity of the scar. Smaller animals almost invariably leave their scars to feed, even if they occur on the shells of other limpets. Distances of between 10 and 30 cms. are usually covered on these excursions. These smaller animals do contact older specimens. The reaction evoked is mild. Pallial tentacles are protruded and then a gentle rocking or pushing may follow, but the movement is often so slight that it is difficult to detect. Staged reactions produce a similar response, but if the "intruder" is persistently pushed against a limpet, the latter sometimes lifts its shell and clamps down on the mantle edge of the intruder. At other times there is no response. No reaction (except perhaps tentacle testing) occurs if the animals are exposed. Despite the mildness of this reaction, intruders respond quite readily and move away.

Reactions are so mild that they can hardly be considered as territorial defence, and leave one with the impression that the process has been ritualised. Nevertheless, withdrawal on contact and the rotatory feeding movements of adults must both help to reduce competition. Furthermore, it would obviously be undesirable in high density populations if every contact resulted in violent territorial response.

_P. miniata_ has not been tested because it is relatively uncommon, but it does possess a fixed scar when adult, and spaces out so that only a single adult occurs on each boulder. In two cases pairs of animals were seen in contact, apparently pushing against one another. The dispersive distribution and isolation of adults suggests an aggressive defence of a territory, but experimental evidence is lacking. _P. argenvillei_ has not been studied.

In the migratory group of animals, no fixed territory exists and aggressive intraspecific reactions are lacking in P. granatina, and P. granularis. P. oculus may or may not display an aggressive shoving, (presumably related to its dispersive habit), but does not defend a fixed site or food source. P. barbara displays no intraspecific reactions.

## DISPERSAL:

The individuals within a population may be aggressive, randomly distributed, or uniformly dispersed. Clark and Evans (1954) have developed a formulation which quantifies the pattern of dispersal. Their dispersal coefficient (R) is calculated as follows:-

$$R = \frac{\Sigma r}{N} \times 2\sqrt{p}$$

where r = distance between each animal and its nearest neighbour.

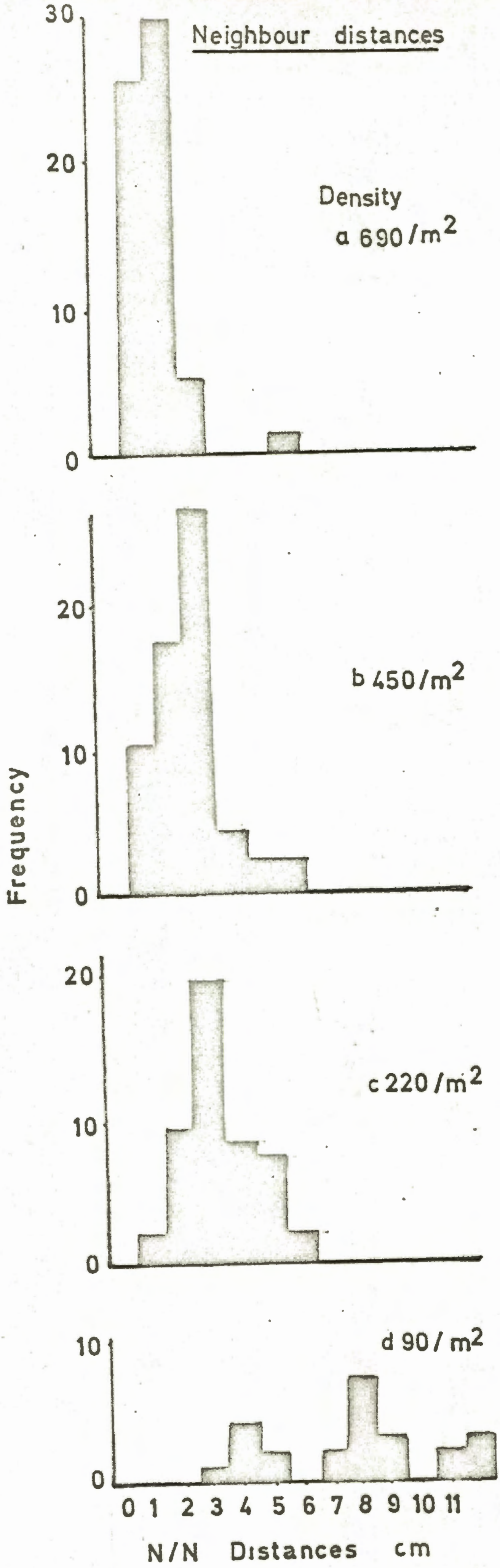
N = number of animals.

p = density (where area is measured in the same units as distance).

Values of 0.0, 1.0 and 2.0 for R, correspond to complete aggregation (contagious behaviour), random distribution and perfect (uniform) dispersal. In practice animal populations almost never attain perfect uniformity which requires a hexagonal equidistant array of all the animals. Complete aggregation on the other hand requires only that all the animals in a given area are in contact with one other animal, and this often occurs in natural populations.

In territorial species, dispersal of the population is an advantage because contact is minimised. The two are of

Fig 8 P. cochlear : Nearest Neighbour distances



course often linked, because one may be the result of the other. Where territorial gardens are formed, dispersal of these is of great importance to avoid overlap.

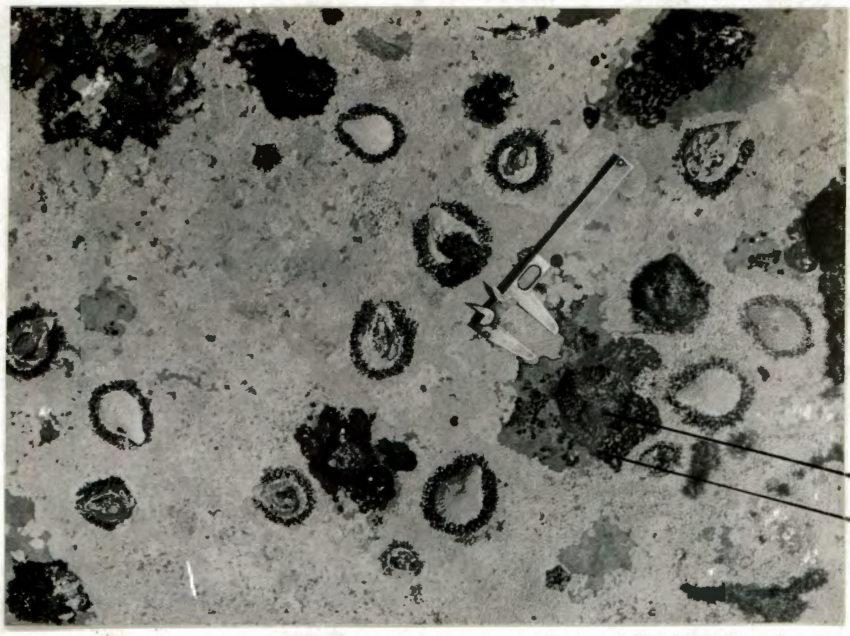
Non-territorial species may also be uniformly dispersed, so that the resources are evenly spread among the animals. However, there are reasons why dispersion may not be desirable or possible, as will be discussed below.

Of all the limpets, high density P. cochlear populations are the most obviously dispersed. Plate 2 shows the regular spacing of animals occupying the rock face. Considering only the animals on the rock, values of between 0,9 and 1,4 were obtained for the dispersal coefficient, the more uniform distribution being associated with denser populations. The nearest neighbour measurements (fig. 8) show that a minimum distance always exists between individuals, irrespective of the population density. As the density of limpets on the rock face increases, spacing still remains uniform although the average distance between animals may decrease. At densities of about $120/m^2$, or less, distribution becomes random, but minimum distances are still maintained between the animals (Plate 2).

This spacing of adult P. cochlear is comparable to that described for Spirorbis larvae and barnacle spat (summarised by Knight-Jones, 1961).

In P. cochlear spacing occurs when the juveniles leave their host shells and establish scars on the rock face. They will only settle and form scars if there is a minimum area free from other P. cochlear. Previous experiments (Branch, 1971) show that if adults are removed, their scars are rapidly

PLATE II. *P.cochlear* populations, showing how spacing becomes more regular as density increases. The decrease in numbers of *P.longicosta* and growth of *Ralfsia* is also apparent.



*P.cochlear*
60 per $m^2$

*P.longicosta*

*Ralfsia*

*P.cochlear*
200 per $m^2$

*Ralfsia*

*P.cochlear*
400 per $m^2$

filled by juveniles from surrounding shells. Natural death of adults produces a similar effect. Day *et al* (1973) recorded a comparable effect after oil pollution destroyed large numbers of adult *P. cochlear*. The scars seem to act as a releaser, inducing settling of the juveniles. In the absence of vacant scars, juveniles establish their own scars. The establishment of such sites has only been seen twice, as it occurs in the incoming turbulent water. In each case the juvenile shifted off its host shell as if feeding, but settled in a vacant area of lithothamnion. Here, each animal made wide rotatory movements in a circle covering about four times the width of the shell. In one case settlement occurred and the animal remained permanently at that site. In the second case another *P. cochlear* was encountered during the circling, and the juvenile moved off but stopped close by and repeated the rotatory movements. Here permanent settlement was accomplished.

Indirect observations support this sequence. On twelve occasions labelled juveniles moved from their host shells and established scars on the rocks. In each instance the new scar was well spaced out from the surrounding established adults.

The scar is formed by radular rasping, producing a sunken area which exactly fits the shell shape. This is aided by death and softening of lithothamnion under the foot, and by growth of the shell to fit the substrate. The rapidity with which scars are formed is due to the rasping away of lithothamnion. Specimens living on other shells often rasp through the periostracum and the crystalline shell layers and radula marks can be clearly seen on the shell surface.

Thus in *P. cochlear* uniform spacing occurs when the scar

FIG.9 Dispersal pattern in P.longicosta. Relationship between dispersion coefficient(R) and density.

Fig 9

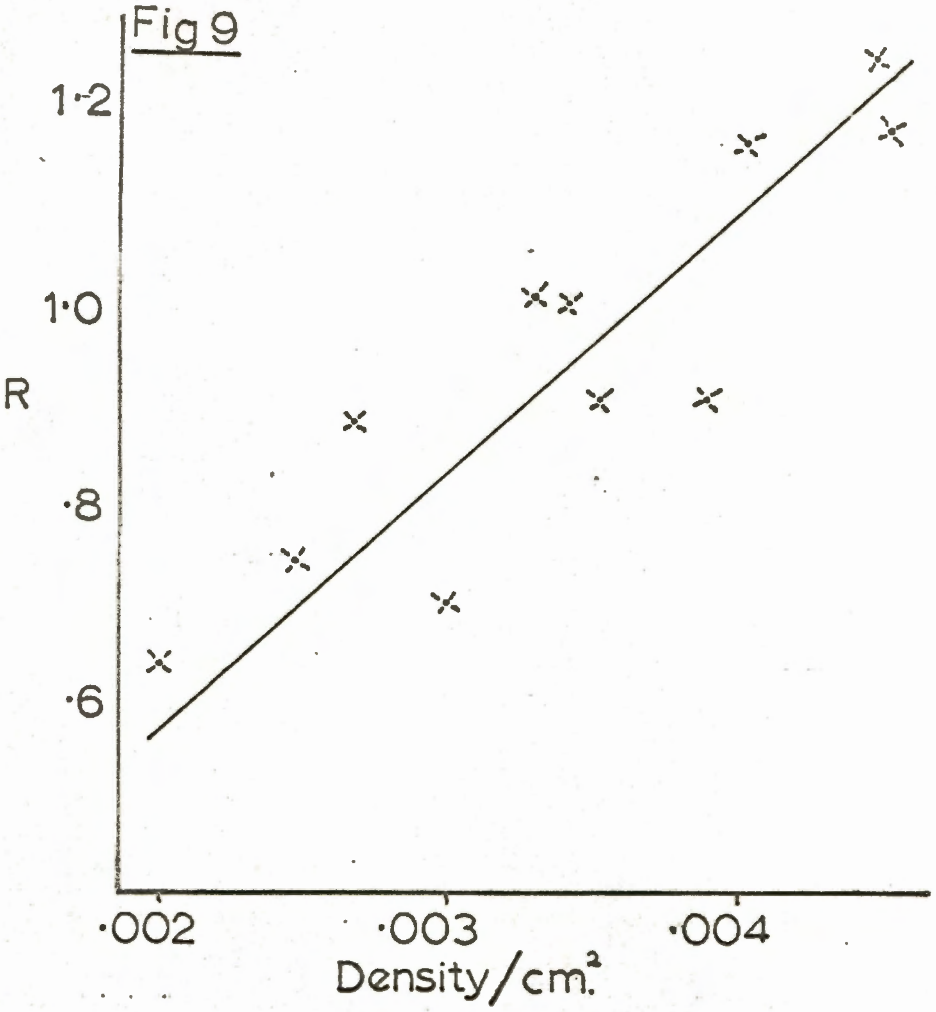
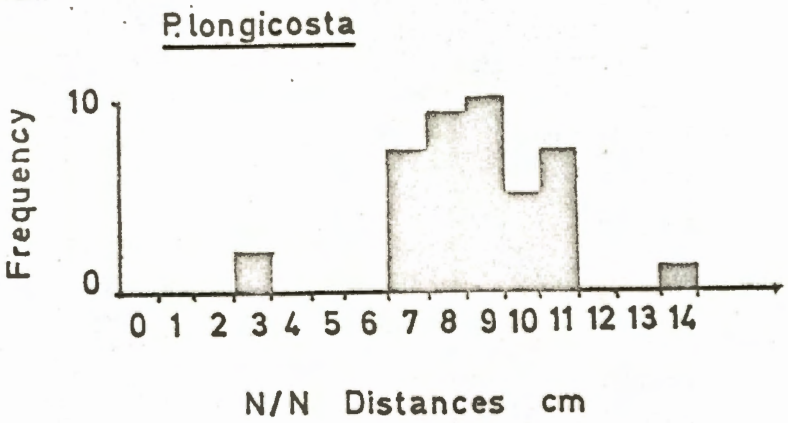


Fig. 10



is formed on rock: only if space is available, will a scar be established.

In *P. longicosta* the populations are never as dense as in *P. cochlear*. The dispersion coefficient ranges from 0,65 to 1,26 and is strongly correlated with density (fig. 9): low density populations are random, higher densities are uniform.

The limpets space out very obviously when they establish territorial gardens (Plate 3a). Most territorial individuals are at least 60 mm. from their closest neighbour (fig. 10). Minimum distances are much greater than in *P. cochlear*, in accordance with the size of *Ralfsia* gardens.

New scars are formed by animals which settle on bare patches on the rock or on *Ralfsia* and remain there. Such patches must contain no established *P. longicosta*, or the intruder will be forced out. The boundary to such areas is often defined by slight cracks or ridges in the rock surface (plate 3b). When the rock face is completely smooth, the limpets move as far as the garden perimeter, but at least part of the foot is kept on the garden. Under different circumstances the limpets are bounded by algal turf and this delimits their movements.

The spacing of scars (and gardens), and restriction by boundaries, will reduce contact between territorial animals and minimise competition.

*P. tabularis* is similar to *P. longicosta*, and adults defend large areas of *Ralfsia*. Sparcity of this species makes it impossible to quantify its dispersal. Nevertheless, only one animal occurs on each territory, and the territories

# PLATE III

A. Regular spacing of Ralfsia 'gardens' occupied by P. longicosta. Lithothamnion has been grazed back to establish the gardens. Note small P.longicosta restricted to lithothamnion (arrowed).

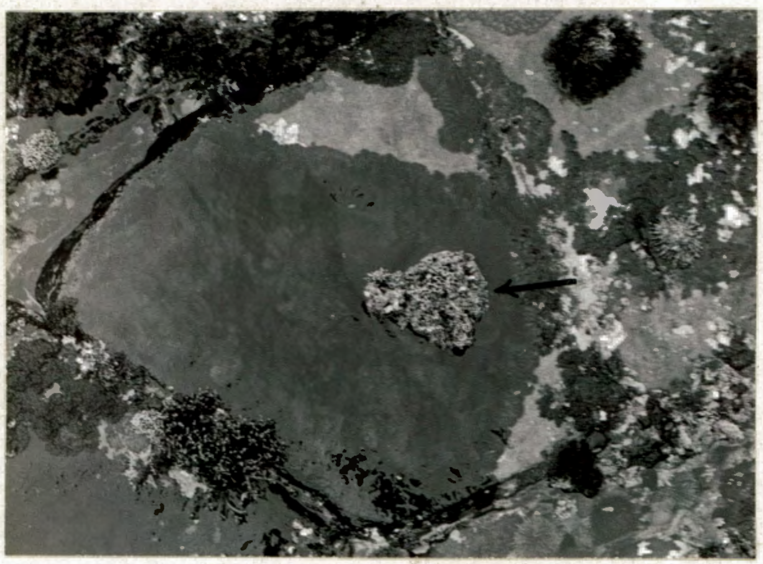
B. Boundaries to gardens are often fixed by grooves in the rocks. The characteristic grazing pattern of the P. longicosta can be seen. Small P. longicosta again restricted to lithothamnion (←— ) and P. oculus to bare rock (←---).

## PLATE IV :

P.tabularis on Ralfsia gardens.

a. The flat expanse is covered by Ralfsia, and the territorial boundaries are well defined by the surrounding algae. The profusion of the latter, and the algal growth on the P.tabularis shell (arrowed) give some indication of the algal growth occuring in the absence of limpet grazing.

b. A similarly well defined Ralfsia garden with a territorial P.tabularis. Rock topography defines t the edge of the garden. The P.tabularis shell (arrowed) is covered with Balanus algicola, which would normally have covered the rock if it were not for the limpet's browzing.



are dispersed so that only one occurs on each flat expanse of rock. Boundaries are set by the rock topography, and may be marked by fissures or abrupt changes in plane (Plate 4).

The same principle of dispersed territories and limitation to these territories will reduce competition. In *P. tabularis* competition is more effectively reduced in this way, because about 85% of the animals are found on territorial gardens, compared with about 40% in *P. longicosta*.

*P. miniata* is also too sparse for a quantitative measure of dispersal, but gives the impression of random distribution. They are never aggregated. Densities are usually low, although up to 1.2 per square metre have been recorded at Buffels Bay (Cape Point). Subtidal rocks carry only a single adult limpet each. This dispersal will again reduce contact and competition.

Because of its unusual habitat, dispersion of *P. compressa* cannot be analysed using Clark and Evans' (1954) formula, for substrate area and nearest-neighbour measurements cannot be obtained in a kelp-bed community. However, only a single scar and adult occurred on most stipes, indicating dispersal at the stage when scars are formed on the stipe. Dispersal was also demonstrated experimentally. Four groups of six animals (size range 30 to 50 mm) were transferred to the stipes of four kelp plants (which were devoid of *P. compressa*). In three cases dispersal occurred to nearby kelp plants (within four days) leaving only one animal on the stipe. In the fourth case one specimen remained on the stipe and two on the hand while two dispersed to other kelp plants and one was lost.

Comparable transferences were conducted with 10 isolated

Fig. 11

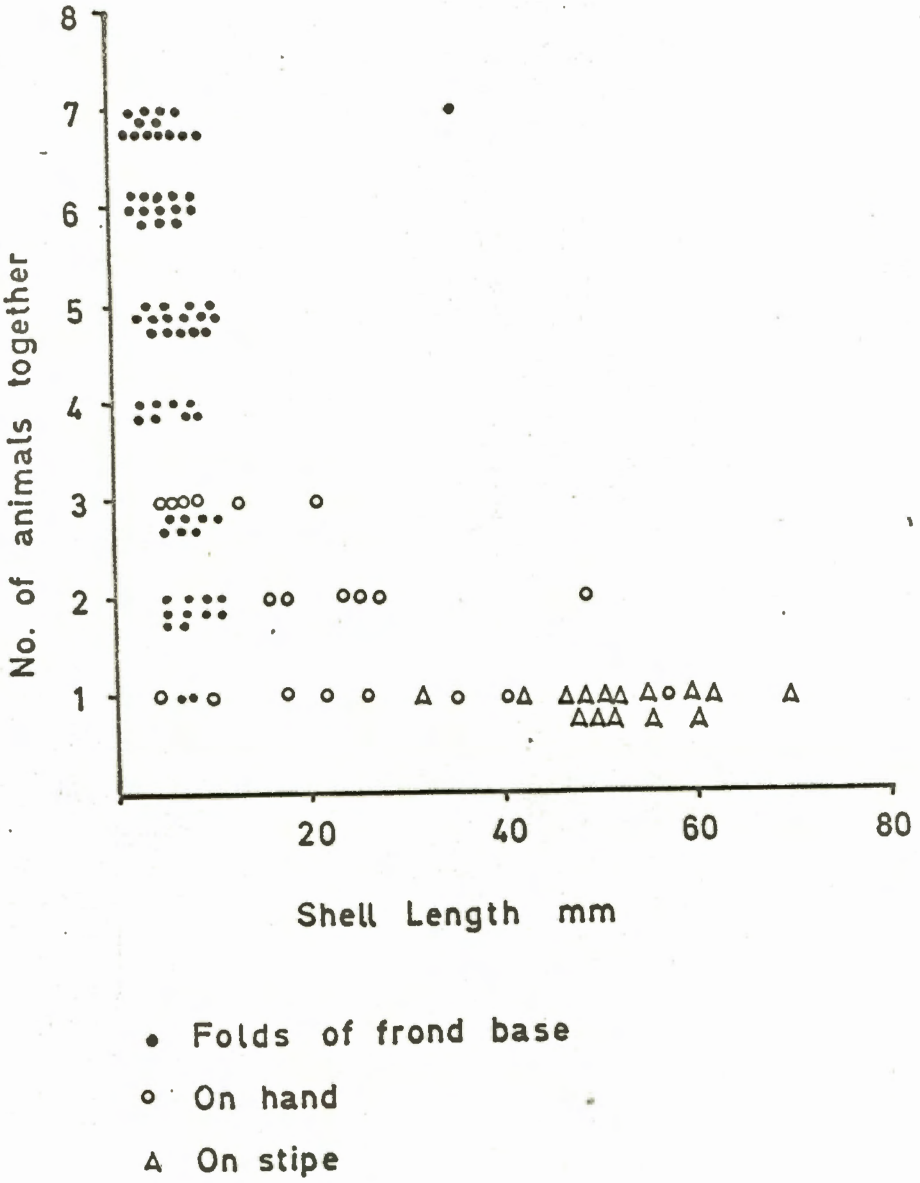


FIG II. The numbers of P.compressa occurring together, in relation to their sizes, and their niche on the kelp.

animals (sizes 40 to 62 mm). Five were placed singly on kelp stipes bearing established limpets and five onto unoccupied stipes. In the first case, four of the animals dispersed to adjacent kelp plants, and the fifth onto the kelp hand. Most of these could not be relocated two weeks later. In the second case, three animals remained on their respective stipes and formed scars within four weeks. One shifted to an adjacent kelp plant and then disappeared, and one was lost.

These results show a strong dispersive tendency in adults, and by implication a territorial defence against invading animals.

Dispersion is not developed in juveniles which may aggregate in the folds of the hand, and are often in contact. This may be because they are excluded from the hand by large animals, but is probably a direct response to the folds - they occur here even in the absence of larger animals. Intermediate sized animals are randomly distributed on the hand, but are never in contact.

Figure 11 illustrated the relationship between the numbers and size of animals found together at given sites on the kelp. This demonstrates the isolation of adults, and implies that they will only form a scar on an unoccupied stipe.

P. granatina populations are moderately to strongly aggregate, with values of R ranging from 0,31 to 0,82. Specimens are often in direct contact while others are randomly spaced out. This pattern of nearest-neighbour distances is maintained irrespective of zonation (fig. 12), although the value of R is slightly (but not significantly) lower in the upper shore.

Fig. 12 *P. granatina*

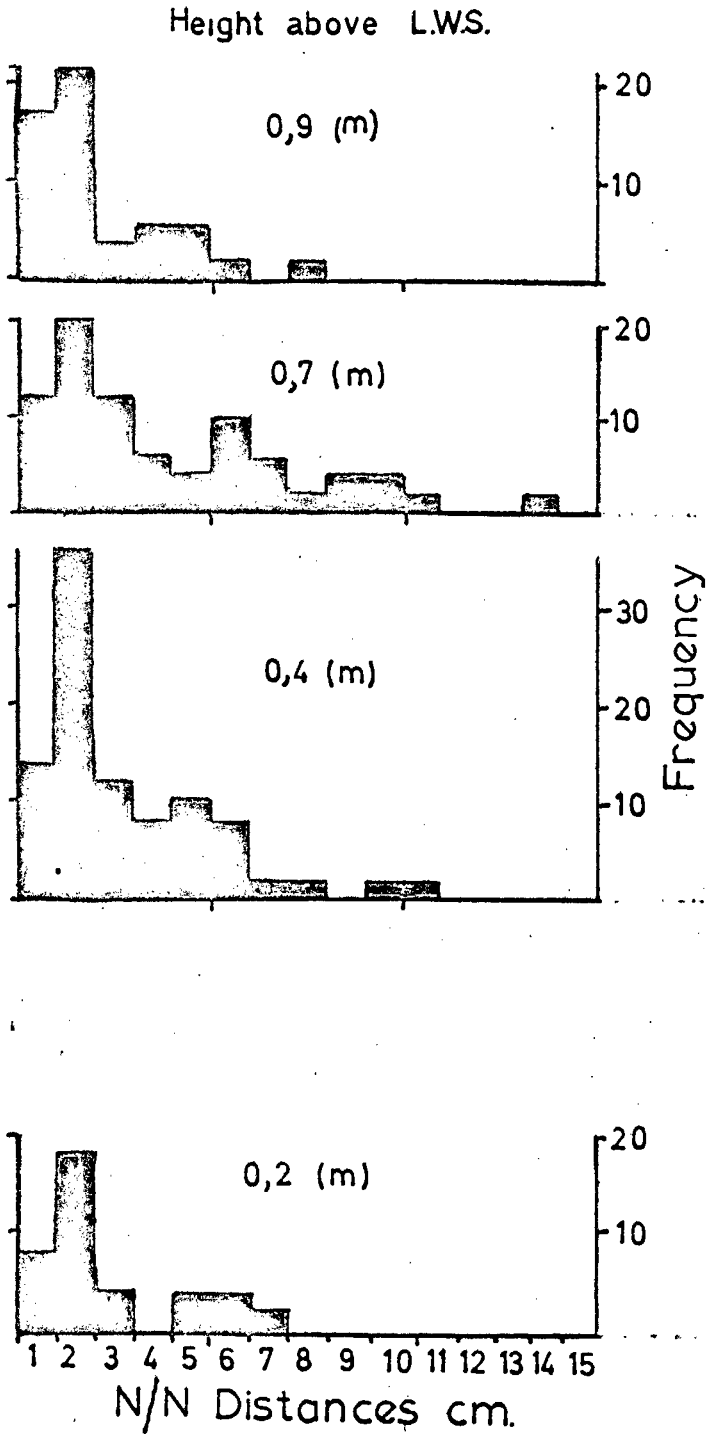


FIG.13. Dispersal pattern of *P.granularis*.

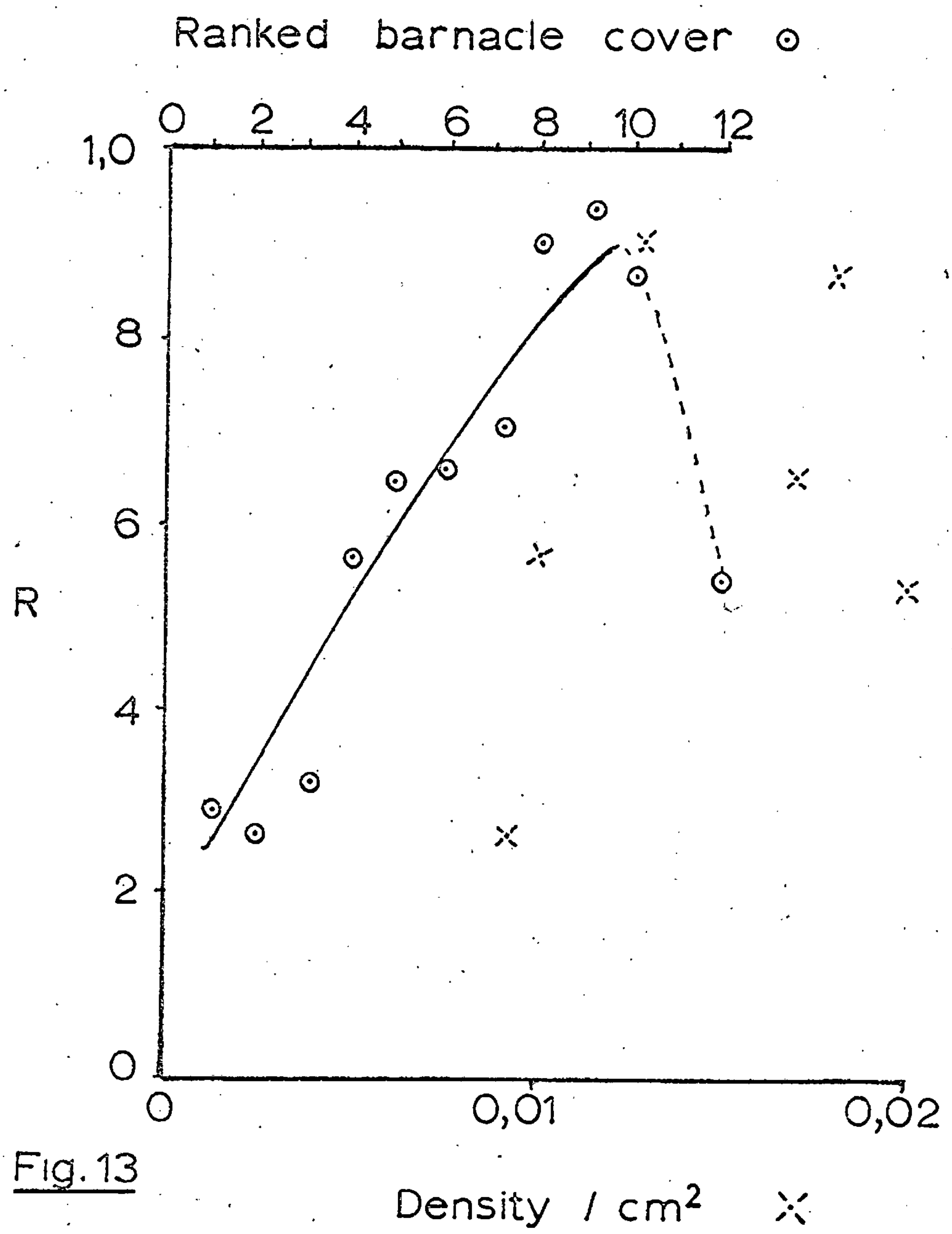


Fig. 13

Such patterns of distribution can be anticipated in this species, as it is non-territorial and displays no intraspecific aggression.

P. granularis is more variable in its dispersal pattern, but the dispersal coefficient R is always less than one, indicating random to aggregate distribution. No correlation exists between R and density (fig. 13). However, at Dalebrook there is a striking correlation between the amount of cover (in the form of barnacles) and the value of R. If cover is totally absent,the limpets are strongly aggregated, but they tend increasingly towards randomness as barnacle cover increases (fig. 13, Plate 5). Aggregation usually occurs in cracks which are probably more moist or humid than the surrounding rocks, or which may be shaded at certain times of the day. In extremely dense stands of barnacles the limpets are more aggregate again, but this is probably a function of their restriction to small barnacle-free patches. In the absence of cover aggregation will help reduce water loss because moisture is retained between the limpets. Barnacle stands are always moist because water collects between the animals, and desiccation will be low in such sites.

In P. granularis populations at Kommetjie (where barnacles are relatively uncommon) a similar transition occurs from random to aggregate distribution as one moves up the shore (Plates 6a, b, c). Again, aggregation is occurring where desiccation is greatest, and dispersive behaviour can obviously be modified in response to prevailing conditions.

Nearest-neighbour distances illustrate this trend (fig. 14), and their distribution is normal to random if desiccation is low, but highly skewed to the left where cover is lacking and desiccation high.

PLATE V

P granularis: pattern of dispersal in relation to barnacle cover.

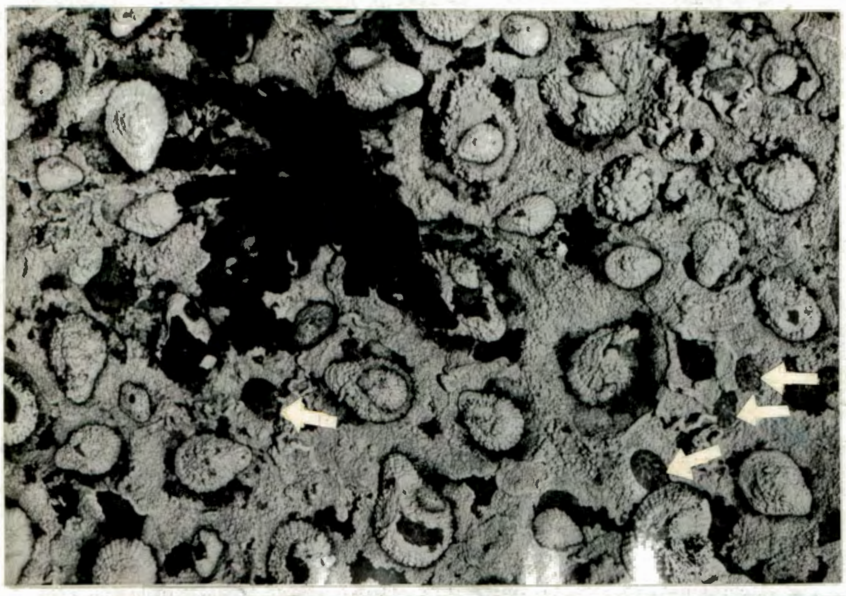
98% barnacle cover. Limpets random to dispersed.

40% barnacle cover. Limpets random to aggregate.

10 % barnacle cover. Limpets strongly aggregated.

PLATE VI

P.granularis: pattern of dispersal in relation to zonation , at Kommetjie.Figures indicate height above low water springs.



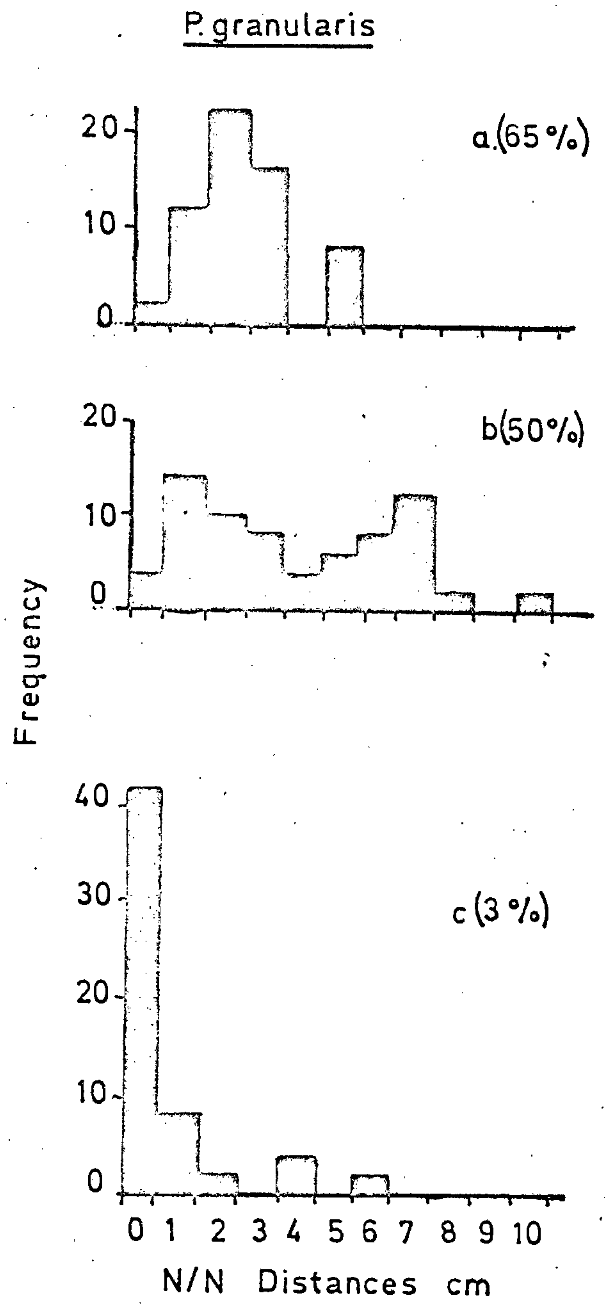
A. Cochlear zone.(+0.2m) Random P.granularis among P.cochlear

B.Lower balanoid. Random P.granularis distribution. (0.5m)

C.Upper balanoid (I.2m). P.granularis aggregated.

FIG.14 Dispersal pattern of *P.granularis* (% barnacle cover indicated in brackets).

Fig. 14



In cases where P. granularis are strongly aggregated, each group of animals is spaced out from the next. The areas between aggregates are covered by the animals when they spread out to feed.

Thus in the migratory P. granularis and P. granatina, their distribution patterns are never uniform, and may even be perfectly aggregate to reduce desiccation by the retention of moisture between the limpets. Such behaviour is in keeping with the lack of aggressive reaction between animals. In these cases, competition is reduced by upward migration - not by uniform distribution or territorial behaviour.

P. oculus is too sparse to assess spacing quantitatively, but specimens are never found in contact, and may be aggressive when contacts are staged. Dispersive behaviour obviously occurs, even if it cannot be quantified. P. oculus grows more rapidly than other limpets (Section IV), has a shorter life, and probably a higher metabolic rate. Large areas are covered while feeding, and a high intake of food can be expected. Thus dispersive behaviour may be important in reducing competition, despite the relatively low density of this species.

## DISCUSSION:

Two basic mechanisms have been evolved by limpets to reduce intraspecific competition. They may migrate progressively away from the site of settlement, or they may remain in a fixed zone and develop behavioural patterns to reduce competition.

### 1. Migratory Species:

Many limpets migrate progressively up the shore, limited only by their tolerance to stress such as desiccation. This leads to differential zonation with respect to size, larger animals occurring higher up the shore. P. granularis, P. granatina, P. concolor and (to a lesser extent) P. oculus fall into this category. In relation to this behaviour, these species have poorly (or temporarily) developed homing behaviour, no territorial behaviour, usually non-aggressive intraspecific reactions, and random to aggregate distribution. P. granularis may have a well developed homing habit high on the shore, but this is variable, and absent lower on the shore.

All these species are generalised grazers feeding on any available food (Branch, 1971); they have relatively high growth rates, low longevity and a high gonad output. As previously described, the last three factors are probably linked (Section IV). None of these species display a sharp differentiation between adults and juveniles, as far as habits, habitat or food are concerned. Mortality is therefore fairly uniform throughout life (Section IV).

One of the interesting features of this sequence of behavioural patterns is that it occurs in many parts of the world, often in taxonomically different groups. Similar migrations have been recorded in Acmaea digitalis (Frank, 1965; Breen, 1973), A. dorsuosa (Abe, 1931), P. vulgata (Das and Sesheppa, 1948; Jones, 1948; Lewis, 1954), and possibly Siphonaria aspersa (personal observations). As far as is known, all these species also conform to the features mentioned above.

Only in one high level species (Cellana radiata) has the reverse size-zonation pattern been recorded (Balaparameswara et al, 1971). In this species, larger animals occur lower on the shore, and Balaparameswara ascribes this to modification of shell shape in relation to desiccation and not to migration.

Variations in aggregating behaviour are also shared by diverse limpets. In P. granularis aggregations occur under desiccating conditions, and random distribution under moist conditions. In Japan, Acmaea dorsuosa (Abe, 1931) forms aggregates in summer, but these break up in winter when raging storms raise the mean tide level. During the latter period, most animals migrate upwards. On the West Coast of America A. digitalis forms aggregates at high levels and undertakes upward migration in autumn or winter, and lesser return migrations in summer (Frank, 1965; Millard, 1968; Breen, 1973). P. vulgata parallels this behaviour in Europe (Lewis, 1954). Siphonaria aspersa also forms aggregates on dry high level rocks. The formation of aggregations only occurs between like species, and Willoughby (1973) has suggested that it entails a species-specific recognition. In all, aggregation occurs in response to desiccating conditions.

Thus these divergent species have developed a remarkable series of parallel behaviour patterns with respect to migrations, aggregation, feeding habits, intraspecific responses, homing behaviour and lack of adult - juvenile differentiation.

An interesting exception is the Antarctic limpet, Patinigera polaris, which migrates downwards in autumn to occupy the sublittoral in winter to escape freezing. In spring there is a return migration to the littoral Zone (Walker, 1972). This sequence is the reverse of that described above for other species (where upward migration occurs in cool conditions) but is clearly adaptive in terms of local conditions.

The principal advantage of upward migration is that the species occupies a wider range over which the biomass may be spread and hence has greater food resources. Figure 15 summarises the zonation of Patella at Elands Bay, and shows how the lower shore is dominated by the non-migratory P. cochlear and P. argenvillei, while the migratory P. granularis and P. granatina extend over most of the shore. The distribution of total limpet biomass (wet weight) decreases sharply just above low water neaps (the limit of P. cochlear and P. argenvillei). Above this the migratory species will experience less interspecific competition. The biomass of P. granularis and P . granatina is spread fairly evenly over the upper shore. Migration will thus prevent accumulation in one zone, and hence keep competition low.

Breen (1971) has suggested that homing in Acmaea digitalis may become less marked under conditions of crowding, thus facilitating dispersal and reducing competition. His evidence for this is however not conclusive.

Other advantages probably accrue from upward migration. Breen (1973) has shown that migrant A. digitalis grow faster than those remaining at a fixed level. Predation is probably less at higher levels. Mortality rate of Patella granularis decreases in older groups, which occur higher on the shore (Section IV). Relative to low level populations, mortality of high level A. digitalis is higher in summer and lower in winter, but annual mortality is greatest in the populations lowest on the shore (Frank, 1965). The pattern is similar in A. scabra (Sutherland, 1970) although this species does not migrate. In P. vulgata (Lewis, 1954) high level animals experience low mortality rates most of the year, but are subject

FIG.I5. Transect at Elands Bay, showing the distribution of limpet numbers, biomass, and total biomass. The latter is indicated in brackets.

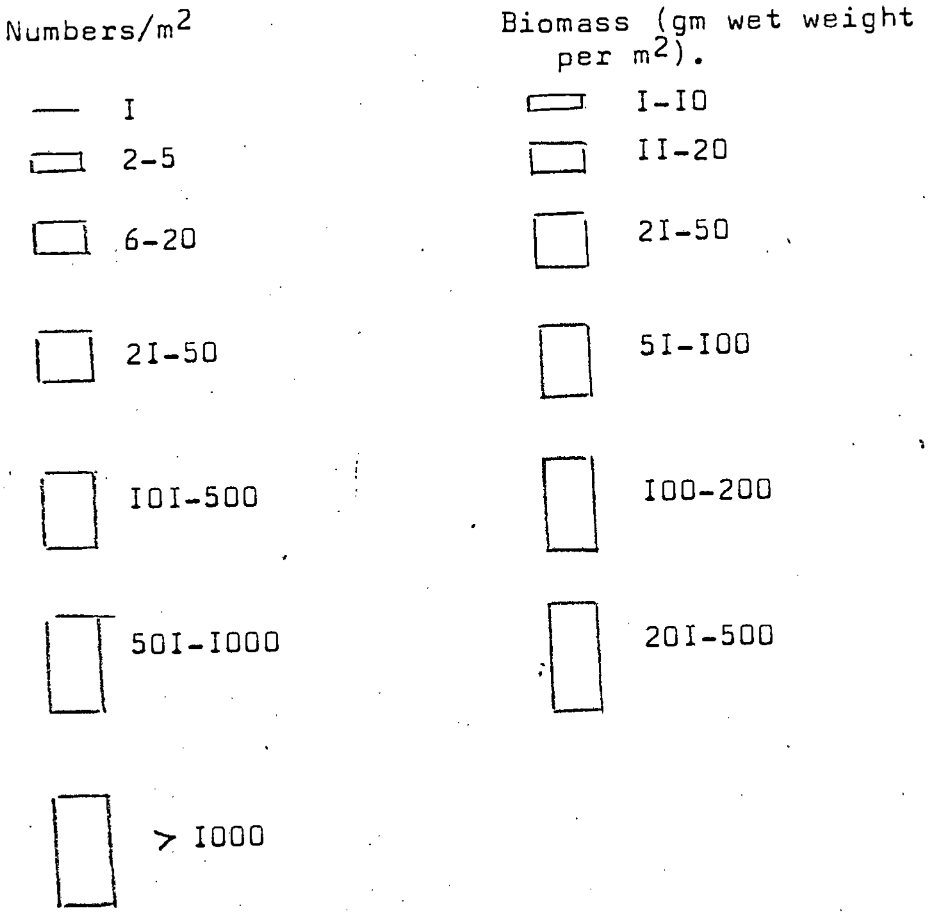
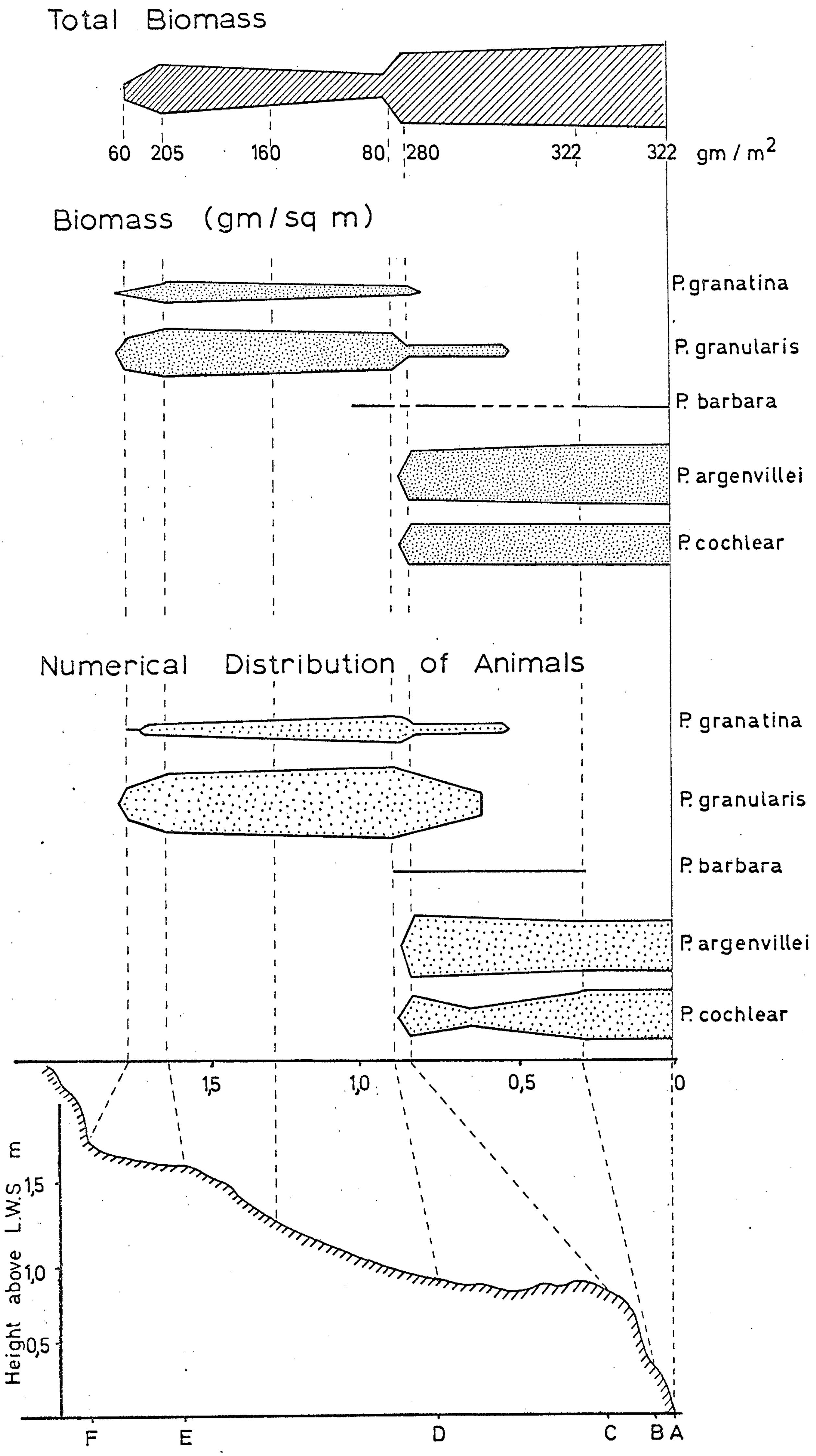


Fig. 15



Total Biomass

Biomass (gm/sq m)

Numerical Distribution of Animals

to "crash" mortality (or downward migration) in summer. Low level P. vulgata die progressively throughout the year.

Thus within each species overall mortality on the upper shore is probably no greater than at low levels, despite the arduous physical conditions and the catastrophic losses which may occur in summer.

The factors controlling upward migration are not known, although several limpets disperse from regions of high density: A. digitalis (Breen 1971, 1973), P. granularis, P. granatina and P. compressa. The work of Eaton (1968), Craig (1968) and Rogers (1968) on three Acmaea spp. offers instructive glimpses of the controlling mechanisms which may exist. A. limatula moves upwards during the nocturnal rising tide and downwards during daylight rise and fall. This is related to its strong photonegative response (Ross, 1968). A. scabra and A. pelta move upwards with the rising tide and downward with the falling tide. Clearly all three are responsive to tidal movement and this may regulate their zonation.

The only detailed experimental analysis of limpet movements is that of Abe (1931). Of his work on A. dorsuosa, the following observations are pertinent: activity occurs at night and with the rising tide; the limpets are geonegative and aggregate at the air-water interface in aquaria; small animals are photopositive in diffuse light, larger ones photonegative; when dry, the limpets are positively rheotactic, but when submerged, they become negatively rheotactic. All of these responses will lead to an upward migration, particularly in juveniles.

Conversely, the low level A. schrenckii concinna is always geopositive and therefore remains at low levels (Abe, 1931).

These behavioural responses to light, tidal movement, gravity and air offer the most logical explanation of zonation patterns and migratory or non-migratory behaviour. Analysis of such responses in Patella are now required before their relative movements can be explained rather than described.

2. Non-migratory species:

P. cochlear, P. longicosta and P. argenvillei all occupy relatively fixed zones low in the intertidal, and undergo no vertical migration from the site of settlement. This is also true of the subtidal P. tabularis and P. miniata. P. compressa maintain their specialised position on Ecklonia, although they do move down the stipe as they age.

In these cases the same zone or habitat is shared by adults and juveniles, and different mechanisms have been evolved to minimise competition.

Most adults have a fixed scar, and defend the territory around this scar, reacting aggressively to others of the same species. This leads to a dispersed population. In P. cochlear a large number of encounters are inevitable because of the high density. This makes aggressive response undesirable. Reaction between animals is mild and appears ritualised, and this has probably been selected for because it is advantageous in these high density populations.

Bovbjerb (1964) suggests that there are two types of dispersal in aquatic animals: density dependent dispersal due to aggressive interaction of the animals, and density independent dispersal when aggression is lacking.

Many non-migratory species are very specific in their choice of food, and in some cases their activities establish or maintain the foodplant. Obvious examples are P. cochlear and *P. miniata* on lithothamnion, *P. longicosta* and *P. tabularis* on *Ralfsia*, and *Lottia gigantea* on an unidentified algal film (Stimson, 1970). This is another example of remarkably parallel behaviour patterns in two different families of limpet.

*P. compressa* is specialised for life on the kelp *Ecklonia*. This too has parallels in other groups. *Patina pellucida* occurs on *Laminaria* in Britain (Graham and Fretter, 1947), *Acmaea incessa* on *Egregia* (Bullock, 1953), and *A. pellucida* on *Phyllospadix* (Yonge, 1962).

Of the South African limpets, four of those with narrow food requirements feed on lithothamnion or *Ralfsia*. It is interesting that Paine and Vadas (1969) record these species as having very low calorific values, and falling below the "preferred" range of 12 common marine invertebrates. If this is true on South African shores, then competition for these algae will be reduced.

As previously described (Section II, p.7), feeding habits are often very specific low on the shore or intertidally. In this region the quantity and diversity of algae and limpets are greatest. Specialisation is possible due to the quantity and variety of algae, and is probably important in maintaining so many coexistent *Patella* spp. On South African shores speciation of the genus is greater than anywhere else, and significantly, a greater percentage of the group are specialised in their feeding habits.

All the *Patella* spp. which aggressively defend a territory have a low gonad output (Section IV). It is doubtful if the two are directly linked, but as territorial species have a high longevity, selection for small gonad size may have occurred (as Evans and Smith, 1952, have argued).

Knight-Jones (1961) has drawn attention to some of the ways competition may occur between different age groups of a species. In non-migratory Patellas there is often a marked difference in food or habitat between juveniles or adults, which will reduce competition. Examples of this have been described above. The transition involved may make the animals temporarily vulnerable, and massive mortalities may occur during the transition.

Adult - juvenile differentiation may also impart incidental benefits. A large proportion of P. longicosta juveniles are found on the shells of Oxystele sinensis. As this winkle shows the strongest avoidance reactions to the predatory Marthasterias glacialis, the limpets may also benefit from these escape reactions. Small P. miniata occur under boulders where predation by fish and starfish is probably lower and where they will not be grazed by other limpets. Juvenile P. compressa occupy folds in the kelp hand where they will be most protected from wave action and predators. P. cochlear juveniles live on the lithothamnion covered shells of adults, thus gaining substrate and food,partly independent of density.

Scars and homing behaviour are most obvious in territorial species. This is related to their territorial function in maintaining a given area, and to their importance in reducing predation (see Section VIII). These species occur low on the shore or subtidally, where desiccation is not a problem. Migratory species on the other hand have poorly defined scars and homing behaviour, except at the upper limits of their zonation, where desiccation must be minimised.

These differences suggest that homing and scars have

FIG. I6. Gradation of migratory and nonmigratory Behaviour in *Patella*.

◯ ⟨ Migratory Nonmigratory ⟩ □

|  | P. granularis | P. granatina | P. concolor | P. oculus | P. barbara | P. argenvillei | P. compressa | P. miniata | P. tabularis | P. longicosta | P. cochlear |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Migrate up shore | ◯ | ◯ | ◯ | ∘ | ▫ | ▫ | ▫ | ▫ | □ | □ | □ | Zonation restricted |
| Generalised food | ◯ | ◯ | ◯ | ◯ | ◯ | ∘ | □ | □ | □ | □ | □ | Specific food. |
| Non-aggressive | ◯ | ◯ | ?∘ | ▫ | ∘ | ?▫ | □ | □ | □ | □ | ▫ | Aggressive. |
| Aggregate to random. | ◯ | ◯ | – | ▫ | ?∘ | ▫ | □ | □ | □ | □ | □ | Random to dispersed. |
| Scar temporary or absent | ◯ | ◯ | ?∘ | ◯ | ?▫ | ?∘ | □ | ▫ | □ | □ | □ | Scar permanent. |
| Homing varies may be absent | ◯ | ◯ | ∘ | ◯ | ?▫ | ▫ | □ | ▫ | □ | □ | □ | Homing rigid. |
| High gonad output. | ◯ | ◯ | ◯ | ▫ | ◯ | ◯ | ▫ | □ | □ | □ | □ | Low gonad output. |
| No territory | ◯ | ◯ | – | ◯ | ▫ | ?▫ | □ | ▫ | □ | □ | ▫ | Territorial defence. |
| No marked adult-juv. differentiatn | ◯ | ◯ | ◯ | ◯ | ▫ | ▫ | ▫ | ▫ | □ | □ | ▫ | Sharp adult-juvenile differentiatn. |

KEY:

◯ Migratory characteristics

□ Nonmigratory characteristics

◯□ Tendency well developed

∘ ▫ Tendency poorly developed

? Uncertain

– Unknown.

different functions in the different species - territorial maintenance, reduction of predation, or prevention of desiccation.

3. Gradation of behaviour patterns:

Most of the species discussed above can be grouped as either migratory or non-migratory, but biological categories are seldom discontinuous, and gradation occurs from one extreme to the other. Some species are intermediate and combine features of both categories. Figure 16 summarises the characteristics of migratory and non-migratory animals, and illustrates the gradation of behavioural patterns between different species.

P. granularis epitomizes the migratory group. P. concolor is similar, although aspects of its behaviour have not yet been studied.

P. granatina also migrates up the shore, but its movements are more random. Juveniles settle low on the shore and lack scars or homing behaviour. These traits appear in adults, particularly higher on the shore, and migration ceases temporarily or is reduced. In this way adults will tend to accumulate in the upper regions of the shore (fig. 3).

P. oculus settles in damp areas but disperses to drier (and usually higher) areas due to aggressive behaviour when animals meet. In some ways this species is intermediate between migratory and non-migratory forms (fig. 16).

P. barbara is more obviously intermediate, and its behaviour patterns are not markedly developed along either line. This is probably related to its sparcity, densities being too low for serious intraspecific competition to occur.

P. argenvillei also possesses characteristics of both groups, but has only been studied in the Cape Peninsula, which is at the fringe of its distribution where densities are never very high. On the Northern West Coast this species replaces P. cochlear in the low intertidal and forms dense stands. Here competition will be greater and behavioural modifications may be more marked.

P. miniata and P. compressa are typical of the non-migratory forms, with aggressive dispersal, specific food-plants, defence of a home territory, well defined homing to a scar and a differentiation between juvenile and adult habitats.

In P. longicosta and P. tabularis these trends are even more marked, culminating in the establishment, maintenance and defence of algal gardens. P. cochlear also conforms to these patterns, and in relation to its exceptional densities it is most highly adapted to minimise competition. This is suggested by the self regulation of total numbers (Section V), the rigid spacing of animals, rotatory feeding mechanism, and the mild (ritualised ?) reaction between individuals.

The relative development of migratory or non-migratory features appears to be correlated with density. With the exception of P. argenvillei, the most distinctive behaviour patterns occur in species with high densities (P. granularis, P. granatina, P. longicosta and P. cochlear).

Thus gradation occurs between the two groups, and the extremities of behaviour are related to high density and hence most intense competition.

## ACKNOWLEDGEMENTS:

Some of the data included in this paper is taken from the unpublished notes of Prof. T.A. Stephenson, and of M. Wood who worked under his supervision. Mrs. A. Stephenson very kindly allowed me access to these notes and gave permission to cite them. Several ideas stemmed from discussion with Dr. W. Ballantine, for which I am most grateful. Data on P. compressa has also been drawn from the unpublished work of Mr. R. Day of the Zoology Department, University of Cape Town.

## SUMMARY:

All limpets probably experience intraspecific competition, but its intensity will be related to density. Various mechanisms have been evolved to reduce competition. On the basis of these, two groups can be distinguished: "migratory" and "non-migratory".

Migratory species settle low on the shore and migrate progressively upwards, thus occupying a wider range and reducing competition. P. granularis, P. granatina, P. concolor and P. oculus comprise the group.

In conjunction with migration, these species are generalised browsers, non-aggressive to their own species, and have a random to aggregate distribution. Aggregations occur under desiccating conditions. Scars are often poorly defined or temporary, and homing is variable and usually not well developed (except under desiccation). Territorial behaviour is lacking, and there is no marked adult - juvenile differentiation with respect to habitat or food.

Upward migration occurs mainly in winter and short-term returns may occur in summer.

The "non-migratory" group includes species which settle in a narrow zone and remain there throughout life. P. cochlear, P. longicosta, P. tabularis, P. miniata, P. argenvillei and P. compressa conform to this. P. compressa lives only on the kelp Ecklonia maxima.

Specialised mechanisms have been evolved to reduce competition. Food requirements are often specific. The limpets respond aggressively to like species, and are therefore dispersed. Many show territorial behaviour and form a permanent scar in the centre of the territory. Homing is rigid. Experimental evidence shows that in some species the foodplant is established, maintained and defended by the limpet. Competition is reduced by dispersion, territorial behaviour and spacing, and differentiation of habitat or food between adults and juveniles.

The relative development of migratory or non-migratory tendencies is graded, and most intense in high density species. P. barbara (with the lowest density) is the only obvious intermediate form.

Examples are given of the parallel evolution of various behavioural traits, in phylogenetically different and geographically distinct groups of limpets.

## REFERENCES:

ABE, N. 1931. Ecological observations on Acmaea dorsuosa Gould. Tohoku Imp. Univ. Sci. Repts. Ser. 4. 6 : 403-427.

BALAPARAMESWARA RAO, M. and GANAPATI, P.N. 1971. Ecological studies on a tropical limpet Cellana radiata. Mar. Biol.

*9* : 109-114.

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.

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.

BOVBJERB, R.V. 1964. Dispersal of aquatic animals relative to density. *Verh. int. Verein. theor. angen. Limnol.* *15* : 879-884.

BULLOCK, T.H. 1953. Predator recognition and escape responses of some intertidal gastropods in presence of starfish. Behaviour *5* : 130-140.

CLARK, P.J. and EVANS, F.C. 1954. Distance to nearest neighbour as a measure of special relationships in populations. *Ecol.* *35* : 445-453.

CRAIG, P.C. 1968. The activity pattern and food habits of the limpet *Acmaea pelta*. *Veliger* *11* (Suppl.) : 13-19.

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* 2: 411-423.

DAY, J.H., COOK, P., ZOUTENDYK, P. and SIMONS, R. 1971. The effect of oil pollution from the tanker *Wafra* on the marine fauna of the Cape Agulhas area. *Zool. Afr.* *6* : 209-219.

DAY, R. 1967. The *Ecklonia* community. Unpublished project, University of Cape Town.

EATON, C. Mc.K. 1968. The activity and food of the file limpet, *Acmaea limatula*. *Veliger 11* (Suppl.) : 5-12.

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

GRAHAM, A. and FRETTER, V. 1967. 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 *A. digitalis* (Gastropoda) in Central California. *Veliger 13* : 231-248.

JONES, N.S. 1948. Observations and experiments on the biology of *Patella vulgata* at Port St. Mary, Isle of Man. *Trans. Lpool. Biol. Soc. 56* : 60-77.

KAIN, J.M. and SVENDSEN, P. 1969. A note on the behaviour of *Patina pellucida* in Britain and Norway. *Sarsia 38* : 25-30.

KNIGHT-JONES, E.W. and MOYSE, J. 1961. Intraspecific competition in sedentary marine animals. *In*: Mechanisms in Biological Competition. *Symp. Soc. Exp. Biol. 15* : 72-95.

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

MILLARD, C.S. 1968. The clustering behaviour of *Acmaea digitalis*. *Veliger 11* (Suppl.) : 45-51.

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.

ROGERS, D.A. 1968. The effect of light and tide on movements of the limpet *Acmaea scutum*. *Veliger 11* (Suppl.) : 20-24.

ROSS, T.L. 1968. Light responses in the limpet *Acmaea limatula*. Ibid. : 25-29.

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

169-188.

STIMSON, J. 1970. Territorial behaviour of the owl limpet _Lottia gigantea_. _Ecology_ _51_ : 113-118.

THORPE, W.H. 1956. Learning and Instinct in Animals. Methuen & Co. London.

WALKER, A.J.M. 1972. Introduction to the ecology of the Antarctic limpet _Patinipera polaris_ (Hombron and Jacquinot) at Signy Island, South Orkney Islands. _Br. Antarct. Survey Bull._ _28_ : 49-69.

WILLOUGHBY, J.W. 1973. A field study of the clustering and movement behaviour of the limpet _Acmaea digitalis_. _Veliger_ _15_ : 223-230.

YONGE, C.M. 1962. Ciliary currents in the mantle of species of _Acmaea_. _Veliger_ _4_ : 119-123.

APPENDIX I: Regressions between shell length (x) and width (y) in P. compressa.

| Length mm. | Regression | Correl.coeff. | p. |
|---|---|---|---|
| 10 - 30 (A) | $y = 0.70x - 0.20$ | 1.00 | $<.001$ |
| 30 - 50 (B) | $y = 0.53x - 4.35$ | 0.88 | $<.001$ |
| $>50$ (C) | $y = 0.29x - 17.36$ | 0.67 | $<.001$ |

Tests of slopes and intercepts for significant differences.

| Samples | Slopes | Intercepts |
|---|---|---|
| A - B | $p = .1$ | $p = .1$ |
| B - C | $p < .05$ | $p < .001$ |
| C - A | $p < .02$ | $p < .001$ |

# SECTION VII:

# INTERSPECIFIC COMPETITION.

# VII. INTERSPECIFIC COMPETITION

The South African coast is endowed with eleven species of Patella, and as many as ten of these may be coexistent in one area. It has been shown that their zonation and feeding habits are sufficiently different to reduce competition between the species (Branch, 1971), but it would be naive to assume that no competition occurs, because niche overlap is almost certain in closely allied coexistent species.

The review of Miller (1967) indicates the diversity of ideas on competition. Equally diverse are the numbers of definitions and the version followed here is that of Miller (1967, p.6): "biological competition is the active demand of two or more individuals of the same species (intraspecific competition), or members of two or more species (interspecific competition) of the same trophic level, for a common resource which is actually or potentially limiting." As Miller points out, confusion has arisen from the tendency to regard competition from the standpoint of its consequences, and failing to establish the common resource which is being competed for. Miller's review also poses basic questions: How is diversity maintained? Is competition a basic force shaping the path of evolution? Is Gause's Principle fundamental and inviolable or can coexistence occur between species with common resources?

Since the introduction of the term "ecological niche" into the literature, authors have interpretted the term in various ways. Miller (1967) summarises these and describes two main lines of thought: that the niche is a distributional unit, embodying all the features of the ecosystem that the species may utilise; or that it is a functional unit pertaining to the trophic status of the animal. Miller draws the analogy that these refer to the animal's "address" and its "profession".

In terms of competition, it is necessary to combine these two and project them on a time scale. The latter very often cannot be evaluated, but it must be remembered that "coexistence" may be a temporary phaze on the path to exclusion.

Hutchinson (1957) introduced the terms "realised niche" and "fundamental niche" to distinguish between the niche a species actually occupies and the niche it could occupy if competition were lacking.

In many ways the intertidal zone is ideal for studies on competition, for habitats are diverse but compressed into a small area. Vertical gradients allow definition of zones and delimit the fauna. Competition is primarily for space and food.

It is generally acknowledged that the upper limits of zonation are set largely by physical conditions, but lower limits may be determined by biological interactions. The latter has recently been demonstrated in the field by Connell's work (1961a, 1961b, 1970) on Chthamalus stellatus. Dayton (1970) has also shown the dramatic effects predation, herbivorous grazing, competition and physical disturbance may have in controlling intertidal populations. Both authors describe the effects limpets may have on barnacle populations. On South African shores, the removal of P. cochlear allows massive settlement of Balanus algicola, indicating the role this limpet plays in preventing barnacle settlement. (Unpublished notes of M. Wood, 1935; White

1973, unpublished.) Algal growth flourishes after the large scale removal of limpets (Jones, 1948; Lodge, 1948). Only Fismer-Piette (1948) has studied the effect that other organisms have on limpets and demonstrated that barnacles depress growth in P. vulgata.

The present paper is concerned with three facets of intertidal competition. First, the effects barnacles have on P. granularis with respect to mean size, growth, gonad output and mortality. Various barnacles, particularly Chthamalus dentatus and Tetraclita serrata are "co-dominants" with P. granularis in the upper regions of the shore on the South coast.

Secondly, consideration is given to competition between limpet species, particularly P. cochlear and P. longicosta, and P. longicosta and P. oculus. Other interactions are mentioned but not considered in the same detail: P. cochlear and P. argenvillei; P. longicosta and P. tabularis.

The general ecology of these species has already been described (Branch, 1971), but the salient features can be recapitulated here. P. cochlear dominates the low intertidal zone, occurring in great density and feeding largely on lithothamnion. P. longicosta occurs both above and below the cochlear zone, and (when adult) feeds only on Ralfsia expansa. The zonation of P. oculus partly includes that of P. longicosta, but extends further up the shore. P. oculus is a generalised browser, feeding on any available food. In the northern regions of the West coast, P. argenvillei dominates the lower shore in place of P. cochlear, but in the southern regions the two species intermingle. Subtidally P. longicosta occurs with P. tabularis, which has very similar habits and also feeds largely on Ralfsia.

Finally, P. concolor and Cellana capensis are of interest because they appear to coexist despite sharing the same food and the same zone (Section II). Interest has centred on the degree to which their niches overlap.

## MATERIAL AND METHODS:

Barnacle - limpet interactions were analysed at Dalebrook, False Bay. P. granularis sizes in relation to barnacle density was assessed from photographs of 64 random sites (of approximately constant height), in the upper balanoid zone. The exponential relationship between body weight and shell length was then used to calculate limpet biomass. Absolute barnacle density is difficult to obtain; its importance will vary from species to species; so "percentage cover" was used instead and ranked. Spearman's rank correlation was used to determine correlation between barnacle cover, limpet size (length), and limpet density. As all three showed correlation with one another, an analysis of covariance was necessary to separate the effects of barnacle cover from those of limpet density. This requires a linear relationship between limpet size and density, at various barnacle "treatments". For convenience four barnacle groups were recognised as "treatments": 0-10% barnacle cover; 11-40%; 41-70%; and 71-100%. Linearity was obtained by plotting limpet density against the reciprocal of limpet shell length.

Gonad output of P. granularis was calculated from a previously measured relationship between gonad output and somatic weight (Section III). Samples were taken from five sites of varying barnacle densities, to test if differences in limpet gonad size occurred. As there were no differences between the five sites, it has been assumed that barnacles have no direct effect on limpet gonad size. (Even if this assumption is not true, the trends adduced from it can only be more marked and will strengthen the conclusions and not invalidate them.) In this context, the technique measures the minimum effect of barnacles on limpet gonadial output, as deduced from limpet size. If the mean limpet size is reduced, then gonad output is reduced proportionally .

Growth of *P. granularis* was measured at four sites with respectively 0%, 30%, 80% and 95% barnacle cover. At each site, 50 animals were labelled and measured at monthly intervals for one year. Details of the technique have previously been given (Section IV).

Work on limpet interactions was completed at various localities in the Cape Peninsula. The *Cellana capensis* - *P. concolor* interaction was analysed at Lwandile (31°53'S, 29°15'E). Work on these two species was unavoidably limited to animals less than 40mm long, because local consumption has reduced the maximum size from about 65mm to 40mm. This need not invalidate the results, because these smaller animals constitute about 80% of (unexploited) populations.

Zonation and distribution of limpets was examined for signs of competitive exclusion, mutually exclusive distribution, or included niches. Line transects and random quadrats were used. For the latter, a minimum of 84 quadrats was used, except at Lwandile, where 34 were used. Chi square analysis of 2 x 2 contingency tables was used to test habitat preferences.

Behavioural interaction was observed during both natural and staged encounters, usually under water with the rising tide, when feeding occurs and reactions are most obvious.

Plate I. Mixed community of <u>Chthamalus</u> and <u>P.granularis</u>.

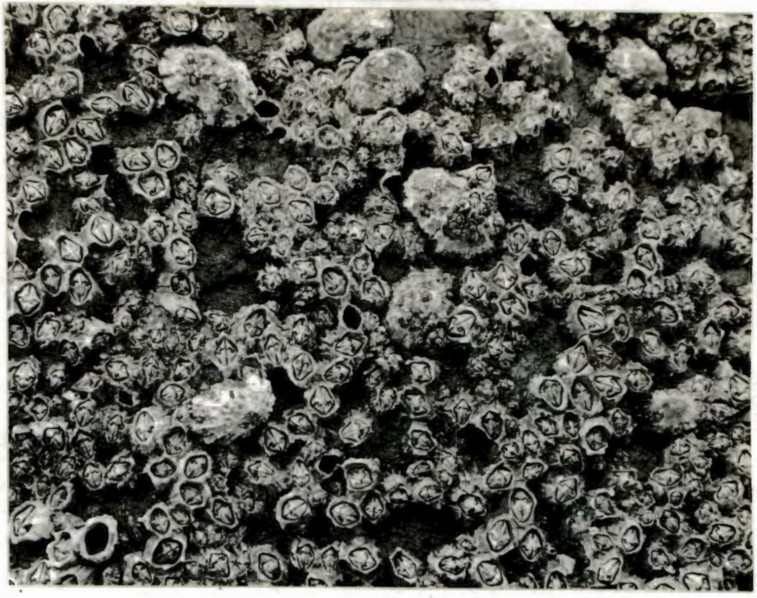


Plate 2. <u>Octomeris</u>: note how <u>P.granularis</u> keeps patches clear.

Plate 3. <u>Tetraclita</u>.The adults are evenly spaced because of larval spacing.

Areas were cleared at Dalebrook to test the effects of removing dominant competitors. P. cochlear were removed from four areas 50 x 50 cm. and P. longicosta from two areas 2 x 3 m. Monthly records were kept of the recolonisation, but only details pertaining to the present work are included here. Information is also drawn from five sites independently examined by Miss P. White; her careful work is a pleasure to acknowledge. In addition, some data comes from the unpublished notes of M. Wood (1935), very kindly given to me by Mrs. A. Stephenson. Information from these sources is acknowledged in the text.

## RESULTS:

### P. granularis - barnacle interaction:

On the South coast of South Africa the midlittoral zone is characteristically blanketed by barnacles. Of these, Chthamalus dentatus occurs highest on the shore and is replaced at lower levels by Tetraclita serrata, particularly in calmer areas. Octomeris angulosus (Plate 2) occurs in wave washed areas, but is not as numerically dominant as the preceding species and is omitted from further consideration. Chthamalus (Plate 1) settles in dense blankets during autumn and spring (April and September) and grows quickly to its maximum size of about 10mm. (Unpublished notes of Wood, 1935; Bokenham, 1938; White, 1973). Settlements of 120,000 per $m^2$ were recorded during this work, but mortality is high because of crowding, and adult densities are about 35,000 per $m^2$.

Tetraclita settlement is more sparse (about $1100/m^2$) and the cyprids space out so that mortality is lower and the adults regularly spaced (Plate 3). Chthamalus settles over most of the shore, but is decimated by Thais dubia at lower levels.

Plate. 4. Mixed community of *Chthamalus* and *Tetraclita*. Note the heavy mortality of *Chthamalus* and the presence of *Thais dubia* (arrowed).

*Tetraclita* reaches a size of about 25mm and is then large enough to escape attack by *Thais*. Presumably the shell is too thick to be easily drilled. As a result *Tetraclita* can occur further down the shore where *Chthamalus* would be eradicated by *Thais* (Plate 4). Dayton (1971) describes a similar effect where *Balanus cariosus* escapes predation by *Thais* spp. because of rapid growth and size.

The effect of percentage barnacle cover on *P. granularis* size was assessed from 74 random quadrats ($0.5m^2$), and shows that as barnacle cover increases, so limpet size decreases (fig. 1). This effect is related directly to barnacle cover and is independent of the barnacle species or density: consequently all three barnacle species were lumped for this analysis. Their long-term competitive action will of course be different, because of different settling patterns, size, growth and mortalities.

Barnacles compete with *P. granularis* on a two-fold basis. Firstly, they compete directly for space, and secondly, they deny access to food. They filter out food which would normally settle on the substrate, and the food which is deposited is often inaccessible because of the irregular barnacle shape. Thus it can be anticipated that mean limpet size will be less, as barnacle cover increases.

However, the situation is not as simple as this, for barnacle cover is also directly related to limpet density (fig. 2b), and this in turn will reduce limpet size because of intraspecific competition (fig. 3). Consequently an analysis of variance was applied to separate the effects of limpet density from those of barnacle cover. Limpet density was plotted against the reciprocal of shell length for four barnacle treatments (fig. 4). Details of this analysis are included in

Fig. 1 P. granularis : Size relative to Barnacle Density

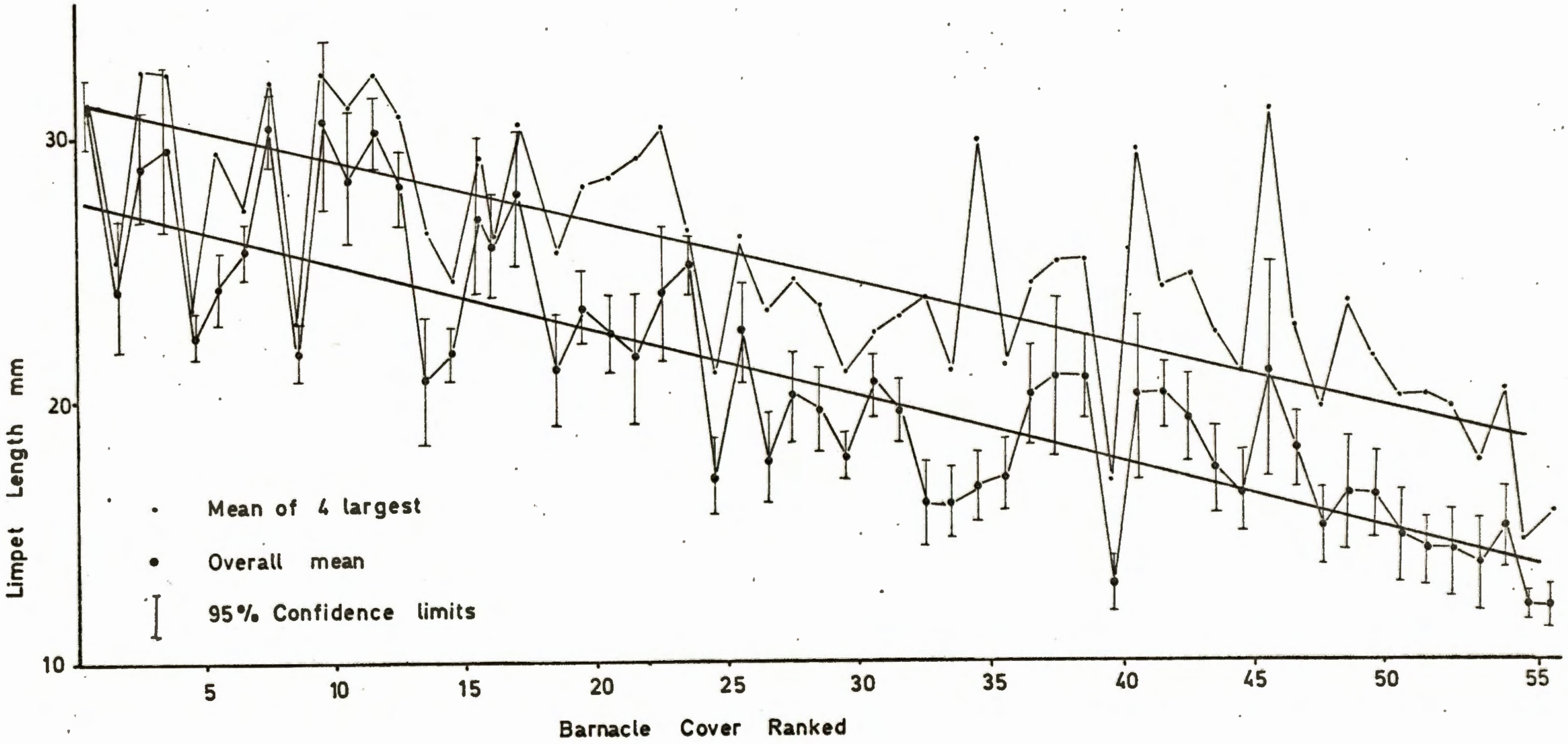


Fig. 2 Ranked Correlations (c) Between P.granularis Limpet Size, Barnacle Density and Limpet Density. (ranked units)

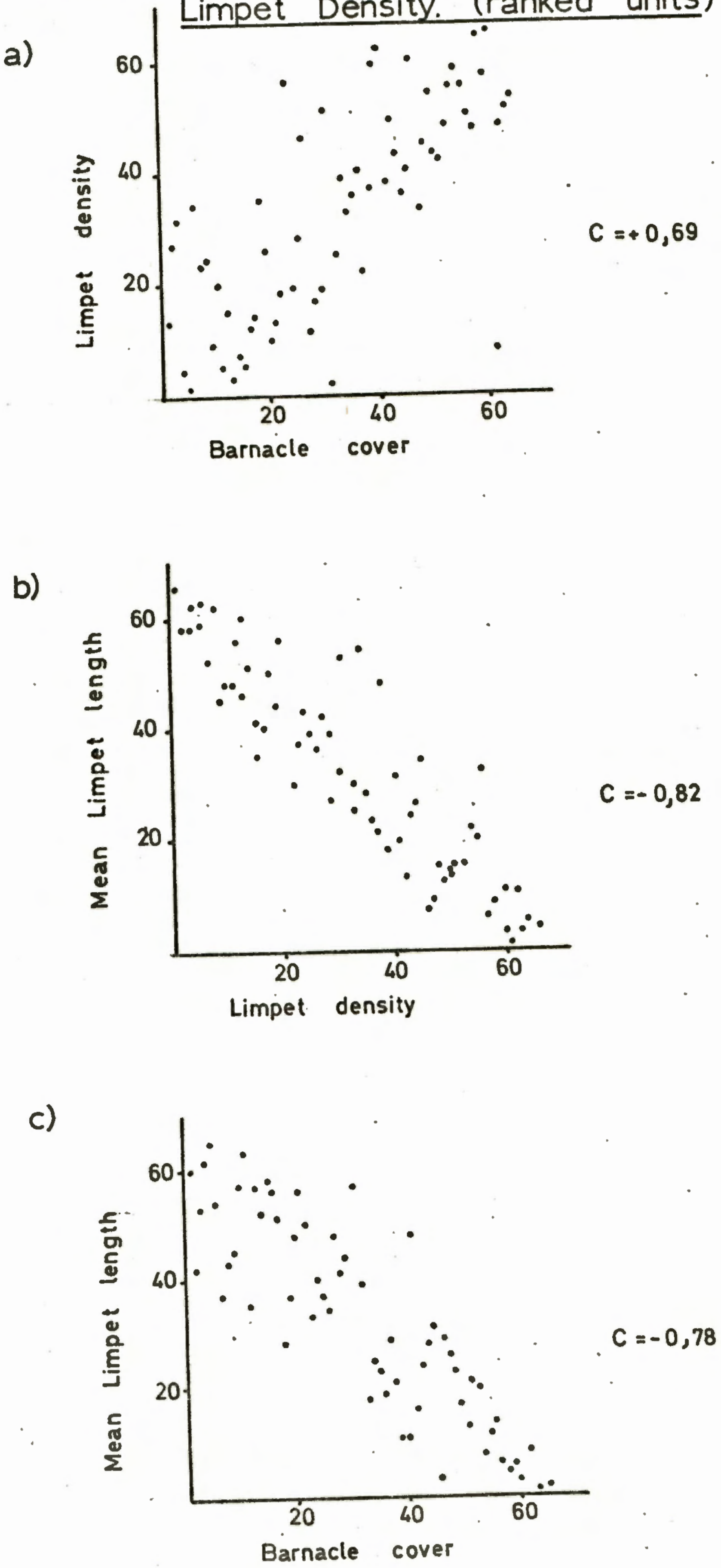


Fig. 3 Relationship Between Limpet Density and Size

*P. granularis*

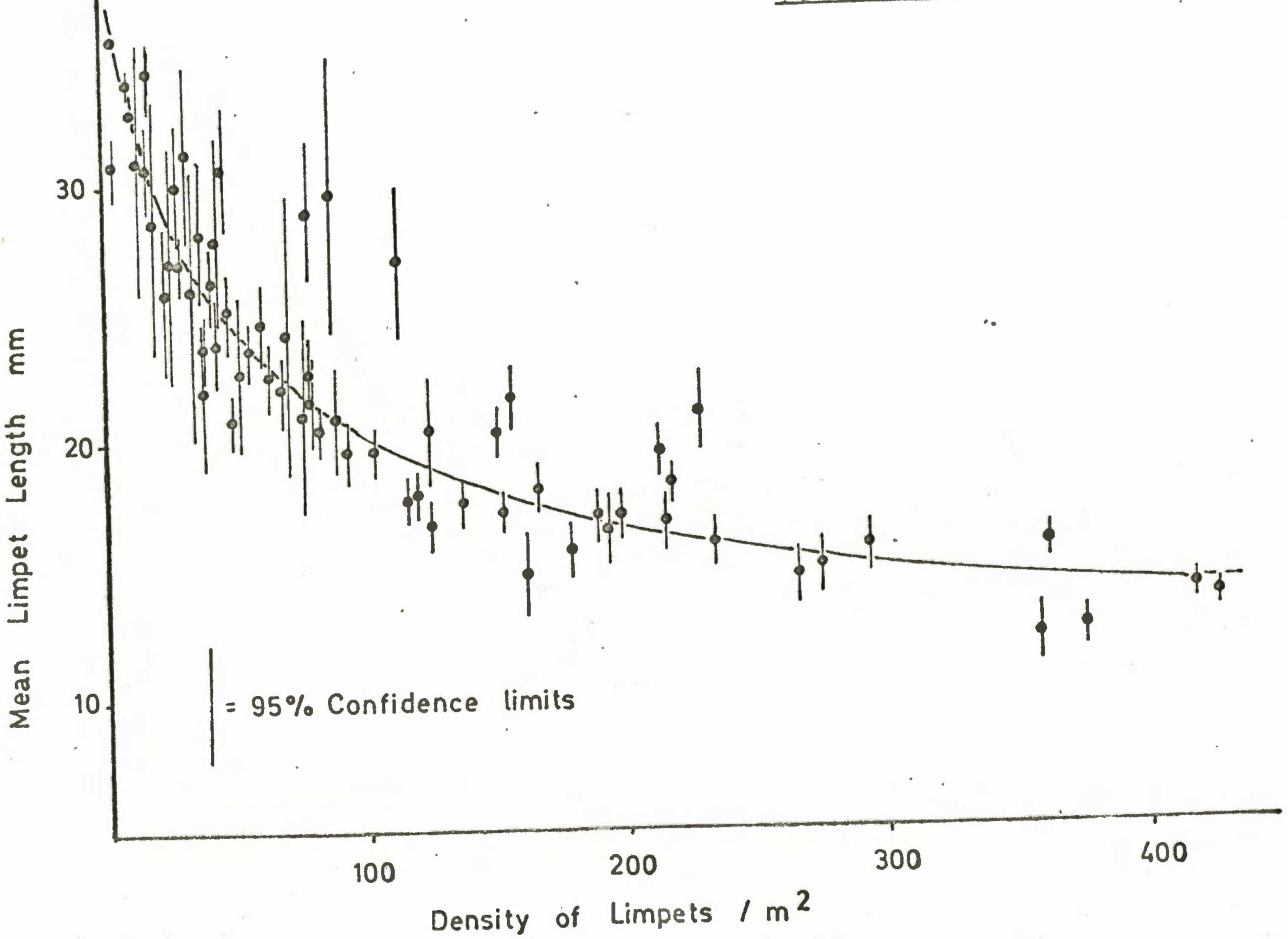
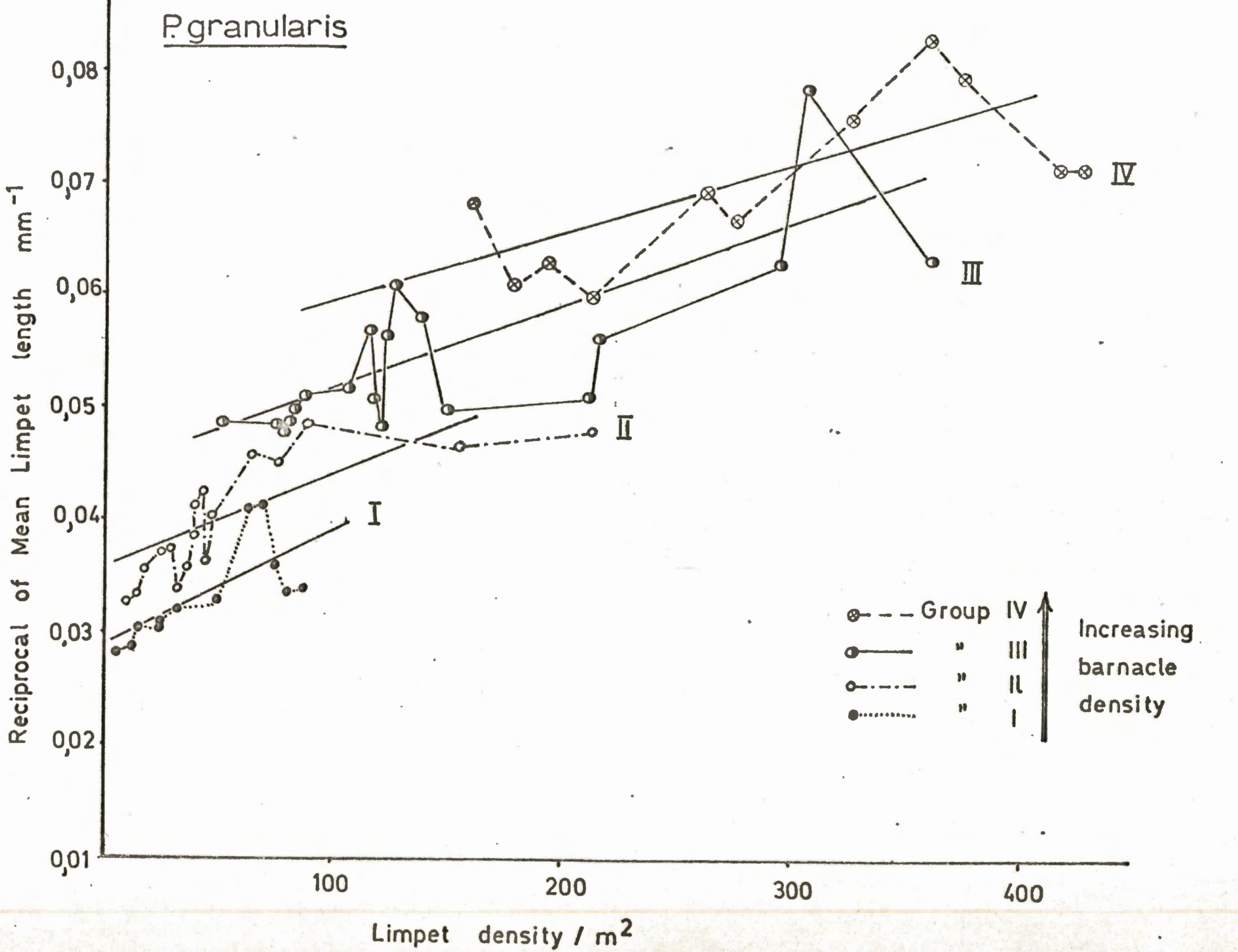
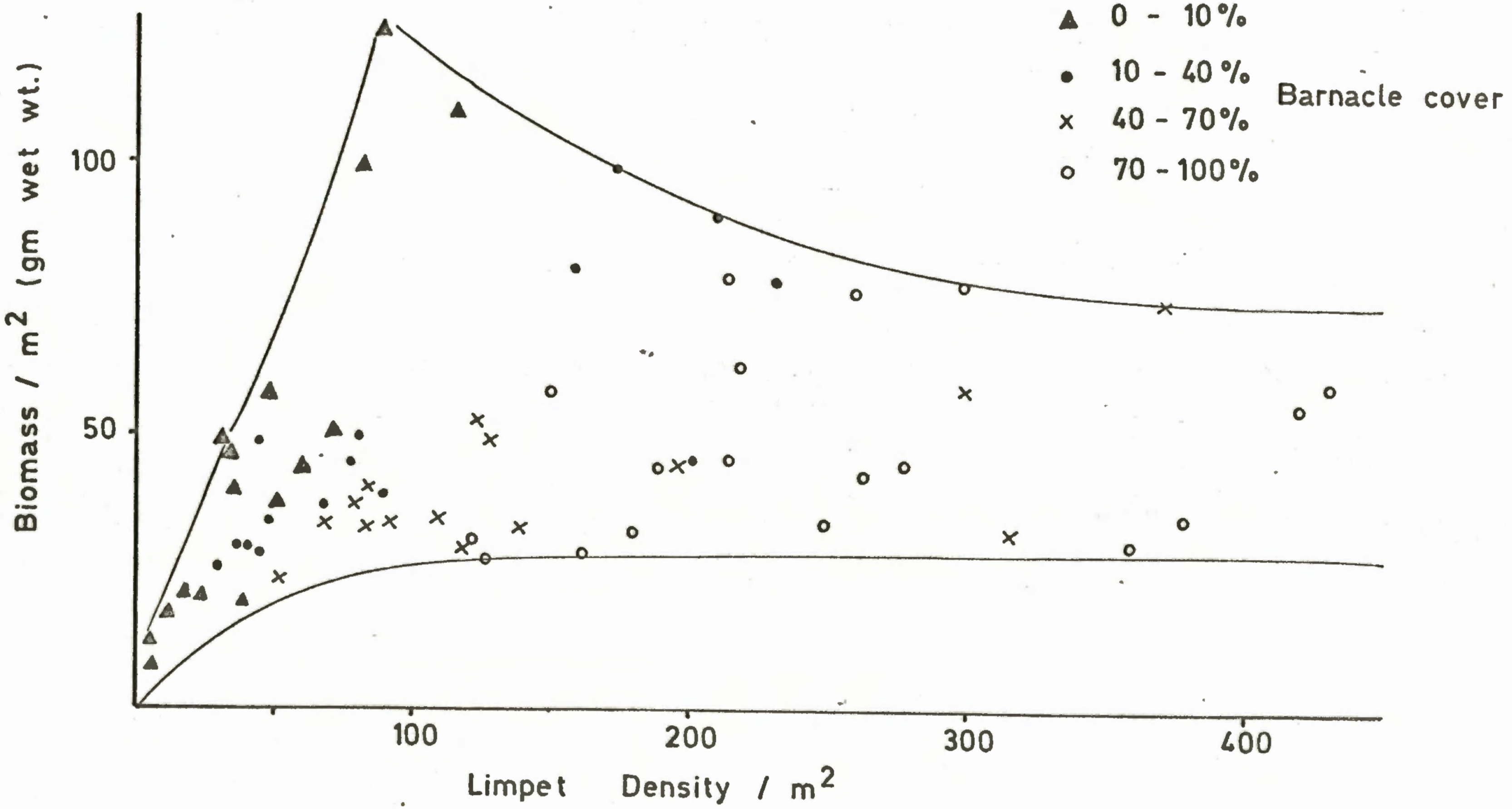


Fig. 4 Limpet Density and Size at Four Barnacle "Treatments"



## Fig. 5 P. granularis: Density - Biomass Relationship



Appendix I. The results show that both limpet density and size are significantly effected by the treatment ($p < .001$) and that the treatment significantly reduces limpet size independently of the limpet density effect ($p < .001$).

Limpet biomass increases with density reaching a peak at a density of about $100/m^2$. Curiously, it then decreases to a plateau of between 30 and 75 gm. (wet weight) per $m^2$, despite further increases of density (fig. 5). The decrease may be due to an "interference" factor between the limpets. More probably the effect is caused by the barnacles, as high density limpet populations are linked with high barnacle cover, and the two factors may simultaneously reduce biomass. At peak biomass (limpet density $90/m^2$) the effect of different barnacle concentrations is quite obvious (fig. 5).

The effect of competition on gamete output is of major importance, for on this hinges the future abundance of the species. Gonadial output in P. granularis (fig. 6) is strongly density dependent, reaching a peak at about $100/m^2$ and then decreasing progressively to zero, at about $450/m^2$. Again, barnacles decrease the output at any given limpet density.

Growth of P. granularis was measured at four sites (A to D) with respectively 0%, 30%, 80% and 95% barnacle cover (Plate 5). The increments in shell length (relative to original length) are given in figures 7a to 7d. Regressions and tests of significance appear in Appendix II.

Growth is progressively stunted as the barnacle cover increases. Fischer-Piette (1948) also recorded that barnacles decrease the growth rate of P. vulgata in N. France. Jones (1948) noted that P. vulgata was smaller in the presence of barnacles, and adduced that this was due to a lower growth rate.

Fig. 6 P.granularis : Density related to Gonadial output

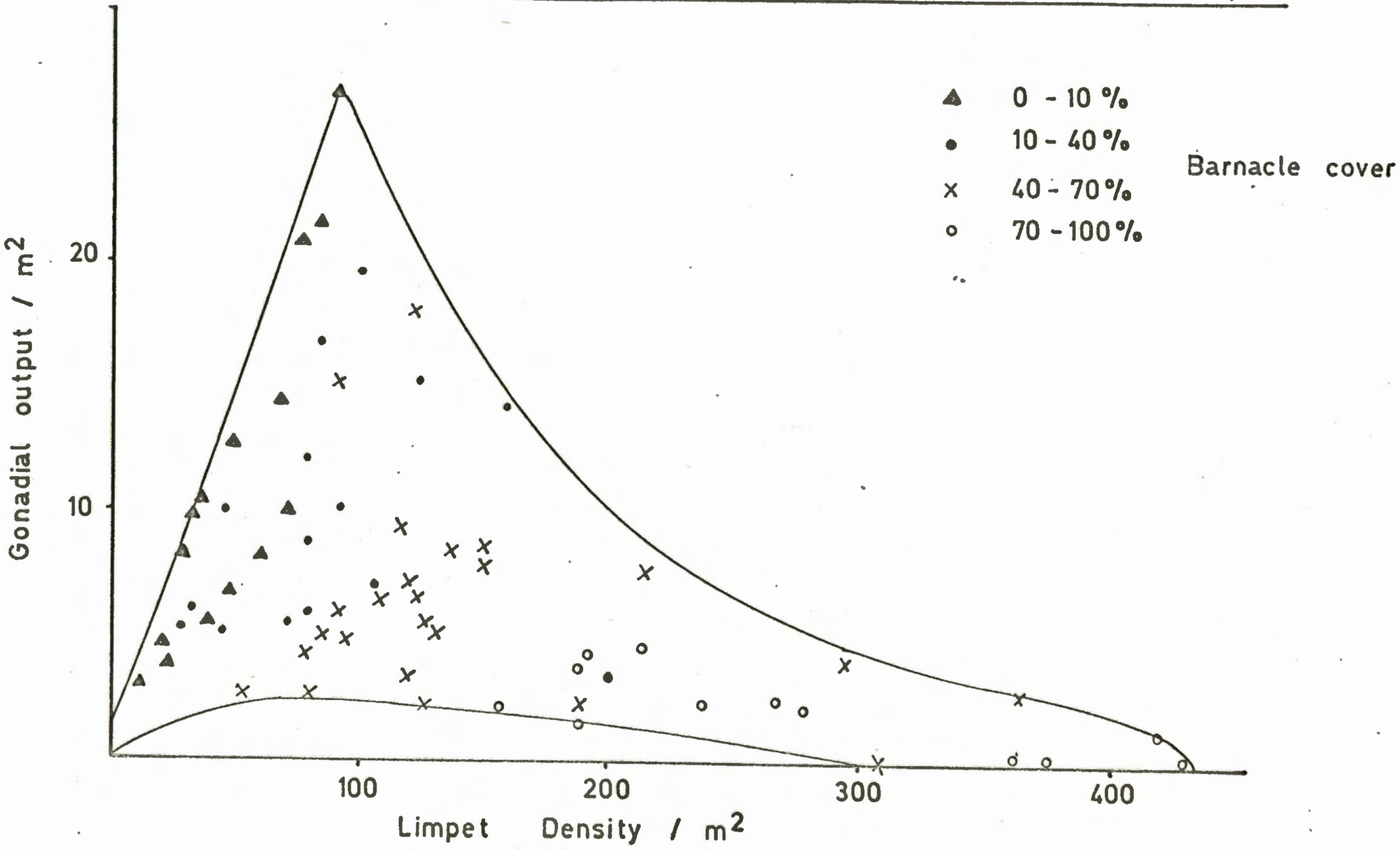
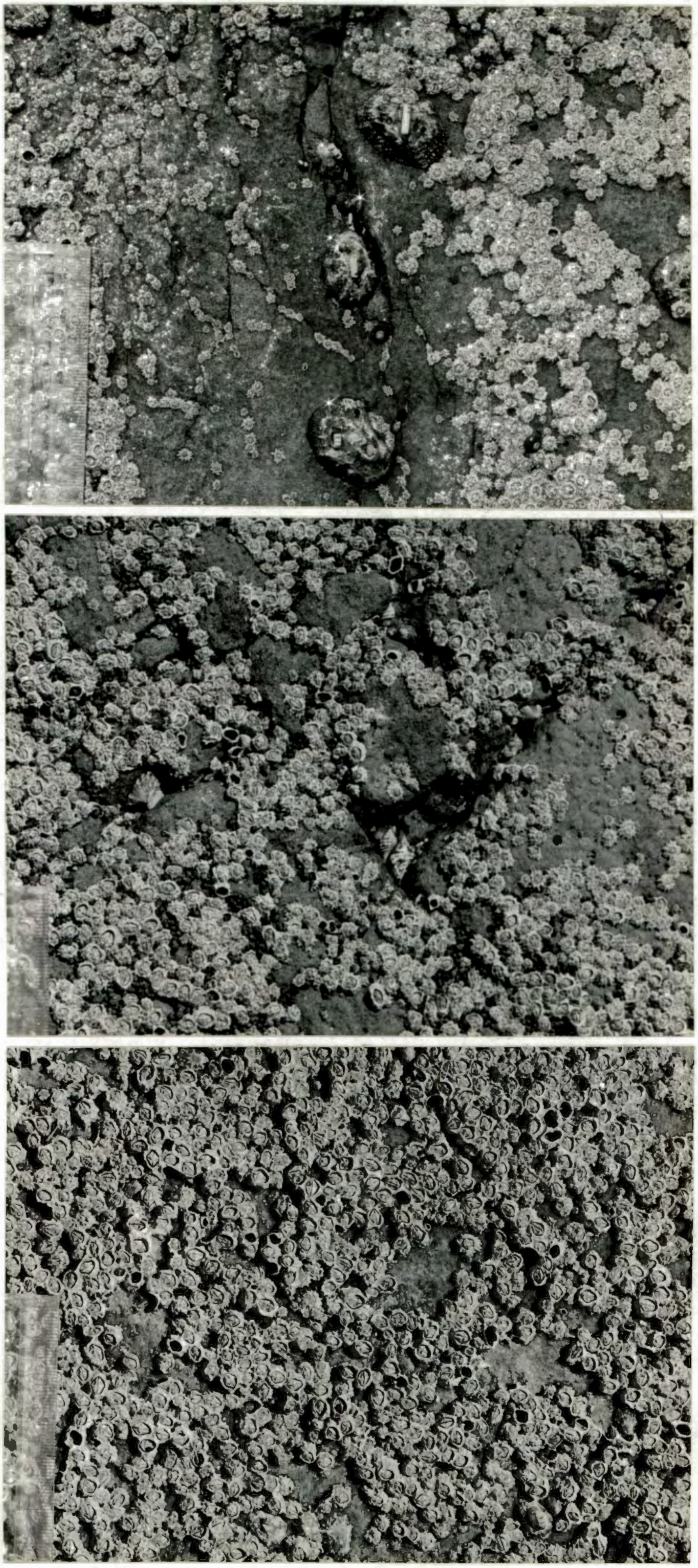


Plate 5. Representative portions of sites B.C. and D, showing the relative barnacle cover. (Barnacles were absent at site A).

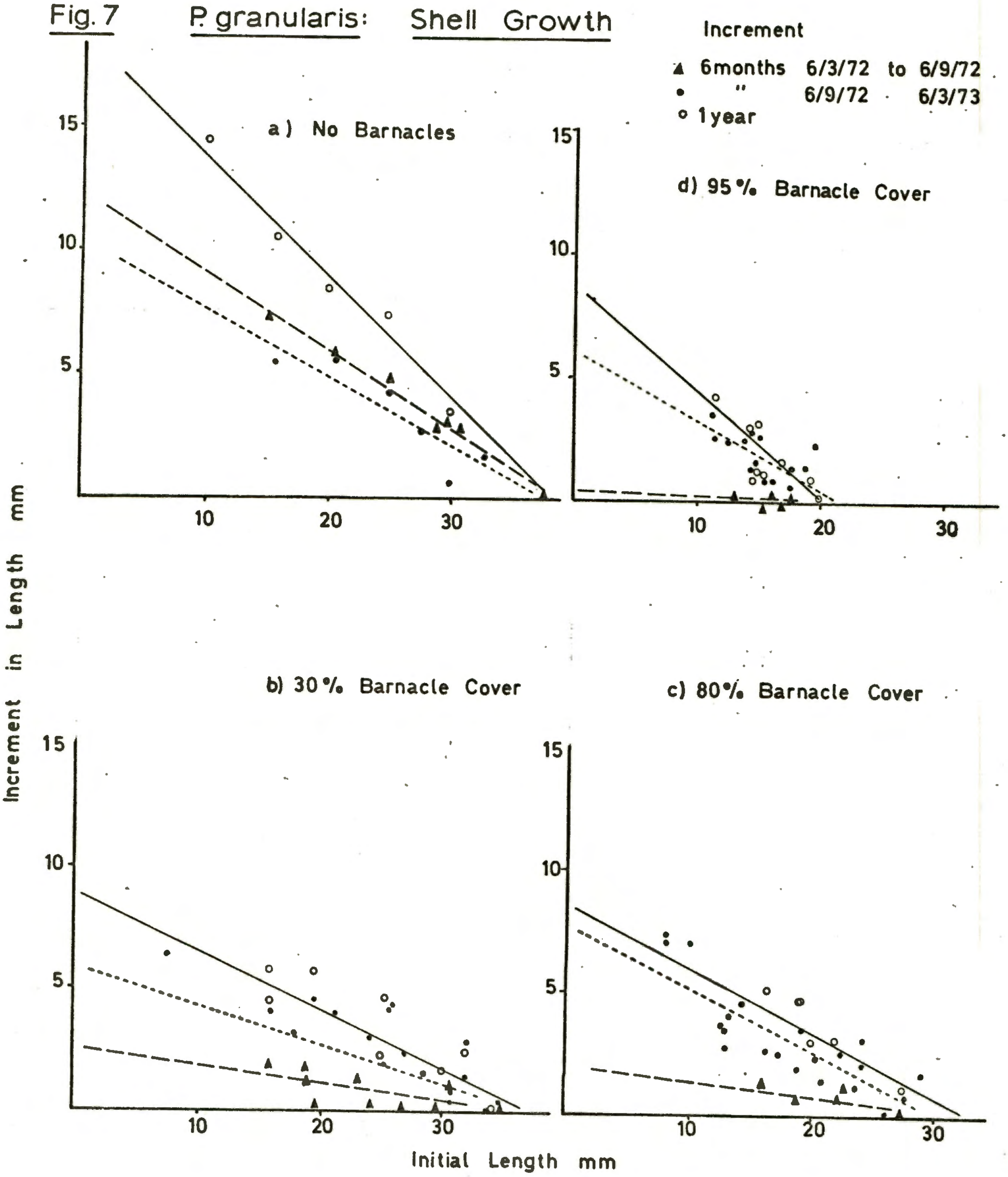


B. 30% barnacle cover

C. 80% barnacle cover

D. 95% barnacle cover.

Fig. 7 P. granularis: Shell Growth



Growth of P. granularis was also analysed for two six month periods: March to September (when gonad development and spawning occur) and September to March (when the gonad is resting)(see Section III, figs. 13a, b). At Site A (no barnacles) growth was equal in the two periods (fig. 7a). At sites B and C growth was progressively depressed during gonadial activity, and at site D (95% barnacles), growth ceased completely while the gonad was active.

This indicates that gonadial growth takes precedence over somatic growth, and that if food is short, somatic growth will decrease to the point of ceasing altogether to allow gonad maturation. Conversely, if food is adequate there will be no seasonal differences in growth (Section IV).

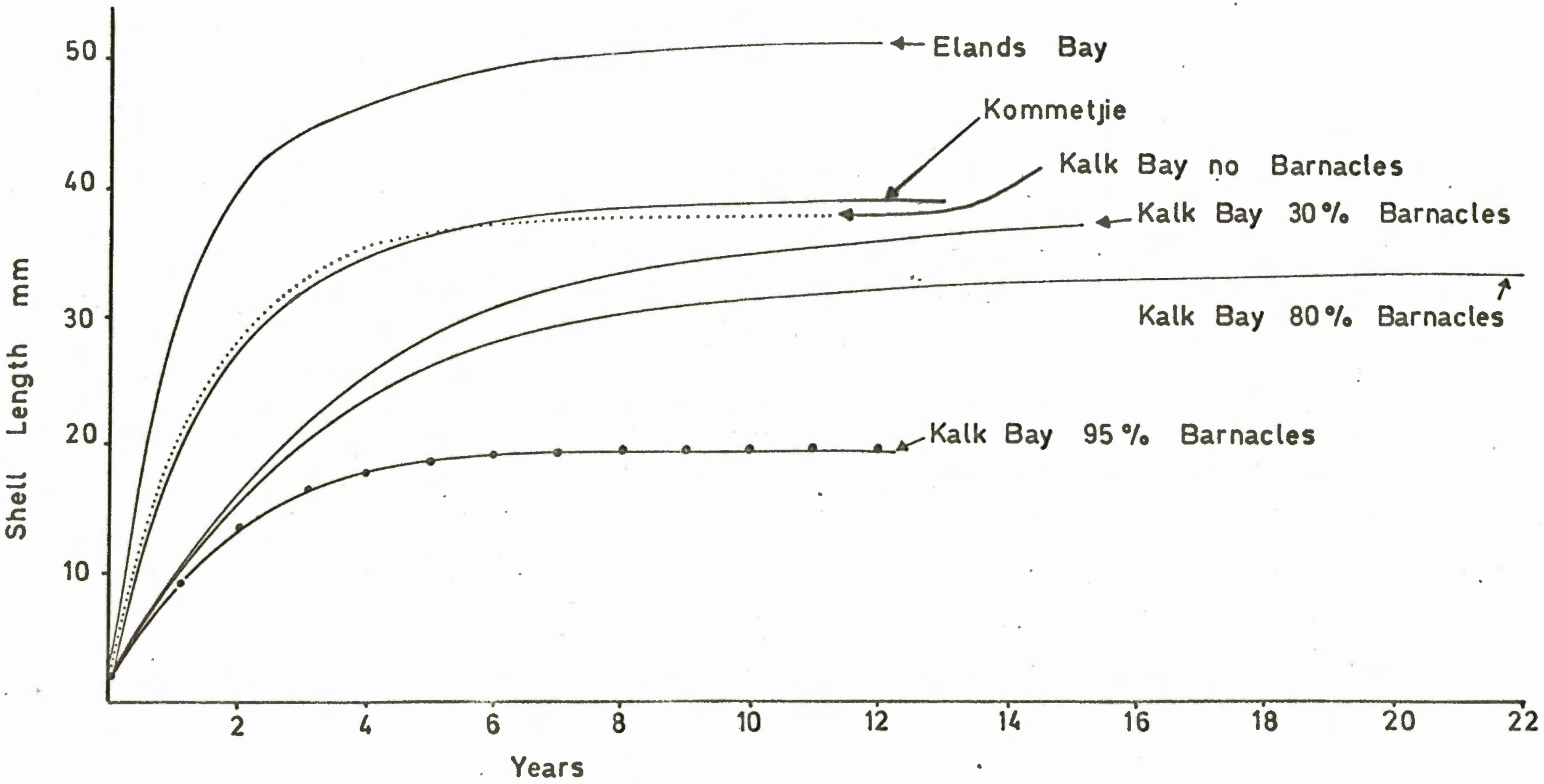
An interesting relationship exists between barnacle cover and limpet gonadial output (per unit biomass)(fig. 9). If barnacle cover is less than 50% (ranked 25) the output of gametes is constant, and presumably somatic growth is constant throughout the year (as at Site A, fig. 7a). Above 50% barnacle cover the output drops to a plateau, and then progressively decreases to zero. This suggests that barnacle competition is only effective if cover is greater than 50%. Part of the reason for this may be that at 50% cover the barnacles surround many of the limpets. Larger barnacles such as Tetraclita will restrict the movements of limpets and physically hamper their feeding excursions. However, the limpets can climb over the barnacles (Plate 6), and are not permanently enclosed by them.

The lower plateau of gamete output coincides with the range of barnacle cover at which limpet growth is decreased during gonadial activity (as at Sites B and C, figs. 7b, c).

PLATE VI :

P.granularis climbing over and browsing on the the barnacles Octomeris. This demonstrates that the limpets are not restricted by surrounding barnacles, although their feeding is probably impaired.

## Fig. 8 P.granularis: Growth



Between certain limits of barnacle cover (50% to 80%) limpet gonadial output may be maintained (at a lower level) by compensating reduction of somatic growth. Above these limits, somatic growth may have reached zero during reproduction (Site D, fig. 7d). Further compensation is impossible and gonad output drops to zero.

Annual growth (fig. 8) can be compared with that in other areas (extracted from Section IV), and it is apparent that the effect of barnacles may be even greater than that of distribution or sea temperatures. This is interesting because P. granularis is much larger on the cold West coast than on the warmer South and East coasts (Stephenson, 1939). This has always been attributed to differences in sea temperatures, in conformation to Bergman's rule. As barnacles are much more abundant on the South and East coasts, they may be at least partly responsible for the decreased limpet size.

Normally growth rate is inversely related to size (length), but during the hottest months (January and February), overall growth was depressed and slowest in smaller animals. As smaller animals are more susceptible to desiccation (Section XI), their reduction of growth in hot weather is interesting.

The growth regressions (fig. 7) can be used to estimate the maximum sizes attainable at each site (that is, the size at which shell growth ceases) and these can be compared with the actual maximum sizes recorded (Table 1).

In each case (except the Elands Bay sample) there is fair agreement between predicted and actual maximum values. Also of interest is the correlation between maximum size and growth rate. This relationship was inferred by Fischer-Piette (1941, 1948) and provides a useful tool for estimating relative growth

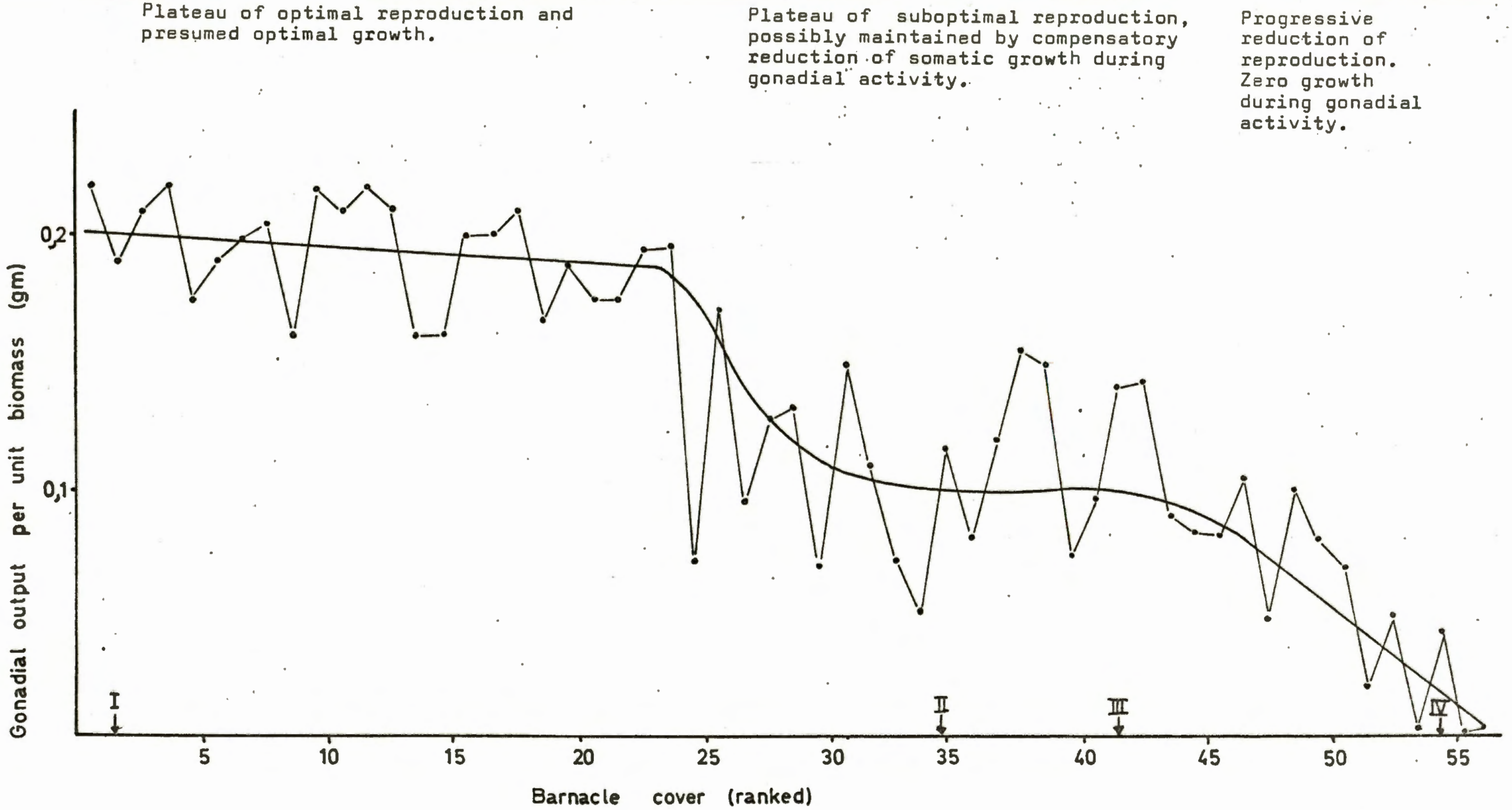


Fig. 9 Limpet Gonadial Output Relative to Barnacle Cover

TABLE 1. Comparisons of the calculated and recorded maximum sizes of P. granularis at various localities.

| Locality | Calculated max. size (mm) | Recorded max. size (mm) | Growth Rate (Ranked) |
|---|---|---|---|
| Elands Bay | 54.0 | 65.0 | 1 |
| Kommetjie | 45.0 | 47.1 | 2 |
| Dalebrook A | 38.0 | 36.3 | 3 |
| Dalebrook B | 33.0 | 36.0 | 4 |
| Dalebrook C | 36.0 | 34.8 | 5 |
| Dalebrook D | 22.0 | 24.0 | 6 |

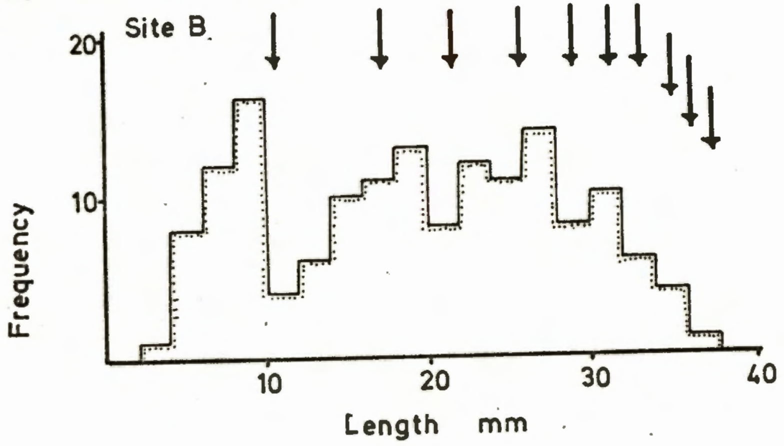
rates (within a species) without long-term measurements of labelled animals.

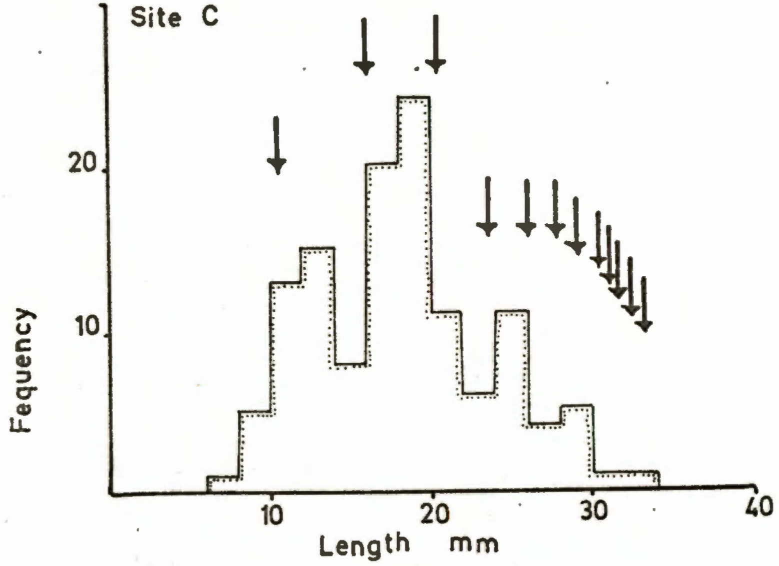
The population structure of P. granularis at sites B, C and D is given in figure 10, (site A was too sparse to assess), and demonstrates the reduction of size associated with increased barnacle cover. From these populations and their known growth rates, survivorship curves have been constructed after the method of Deevey (1947). (These curves have comparative value only, because they are based on the unproven assumption that the populations are stable in time, and because the year groups can only be approximately separated.)

The survivorship curves (fig. 11) show that although mortality increases slightly as barnacle cover increases, the curves are essentially similar and cannot be separated (particularly because of the limited accuracy of the data).

Thus barnacle cover effects the growth rates of limpets and hence the maximum and mean sizes in the population; it also decreases the gamete output, but apparently has little effect on limpet mortality.

FIG. 10 Population structure of *P.granularis* relative to barnacle cover. (Arrows indicate year groups of *P.granularis*, calculated from growth rates).


a) Barnacles Sparse


b) Barnacles Fairly Dense (80% cover)

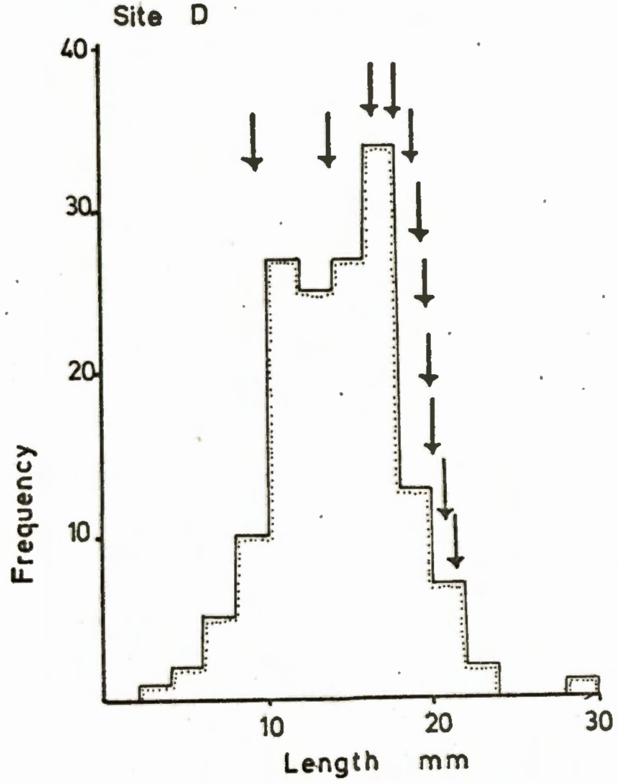
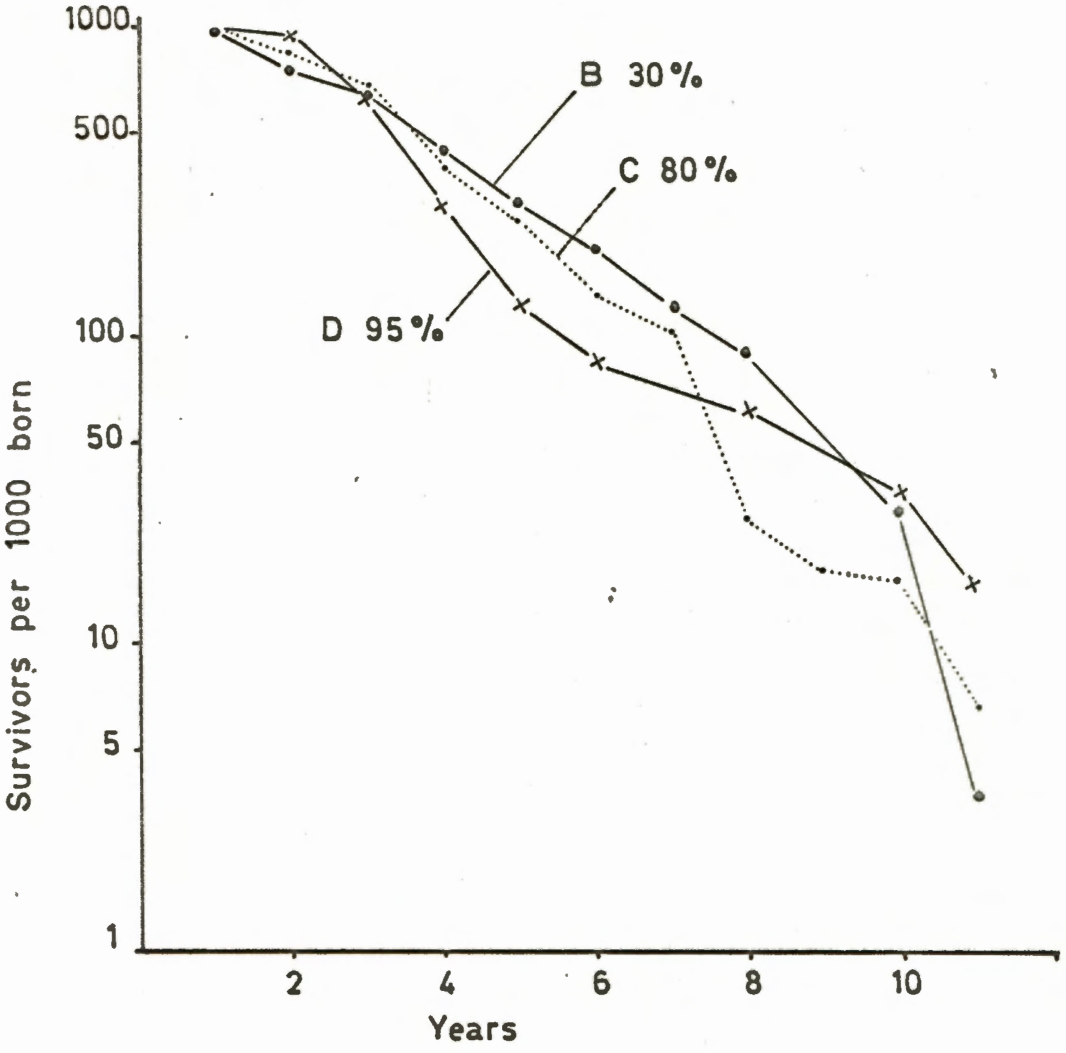

c) Barnacles Very Dense (95 % cover)

Fig. 11. P. granularis: Survivorship related to % Barnacle Cover



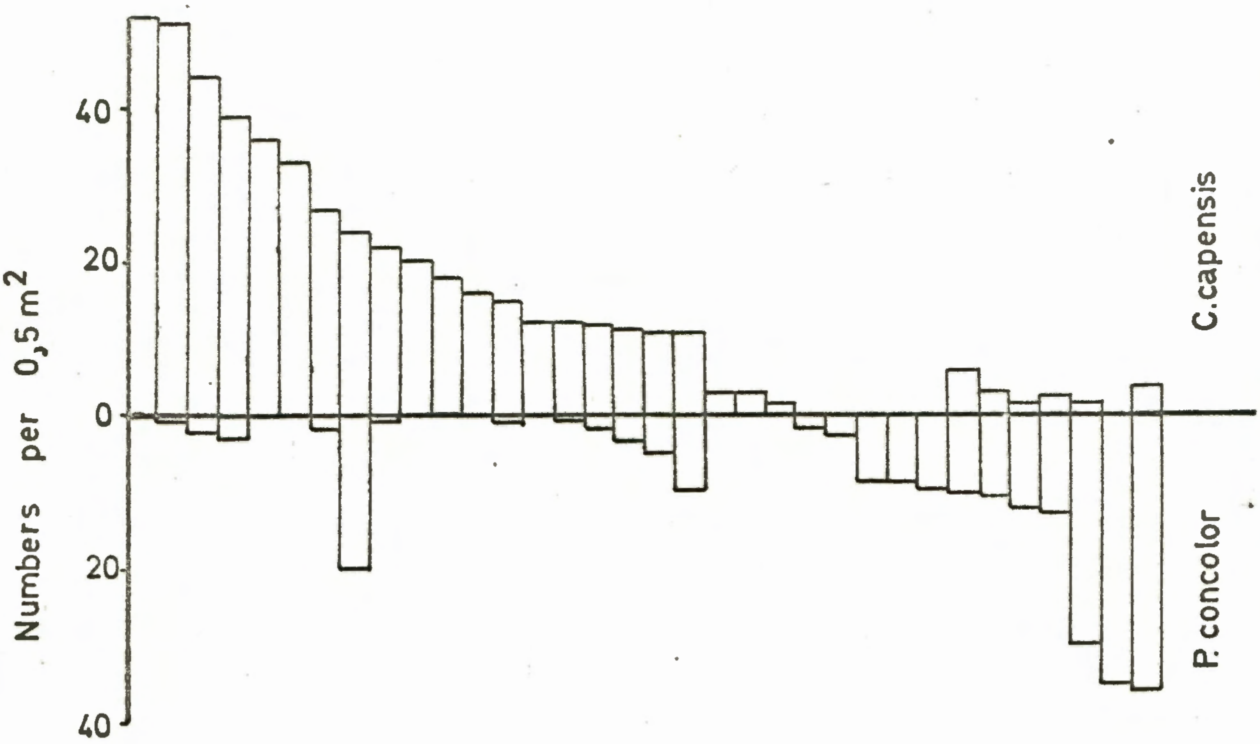


FIG. I2. The relative densities of *P.concolor* and *C.capensis* in a series of 34 random quadrats.

## P. concolor - Cellana capensis interaction:

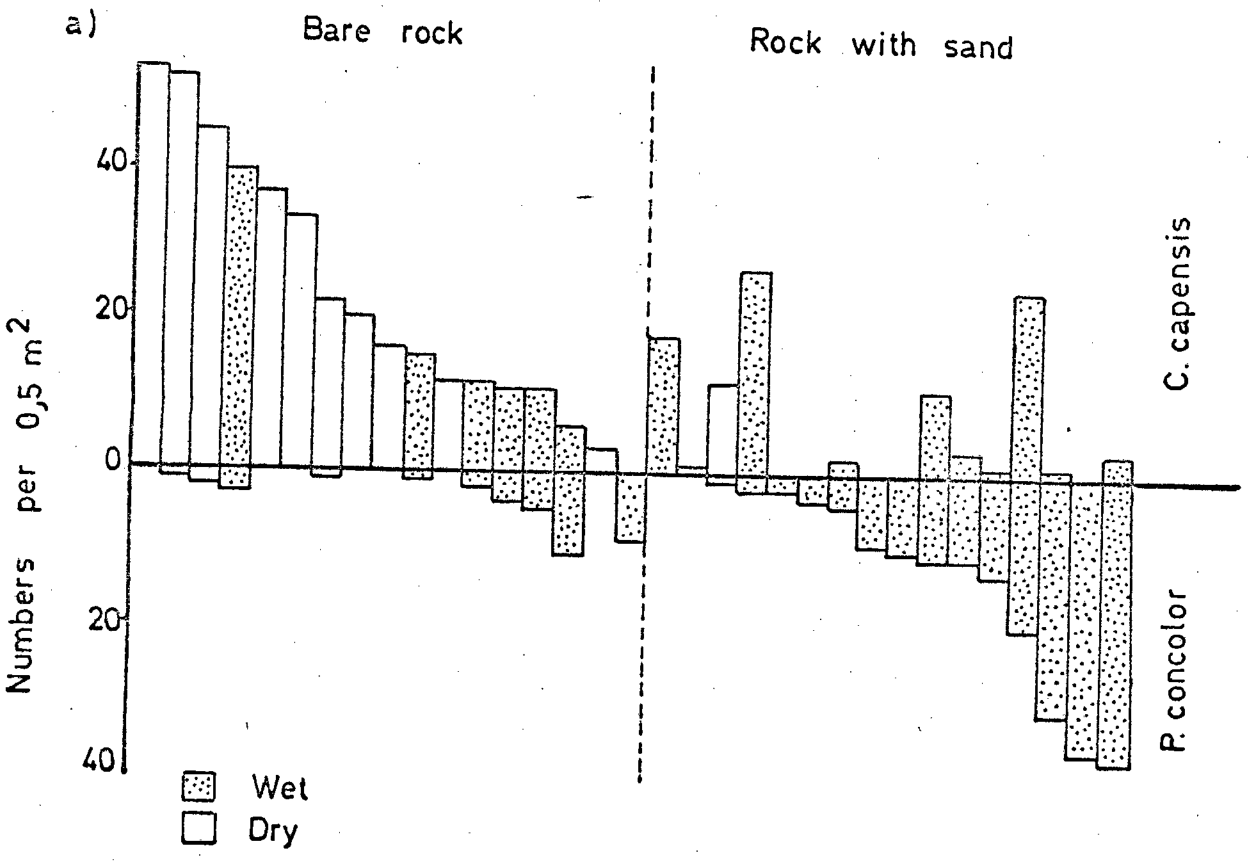
The general ecology of these two species has already been described (Section II), but can be summarised briefly. Both species are common in the upper balanoid zone of the East coast and are generalised browsers feeding on any available food. P. concolor probably migrates up the shore. Their distributions overlap considerably.

All other Patellas are ecologically separable from their allies by some major differentiation in habitat, zonation or food, so that niche overlap is minimised. In this case the fundamental niches of the two species are so similar that the question arises whether they are truly "coexistent", and to what extent their niches are shared.

A random quadrat analysis was undertaken at Lwandile in the Transkei to test the degree of overlap between the two species. The results from 34 quadrats show that within small areas ($0.5m^2$) there is a substantial separation of the two species. With few exceptions, if one is common, the other is not (fig. 12).

Demonstration of mutual exclusion does not elucidate the mechanism causing separation, and so the physical make up of the quadrats was analysed with respect to moisture (wet or dry substrate), and presence or absence of sand on the rocks.

The analysis shows that P. concolor is almost entirely restricted to moist areas (fig. 13b). Sand retains moisture, and P. concolor was found predominantly on rocks covered by a fine layer of sand (fig. 13a). The converse was true for Cellana capensis: they occurred predominantly on dry rocks (fig. 13b). Some did extend into moist areas, but very few occurred where there was sand on the rocks. Thus P. concolor



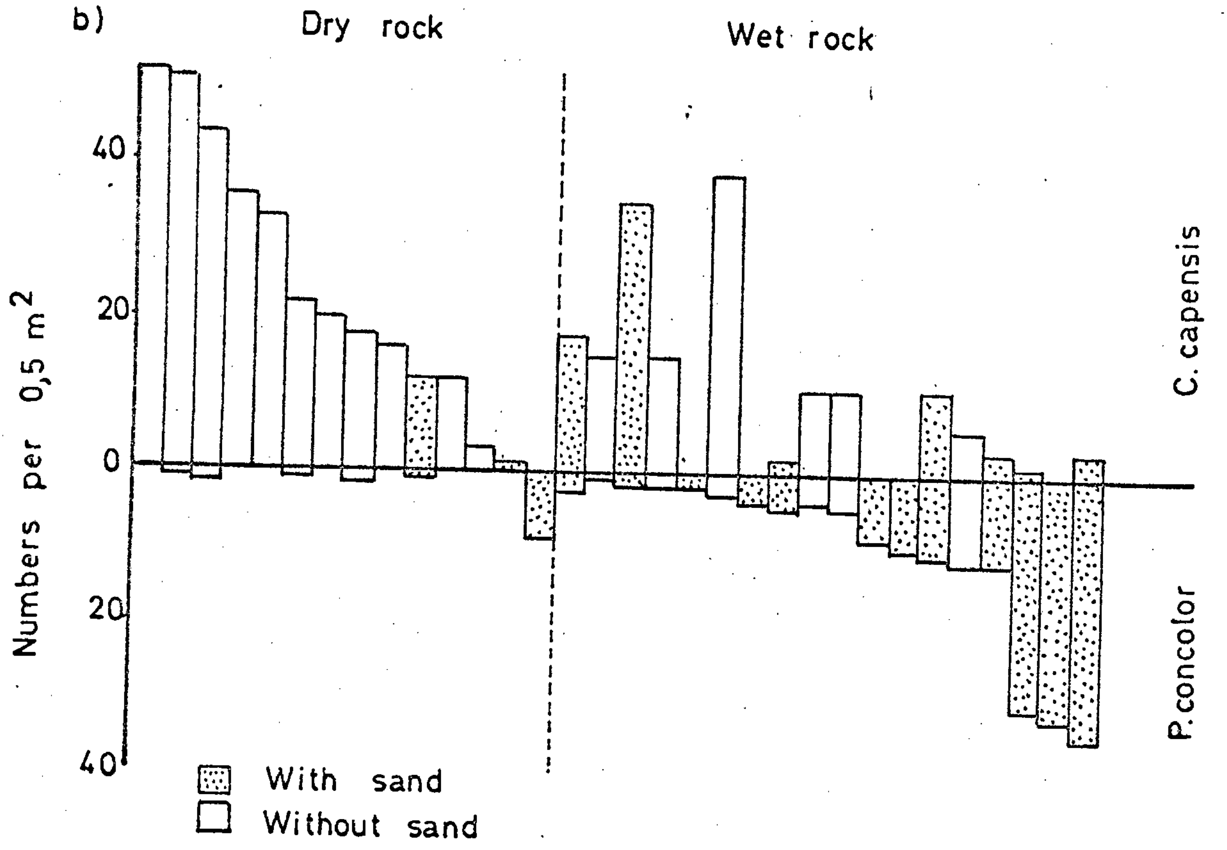


FIG.13. Densities of P.concolor and C.capensis, relative to oneanother and to physical conditions

is common in moist (often sandy) niches, while C. capensis avoids sandy areas and occurs more often on dry rocks.

Statistical analysis of these data is given in tables 2 and 3.

TABLE 2. Chi square analysis of 2 x 2 contingency table. Preference of P. concolor and C. capensis for dry or moist niches.

| | Moist | Dry | Total |
|---|---|---|---|
| C. capensis | 160 | 320 | 480 |
| P. concolor | 195 | 16 | 211 |
| Total | 355 | 336 | 691 |

Significance of difference: $p < .001$

TABLE 3. Chi square test of 2 x 2 contingency table: Preference of C. capensis and P. concolor for bare or sand covered rocks.

| | Sandy | Bare | Total |
|---|---|---|---|
| C. capensis | 103 | 373 | 476 |
| P. concolor | 190 | 45 | 235 |
| Total | 293 | 418 | 711 |

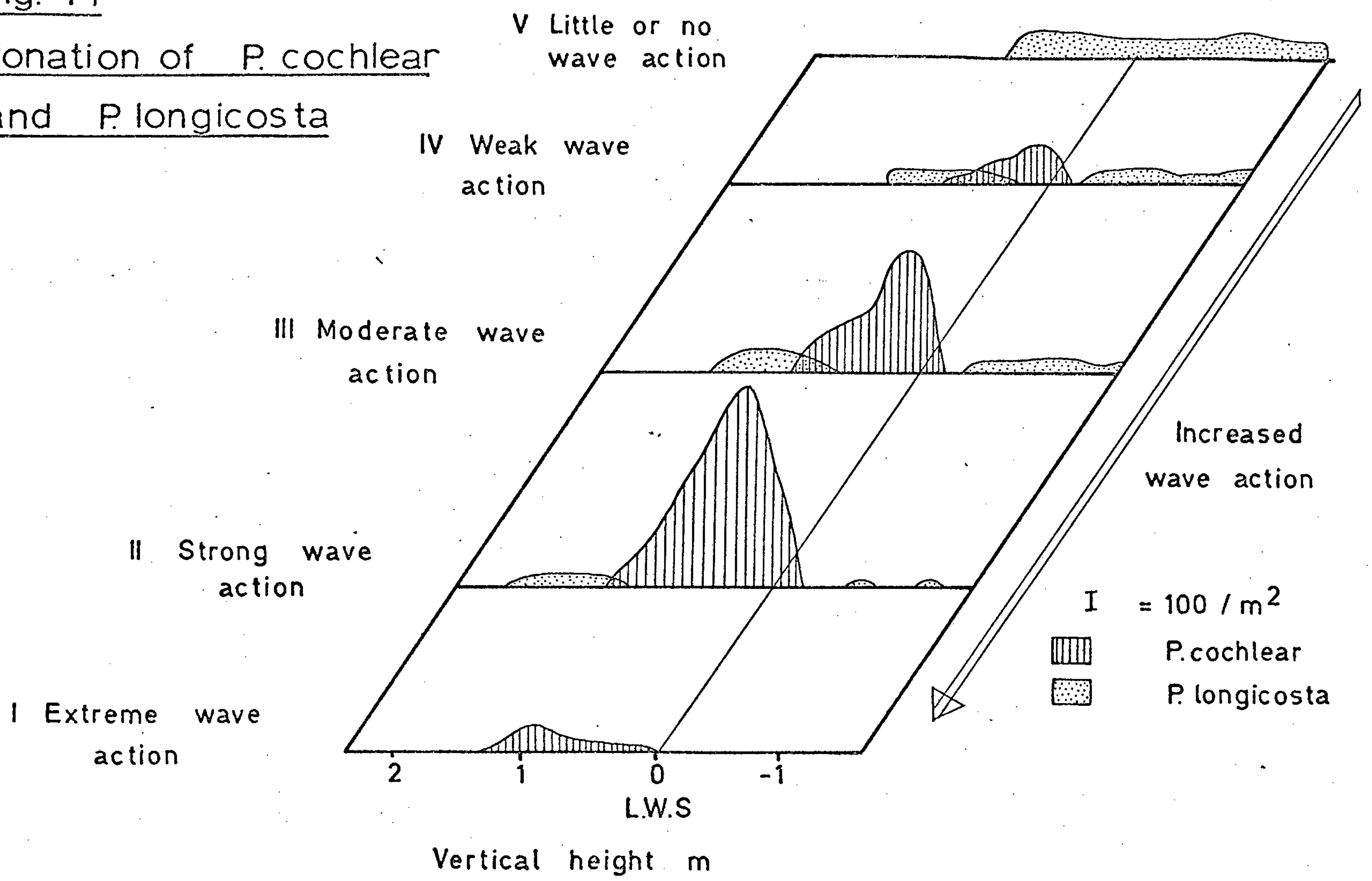
Significance of difference: $p < .001$

Separation of the two species at the microniche level may be important in preventing competitive exclusion of one or other. Coexistence is a relative term, dependent on the spacial unit used, but within the context of the intertidal zone, these species are coexistent.

This is similar to the situation described by Haven (1971)

Fig. 14

Zonation of P. cochlear and P. longicosta



for Acmaea scabra and A. digitalis, which share the same zone and food, but their habits are sufficiently different to separate their microniches.

### P. cochlear - P. longicosta interaction:

P. cochlear dominates the lower shore in the southerly regions of South Africa, and its density is related to wave action. Four transects were completed at Dalebrook, and one at Hangklip, at sites with different intensities of wave action. These are given in figure 14. P. cochlear is absent from very sheltered areas, but as wave action increases it becomes more and more common and extends further up the shore. Under extreme wave action it is scarce or absent. P. longicosta occurs both above and below the cochlear zone and progressively encroaches into it as the densities of P. cochlear decrease (fig. 14). With the disappearance of P. cochlear, P. longicosta occupies a continuous zone from about 0.8m. above L.W.S. to at least 3m. below L.W.S.

This zonation is strong empirical evidence for competitive exclusion of P. longicosta from the cochlear zone and that P. cochlear is included in the fundamental niche of P. longicosta.

P. cochlear feeds almost entirely on lithothamnion, and clears all other algal away. Overgrowth by other algae increases as P. cochlear densities drop below 300/m$^2$ (Section V, fig. 13a). Adult P. longicosta feed on Ralfsia expansa, and this alga is excluded from the denser P. cochlear stands. Random quadrat analyses were undertaken in the cochlear zone at Dalebrook, along 200m. of shoreline. All sites analysed were between low water spring level and 0.4m. above low water springs and the prevailing wave action varied from moderate to

Fig. 15a Relative Densities of P. cochlear and P. longicosta

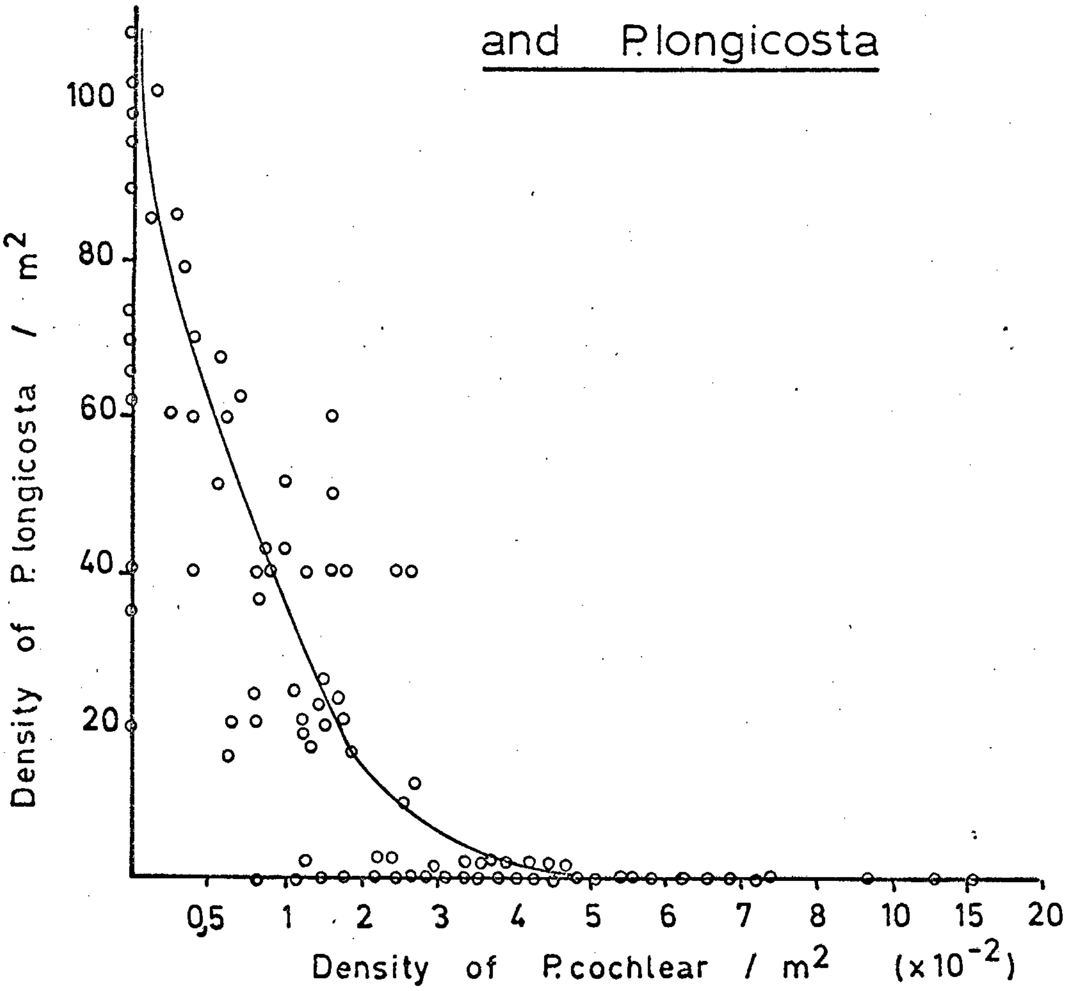
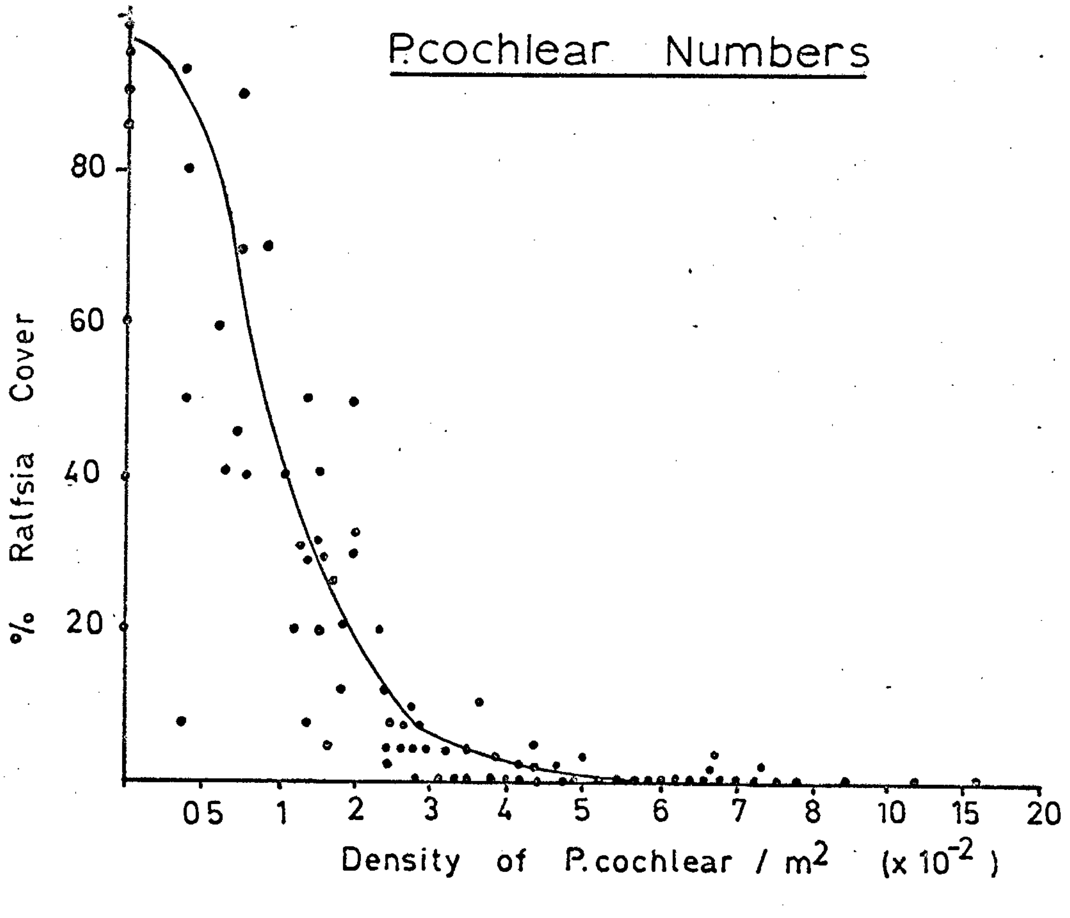


Fig. 15b Ralfsia Cover Relative to P. cochlear Numbers



fairly strong. These analyses show the relationship between *P. cochlear* density, precentage *Ralfsia* cover, and density of *P. longicosta* (figs. 15a, b).

The interplay between the two limpets is however not based simply on the presence or absence of *Ralfsia*, for (at least intertidally) it is *P. longicosta* which establishes and maintains the *Ralfsia*. 96% of this alga occurs in *P. longicosta* gardens (Section VI), and there is a direct correlation between *P. longicosta* densities and percentage *Ralfsia* cover.

*P. cochlear* settle in June-July, and are established by the time *P. longicosta* settle in November (Section III). Juvenile *P. cochlear* are restricted to the shells of other *P. cochlear*, because grazing eradicates larvae settling on the rocks. These juveniles feed both on the shells (which are covered by lithothamnion) and they descend to feed on the adjacent rock. In the process, both shells and rocks are kept clear of *Ralfsia*. Sometimes, however, *Ralfsia* becomes established on *P. cochlear* shells, and *P. longicosta* juveniles may settle there. Subsequently they disappear from the cochlear zone, unless the densities of *P. cochlear* are low. This may be because *Ralfsia* becomes limiting, but it is also probably because *P. longicosta* requires a minimum space in which to establish a territory (Section VI, p. 22). The closely packed *P. cochlear* prevent this. Even in areas where the *P. cochlear* density is too low to exclude *Ralfsia*, and this alga forms small islands between the limpets, *P. longicosta* never establishes a territory on the *Ralfsia* unless the space is adequate.

The competitive superiority of *P. cochlear* comes from its exploitation of both space and food in the lower intertidal, thus excluding *P. longicosta* (and probably *P. oculus* as well).

P. cochlear is limited by physical factors, such as wave action and desiccation, and by the presence of its food plant, lithothamnion. At the fringe of its habitat, where P. cochlear is sparse, P. longicosta coexists with it. Physical factors limit one species, and competitive factors the other.

Territorial defence by P. longicosta has already been described (Section VI, p.13). Recapitulating, the limpet establishes a Ralfsia garden (with a scar at the centre), and then defends it by steadily pushing against any intruding limpet until it retreats. This reaction has been elicited during staged encounters with other P. longicosta, P. oculus, P. barbara and P. granularis. Defence against P. cochlear often failed to occur, although strong reactions were seen on three occasions. This may be an anomalous effect due to the difficult turbulent conditions one is operating under. If it is a real effect, it may be a further measure of the competitive superiority of P. cochlear, or it may be that territorial defence against the densely packed P. cochlear is poorly developed because it is futile. In any event, P. cochlear will not move away from their scars when they encounter other animals. During staged encounters, P. cochlear remained firmly on their scars irrespective of the species involved or the force applied. Under natural conditions they are unlikely to move away from a P. longicosta, so that aggressive action against an established P. cochlear would be futile.

### P. longicosta - P. oculus interaction:

P. oculus occurs in the lower and upper balanoid zones, extending higher than P. longicosta but overlapping with it. P. oculus is a generalised browser, consuming all available low growing algae (including Ralfsia), lichens, spume and organic debris (Branch, 1971).

P. longicosta is a specialist, feeding principally on Ralfsia, and has a narrow niche, while P. oculus has a wide niche incorporating that of P. longicosta. One factor partly separates the two species: P. oculus is restricted to bare rock (Section VI, plate 3b), while P. longicosta occurs on bare rock, on lithothamnion, or on isolated patches of Ralfsia amongst algal turf.

Territorial defence by P. longicosta is particularly vigorous against P. oculus. Forty encounters were staged between the two species underwater during the incoming tide (when both normally start feeding). The P. oculus were placed separately on Ralfsia gardens, or on the scars of P. longicosta which had moved away to feed, and held in position until they adhered.

In every case, as soon as contact occurred between the two animals, the P. longicosta thrust out all its pallial tentacles, and after a brief pause began pushing the P. oculus away. Considerable force was used in most cases, and the shell of the P. oculus was often forced away while the foot remained attached and became stretched. The P. oculus often adhered firmly, but gave way slowly and eventually retreated more rapidly. Contest ceased at the perimeter of the gardens and the P. longicosta never went further than this. Some contests lasted 30 minutes, but two to ten minutes was more normal. Reaction was most rapid when the P. longicosta was off its scar, feeding.

To test the efficiency of territorial defence and maintenance of Ralfsia, all P. longicosta were removed from two areas of $6m^2$ at Dalebrook. At one site, all other limpets were also removed, and at the other, they were left in position.

In the total absence of limpets, Ralfsia flourished initially, but after 6 months it was slowly replaced by more upright algae including Ulva sp., Enteromorpha sp. Gelidium pristoides, and Colpomenia sinuosa; and after two and a half years it was almost completely displaced. At the second site the Ralfsia was consumed by the remaining limpets and disappeared within a month: chief amongst those responsible was P. oculus, but a few P. barbara were also present.

When large P. longicosta die naturally (or are removed), their scars are rapidly occupied by single smaller P. longicosta which were previously restricted to lithothamnion (Branch, 1971). These animals then maintain the territory.

These results show that territorial defence is important and efficient in the maintenance of Ralfsia gardens. In a curious way, the relationship is co-operative.

The continued coexistence of the two limpets is dependent on the competitive superiority of P. longicosta, allowing it to dominate its narrow niche, and the generalised behaviour of P. oculus allowing it to use wider resources.

In passing, it may be recalled that the subtidal P. tabularis defends large Ralfsia gardens as well, and force off intruding limpets: yet may tolerate P. longicosta, and the latter quite often establish their smaller territories within the confines of P. tabularis gardens. Five P. longicosta were matched against territorial P. tabularis, without result. This does not necessarily indicate a lack of territorial defence against this limpet, and a larger sample needs to be tested.

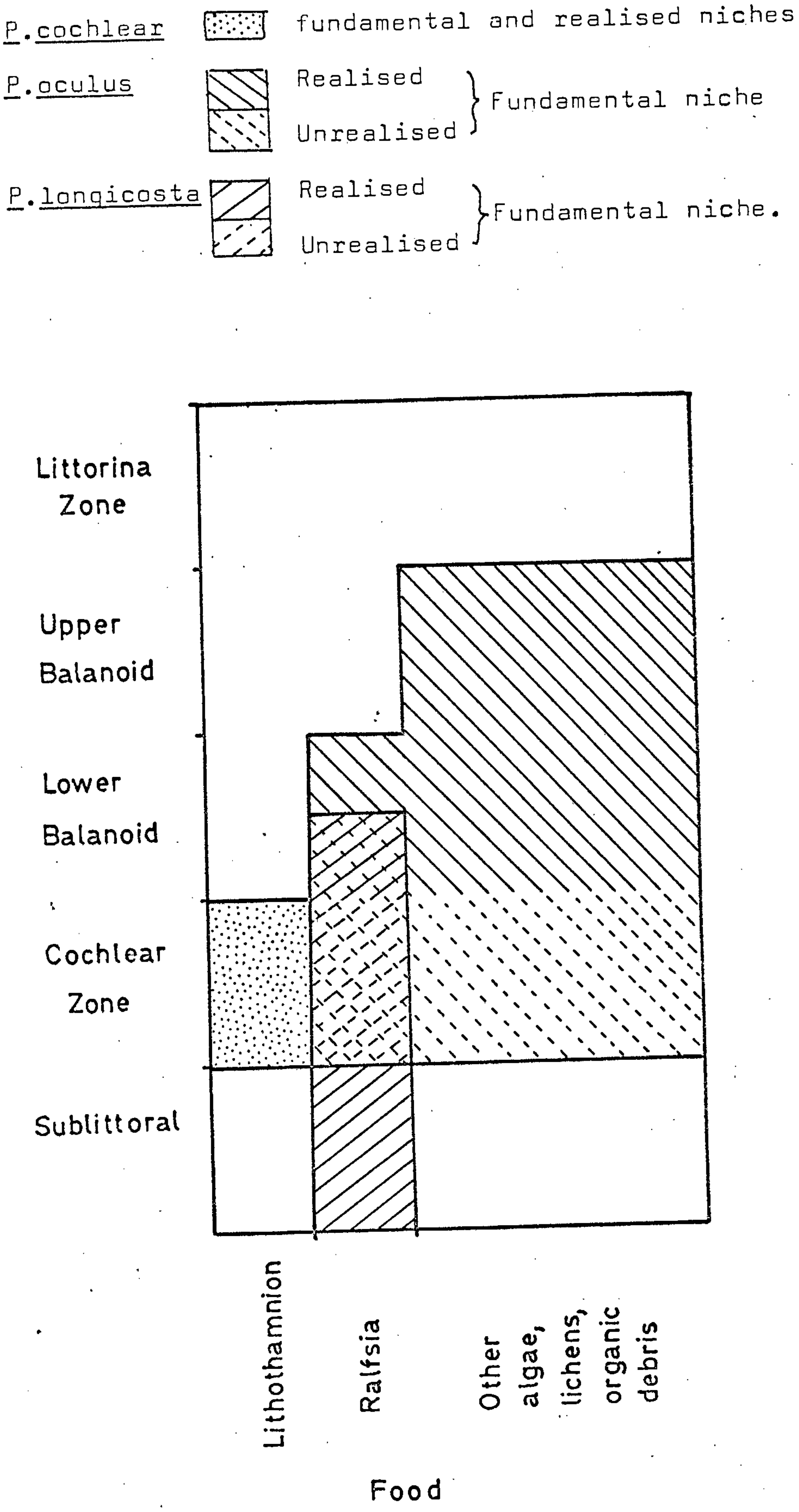
## DISCUSSION:

Competition is generally assumed to be a dominant force behind evolution, but evidence for this is mostly empirical. Gause's principle (advanced in various forms, which are reviewed by Miller, 1967) prescribes that species with identical needs cannot coexist (Hardin, 1960). There is however a danger of accepting this axiom uncritically: clearly no two species ever have identical needs and habits. Intraspecific competition occurs between individuals with nearly identical needs, and yet their "coexistence" continues.

As it is stated, Gause's principle is untestable, for examples of apparent coexistence can always be dismissed by the statement that the species could not have had identical requirements. This introduces circularity into the argument, and may obscure new findings (Cole, 1960). Experimental analysis of two-species systems usually results in competitive exclusion of one species, but Miller (1967) gives several examples of apparent coexistence over many generations. Finally, Andrewartha (1970, p.48) records examples of competitive exclusion which are the result of essential differences between species and not "identical needs". Perhaps this does not detract from Gause's principle, but suggests an alternative pathway to exclusion.

In the light of these criticisms, it may be better to rephrase the concept as follows: "Species which compete for an essential and potentially limiting resource cannot coexist indefinitely unless their populations are maintained at sub-maximal levels by some intrinsic or extrinsic factor." The corollary to this is that allied species are more likely to have similar requirements and hence to come into competition

FIG. 16. THE NICHE RELATIONSHIPS OF P.COCHLEAR, P.LONGICOSTA, AND P.OCULUS.
(The fundamental and realised niches are indicated by differential shading).



if they are sympatric. Such a condition may arise during the evolution of two species from a common ancestor, when intraspecific competition may become interspecific competition in overlapping areas, as the two species diverge. Specialisation is one mechanism which will reduce such overlap and allow continued coexistence in a broad habitat.

The cases described in this paper include examples of competitive exclusion and of coexistence, involving similar and dissimilar species and various mechanisms have been employed which bring about these respective conditions. Figure 16 summarises the overlap which occurs between the principal limpet species.

## Mechanisms of competition:

Elton and Miller (1954) define two components of competition. "Interference" is any activity which denies a competitor access to a resource. Territorial behaviour is the most obvious form of interference. "Exploitation" is the direct utilisation of a resource. A superior competitor will utilise the greatest amount to the cost of the inferior competitor.

The interaction between *P. oculus* and *P. longicosta* elegantly illustrate the difference: *P. oculus* exploits all available food and competes by utilising as much food as possible; *P. longicosta*, by territorial defence, interferes with the access of other limpets to *Ralfsia*. These mechanisms are usually common to both interspecific and intraspecific interactions.

Similar interference can be ascribed to the territorial behaviour of *P. tabularis*, *P. compressa* (and probably *P. miniata*), and is typical of the "non-migratory" species which occupy a fixed habitat throughout their lives (Section VI, p. Conversely the "migratory" species (P. granularis, P. granatina, P. oculus and P. concolor) all move progressively up the shore, and all compete by exploitation. (This is assumed for P. concolor.) This differentiation is logical, for the migratory species can always move if food is overexploited by their activities (unless movement is restricted by dense barnacles or other physical features), while non-migratory species are restricted to a fixed zone (and often a fixed food plant), and it is more important to conserve their resources.

P. cochlear is an unusual case. Adults space themselves out and avoid competition by rotating and feeding in the immediate vicinity of the scar. Juveniles form scars on the shells of adults but descend to feed on the rock, as well as feeding on the lithothamnion growing on the shell. Individuals move apart when they come in contact. Thus the adults are territorial even though a territorial defence is not developed. They deny access to the substrate by their grazing habits, and a variety of other organisms are excluded as a result: barnacles and the sessile Vermetus corallinaceus and Dodecaceria pulchra are obvious examples. When P. cochlear are removed, large numbers of Balanus algicola settle (Section V, plate 1). In sparse populations of the limpet, Vermetus settle outside the reach of the rotating adults and form islands or complete craters surrounding the limpets.

Competition in these cases is by interference, preventing settlement of other organisms. In the same way the P. cochlear are too crowded to allow P. longicosta to establish territories, and they exploit all algae so much that Ralfsia is excluded from most of the cochlear zone.

Thus in *P. cochlear* elements of both interference and exploitation are present.

In the midlittoral zone barnacles compete with *P. granularis* by exploiting available space and food. They also interfere with feeding, because *P. granularis* cannot feed effectively on the barnacles. Conversely the limpets may compete by interfering with settlement and by actively shouldering off small barnacles. *Chthamalus* settles so densely that competition by *P. granularis* is not very effective. Apart from the scar physically occupied by the limpet, *Chthamalus* may completely cover the substrate. *Octomeris* and *Tetraclita* settle more sparsely, and groups of limpets may keep clear patches of rock (Plate 2).

Limpet - barnacle competition has also been documented by Connell (1961a) for *P. vulgata* and *Chthamalus stellatus*, and by Dayton (1970) for *Acmaea* spp. and various barnacles.

In most cases exploitation is the predominant form of competition when interference mechanisms are lacking. Exploitation is likely to lead to wastage of resources and higher mortality, because "some of the requisite secured by the animals takes no part in sustaining the population, being dissipated by individuals which obtain insufficient for survival" (or reproduction)(Nicholson, 1954, p.42). Interference allows the effective use of the resource by the individual in possession, and there is no wastage. Thus there will be a selective advantage in developing interference mechanisms at both intra- and interspecific levels (Miller, 1967).

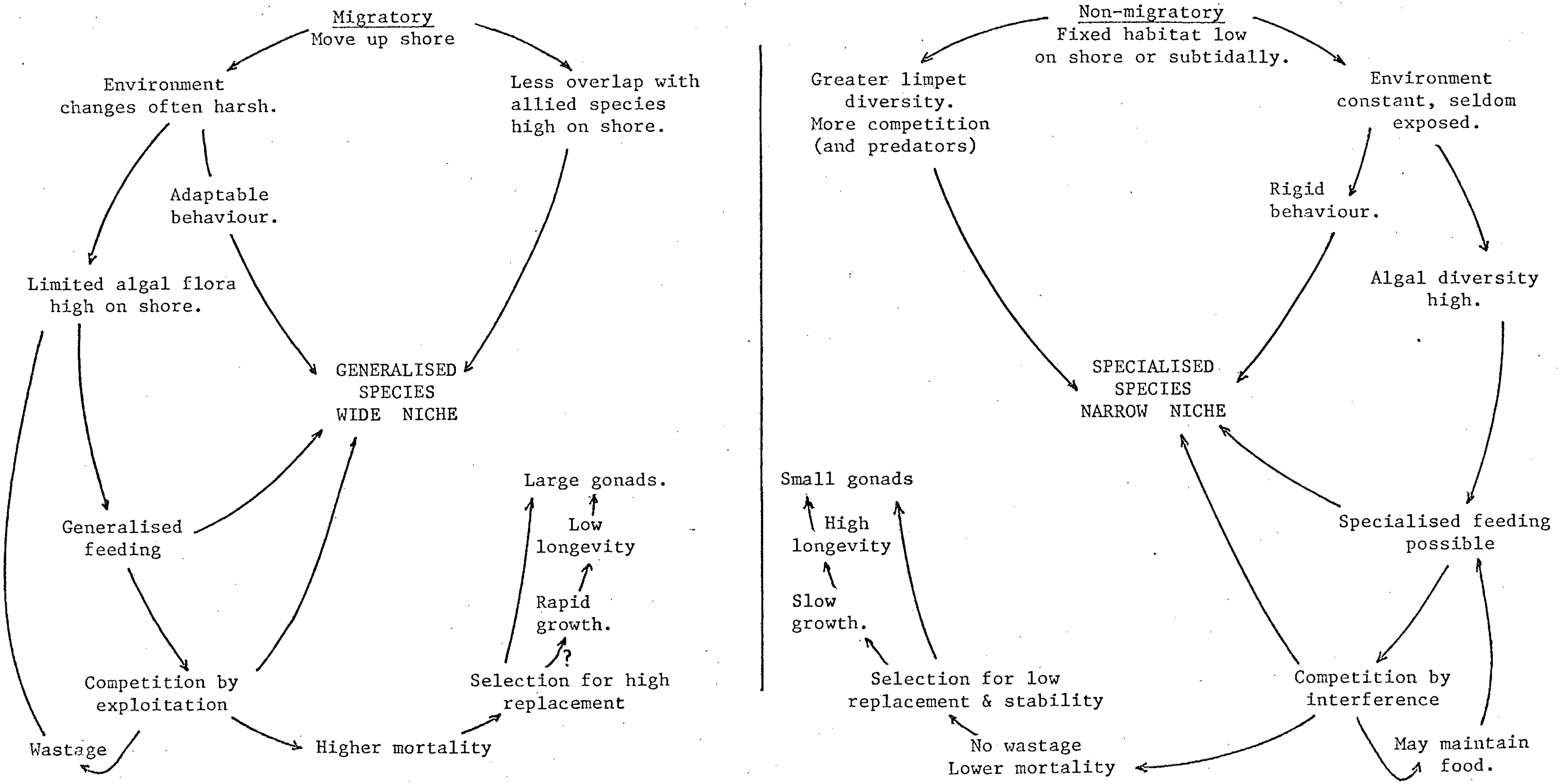
These points suggest that "exploitation is a primitive and unstable form of interaction and that interference mechanisms such as territoriality represent evolutionary advances towards more effective biotic control of population interactions and numerical stability" (Miller, 1967, p.12).

Interference is usually most marked between members of the same species or allied species. Wynne-Edwards (1962) has inferred that it arose as an intraspecific device to stabilise populations. Territorial defence in *Patella* is most marked between individuals of the same species, often less pronounced to other limpets, and lacking in response to *Oxystele tigrina* and *O. variegata* (common intertidal winkles). Closely related species are more likely to have overlapping ecological requirements and are also more likely to evolve interference mechanisms which are recognisable between the species. In a sense this supports Gause's principle, for it implies greatest competition between allied species.

In the case of limpets, interference mechanisms are known only in areas where limpet diversity is high: South Africa and the Western coast of N. America (Stimson, 1969). In areas such as Europe, Angola, West Africa, Mocambique and Mauritius, limpet diversity is low and interference absent (or unrecorded as yet).

As exploitation is associated with higher mortality, selection will probably favour higher replacement rate. Amongst other mechanisms this can be achieved by a higher gonadial output or faster growth to maturity. Both imply greater metabolic expenditure and a low longevity. Conversely interference decreases mortality and stabilises the population, and selection will favour lower replacement and greater stability. Stability is achieved by higher longevity;

Fig. 17.


Migratory
Move up shore
Environment changes often harsh.
Less overlap with allied species high on shore.
Adaptable behaviour.
Limited algal flora high on shore.
GENERALISED SPECIES WIDE NICHE
Generalised feeding
Large gonads.
Low longevity
Rapid growth.
?
Competition by exploitation
Selection for high replacement
Wastage
Higher mortality
Non-migratory
Fixed habitat low on shore or subtidally.
Greater limpet diversity. More competition (and predators)
Environment constant, seldom exposed.
Rigid behaviour.
Algal diversity high.
SPECIALISED SPECIES NARROW NICHE
Small gonads
High longevity
Slow growth.
Specialised feeding possible
Selection for low replacement & stability
Competition by interference
No wastage
Lower mortality
May maintain food.

low replacement by slower growth and small gonad size.

These trends are strikingly demonstrated by Patella spp., (although some aspects are not known for all of the species). P. granularis, P. granatina, P. oculus, P. concolor, (and possibly P. barbara ?) all exploit their food supplies. Information is incomplete for P. concolor, but all of this group have high growth rates, high mortality, low longevity (Section IV, figs. 10 and 18) and large gonads (Section II, fig.6 and III, fig. 16). P. oculus is exceptional in the last respect, having a small gonad: but it is unusual in being a protandric hermaphrodite and spawning twice a year.

Conversely, P. longicosta, P. tabularis, P. cochlear, P. compressa (and P. miniata ?) are territorial and compete by interference. All have relatively small gonads (Section III, fig. 16) and growth in P. longicosta and P. cochlear is low, while they have a correspondingly high longevity. (Data are lacking for the other species, but growth is probably faster in P. compressa.)

These trends are summarised in figure 17.

## Coexistence and Species Diversity:

Within the confines of the intertidal and infratidal zones, all the South African Patella spp. (excluding P. concolor) are coexistent at some point of their distribution. This coexistence of 10 congeneric limpet species is probably paralleled only by the array of Acmaea spp. on the Californian coast (Test, 1945).

Competition is probably a major cause of specialisation which in turn reduces overlap between the species and allows a greater diversity of species to coexist. Many of the local

Patellas are specialised with respect to food and zonation: P. longicosta, P. tabularis, P. cochlear, P. compressa and P. miniata. P. argenvillei occupies a narrow zone on the shore, but has generalised feeding habits, and is somewhat intermediate.

Conversely, P. oculus, P. granularis, P. granatina, and P. concolor are generalised and have wide niches. Both their zonation and their feeding habits are broad. P. barbara feeds on a wide variety of algae and is probably also a generalised species (although its habits are not as well known).

These two groups correspond with the "non-migratory" and "migratory" categories previously described (Section VI, p. 6 ).

Species with narrow niches generally have stereotyped behaviour while those with broader niches are more adaptable. The specialised Patella spp. have rigid habits with respect to homing, feeding, territorial behaviour, dispersal and aggression to other limpets. Behaviour is more flexible in the generalised species. The pattern of dispersion varies from random to highly aggregate, and homing behaviour may be highly developed or completely absent in any given species. Such differences in behaviour have been related to environmental conditions, especially desiccation (Section XI). Incidentally the aggregating behaviour of P. granularis and P. granatina is species-specific thus reducing contact and competition between the two, where their zonation overlaps.

Wide niches imply that fewer species can be sympatric, because the likelihood of overlap and competition is greater. Furthermore, such species usually compete by exploitation, with inevitable wastage of resources. This intensifies the problem of overlap in niches.

In the case of Patella concolor and Cellana capensis, both are generalised species and there is broad overlap in their feeding and zonation. However, their habits with respect to moisture and sand are sufficiently different to separate their microniches.

A trend towards specialisation can be anticipated when a large number of allied species are sympatric. This is elegantly demonstrated by the distribution of Patella in Southern Africa (Table 4).

This same trend is probably true on a worldwide basis, although data is not available for many limpets. In California many of the 17 Acmaea spp. are specialised with respect to food or habitat and only three overlap substantially (Test, 1945). In the same area Lottia gigantea is clearly a specialised species (Stimson, 1969). Acmaea limatula coexists with A. pelta, but the former feeds on encrusting lithothamnion, Hildenbrandia and Peyssonelia (Eaton, 1968), while A. pelta eats upright non-encrusting algae (Craig, 1968).

By contrast, the three British Patella spp. are all generalised feeders and although they may be differentially zoned, they coexist in the lower shore and have wide niches. Patina pellucida is however specialised for life on kelp.

Under conditions of sympatry, natural selection will favour niche specialisation, reducing competition and thus stabilising the community. Logically this should terminate in a condition where competition is all but eliminated. Kohn (1959) has suggested that this is the case in Hawaiian Conus spp. which have different habits with respect to feeding, nature of substrate, and zonation. He suggests they are so sensitively adapted to

TABLE 4. The numbers of sympatric Patella spp. in relation to distribution and specialisation.

| Locality | P. safiana | P. compressa | P. granatina | P. argenvillei | P. miniata | P. granularis | P. barbara | P. cochlear | P. oculus | P. tabularis | P. longicosta | P. concolor | ? P. rustica * | Number of Patella spp. | % specialised species |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| (Angola) | x | | | | | x | | | | | | | | 2 | 0 |
| Rocky Point (SWA) | x | | x | | x | x | | | | | | | | 4 | 25 |
| Luderitz (SWA) | | x | x | x | x | x | x | | | | | | | 6 | 50 |
| Elands Bay | | x | x | x | x | x | x | x | | | | | | 7 | 57 |
| Cape Point | | x | x | x | x | x | x | x | x | x | x | | | 10 | 60 |
| Cape Padrone | | | | x | x | x | x | x | x | x | x | | | 8 | 62 |
| Durban | | | | | | x | x | | | | x | x | | 4 | 25 |
| St. Lucia | | | | | | x | x | | | | | x | | 3 | 0 |
| Jangamo (Mocambique) | | | | | | | | | | | | | x | 1 | 0 |

* This is possibly P. rustica Linn. and is not the P. rustica of Reeve (= P. tabularis).

their microhabitats that their distribution is effectively mutually exclusive, and controlled by environmental discontinuities and not competition. Nevertheless, competition probably caused their original specialisation and divergence.

Niche specialisation is often equated with competitive superiority in a particular habitat (Miller, 1967). Often the narrower niche of a specialised species is included in the fundamental niche of a more generalised species. Under such conditions it is axiomatic that the former species is the superior competitor. This allows continued coexistence of the two species within the biotope, for while the specialised species dominates its niche, it cannot penetrate the wider niche to displace the generalised species.

Another facet of specialisation is that a species may modify the environment to the extent of "creating" a new microhabitat. The activities of *P. longicosta* are of this type, for they are responsible for the initiation and maintenance of *Ralfsia* gardens. Removal of *P. longicosta* results in the disappearance of *Ralfsia* because of algal overgrowth or herbivore grazing: 96% of this alga occurs in limpet gardens. This does not imply that the alga cannot develop without *P. longicosta* but that if it were not maintained, its quantity would be inadequate for the specialised needs of the *P. longicosta* population.

The biotic complexity thus diversifies the environment, encouraging further speciation and in turn increasing complexity. Thus an "accelerated" speciation and diversification may occur (Day, 1963).

On the other hand, *P. cochlear* modifies its habitat drastically, excluding all macrofauna and algae. Domination is so great that environmental diversity is reduced considerably. A uniform environment will intensify competition, favouring a monospecific community of the most successful competitor. It is not known how *P. cochlear* removes all other algae while leaving the lithothamnion to grow. Possibly the calcareous incrustation is more difficult to remove.

In a different sense *P. argenvillei* and *P. cochlear* also "create" their environment: their shells are covered by lithothamnion and provide both substrate and food for settling larvae. This will be discussed below.

Apart from specialisation within a region of sympatry, a farther avenue is open for increasing diversity within a group: species may fill "unoccupied" niches. Such entities are difficult to conceive in the crowded intertidal zone, but the unstable wave beaten Ecklonia stipes and fronds are a relatively unexploited niche. The winkles Oxystele sinensis and Turbo cidaris climb up the stipe and feed there, but are swept off by stronger water movements. P. compressa is the only herbivore specialised for this niche.

Meadows and Campbell (1972a, b) have postulated that behavioural mutation may alter habitat selection and simultaneously cause isolation of the mutant strain. The distinct and very specific habitat of P. compressa suggests it may have evolved this way. Subsequent adaptation to the niche would be due to physical selective pressures and not interspecific competition.

It must however be appreciated that isolation is not easily achieved in the sea, where gametes are often shed into the sea (Day, 1963). Under these conditions a mutant trait is likely to be swamped by crossfertilisation with the parent population, unless it is dominant, or different breeding seasons allow isolation, or specialised isolating mechanisms occur.

Competition can also be decreased (and diversity increased) if populations are rarified by some factor which regulates their densities. This can be achieved by a reduction in gonad output, recruitment or survival. This regulation is particularly important when directed at potentially dominant species and may prevent their monopolisation of a habitat.

The habitat of P. cochlear is delimited by physical factors such as wave action and desiccation and by the presence of lithothamnion. Intrinsic control is exerted over the densities in that habitat. This has previously been described (Section V, fig 12).

The association between *P. granularis* and barnacles is a more complex case. Firstly, limpet density increases as barnacle cover gets greater. The cause of this is not known, but there are various possibilities. Barnacles may protect the limpets from wave action and desiccation. The predatory *Thais dubia* feeds preferentially on barnacles (particularly *Chthamalus*), but also on *P. granularis*. Morgan (1972) has shown that *Nucella lapillus* feeds on *Balanus*, but switches its attention to the cockle *Ceratoderma edula* if no barnacles are present. While *T. dubia* may feed on increasing numbers of limpets if barnacles are absent, there was little difference in survival of *P. granularis* at sites B, C and D (30%, 80% and 95% *Chthamalus* cover). Thus differential feeding by *Thais* does not seem implicated in the higher densities of *P. granularis* associated with greater barnacle cover.

More probably, settlement of *P. granularis* is more successful where barnacles are present, because the latter provide shelter against desiccation and wave action. Settlement of *P. granularis* juveniles was recorded over a wide area in the intertidal zone at Dalebrook in August 1972. Massive mortality occurred in barnacle-free bare rocks at mid-tide level, and survival was restricted to the low tide level, amongst barnacles and in damp crevices.

This would also explain why juvenile *P. granularis* are found high on the shore on the South coast (where barnacles predominate), while they are restricted to the lower shore on the West coast, and progressively migrate upwards.

Whatever the reason for the barnacle - P. granularis correlation, the effect is to intensify intra- and interspecific competition simultaneously. As barnacle cover increases, limpet growth and mean size are reduced. The output of limpet gametes (per $m^2$) also decreases despite the concurrent increase in limpet density, and despite compensatory reduction in somatic growth.

Each limpet - barnacle interaction cannot be considered in isolation, for P. granularis can be replaced by migration, and by larval recruitment from other stocks lower on the shore (where barnacle competition is not important).

In this case a balance exists, for although the barnacles may reduce limpet gonadial output, limpet recruitment and immigration allow coexistence to continue.

The barnacles have been collectively considered because it is their percentage cover that effects the limpets. However, Chthamalus settles in vast numbers in the upper balanoid zone, and because of its ability to completely blanket the substrate, is strongly competitive with P. granularis. Tetraclita dominates the mid-tide zone but its settlement is more sparse and it usually covers less than 50% of the substrate. As a result its competitive importance is much less.

Predation is another factor regulating populations. Paine (1966, 1969, 1971) has dramatically shown how the removal of a top predator results in monopolisation of intertidal space by a single species. Clearly predation of this potential dominant normally prevents monopolisation and enhances diversity.

Chthamalus settles over most of the shore, but Thais dubia (and other predators) decimate it in the lower regions of the shore (Plate 4). Lower on the shore, Tetraclita is eaten by Marthasterias glacialis, which removes the barnacles, thus clearing space.

Subtidally P. longicosta and P. tabularis share on almost identical niche, both occupying territorial gardens of Ralfsia. P. longicosta is commoner than the larger P. tabularis, but is frequently eaten by Marthasterias. P. tabularis is very large and probably grows very quickly (Shackleton, 1973), and is rarely (if ever) eaten by Marthasterias (Section VIII). Differential predation may allow the coexistence of these two limpets to continue.

An analagous case can be made out for algal diversity: preferential grazing may prevent domination by a single species. In the present case almost the reverse is true: P. cochlear grazing maintains a lithothamnion dominated lower shore, and P. longicosta maintains monospecific Ralfsia gardens. Dayton (1971) recorded up to 21 algal species in the absence of limpets, but a maximum of six when they were present.

Physical disturbance also prevents monopolisation of space. Dayton (1971) describes how battering by drift logs clears away large patches of animals, allowing other species to fill their place. Movement of boulders by storms, and the physical effect of waves achieve the same thing here. Tetraclita is particularly susceptible.

The limits of zonation usually correlate with the range of tolerance of a species (Section XI), but its habitat preferences and behaviour normally confine it well within its lethal limits. This restriction also limits the niche size.

On a geographical scale along the shore, physical variations are more difficult to pinpoint, except in cases such as the meeting of cold and warm oceans at Cape Point. Here a sharp distributional barrier may occur and some *Patella* spp. are confined to either warm or cold coasts while others occur on both coasts (Stephenson, 1939; Branch, 1971, fig.1). This too will minimise the distributional overlap of many species. Species which extend around Cape Point, out of their usual temperature regime, will have to contend with temperature stresses and competitive stresses. Competition may reinforce the temperature barriers which exist.

A more intriguing problem is the interaction of *P. cochlear* and *P. argenvillei*. *P. cochlear* is a South coast species which extends up the West coast as far as Buffels Bay, its numbers decreasing northwards. *P. argenvillei* intermingles with *P. cochlear* on the South coast and the South West coast, becoming progressively more common in the northern parts of the West coast until it replaces *P. cochlear* and forms a dense "argenvillei" zone low on the shore. Over a broad geographical area the two coexist, with no sign of either displacing the other.

This case has not yet been explored. However, the juveniles of both species settle on the shells of adults of either species. By virtue of its size, *P. argenvillei* usually dominates the primary space, but its shell is coated with lithothamnion, providing food and secondary space for *P. cochlear*. This will reduce the competitive interaction and is perhaps what allows them to coexist.

## Radiation of limpets:

The mechanisms described above suggest how diversity and coexistence are maintained, but do not explain why such diversity of Patella should occur in South Africa, or of Acmaea on the western coast of N. America. The question is even more acute when the paucity of tropical limpets is considered, for the tropics are usually regions of high speciation and diversity.

While the answer to this is likely to be complex, at least part of it may come from the differences between temperate shores (including South Africa and Central North America) and tropical shores. Table 5 summarises some of these differences. Much of the data is taken from the excellent review of Moore (1973), and represent generalisations based on a broad comparison of many shores.

Thus the temperate intertidal zone is larger, more constant in tidal exposure, and is penetrated to a greater degree by animals which live on exposed dry rock surfaces.

All these factors will favour speciation of species adapted to occupy the open shore,and can allow subsequent isolation because synchronised spawning occurs over a short period.

The limpets are particularly well equipped for such an existence, and their shells are adapted to withstand heavy wave action (as is experienced on the South African coast). They may well have undergone speciation in temperate regions as a result of all these factors.

Tropical shores are of course more diverse as a whole, but most of the fauna is infratidal, low intertidal or cryptic and therefore not so susceptible to the blazing tropical sun and other differences between tropical and temperate shores.

TABLE 5. Biological and physical differences between temperate and tropical shores. (i/t = intertidal, temp = temperature).

| | Temperate | Tropical | Consequence |
|---|---|---|---|
| 1 | N-S temp. gradient greater. | N-S temp. gradient less. | Temp.differences may encourage speciation. |
| 2 | Large seasonal range of temp. | Small seasonal range of temp. | Temp. changes allow synchronised spawning. (Assumed to be favourable. Allows isolation of species.) |
| 3 | Tidal range great. | Tidal range small. (Excluding Mocambique channel) | Large i/t area in temperates: more "space" for diversity. More algal biomass. Stronger tidal movement to flush i/t area. |
| 4 | Spring: neap ratio low. | Spring: neap ratio high. | Greater area of i/t with constant tidal conditions in temperates. |
| 5 | Temp. tolerance range great. | Temp. tolerance range small. | Allows wider occupation of i/t in temperates. |
| 6 | Average sp. occupies 40-50% of i/t zone. | Average sp. occupies 20-30% of i/t zone | Greater spread of i/t spp. in temperates. |
| 7 | Air temperatures moderate. | Air temp. very high | Occupation of bare rocks possible in temperates. |
| 8 | Algal biomass high | Algal growth in i/t restricted by solar radiation and air temp. | More algal food available in temperate i/t. |

Speciation in these niches is more likely to be conventionally higher in the tropics.

## SUMMARY:

1. Interspecific competition in Patella is analysed with particular reference to the following interactions: *P. granularis* - barnacles; *P. longicosta* - *P. cochlear*; *P. longicosta* - *P. oculus*; and *P. concolor* - *Cellana capensis*.

2. Mechanisms of competition are discussed in relation to their effects on these species.

3. Two groups of limpets are distinguished: specialists with narrow food requirements and restricted zonation, and generalised species with broad feeding habits and zonation. These correspond to "migratory" and "non-migratory" groups, and compete respectively by interference and exploitation.

4. Up to ten *Patella* spp. may occur on the same shore. Factors allowing this are discussed. Specialisation is the most important factor, and in Southern Africa the percentage of specialised species is correlated with limpet diversity. Other factors maintaining diversity are predation, disturbance, intrinsic population control, migration, invasion or "creation" of unexploited niches, and similar interaction values between competing species.

5. The paucity of tropical limpets and the diversity in other areas are discussed in the light of differences between temperate and tropical shores.

REFERENCES:

ANDREWARTHA, H.G. 1970. Introduction to the study of animal populations. Methuen & Co., London.

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

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.

COLE, L.C. 1960. Competitive exclusion. Science 132 : 348-349.

CONNELL, J.H. 1961a. The influence of interspecific competition and other factors on the distribution of the barnacle Chthamalus stellatus. Ecology 42 : 710-723.

—— 1961b. Effects of competition, predation by Thais lapillus and other factors on natural populations of the barnacle Balanus balanoides. Ecol. Monogr. 31 : 61-104.

—— 1970. A predator-prey system in the marine intertidal region. 1. Balanus glandula and several predatory species of Thais. Ibid. 40 : 49-78.

CRAIG, P.C. 1968. The activity pattern and food habits of the limpet Acmaea pelta. Veliger 11 (suppl.) : 13-19.

DAY, J.H. 1963. The complexity of the biotic environment. In Speciation in the sea. Systematics Assn. Publ. No.5 : 31-49.

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. Quart. rev. Biol. 22 : 283-314.

EATON, C. McK. 1968. The activity and food of the file limpet, Acmaea limatula. Veliger 11 (suppl.) : 5-12.

ELTON, C. and MILLER, R.S. 1954. The ecological survey of animal communities : with a practical system of classifying habitats by structural characters. J. ecol. 42 : 460-496.

FISCHER-PIETTE, E. 1941. Croissance, taille maxima et longevite possible de querques animaux intercotidaux, en fonction du milieu. Ann. Inn. Oceangr. 2nd S. 21 : 1-28.

—— 1948. Sus les elements de prosperite des Patellas et sur leur specificite. J. Conchyliol. 88 : 45-96.

HARDIN, G. 1960. The competitive exclusion principle. Science 131 : 1292-1297.

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

HUTCHINSON, G.E. 1948. Circular causal systems in ecology. Ann. N.Y. Acad. Sci. 50 : 221-246.

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

KOHN, A.J. 1959. The ecology of Conus on Hawaii. Ecol. Monogr. 29 : 47-90.

LODGE, S.M. 1948. Algal growth in the absence of Patella on an experimental strip of foreshore, Port St. Mary, Isle of Man. Proc. Liverpool Biol. Soc. 56 : 78-83.

MEADOWS, P.S. and CAMPBELL, J.I. 1972a. Habitat Selection by aquatic invertebrates. Adv. mar. Biol. 10 : 271-382.

—— 1972b. Habitat selection and animal distribution in the sea : the evolution of a concept. Proc. Roy. Soc. Edinb. (B) 73 : 145-157.

MILLER, R.S. 1967. Pattern and process in competition. Adv. ecol. Res. 4 : 1-74.

MOORE, H.B. 1973. Aspects of stress in the tropical marine environment. Adv. mar. Biol. 10 : 217-269.

MORGAN, P.R. 1972. The influence of prey availability on the distribution and predatory behaviour of *Nucella lapillus* (L). J. anim. Ecol. 41 : 257-274.

NICHOLSON, A.J. 1954. An outline of the dynamics of animal populations. Austr. Jour. Zool. 2 : 9-65.

PAINE, R.T. 1966. Food web complexity and species diversity. Am. Nat. 100 : 65-75.

——— 1969. The *Pisaster-Tegula* interaction : prey patches, predator food preference and intertidal community structure. Ecology 50 : 950-961.

——— 1971. A short term experimental investigation of resource partitioning in a New Zealand rocky intertidal habitat. Ecology 52 : 1096-1106.

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

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

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

STIMSON, J. 1970. Territorial behaviour of the owl limpet, *Lottia gigantea*. Ecology 51 : 113-118.

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

WHITE, P. 1973. Intertidal recolonisation at Dalebrook, False Bay. Unpublished undergraduate project, University of Cape Town.

WOOD, M. 1935. Unpublished notes on intertidal recolonisation. University of Cape Town.

WYNNE-EDWARDS, V.C. 1962. Animal dispersion in relation to social behaviour. Oliver Boyd, London.

APPENDIX I. Analysis of Covariance : limpet density (x) related to reciprocal of limpet mean length at 4 barnacle treatments. (Notation after Snedecor, 1958)

A.

| | Treatment | $f$ (n-1) | $\Sigma x^2$ | $\Sigma xy$ | $\Sigma y^2$ | b | $f'$ | $dy^2$ | Mean square (m.s.) |
|---|---|---|---|---|---|---|---|---|---|
| 1. | | | | | | | | | |
| | I | 9 | 8351.22 | 0.8703 | 0.00024 | 0.0001042 | 8 | 0.0001493 | 0.00001866 |
| | II | 16 | 50905.05 | 3.5675 | 0.0004 | 0.00007008 | 15 | 0.0001500 | 0.00001000 |
| | III | 18 | 140357.78 | 9.2463 | 0.0011 | 0.0006588 | 17 | 0.0004900 | 0.00002882 |
| | IV | 10 | 111748.54 | 5.0275 | 0.0005 | 0.00004499 | 9 | 0.0002738 | 0.00003042 |
| 3. | Within | | | | | | 49 | 0.0010631 | 0.0000217 |
| 4. | Regr.Coeff. | | | | | | 3 | 0.0000919 | 0.0000306 |
| 5. | Common | | 311362.95 | 18.7119 | 0.00224 | 0.00006010 | 53 | 0.001155 | 0.0000222 |
| 6. | Adj. Means | | | | | | 3 | 0.001175 | 0.0003916 |
| 7. | Total | 56 | 719788.77 | 77.1761 | 0.01060 | 0.0001072 | 55 | 0.00233 | 0.00004236 |

B.

Analysis of variance of $\bar{x}$, $\bar{y}$.

| | | $f$ | x | x/$f$ (=m.s.) | y | y/$f$ (=m.s.) |
|---|---|---|---|---|---|---|
| 8. | Total | 56 | 719788.77 | | 0.0106 | |
| 9. | Within | 53 | 311362.95 | 5874.77 | 0.00224 | 0.00004226 |
| 10. | Betw. Means | 3 | 408425.82 | 136141.94 | 0.00836 | 0.002786 |

For y, MS10 / MS9 = 65.925, for 3;53 degrees of freedom, $p < .001$ } Both x and y effected
For x, MS10 / MS9 = 23.174, for 3;53 degrees of freedom, $p < .001$ } by treatment.

C.

Homogeneity of Slopes.
M.S.4/M.S.3 = 1.4166, for 3;49 degrees of freedom : $p > .05$
Slopes for 4 treatments not significantly different.

D.

Differences between adjusted means.
M.S.6/M.S.5 = 17.639, for 3;53 degrees of freedom : $p < .001$
i.e. 4 treatments have a significant effect on y (limpet size) independent of x (limpet density).

APPENDIX 2. *P. granularis* : regression of increment in shell length (y) on original length (x), for 3 periods.

6(1) : 1.3.1972. - 3.9.1972. (6 months during gonad rest)
6(2) : 3.9.1972. - 2.3.1973. (6 months during gonad activity)
12 : 1.3.1972. - 2.3.1973. (12 months)

| Barnacle cover | Period (months) | Regression | Correl. Coeff. | p | Signif.diffs. | |
|---|---|---|---|---|---|---|
| | | | | | Slopes | Intercepts |
| 0% | 6(1) | $y = -.27x + 10.24$ | -.89 | $< .02$ | $> .05$ | $> .05$ |
| | 6(2) | $y = -.31x + 12.47$ | -.99 | $< .01$ | | |
| | 12 | $y = -.49x + 18.58$ | -.98 | $< .01$ | | |
| 30% | 6(1) | $y = -.13x + 5.77$ | -.63 | $< .001$ | $> .05$ | $> .05$ |
| | 6(2) | $y = -.07x + 2.50$ | -.62 | $< .05$ | | |
| | 12 | $y = -.23x + 8.81$ | -.80 | $< .05$ | | |
| 80% | 6(1) | $y = -.26x + 7.70$ | -.81 | $< .001$ | $> .05$ | $< .05$ |
| | 6(2) | $y = -.07x + 2.36$ | -.68 | $> .05$ | | |
| | 12 | $y = -.26x + 8.47$ | -.86 | $< .05$ | | |
| 95% | 6(1) | $y = -.27x + 5.95$ | -.67 | $< .001$ | $> .05$ | $< .05$ |
| | 6(2) | $y = -.02x + 0.31$ | -.16 | $> .05$ | | |
| | 12 | $y = -.43x + 8.47$ | -.73 | $< .02$ | | |

Fig 2c Response of P.miniata to M.glacialis and T.dubia

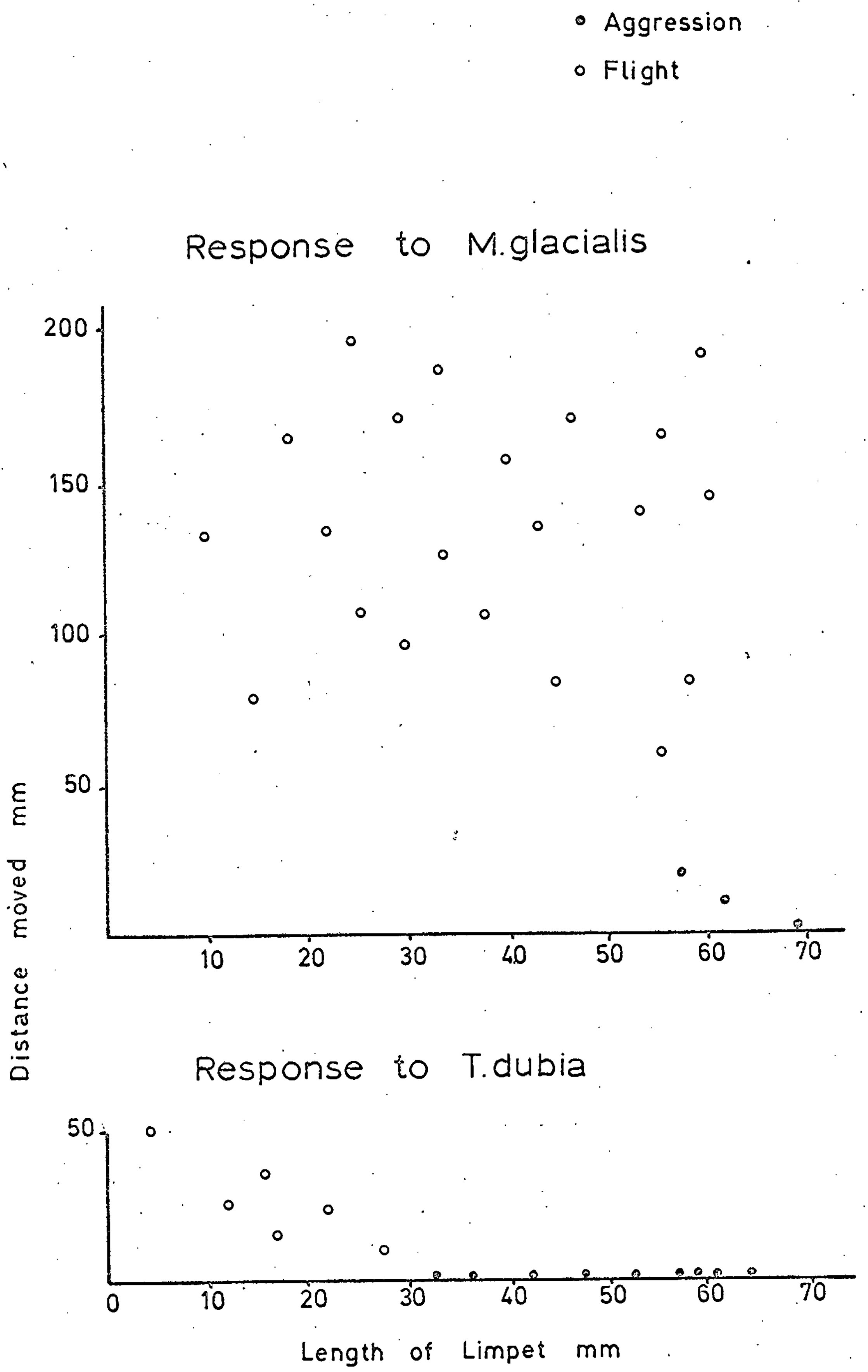
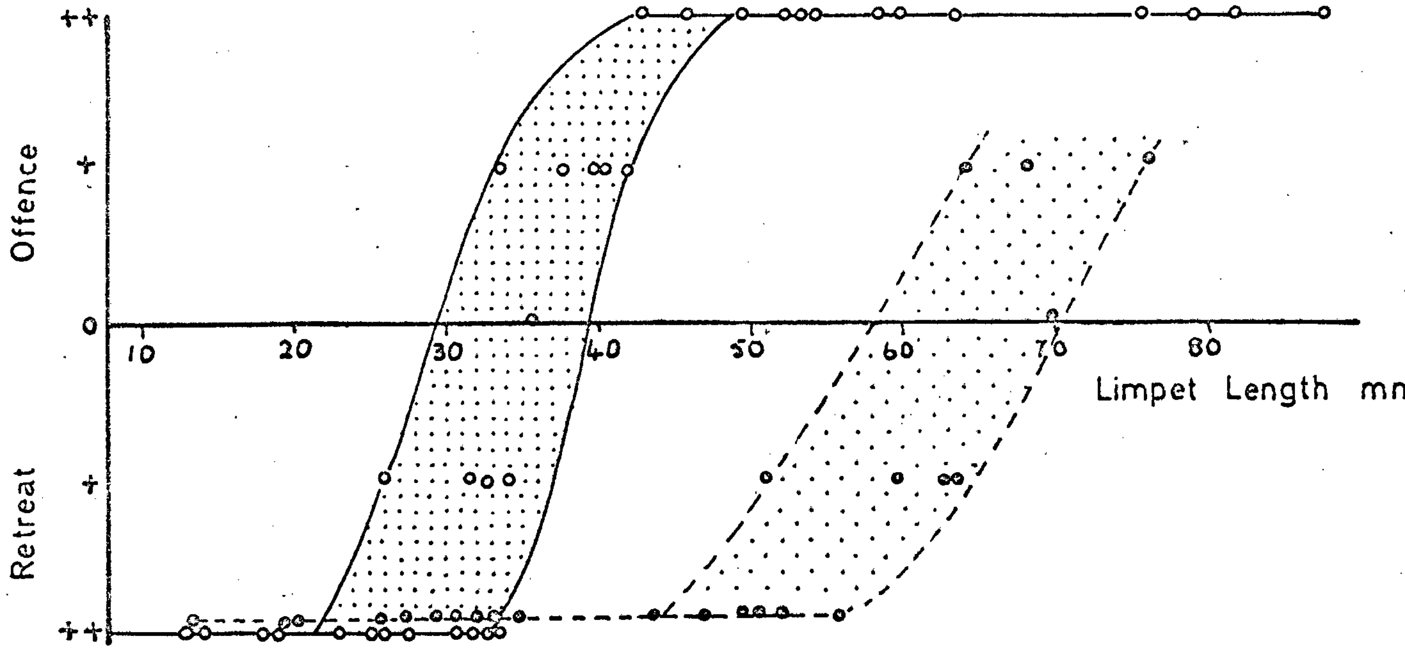
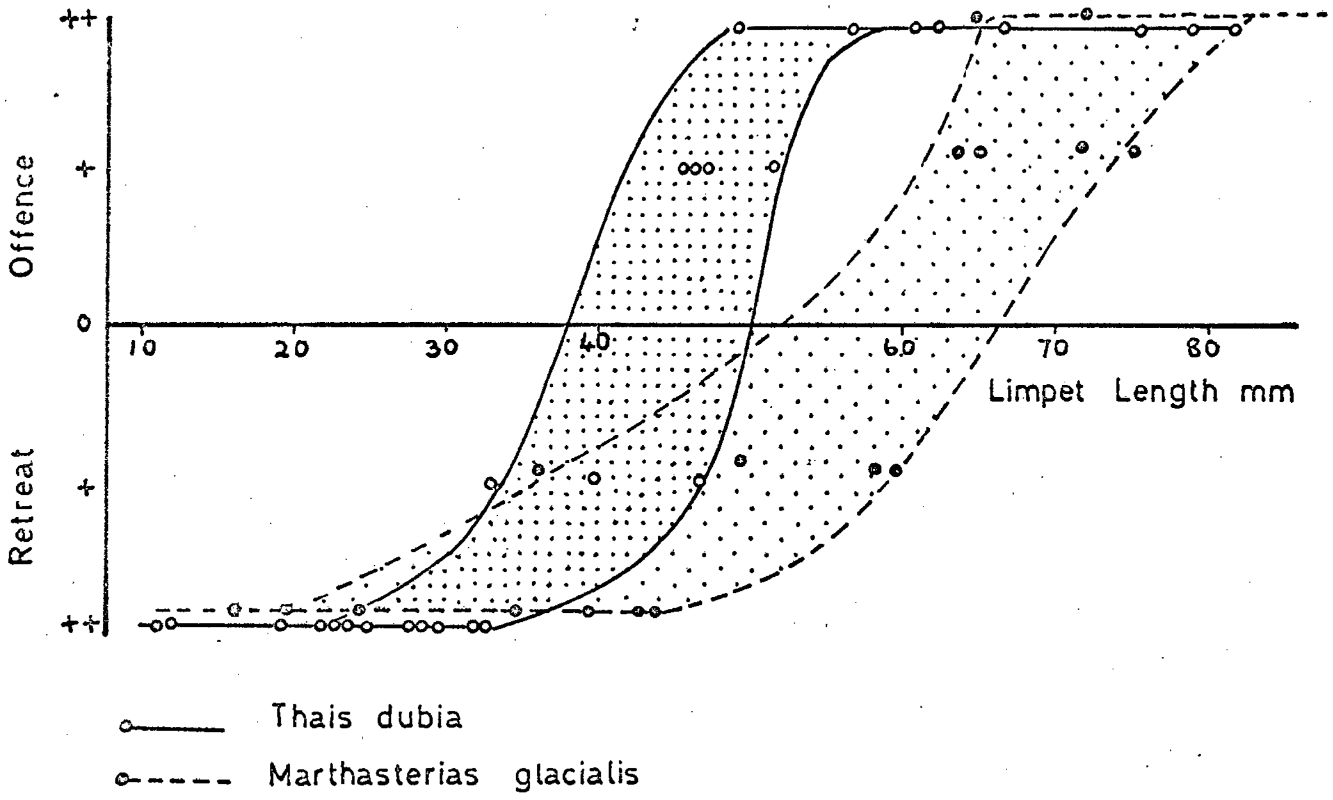


Fig. 2 Response of P. oculus and P. granatina to Marthasterias and Thais

a) P. oculus



b) P. granatina



withdrew after the limpet clamped down on its proboscis. Another group were found feeding on an apparently healthy and live P. longicosta. Predation on healthy animals is however exceptional. In aquaria they feed on live P. granatina.

Responses of Patella spp. to predators:

P. granularis: Contact with Thais dubia is almost invariably followed by an elevation of the shell away from the point of contact ("mushrooming") and protrusion of all the pallial tentacles. Within seconds the limpet swings away from the point of contact and glides rapidly in the opposite direction (Plate 1). After the initial flight the limpets often swing around and migrate upwards for a few centimetres before stopping. This geotaxis is interesting in the light of the progressive migration which P. granularis undertakes up the shore (Section VI, p. 2 ).

Flight will be repeated successively if contact with a predator is repeated, but becomes less marked and may eventually cease altogether. This suggests a conditioning or fatigue of receptors, and may be important in allowing capture of P. granularis by the slow moving Thais. It may also explain the feeble responses of the limpet once Thais starts feeding on it.

Occasionally Thais managed to mount the shell of P. granularis, but the latter responded by twisting the shell from side to side and often shook the predator off.

Escape responses often fail to occur in limpets which have been exposed for some time, but Thais are also inactive during exposure and retreat into crevices or under algae, and predation is probably not important during this period. Thais will however remain feeding while exposed, if they have captured a P. granularis during high tide, and both species are active while exposed if humidity is high.

Response to B. delalandii was almost identical: mushrooming followed by retreat.

Reaction to Marthasterias glacialis followed the same pattern, but was often slower and less pronounced. Tentacle testing and mushrooming usually occurred, but in 20% of the cases, flight did not follow, and the limpet clamped down instead. This is similar to the reaction of P. vulgata to the same starfish (Feder, 1967) and is yet another parallel between the two species. The pattern of reaction is also very similar to that of several Acmaea spp. (Bullock, 1953; Margolin, 1964b).

P. granularis failed to react to either of the "control" species, Oxystele sinensis or Asterina exigua.

P. oculus and P. granatina: These two species react in a similar way to predators, but with different intensities. Small P. oculus (less than 30mm. in length) invariably react to Thais dubia by a quick elevation of the shells away from the predator, followed by an extremely rapid retreat for about 50cm. Larger animals react quite differently by elevating the shell and then crunching it down on the foot or shell of the Thais, sometimes cutting off part of the foot. The Thais retreat into their shells and usually roll out of reach of the limpet. On occasions the whelk rolled under the limpet shell and the repeated crushing by the limpet could become so violent that the whelk shell was broken. During 60 staged encounters, Thais had its foot damaged in 21 cases and the shell broken in three.

Stimson (1970) records that Lottia gigantea also reacts in this aggressive manner to Thais emarginata and Acanthina spirata, and this is yet another example of parallel evolution between two different limpet families.

Figure 2a shows the fairly sharp transition that occurs between retreat of small animals and aggression of larger specimens (the responses of retreat or defence have been graded as strong, weak or absent).

Marthasterias induces flight in most P. oculus. Much larger animals (over 50mm) may display weak flight or slight aggression, but none were strongly aggressive (fig. 2a).

When animals in the 40 to 50mm. size range were alternately subjected to Thais and Marthasterias, they faithfully alternated their behaviour between attack and retreat.

Larger P. oculus were often unresponsive to either predator if they were exposed on dry rocks.

P. granatina parallels the behaviour of P. oculus, except that the response curve to Thais is shifted to the right (fig. 2b) and attack induced in slightly larger animals. Possibly this is because Thais grow much larger on the West coast. The response of large P. granatina to Marthasterias tended to be more aggressive than in P. oculus.

The similar responses of these two limpets are interesting, because they are similar morphologically and occupy the same zone.

The different responses to Thais and to Marthasterias are also interesting and have clear survival value: while aggression may be effective against Thais, flight is more likely to be effective against Marthasterias.

# SECTION VIII:

# REACTION TO PREDATORS

PLATE I. Response of P.granularis to Thais dubia: 'mushrooming', extension of pallial tentacles, and rapid flight.

# VIII. REACTIONS TO PREDATORS

A variety of limpet predators have been recorded. Several birds attack limpets by knocking them off the rock, and either picking out the flesh or consuming the whole limpet and regurgitating the shell: oyster catchers (Haematopus spp.), various gulls (Larus spp.) and the Sheathbill (Chionus alba) (Test, 1945; Feare, 1971; Walker, 1972). In Britain large numbers of Patella vulgata and P. aspersa are attacked by oyster catchers, P. aspersa being more susceptible (Feare, 1971). Strangely there are no records of birds eating South African limpets.

In California, rodents occasionally eat Acmaea spp., although Frank (1965) suggests this only occurs if the limpets are weakened by desiccation. In South Africa baboons (Papio ursinus) have been recorded feeding on Patella, (Hall, 1962) but this is probably a local occurrence. The middens of Strandlopers testify to the large numbers of limpets and mussels eaten by these hunter-gatherers, and there is evidence that they substantially reduced the mean size of limpets (Parkington, personal communication).

Crabs feed on Acmaea, crushing the shell with their chelipeds or prising them off the substrate (Chapin, 1968). Cast-up Patella shells are sometimes broken in the same way as Chapin's Acmaea shells. This need not indicate predation, as there is a fracture line above the muscle scar and breakage is likely to occur at this point.

Fish are also common predators of limpets (Test, 1945; Walker, 1972) and in South Africa the Suckerfish Chorisochismus dentex often contains Patella shells in its gut.

In South Africa, two major predators are the starfish Marthasterias glacialis and the gastropod Thais dubia. The five Burnupena spp. are all scavengers, but are rapidly attracted to any damaged animal, voraciously devouring it while it is still alive. In a few instances they have also been seen attacking healthy limpets and are thus partly predatory. P. compressa lives on kelp stipes and fronds, and is out of the reach of these predators, but occasional Octopus granulata were recorded clinging to kelp plants and feeding on this limpet.

There have been many accounts of the reactions of mulluscs to their predators, including those of Acmaea spp. (Bullock, 1953; Feder, 1963; Margolin, 1964b; Manzey, 1966), Patella vulgata and Patina pellucida (Feder, 1967), Cellana spp. (Clark, 1958) and Patinigera polaris (Walker, 1972).

The reactions of limpets are variable. Some are totally unresponsive, while others escape by "mushrooming" and fleeing or by twisting the shell to break the predator's grip. The fissurelid Diodora aperta slides its mantle over the shell, preventing the attachment of starfish tube-feet (Margolin, 1964a).

The present work records the relative importance of various prey species to Marthasterias and to Thais dubia. Briefer consideration is also given to the Burnupena spp. In addition, the reactions of Patella spp. to these predators have been tested. One of the reasons for undertaking the latter analysis was that South African Patellas have been grouped according to their behaviour, and two extremes recognised: "migratory" species which move progressively up the shore from the site of settlement, and "non-migratory" species which remain in a narrow habitat throughout their lives. (Trends associated with these groups are summarised in Section VI, fig.16, and Section VII, fig. 18.) It was therefore of interest to see if their reactions to predators are similarly divisible.

## MATERIAL AND METHODS:

Intermittent records have been kept over the past four years of the prey species of *Marthasterias glacialis* and *Thais dubia*, mainly within the Cape Peninsula. In addition a systematic survey of *M. glacialis* and its prey was made at Sunny Cove (near Fish Hoek on the Western coast of False Bay). About 600 *M. glacialis* were examined by diving: 108 were feeding and their prey was collected for subsequent identification.

The relative numbers of *M. glacialis* and *P. longicosta* were assessed at four sites; Hangklip, Dalebrook, Sunny Cove and Partridge Point, by counting all the specimens visible on a 100 m. subtidal transect parallel to the shore.

An attempt has been made to convert prey numbers to biomass. This is accurate in the case of *Patella*, where the exponential relationships between shell length and flesh weight are known. For other species the biomass has been estimated from a sample of twenty animals.

Reactions between predator & prey were staged in the field by placing a predator close to a limpet and then progressively moving it until contact occurred. Reactions to finger touch, and contact with the non-predatory *Asterina Oxigua* and *Oxystele sinensis* were used as control responses.

Cast-up *Patella* shells were examined for signs of drilling by predatory gastropods.

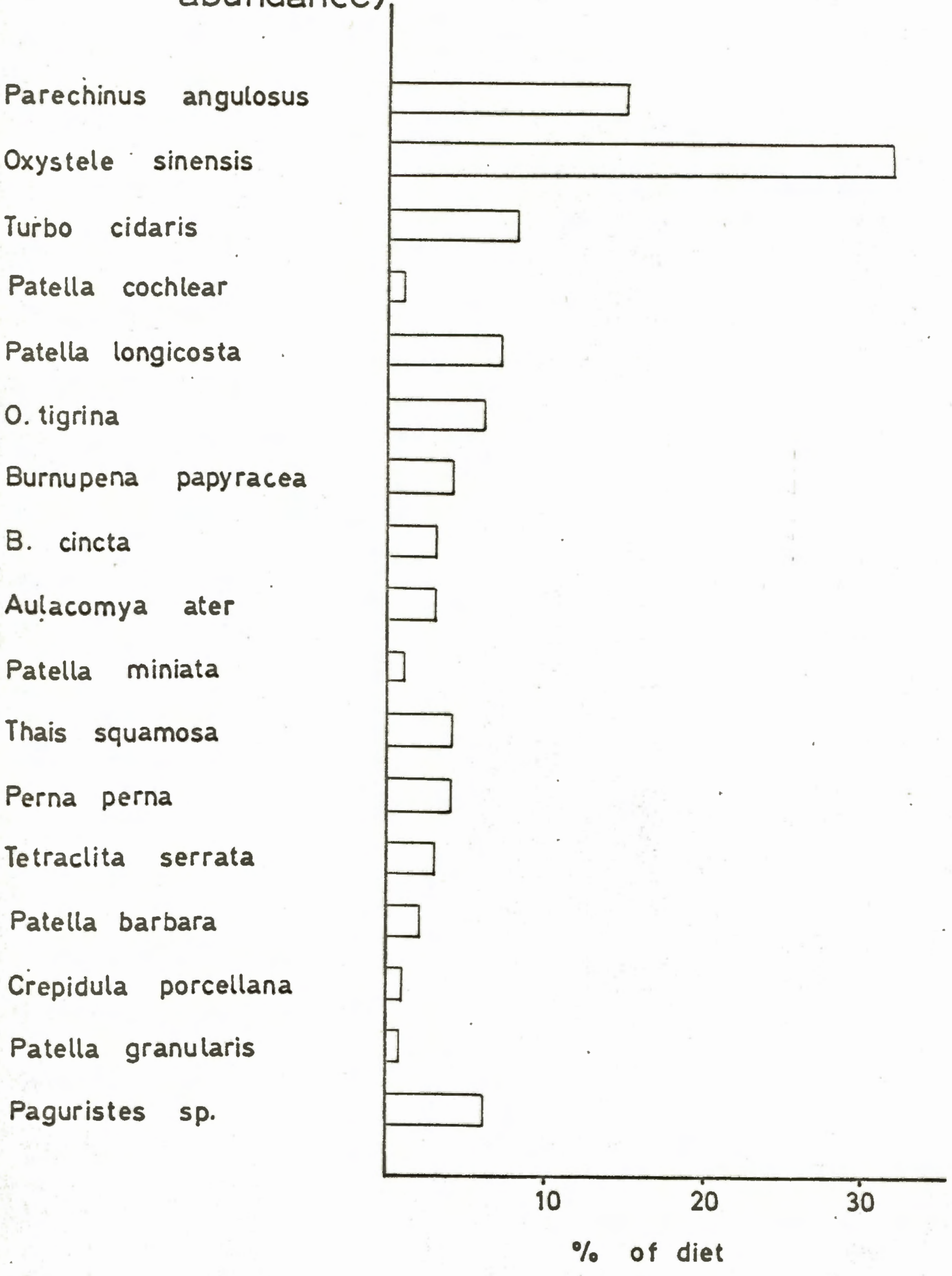


Fig. 1 Incidence of Predation by Marthasterias

(Prey spp. are ranked in order of their abundance)

## RESULTS:

### Incidence of predation:

Marthasterias glacialis is a slow moving predator occurring subtidally and reaching densities of 0.5 per $m^2$. Prey are gripped by the tube feet and manipulated under the mouth. The starfish assumes a characteristic arched stance over the prey, adhering firmly to the substrate with its arms and extruding its stomach over the prey, and digesting it externally. Digestion is very rapid so that the prey is usually found in an advanced state of disintegration.

Figure 1 summarises the prey species of M. glacialis at Sunny Cove. It appears to feed on any available prey, and the commoner prey species are those which are most abundant. This explains the preponderance of Parechinus angulosus and Oxystele sinensis. In terms of biomass Parechinus angulosus is the major source of food, but much of its value is probably not realised because external digestion of a large animal is very wasteful. The smaller O. sinensis can be completely covered by the stomach. The large numbers of O. sinensis are interesting because this winkle has a strongly developed escape response to M. glacialis, can perceive it at a distance, and will migrate out of pools or aquaria if the starfish is introduced (Pitt-Kennedy, 1968, unpublished). This is similar to the response of Tegula spp. to predatory Starfish (Bullock, 1953).

Also of interest was the relatively large number of Paguristes gamianus eaten by the starfish. These hermit crabs accumulate around Marthasterias which are feeding, gathering half digested particles of the prey and they may themselves fall prey in the process.

Normally one would expect a higher percentage of mussels in the diet, but neither *Perna perna* nor *Aulacomya ater* were common at Sunny Cove. Several other predators and scavengers were included in the diet of *Marthasterias* such as *Thais squamosa* and *Burnupena* spp. Quite frequently the starfish were found with their stomachs everted over isolated *Gunnarea capensis* and colonies of *Dodecaceria pulchra* and the digested state of these polychaets indicate that their tubes are ineffective against *Marthasterias*. However, the starfish was never found on the gregarious banks of *Gunnarea*, and the gregarious habit probably affords more protection.

Of the limpets, *P. longicosta* is a frequent food item and *P. barbara* and *P. miniata* are occasionally eaten, and *P. tabularis* is probably immune to attack because of its size (up to 150 mm. in length). *P. cochlear* is of interest, for despite its great abundance, only a single specimen has been found eaten by *Marthasterias*. This is partly because it predominates in wave-washed areas avoided by *Marthasterias*, but even under calm conditions it was not eaten.

*Thais dubia* is an intertidal species occurring commonly in the upper balanoid zone. It feeds predominantly on *Chthamalus dentatus* (42%), *Aulacomya ater* (16%), *Octomeris angulosus* (9%) and *P. granularis* (28%), while small numbers of other barnacles, particularly small *Tetraclita serrata*, and *P. oculus* make up the rest of its diet. Barnacles such as *Tetraclita serrata* and *Octomeris angulosus* probably achieve immunity by their rapid growth, thicker shells and larger size, as Dayton (1971) has described for *Balanus cariosus*. At times *Littorina knysnaensis* aggregate in clumps of 50 or more, presumably to breed, and *T. dubia* converge on these clumps (J.H. Day, personal communication), but this was not seen during the present work.

*Thais* drills into barnacles, usually by way of the operculum, and the thinner walled *Chthamalus* are particularly susceptible. *P. granularis* is not attacked by drilling. *Thais* inserts its siphon under the shell and begins feeding directly. Most *P. granularis* escape after the first contact, but many fall prey. In terms of biomass, *P. granularis* constitutes about 20% of the diet, and as *Thais* may reach densities of up to 150/m$^2$ it is certainly an important predator of this limpet. Because of the method of feeding, *P. granularis* shells are seldom found with drill-holes.

*Thais* were also seen attacking *P. oculus*, but were repulsed in each case. However, a few *P. oculus* shells were found with drill-holes. *Thais dubia* is the most likely mid-littoral predator to be responsible.

*T. cingulata* was also occasionally seen feeding on *P. granularis*, low on the shore on the West coast, but it normally feeds on barnacles and mussels.

*Burnupena* spp. occur in large numbers in the lower intertidal zone and subtidally. They are scavengers, but feed avidly on any damaged living animal. Limpets with damaged shells or mantles are rapidly detected and devoured. *P. cochlear* which were weakened by oil pollution in False Bay were also devoured by *Burnupena delalandii*.

*Burnupena* are exceptionally responsive to damaged animals and within minutes they gather in large numbers : they are even responsive to the filings from a limpet shell.

Occasional observations have been made of predation or attempted predation by *Burnupena delalandii*. One was seen thrusting its proboscis under the shell of a *P. longicosta*, but

P. miniata: In response to Thais, small P. miniata retreat rapidly, while larger animals usually aggressively lift their shells and scrape them down on the predator's foot. The response is similar to that of the two preceding species. On the other hand, P. miniata of all sizes took rapid flight from Marthasterias. This may be because the latter two overlap considerably, both predominating in the infratidal zone. P. miniata also moves much faster and further after contact with M. glacialis than with T. dubia (fig. 2c).

P. compressa: Living on the stipes of Ecklonia maxima, P. compressa will not normally come into contact with predatory molluscs or echinoderms, but despite this it reacts strongly to Burnupena papyracea and to Marthasterias (but not to Asterina exigua). In both cases the limpets move rapidly away from the point of contact. Movement stops after a few centimetres, but is repeated after further contact.

P. barbara: P. barbara had the least definite responses to Thais and Burnupena. Sometimes the shell was slowly lifted and mild shell rotation and retreat followed. Other times there was no response at all. After contact with Marthasterias they retreated, but even this was unhurried. Indecisive responses were a feature of P. barbara.

P. longicosta: Reaction to predators was quite different in P. longicosta. As previously described, juveniles of this limpet are found on the shells of other molluscs, particularly Oxystele sinensis. Subsequently they move onto lithothamnion covered rock, until they establish territorial patches of the alga Ralfsia expansa, where they remain for the rest of their lives (Branch, 1971 : Plate 3). Juveniles lack any response to the three predators, remaining clamped onto their host shell.

As they have well defined scars and their shells fit these closely, the negative response may simply be due to a lack of direct contact with the predator during experimental encounters. The association with the highly responsive Oxystele sinensis may be of fortuitous survival value.

P. longicosta on lithothamnion move around considerably (Section IV, fig. 7b) and often lack well defined scars. If they encounter a Thais while moving around feeding, they immediately clamp down and test the predator by extending pallial tentacles from the tips of the long shell costae. If the Thais is applied persistently, the limpet violently rotates its shell from side to side through an arc of about 110°, striking the Thais in the process. If this is still not successful the limpet retreats to its scar.

Adult P. longicosta have well defined scars in the centre of Ralfsia patches. While they are feeding, staged encounters with Thais result in immediate retreat to the scar, where the limpet clamps down. Persistent application of the Thais may result in shell rotation. This action is particularly characteristic of P. longicosta and may explain the survival value of long shell costae.

Adults which are on their scars at the time of contact with a predator, simply clamp down and usually react no further, except for periodic extension of pallial tentacles to test if the predator is still present.

Responses to Marthasterias and Burnupena spp. are very similar, except that flight of the smaller unestablished specimens (on lithothamnion) is more readily induced by the starfish and aggression occurs less often.

P. cochlear: Irrespective of the predator encountered, P. cochlear simply clamps firmly onto its scar and remains there. No tentacle testing or movements occur. If the P. cochlear is off its scar feeding, when it contacts a predator, it will move slowly but directly back to its scar, orientate on it and clamp down. Larger specimens remain on their scars when feeding, and rotate around the scar. Contact with a predator causes rotation to the original position and clamping on the scar. Juveniles may move some distance from their scars, but migrate back to them in an almost straight line if a predator is met. If the predator is in line with the scar the limpet will force it aside, keeping its shell low and never mushrooming like other limpets. Figure 3 illustrates two staged encounters between Thais dubia and a small P. cochlear which was feeding about 190mm. from its scar.

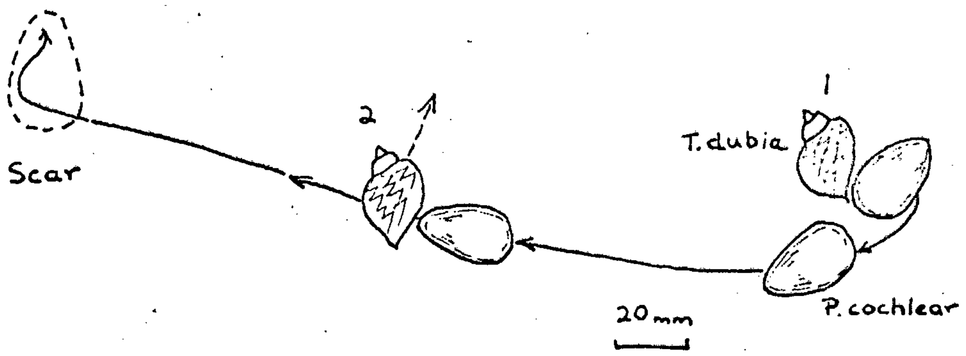


Fig. 3 Two encounters between P. cochlear and T. dubia.

The feature of this limpet's response is its persistent clamping to the scar.

P. tabularis and P. argenvillei: In both these species there is usually no response to predators except for the withdrawal of the mantle. A single P. tabularis which was feeding when it encountered a Marthasterias, retreated to its scar and clamped there, but others seemed to ignore the starfish. Possibly reaction is similar to that of P. longicosta and clamping on the scar is the most effective means of defence. No offensive action was ever seen.

Forty P. argenvillei were tested with Thais dubia and Marthasterias. Thirty-eight showed no response other than withdrawing the mantle and remaining in the same position (not necessarily on a scar). Two animals reacted aggressively to Thais, lifting their shells and clamping down on the predator.

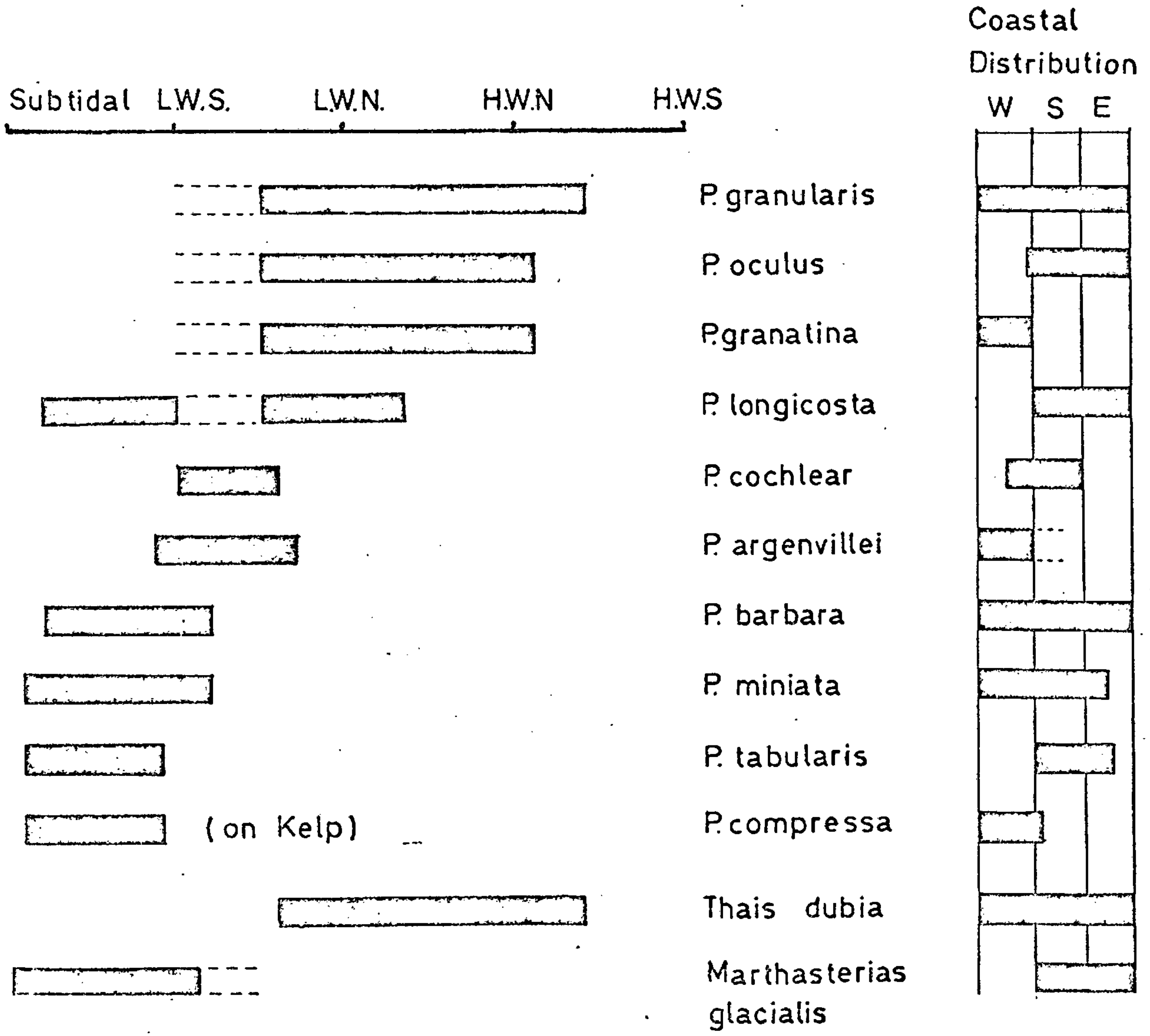
P. tabularis reaches a length of 150mm. and P. argenvillei 95mm, and by virtue of their size they are probably not vulnerable to predation by Marthasterias. Thais dubia does not occur subtidally and therefore does not overlap with the two limpets, but they were equally unresponsive to the subtidal T. squamosa.

## DISCUSSION:

Marthasterias is clearly an important predator of P. longicosta and to a lesser extent of P. barbara and P. miniata. P. cochlear, P. granularis and probably P. oculus may be eaten in smaller numbers. Thais dubia feeds extensively on P. granularis and is probably its major predator. P. oculus and P. granatina may occasionally be eaten by T. dubia. P. tabularis and P. argenvillei probably escape most predators because of their size, and P. compressa because of its specialised habitat on Ecklonia.

Bullock (1953) has suggested that reaction to a predator is only evolved if there is an ecological overlap between predator and prey, so that the two often come into contact. He showed that the high level Acmaea digitalis and A. scabra do not encounter predatory starfish very often, and are unresponsive to

Fig. 4


Coastal Distribution
W S E
Subtidal
L.W.S.
L.W.N.
H.W.N
H.W.S
P. granularis
P. oculus
P. granatina
P. longicosta
P. cochlear
P. argenvillei
P. barbara
P. miniata
P. tabularis
P. compressa
(on Kelp)
Thais dubia
Marthasterias glacialis

them. Similarly the specialised A. insessa (which occurs on blades of Egregia) does not react to starfish. His suggestion has been queried by subsequent workers. Clark (1958) could find no correlation between sensitivity and the relative zonation of predator and prey, and Feder (1972) gives examples of prey species which are highly responsive to predators they never naturally meet.

The zonation of Patella spp. has already been described (Branch, 1971 : figs. 2 and 3), but can be summarised here in relation to that of M. glacialis and T. dubia (fig. 4).

Clearly there are several species which do not encounter predators which they are responsive to. P. miniata does not come in contact with T. dubia but reacts strongly to it. Perhaps this can be explained by the evolution of responses to allied species such as T. squamosa, which occurs subtidally with P. miniata. However, West coast P. granatina respond to the South coast M. glacialis, and P. compressa is strongly responsive to both this starfish and Burnupena, although it never comes in contact with either. Patina pellucida (which occurs on kelp in Europe) is usually strongly reactive to M. glacialis, although at Plymouth it is unresponsive (Feder, 1967).

Marthasterias occurs predominantly subtidally, but specimens encroach on the littoral zone and feed there at high tide. Consequently all limpets (except P. compressa) overlap with it to a certain extent.

Thus there are many exceptions to the rule that escape responses only develop against predators which are normally encountered.

This may be explained by recent work on the nature of the stimulus inducing escape responses. In several species, predators can be perceived at a distance. Tegula spp. (Bullock, 1953) and Oxystele spp. have already been mentioned as obvious examples. Limpets require actual contact with the predator. In either case chemoreception is implicated because of the specificity of the response, and because mechanical stimulus alone fail to elicit an escape response. Markie (1970; 1972) has isolated steroid glycosides from M. glacialis which induce escape reactions in a number of animals including P. vulgata. These animals also respond to synthetic non-ionic surface active agents. Both the glycosides and the surface active agents produce fatigue in the chemoreceptors of the foot if they are applied for any length of time, and this may explain the "conditioning" of P. granularis to T. dubia.

Such substances are likely to be widespread in predatory starfish and may be common metabolites in all echinoderms. Feder (1972) suggests they may even occur in smaller quantities in non-predatory echinoderms. This would explain responses to non-overlapping predators and the occasional response to non-predatory echinoderms.

Feder (1967) suggests that response is most significant when the starfish is small in relation to the prey species, but this is not true in Patella. Here the largest species (P. tabularis and P. argenvillei) are least responsive to Marthasterias (or Thais), despite their ecological overlap. This may be attributable to their impunity to predation by M. glacialis.

One of the interesting features of the present study is the change of behaviour in P. oculus and P. granatina as they get larger: a change from defensive retreat to an active repulsion of predators. Clearly this has survival value, for while retreat by juveniles will reduce predation, offensive repulsion by large animals is highly effective and less wasteful of energy.

Such transitions may explain some of the contradictions which exist in the literature. For example, Bullock (1953) records the flight of Lottia gigantea from Pisaster ochraceus, while Stimson (1970) records that it will not abandon its territory despite the presence of this starfish. In a comparable way, P. longicosta will only flee from predators if it is off its scar feeding, but is "unresponsive" if on its scar.

All of the reactions recorded during contacts with predators are totally different from the reactions evoked by intra- and interspecific meeting between limpets (Sections VI and VII). P. granularis and P. granatina may form aggregates of their own species but flee from predators or aggressively repulse them. P. compressa (and probably P. miniata) are aggressive to their own species but take flight from predators. P. longicosta and P. tabularis defend their territories against other limpets, but clamp on their scars in response to predators. P. cochlear are dispersive and move away after contact with other P. cochlear, but clamp on their scars in the face of predation.

These responses to predators are basically of three kinds: rapid flight, aggressive defence and clamping down on a scar. Possibly the larger species should be considered separately because they remain inert.

The relative effectiveness of these responses is difficult to gauge, because of different degrees of habitat overlap, and possible food preferences. However, very few P. oculus and P. granatina are eaten by T. dubia while P. granularis often falls prey to it. The few drilled P. oculus shells which were found suggest that the only way T. dubia can attack P. oculus is to gain purchase on top of the shell and drill through it.

P. longicosta is often eaten by Marthasterias (more than any other Patella) and this may be because it fails to escape, and remains clamped on its scar. Acmaea scabra also clamps down in response to predatory starfish, and it too is eaten more often than other Acmaea spp. (Feder, 1963). Such behaviour will only be effective against starfish if the shell seals onto the rock, excluding the digestive juices from the starfish stomach. In the case of P. longicosta the shell does not seal effectively because there are slender channels along the costae, through which the pallial tentacles project.

To assess the effects of Marthasterias on P. longicosta populations, their relative numbers were determined at four sites in the Cape Peninsula, using 100 m. underwater transects, parallel to the shore. (This consistently under-estimates the numbers of P. longicosta, as small specimens are difficult to see underwater). The results are given in Table 1.

TABLE 1. Relative numbers of P. longicosta and M. glacialis at 4 sites (December 1972).

| Site | No. of M. glacialis | No. of P. longicosta |
|---|---|---|
| Hangklip | 240 | 260 |
| Dalebrook | 160 | 220 |
| Sunny Cove | 420 | 190 |
| Partridge Point | 6 | 669 |

At Partridge Point there was a remarkable sparcity of M. glacialis, coupled with more than double the usual number of P. longicosta. This suggests that predation is an important factor reducing the numbers of P. longicosta. Marthasterias are known to migrate from deeper water to low tide, possibly in relation to spawning (J.H. Day, personal communication), but the present observations were made over a two week period and are unlikely to have been biased by migration.

P. cochlear also clamps down on its scar in response to predators, but unlike P. longicosta it is rarely eaten by M. glacialis. By contrast with P. longicosta, its shell fits the substrate exactly and can probably exclude starfish gastric juices. Only a single P. cochlear was found being eaten by M. glacialis, and this specimen had a cracked shell due to Polydora boring.

Another interesting facet is the correlation of prey responses with other behavioural trends in the genus Patella.

The "migratory" group comprises P. granularis, P. granatina and P. oculus. These species are unspecialised and have wide niches and flexible behaviour: homing behaviour varies according to conditions and scars are never permanent. Conversely the non-migratory group occupy the same habitat throughout life and have specialised feeding habits, a narrow niche, and rigid behaviour patterns.

In relation to this, the migratory species all have strong escape responses or react aggressively to predators, but have no tendency to remain on a scar (fig. 5). The behaviour is flexible, and modified according to the size of the limpet, and according to the predator involved (fig. 2).

Conversely the more extreme non-migratory species (P. tabularis, P. longicosta and P. cochlear) clamp onto their scars in response to a predator and make no attempt at flight, and only occasionally (in P. longicosta) aggression (fig. 5).

Intermediate between these two extremes are P. miniata and P. compressa.

In the extreme non-migratory species, responses are rigid and remain constant irrespective of the predator encounter. In these species the possession and defence of home territories (Section VI) has obvious advantages, and survival is high once territories are established (Section IV, fig. 18). In the case of P. cochlear the shell fits the scar so perfectly that predatory attacks are ineffective. This is not so for P. longicosta and large numbers are eaten by M. glacialis. Perhaps the overall advantages of the territory as a source of food and of the scar as a protection against other predators (such as fish) are greater than the disadvantage of not fleeing from M. glacialis.

SUMMARY:

1. The starfish Marthasterias glacialis is a generalised predator, feeding on all available prey, including several limpets, particularly P. longicosta.
2. Thais dubia feeds mainly on barnacles, mussels and P. granularis.
3. Burnupena delalandii and B. cincta are scavengers, feeding on damaged or dead animals, but may occasionally be predatory.
4. The responses of Patella spp. to these predators are described. P. granularis, P. compressa and P. miniata usually flee rapidly. P. oculus and P. granatina juveniles also flee, but adults react aggressively and repel predators, and respond differentially to different predators. P. longicosta, P. cochlear and P. tabularis respond by retreating to their scars and remaining clamped

there. P. argenvillei is unresponsive possibly because it is too large to fall prey.

5. There is no correlation between prey response to a predator and the degree of contact between them in the environment.
6. The responses and their effectiveness are discussed in relation to other behavioural patterns displayed by Patella spp.

REFERENCES:

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.

BULLOCK, T.H. 1953. Predator recognition and escape responses of some intertidal gastropods in presence of starfish. Behaviour 5 : 130-140.

CHAPIN, D. 1968. Some observations of predation on Acmaea species by the crab Pachygrapsus crassipes. Veliger 11 (suppl.) : 67-68.

CLARK, W. 1958. Escape responses of herbivorous gastropods when stimulated by carnivorous gastropods. Nature 181 : 137-138.

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.

FEARE, C.J. 1971. Predation of limpets and dog whelks by oyster catchers. Bird Study 18 : 121-129.

FEDER, H.M. 1963. Gastropod defensive responses and their effectiveness in reducing predation by starfishes. Ecology 44 : 505-512.

---- 1967. Organisms responsive to predatory starfish. *Sarsia* *29* : 371-394.

---- 1972. Escape responses in marine invertebrates. *Sci. Am.* *227* (1) : 92-100.

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

HALL, K.R. 1962. Numerical data maintenance activities and locomotion of the wild Chacma baboon, *Papio ursinus*. *Proc. Zool. Soc. Lond.* *139* : 181-220.

MACKIE, A.M. 1970. Avoidance reactions of marine invertebrates to either steroid glycosides of starfish or synthetic surface active agents. *J. exp. mar. Biol. Ecol.* *5* : 63-69.

---- 1972. The escape reactions of marine invertebrates to predatory starfish. *Fifth European Mar. Biol. Symposium.* pp 269-274.

MARGOLIN, A.S. 1964a. The mantle response of *Diodora aspera*. *Animal Behaviour* *12* : 187-194.

---- 1964b. A running response of *Acmaea* to sea stars. *Ecology* *45* : 191-193.

MAUZEY, K.P. 1966. Feeding behaviour and reproductive cycles in *Pisaster ochraceous*. *Biol. Bull.* *131* : 127-144.

PITT-KENNEDY, T.S. 1968. Predator recognition and escape responses of some intertidal marine gastropods in the presence of starfish. Unpublished honours project - University of Cape Town.

STIMSON, J. 1970. Territorial behaviour of the owl limpet, *Lottia gigantea*. *Ecology* *51* : 113-118.

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

Intermediate between these two extremes are P. miniata and P. compressa.

In the extreme non-migratory species, responses are rigid and remain constant irrespective of the predator encounter. In these species the possession and defence of home territories (Section VI) has obvious advantages, and survival is high once territories are established (Section IV, fig. 18). In the case of P. cochlear the shell fits the scar so perfectly that predatory attacks are ineffective. This is not so for P. longicosta and large numbers are eaten by M. glacialis. Perhaps the overall advantages of the territory as a source of food and of the scar as a protection against other predators (such as fish) are greater than the disadvantage of not fleeing from M. glacialis.

SUMMARY:

1. The starfish Marthasterias glacialis is a generalised predator, feeding on all available prey, including several limpets, particularly P. longicosta.
2. Thais dubia feeds mainly on barnacles, mussels and P. granularis.
3. Burnupena delalandii and B. cincta are scavengers, feeding on damaged or dead animals, but may occasionally be predatory.
4. The responses of Patella spp. to these predators are described. P. granularis, P. compressa and P. miniata usually flee rapidly. P. oculus and P. granatina juveniles also flee, but adults react aggressively and repel predators, and respond differentially to different predators. P. longicosta, P. cochlear and P. tabularis respond by retreating to their scars and remaining clamped

there. P. argenvillei is unresponsive possibly because it is too large to fall prey.

5. There is no correlation between prey response to a predator and the degree of contact between them in the environment.
6. The responses and their effectiveness are discussed in relation to other behavioural patterns displayed by Patella spp.

## REFERENCES:

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.

BULLOCK, T.H. 1953. Predator recognition and escape responses of some intertidal gastropods in presence of starfish. Behaviour 5 : 130-140.

CHAPIN, D. 1968. Some observations of predation on Acmaea species by the crab Pachygrapsus crassipes. Veliger 11 (suppl.) : 67-68.

CLARK, W. 1958. Escape responses of herbivorous gastropods when stimulated by carnivorous gastropods. Nature 181 : 137-138.

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.

FEARE, C.J. 1971. Predation of limpets and dog whelks by oyster catchers. Bird Study 18 : 121-129.

FEDER, H.M. 1963. Gastropod defensive responses and their effectiveness in reducing predation by starfishes. Ecology 44 : 505-512.

---- 1967. Organisms responsive to predatory starfish. *Sarsia 29* : 371-394.

---- 1972. Escape responses in marine invertebrates. *Sci. Am. 227* (1) : 92-100.

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

HALL, K.R. 1962. Numerical data maintenance activities and locomotion of the wild Chacma baboon, *Papio ursinus*. *Proc. Zool. Soc. Lond. 139* : 181-220.

MACKIE, A.M. 1970. Avoidance reactions of marine invertebrates to either steroid glycosides of starfish or synthetic surface active agents. *J. exp. mar. Biol. Ecol. 5* : 63-69.

---- 1972. The escape reactions of marine invertebrates to predatory starfish. *Fifth European Mar. Biol. Symposium.* pp 269-274.

MARGOLIN, A.S. 1964a. The mantle response of *Diodora aspera*. *Animal Behaviour 12* : 187-194.

---- 1964b. A running response of *Acmaea* to sea stars. *Ecology 45* : 191-193.

MAUZEY, K.P. 1966. Feeding behaviour and reproductive cycles in *Pisaster ochraceous*. *Biol. Bull. 131* : 127-144.

PITT-KENNEDY, T.S. 1968. Predator recognition and escape responses of some intertidal marine gastropods in the presence of starfish. Unpublished honours project - University of Cape Town.

STIMSON, J. 1970. Territorial behaviour of the owl limpet, *Lottia gigantea*. *Ecology 51* : 113-118.

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

# SECTION IX:

# COMMENSALISM AND PARASITISM.

# The Ecology of Patella Linnaeus from the Cape Peninsula, South Africa Pt IX Biotic Associations.

The occurence of various organisms associated with Patella spp. in South Africa is well known and has been recorded by Koch (1949). The present paper describes some aspects of the biology of these commensals: particularly the nature of the association and the behaviour of the associates. In addition, two trematode parasites are recorded.

In the intertidal zone, limpets retain water in their pallial cavities when exposed, and provide an obvious microniche which is exploited by a large number of organisms. In most cases the association is casual and temporary, providing only protection against desiccation. In a few cases the relationship has developed into a definite commensal association, the specificity of which varies.

An entirely different group of organisms is associated with the shells of patellids. Due to theprevalence of limpets on most intertidal shores, the surrounding rocks are extensively grazed: often the top of limpet shells is the only area left for the development of algae. Some invertebrates are similarly restricted to limpet shells.

Such relationships with limpets are world wide. Cheng (1967) has given a general account of the various associations involving molluscs, and Vader (1972) has recently reviewed the records of amphipods associated with molluscs.

## MATERIAL AND METHODS:

Samples of all Patella spp. were collected monthly from Kommetjie and Kalk Bay in the Cape Peninsula. A minimum of 30 specimens of each species was collected, examined for associates, distinction being made between those on the shell and those on the body of the limpet. After superficial examination, all specimens were preserved in 7% formalin for microscopic examination. Smears of the gonad, gut and digestive gland were examined for parasites.

Distribution patterns were determined by collections ranging from Lamberts Bay on the West Coast to Lwandile ($31^{\circ}53'S/29^{\circ}15'E$) on the East Coast. Line and quadrat transects were undertaken to assess zonation and density of commensals and hosts, at Dalebrook, Kalk Bay, Kommetjie and Camps Bay.

Commensals were maintained in marine aquaria (at $16^{\circ}C$), to assess their relationship with the hosts. Experiments conducted to elucidate the relationships, are described below under the relevant sections.

All results have been analysed statistically using either the Student's t test or $\chi^2$ . Regression lines have been fitted by method of least squares and tested by the t test; correlations were determined by the product moment correlation coefficient.

The term "% association" is applied to the percentage of any species found in association; "% specificity" refers to the percentage of commensals associated with a particular host relative to the number associated with all known hosts. "Associate" is applied to all species regularly found under Patella, while "commensal" is confined to cases in which the relationship is permanent, and some degree of dependency is probable.

## CASUAL ASSOCIATION

Most animals found under limpets are casual associates seeking temporary shelter from desiccation. Forty six species have been recorded in this work. The more important species are summarised in Table 1, which gives the cumulative totals from 12 monthly samples from Kommetjie and Kalk Bay. The numbers have been scaled to represent the number collected per 100 limpets per year. Comparative figures are also given for collections made at low tide and high tide, on a

TABLE I:

| | Number of associates per I00 limpets per year. | | | | | | | | | | No. of associates per I00 limpets. | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Tidal level: | High | | | | | Low | | Subtidal | | | | |
| Patella sp: | P.granularis. | P.granatina. | P.oculus. | P.longicosta. | P.cochlear. | P.argenvillei. | P.barbara. | P.miniata | P.tabularis | P.compressa | Sample at low tide (0900 hrs) | Sample at high tide (I500hrs) |
| Number sampled: | 3I0 | 3II | 300 | 300 | 346 | 284 | 302 | 286 | I42 | 82 | 90 | 90 |
| AMPHIPODA | | | | | | | | | | | | |
| *Calliopiella michaelseni | 20 | I74 | I40 | 4 | 5 | 8 | 27 | 73 | 48 | I62 | 72 | 78 |
| *Hyale grandicornis | 27 | 2 | 3 | 7 | I3 | 24 | I | I | 0 | 8 | 52 | I0 |
| *Allorchestes inquiridens | 4 | I | I | 3 | I | 4 | 0 | 0 | 0 | I | 6 | 0 |
| Jassa falcata | 0 | 0 | 0 | 0 | I | 4 | 0 | 0 | 0 | 0 | 4 | 0 |
| Paramoera capensis | 0 | 0 | 0 | I4 | 2 | I | 2 | 0 | 0 | 0 | 7 | I0 |
| caprellids | 0 | 0 | 0 | I | I | 2 | 2 | 0 | 0 | 0 | 7 | 0 |
| Others | 0 | 0 | I | I | I | I | 2 | 0 | 0 | I | 3 | 0 |
| ISOPODA | | | | | | | | | | | | |
| Paridotea rubra & P.ungulata | 0 | 0 | 0 | 0 | 0 | I | 2 | 0 | 0 | 0 | 0 | 0 |
| Exosphaeroma spp. | 0 | I | I | 4 | I | 5 | 5 | 0 | 0 | I | 7 | 0 |
| Parisocladus perforatus | 0 | 0 | 6 | I | 0 | 0 | 2 | 0 | 0 | 0 | 3 | 0 |
| P.stimpsoni | I | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | I | 0 |
| Dynamenella huttoni | 0 | I | 0 | I | I | 4 | I | 0 | 0 | 0 | 4 | 0 |
| *D.scabricula | 35 | 2I | 4 | I | 3 | 6 | 2 | 0 | 0 | 5 | 62 | 48 |
| *D.australis | 6 | I | 0 | 0 | I4I | 440 | 2 | 0 | 0 | 0 | I46 | I7I |
| COPEPODA | | | | | | | | | | | | |
| *Scutellidium sp. | 0 | 2 | I | 5 | >3000 | >3000 | 3 | ?I | ?I | 0 | - | - |
| Pelteutha sp. | 0 | 0 | 0 | I | 9 | 9 | 3 | 0 | 0 | 0 | - | - |
| Harpacticus sp. | 0 | 0 | 0 | 0 | 7 | 5 | 9 | 0 | 0 | 0 | - | - |
| TANAIDACEA | | | | | | | | | | | | |
| Tanais philataerus | 0 | 0 | I | I | I | 5 | 2 | 0 | 0 | 0 | 3 | 0 |
| INSECTA | | | | | | | | | | | | |
| Aponogeton sp. | 0 | 0 | 5 | I | 0 | 5 | 0 | 0 | 0 | 0 | I | 0 |
| POLYCHAETA | | | | | | | | | | | | |
| Pseudonereis variegata | 0 | I | I | 0 | 0 | 2 | 2 | 0 | 0 | 0 | I | 0 |
| Syllis sp. | 0 | 0 | 2 | 0 | 0 | 2 | I | 0 | 0 | 0 | - | - |
| Others | 0 | 0 | 0 | 0 | 0 | 2 | 2 | 0 | 0 | 0 | - | - |
| TURBELLARIA | | | | | | | | | | | | |
| *Notoplana patellarum | 5 | I | 307 | 20 | 3 | 2 | 20 | 0 | 0 | 0 | I80 | I98 |

* indicates commensal and associated species.

single occasion, collecting 10 of each Patella spp.

Several trends are apparent from Table 1. The commensal species are numerically dominant compared with the casual associates, and their numbers remain relatively constant irrespective of the state of the tide. Casual associates tend to disappear from the limpets with the incoming tide. Limpets inhabiting the lower regions of the shore have many more associates than those at higher levels. P. argenvillei, being not only a low level species but also much larger than most other species, harbours more associates than any other species.

## ASSOCIATES ON THE SHELL

The shells of Patella form an important biotic niche, and a wide variety of organisms may be limited to these shells because of heavy grazing on the surrounding rocks. In particular, the shells of P. cochlear, P. barbara, P. tabularis and P. oculus are often covered by a dense algae growth. The most extreme example occurs in the cochlear zone, where up to 95% of the algal biomass may be restricted to the shells of P. cochlear. These associations are not specific, although, due to the restricted zonation of some limpets and algae, examples may be "specific" through lack of alternatives. The alga ? Pantoneura sp. seems to be restricted to P. barbara.

The importance of the shell as a substrate for settling Patella larvae, and the significance of this in intraspecific competition, has already been described (Branch, 1971).

The polychaete Polydora capensis bores into mollusc shells and is frequently found on P. argenvillei, P. cochlear and P. barbara, in the Cochlear zone. Shells of old limpets are often riddled by the polychaete, and become fragile. Penetration through the shell seldom occurs, as fresh nacreous layers are deposited internally to cover the polychaete tubes. Densities of up to 725 Polydora capensis per shell have been recorded. The worms appear to be gregarious in their settling pattern, as large numbers are usually found on a few shells while surrounding shells are free of them. Haigler (1969) has described how the larvae of Polydora websteri select a calcareous substrate when settling, and bore into the shell by a chemical secretion. Blake and Evans (1973) have recently reviewed Polydora and related genera, and show that twenty six of the species are confined to a calareous substrate: mainly in the form of mollusc shells or calcareous algae.

Table II. Organisms associated with *Patella* shells.(N=4 for all samples, 95% confidence limits indicated in brackets)

| *Species* | *Biomass* (dry wt. gm/m$^2$) | | *Zone* | *Patella* spp. |
|---|---|---|---|---|
| I.Algae | On shells | On rock | | |
| *Gelidium pristoides* | I8.2(±4.2) | 4.2(±2.4) | Cochlear | *P.cochlear* |
| | 62.6(±I7.2) | 40.2(±I0.2) | Low balanoid | *P.longicosta* |
| | I4.2(±I2.0) | 0.2(± 0.I) | Mid balanoid | *P.oculus* |
| *Laurencia glomerata* | 9.6(± 6.2) | I.2(± I.0) | Cochlear | *P.cochlear* |
| | 22.4(±I4.I) | 26.2(±I6.I) | Low balaniod | *P.longicosta* |
| *Cheilosporium* sp. | 26.2(±I4.2) | 3.I(± I.6) | Cochlear | *P.cochlear*, *P.barbara* |
| *Pterosiphonia cloiophylla* | I9.2(± 6.2) | 3.0(± I.I) | subtidal | *P.miniata* |
| | 25.3(± 9.I) | I.2(± 0.6) | subtidal | *P.tabularis* |
| | 42.6(±20.I) | 4.2(± I.2) | Cochlear | *P.cochlear* |
| *Gigartina stiriata* | 5.8(± 5.0) | 9.2(± 2.4) | subtidal | *P.miniata* |
| | 6.2(± I.0) | I2.2(± 9.2) | Cochlear | *P.cochlear* |
| *Champia lumbricalis* | 5.2(± 2.I) | 0.4(± 0.3) | subtidal | *P.miniata* |
| *Hypnea spicifera* | 22.I(±I0.0) | 72.6(±I5.I) | subtidal | *P.tabularis* |
| *Ulva* sp. | I06.7(±I2.2) | 3.2(± 3.0) | Low balanoid | *P.granatina* |
| 2.Animals | Numbers per 0.5m$^2$ | | | |
| *Spirorbis levinseni* | I22 (± 92) | 42(±27) | Intertidal pools cochlear to subtidal | *P.miniata*, *P.longicosta* *P.cochlear*, *P.argenvillei* , and *P.barbara*. |
| *Vermetes coralinaceus* | I460 (±I06) | 692(±I6) | | |
| *Polydora capensis* | 622 (±242) | 0 | | |

On the west coast the gregarious *Vermetes corallinaceus* often occurs in large numbers on the shells of limpets. Normally associated with lithothamnion, *V. corallinaceus* may completely cover and distort the limpet shell but do not undermine it. Restriction to limpet shells only occurs when the density of limpets is high and grazing precludes settlement on the surrounding rock. In low density populations of *P. cochlear*, small "islands" of *Vermetus* may occur beyond the grazing range of the limpets.

*Ampelisca excavata*, normally found burrowing in the lithothamnion on *Turbo sarmaticus* (Gray and Barnard 1970) has been found subtidally in the shells of *P. barbara*, at Kommetjie and Hongklip in the Cape Peninsula.

*Spirorbis* (*Paralaeospira*) *levinseni* is often restricted to the shells of limpets. This again is probably due to grazing of limpets in the vicinity but the effect is enhanced by the gregarious behaviour of settling *Spirorbis* (Knight-Jones 1951).

Occasional boring sponges (Clionidae) cover the shell and undermine it. Pelseneer (1935) has recorded clionids from *Patella*. Acrothoracic barnacles were found on a single large *P. barbara* in burrows on the shell, but are more commonly found on *Turbo sarmaticus*.

The lack of specifity in these associations does not detract from the importance of the shell as a niche. Table II illustrates this quantitatively. Korringa (1951) has described how the shells of *Ostrea edulis* provide a similar substrate for many organisms.

Fig. 1. Zonation of animals associated with *Patella*, at Kalk Bay and Camps Bay.

— $<1/m^2$

▭ 1- $10/m^2$

▭ 10 - $50/m^2$

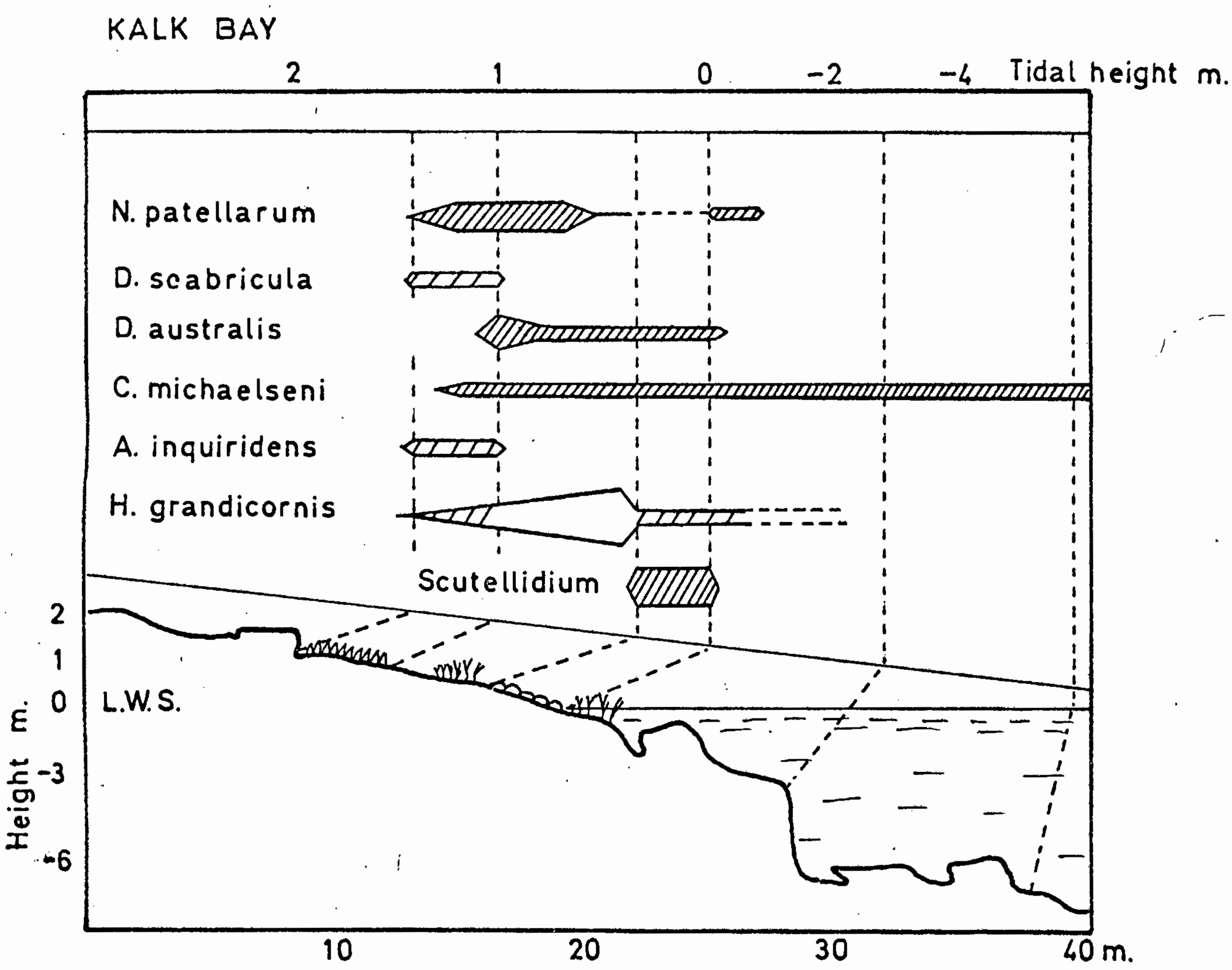
□ 50- $500/m^2$

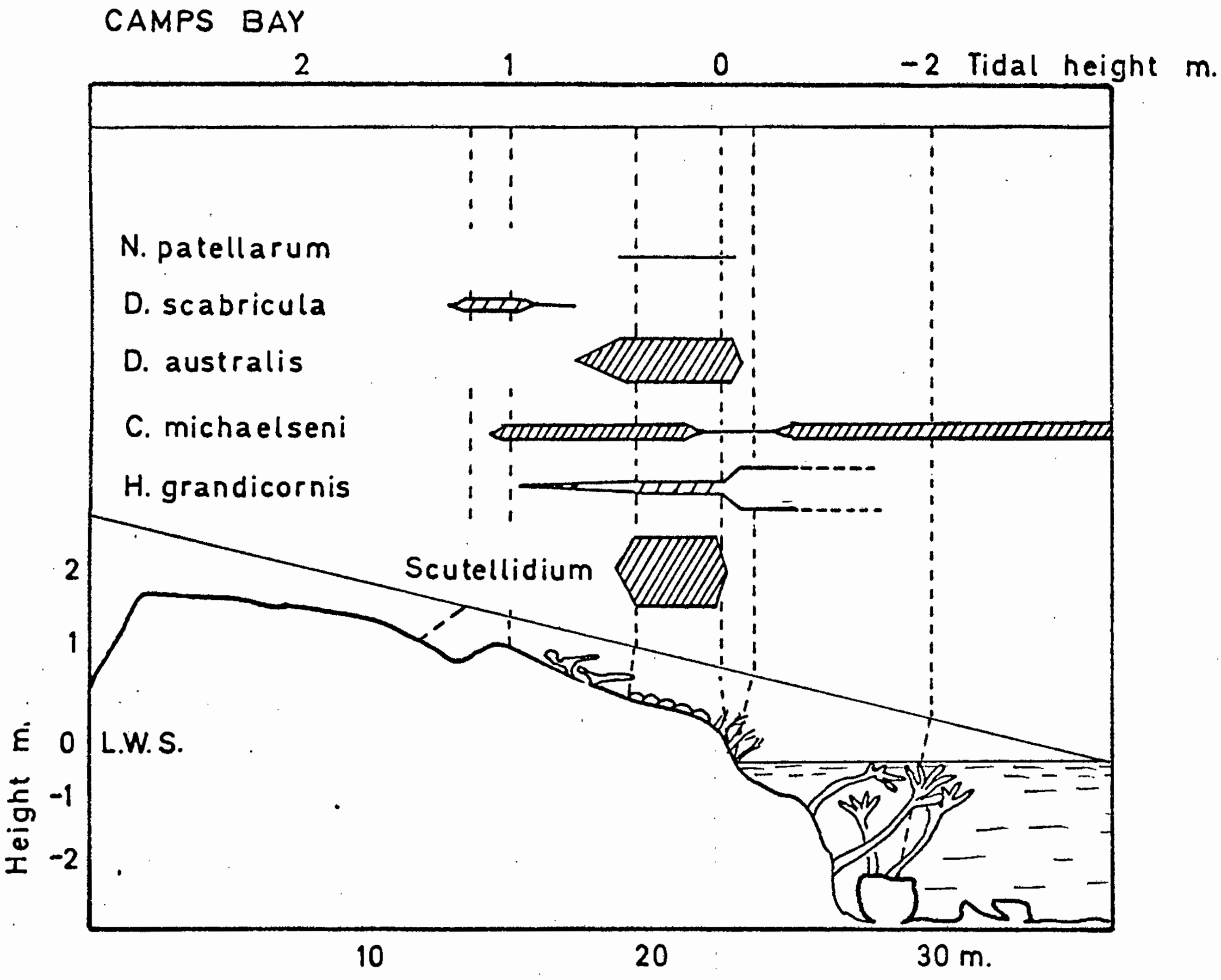
□ $1000/m^2$

▨ Associated

▧ Partly associated with Patella

□ Free living


KALK BAY
2
1
0
-2
-4
Tidal height m.
N. patellarum
D. scabricula
D. australis
C. michaelseni
A. inquiridens
H. grandicornis
Scutellidium
2
1
0
L.W.S.
-3
-6
Height m.
10
20
30
40 m.


CAMPS BAY
2
1
0
-2
Tidal height m.
N. patellarum
D. scabricula
D. australis
C. michaelseni
H. grandicornis
Scutellidium
2
1
0
L.W.S.
-1
-2
Height m.
10
20
30 m.

AMPHIPODA

*Calliopiella michaelseni*

Koch (1949) first drew attention to the occurrence of *C. michaelseni* in association with *Patella*. The distribution of the amphipod ranges from Luderitz (Penrith and Kemsley, 1970) to Hermanus: a predominantly cold water distribution. Typically its zonation (fig. 1) extends from the upper balanoid to the subtidal zone, extending down to a recorded depth of 7m.

In the areas investigated in the Cape Peninsula, *C. michaelseni* is strongly associated with *Patella*, with 98% association. Koch (1949) has remarked that the association is particularly well developed near the Cape Peninsula. Although it may be found under all species of *Patella*, *C. michaelseni* shows a marked numerical preference for *P. oculus*, *P. granatina*, *P. miniata*, *P. tabularis* and *P. compressa* (fig. 2.). This trend cannot be explained by the zonation of the amphipod, as it coincides with all of the limpets, and some host selection evidently occurs.

The colours of the amphipod vary with and resemble those of the host species. A bright red longitudinal dorsal stripe may be developed: this is rapidly gained or lost and apparently controlled by chromatophores. The general body colour resembles that of the host, but transitions are slow and evidently controlled by a different mechanism. Modification of diet under the different host may effect the colour.

The colour variations and percentage specificity relating to different hosts, is summarised in Table III.

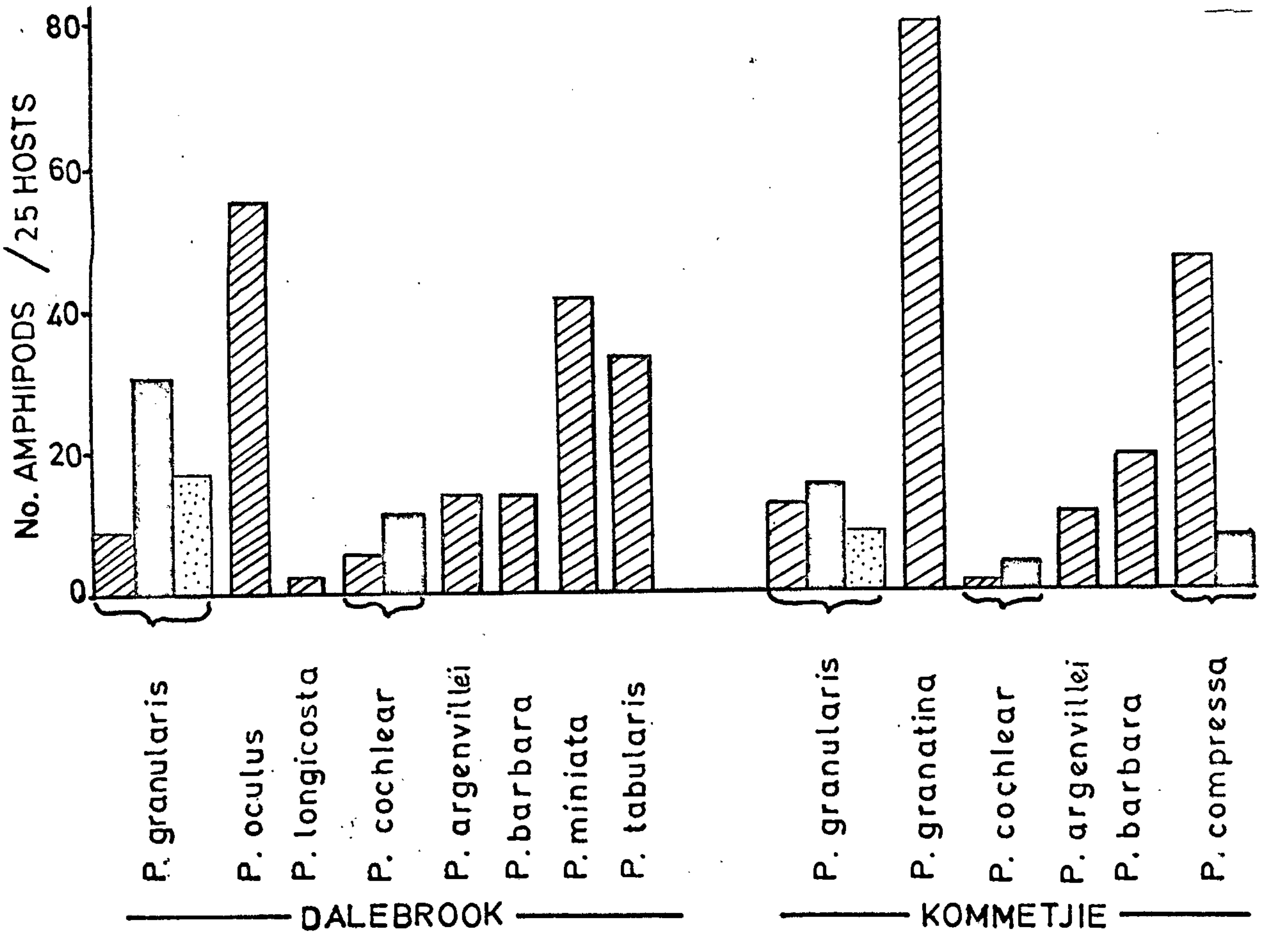


Fig. 2. Numbers of amphipods associated with <u>Patella</u>.
Dotted: <u>Allorchestes</u> <u>inquiridens</u>
Black: <u>Hyale</u> <u>grandicornis</u>
Hatched: <u>Calliopiella</u> <u>michaelseni</u>

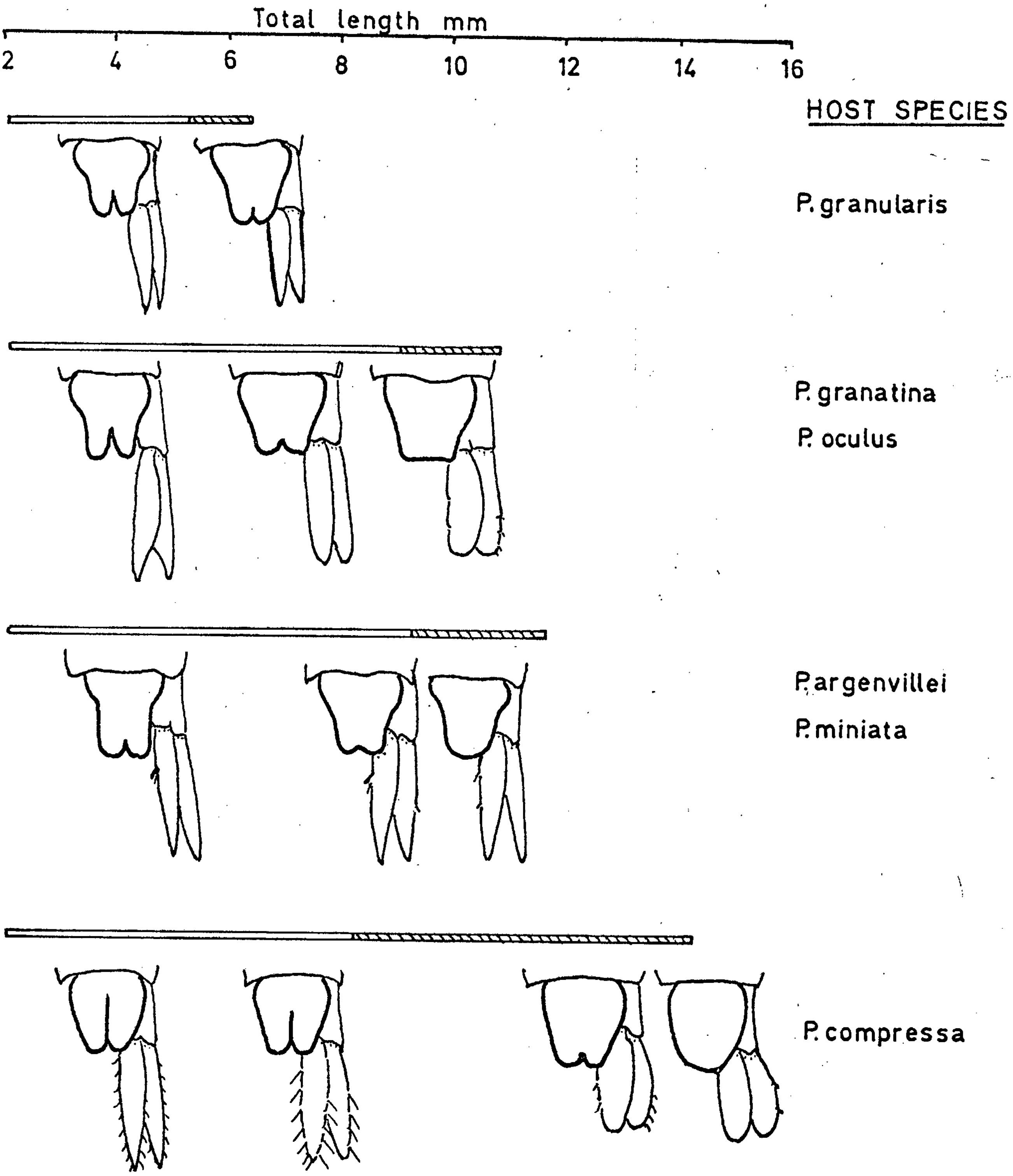


Fig. 3. Morphological variation of the uropods and telson of C. michaelseni in relation to size and zonation. Horizontal bars indicate total lengths of amphipods and ovigerous females are indicated by cross hatching.

Table III

| Host | % Specificity | Colour of Calliopiella |
|---|---|---|
| P. granularis | 3.6 | Uniform pale green-brown. Gut dark brown. Eyes red-brown. |
| P. granatina | 26.4 | Uniform dark khaki: Gut darker |
| P. oculus | 18.0 | Paler Khaki. Gut green to khaki |
| P. longicosta | 0.9 | Pale blue green. Green to redish brown |
| P. cochlear | 0.9 | Pale brown green. Gut whitish |
| P. argenvillei | 4.5 | Variable, usually whitish-brown. Gut green. Mid dorsal stripe. Eyes bright red. |
| P. barbara | 5.4 | Pale green brown. |
| P. miniata | 13.8 | Delicate blue, pink tinges, mid dorsal red stripe. |
| P. tabularis | 10.8 | As for P. miniata but paler blue. |
| P. compressa | 15.4 | Dorsally deep purple, fading to blue-pink. Gut brown. Eyes orange with brown mosaic. |

A certain amount of morphological variability occurs in C. michaelseni, due partly to age and partly to zonation. Some variations fall outside the accepted definition of the species. The telson is strongly cleft in recently hatched juveniles, and becomes progressively rounded, the cleft disappearing only in adults. Similarly, the uropods change from an elongated lanceolate shape to a blunt rounded structure, as the animals mature. Specimens found high in the intertidal zone are small at maturity (10 - 12 mm.) and tend to have shorter, rounded uropods. Subtidal specimens are larger at maturity (12 - 18 mm.) and as juveniles they have much longer pointed uropods. This differentiation is particularly marked in specimens from P. compressa in which the juvenile uropods are very long and may be lined with long hairs ( a feature not found in individuals from other hosts). (fig.3).

Although these differences may be due to incipient speciation, they are not constant enough to justify subspecific separation, and it is more likely that they are due to environmental differences.

Certainly it is common for size to be related to the amount of submergence experienced.

Specimens of C. michaelseni and its host were maintained in the laboratory for examination. To simulate tidal exposure and submergence, 10 P. oculus housing 15 amphipods were subjected to cyclic removal and replacement of water, using a simplified version of the tidal machine described by Underwood (1972). After an initial 10 hour period, none of the amphipods left their hosts during three successive 10 hour "tidal" cycles.

The amphipods lie in the pallial or mantle cavity, periodically moving around between the gills. Feeding, mating, moulting and emergence of the young were all observed to occur under the limpets.

The faeces of Calliopiella comprise a wide variety of algal fragments, but were constant within specimens taken from each host species. Calliopiella were observed feeding on the faeces of its hosts while in the mantle cavity and pallial groove. Isolated specimens would also feed readily on the faeces of P. compressa. In the cases of P. compressa, P. longicosta and P. tabularis, the host faeces and amphipod faeces were very similar in composition. The amphipods probably also feed on alga scrapings left behind while the host is feeding. These methods of feeding may in part explain the host preferences, as P. cochlear feeds predominantly on Lithothamnion and the limpet faeces must have a low nutritive value. The colour of amphipod guts (see Table III) may similarly be explained by this diet. On one occasion a specimen was found feeding on the mucus deposited by a P. oculus, but this did not seem to be a regular occurrence.

TABLE IV. Choice chamber experiments with *C. michaelseni*.

| Number | Choice | | Significance |
|---|---|---|---|
| | Sunlight, black background | Total darkness, black background | |
| 11 | 0 | 11 | $p < .001$ |
| 11 | 0 | 11 | $p < .001$ |
| 11 | 1 | 10 | $p < .001$ |
| 11 | 1 | 10 | $p < .001$ |
| 11 | 1 | 10 | $p < .001$ |
| 11 | 0 | 11 | $p < .001$ |
| 10 | 0 | 10 | $p < .001$ |
| 76 | 3 | 73 | $p < .001$ |
| | Direct sunlight black background | Shadow, black background | |
| 8 | 2 | 6 | $p > .05$ |
| 8 | 1 | 7 | $p < .001$ |
| 8 | 0 | 8 | $p < .001$ |
| 8 | 1 | 7 | $p < .001$ |
| 32 | 4 | 28 | $p < .001$ |
| | Sunlight, white background | Sunlight, black background | |
| 11 | 2 | 9 | $p < .05$ |
| 11 | 2 | 9 | $p < .05$ |
| 11 | 1 | 10 | $p < .01$ |
| 11 | 2 | 9 | $p < .01$ |
| 10 | 1 | 9 | $p < .01$ |
| 54 | 8 | 46 | $p < .001$ |

Analysis of monthly samples of Calliopiella for size distribution, number of juveniles and ovigerous females, indicates that reproduction occurs throughout the year. However, there are two marked peaks of activity in June (Winter) and November (Spring) when large numbers of juveniles appear (fig. 4). This is similar to the condition found in Neohaustorius schmitzi and Austrochiltonia subtenuis, recorded by Dexter (1971) and Lim and Williams (1971). Between two and four age groups are apparent in most populations. The growth of each age group indicates a longevity of about 12 months and a deduced growth rate of 8mm. in six months. Most ovigerous females fall into a size range of 8 - 12mm. although a few samples of 5mm. were recorded.

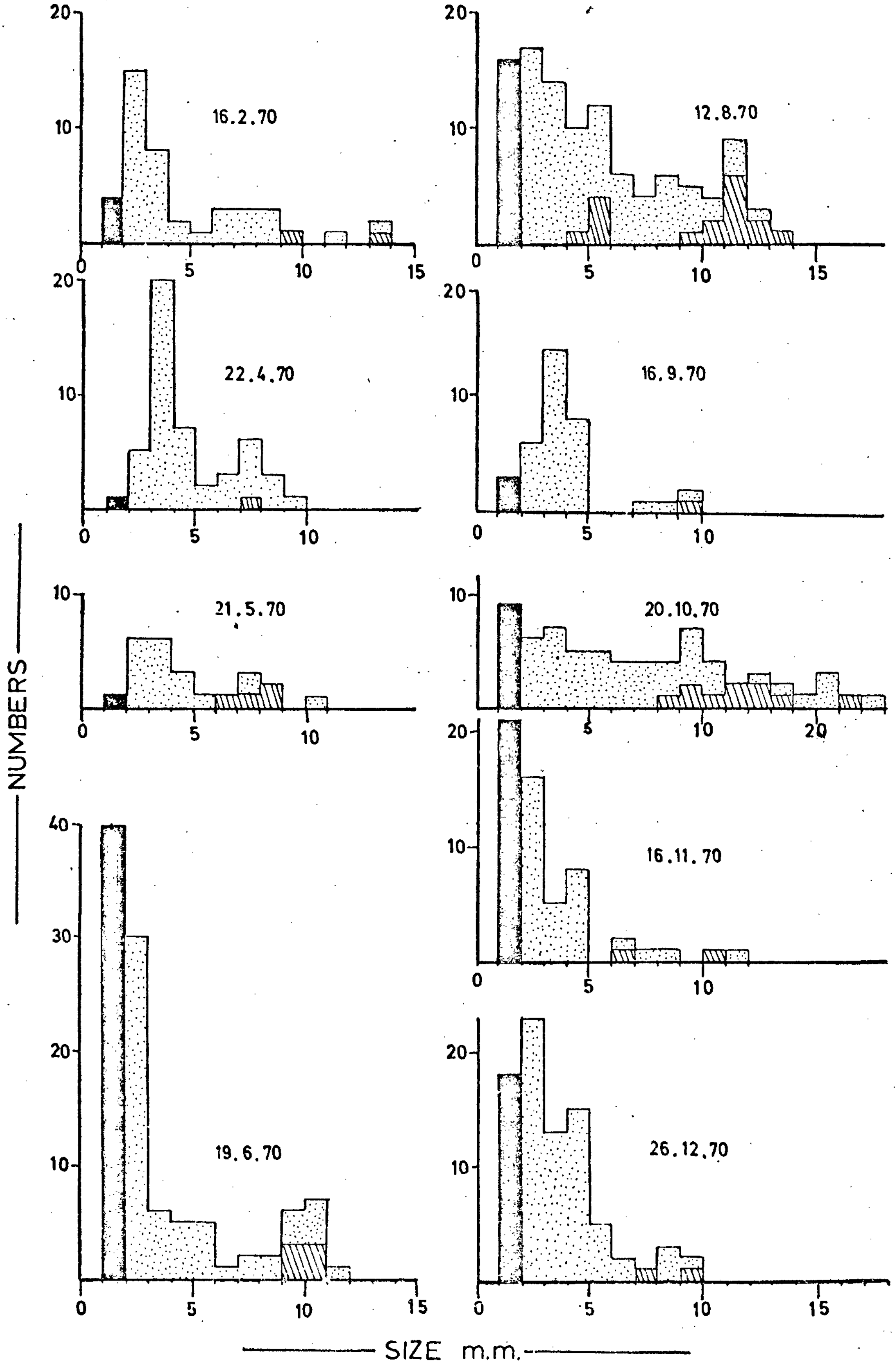
The reaction of Calliopiella to light was demonstrated by a series of choice chamber experiments. Circular glass dishes of 10cm. diameter were used, dividing each to allow the animals a choice of two alternatives. At least four trials of ten minutes were run for each experiment and each independently statistically tested. Table IV gives the cumulative results for each experiment.

The results demonstrate a strong and sensitive photonegative reaction, similar to that displayed by Lystriella clymenellae, which is commensal in the tubes of the polychaete Clymenella torquata (Batcheller and Mills, 1965).

An interesting positive correlation exists between the size of a host limpet and the size of its commensal amphipods (fig. 5), excluding newly emerged juveniles, which before dispersal remain with their parents and are thus associated with large limpets.

This correlation suggests the selection of hosts according to size. Furthermore, a high percentage of large limpets contain a pair of Calliopiella (one of each sex) or a pair of adults and a

Fig. 4. Monthly size distribution of C. michaelseni. Small juveniles are indicated in black, and ovigerous ♀♀ by cross hatching.


16.2.70
12.8.70
22.4.70
16.9.70
21.5.70
20.10.70
16.11.70
19.6.70
26.12.70
0
5
10
15
20
30
40
NUMBERS
SIZE m.m.

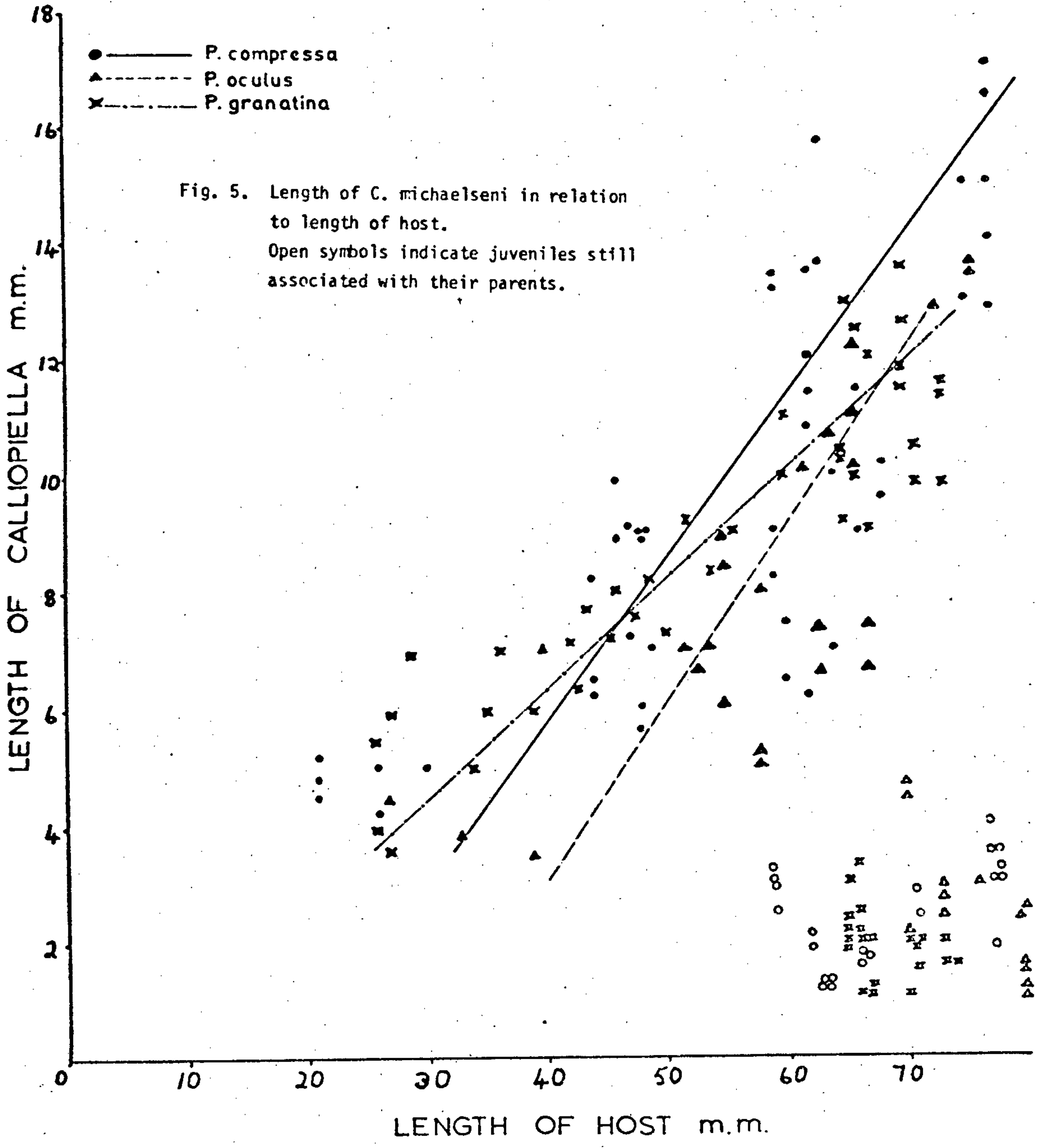


Fig. 5. Length of C. michaelseni in relation to length of host.
Open symbols indicate juveniles still associated with their parents.

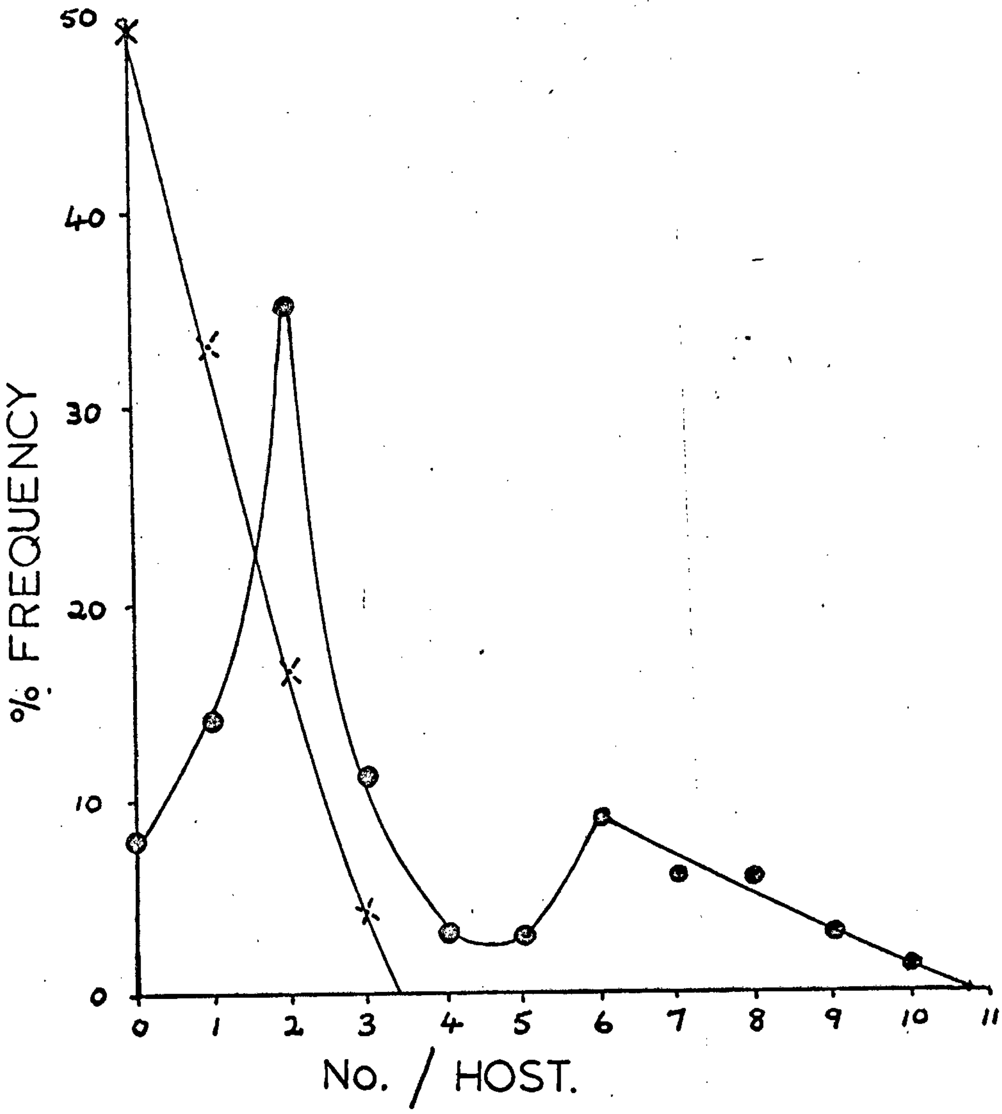


Fig. 6. Number of Calliopiella per host. Circles indicate hosts of over 35mm. and crosses under 35mm. in length.

number of offspring. In the case of smaller limpets (less than 50mm.), most lack amphipods or contain only a single specimen (fig. 6).

The dispersal of Calliopiella can be interpreted in the light of these observations. Mature males and females almost always occur in pairs, one pair per limpet, and are found only under large limpets. After reproduction, the offspring remain with the parents until they are about 4 mm. in length, (equivalent to approximately two months growth). Dispersal then occurs and the juveniles are subsequently found, usually singly, under small limpets. (Figs. 5 and 6). Heavy mortality evidently occurs during dispersal as is apparent from the size of the population age groups (fig. 4.)

Large amphipods may actively select large host, while the smaller amphipods are distributed amongst the remaining limpets thus giving an illusion that they are limited to small limpets.

The growth rate of some of the limpets is such that not more than one change of host would be necessary to explain the positive correlation between host and amphipod sizes. Two of the preferred host species, P. granatina and P. oculus have average growth rates of 18 mm and 25 mm per year respectively (when considering the average growth from 20 mm to 70 mm).

Movement from one host to another presumably must occur with pairing (although this has not been observed) and "selection" of a large limpet may occur in the process.

As never more than one pair of adult Calliopiella is associated with each limpet, some mechanism must operate to prevent additional amphipods from entering. Whether an "occupied" limpet is rejected by incoming amphipods, or the pair already present actively excludes further amphipods, is not known. It is interesting that when 20

TABLE V: Choice chamber experiments with *C. michaelseni*

| No. Tested | Choice | | | Time per trial (hrs.) | conditions | Significance of Difference |
|---|---|---|---|---|---|---|
| | 2 live *P. oculus* | 2 empty *P. oculus* shells | Free Swimming | | | |
| 14 | 8 | 6 | 0 | 0.1 | Diffuse light | $p > .05$ |
| 14 | 7 | 7 | 0 | | | $p > .05$ |
| 14 | 9 | 5 | 0 | | | $p > .05$ |
| 14 | 9 | 5 | 0 | | | $p > .05$ |
| 18 | 16 | 1 | 1 | 12.0 | Diffuse light | $p < .001$ |
| 16 | 16 | 0 | 0 | | | $p < .001$ |
| 16 | 14 | 2 | 0 | | | $p < .001$ |
| 14 | 14 | 0 | 0 | 12.0 | Total Darkness | $p < .001$ |
| 14 | 12 | 1 | 1 | | | $p < .001$ |
| 14 | 14 | 4 | 0 | | | $p < .01$ |
| | 2 live *P. oculus* | 2 recently killed *P. oculus* | Free Swimming | | | |
| 16 | 16 | 0 | 0 | 12.0 | Diffuse light | $p < .001$ |
| 14 | 12 | 0 | 2 | | | $p < .001$ |
| 14 | 12 | 0 | 2 | | | $p < .001$ |

Calliopiella were introduced into an aquarium under a single P. oculus, they dispersed within three days to the other (unoccupied) limpets in the aquarium.

Dispersal may be associated with host selection to explain the relationship between amphipod and host size. Adult Calliopiella may for physical reasons be associated with large limpets. Occupation of large limpets by adult Calliopiella may restrict small individuals to the remaining limpets.

Whilst the mechanism of this dispersal is unknown, the advantage is obvious: only a limited amount of food can be available under each limpet. A similar advantage results from the size correlation of host and amphipod.

Neither of the amphipods Allorchestes inquiridens or Hyale grandicornis have been found under limpets housing a pair of adult C. michaelseni.

The initial attraction of C. michaelseni to a limpet may be phototactic as the amphipods are strongly photonegative, and crawl readily under any shell. This alone is not adequate to explain the attraction; some form of chemical attraction is probable. Initial and immediate escape under dark objects is always followed later by rejection of the object in preference for a limpet, (if the latter is available.) The attractive factor occurs only in living limpets and dead specimens appear to repel the amphipods.

These conclusions are based on the choice chamber experiments summarised in Table V.

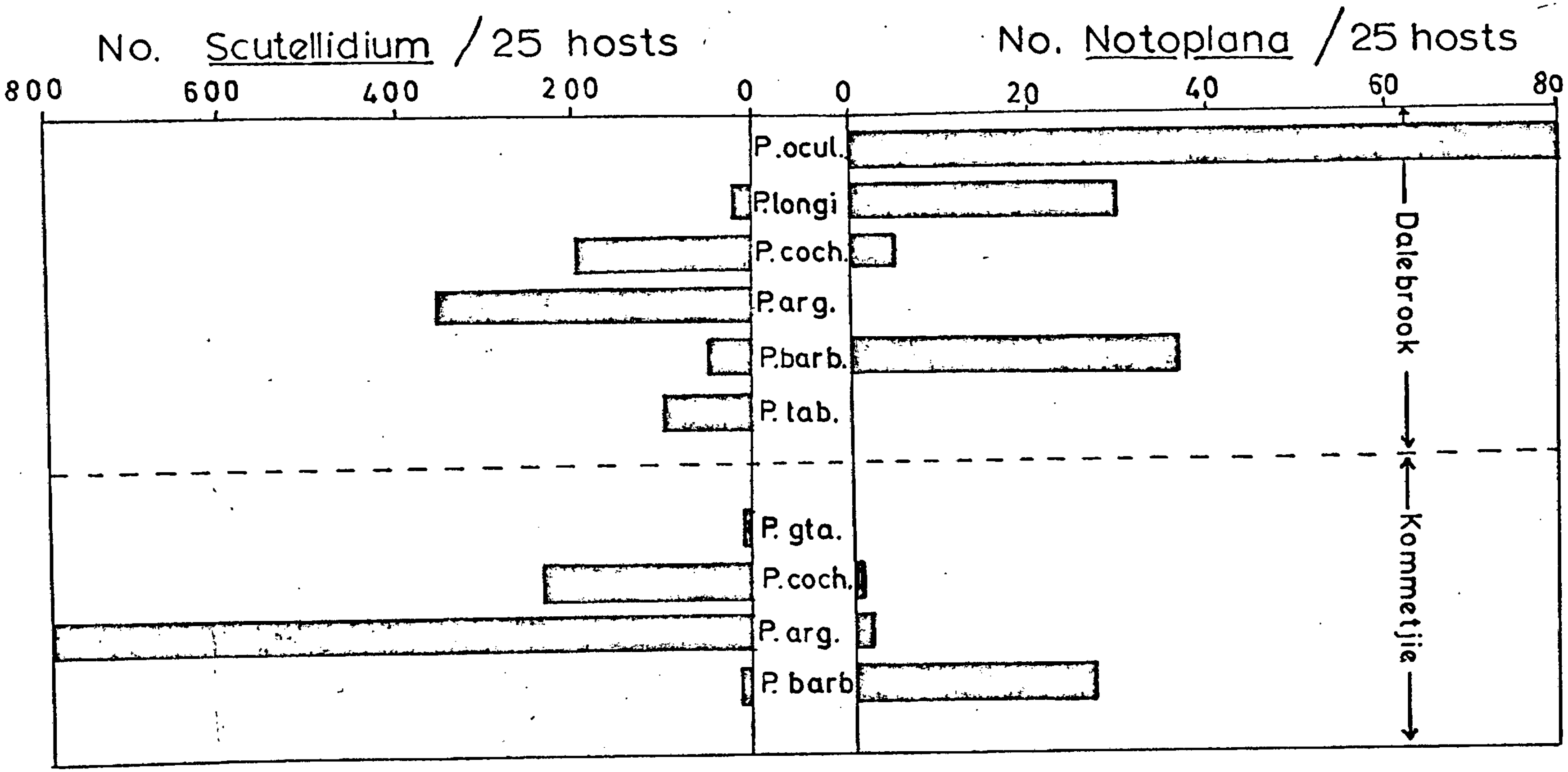


Fig. 9. Number of Scutellidium sp. and Notoplana patellarum associated with different Patella spp.

TABLE VI: Relationship between size of *C. michaelseni* and width of niche selected.

| Size Range of *C. michaelseni*. mm. | 1.0-1.9 | 2.0-2.9 | 3.0-4.9 | 5.0-6.9 | 7.0-12.0 |
|---|---|---|---|---|---|
| Width of Niche mm. | | | | | |
| 0.25 | 2 | 4 | 0 | 0 | 0 |
| 0.50 | 7 | 6 | 0 | 0 | 0 |
| 0.75 | 2 | 4 | 6 | 5 | 0 |
| 1.0 | 0 | 0 | 6 | 3 | 0 |
| 1.5 | 0 | 1 | 7 | 8 | 2 |
| 2.0 | 0 | 0 | 1 | 3 | 7 |
| 2.5 | 0 | 0 | 0 | 1 | 6 |
| 3.0 | 0 | 0 | 1 | 1 | 4 |
| No niche selected: | 2 | 1 | 3 | 2 | 1 |
| Total: | 13 | 16 | 24 | 23 | 20 |

Calliopiella also exhibites a strong thigmotaxis. When specimens are liberated in a round smooth glass container in which little substrate is possible, they will clamp together in small groups. This is a typical thigomotactic response. The clamping effect only occurs if the background is dark or the light intensity low: in the presence of strong light or a white background the effect is abolished and the animals swim rapidly around trying to avoid the light.

Thigmotaxis is also demonstrated in an aquarium containing empty limpet shells: they immediately crawl under the shells out of the light and lie around the periphery where they have maximum contact with the shell and the substrate.

Calliopiella will select a niche which provides maximal substrate contact. The following experiment demonstrates this: 96 Calliopiella were released in a round aquarium in which were mounte glass slides at various distances from the bottom. After 12 hours in the dark, the size distribution of the amphipods was related to the size of the niche each had selected. Table VI summarises the results.

The results indicate an active selection of niche size according to the size of the amphipod, so that maximumcontact with the substrate is achieved. This may in part explain the correlation between host and commensal sizes, and supports the contension that an active selection of certain sized hosts occur after dispersal, and possibly during pairing as well. It may also partially explain the specificity of host selection, as in P. cochlear and P. longicosta (the species selected least often) the pallial groove is much shallower than in the other species.

*Hyale grandicornis*:

*H. grandicornis* and *Allorchestes inquiridens* are both found associated with *Patella* and have a similar relationship. *H. grandicornis* is a widely distributed and common species, recorded from the Californian coast of America (Barnard, 1969) in association with *Acmaea* spp (Johnson (1968), and in association with *P. vulgata* in Europe (Vader, pers. comm.). In South Africa it is ubiquitous and has been recorded from Luderitz to Durban. Its zonation extends from the upper balanoid to the sublittoral (fig. 1). Densities of up to 4 212 per square metre were recorded.

*H. grandicornis* is found under all *Patella* spp., but almost all are associated with *P. cochlear* (30%) and *P. granularis* (62%) (fig. 2). Large numbers are also found free living in algal tufts. The "preference" for *P. cochlear* and *P. granularis* is explicably by the distribution of algal cover on the shore. In the Cochlear zone, limpet grazing is extensive, and few algae are found apart from the encrusting lithothamnion. Similarly, the Upper Balanoid is high on the shore and characterised by a leck of algae. *P. cochlear* and *P. granularis* respectively predominate in these zones and provide a logical shelter at low tide, in the absence of algae. Empty barnacle shells are also utilised.

Johnson (1968) has described how juveniles of *H. grandicornis* are always found associated with *Acmaea* spp. on the Californian coast while adults are free living. In the present work, this pattern is also apparent in the lower regions of the shore, where predominently juveniles (and a certain number of adults) are found under limpets. The distinction is not as marked as in Johnson's work. In the upper regions of the shore, adults predominate, (both free living and associated with *Patella*), presumably because of the more rigorous conditions.

Spooner (1957) has similarly described how juveniles of *H. perieri* are found under *P. vulgata*. Juveniles of *H. nilssonii* are also associated with this limpet (Vader 1971) and with *Nucella lapillus* (Brattegard, 1963).

Johnson (1968) records that between 20% and 90% of *Acmaea* house *H. grandicornis*, with a decrease in association up the shore. This is different from the pattern experienced here, where the incidence is highest with *P. granularis* in the upper regions of the shore and decreases down the shore.

The differences experienced between these results and those of Johnson (1968) may be due to differences in algal cover. *Patella* spp. are much larger than most *Acmaea* spp. and this may explain why more adults amphipods are associated with *Patella*. In addition, *C. michaelseni* inhabits many limpets and may reduce the number available to other amphipods.

No relationship exists between host size and the number or size of *H. grandicornis* but hosts of less than 20mm. usually lack the amphipods.

In the laboratory *H. grandicornis* are photonegative and react positively to a dark substrate, as shown by the results of choice chamber experiments (Table VII). The amphipods were liberated into circular chambers, one half of which was darkened, the other in the light. Similarly, choices of black or white backgrounds (both in Light) were offered. Ten minutes were allowed for each trial.

Table VII: Choice chamber experiments with *H. grandicornis*.

| No. Tested | Choice | | Signif. of Difference |
|---|---|---|---|
| | Light | Dark | |
| 11<br>11<br>18 | 2<br>3<br>4 | 9<br>8<br>14 | p. <.05<br>p. >.05<br>p. <.02 |
| 40 | 9 | 31 | p.<.001 |
| | In light white background | In light black background | |
| 10<br>10<br>11 | 2<br>3<br>2 | 8<br>7<br>9 | p. <.05<br>p. >.05<br>p. <.05 |
| 31 | 7 | 24 | p. <.01 |

Under water, *H. grandicornis* is attracted to dark shells and remains on (but not under) them. Feeding on algae was observed. If the water is drained off, the amphipods crawl under the limpet shell or into any niche where water has accumulated. With the addition of further water, they emerge and swim actively around and onto the shell surface again. If algal tufts are available, they too may be settled on.

Quantitatively this is shown by the results in Table VIII obtained by liberating H. grandicornis into an aquarium with four intact P. oculus and four empty P. oculus shells.

Table VIII: Niche selection by Hyale grandicornis

| Conditions | Time Mins | No. under living P. oculus | No. under empty shell | No. on top of shells | No. free swimming | Total |
|---|---|---|---|---|---|---|
| Under water | 1 | 0 | 0 | 7 | 1 | 8 |
| | 10 | 0 | 0 | 7 | 1 | 8 |
| Water drained off | 10 | 4 | 3 | 3 | 0 | 10 |
| | 30 | 5 | 3 | 1 | 0 | 9 |
| | 30 | 5 | 3 | 2 | 0 | 10 |

Observations in the field confirm this behaviour. As the tide washes over the rocks, large numbers of H. grandicornis emerge from under limpets or other niches, and actively swim or jump over the substrate. With the receeding tide they again retreat into shelters.

The relationship between H. grandicornis and Patella spp. is thus a loose one. Nevertheless, the abundance of this amphipod under limpets (Table 1) suggests that the association is not due to chance alone. Large numbers of other amphipods occur intertidally and yet are seldom found associated with Patella. Some degree of attraction between H. grandicornis and its hosts is probable.

Allorchestes inquiridens:

A. inquiridens is distribted from Luderitz to Mossel Bay and is frequently found in association with P. granularis and to a lesser extent P. cochlear (fig. 1). The reasons for this specificity are probably similar to those discussed above for H. grandicornis: lack of algal cover in the zone dominated by these limpets. Association with limpets occurs mainly in the upper regions of the shore. Lower down, the amphipods are found in tufts of algae, and may be restricted to the algae growing on limpet shells.

A. inquiridens is also predominantly associated with limpets while juvenile: relatively few adults were found under Patella.

The association is again based on the need to avoid desiccation and predation but the large numbers found under P. granularis suggest some niche preference.

The taxonomic distinction between A. inquiridens and H. grandicornis depends solely on the expansion of the fifth joint of gnathopod two in males of the former species (Barnard 1940). Identification of juveniles and females is thus difficult, and could only be made with reasonable assurance when males of only one of these species were present. H. grandicornis is far more common than A. inquiridens.

## ISOPODA

### Dynamenella spp.

Several species of isopod have been recorded as commensals (Glynn, 1968; Brattegard, 1968). The relationship between Dynamenella perforta and Acanthopleura granulata has been analysed in some detail by Glynn (1968). In South Africa a large variety of isopods is common intertidally, but only D. scabricula and D. australis are regularly associated with Patella, with respectively 85% and 96% association. D. scabricula is distributed from Luderitz to Hermanus (Day 1969) and occurs predominantly in the balanoid zone at about midtide level. D. australis ranges from Luderitz to Hermanus, principally in the cochlear zone, but

Table IX Intertidal distribution of the isopod genera *Dynamenella*, *Exosphaeroma*, and *Parisocladus*.

| Species | Upper bala-noid. | Lower bala-noid. | Cochlear | Sub-tidal. | Locality |
|---|---|---|---|---|---|
| *D.australis* | 0 | 0 | 0+*9* | *4* | Dalebrook |
| *D.scrabicula* | 0+*6* | 0 | 0 | 0 | |
| *D.dioxus* | 0 | 0 | 6 | 0 | |
| *D.macrocephala* | 0 | I2 | 90 | 0 | |
| *D.huttoni* | 0 | 96 | 888 | 96 | |
| *E.truncatitelson* | I2 | 6 | 0 | 0 | |
| *E.planum* | 6 | I2 | 24 | 0 | |
| *E.kraussi* | 84 | I2 | 0 | 0 | |
| *P.stimpsoni* | 78+*3* | 6 | 0 | 0 | |
| *P.perforatus* | I2 | I584 | I8 | 0 | |
| *D.australis* | 22+*40* | I0+*I27* | I0+*I70* | - | Kalk Bay |
| *D.scrabicula* | 34+*60* | 0 | 0 | - | |
| *D.huttoni* | 0 | 340 | 620 | - | |
| *E.porrectum* | 0 | 0 | 20 | - | |
| *E.kraussi* | 25 | 0 | 0 | - | |
| *P.perforatus* | 6 | 270 | 0 | - | |
| *D.australis* | I0 | 22+*504* | 42+*20I6* | 46+*I5I2* | Camps Bay |
| *D.scabricula* | I+*27* | 0+*I7* | 0 | 0 | |
| *D.huttoni* | I0 | I20 | I252+*I2* | 626 | |
| *E.kraussi* | 26 | 0 | 0 | 0 | |
| *E.laeviusculum* | 6 | 0 | 0 | 0 | |
| *P.perforatus* | 6 | 26 | 0 | 0 | |
| *Paridotea rubra* | 0 | 0 | 3 | 3 | |

extending into the lower balanoid (fig. 1). Related to these zonation patterns, *D. scabricula* is mainly associated with *P. granularis* and *P. granatina*, while *D. australis* is found under *P. cochlear* and *P. argenvillei* (Table 1).

Analysis of the relative zonation and density of all common intertidal isopods at Dalebrook, Kalkbay and Camps Bay show that these two species are the only regular isopod associates found under *Patella*. *D. huttoni* is probably the commonest isopod at these sites but is seldom found under limpets. Similarly, *Parisocladus* spp. and *Exosphaeroma* spp. are abundant in tufts of sea weed but only occasionally occur under limpets (Table IX). *D. huttoni* is found abundantly in beds of *Bifurcaria brassicaeformis* as well as on *Gelidium pristoides*, *Gigartina stiriata* and other algae. Small specimens are commoner in tufts of *Cladophora* spp. Faecal contents indicate that *D. huttoni* feeds entirely on the alga to which it is clinging.

*Table IX* Intertidal Distribution of the isopod genera *Dynamenella* *Exosphaeroma* and *Parisocladus*. Figures for Dalebrook are from Fuhr (1970, unpublished), obtained cumulatively from 3 samples of approximately 5000cm$^2$. Densities for Kalk Bay and Camps Bay are from duplicate 400cm$^2$ samples. All figures have been scaled to represent density per square metre. Figures underlined represent numbers associated with *Patella*.

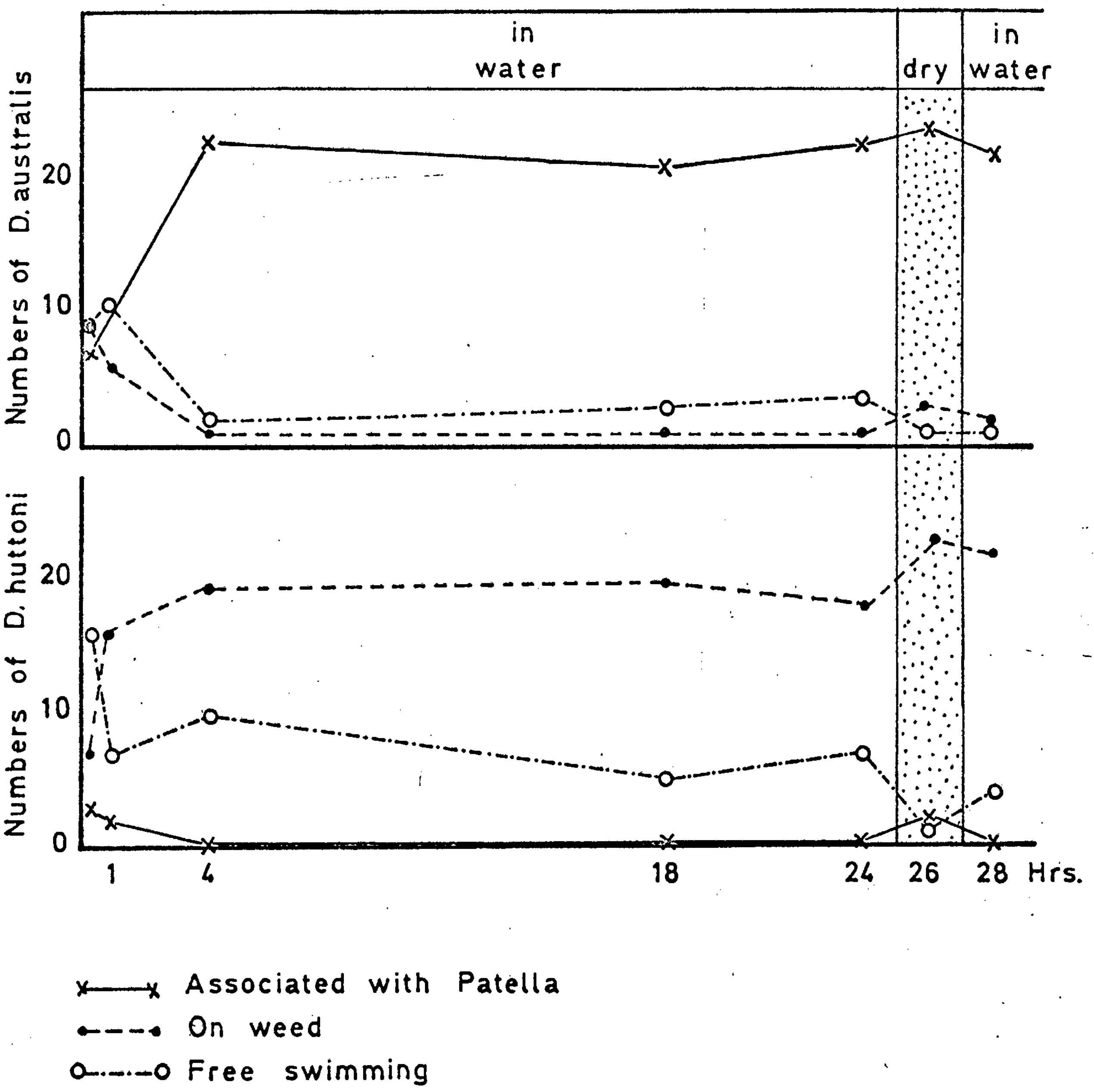


Fig. 7. Selection of Substrate by D. australis and D. huttoni.

Field and McFarlane (1968) have shown that D. australis and D. scabricula are associated with shores with strong wave action, while D. huttoni occurs over a much wider range of wave conditions. It is significant that P. cochlear and P. argenvillei also predominate in areas of strong wave action.

The reactions of D. huttoni and D. australis were tested by randomly releasing twenty six of each into an aquarium containing two P. argenvillei, eight small P. cochlear (on the shells of P. argenvillei) and an equivalent amount of Bifurcaria brassicaeformis. The specimens were maintained in sea water at 16°C for twenty four hours. The water was then slowly siphoned off to simulate low tide conditions and then poured back after three hours. Isopod distribution was determined periodically throughout the experimental period of 28 hours.

The results are given in Table X and figure 7.

TABLE X

| Isopod species | Time from start mins. | Conditions | Numbers of isopods | | | |
|---|---|---|---|---|---|---|
| | | | Under limpets | On limp. shell | Free swim. | On Alga |
| D.australis (n=26) | 0.5 | under water | 5 | 2 | 10 | 9 |
| | 1 | | 6 | 4 | 10 | 6 |
| | 4 | | 20 | 3 | 2 | 1 |
| | 18 | | 20 | 1 | 4 | 1 |
| | 24 | | 19 | 4 | 2 | 1 |
| | 26 | dry | 22 | 1 | 1 | 3 |
| | 28 | under water | 20 | 2 | 2 | 2 |
| D. huttoni (n=26) | 0.5 | under water | 3 | 0 | 16 | 7 |
| | 1 | | 2 | 1 | 7 | 16 |
| | 4 | | 0 | 0 | 10 | 16 |
| | 18 | | 0 | 1 | 5 | 20 |
| | 24 | | 0 | 1 | 7 | 18 |
| | 26 | dry | 2 | 0 | 1 | 23 |
| | 28 | under water | 0 | 0 | 4 | 22 |

The results of this experiment clearly indicate the preference the associate D. australis has for limpets, while the free living D. huttoni attach onto the alga. During exposure, a few D. huttoni may crawl under limpets, but most bury themselves in the holdfast of the alga. D. australis rapidly crawls under (or onto) a Patella. They remain there even when the limpets are moving. If the limpet crawls away from them, the isopods rapidly follow it until they can move under the shell.

Moulting and mating of D. australis have both been observed in the pallial groove of a limpet.

D. scabricula is not as common D. australis, and occurs higher up the shore. While its relationship with Patella seems similar to that of D. australis, the association is less marked. In surveys (Table IX) most D. scabricula are found under limpets, (85% association), but in aquaria about 40% cling to algae and 50% select limpets. Adults are often too large to lie in the pallial groove of P. granularis, and the limpet completely covers the isopod with its foot, so that it is firmly trapped to the substrate. This has no effect on the isopod, which is liberated when the limpet moves off to feed.

The relationship of D. scabricula and Patella is thus not as well developed as that of D. australis.

Under the limpet, D. australis lies in the pallial groove or on the mantle edge. Often they are orientated with their heads buried between the gills. Glynn (1968) has observed that D. perforata adopts a similar position in the pallial groove of Acanthopleura granulata, and suggests that they are feeding on algal fragments left by the rasping of the chiton, and swept back

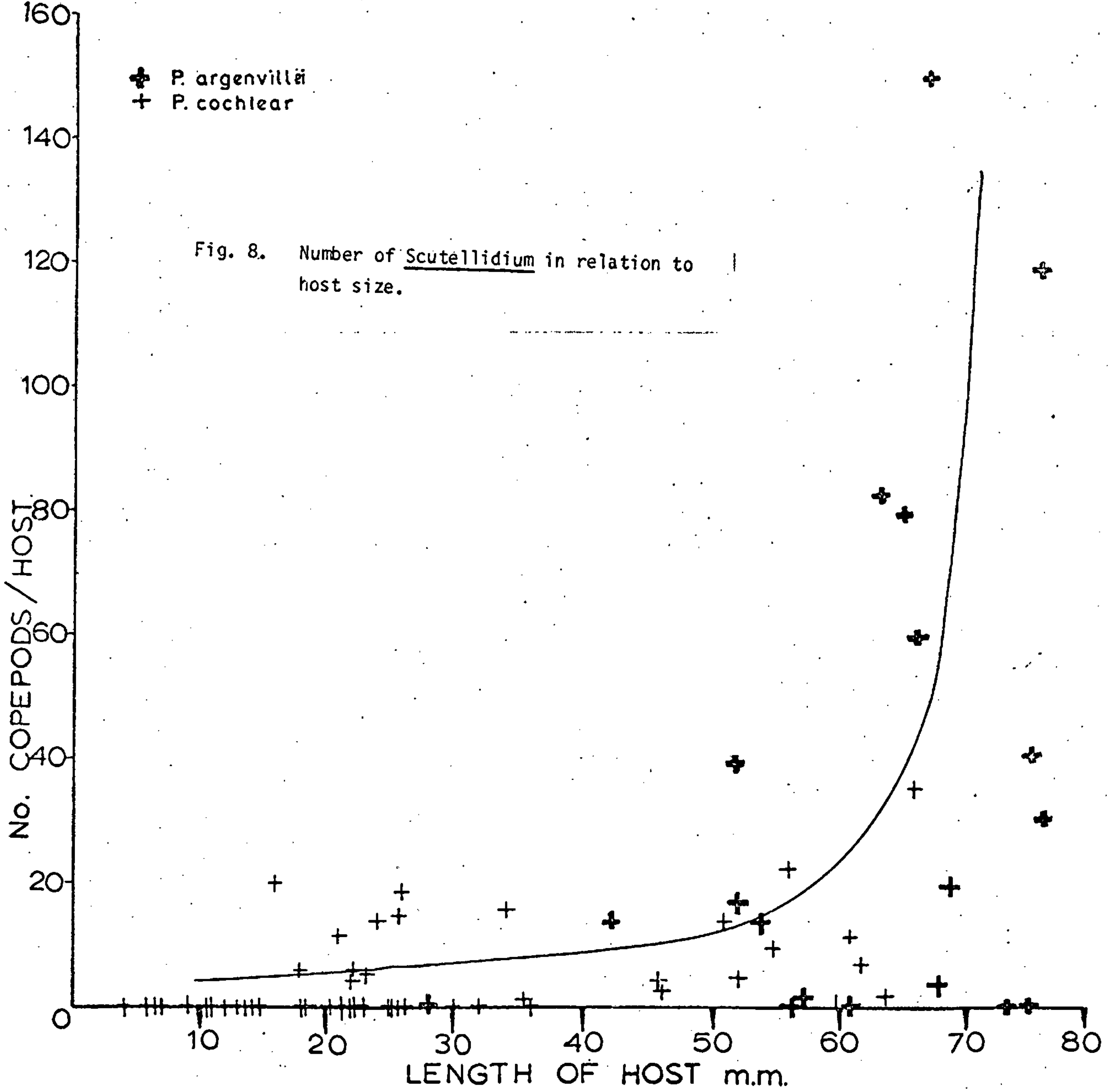


Fig. 8. Number of Scutellidium in relation to host size.

in the respiratory current of Acanthopleura. D. australis may also feed on these algal particales, but were also seen emerging from under the limpet and eating alga on the edge of the shell. Some D. australis crawl over the shell, but never attempt to leave the limpet.

D. huttoni is clearly a free living species found only under limpets when no other moist niche is available at low tide. D. australis is predominantly associated with limpets, and feeds, moults and mates there. The relationship is still probably not obligatory, as free living specimens are found in algae or empty barnacle shells. D. scabricula represents an intermediate stage with an obvious, but less developed, association with Patella. This isopod occupies a more rigorous zone on the shore, where few algae occur: its association with limpets may partly be explained on this basis.

## COPEPODA (HARPACTICOIDEA)

### Scutellidium spp.:

A new species of the genus Scutellidium was found in large numbers associated with Patella. A separate description of the species and its life cycle has been prepared (Branch, in press). The known distribution of the species extends from Lambert's Bay to Hangklip, but this range will probably be extended with further work. At present it is suggestive of a cold water distribution. The species has a restricted zonation, being confined almost entirely to the Cochlear zone (fig. 1).

There is a marked correlation between the host size and the number of copepods (fig. 8), and together with the restricted zonation, probably explains the apparent preference of Scutellidium for *P. argenvillei*. About 80% are found associated with this limpet and the remainder are almost all limited to *P. cochlear*. Occasional specimens are found under other limpets but have not been found on any other hosts. An interesting negative correlation exists between the number of *Scutellidium* on a limpet, and the numbers of *Notoplana patellarum* (fig.9). It is unlikely that a direct cause-and-effect relationship exists between the two distributions. Nevertheless, the reduction of contact is certainly of survival value to the copepods, as most polyclad turbellarians feed on small crustaceans (Hyman 1951) and the occasional *Notoplana* found on *P. argenvillei* feed readily on *Scutellidium*.

*Scutellidium* appears to be a scavenger and the limpets are unefected by the relationship. In aquaria the copepods run continually over the pallial cavity and gills and even occasionally on the external surface of the shell. Specimens have been kept alive for three weeks without their hosts, fed on dry shavings of *Ecklonia maxima* and small amounts of wet algae. During this time they produced larvae. It seems probable that they normally scavenge on the limpet faeces as well as algal fragments and possibly mucous produced by the limpets. Other members of the genus are free living and usually found on littoral algae. (Lang 1948, Wells 1967).

Ovigerous females and larval stages can be found throughout the year and no marked peaks of reproduction have yet been detected. A marked sexual disparity exists and about 95% of adults are female. It is interesting that all of the larval stages are found under limpets suggesting that planktonic dispersal is minimal. Up to 200 specimens have been found on a large *P. argenvillei*, and due to the high density of limpets in the cochlear zone, dispersal could occur by direct transfer from limpet to limpet.

All stages of the life cycle cling strongly to the host: the

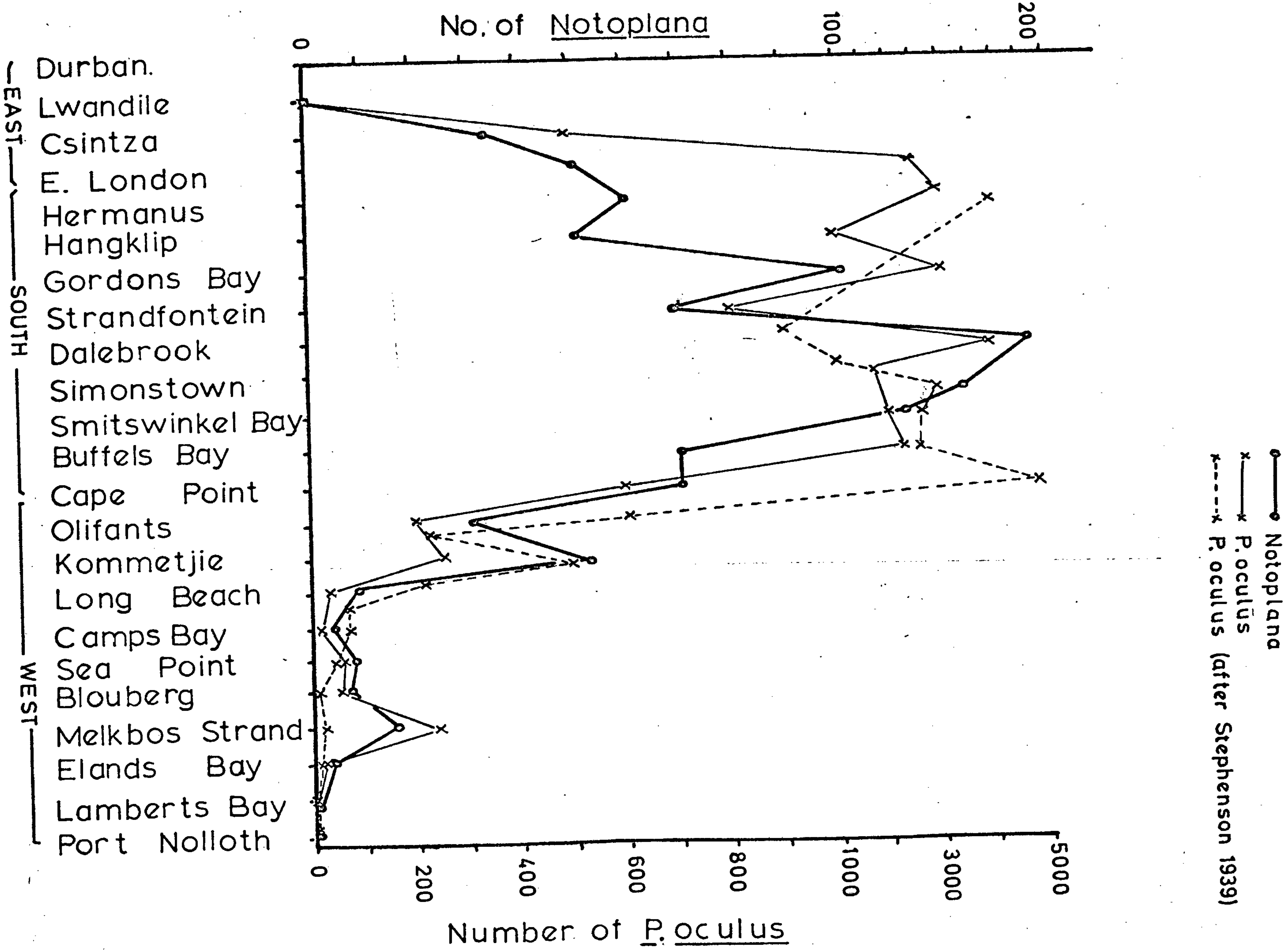


FIG. 10 Distribution of N. patellarum and P. oculus

adult and copepodites have strong raptorial setae and suctorial setal pads while the nauplii have a large central suctorial membrane. Specimens cling tenaciously to the host when water movement occurs and even violent currents are incapable of dislodging them.

Of incidental interest is the regular occurence of two suctorian species, and a peritrich ciliate on the body of the copepods. One of the suctorians (an ophryodendrid) is found only on the basal segments of the first antenna - a situation similar to the suctorian *Spathocyanus caridina* found on the antenna of the shrimp *Caridina* sp. (Nie and Lue 1945). Presumably the swimming action of the antenna improves the feeding mechanism of the suctorian.

## TURBELLARIA (POLYCLADIDA)

### *Notoplana patellarum*:

The association between *N. patellarum* and *Patella* has long been known (Stephenson 1939, and Koch 1949). In the present work, 98.5% association was recorded, 78% being specific to *P. oculus*. The remainder are mainly associated with *P. longicosta* and *P. barbara*, although individuals have been found under all of the intertidal limpets. The distribution of the turbellarian was obtained by counting the number that could be found in one hour's examination of all the limpets in the given area. This correlates almost exactly with the numerical distribution of *P. oculus* obtained by using Stephenson's (1939) method of counting the number of *P. oculus* that could be identified in one hour without removing the limpets from the rocks (fig. 10).

*N. patellarum* occurs predominantly in the balanoid zone, occasionally being found subtidally (fig. 1). This pattern coincides with the zonation of *P. oculus*, except that small populations of

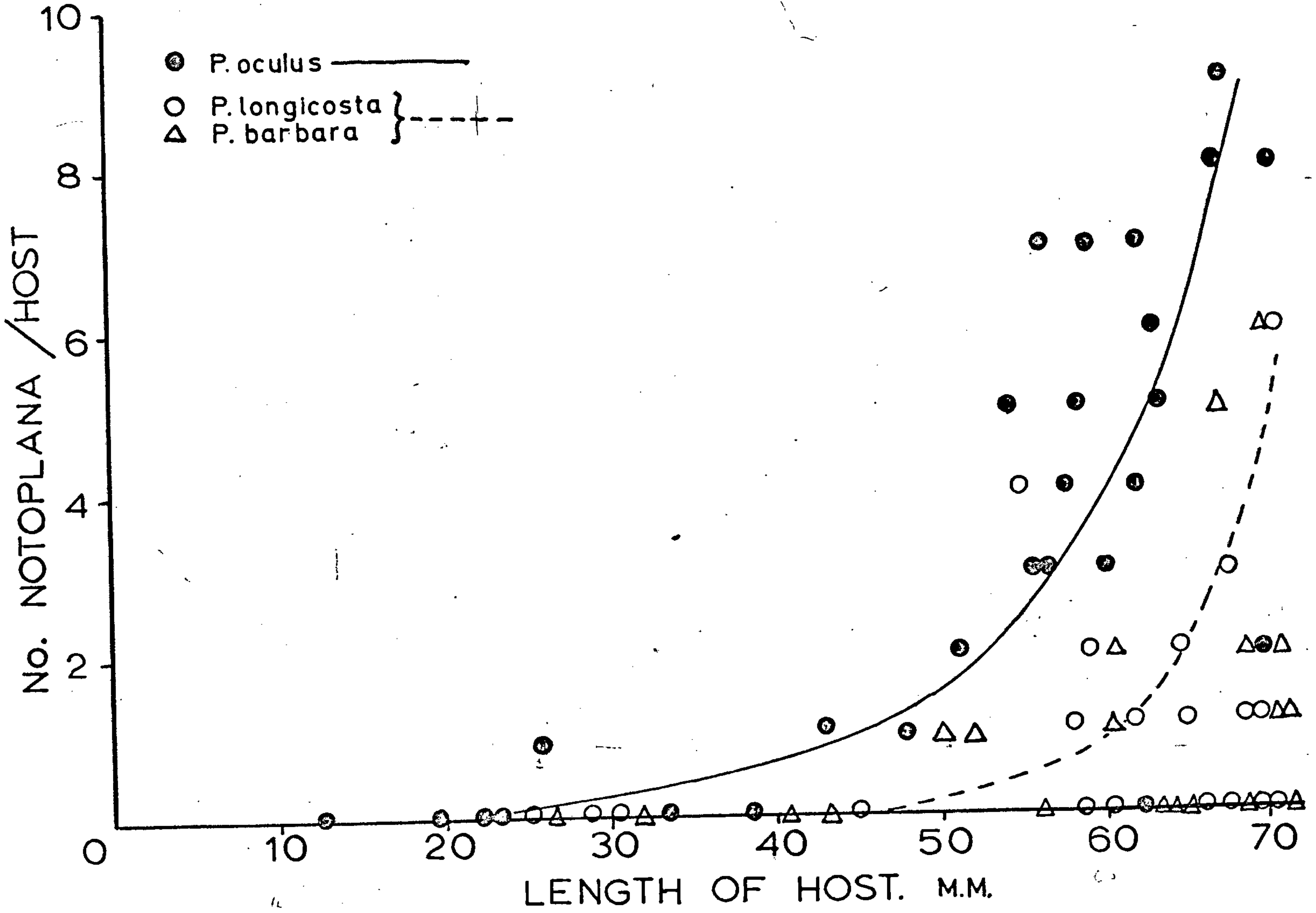


Fig. 11. Numbers of Notoplana in relation to host size.

Table XII. Choice Chamber experiments with <u>N. patellarum</u>

| No. tested | Choice | | | Conditions | Significance of difference |
|---|---|---|---|---|---|
| | Light | Dark | | | |
| 24 | 2 | 22 | | 15 mins for each trial | $p < .001$ |
| 24 | 2 | 22 | | | $p < .001$ |
| 24 | 1 | 23 | | | $p < .001$ |
| 24 | 2 | 22 | | | $p < .001$ |
| | Sunlight | Shadow | | | |
| 24 | 10 | 14 | | 15 mins for each trial | $p > .5$ |
| 24 | 8 | 16 | | | $p > .1$ |
| 24 | 12 | 12 | | | $p = 1$ |
| 24 | 10 | 14 | | | $p > .5$ |
| | 2 living P. oculus | 2 empty shells | Free Swimming | | |
| 26 | 6 | 7 | 13 | 10 mins in light | $p > .1$ |
| 26 | 8 | 5 | 13 | | $p > .1$ |
| 26 | 26 | 0 | 0 | 12 hours in light | $p < .001$ |
| 26 | 24 | 2 | 0 | | $p < .001$ |
| 26 | 20 | 6 | 0 | | $p < .01$ |
| 26 | 24 | 1 | 1 | 12 hr in dark | $p < .001$ |
| 26 | 25 | 0 | 1 | 12 hr alt. lgt. and dark. | $p < .001$ |

of the lower balanoid by P. granatina, almost all N. patellarum were found with P. oculus (Table XI).

Table XI Relative frequency of association between Notoplana, P. oculus and P. granatina, at Melkbos Strand.

| Number of Notoplana per limpet | 0 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | | Mean dens. of limpets $/m^2$ |
|---|---|---|---|---|---|---|---|---|---|---|
| Frequency with P. oculus | 5 | 2 | 7 | 14 | 8 | 2 | 0 | 1 | n=39 | 2.6 |
| Frequency with P. granatina | 36 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | n=38 | 14.1 |

The reaction of N. patellarum to light, limpets, and limpet shells was tested using choice chambers. The following choices were offered.

1. Direct light and total darkness (in the absence of limpets and with a uniform black background).
2. Direct sunlight and shadow (in the absence of limpets and with a uniform black background).
3. Two intact live P. oculus and two freshly cleaned and boiled P. oculus shells of comparable size (with uniform diffuse light, or with total darkness or with light and dark alternating at 3 hour intervals).

All experiments were conducted in sea water at 16°C. The results are given in Table XII.

Table XIII: Selection of different Patella spp. by N. patellarum

| Conditions | Number under limpets |  |  |  |  |  |  |  | No. not under limpets | Total |
|---|---|---|---|---|---|---|---|---|---|---|
|  | P. oculus |  | P. longicosta |  | P. granularis |  | P. cochlear |  |  |  |
|  | 1 | 2 | 1 | 2 | 1 | 2 | 1 | 2 |  |  |
| 14 hrs. in light. All limpets alive | 8 | 8 | 1 | 1 | 4 | 0 | 0 | 0 | 5 | 27 |
| 5 hrs. in dark All limpets alive | 18 | 2 | 0 | 4 | 0 | 2 | 0 | 0 | 1 | 27 |
| 6 hrs in light limpets died after 3 hrs. | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 24 | 26 |
| 6 hrs. in light limpets mutilated but alive | 2 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 23 | 26 |

Although a photonegative response is apparent from these results, the sensitivity is low, as indicated by the limited distinction between indirect light (shadow) and direct sunlight. In the choice between intact P. oculus and fresh empty shells of this limpet, a strong attraction to the live limpet was apparent. Initial reaction was random, and the Notoplana moved around and under the limpets or shells in an irregular manner: many crawled under one of the limpets and then out again almost immediately. This random pattern disappeared progressively, and within 12 hours almost all were confined to the live P. oculus.

Host specificity was strikingly demonstrated by introducing 27 Notoplana into the centre of a round aquarium containing two specimens each of P. oculus, P. cochlear, P. longicosta and P. granularis arranged equidistantly around the periphery. (Table XIII).

A marked preference for live P. oculus is evident (Chi square $p < .001$). Some form of chemical attraction must exist to explain the marked specificity. The attraction ceases with death or mutilation of the P. oculus and the limpets are rejected (Chi square $p < .001$). This is similar to the situation recorded by Davenport and Hickok (1951) for the polychaete Arctonoë fragilis which is commensal with Evasterias troschelii.

It is difficult to identify the gut contents of Notoplana, due to digestion or regurgitation on capture. Five specimens taken from under P. argenvillei and P. cochlear all had two to five Scutellidium sp. in their guts. Two specimens from P. oculus contained on juvenile Calliopiella each. Small crustaceans probably comprise the principal diet.

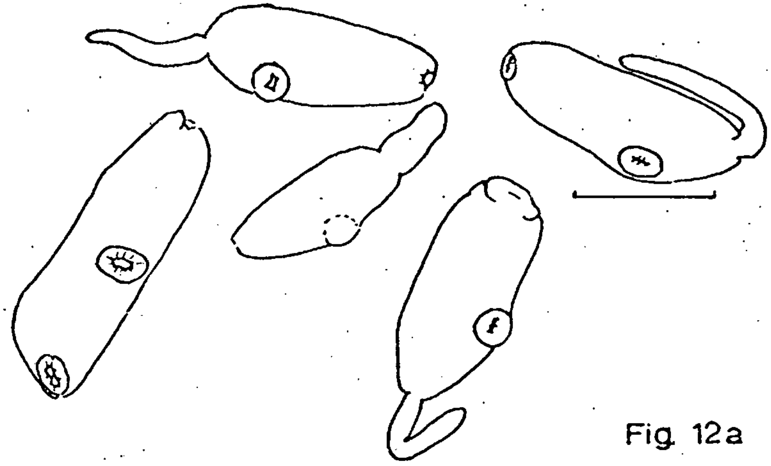


Fig. 12a

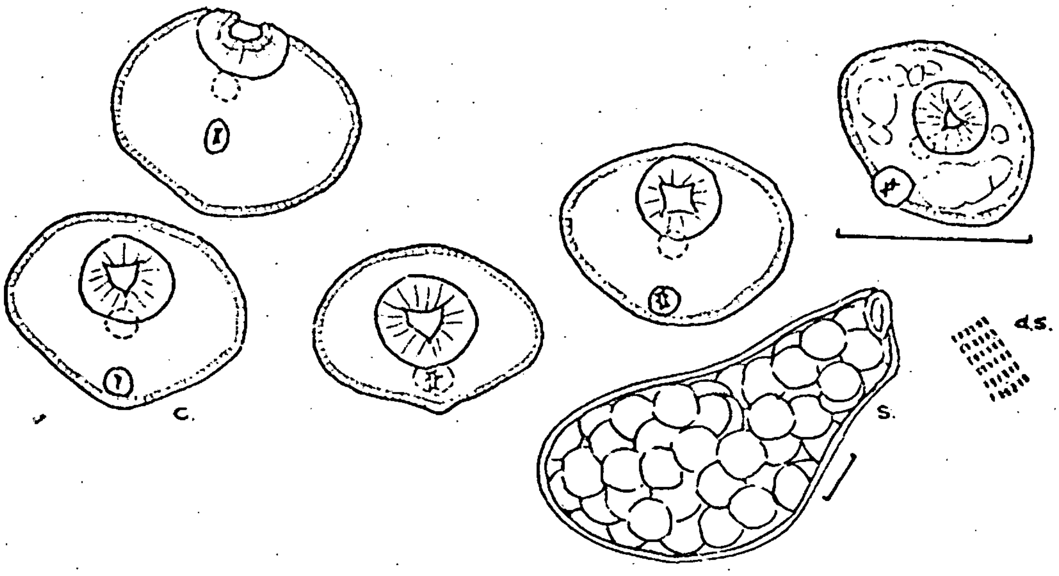


Fig. 12b

Fig. 12A, 12B. Two trematode species parasitic in the gonads of Patella.
S : Sporocyst, C : cercaria,
ds : detail of the cancellate surface of the cercariae.

## TREMATODE PARASITES.

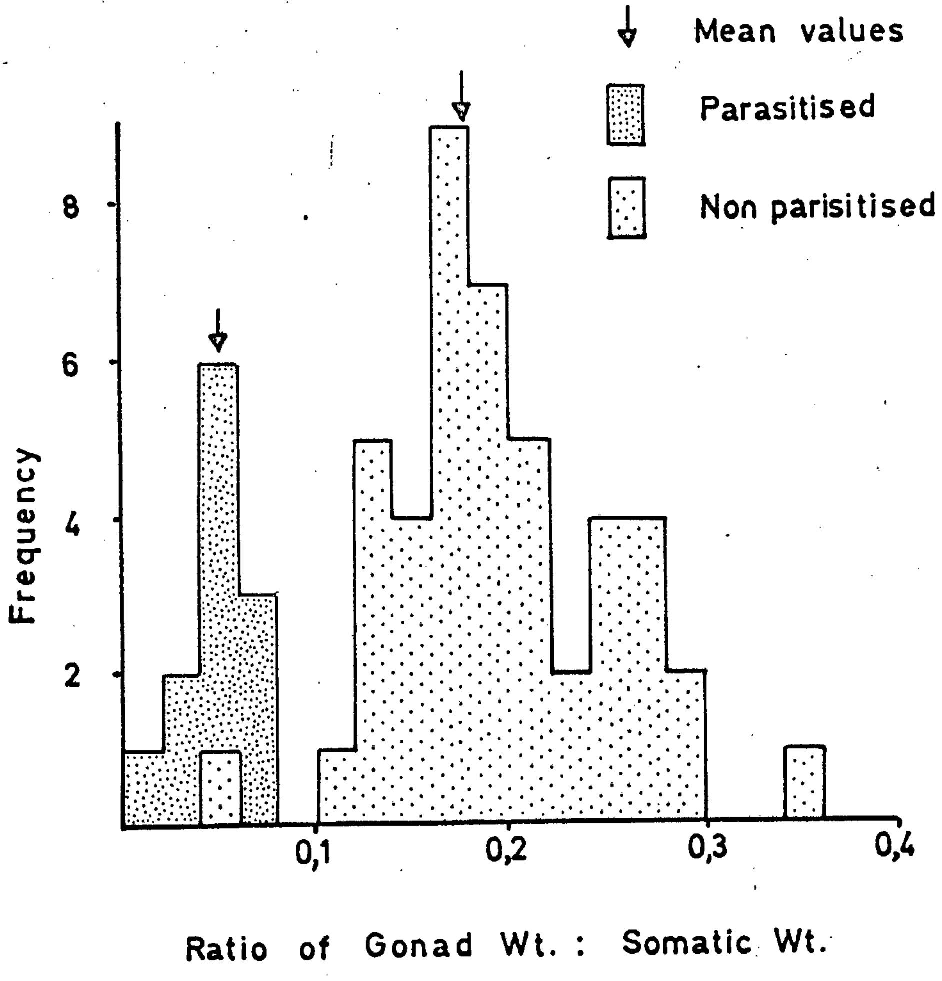
In the course of investigating the gonadial cycles of Patella, 4,260 specimens were microscopically examined: only two contained parasites. Examination of the gut and digestive gland of 60 specimens of each species failed to produce any parasites except in P. granatina. These organs need to be reexamined using larger samples, as Rees (1934) has shown that they are the normal site of cercarial infection, and that the gonads are only parasitised in the case of very heavy infections.

The parasites found in the gonad were the cercariae of two unidentified digenetic trematodes. In one case small numbers of the cercariae lay freely in the ovary of a P. granularis (fig. 12a), while in the other they were enclosed in a well defined sporocyst (fig. 12b) in the ovary of a P. granatina and were so abundant that the ovary appeared diseased and lobulated. Microscopic smears of the gonad showed the eggs of the latter to be partially atrophied in the region of the sporocysts but normal elsewhere. This is similar to the partial castration induced by Cercaria patellae in P. vulgata (Rees, 1934).

In P. granatina, 10% of a sample of 60 (from Melkbos Strand) contained cercariae in their digestive glands. These aggregated around the digestive gland ducts and gave the organ a white diseased appearance instead of its usual dark green colour. The gonads were markedly smaller in infected animals, as shown in fig. 12c, and partial castration had obviously occurred. The mean gonad size was 77% less than that of unparasitised animals.

The extremely low incidence of parasitism in most species is in sharp contrast wit the work of Crewe (1947) on P. vulgata, in which three trematode species were found with an incidence of up to 20% infection.

Fig 12c Effect of Parasitism on Gonad Size in P. granatina



## DISCUSSION

The retension of water in the pallial cavity of limpets makes them a logical shelter for small intertidal organisms, during low tide. This niche is exploited by a large number of species, but in most cases the association is casual and temporary. Forty six species have been recorded under limpets, but only seven occur sufficiently often to be considered associates or commensals. Among the forty six species, almost every group of intertidal animals is represented, including fish, nemertines, polychaetes, crustaceans and molluscs, but amphipods and isopods predominate.

In many of these animals, attraction to limpets is probably random. Most are cryptic, and attraction may be due simply to a photonegative response coupled with the presence of water in the pallial groove. The advantages conferred by this niche would obviously be increased by some permanence and specificity. It is thus not surprising that a range of small animals have become associated with limpets.

*Hyale grandicornis* and *Allorchestes inquiridens* illustrate the initial stages of such an association, in which clear numerical association occurs, but the dependency is low and specificity nonexistent. The limpets provide no more than a temporary shelter. Significantly, only intertidal limpets act as hosts for these two species. Juvenile amphipods predominate in this relationship, and this is logical in terms of their greater susceptibility to desiccation.

In the case of *Scutellidium* and *Dynamenella australis* (and to a lesser extent *D. scabricula*), a greater degree of association occurs. Even at high tide these animals remain under their hosts, or undertake only short excursions and then return. Fewer are found free living. The complete life cycle may occur under the limpets. Feeding on algal fragments has been observed, and the radular movements of the limpet may leave small algal particles on which these animals can feed.

Specificity is still low, for although all three are confined to a few *Patella* spp., this is probably due to their zonation patterns rather than a true specificity.

*Scutellidium*, *D. australis* and *D. scabricula* are probably facultative inquilines.

*Calliopiella michaelseni* can be considered a true commensal. Its dependency is increased to include a food supply in the form of limpet faeces, as well as a source of shelter. *C. michaelseni* is associated with both subtidal and intertidal limpets, suggesting that protection from desication is not the prime cause of the association. Protection against predation by birds and fishes will also be gained by sheltering under limpets. *C. michaelseni* is partially specific and shows a marked preference for some limpets. This is not related to zonation patterns.

*C. michaelseni* is strongly thigmotactic. Its selection of niches according to size, may partially explain the preference for certain limpet species.

Turbellarians are mainly cryptic animals, a habit which leads naturally to inquilinism and commensalism. Smith (1961) has described a case of inquilinism in which *Hoploplana luracola* occurs in the mantle cavity of *Nerita scabricosta* but probably feeds elsewhere. Several of the Leptoplanidae (to which *Notoplana* belongs) are commensal. *Hoploplana inquilina* is found in the mantle cavity of several whelks (Hyman, 1967). *Stylochoplana inquilina* is associated with a hermit crab - anemone complex (Hyman, 1950), *S. pusilla* occurs in the mantle cavity of *Monodonta labis*, and *S. parasitica* in the pallial groove of the Chiton *Liolophura japonica tessellata* (Kato 1934, 1935). *Notoplana* is a widely distributed genus, and common on rocky shores (Hyman 1951) so that the development of commensalism in *N. patellarum* is not surprising. *N. patellarum* is specific to a limited number of limpets and shows a marked preference for *P. oculus*.

With the exception of *C. michaelseni*, all the associates described in this paper are only associated with *Patella* in the intertidal zone. This suggests that protection from desiccation may initiate relationships which lead eventually to commensalism.

The low incidence of metazoan parasites is surprising. As birds are probably implicated in the life cycle of trematodes infecting intertidal molluscs, it would be interesting to determine the incidence of infection of *Patella* on guano islands. Thomas (1965) has shown that the incidence of infection of *P. vulgata* is highest on sheltered, gently sloping shores, which are also favoured settling splaces of many birds.

## ACKNOWLEDGEMENTS:

The data of isopod distribution at Dalebrook were extracted from the unpublished honour project of Miss I. Fuhr, to whom full credit must be extended. Mr. C. Griffiths of the Zoology Department, University of Cape Town and Mr. R. Simons of the Division of Sea Fisheries, Cape Town, assisted with the identification of respectively amphipods and algae. From his personal library, Dr. de Decker loaned literature on copepod taxonomy. My wife Margo has given constant and much appreciated encouragement and help with field work. Professor J.H. Day's constructive criticism of the paper is very much appreciated.

## SUMMARY:

Forty six species have been recorded under Patella spp., but most of these are casual associates, seeking temporary shelter. The shell surface offers an important substrate for algae and a few invertebrates, particularly where limpet densities are high.

The amphipods Hyale grandicornis and Allorchestes inquiridens are often associated with Patella, particularly in the juvenile stages. They are facultative inquilines which vacate their hosts at high tide, and are also found in large numbers in algal tufts.

The isopods Dynamenella australis and D. scabricula are predominantly associated with limpets and complete their life cycles under limpets. Choice chamber experiments demonstrate their preference for sheltering under limpets. The copepod Scutellidium sp. is similar, but the association is more marked.

Calliopiella michaelseni is commensal and shows a preference for certain species. Its colour changes in relation to the host species. Feeding occurs on limpet faeces and algal fragments. The life cycle is completed under the limpet. Two reproductive peaks occur each year. Adults usually occur in pairs. Juveniles remain with their parents initially, and then disperse to other limpets. A positive correlation between host and amphipod size can experimentally be elucidated in terms of thigmotaxis and niche size selection. The amphipods are strongly photonegative.

Notoplana patellarum is preferentially commensal with P. oculus. This can be experimentally demonstrated. It feeds on small crustacea, including Scutellidium. Only two trematode parasites were found, in the gonads.

## REFERENCES

Barnard, K.H. 1940. Contributions to the crustacean fauna of South Africa. XII Further additions to the Tanaidacea, Isopoda and Amphipoda, together with keys for the identification of the hitherto recorded marine and fresh water species. Ann. S.A. Mus. 32: 381-486.

Barnard, J.L. 1969. Gammaridean Amphipoda of the rocky intertidal of California: Monterey Bay to La Jolla. Bull. Am. Mus. nat. Hist. 260: 1-204.

Batcheller, R. and Mills, E.L. 1965. Behavioural studies on the commensal amphipod crustacean Listriella clymenellae Mills. Biol. Bull. 129 (2): 398.

Blake, J.A. and Evans, J.W. 1973. Polydora and related genera as borers in mollusk shells and other calcareous substrates. Veliger 15 (3): 235-249.

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): 1-38.

―――――――― 1973. Scutellidium patellarum nov. sp., a harpacticoid copepod associated with Patella spp. in South Africa, and a description of its larval development. Crustaceana (in press).

Brattegard, T. 1963. Crustaceans sheltering under shells of Nucella. Sarsia 11: 1-3.

―――――――― 1968. Marine biological investigations in the Bahamas 2. On an association between Acanthopleura granulata (Polyplacophora) and Dynamene spp. (Isopoda). Sarsia 32: 11-20.

Cheng, Th.C. 1967. Marine molluscs as hosts for symbioses, with a review of known parasites of commercially important species. Adv. Mar. Biol. 5: 1-424

Crew, W. 1947. Helminth parasites of limpets. Nature 159: 238.

Davenport, D. and Hickok, J.F. 1951. Studies in commensalism 2. The polynoid genera Arctonoë and Halosydna. Biol. Bull. 100: 71-83.

Day, J.H. 1969. A guide to marine life on South African shores. Balkema, Cape Town.

Dexter, D.M. 1971. Life history of the sandy-beach amphipod Neohaustorius schmitzi (Crustacea, Haustoriidae). Mar. Biol. 8 (3): 232-237.

Field, J.G. and McFarlane, G. 1968. Numerical methods in marine ecology 1. A quantitative "similarity" analysis of rocky shore samples in False Bay, South Africa. Zool. Afr. 3. (2): 119-138.

Fuhr, I.M. 1970. The ecology of isopods on a rocky shore: a study at Dalebrook (Cape Town), with particular reference to the species of Parisocladus and Exosphaeroma. Unpublished Honours project, University of Cape Town.

Glynn, P.W. 1968. Ecological studies on the associations of chitons in Puerto Rico, with special reference to sphaeromid isopods. Bull. Mar. Sc. 18 (3): 572-626.

Gray, W.S. and Barnard ,J.L. 1970. South African Ampelisca excavata K.H. Barnard (Amphipoda, Gammaridea), a redescription with notes on the domicile. Crustaceana 19 (1): 67-83.

Haigler, S.A., 1969. Boring mechanism of Polydora websteri inhabiting Crassostrea virginica. Am. Zool. 9: 821

Hyman, L.H. 1950. A new Hawaiian polyclad, Stylochoplana inquilina with commensal habits. Bernice P. Biship Mus. Occasional papers 20 (4): 55-58.

——————— 1951. *The Invertebrates II Platyhelminthes and Rhynchocoela*. McGraw Hill, New York.

——————— 1967. *The Invertebrates VII Mollusca I*. McGraw Hill, New York.

Johnson, S.E. 1968. Occurrence and behaviour of *Hyale grandicornis* a gammarid amphipod commensal in the genus *Acmaea*. *Veliger* *11* (Supplement): 56-60.

Kato, K., 1934. Polyclad turbellarians from the neighbourhood of the Mitsui Institute of Marine Biology. *Japan Jour*. *Zool*. *6* (1): 123-138.

——————— 1935. *Stylechoplana parasitica* sp. nov., a polyclad parasitic in the pallial groove of the chiton. *Annot*. *Zool. Japan* *15* (1): 123-127.

Knight-Jones, E.W. 1951. Gregariousness and some other aspects of the setting behaviour of *Spirorbis*. *J. mar. biol. Ass*. *U.K*. *30*: 201-222.

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

Korringa, P. 1951. The shell of *Ostrea edulis* as a habitat. *Arch. Nearl. Zool*. *10* (1): 32-152.

Lang, K. 1948. *Monographie der Harpacticiden*. 2 Vols.: 1-1683. H. Ohlsson, Lond.

Lim, K.H. and Williams, W.D. 1971. Ecology of *Austrochiltonia subtenuis* (Sayce) (Amphipoda, Hyalellidae). *Crustaceana* *20*: 19-24.

Nie, D. and Lue, K.S.Y. 1945. Studies on *Spathocyanus caridina* gen. et sp. nov. a suctorian attached to the antenna of a fresh water shrimp *Caridina* sp. *Sinensia* 16: 57-64.

Pelseneer, P. 1935. Essai d'ethologie zoologique d'apris l'etude de mollusques. Acad. Roy. Belg. Classe Sci. Publ. Fond. 1: 1-662.

Penrith, M.L. and Kensley, B.F. 1970. The constitution of the intertidal fauna of rocky shores of South West Africa. Pt. 1. Lüderitzbucht. Cimbebasia A. 1 (9): 191-239.

Rees, F.G. 1934. Cercaria patellae Lebour, 1911, and its effects on the digestive glands and gonads of Patella vulgata. Proc. Zool. Soc. London. 45: 45-53.

Smith, E.H. 1961. A new commensal polyclad from Panama. Veliger 4 (2): 69-71.

Spooner, G.M. 1957. Order Amphipoda. pp 207-234 in: Marine Biological Association. Plymouth Marine Fauna, 3rd Edition.

Stephenson, T.A. 1939. The constitution of the intertidal fauna and flora of South Africa. Pt. 1. J. Linn. Soc. Zool. 40: 487-536.

Thomas, M.L.H. 1965. Observations on the occurrence of Cercaria patellae Lebour in Patella vulgata L. on the Inner Farne. Trans. nat. hist. Soc. Northumberland. 15: 140-146.

Underwood, A.J. 1972. Sinusoidal tide models: design, construction and laboratory performance. J. exp. mar. Biol. Ecol. 8: 101-111.

Vader, W. 1972. Associations between amphipods and molluscs. A review of published records. Sarsia 48: 13-18.

Wells, J.B.J. 1967. The littoral copepods (Crustacea) of Inhaca Island, Mocambique. Trans. Roy. Soc. Edinb. 67 (7): 189-358.

# SECTION X:

# *SCUTELLIDIUM PATELLARUM* NOV. SP., A HARPACTICOID COPEPOD ASSOCIATED WITH *PATELLA* SPP. IN SOUTH AFRICA, AND A DESCRIPTION OF ITS LARVAL DEVELOPMENT.

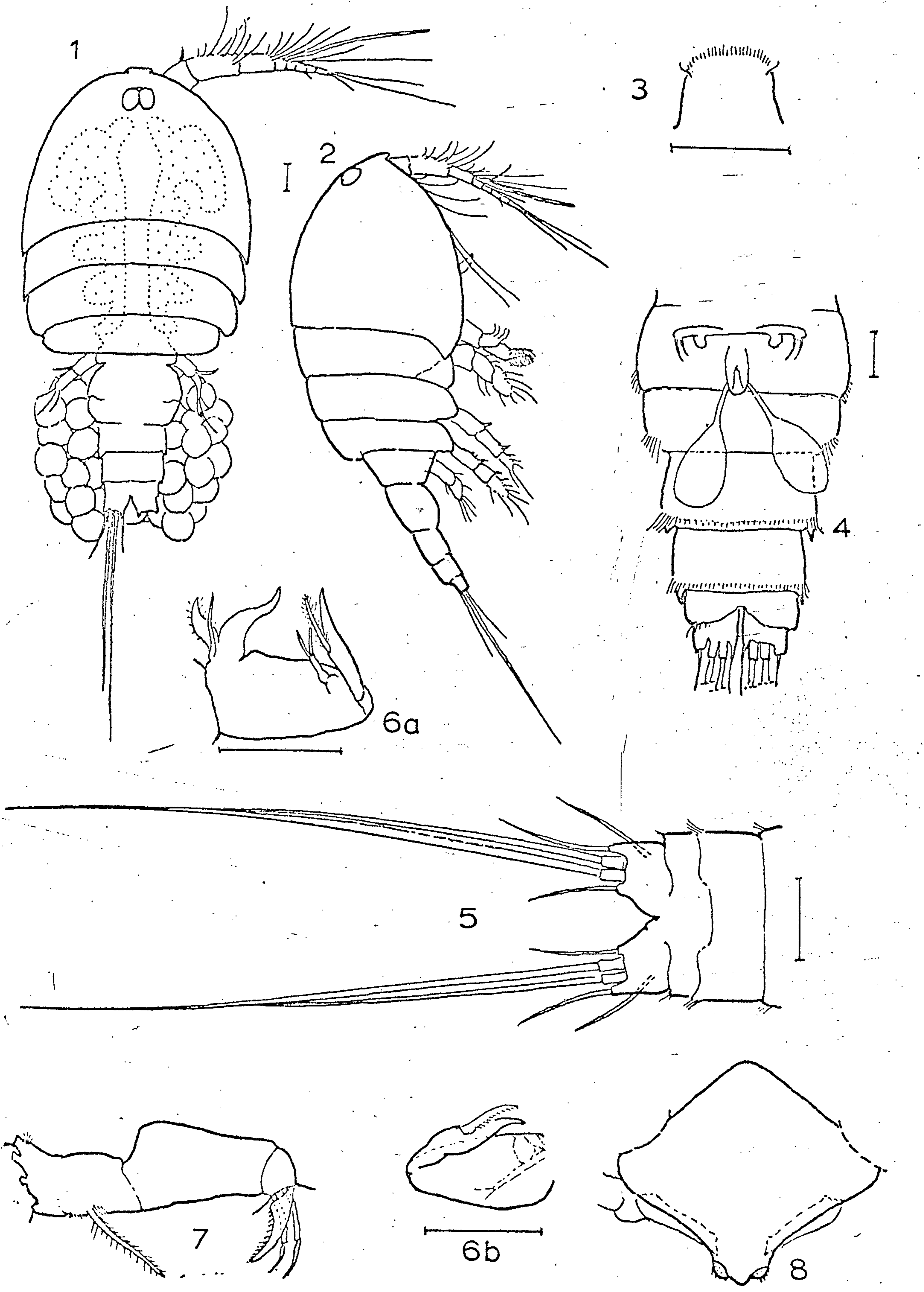
# SCUTELLIDIUM PATELLARUM nov. sp., a harpacticoid copepod associated with Patella spp. in South Africa, and a description of its larval development.

During investigations on the biology of Patella in South Africa, large numbers of a new species of Scutellidium Claus 1866 were found in association with the limpets. This is described below as Scutellidium patellarum nov.sp. All stages of larval development were also found associated with the limpets, and a description of the nauplii and copepodites is given.

The copepods were found predominantly associated with Patella argenvillei and P. cochlear, although smaller numbers also occurred with P. tabularis, P. barbara and P. longicosta. In the first two cases, respectively 80% and 45% of the limpets harboured copepods, with as many as 160 per limpet. The copepods were restricted to the pallial cavity, moving between the gills and over the foot.

Despite intensive examination of other possible hosts in the vicinity (including other limpets such as Helcion spp. and Siphonaria spp.) the copepods were only found on Patella spp. with the exception of a single free living specimen.

No other members of the genus have previously been found associated with other animals, (although Lang [1948] mentions the probably accidental occurence of S. hippolytes on the head of Hippolytes aculeata). This is surprising in view of the several species of the closely related genera Tisbe Lilljeborg, and Sacodiscus Wilson, found associated with a wide variety of animals. These are described or listed



Figs. 1-8 Adult♀

1. Dorsal; 2. Lateral; 3. Rostrum; 4. Urosome with two attached spermatophores. Ventral; 5. Furcae and posterior abdominal segments. Dorsal; 6a. Maxilla 2; 6b. Alternate view of maxilla 2 with twisted basis; 7. Maxilliped; 8. Labrum. (Scales indicate 50μ).

16°C, and fed shavings of dry Ecklonia maxima and small amounts of wet seaweed. These remained alive for three weeks, during which time the nauplii emerged and completed two moults.

| | | |
|---|---|---|
| Abbreviations: | $A_1$, $A_2$ : | Antenna 1, Antenna 2. |
| | End. : | Endopodite |
| | Exp. : | Exopodite |
| | $P_1$-5 : | Swimming legs 1 to 5 |
| | Se,Si,St : | External, internal & terminal setae. |
| | CI-V : | Copepodite stages I to V |
| | NI-VI : | Naupliar stages I to VI. |

In expressing setal formulae, spines are distinguished by Roman numbers and setae by Arabic.

## DESCRIPTION:

### Scutellidium patellarum nov.sp.

### Female:

Live specimens suffused with a red colour over the whole body. Showing through the cuticle, the digestive gland forms a darker brown lobular pattern (fig. 1). Eyes bright red. All red colouration disappears in preserved material.

Length from rostrum to end of candal rami 0.750 mm., greatest width 0.420 mm (Range 0.910-0.721 x 0.460-0.410, based on 25 specimens). Relative lengths of the somites listed in table 1.

Prosoma oval but truncated posteriorly, flattened and markedly wider than urosome (figs. 1 and 2). Somite bearing leg 1 fused indistinguishably to head, and clypeiform. Posterior corners of first two somites forming acutely pointed single long naked seta (72$\mu$); subterminally there are two setose setae and a series of spinules. Outer margin indented midway along its length, where a naked seta arises, and with a proximal fringe of setules.

$P_6$ (fig. 21) arising from the genital segment as a conical protuberance with one flattened setulose seta and two smaller naked setae.

Larval Stages:

Nauplius I: Body almost round, 125 x 119$\mu$, very flattened (fig.23) and with a large ventral sucker. The sucker consists of a basal chitinous disc attached to the sternum from which arises a thin membrane forming a complete circular sucker and overlapping anteriorly (fig. 22). The membrane is supported by radiating chitinous rays, between which the membrane stretches. Where the rays end, five marginal setae radiate outward, extending the effective width of the membrane. Two posterior tufts of setae extend back. Suction is effected by retraction of a pair of soft central sacs creating a partial vacuum.

Urosome represented only by three posterior lobes (figs. 23 and 27) lined with strong setae. A pair of very long ventral setae project posteriorly.

$A_1$ (fig. 24) indistinctly 3 segmented, segment 1 with an anterior hairy seta and a setule, and a long posterior seta. Segment 2 with an anterior tuft of setules and a long posterior seta. Three setae on the terminal segment.

$A_2$ (fig. 25) with a 3 segmented exopod bearing four setae. Endopod with a strong terminal raptorial claw and two setules, and two setae midway along its length. One of the latter setae

TABLE 1:

| | | Head & somite of leg 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ♀ | Length μ | 213 | 107 | 80 | 63 | 62 | 107 | | 52 | 37 | 15 | |
| | Relative length | 28.9 | 14.6 | 10.9 | 8.6 | 8.5 | 14.6 | | 7.2 | 4.7 | 2.0 | = 100 |
| ♂ | Length μ | 165 | 90 | 75 | 60 | 52 | 75 | 30 | 34 | 34 | 15 | |
| | Relative length | 26.2 | 14.3 | 11.9 | 9.5 | 8.2 | 11.9 | 4.8 | 5.4 | 5.4 | 2.4 | = 100 |

epimera, while those of somites 3 and 4 are rounded. Somite 4 slightly excavate posteriorly and partly housing somite 5 which is abruptly narrower than the preceding somites. The genital "double segment" (taken here as two fused segments) is slightly swollen and divided ventrally, laterally and dorso-laterally by a furrowed groove (fig. 4). The subsequent three somites constitute the tapering abdomen. Furcae wider than long, 28 x 38 , narrowing distally, and bearing two very long terminal pedicillate setae (500μ and 411μ), two short terminal setae, and a single ventro-lateral seta (fig. 5).

Prosoma naked. Genital segment with lateral tufts of setules arising from the posterior margin of the segment and from the transverse groove. Similar tufts on the subsequent three segments, extending as a row of spinules across the posterior ventral margin of segments 8 and 9 (fig. 4).

Genital field (fig. 4) with a central gonopore terminating a muscular flexed structure, onto which the spermatophores are attached by the male. Anterior to this is a transverse chitinous bar with lobes bearing two setae at either end. These setae are presumably the rudiments of $P_6$.

Rostrum rounded, 41μ x 47μ with a distal fringe of setule, flanked at either end by a slightly longer setule (fig. 3).

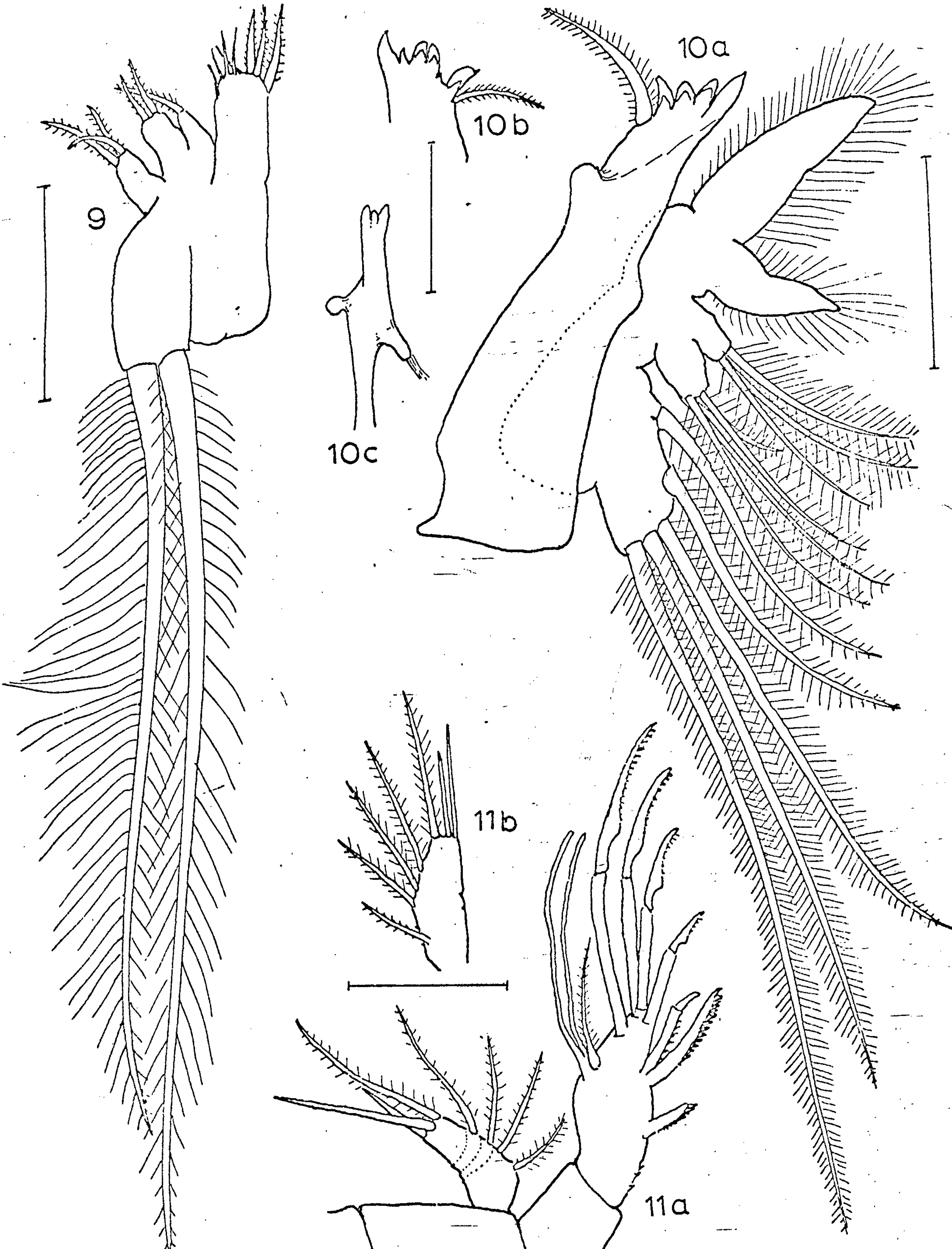
A single egg sac attached ventrally, containing 10 to 44 white eggs, each about 82μ in diameter.

$A_1$ 9-segmented (fig. 12). Armature and relative lengths of the podomeres given in table II. All setae naked; a single aesthetasc arising from the fourth podomere.

TABLE II:

Details of $A_1$

| Podomeres: | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | Total |
|---|---|---|---|---|---|---|---|---|---|---|
| Length μ | 53 | 79 | 42 | 15 | 11 | 7.6 | 7.6 | 13 | 19 | 248 |
| Rel. length | 21.3 | 32.0 | 16.8 | 6.2 | 4.6 | 3.0 | 3.0 | 5.4 | 7.7 | 100 |
| Setae | 1 | 12 | 10 | 3+A | 0 | 0 | 2 | 1 | 4 | 34 |
| Length μ | 36 | 91 | 30 | 38 | 15 | 27 | 8 | 23 |  | 268 |
| Rel. length | 13.4 | 33.9 | 11.2 | 14.2 | 5.6 | 10.0 | 3.0 | 8.7 |  | 100 |
| Setae | 1 | 9 | 4 | 5+A | 3 | 2 | 1 | 4 |  | 30 |



Figs. 9-11 Adult♀

9. Maxilla 1; 10a Mandible; 10b,c. Different views of manditular cutting edge; 11a. Antenna 2; 11b. Antenna 2 exopod from another specimen (note lack of segmentation). (Scales indicate 50μ).

$A_2$ very similar to that of S. arthuri (see Lang 1965). Basipodite bearing a single hairy seta; first endopodal segment without setae, second with setae as indicated in fig. 11a. The exopodite is unusual in that the four segments are not clearly defined, and in some specimens (see fig. 11b) cannot be distinguished at all. The setal arrangement of the exopod is 2, 1, 1, 3; two of the terminal setae are naked, the others hairy; slight differences may occur in the relative lengths of these setae (see figs. 11a and 11b).

Mandible and maxilla 1 as in figures 9 and 10a, b, c, very similar to those of S. arthuri. Labrum roughly parallelogram shaped (fig. 8) with a tapering posterior lip flanked by a patch of fine setules on either side. Maxilla 2 (fig. 6a) with a single-segmented syncoxa bearing a stout basis which merges terminally into a stout claw and carries a setose spine. Syncoxa with a basal endite consisting of two broad lobes and a seta, and a single-segmented distal endite with two naked setae. Frequently the basis is twisted and the endites concealed (fig. 6b).

Maxilliped (fig. 7) 3 segmented, the middle segment with a markedly expanded anterior margin. The basal segment with a long seta, and the terminal segment with a stout toothed claw, two jointed setae and two setules.

The relative lengths and setal formulae of $P_1$ - $P_4$ are given in tables III and IV.

The basipodite of $P_1$ (fig. 13a) comprises two partly fused segments, the first apparently bearing the extremely broad outer seta, and the second a smaller inner seta, flanked by a row of spinules. Segment 2 and 3 of $P_1$ exp. are difficult

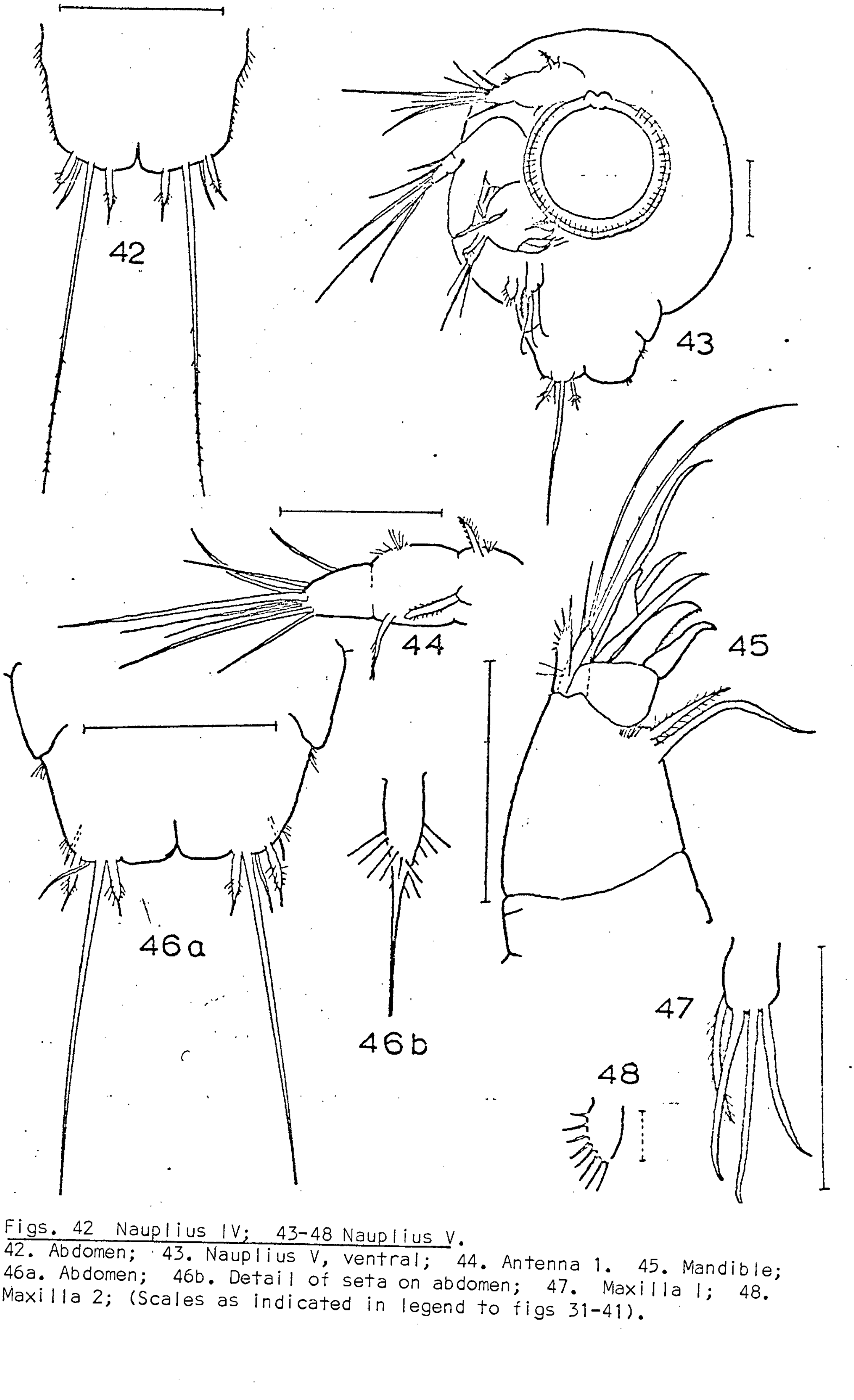
TABLE III : Setal formulae of $P_1 - 4$.

| | Basipodite | | Exopodite | | | | | Endopodite | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 1 | 2 | 3 | | | 1 | 2 | 3 | | |
| | Se Si | Se Si | Se Si | Se Si | Se | St | Si | Se Si | Se Si | Se | St | Si |
| $P_1$ | 1 : 0 | 0 : 1 | 1 : 0 | 1 : 1 | II | II | 2 | 0 : 1 | 0 : 1 | 1 | II | 0 |
| $P_2$ | 0 : 0 | 1 : 0 | 1 : 1 | 1 : 1 | 3 | 1 | 2 | 0 : 1 | 0 : 2 | 2 | 2 | 1 |
| $P_3$ | 0 : 0 | 1 : 0 | 1 : 1 | 1 : 1 | IV | 1 | 3 | 0 : 1 | 0 : 2 | 1 | 2 | 3 |
| $P_4$ | 0 : 0 | 1 : 0 | 1 : 1 | 1 : 1 | IV | 1 | 3 | 0 : 1 | 0 : 2 | 1 | 2 | 2 |

setiform spines

TABLE IV Relative lengths of $P_1 - 4$ podomeres ($\mu$)

| | Endopodite | | | | Exopodite | | | |
|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | Total | 1 | 2 | 3 | Total |
| $P_1$ | 95 | 57 | 11 | 173 | 68 | 28 | 6 | 108 |
| $P_2$ | 57 | 57 | 42 | 156 | 53 | 27 | 34 | 114 |
| $P_3$ | 57 | 61 | 53 | 171 | 41 | 42 | 62 | 147 |
| $P_4$ | 30 | 53 | 46 | 131 | 38 | 53 | 68 | 159 |



Figs. 42 Nauplius IV; 43-48 Nauplius V.
42. Abdomen; 43. Nauplius V, ventral; 44. Antenna 1. 45. Mandible; 46a. Abdomen; 46b. Detail of seta on abdomen; 47. Maxilla I; 48. Maxilla 2; (Scales as indicated in legend to figs 31-41).

is stout and distally setose ("tufted"). Basipodite with a stout protuberance bearing two setae, one of which is tufted. Epipodite with a broad flattened seta and a narrower curved seta with distal hairs.

Mandible (fig. 26) with 4 segmented exopod, terminally bearing a very long seta (98µ) which is sparsely setose. The basal exopod segment with a stout strangely tufted seta, and the third segment with a setule. Endopod with two stout toothed claws and three long setae. Basipodite oval with an inner spinulose seta.

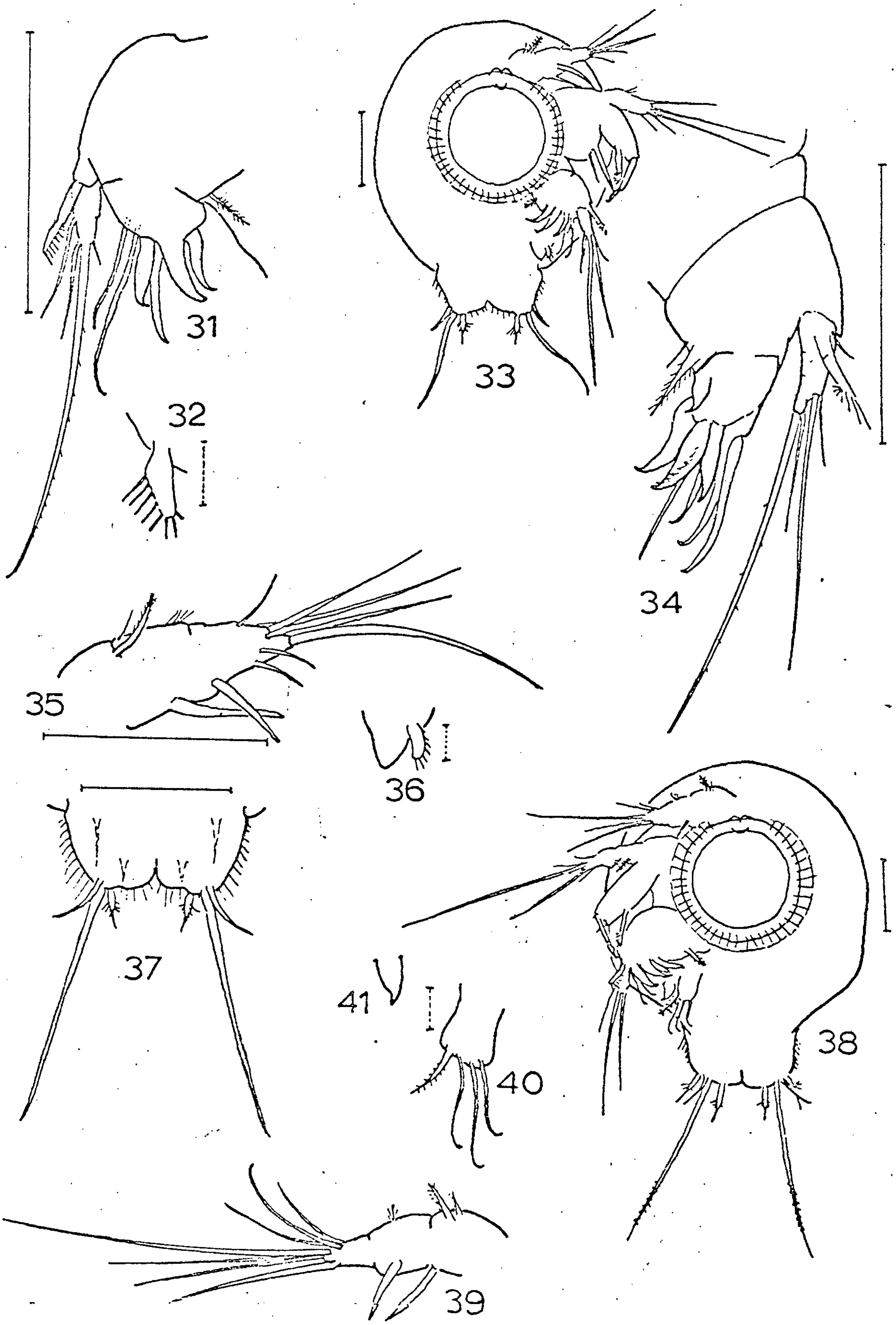
Dorsally the prosoma bears a single median naupliar eye, comprising a diffuse series of bright red pigment spots. The body is red like the adult, but much paler.

Nauplius II: Oval but tapering posteriorly (fig. 28), 145µ x 124µ. (Range 130-155 x 118-132, based on 5 specimens.) Urosome (fig. 30) with two ventral setae projecting further, remaining setae shorter than in NI. $A_1$ (fig. 29) with an additional subterminal setule. $A_2$ as in NI. Mandible exopod with two additional setae, and the terminal seta much shortened; endopod now with three claws and three long rigid setae; basipodite with a slender hairy seta (fig. 31). Maxilla 1 appearing as a pair of spinose processes (fig. 32), one on either side of the urosome (fig. 28).

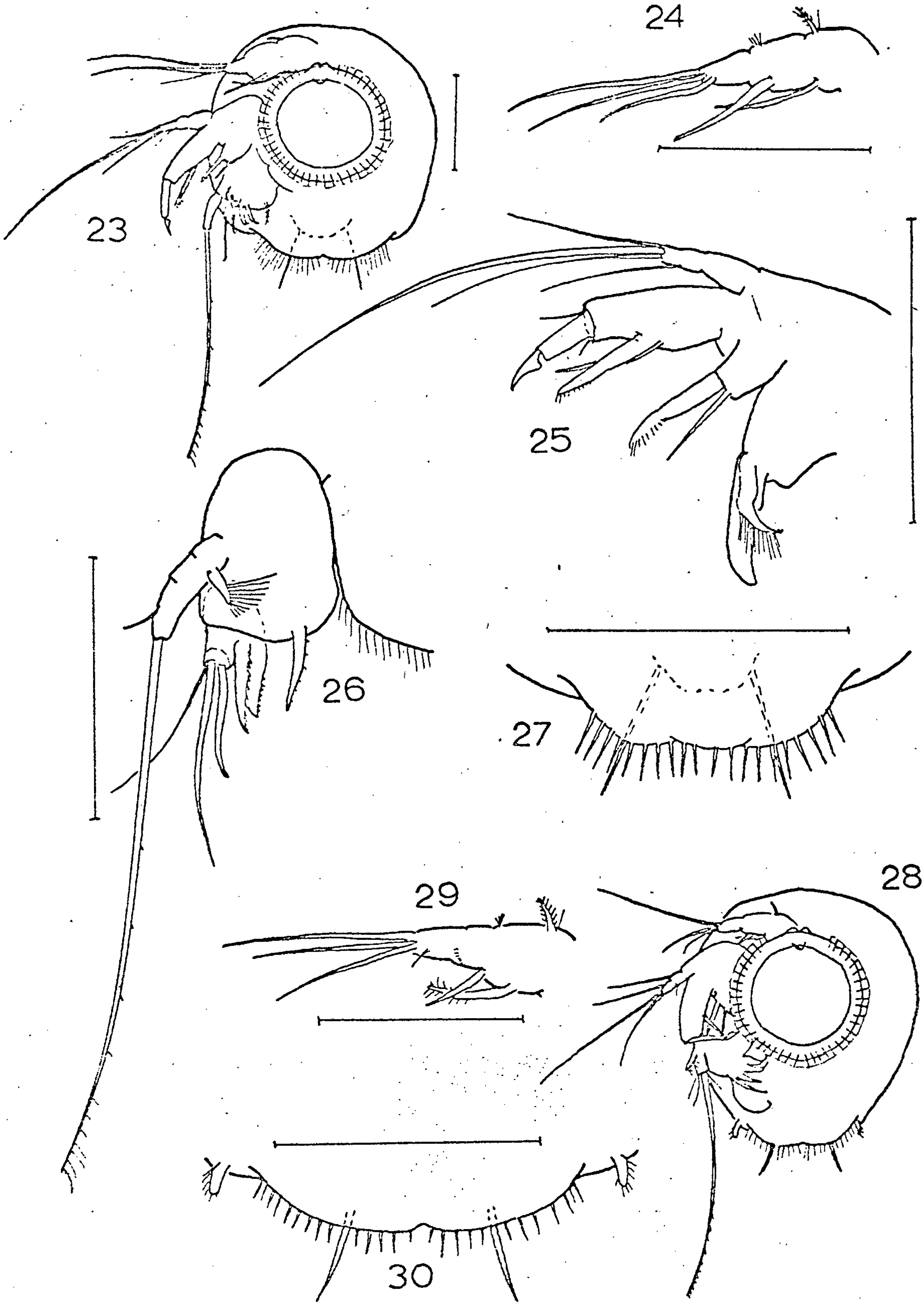
Nauplius III: Oval prosoma with unsegmented urosome projecting posteriorly (fig. 33). 181µ x 153µ. (Range 153-195 x 143-160, based on 12 specimens.) Urosome a bilobed structure (fig. 37) fringed with fine setules, each lobe with a long seta and two short setae, one of which is hairy. $A_1$ (fig. 35) now with four long and three short setae on the last segment. $A_2$ as in NI, but the flattened seta of the epipodite now has a row of setules on it, and the exopod carries five setae. Mandible (fig. 34) similar to NII but basipodite divisible into two segments and with two setae arising from it; exopod with an additional basal setule; endopod with four claws and four long rigid setae. (The basal fourth claw is not apparent in subsequent stages, but is probably masked by the other three.) Maxilla 1 forms a triangular lobe (fig. 36) with a setose appendage.

Nauplius IV: General shape as in NIII but larger and elongated: 203µ x 172µ. (Range 188-207 x 163-178, based on 12 specimens.) Urosome (fig. 42) similar to that of NIII but longer, lacking the posterior fringing setules, and with an additional hairy seta. $A_1$ (fig. 39) with an additional setule on the basal segment and seven long setae on the terminal segment. $A_2$ as in NIII. Mandible unchanged except for an elongated basipodite. Maxilla 1 (fig. 40) now forming a rounded knob from which project three rigid hooked setae and a shorter hairy seta. Maxilla 2 appears external to maxilla 1 (fig. 38) as a roughly triangular lobe (fig. 41).

Nauplius V: Round prosoma, with urosome projecting (fig. 43). 218µ x 185µ. (Range 208-236 x 173-199 based on 15 specimens.) Urosome (fig. 46a) two segmented, with two lateral tufts of setules and an additional ventral seta. The structure of the short urosomal setae is now clearly apparent (fig. 46b) and comprises a sharply tapering shaft with two helical rows of setules spiralling down the shaft. $A_1$ (fig. 44) now with 8 terminal setae. $A_2$ as in NVI but with only six exopodial setae. Mandible (fig. 45) more elongate and the basipodite with two large setae, otherwise as in NIII. Maxilla 1 (fig. 47) similar to NIV but setae longer. Maxilla 2 (fig. 48) now spinulose along



Figs. 31-32 Nauplius II; 33-37 Nauplius III; 38-41 Nauplius IV.
31. Mandible; 32. Maxilla 1; 33. Nauplius III, ventral; 34. Mandible; 35. Antennal; 36. Maxilla 1; 37. Abdomen; 38. Nauplius IV, ventral; 39. Antenna 1; 40. Maxilla 1; 41. Maxilla 2. (Scales with unbroken lines represent 50μ, scales with broken lines represent 10μ).



Figs. 23-27 Nauplius I; 28-30 Nauplius II.
23. Nauplius I, ventral; 24. Antenna 1; 25. Antenna 2; 26. Mandible; 27. Abdomen; 28. Nauplius II, bentral; 29. Antenna 1; 30. Abdomen. (Scales indicate 50μ).

22

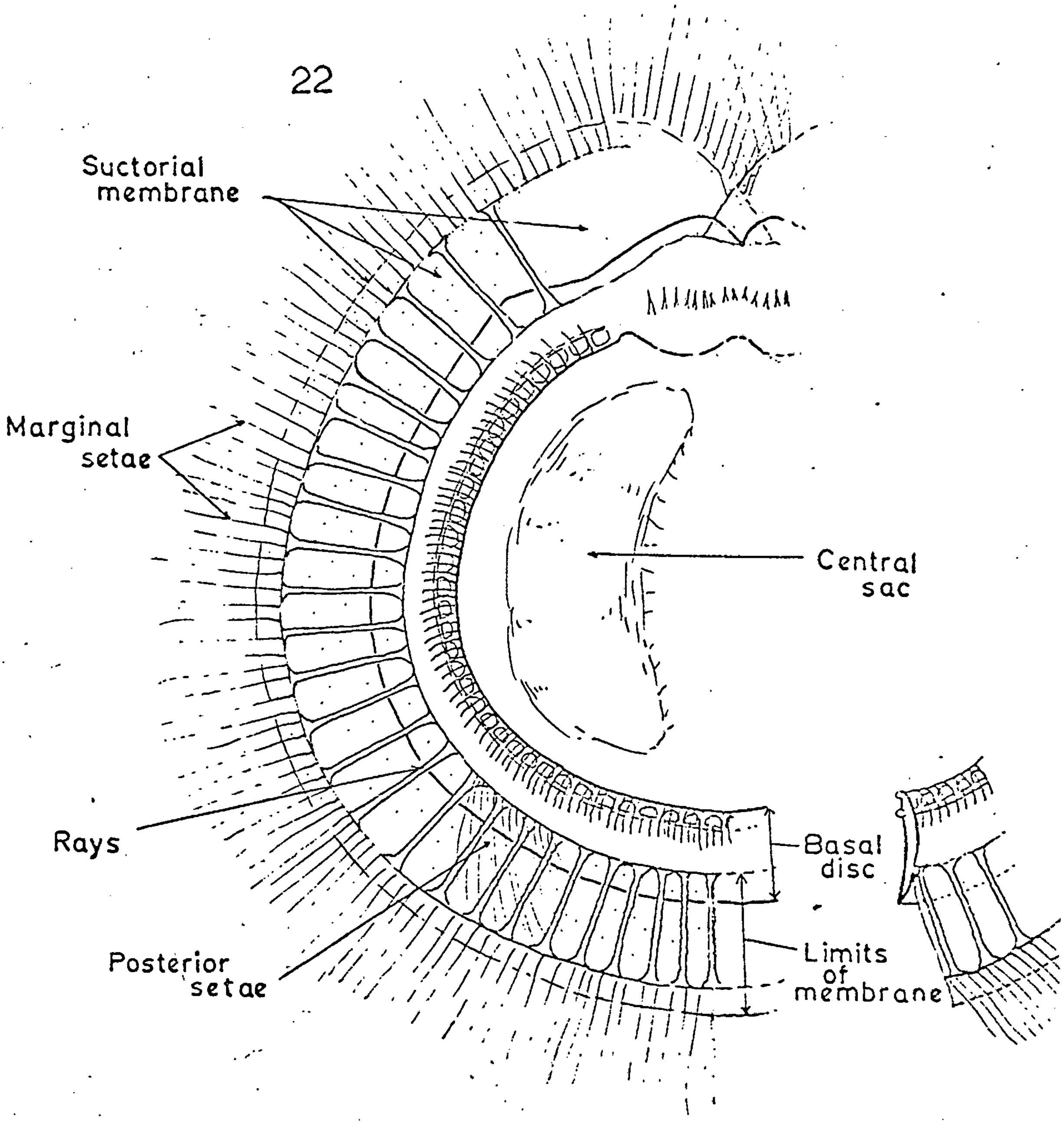


Fig. 22. Detail of the left half of Nauplier sucker, ventral. (A small section also given in stereoscopic view).

the outer margin and the proximal part of the inner margin. The exopodite measures 95$\mu$ ~~and~~ by 38$\mu$ (the length 2.5 x the width) and is armed with a simple seta at its midline, two terminal and two subterminal setae. The inner margin has five parallel rows of setules (only visible at certain angles).

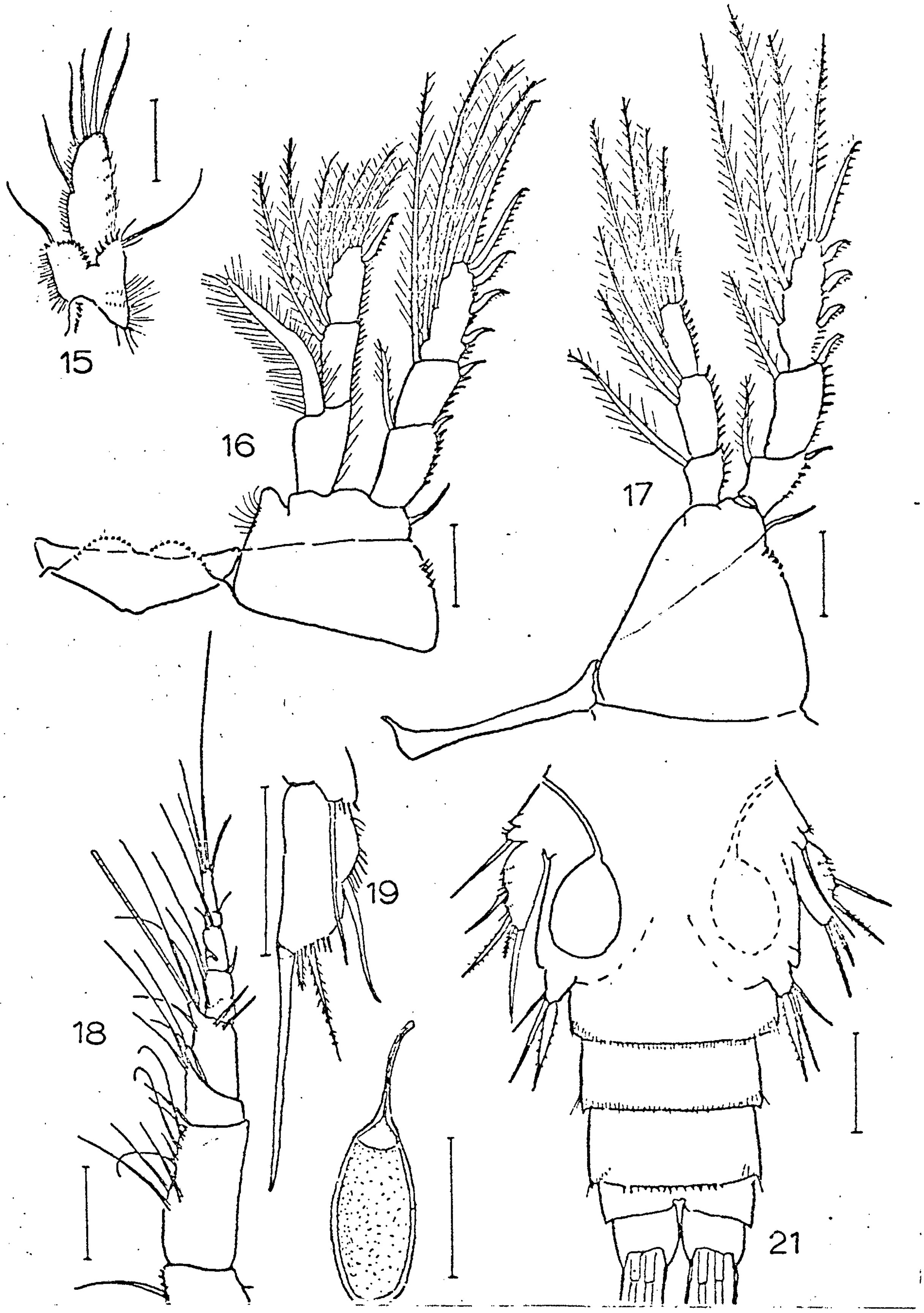
Male:

Very similar to the female in general body shape and ornamentation, but slightly smaller, 630$\mu$ x 340$\mu$. (Range 720-601 x 392-315 based on 10 specimens.) See table I for somite lengths. Genital segment (fig. 21) less swollen than in female, but wider than subsequent four abdominal segments. Two oval spermatophores housed in the genital segment, with ducts opening laterally on the preceding segment. Body of spermatophore filled with an opaque spermatic mass while the neck contains a hyaline material (fig. 20).

Apart from $A_1$, $P_5$ and $P_6$, the limbs are identical to those of the female.

$A_1$ (fig. 18) 8 segmented, with segment 5 partly divided. Basal segment more geniculate than in the female, segment 6 transversely grooved, and the relative lengths and armature of the segments differing from those of the female (see table II). Segments 3 and 4 are produced into cones bearing setae and the aesthetasc. The antenna is bent forward between segment 4, 5 and 6, as opposed to that of the female which is bent back.

$P_5$ (fig. 19) baso-endopodite not as defined as in the female, the outer lobe obvious and bearing one long seta and a few spinules, the inner lobe indistinct. Exopodite 50$\mu$ x 21$\mu$, the inner margin almost straight, terminating in a



Figs. 15-17. Adult ♀; 18-21 Adult ♂
15. Fifth leg; 16. Third leg. 17. Fourth leg; 18. Antenna 1; 19. Fifth leg; 20. Spermatophore; 21. Urosome, including fifth and sixth legs. Ventral (Scales indicate 50μ).

to distinguish (fig. 13b, c) and carry the stout penicillate spines typical of the genus. As segment 3 is telescoped it is difficult to decide which setae are terminal. Segment 3 of the endopodite carries two terminal penicillate setae (fig. 13a, d).

$P_2$ (fig. 14) endopodite much larger than exopodite. Notable are the extremely large setiform spines arising from the basipodite and externally from the exopodite. These six spines measure respectively 121, 76, 65, 50, 65 and 61$\mu$. The basipodal spine is almost the length of the exopod and the other spines 1.5 to 2 x the length of the podomeres bearing them. These spines are one of the diagnostic characters of the species.

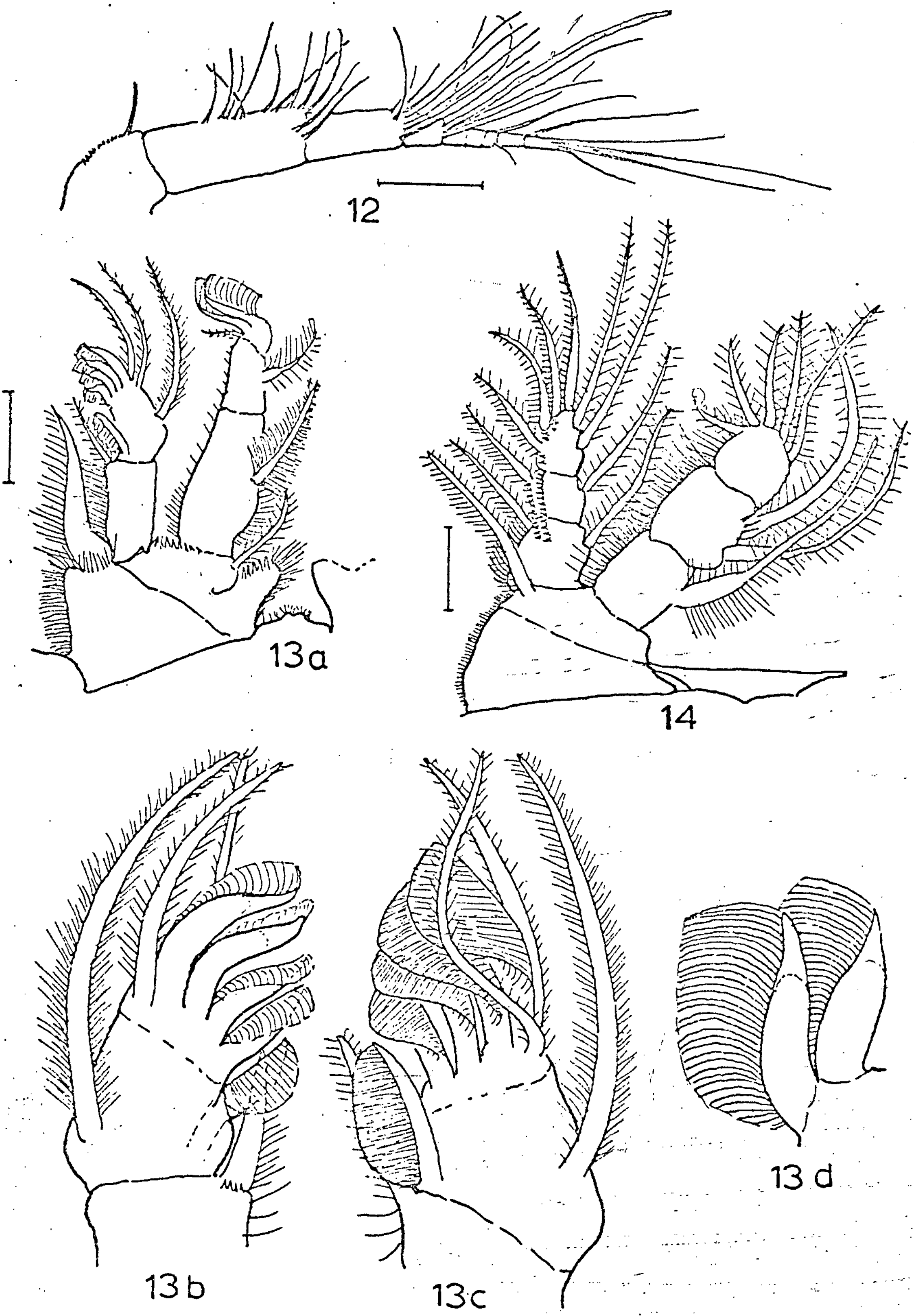
On the first two podomeres of the exopod there are two parallel rows of spinules, continuing as paired spinules between the spines of the third podomere. Outer margin of the first podomere armed with strong setules.

Seta on Endopodite segment 1 with a very swollen base. Three spinules at the base of seta 2 on endopodite segment 2. The radiating arrangement of setae on the terminal segment of the endopodite is typical of the species.

$P_3$ (fig. 16) similar to that of <u>S. arthuri</u> except for the extremely broad seta on endopodite segment 1 which is 2.5 x the width of the other setae on this limb. This also is a diagnostic feature of the species.

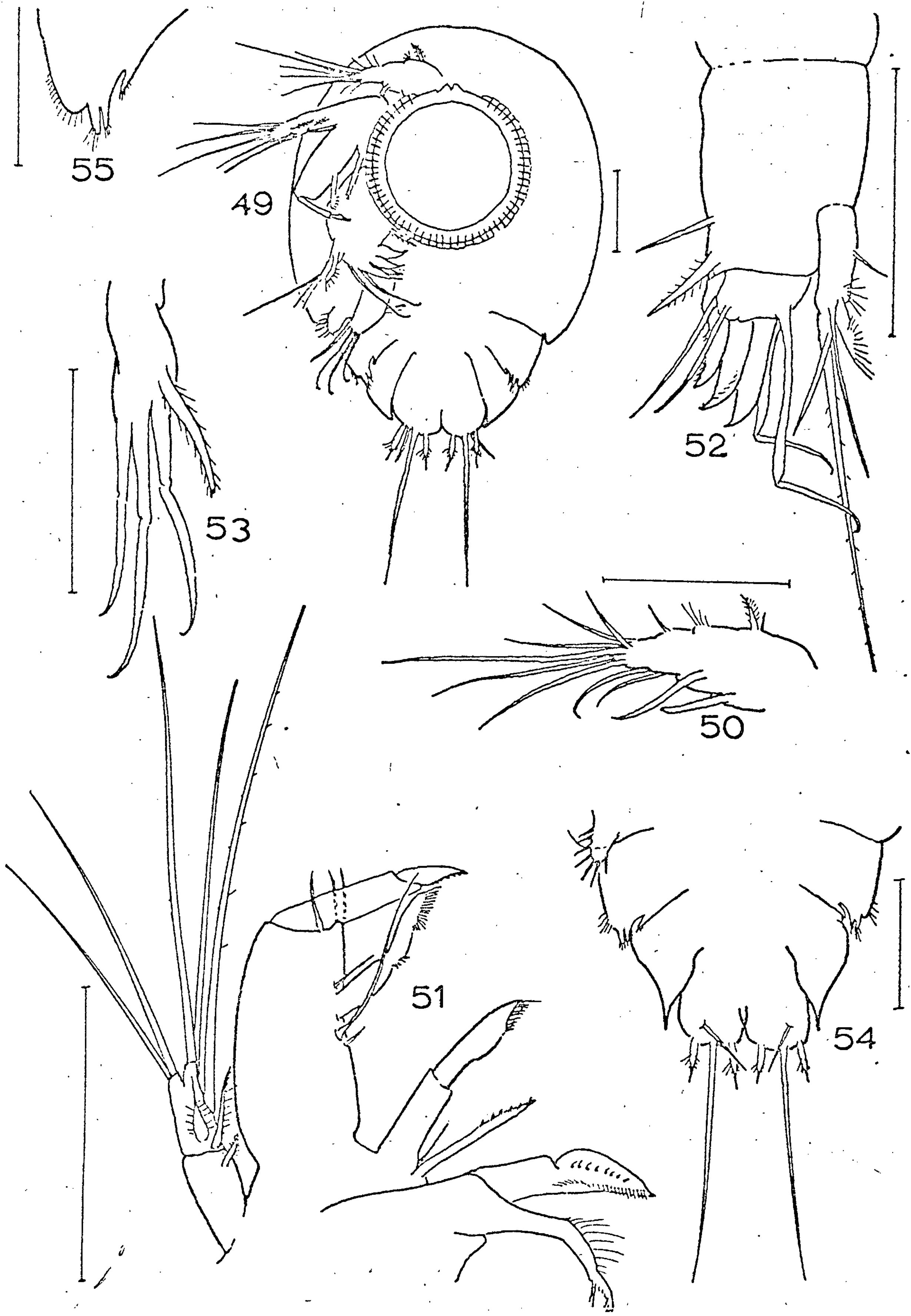
$P_4$ (fig. 17) similar to that of <u>S. arthuri</u> and <u>S. dentipes</u>.

$P_5$ (fig. 15) possesses a bilobed basoendopodite, both lobes being fringed with spinules and bearing a single long seta. The inner lobe also has a pair of short setules. Setules fringe



Figs. 12-14 Adult ♀

12. Antenna 1; 13a. First leg; 13b,c. Tip of first leg expod; 13d. Penicillate setae from tip of first leg endoped; 14. Second leg. (Scales indicate 50μ).



Figs. 49-55 Nauplius VI.

49. Nauplius VI, ventral; 50. Antenna 1; 51. Antenna 2; 52. Mandible; 53. Maxilla 1; 54. Abdomen, including maxilla 2 and rudiment of maxilliped, ventral; 55. Rudiment of maxilliped. Scales indicate 50µ).

the outer edge.

Nauplius VI: Body oval but tapering posteriorly (fig. 49). 247 x 193 . (Range 233-270 x 182-214 based on 14 specimens.) Urosome (fig. 54) 3 segmented, the first segment rounded laterally and produced into three hairy projections, presumably a rudiment of the maxilliped (fig. 55); second segment sharply pointed posteriorly; third segment bilobed and with four setae. $A_1$ with nine terminal setae (fig. 50). $A_2$ (fig. 51) larger, with five long setae and three short hairy setae; endopod stronger, with three terminal setae in addition to the strong raptorial claw, and four setae at the midpoint of the shaft; basipodite with a very strong jointed tufted seta, a sharp toothed spine and a short seta; epipodite extended into a flat curved hairy structure which is hooked terminally and supports a flattened broad seta with two rows of setules. Mandibles (fig.52) even longer; exopod with five setae and a row of setules; endopod as in NV but the longer setae usually bent sharply. Maxilla 1 elongated (fig. 53) and the naked setae constricted about one third from their bases. Maxilla 2 (fig. 54) hardly changed.

Copepodite I: Body very flattened and roughly oval in outline, with five somites. 0.290mm x 0.220mm (Range 0.288-0.305 x 0.216-0.229 based on 5 specimens). First leg bearing somite fused to head. Rostrum narrow at base and expanding distally to a sharply truncated margin with acute corners. Caudal furcae about as long as wide, setae as in adult but with a row of setules running across the base of the furca. $A_1$ (fig. 56) 5 segmented. $A_2$ (fig. 57) similar to that of the adult, except that the endopodite is one segmented, the proximal segment not yet divided from the basipodite, and there are only three raptorial claws and one toothed claw on the endopod.

Labrum, mandibles maxilla 1 and 2, and maxilliped practically identical with those of the adult (as is true for all subsequent copepodite stages).

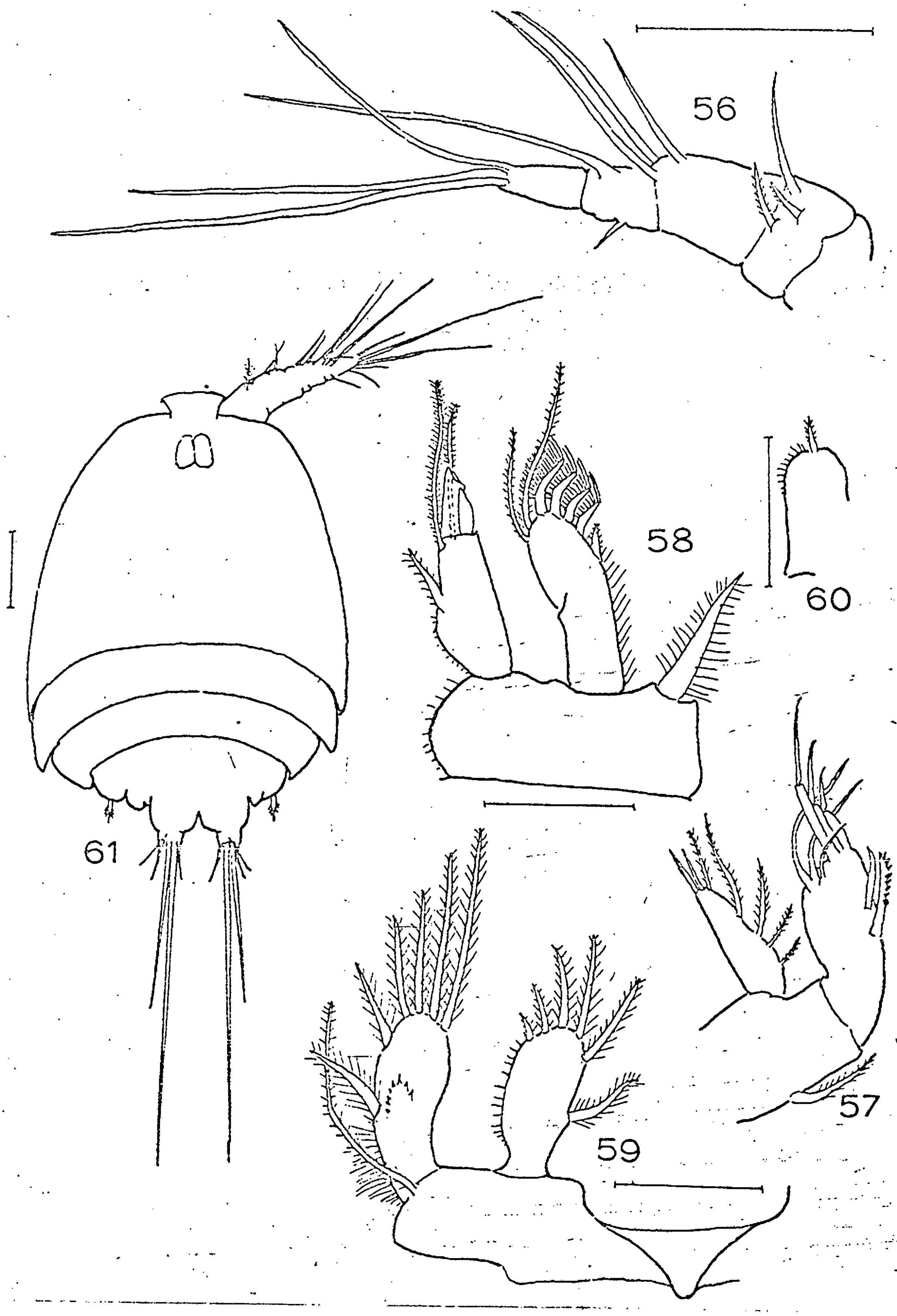
Leg 1 with both rami one segmented. Endopod rather different from that os subsequent stages, being shorter than the exopod, and terminating in two blunt claws (which have not yet developed the penicillate structure typical of the genus) and two long setae. One of the latter is lost in the next stage and does not reappear: an unusual condition in copopodite development.

Both rami of leg 2 (fig. 59) also one segmented, the seta arising from the basipodite already characteristically large. The rudiment of leg 3 forming a rounded flap with a single seta (fig. 60).

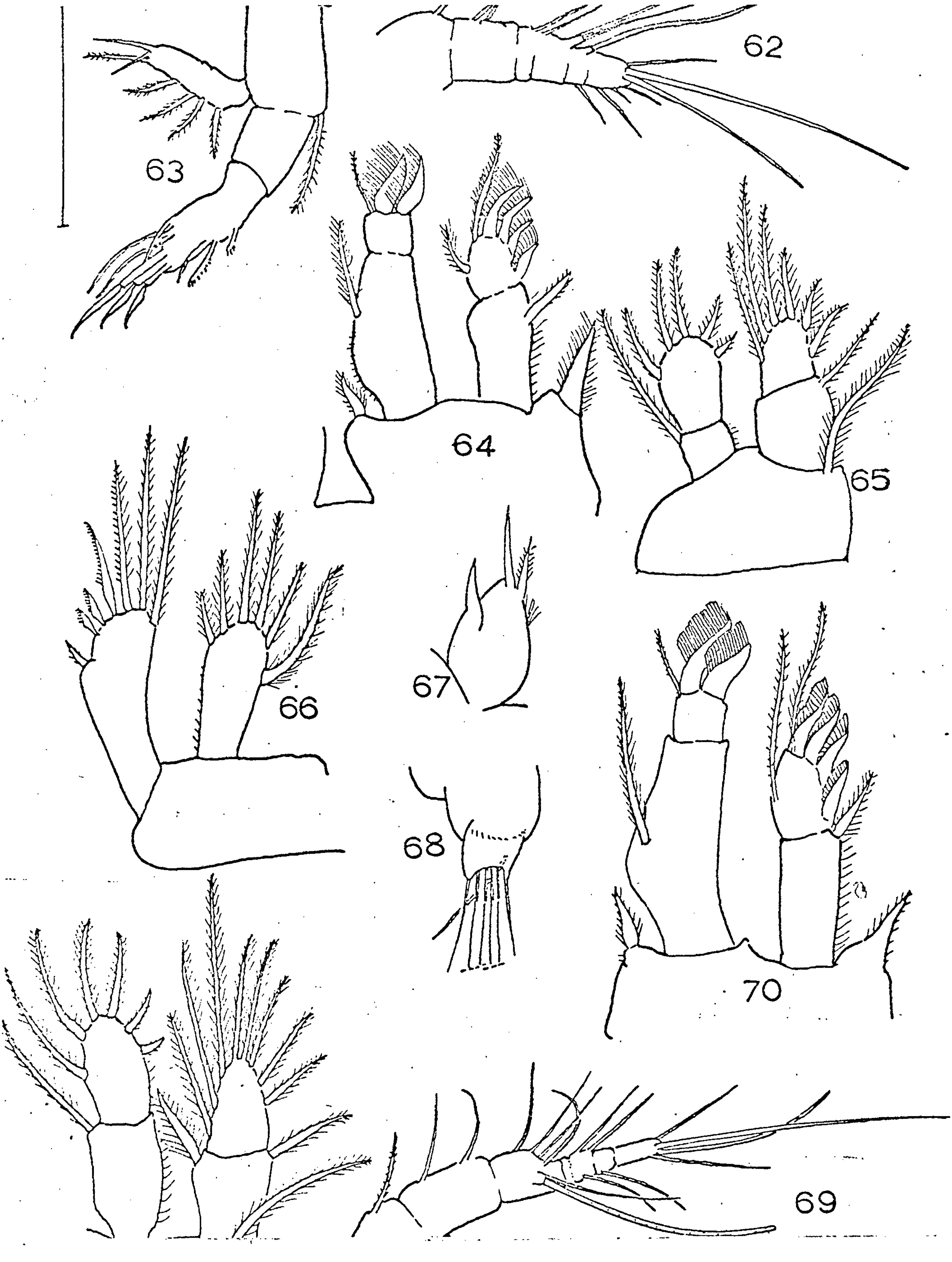
Copepodite II: Body 6 segmented. Shape as in CI, with a similar rostrum (fig. 61). 0.310mm x 0.225mm (range 0.302-0.325 x 0.217-0.240, based on 9 specimens). Somite 6 forming a bilobed structure, each lobe bearing a furca essentially like that of CI (fig. 68).

$A_1$ (fig. 62) 6 segmented. $A_2$ endopodite now comprising two podomeres and armed with an additional toothed seta; exopod showing slight traces of segmentation. This structure is maintained until CV.

Rami of legs 1 and 2 now two segmented (figs. 64 and 65)



Figs. 56-60 Copepodite I, 61 Copepodite II.
56. Antenna 1; 57. Antenna 2; 58. First leg; 59. Second leg; 60. Rudiment of third leg. 61. Copepodite II, dorsal. (Scales indicate 50μ).



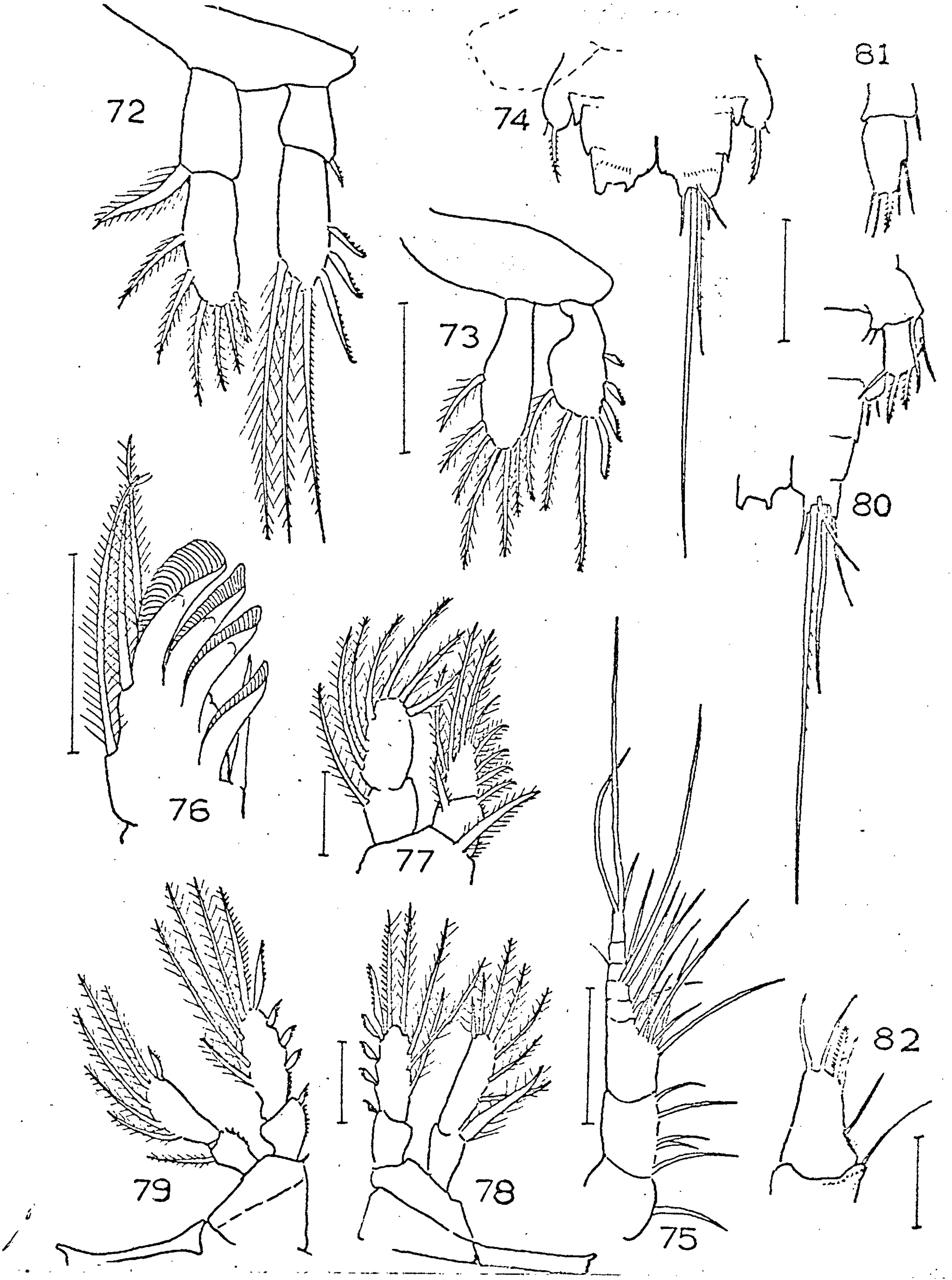
Figs. 62-68 Copepodite II;  69-71 Copepodite III

62. Antenna 1;  63. Antenna 2;  64. First leg;  65. Second leg.  66. Third leg;  67. Rudiment of fourth leg;  71. Second leg; (Scales indicate 50µ, that for fig. 63 in top left hand corner, that for figs. 64-71 at bottom of plate).

In all the legs, the division of the original podomere into two occurs distad of the basal external seta, so that this remains on the proximal podomere after division. Endopodite of leg 1 now longer than exopod and terminated by two penicillate claws. Leg 3 (fig. 66) with 1 segmented rami. An oval flap with three setae forming the rudiment of leg 4 (fig. 67).

<u>Copepodite III</u>: Body 7 segmented with one abdominal segment apparent. 0.443mm x 0.301mm. (Range 0.406-0.582 x 0.229-0.390 based on 15 specimens.) Body oval, but with urosome (fig. 74) projecting posteriorly. Furcae as in CI, but one seta now spinose. Rostrum still expanding outwards from a narrower base, but with rounded corners.

$A_1$ (fig. 69) 7 segmented, aesthetasc now apparent and born on the third segment. Rami of legs 1 to 3 with two podomeres (figs. 70, 71, 72). Leg 3 endopod with the characteristic broad seta now distinguishable on the basal podomere. Rami of leg 4 each comprising a single podomere (fig. 73). Rudiment of leg 5 forming a rounded lobe with one seta, and projecting from under the margin of somite 4 (fig. 74).



Figs. 72-74 Copepodite III; 75-81 Copepodite IV; 82 Copepodite V. 72. Third leg; 73. Fourth leg; 74. Urosome and fifth leg, dorsal (fourth somite dotted in); 75. Antenna 1; 76. Tip of first leg expod; 77. Second leg; 78. Third leg; 79. Fourth leg; 80. ♂Urosome and fifth and sixth legs, ventral; 81. ♀Fifth leg. 82. ♀Fifth leg.

Copepodite IV: Body with 8 somites, including two abdominal somites. Male and female now distinguishable in size and minor morphological features. ♀ : 0.589mm x 0.371mm (range 0.512-0.721 x 0.301-0.442 based on 23 specimens); ♂: 0.568mm x 0.357mm (range 0.556-0.596 x 0.342-0.369 based on 4 specimens). Body more like that of the adult, but urosome shorter and proportionately wider (fig. 80). Rostrum rounded and with setules as in the adult. The furcae have now lost the row of setules. $A_1$ 8-segmented in both sexes, but with podomere 3 wider in the male (fig. 75) than the female.

Legs 1 to 4 with two segments to both rami (figs. 76 to 79). Leg 5 well developed; in the male the basoendopodite has a very long outer seta and two short inner setules, and the exopod bears two naked and two hairy setae (fig. 80). The female differs in having only a short seta on the outer lobe of the basoendopodite, while the exopod carries five setae, one of which is hairy (fig. 81). Leg 6 is apparent in both sexes as a conical protuberance with two naked setae (fig. 80).

Copepod V: No males of this stage could be found. Female with 9 body somites (3 abdominal) and almost identical to the adult. 0.704mm x 0.422mm (range 0.671-0.721 x 0.398-0.441 based on 3 specimens).

Identical to the adult in most respects, including $A_2$, all the mouthparts, legs 1 to 4 and the caudal furcae. $A_1$ 9-segmented but podomeres 2 and 3 slightly shorter than in the adult. Leg 5 (fig. 82) lacking well developed lobes to the basoendopodite, which has only a single outer seta; exopod tapering distally and giving rise to five setae, one of which is hairy.

# TABLE V COPEPODITE SETAL ARRANGEMENT, $P_{1-6}$

Podomeres 1-3 indicate a sequence from terminal to basal

Numerically the adult setal are identical with CV.

| Copepodite: | | I | II | | III | | IV | | V | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Podomere: | | 1 | 2 | 1 | 2 | 1 | 2 | 1 | 3 | 2 | 1 |
| $P_1$ | exp. | IV + 3 | 1 : 0, | IV + 2 | 1 : 0, | IV + 2 | 1 : 0, | IV + 3 | 1 : 0, | I : 1, | IV + 2 |
| | end. | II + 3 | 0 : 1, | II + 1 | 0 : 1, | II + 1 | 0 : 1, | II + 1 | 0 : 1, | 0 : 1, | II + 1 |
| $P_2$ | exp. | 6 | 1 : 0, | 6 | 1 : 1, | 8 | 1 : 1, | 8 | 1 : 1, | 1 : 1, | 6 |
| | end. | 6 | 0 : 1, | 5 | 0 : 1, | 6 | 0 : 1, | 6 | 0 : 1, | 0 : 2, | 5 |
| $P_3$ | exp. | 1 | | III + 4 | I : 0, | III + 3 | I : 0, | IV + 5 | I : 1, | I : 1, | IV + 4 |
| | end. | | | 6 | 0 : 1, | 6 | 0 : 1, | 7 | 0 : 1, | 0 : 2, | I + 5 |
| $P_4$ | exp. | | | 3 | | IV + 3 | I : 0, | IV + 5 | I : 1, | I : 1, | IV + 4 |
| | end. | | | | | 6 | 0 : 1, | I + 5 | o : 1, | 0 : 2, | I + 4 |
| $P_5$ | exp. ♂ | | | | | 1 | | 4 | | | ? 4 |
| | exp. ♀ | | | | | 1 | | 5 | | | 5 |
| $P_6$ | ♂ | | | | | | | 2 | | | ? 3 |
| | ♀ | | | | | | | 2 | | | 2 |

In legs 1 to 4 the transition between the two and three segmented condition occurs by division of the terminal segment. Exopodial division occurs distally to the two basal setae, thus leaving one external and one internal seta attached to the middle segment. Division in the endopods is distal to the two external basal setae, resulting in a middle segment with two external setae.

## DISCUSSION

Definition of the adult: Vervoordt (1964) and Lang (1965) have drawn attention to the similarity between S. arthuri Poppe, S. arthuri magna Monk, S. purpurocincta Monk, and S. dentipes Vervoordt, and Vervoordt suggests that they may on further study constitute a single variable species.

In many respects S. patellarum also resembles S. arthuri, but although allied to it, is readily distinguishable from it.

The following diagnostic features distinguish both sexes of S. patellarum from all other members of the genus:

1. External spines on $P_2$ exopodite setiform and about 1.5 to 2 x the length of the respective podomeres bearing them.
2. Seta arising from podomere 1 of $P_3$ endopodite, very broad: about 2.5 x the width of all other setae on this ramus.

In addition the following combination of features identifies S. patellarum: Furca not longer than wide; external setiform spine arising from $P_2$ basipodite is strongly increased in size (almost as long as the exopodite); setal formula of $A_2$ exp. is 2, 1, 1, 3; segmentation of $A_2$ exp. indistinct; $A_1$ with segment 2 much longer than segment 3; all setae on $A_1$ naked; a single aesthetasc on $A_1$; $P_5$ basoendopodite with a single long seta on each of the two lobes; $P_5$ exp. length 2.5 x width and with 1 marginal, 2 terminal and 2 subterminal setae; $P_5$ exp. length 2.5 x width with 1 long naked terminal, 1 naked marginal and 2 setulose subterminal setae; $P_6$ with 3 setae, one of which is setulose; colour red.

Generic position: *S. patellarum* falls within the genus *Scutellidium* as defined by Lang (1948), but two features link it with *Sacodiscus* Wilson 1924. Firstly $A_2$ exp. is only indistinctly four segmented. As Lang (1965 pp. 145-6) uses this as a distinguishing character between the two genera, the exception is worth noting.

Secondly the fourth body somite is posteriorly slightly excavate, and in live material partly conceals the fifth somite. This condition is intermediate between that of *Sacodiscus* of *Scutellidium*.

In all other respects *S. patellarum* falls within the scope of *Scutellidium*, but there are important features excluding it from *Sacodiscus*.

Larval Development: Brian (1929) has described the nauplius of *Scutellidium* (=*Psamathe*) *longicauda*, and it is interesting that this too has a midventral sucker, (as Gurney (1933) has drawn attention to). *Sacodiscus* (=*Aspidiscus*) *littoralis* (Gurney 1933) and *Tisbe furcata* (Johnson and Olson, 1948) lack a comparable structure in the nauplius, despite the fact that they are generically closely allied.

The naupliar sucker may thus be of value in defining the genus *Scutellidium* in nauplii.

The nauplii of S. patellarum and S. longicauda are readily distinguishable by differences in setal arrangement. For example, in S. longicauda some terminal setae on $A_1$ are hairy, the tufted seta at the midpoint of $A_2$ endopodite is very short, the mandibular basipodite has only one seta, maxilla 1 does not have a hairy seta, and maxilla 2 appears to be lacking in the sixth naupliar stage. (See Gurney, 1933, fig. 3).

Humes (1960) has given a detailed description of the copepodite stages of Sacodiscus ovalis (Wilson). Comparison with S. patellarum reveals only minor differences in development: in the first copepodite of S. ovalis, $P_1$ has a 2 segmented exopodite and $A_1$ is 4 segmented, while in S. patellarum these are respectively one and five segmented. Generic differences between the two are apparent even from an early stage: for example, the hyaline margin of Sacodiscus and the penicillate spines of $P_1$ exopodite in Scutellidium.

Copepodites of S. patellarum can also be distinguished from those of S. longicauda (Brian 1919) by the presence of setiform spines on $P_2$ exopodite, and the broad seta on $P_3$ endopodite.

## REFERENCES:

BRIAN, A. 1919. Sviluppo larvale della Psamathe longicauda Ph. e dell' Harpacticus uniremis Kroy. Atti della Societa Italiana di Scienze Naturali. 58 : 29-58.

GURNEY, R. 1933. Some Copepoda from Plymouth. J. mar.biol. Ass. 19 : 299-304.

HUMES, A.G. 1954. Tisbe celata n.sp., a harpacticoid copepod from the mantle cavity of the Edible Mussel in New Brunswich. J. Fish. Res. Bd. Canada, 11 (6) : 816-826.

——— 1957. Deux copepodes Harpacticoides nuuveux du genre Tisbe, parasites des Holothuries de la Mediterranee. Vie et Mileu 8 (1) : 9-22.

——— 1960. The harpacticoid copepod Sacodiscus (=Unicalteutha) ovalis (C.B. Wilson, 1944) and its copepodite stages. Crustaceana 1 (3) : 279-294.

LANG, K. 1948. Monographie der Harpacticiden, 2 Vols : 1-1683. (H. Ohlsson, Lund).

——— 1965. Copepoda Harpacticoidea from the Californian Pacific Coast. K. Svenska Vetensk. Akad. Handl. 10 (2) : 1-560.

STOCK, J.H. 1960. Sur quelques Copepodes associes aux invertebres des cotes du Roussillon. Crustaceana 1 (3) : 218-257.

VERVOORDT, W. 1964. Free living Copepoda from Ifaluk Atoll, in the Carolina Islands. U.S. Nat. Mus. Bull. 236 : 1-431.

WELLS, J.B.J. 1967. The littoral Copepoda (Crustacea) of Inhaca Island, Mozambique. Trans. Roy. Soc. Edinb. 67 (7) : 191-358.

# SECTION XI:

# DESICCATION.

# XI. DESICCATION

The intertidal zone is cyclically exposed and immersed by tidal movements. This results in a gradation of physical factors with maximum exposure at the top of the shore and minimal exposure at low water spring tide. Superimposed on this gradation is the differentiation between spring and neap tides. This establishes several "critical" zones: the upper level which is only covered by high spring tides, a mid-littoral level exposed and immersed by all tides, and a lower zone which is uncovered only by low spring tides.

The vertical gradation of physical factors results in a zonation of organisms according to their tolerances or preferences. This effect has been described by many authors including Colman (1933), Stephenson (1942), Doty (1957) and Southward (1958).

Of the physical variables involved, temperature, salinity and desiccation are likely to be the most important.

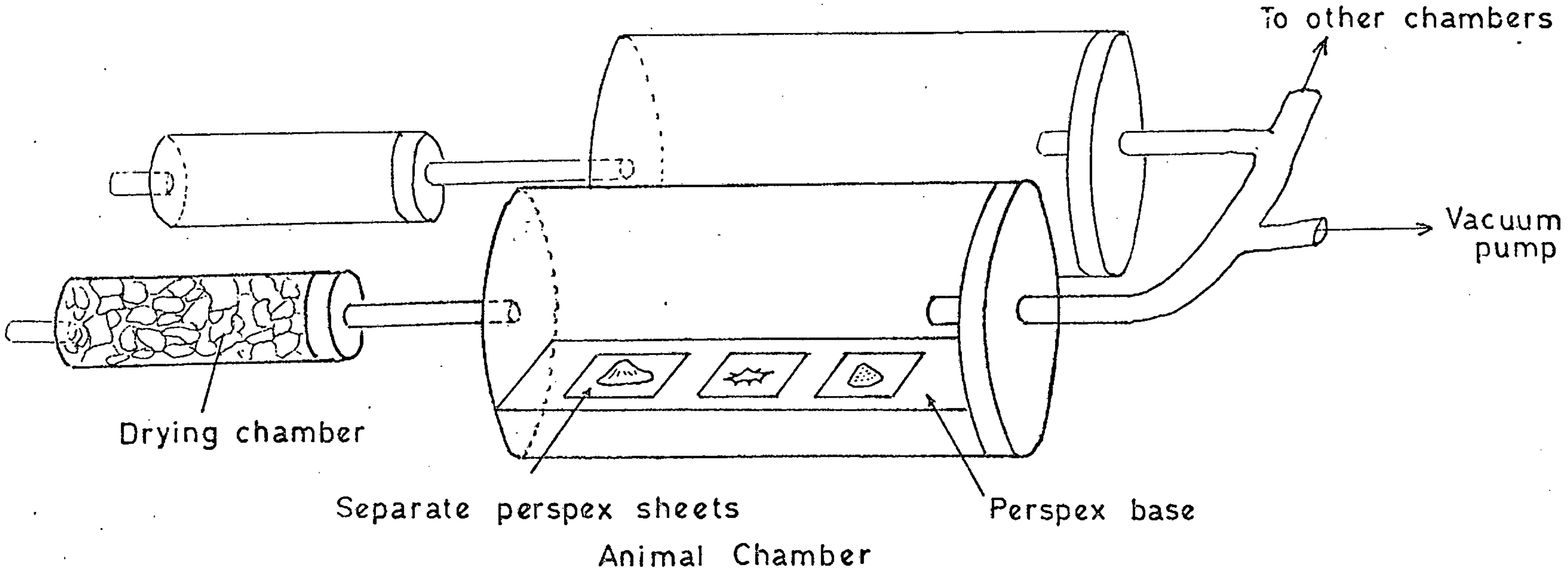
The pioneer study of Broekhuysen (1940) and subsequent work by Allanson (1958) and Brown (1960) has established that tolerance to these variables is correlated with the degree of exposure normally experienced by a species on the shore. The lethal temperature limits of most intertidal animals are well in excess of actual conditions on the shore (Evans, 1948; Southwood, 1958), although Davies (1970) has shown that the body temperatures of P. vulgata may be as much as 11°C. above ambient temperature, due to absorption of infra-red radiation. Limpets are probably more prone to heating than other organisms, because a large surface area is exposed to the sun, little shadow is cast, and the large foot will absorb heat from the substrate.

Salinity varies in the intertidal zone due to rain and evaporation, but is only likely to limit inhabitants of intertidal pools, (although rain water may float on the surface of pools, and evaporation will alter the salinity in the gill cavities of drying animals). With the exception of low level *P. miniata*, no South African *Patellas* are restricted to intertidal pools. Arnold (1957, 1972) has shown that *P. vulgata* reacts negatively to dilute sea water, clamping down and withdrawing its mantle.

Apart from the work of Davies (1969a) and Foster (1971), previous analyses of the effects of desiccation have been confined to adult animals, and the importance of body size has been overlooked. This is clearly of great importance, as juveniles are usually most susceptible to desiccation, and it cannot be assumed that their tolerance will be similar to that of the adults. The elegant work of Davies (1969a) has also stressed the importance of rate of water reabsorption as a possible factor limiting zonation.

The present paper concerns desiccation in seven South African *Patella* spp., particularly the effect of body size on rate of water loss and on the lethal limits. These species are zoned differentially on the shore from the upper balanoid to the infratidal in the following sequence: *P. granularis*, *P. oculus* and *P. granatina*, *P. longicosta*, *P. cochlear* and *P. argenvillei*, and *P. barbara*. The first three tend to settle low on the shore and migrate upwards and have been termed "migratory" species. The last four are "non-migratory" remaining at the site of settlement, throughout life.

FIG. I. DESICCATING APPARATUS.



## MATERIALS AND METHODS:

Work on desiccation is usually based on water loss over calcium chloride or sulphuric acid in desiccators. The method suffers from the problem that the resultant humidity is unrealistically low, and equilibrium is disturbed each time the animals are removed for weighing. Consequently an apparatus was designed to allow continual air flow, constant conditions and a more realistic humidity. This comprised a series of cylindrical animal chambers 200 mm. long and 50 mm. in diameter, connected in parallel to a vacuum pump (fig. 1). Each chamber was connected to a narrower drying tube (or U-tube) which could be filled with the desired drying agent. Air was drawn through the drying tube, establishing a constant humidity and then passed over the animals. Wet and dry bulb thermometers could be inserted through small apertures to monitor the humidity and temperature. All experiments were run in a constant temperature room at 21°c, and calcium chloride used as a drying agent, giving a relative humidity of between 65 and 70%. In all cases freshly collected animals were used, and the complete experiment conducted over a two week period in late August to September, to avoid the effects of acclimation.

Excess water was dried off each animal before placing it separately on a weighed perspex sheet. The removal of water from the pallial cavity introduces an unnatural condition, but is essential if lethal limits and rate of water loss are to be calculated in terms of percentage body water. Animals with flat shell mouths were selected, to fit the flat sheets as closely as possible, and allowed to adhere to the sheets. Water loss was recorded by weighing the limpets intermittently (on their perspex sheets) until they died or for a maximum of 150 hours. Parallel experiments were run with empty shells of comparable size to assess the rate of water loss from the shell. Only in small animals did this contribute substantially to the overall loss, and the rate of water loss was corrected to allow for evaporation from the shell. A minimum of twelve individuals was used for each species in each experiment, except P. argenvillei (9) and P. barbara (4). Results for the latter species are tenuous because of the small sample.

Specimens were collected from Kommetjie and from Kalk Bay which respectively experience mean water temperatures of 13.4°c and 16.5°c.

Shell diameters were determined by tracing the outline and measuring the trace using a calibrated eyepiece on a dissecting microscope. Shell volumes were calculated from the weight of alcohol the shell could hold.

The term "resistance" (to water loss) denotes the degree an animal restricts water loss, and "tolerance" refers to the amount of water loss it can withstand.

## RESULTS:

The rate of water loss at 21°c. and a relative humidity of 65 - 70% was determined for various sized animals of all seven species, and the results are given in figures 2 - 9.

In most cases rate of water loss was initially linear and then decreased slowly, but in a few cases (P. oculus and P. granatina) there was a sudden increase just before or after death. This suggests an active mechanism reducing water loss, but is probably simply contraction of the mantle, reducing peripheral circulation. After death the mantle expands and a yellow fluid accumulated in the mantle cavity. Limpets

Fig. 2 Rate of Water Loss

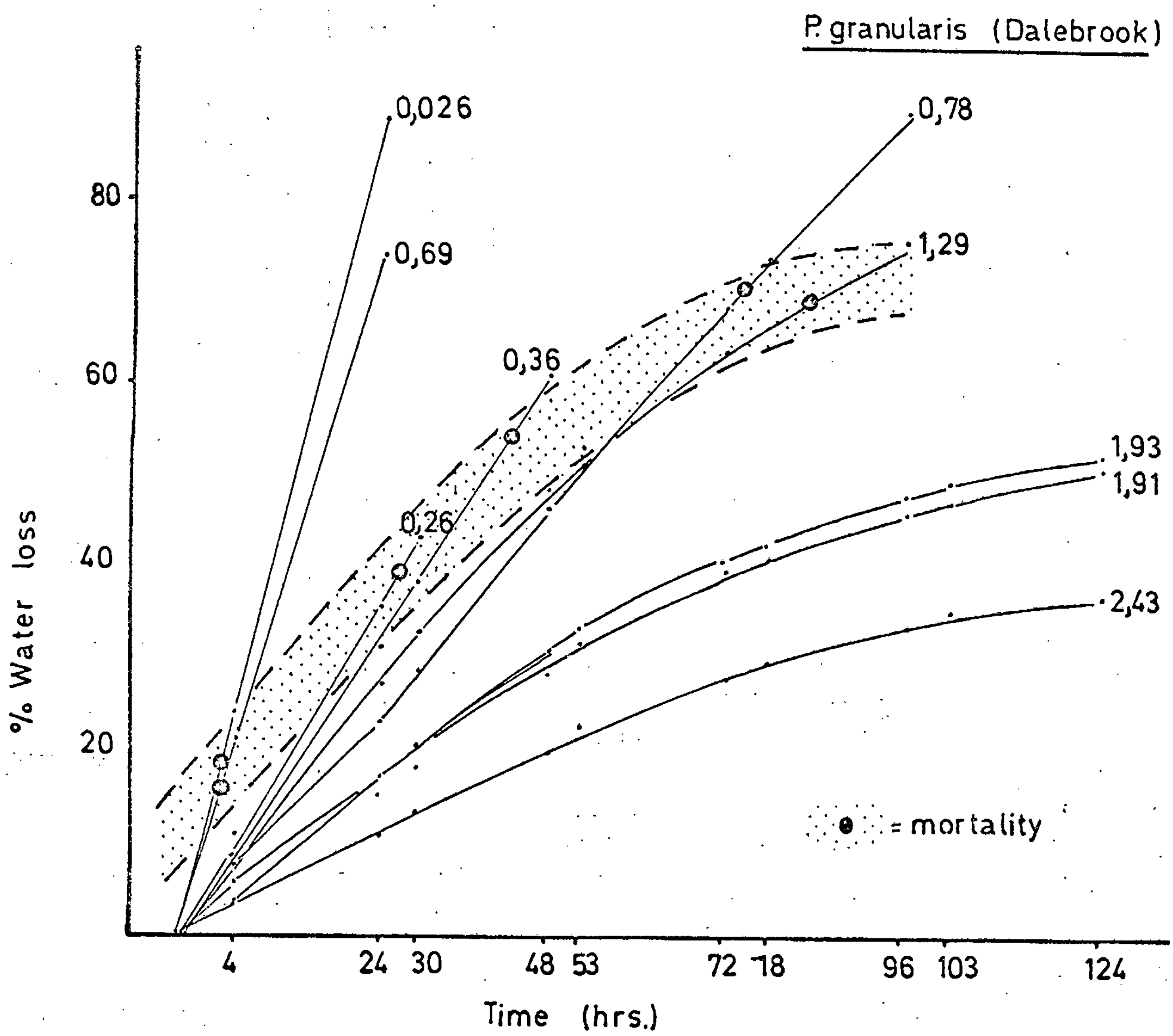


Fig. 3

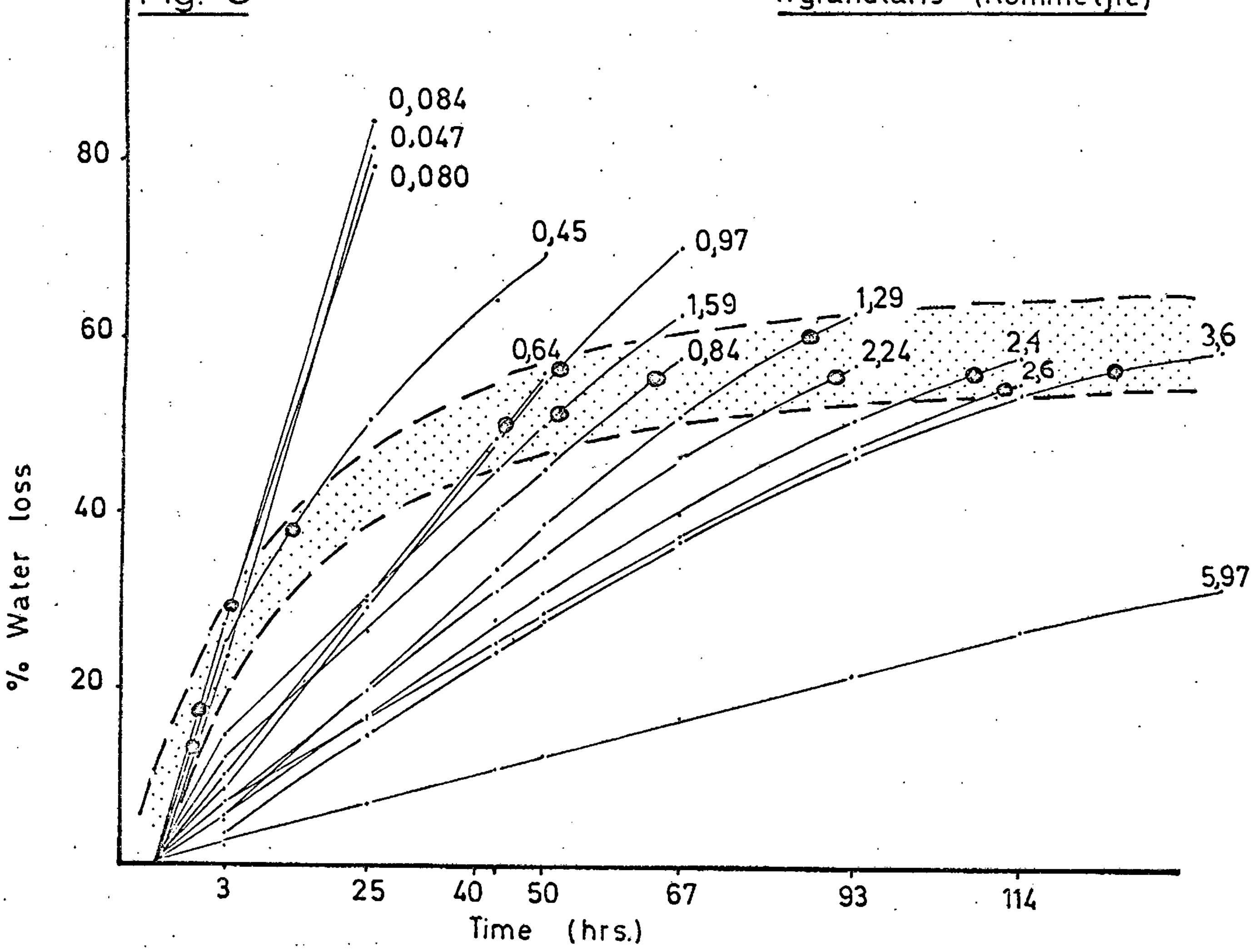


Fig. 4 Rate of Water Loss

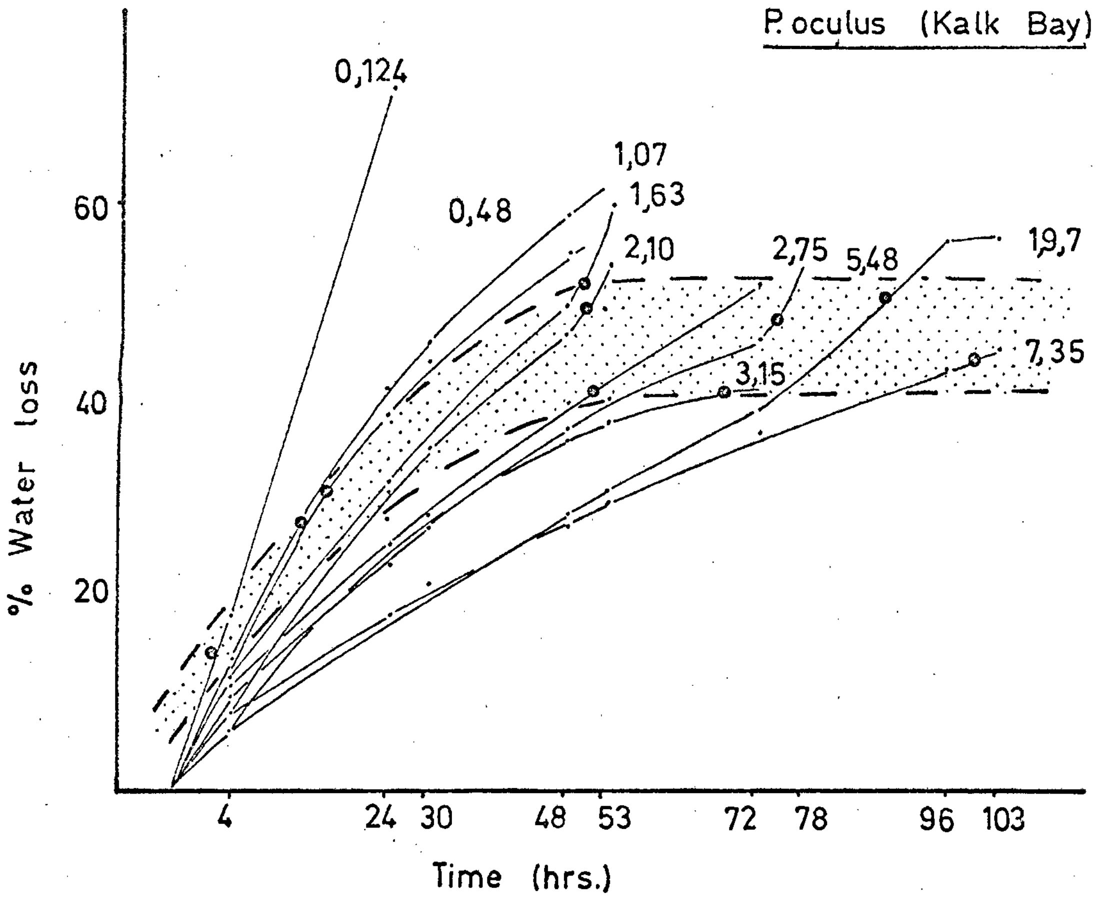
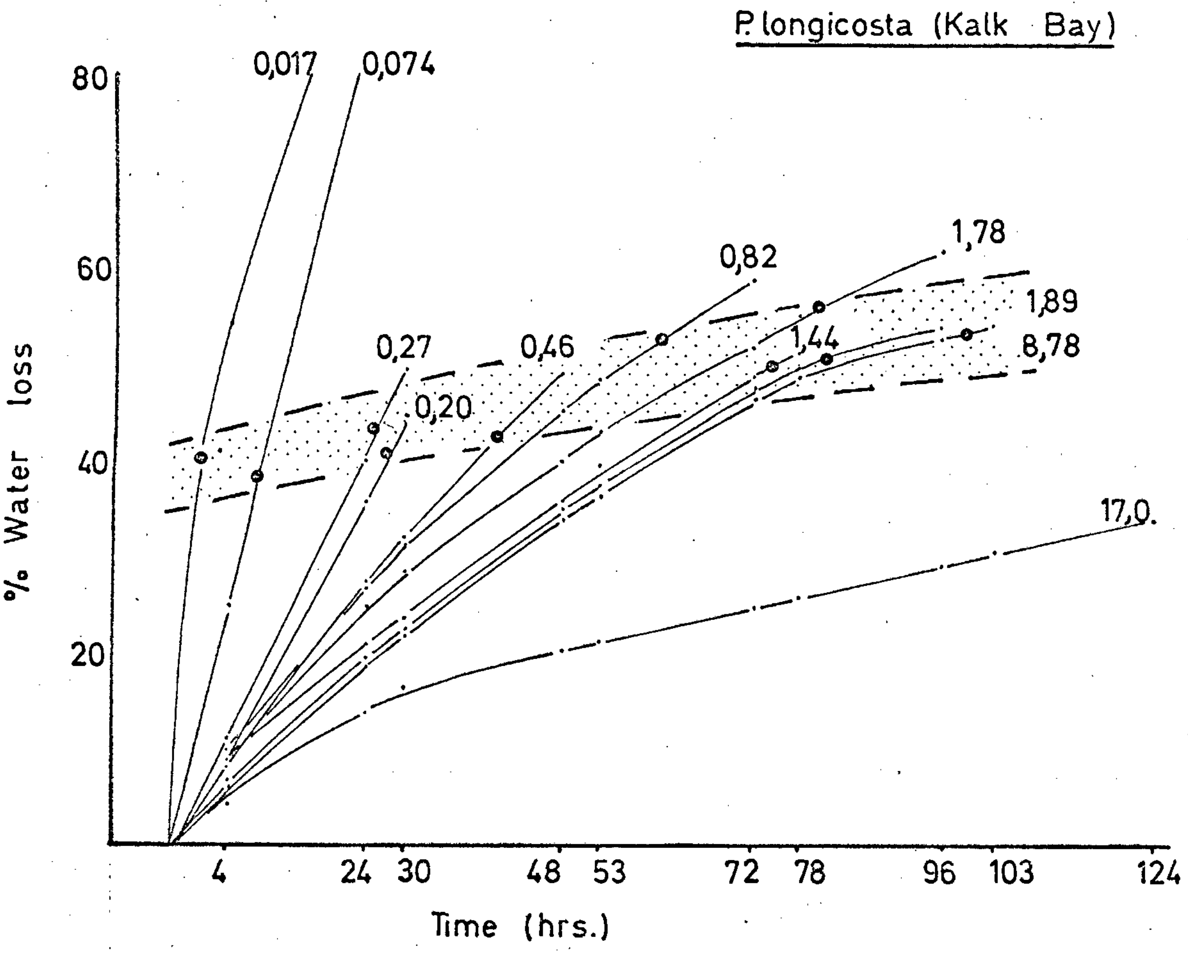


Fig. 5



## Fig. 6 Rate of Water Loss

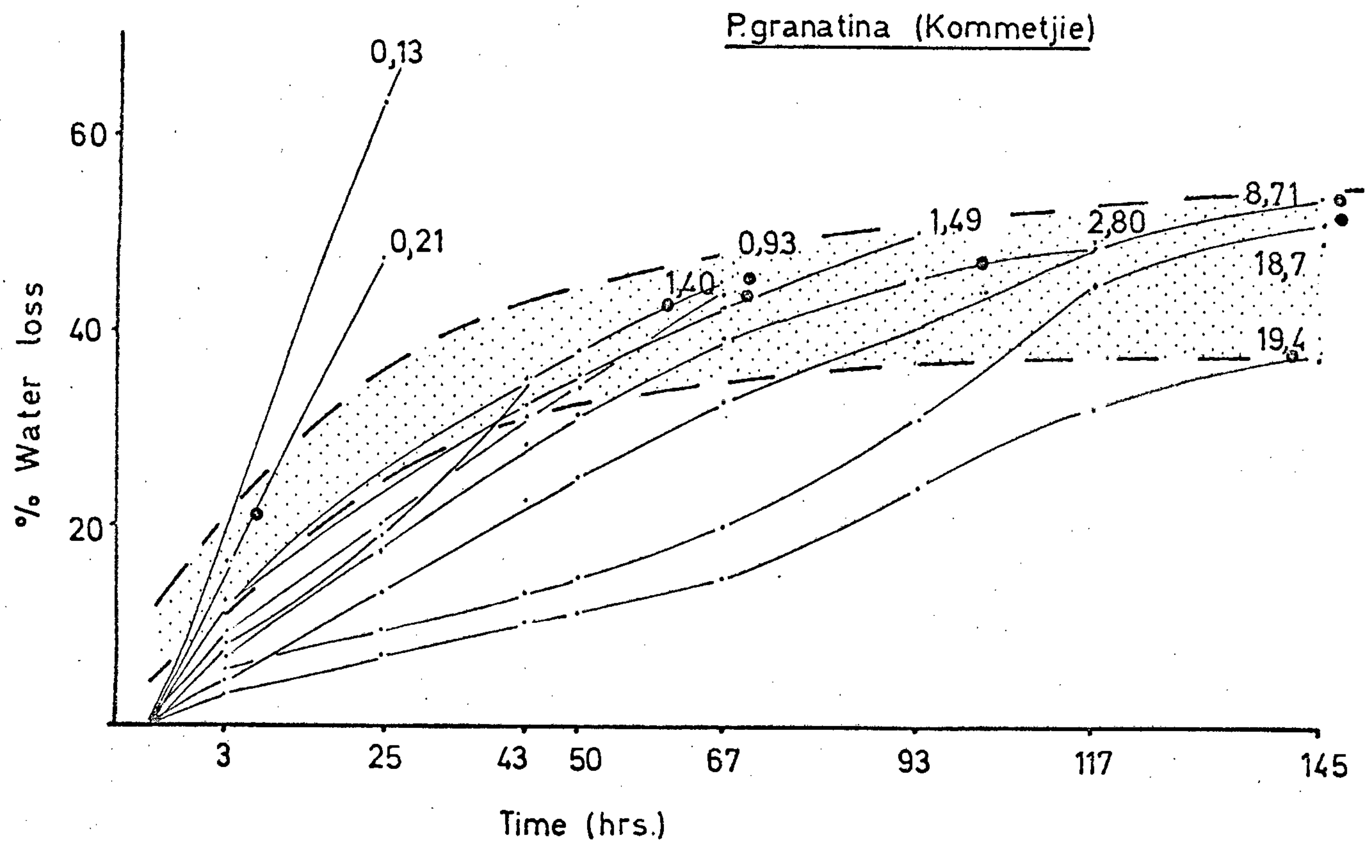


Fig. 7

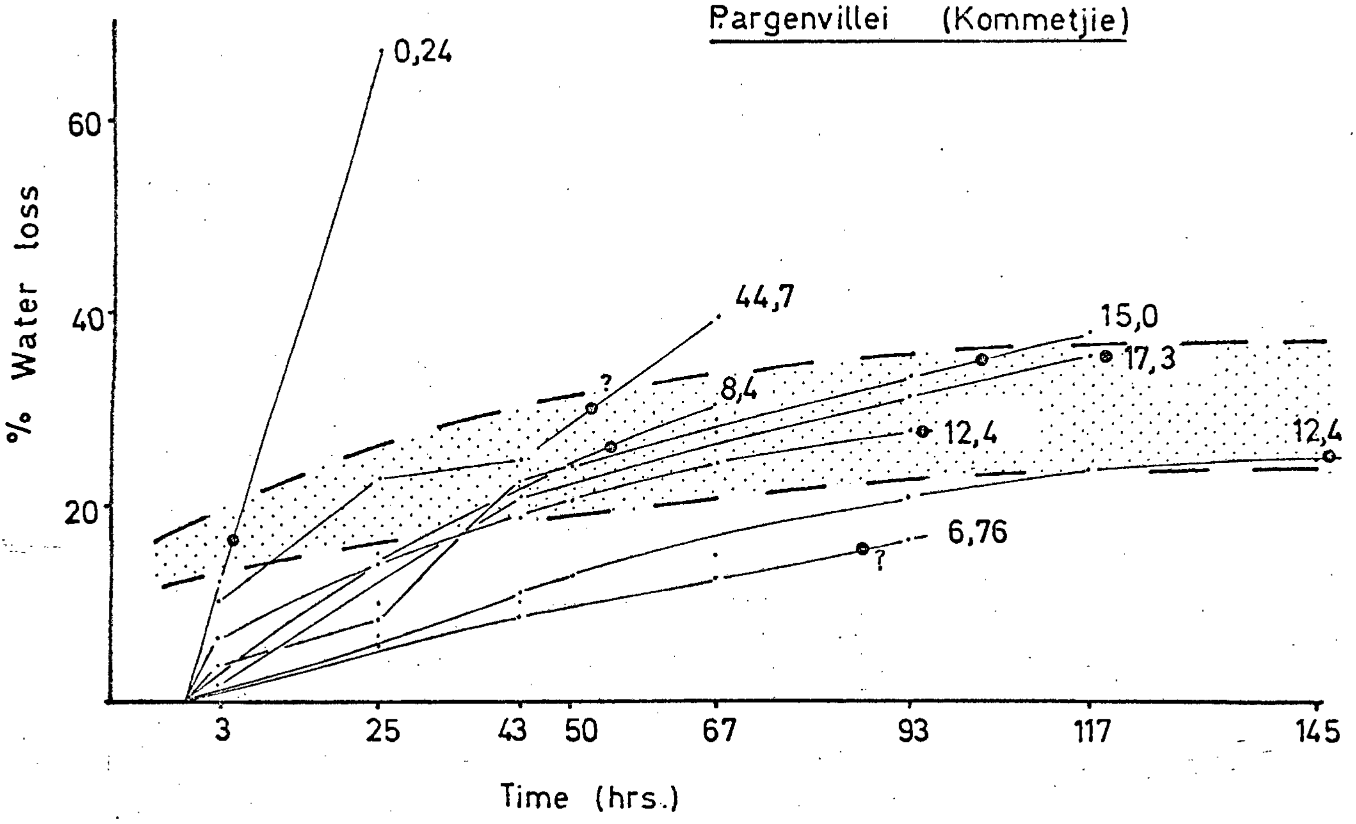
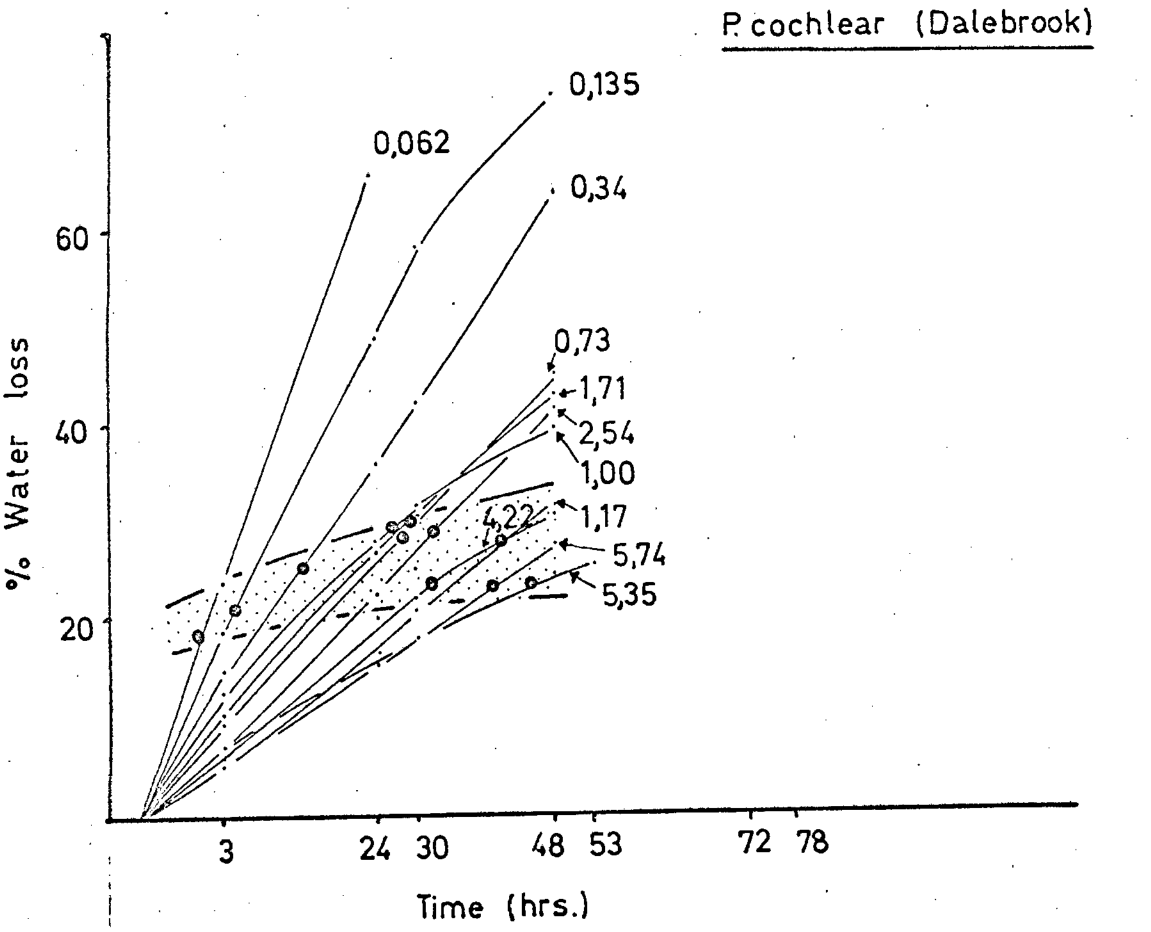
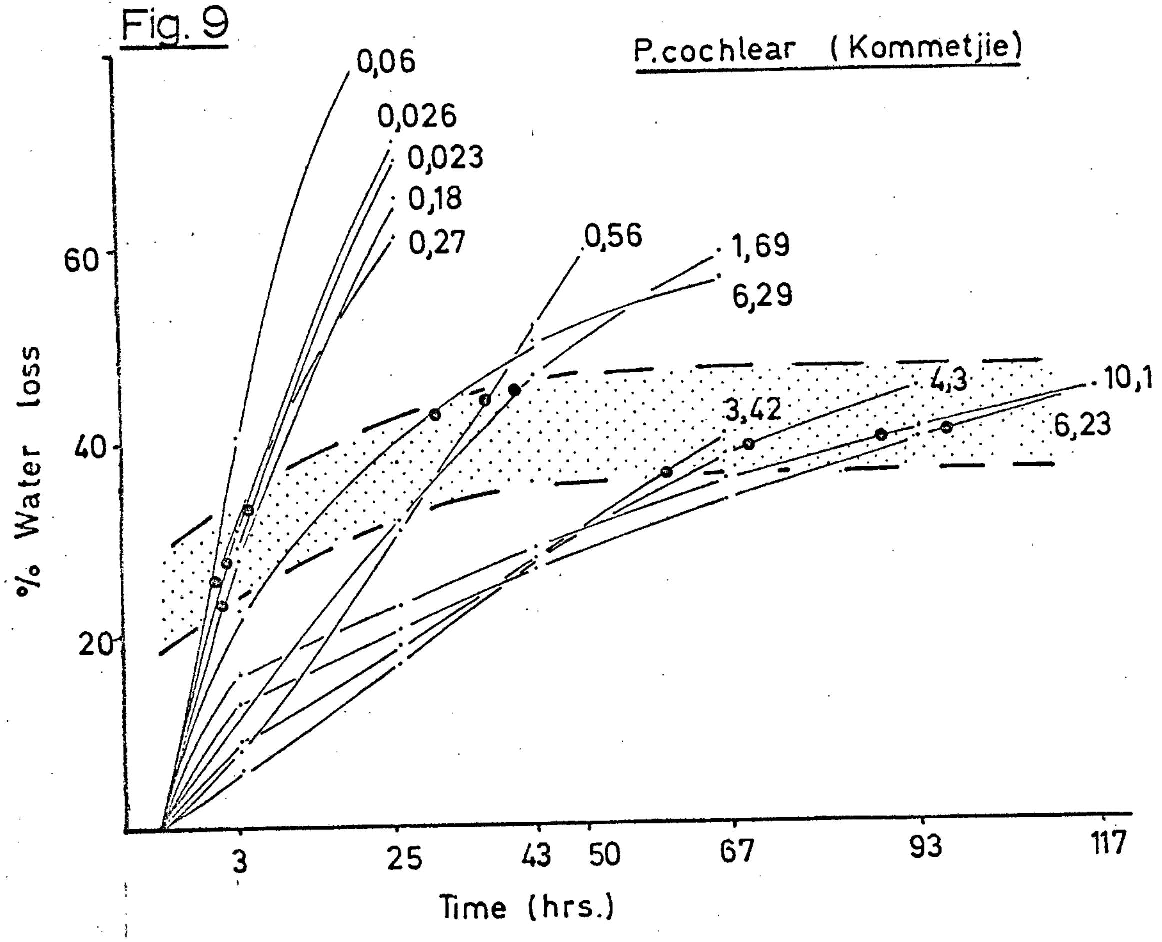


Fig. 8 Rate of Water Loss



P. cochlear (Dalebrook)

Fig. 9



P. cochlear (Kommetjie)

normally void waste products only when submerged, and this probably represented the final release of excretory products after some 60 hours of exposure.

Several general trends are apparent from the results. Percentage water loss is greatest in small animals. A plot of rate of water loss against body weight (fig. 10) shows that animals of less than about 1 gm. body weight are particularly susceptible to water loss. Logarithmic transformation of this data separates the species and allows regression lines to be calculated (fig. 11 and Appendix I).

If water loss is purely a function of surface area from which evaporation can occur, then the relationship between shell circumference and body weight (which is proportional to shell volume) will influence the rate of water loss. Figure 12 illustrates this relationship. The shells of P. granularis and P. argenvillei are high domed and have a smooth oval mouth, whilst those of P. longicosta and P. oculus are flatter and have costae which increase the circumference. Other species are intermediate.

Table 1 summarises the effect this has on the rate of water loss.

With two exceptions there is close agreement between the shell circumference: volume ratio and the rate of water loss and for the standard animals of 10 gm, 1 gm and 0.1 gm Spearman's ranking correlation yielded values of 0.75, 0.65 and 0.33. P. granatina loses water far slower than would be expected. The reason for this is not known, but as mentioned above, P. granatina was one of the species in which water loss may be actively regulated. Differences in epithelial permeability may also affect water loss.

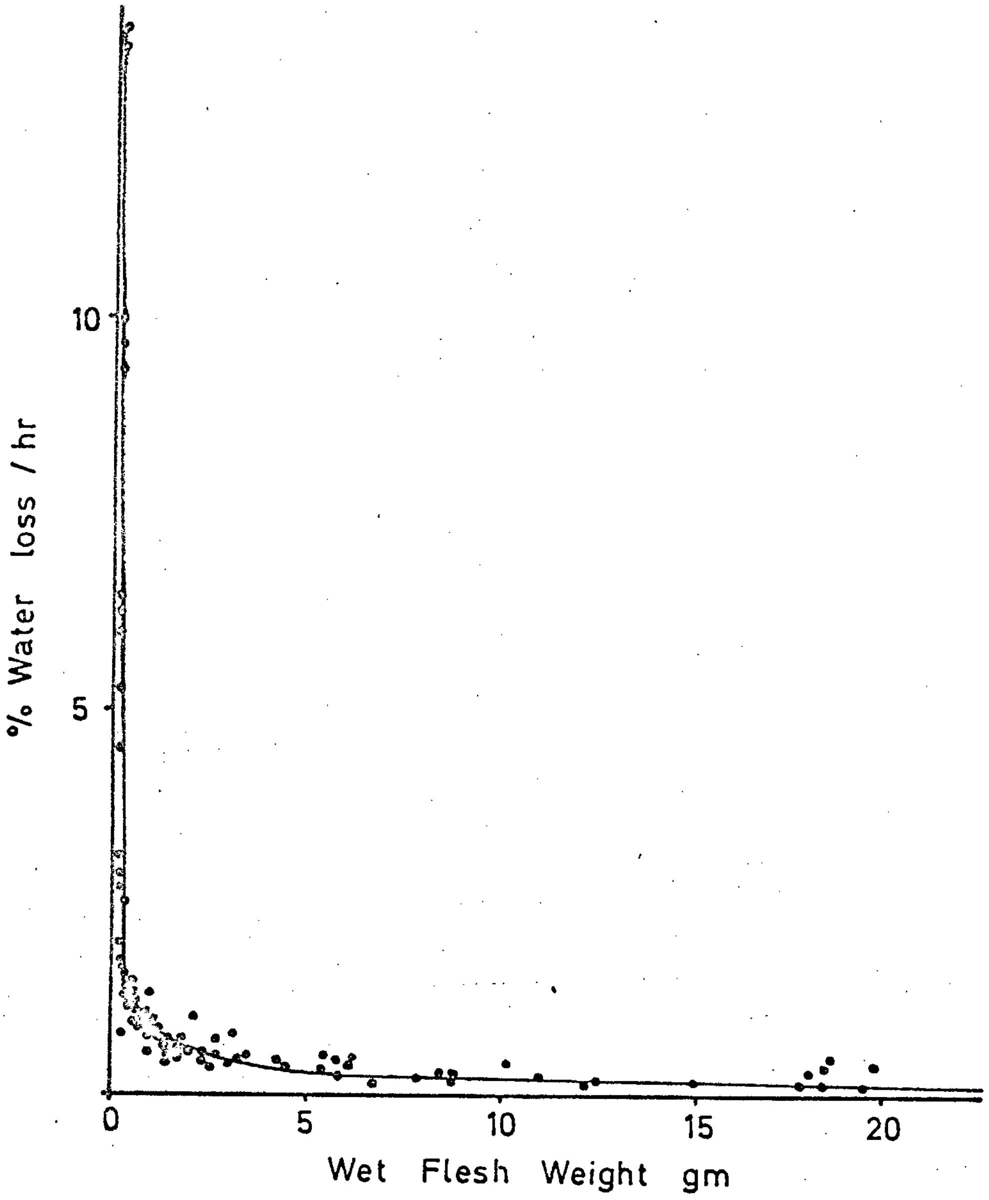


FIG.10. Rate of water loss in Patella.
(Data have been pooled from
seven species).

Fig. 11

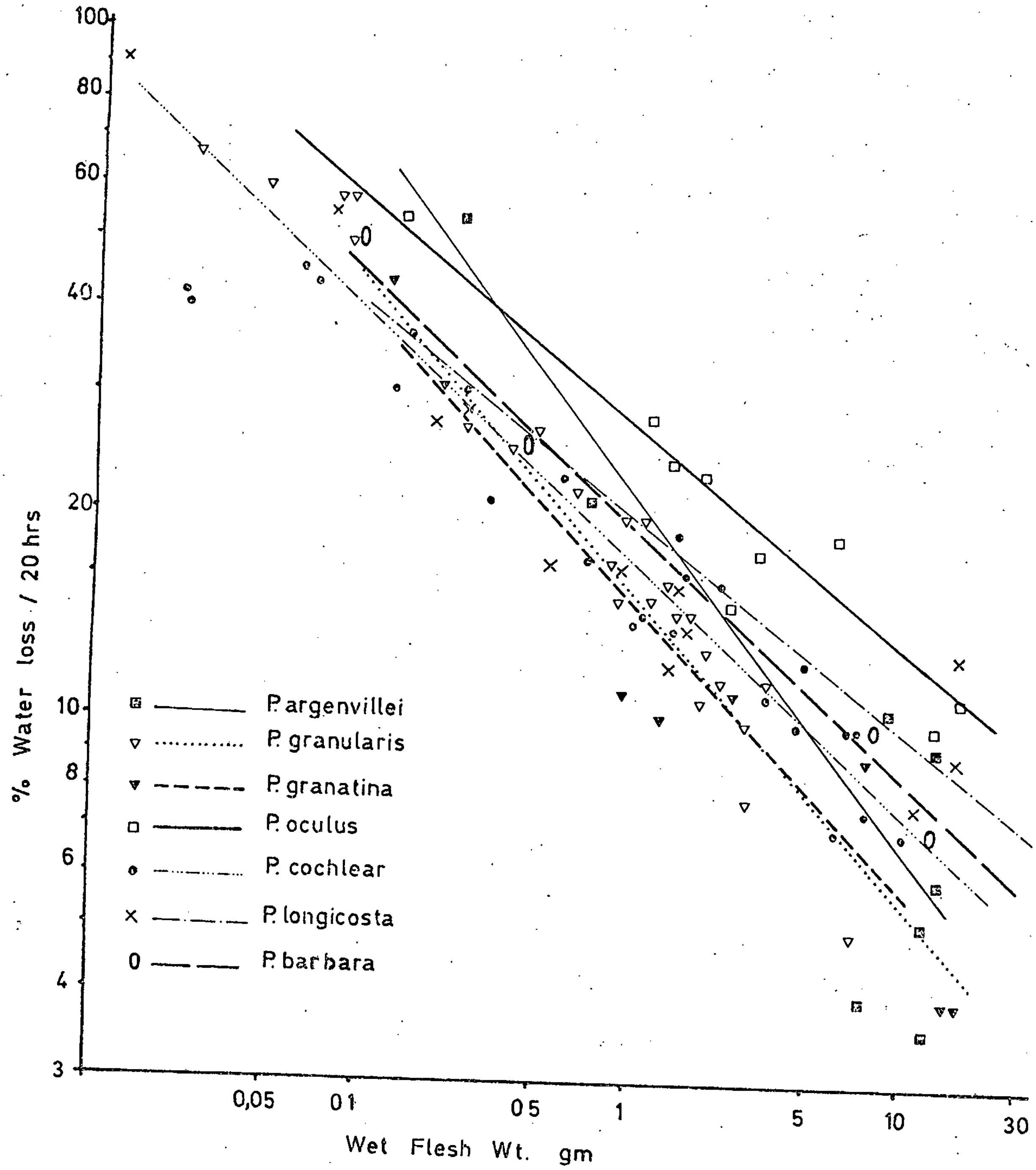


FIG. II. Logarithmic plot of percentage water loss against wet flesh weight. The experiment was conducted at 21.0°c and 70% relative humidity.

Fig. 12 Shell Volume Relative to Circumference

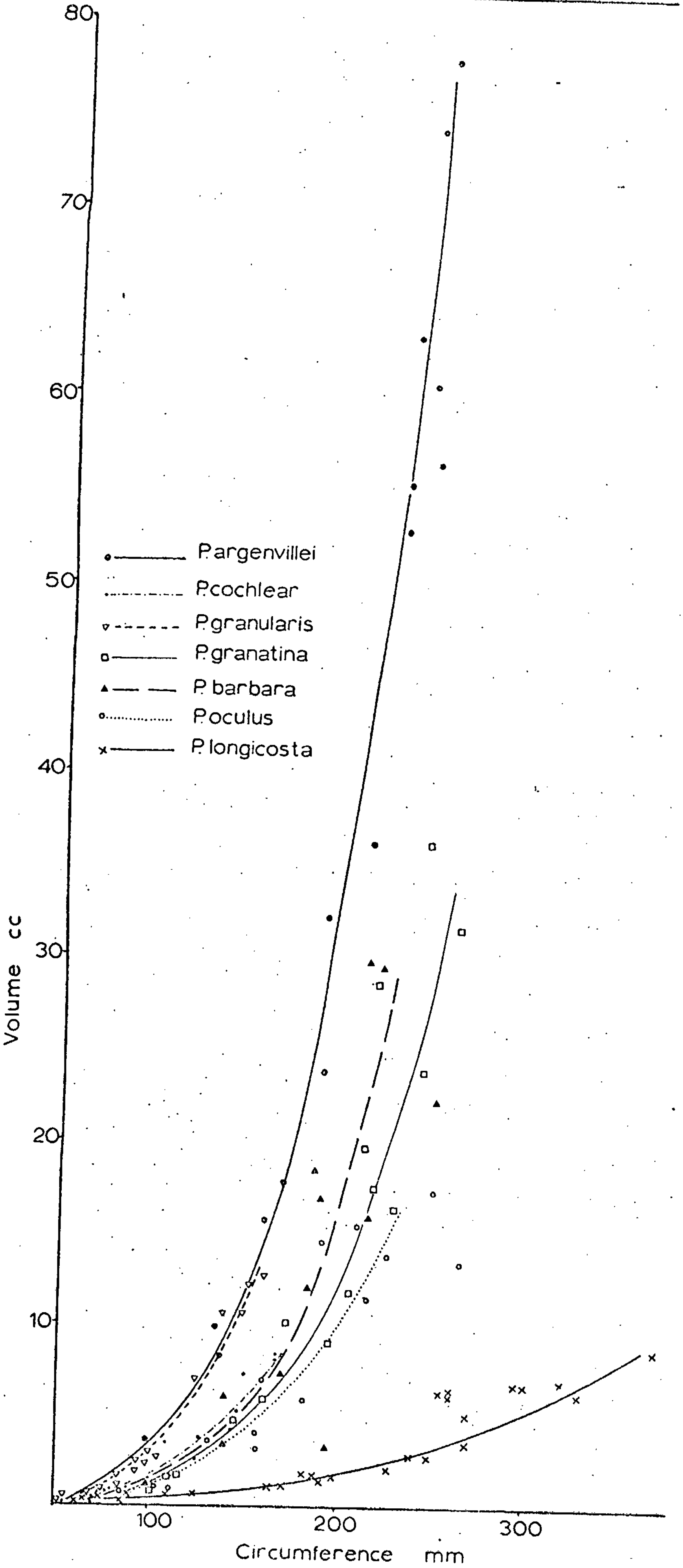


TABLE 1. Ratio of shell circumference to volume (ranked from smallest to largest) and its relationship to rate of water loss for "standard" animals of 10 gm, 1.0 gm, and 0.1 gm. wet body weight (data extracted from figure 11). Figures in brackets indicate ranking. Zonation is given for adult animals only, ranked from the top of the shore downwards.

| Species | Ratio of circumference: volume. | % $H_2O$ loss/20 hrs. for standard animals | | | Zonation |
|---|---|---|---|---|---|
| | | 10 gm. | 1 gm. | 0.1 gm | |
| P. granularis | (1) | 5.6(1) | 15.0(1) | 40.0(1) | (1) |
| P. argenvillei | (2) | 6.6(3) | 21.0(5) | 68.0(7) | (5) |
| P. cochlear | (3) | 7.6(4) | 17.0(3) | 42.0(3) | (5) |
| P. barbara | (4) | 8.5(5) | 19.5(4) | 45.0(4) | (7) |
| P. granatina | (5) | 6.0(2) | 15.1(2) | 40.0(2) | (2) |
| P. oculus | (6) | 14.0(7) | 25.0(7) | 57.0(6) | (2) |
| P. longicosta | (7) | 10.0(6) | 22.0(6) | 48.0(5) | (4) |

P. argenvillei adults desiccate at the expected slow rate, but juveniles lose water much faster relative to the other species (fig. 11). There are two reasons for this. The shell growth is isometric until a length of about 50 mm, after which height increases proportionally more than length (fig. 13g), reducing the circumference : volume ratio and the rate of water loss.

Secondly, P. argenvillei often rears its shell off the substrate, exposing its body. This usually occurs with the returning tide, but was also observed in the desiccator. As a result the rate of water loss was eratic and not closely linked to size (fig. 7). All the remaining species remained clamped down and water loss was approximately linear.

As Davies (1969a) has pointed out, the "surface law" states that surface area varies with the power of -0.33 of the volume, provided the relative proportions of a body remain constant. If water loss is related to surface area, and volume to body weight, one would expect the following relationship if the body proportions remain constant:

$$r \propto w^{-0.33}$$

(where r = rate of water loss and w = flesh weight).

In its more generalised form this can be expressed:

$$r = cw^{b}$$

The exponent b can be calculated from the slope of a logarithmic plot of these two parameters (fig. 11) :

$\log r = \log c + b \log w.$

The resulting exponents are given in Table 2 and the regressions in Appendix I.

Davies (1969a) recorded exponents of -0.55, -0.44 and -0.44 for respectively high level P. vulgata, low level P. vulgata and low level P. aspersa. He ascribed this to changing shell proportions, as the shells become progressively steeper with growth, reducing surface area for evaporation.

In a similar way the relationship between shell height and length gives an estimate of whether the surface area available for evaporation remains constant in relation to body size, or decreases proportionally with growth. Figures 13d - g show that shell height and length are approximately isometric in P. barbara, P. oculus, P. longicosta and P. cochlear. (Shell growth in P. oculus is only isometric after a length of 13mm. has been achieved. As this is reached within one month of settlement, the initial allometry has been ignored.) On the other hand, growth is markedly allometric in P. granularis, P. granatina and P. argenvillei (figs. 13a - c).

Shell height (h) and Length (L) can be related by the function: $h = cL^{\alpha}$ , where $\alpha$ is the constant of allometry (Simpson, Roe and Lewontin, 1960) and can be obtained by logarithmic transformation. $\alpha$ for the seven species of Patella

Fig. 13 Shell Length Relative to Height

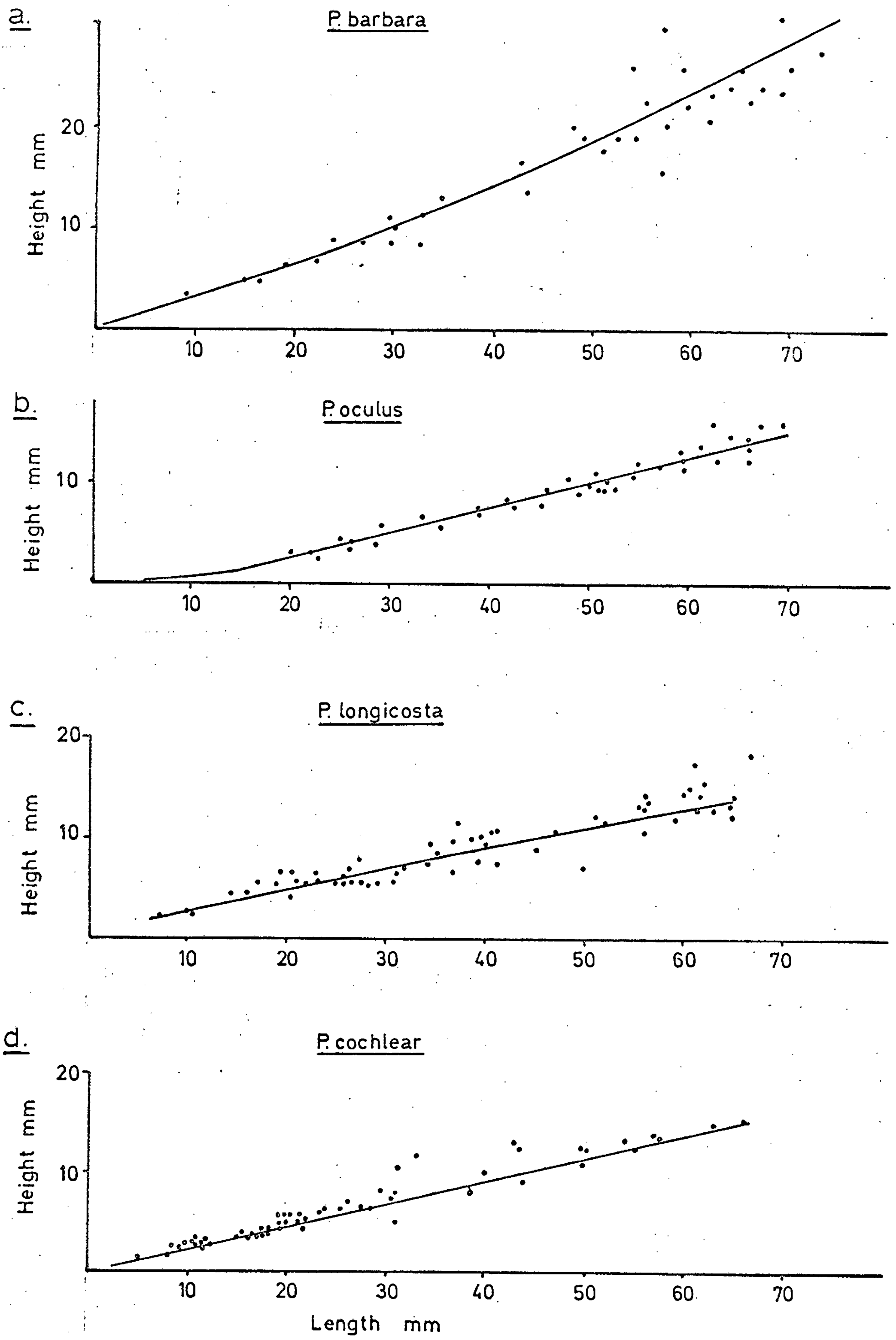
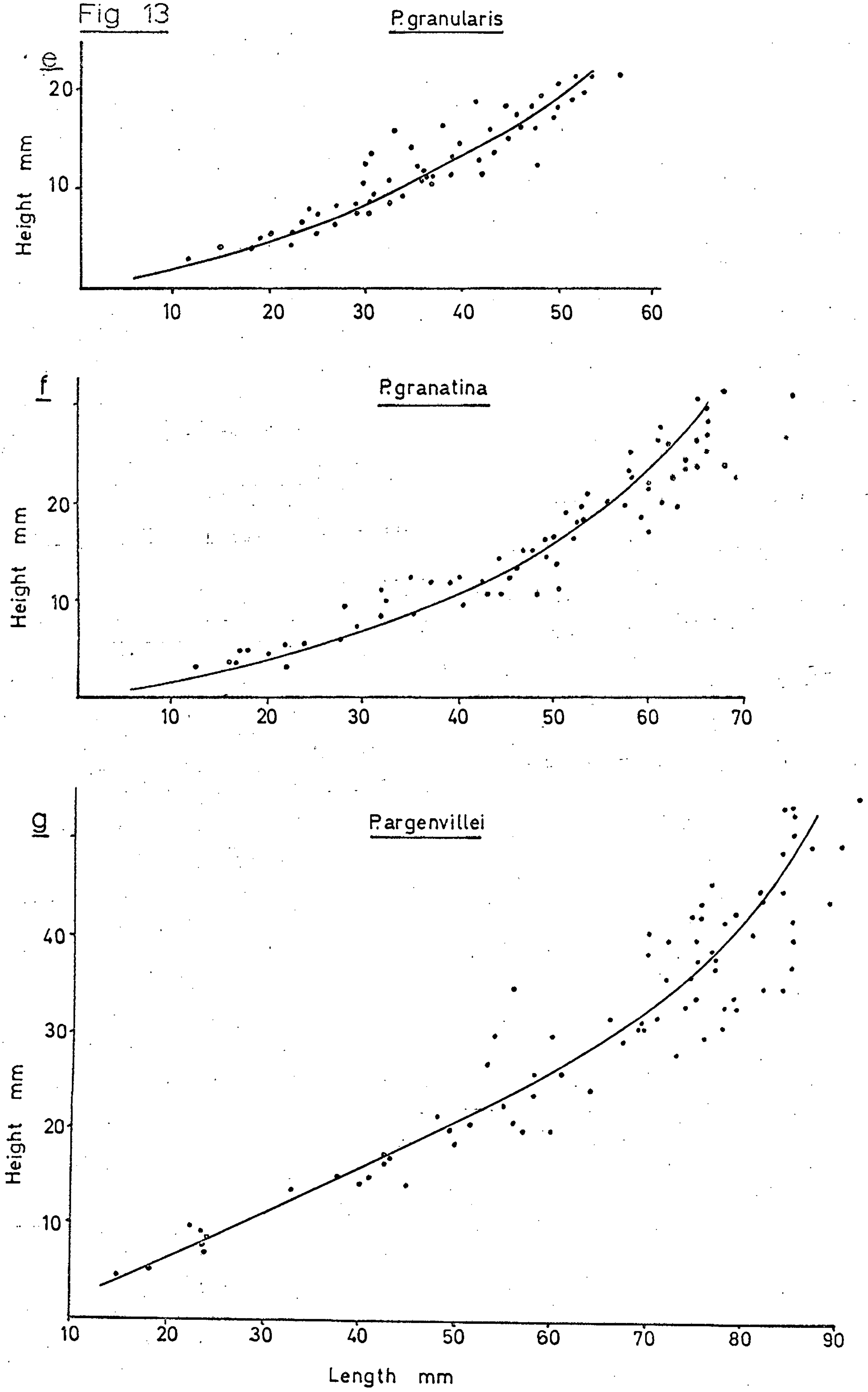


Fig 13


e
P.granularis
Height mm
20
10
10
20
30
40
50
60
f
P.granatina
Height mm
20
10
10
20
30
40
50
60
70
g
P.argenvillei
Height mm
40
30
20
10
10
20
30
40
50
60
70
80
90
Length mm

is given in Table 2, and the relevant exponential equations given in Appendix II.

TABLE 2. Constant of allometry ($\alpha$) for shell height and length, and the exponent (b) between rate of water loss and body weight. $\alpha$ is approximately 1 if growth is isometric.

| Species | $\alpha$ | b |
|---|---|---|
| P. granatina | 1.36 | -0.43 |
| P. granularis | 1.34 | -0.45 |
| P. argenvillei | 1.31 | -0.51 |
| P. barbara | 1.09 | -0.36 |
| P. oculus | 1.02* | -0.32 |
| P. cochlear | 0.97 | -0.36 |
| P. longicosta | 0.91 | -0.31 |

* Ignoring initial allometry.

Clearly those limpets with isometric growth conform to the "surface law" and their rate of water loss is approximately proportional to the power of -0.33, while those in which shell height increases faster than length have a higher exponent. This confirms and extends the findings of Davies (1969a).

From the ecological standpoint, tolerance to water loss is even more important than the rate of water loss.

Figures 2 to 9 also show the lethal limits of water loss, as related to body size. In terms of this, the limpets fall into two groups. In P. granularis, P. granatina and P. oculus the tolerance of juveniles is very low, but increases markedly with size; while in P. cochlear, P. longicosta and P. argenvillei tolerance remains unchanged and only increases slightly with increased size. The range of lethal limits is given in Table 3.

TABLE 3. Range of lethal water loss. The species are listed in order of their zonation from the top of the shore downwards. (Data taken from figures 2 to 9 and apply to a complete size range of each species.)

| Species | Range of lethal water loss (%). | |
|---|---|---|
| | Minimum | Maximum |
| <u>P. granularis</u> (Kommetjie) | 13 | 60 |
| <u>P. granularis</u> (Kalk Bay) | 15 | 70 |
| <u>P. granatina</u> | 16 | 54 |
| <u>P. oculus</u> | 14 | 54 |
| <u>P. longicosta</u> | 36 | 54 |
| <u>P. cochlear</u> (Kommetjie) | 23 | 46 |
| <u>P. cochlear</u> (Kalk Bay) | 16 | 30 |
| <u>P. argenvillei</u> | 13 | 37 |

## <u>DISCUSSION</u>:

Davies (1969b) has shown that in British and Mediterranean <u>Patellas</u>, the shell is tall and conical in upper-shore species, and progressively flatter in lower-shore and subtidal species. Even within species this trend is true (Orton, 1928; Moore, 1934; Branch, 1971). This tendency will reduce evaporation from high-level specimens. Most South African limpets conform to this pattern, but there are exceptions. Among those at high levels, <u>P. granularis</u> and <u>P. granatina</u> conform with high domed shells, but <u>P. oculus</u> has a consistently flat shell throughout life. Conversely, the low level <u>P. cochlear</u> (and subtidal <u>P. tabularis</u> and <u>P. miniata</u>) have flat shells, but <u>P. argenvillei</u>

and P. barbara have very tall shells in spite of their position low on the shore. Clearly there is no close correlation between zonation and shell shape in South African Patellas, nor between zonation and rate of water loss (table 1). Spearman's rank correlation yields values of respectively 0.00 and 0.32 for these correlations, which are not significant.

Shell shape is not the only factor effecting water loss. Kristensen (1969) has shown that P. coerulea loses water almost twice as fast as Diodora nubela, despite the fissura at the shell apex of Diodora. Probably the relative permeability of the epidermis influences water loss, as has been suggested above for P. granatina. The relative development of a scar and of homing behaviour and the choice of shaded or exposed rocks will also effect water loss.

Shell shape is probably not only related to the relative needs for water conservation. Both P. cochlear and P. argenvillei occur low on the shore in areas of strong wave action, and have evolved divergent shell shapes which may be related to the mechanical stresses of wave action. P. cochlear predominates on horizontal or gently sloping rocks, and the flat shell will present minimal resistance to water movement. The dynamics of water flow over the shell may even press the shell onto the substrate rather than wash it away. P. argenvillei on the other hand often attaches on the vertical seaward faces of rocks and waves may break directly onto them. The high domed shell allows the development of enormous adductor muscles to help the limpet retain its position.

As would be expected, there is a strong correlation between zonation and tolerance to water loss (Spearman's rank correlation = 0.91). This agrees with previous results on other molluscs (Broekhuysen, 1940; Allanson, 1958; Brown, 1960; Micaleff, 1966 unpublished; Davies, 1969a; Bannister, 1970 unpublished). More important and interesting is the change of tolerance in relation to body size. In *P. granularis*, *P. oculus* and *P. granatina* tolerance is initially low, but increases sharply with size (figs. 2, 3, 4 and 6). These species comprise the migratory group in which juveniles are established low on the shore and migrate progressively upwards. In the light of this, the substantial difference between juveniles and adult tolerances is intelligible.

Conversely, *P. argenvillei*, *P. cochlear* and *P. longicosta* are non-migratory and occupy narrower fixed zones throughout life. Associated with this, their tolerances remain more constant, and have a smaller range (table 3).

Large numbers of newly settled *P. granularis* were recorded at Kommetjie in July 1972, from midtide level downwards, and at Dalebrook in August 1971, similarly distributed over the shore. In both cases substantial mortality occurred within two days, leaving only low level juveniles and a few animals in moist cracks. This suggests that desiccation severely restricts juvenile zonation, but that as tolerance increases the animals are able to migrate up the shore. This explains why juveniles are found high on the shore amongst barnacles (which remain moist during exposure) and may also account for the correlation between *P. granularis* densities and barnacle cover (Section VII, p. 7).

It can be argued that high level specimens acclimate and can therefore tolerate greater water loss (that is, the degree of exposure determines the tolerance and not vice versa). This type of acclimation has never been investigated, although Davies (1969a) has shown that high level *P. vulgata* are more tolerant than low level specimens. (He does not state the size of the animals involved: if they were of similar size, acclimation may be implicated.) Wallace (1972) has shown a similar effect in Acmaea testudinalis collected from high levels, subtidally and in intertidal pools. The latter were most susceptible to water loss, and Wallace ascribes this to their smaller size. High level specimens were more tolerant than subtidal individuals of the same size, possibly because of "physiological adaptation". Micaleff (1966, fig. 2.2), working on four trochid gastropods, showed that surprisingly resistance to water loss decreased in summer, implying undercompensation (negative acclimation).

High level P. vulgata are more tolerant to salinity extremes than their low level counterparts (Arnold, 1972), and this difference is acquired with age and is not inherent. P. vulgata also migrates up the shore so that older more tolerant animals occur at higher levels. Desiccation and high salinity have similar effects in that water is lost from the body.

Whether acclimation occurs or not, the tolerance of an individual at any given time will set upper limits on its zonation. Behavioural patterns probably keep most animals well within lethal limits, except during unusual conditions. So for example, P. granularis migrates down the shore under hot conditions (Section VI, p. 4 ). High level P. granularis and P. granatina have more rigid homing habits than their lower level counterparts, thus reducing water loss (Branch, 1971, and Section VI, p. 5 ). In Acmaea limatula retention of water in the pallial cavity forms a "buffer" between the blood and the external medium, reducing water loss from the body (Segal and Dehnel, 1962). In these ways lethal limits are avoided and behaviour plays an important part in establishing zonation patterns.

Nevertheless, seasonal hot weather often results in crash mortalities of the upper shore fauna and flora. There are several records of catastrophic mortalities of high level limpets, particularly during calm hot conditions (Orton, 1933; Lewis, 1954; Hodgkin, 1960; Frank, 1965; Sutherland, 1970). At Kommetjie in February 1969, an exceptional heat-wave associated with calm seas resulted in a massive mortality of upper level P. granularis.

Thus although limpets may live below lethal limits most of the time, periodic exceptional conditions will eliminate those which live closest to the lethal limits. The close correlation between zonation and tolerance also suggests that desiccation is the ultimate limiting factor, restricting migration up the shore. Chaisermartin (1971) has given intriguing evidence that if P. depressa is transplanted high on the shore, excess concentration of calcium and magnesium reduces muscular action so that the limpet is washed away.

In non-migratory species small individuals may be restricted by water loss. Juveniles of P. longicosta, P. cochlear and P. argenvillei died within three hours of exposure at 21°c. and 70% relative humidity. Larger specimens will lose water more slowly, but remain in the same zone as juveniles. Clearly their position is not restricted by physical factors, as they can tolerate exposure more readily than the juveniles. In these cases food may limit zonation: the upper limit of P. cochlear coincides with that of lithothamnion; and P. longicosta is restricted to territorial gardens of Ralfsia expansa.

Tentatively it can be suggested that the non-migratory species may settle selectively in relation to food, wave action or gregariousness, and that their zonation is regulated predominantly by behavioural traits; migratory species settle more randomly and are subject to physical selection, their upper limits being set by desiccation.

## SUMMARY:

1. The rate of water loss from seven South African *Patella* spp. has been investigated. Water loss is most rapid in smaller individuals and they are also least tolerant.

2. Rate of water loss is related to shell shape. In some species shell height becomes proportionally greater with age, thus reducing water loss. In others, growth is isometric, and rate of water loss varies with the power of -0.33 of body weight.

3. Tolerance is related to zonation, but there is no obvious relationship between zonation and shell shape, or zonation and rate of water loss.

4. Migratory species have a wide range of tolerances, correlated with their habit of moving up the shore. Non-migratory species have a smaller range of tolerances. Desiccation is likely to limit the former species but not the latter.

## REFERENCES:

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

ARNOLD, D.C. 1957. The response of the limpet *Patella vulgata* L. to waters of different salinities. *J. mar. biol. Ass. U.K. 36* : 121-128.

—— 1972. Salinity tolerances of some common prosobranchs.

SUPPORTING PAPER:

Ibid. 52 : 475-486.

BANNISTER, J.V. 1970. Some adaptational differences in the limpets *Patella coerula* and *Patella lusitanica* in relation to zonation. Unpublished M.Sc. thesis, Malta University.

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.

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 gastropods in False Bay, South Africa. *Trans. roy. Soc. S. Afr. 28* : 254-292.

BROWN, A.C. 1960. Desiccation as a factor influencing the vertical distribution of some South African gastropods from intertidal rocky shores. *Portug. acta. Biol.*(B) *7* : 11-23.

CHAISERMARTIN, C. 1971. le "stress" hydromineral et la zonation de Patellidae. *C.R. Seances Soc. Biol. Filiales 164* (10) : 2088-2091.

COLMAN, J. 1933. The nature of the intertidal zonation of plants and animals. *J. mar. biol. Ass. U.K. 18* : 435-476.

DAVIES, S.D. 1969a. Physiological ecology of Patella. III. Desiccation effects. *Ibid*. *49* : 291-304.

——— 1969b. Effect of environment on metabolic activity and morphology of Mediterranean and British species of *Patella*. *Publ. Staz. Zool. Napoli*. *37* : 641-656.

——— 1970. Physiological ecology of *Patella*. IV. Environmental and limpet body temperatures. *J. mar. biol. Ass. U.K*. *50* : 1069-1077.

DOTY, M.S. 1957. Rocky intertidal surfaces. *In* Treatise on Marine Ecology & Paleoecology (Ed. J.W. Hedgepeth). *Geol. Soc. Am. Mem. 67. 1* : 535-585.

EVANS, R.G. 1948. The lethal temperatures of some common

British littoral molluscs. J. anim. Ecol. 17 : 165-173.

FOSTER, B.A. 1971. Desiccation as a factor in the intertidal zonation of barnacles. Mar. biol. 8 : 12-29.

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

HODGKIN, E.P. 1960. Patterns of life on rocky shores. J. roy. Soc. West. Austral. 43 : 35-45.

KRISTENSEN, I. 1969. Heart rhythm in Patella and Diodora when exposed to air. Pubbl. staz. Zool. Napoli. 37 : 44-50.

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

MICALEFF, H. 1966. Ecology and behaviour of selected intertidal gastropods. Unpublished Ph.D. thesis, Queen Mary College, London University.

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

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

—— 1933. Some limiting factors in the environment of the common limpet. Nature 131 : 693.

SEGAL, E. and DEHNEL, P.A. 1962. Osmotic behaviour in an intertidal limpet, Acmaea limatula. Biol. Bull. 122 : 417-430.

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

SOUTHWARD, A.J. 1958. Note on the temperature tolerances of some intertidal animals in relation to environmental temperature and geographic distribution. J. mar. biol. Ass. U.K. 37 : 49-66.

STEPHENSON, T.A. 1942. The causes of the vertical and horizontal distribution of organisms between tide marks in South

Africa. Proc. Linn. Soc. Lond. 154 : 219-232.

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

WALLACE, L.R. 1972. Some factors effecting vertical distribution and resistance to desiccation in the limpet Acmaea testudinalis (Muller). Biol. Bull. 142 (1) : 186-193.

---o0o---

## APPENDIX I. Relationship between % water loss per hour (r) and wet flesh weight (w).

*P. granularis* $r = 15.62\ w^{-0.45}$

*P. granatina* $r = 14.89\ w^{-0.43}$

*P. cochlear* $r = 17.43\ w^{-0.36}$

*P. barbara* $r = 19.37\ w^{-0.36}$

*P. argenvillei* $r = 20.87\ w^{-0.51}$

*P. oculus* $r = 27.30\ w^{-0.32}$

*P. longicosta* $r = 19.74\ w^{-0.31}$

## APPENDIX II. Relationship between shell height (h) and length (L). $h = cL^{\alpha}$ ($\alpha$ = constant of allometry).

*P. granularis* $h = 0.0957\ L^{1.34}$

*P. granatina* $h = 0.0832\ L^{1.36}$

*P. cochlear* $h = 0.2859\ L^{0.97}$

*P. barbara* $h = 0.2588\ L^{1.09}$

*P. argenvillei* $h = 0.1271\ L^{1.31}$

* *P. oculus* $h = 0.0542\ L^{1.09}$

*P. longicosta* $h = 0.3429\ L^{0.91}$

* Excluding initial allometry (see text).

## RESUME :

## RESUME:

The ecology of eleven South African Patella spp. has been analysed, with particular reference to feeding, zonation and movements; gonadial cycles; intra and interspecific competition; predation; commensalism and parasitism; and the effects of desiccation. The more important results have been summarised at the end of each section, and this resume serves to integrate the results.

Up to ten Patella spp. may occur on the same shore. This coexistence is maintained by the balance between intraspecific and interspecific competition.

Intraspecific competition may be considerable, (as has been demonstrated in P.cochlear and P.granularis) resulting in reduced body size, growth rate, and gonad output, and a higher mortality. Competition is naturally less in the more sparce species. The limpets are divisible into two groups, "migratory" and "nonmigratory" which employ different methods to reduce intraspecific competition.

Migratory species (P.granularis, P.granatina, P.oculus and P.concolor), move progressively up the shore, thus experiencing wider and more diverse resources. Associated with this, they are generalised browsers, lack territories, are not aggressive to like species, and exhibit no sharp adult-juvenile differentiation. Behaviour is variable and adaptable. Scars and homing behaviour are developed to different degrees depending on the degree of desiccation experienced.

Predators induce rapid flight of smaller animals, and aggressive attack by larger animals, and the response varies with the predator species. In keeping with the upward migration, tolerance to desiccation increases with age. These features typify adaptable generalised species.

Nonmigratory species (P.cochlear, P.longicosta, P.tabularis, P.miniata, P.compressa, and possibly P.argenvillei), remain at the site of settlement throughout their lives, and occupy narrow habitats. The group has developed different mechanisms to reduce intraspecific competition: territorial defence of a specific foodplant; dispersion and spacing of the population; and marked adult-juvenile differentiation with respect to food or habitat. Tolerance to desiccation remains fairly constant throughout life. Nonmigratory species are also typified by their inflexible behaviour: scars are well developed and homing behaviour rigid; responses to predators inflexible. Irrespective of the predator involved, the limpets move to, and clamp on, their scars. These features are typical of specialised species occupying narrow niches.

Interspecific competition occurs for food and space. Differentiation of food requirements, zonation and distribution reduces competition, but overlap still occurs in several cases: P.cochlear and P.longicosta; P.longicosta and P.oculus; P.concolor and Cellana capensis; and between P.granularis and barnacles.

Zonation of migratory species is determined by their relative tolerances to desiccation, but nonmigratory species are limited by their behaviour or possibly their foodplants. Distribution patterns are primarily dictated by temperature differences between the cold temperate West coast, the warm temperate South coast, and the subtropical East coast. In general the cold water species spawn in May or June (Autumn to Winter) while their warm water counterparts spawn in August to November (Spring to Summer). All spawn once a year, with the possible exception of P.oculus (which is also exceptional in being a consecutive hermaphrodite). It has been demonstrated that the timing of spawning, seasonal temperatures, and inshore currents are all important in explaining distribution patterns.

Specialisation is the most important mechanism allowing coexistence of competing species. P.concolor and Cellana capensis have divergent requirements with respect to moisture and sand and are thus partly separated. P.longicosta excludes P.oculus from its narrow niche, but because P.oculus occupies a broader niche (potentially including that of P.longicosta), coexistence continues.

Specialised feeding (usually associated with territorial behaviour), has a considerable effect on growth rates. Generalised browsers have rapid growth rates, while species feeding specifically on Ralfsia expansa or lithothamnion grow slowly but have a much greater longevity. Growth does not vary seasonally unless food is very limited by competition, in which case gonadial growth takes preference over somatic growth.

The generalised migratory species compete by exploitation, with consequent wastage and higher mortality. A high replacement rate will thus be favoured, and these species are characterised by rapid growth to sexual maturity, and a high gonadial output. Specialised species compete by interference, minimising wastage and mortality, and population stability is favoured: growth is slow, longevity high, and gonadial size small.

Other mechanisms allowing continued coexistence of competing species include intrinsic control of population densities, extrinsic control of niche size, differential predation, migration and recruitment into areas of competition, and increase in biological complexity. Diversity is also increased by the invasion of "unoccupied" niches, as for example *P.compressa* on the kelp *Ecklonia maxima*.

Intertidally, a large number of animals are associated with *Patella* spp., gaining shelter and moisture during low tide. Only five species can be considered as commensals: the amphipod *Calliopiella michaelseni*, the isopods *Dynamenella australis* and *D.scabricula*, the turbellarian *Notoplana patellarum*, and a new species of copepod, *Scutellidium patellarum*. Their relationships with *Patella* spp. are described.

The incidence of parasitism is low, although up to 25% of *P.granatina* may contain trematode cercaria in the digestive gland.

# CONTRIBUTIONS TO THE FUNCTIONAL MORPHOLOGY OF FISHES

## PART III. THE FEEDING MECHANISM OF *SYNGNATHUS ACUS* LINNAEUS

G. M. BRANCH

*Zoology Department, University of Cape Town*

## INTRODUCTION

*Syngnathus acus*, the pipe-fish, has a fairly wide distribution, being recorded from the west coast of South Africa and in the western Indian Ocean; its range extending as far as the West Indies. In European waters it is found in the Mediterranean and the East Atlantic (Smith 1949). It generally occurs in shallow waters, although one specimen has been dredged in sixty fathoms of water off Algoa Bay (Smith 1963).

In South Africa it is often found in large numbers, in beds of *Zostera*—a common estuarine weed. The fish is particularly suited to this habitat, for its slim elongate body is camouflaged among the long threads of *Zostera*. The colour of the fish varies, as *Syngnathus* has the ability to slowly alter its colour to suit that of its environment. Generally the ground colour is green or brown, with bands, spots, and stripes of green, brown and yellow. This colouring and pattern renders the fish inconspicuous in the *Zostera* beds. This deception is heightened by the slow swaying motion of the fish: for this resembles the way in which the weed is swirled about by the tidal waters. The fish moves quite slowly by undulations of the small dorsal fin, and more rapidly by a rhythmic wave-like motion of the elongate body, accompanied by spreading of the caudal fin.

The male carries the eggs in a covered brood-pouch situated on the tail. Specimens examined bore between 200 and 300 eggs, and one male "gave birth" to about 300 young fish in the aquarium.

Little work has been done on the functional anatomy of *Syngnathus*, although Kindred (1924) has studied the osteology and development of the skull of *S. fuscus*, and McMurrich (1883) that of *S. peckianus*. Gregory (1933) has investigated the skulls of allied species, and his work has been used to compare *S. acus* with related forms.

## MATERIAL AND METHODS

Twenty-seven specimens of *S. acus* were captured in Knysna lagoon, by netting in about four feet of water amongst fairly thick beds of *Zostera*. Of these, ten were kept alive, and the others preserved in 7 per cent neutral formalin. The length of the fish varied from 4 cm. to 15 cm. The live specimens were kept in a sea-water aquarium at 18°C, and were fed on *Artemia* nauplii.

Most of the work was done by microdissection and the results verified by reconstruction of serial sections after the method of Pusey (1939). For sectioning, small specimens of about 4 cm. long were decalcified in 5 per cent nitric acid, and bulk-stained in Mayer's acid haemalum. Sections were cut at 15$\mu$ and counterstained with erythrosin. Muscle nomenclature follows that outlined in the introduction to this series (Millard 1966), unless otherwise stated.

## OSTEOLOGY

### *General considerations*

The skull is modified by the development of an elongate snout, which bears the small mouth at its terminal end. The orbits are large and bounded dorsally by the cranial roof, and ventrally by the parasphenoid and anterior projections of the preopercular bones. The operculum is large and rounded, extending downwards so that the two opercular bones almost meet ventrally. The hyoid arch is small and the bones tend to be fused to one another.

Due to the development of bony rings around the body, the head is held rigid, and there is little need for articulation between the skull and the vertebral column. Consequently the occipital condyles are reduced. The immobility of the skull is increased by the fusion of the first three vertebrae.

The pectoral girdle is well developed but partially fused to the bony rings around the body. The cleithrum and post-temporal are fused to these rings, but the postcleithrum and coracoid are free and extend longitudinally. The scapula is small, but bears a pectoral fin. Both pelvic bones and pelvic fins are absent.

### *Osteology of the Head*

The orbit is roofed by the frontal bones which also cover the neurocranium. The parietals are fused together medially and lie superficially over the epiotics, extending backwards to cover parts of the supraoccipital and the pterotics. The epiotics are thin scale-like bones situated almost superficially on the skull, while the pterotics, supraoccipitals, and frontals are fused and the sutures between them indistinct. The pterotics do not extend upwards to meet across the midline of the skull, as described for *S. peckianus* by McMurrich (1883).

The sphenotic is prolonged downwards behind the eye, and meets the preopercular, which lies beneath the orbit. Anteriorly a prefrontal and a suborbital complete the ring of circumorbital bones. Running medially below the orbit is the parasphenoid, which has lost its connection with the vomer, and ends at the front of the orbit, abutting against the mesethmoid.

The front of the head is produced forwards into an elongate cylindrical snout which tapers towards the small mouth. Laterally this snout is made up of enormously elongated quadrate bones, and dorsally it is roofed by the dermethmoid and vomer.

The preopercular (termed the infraorbital by McMurrich 1883) extends forwards from the operculum, underneath the snout (Fig. 1). The interoperculars have also been produced forwards in a similar manner and have lost their connection with the rest of the opercular complex: they lie ventrally medial to the quadrate bones (Figs. 2 and 10) and are attached by ligaments to the mandibles and the hyoid arch (Fig. 6). McMurrich considers the interopercular to be lacking in *S. peckianus.*

FIG. 1

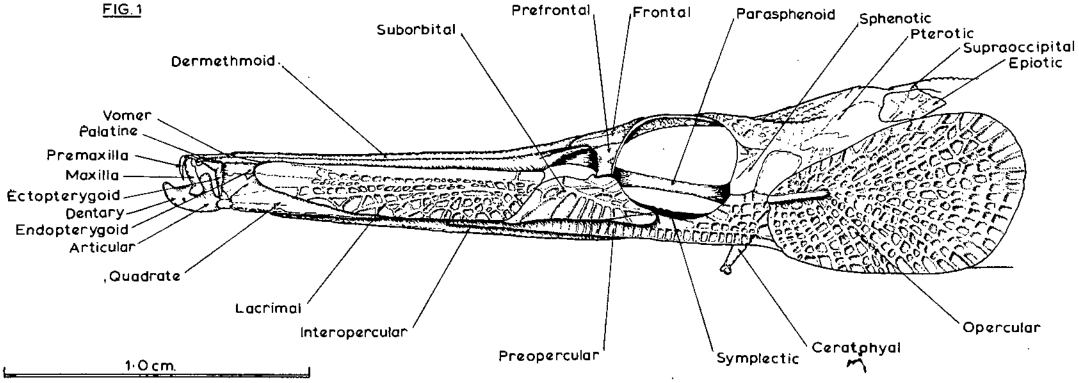


Fig. 1 *Syngnathus acus.* Left lateral view of skull.

FIG. 2

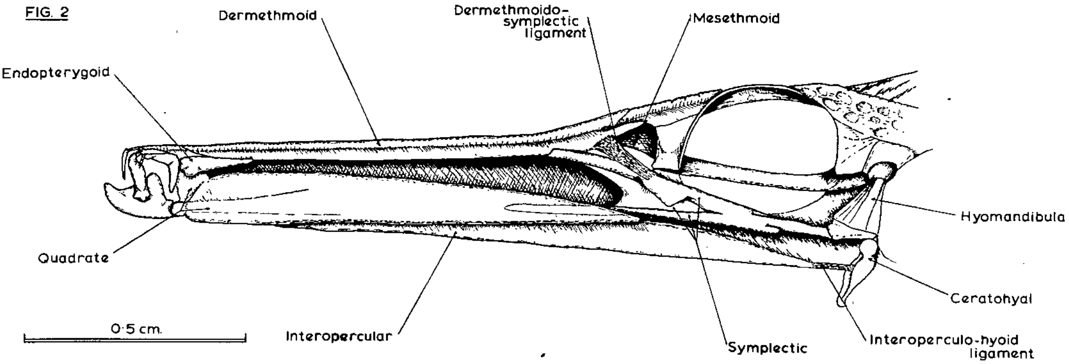


Fig. 2 *Syngnathus acus.* Left lateral view of skull after removal of lacrimal, suborbital, and preopercular bones.

The snout is further strengthened by two bones which encase the snout laterally. The homology of these bones is controversial and is discussed below (p. 73). In this work they are regarded as the lacrimal and suborbital which have lost their original position under the eye, and with protrusion of the skull to form a snout, have been carried forwards (Fig. 1). The nasals are lacking.

Due to the arrangement of the bones, and the large amount of dense connective tissue between them, the snout is a fairly rigid tube. There is little longitudinal movement of the bones, with the exception of the interopercular.

The premaxilla is considerably reduced and lies anterior to a larger (but also reduced) maxilla. The premaxilla is held in place by a ligament extending across the maxilla to the palatine bone (Fig. 4). A ligament also stretches between the maxilla and the palatine, and from maxilla to vomer. The maxillo-mandibular ligament is well developed, being inserted on the upper inner edge of the maxilla, and running down to the dentary. The dentary and the articular are fused to such an extent that they are indistinguishable: the latter articulates with the quadrate bone. The retroarticular is a tiny loose bone at the base of the articular. Neither the mandible nor the premaxilla bear teeth.

The quadrate extends the whole length of the snout to meet the symplectic. A narrow limb of the latter is contained in a groove of the quadrate, while its upper portion abuts against the dermethmoid and is linked to it by a strong ligament (Fig. 2). Posteriorly the symplectic narrows and meets the hyomandibula, which articulates with the otic region of the skull. The hyomandibula has only a single articulatory facet with the skull, which increases its freedom.

The quadrate is held rigidly by the lacrimal and suborbital which encase it.

All the palatal bones are reduced in size, and the palatine, ectopterygoid, endopterygoid, and vomer, have been carried forward to the front of the snout (Figs. 1 and 4). The parasphenoid lies below the orbit and has lost contact with the other palatal bones.

*S. acus* has a comparatively large operculum, due to the size and shape of the opercular bone: this is an oval convex bone, which articulates anteriorly with the hyomandibula (Fig. 1). The subopercular is reduced and lies ventrally medial to the opercular, being loosely attached to it by connective tissue (Fig. 6). The preopercular and the interopercular constitute part of the snout, as discussed above.

The hyoid arch has several muscles inserted on it, and its action constitutes an important part of the respiratory cycle. The ceratohyoids are large, and each bears two long slender branchiostegal rays (Fig. 6). The median basihyoid is extended back as a long thin urohyal. Passing medially forwards is the embryonic copula communis, which extends from the first branchial arch, forwards between the two ceratohyoids, to form the os entoglossum of the adult. Cartilage persists in the interhyal which articulates with the hyomandibula. The ceratohyoid can to a certain extent move on the interhyal, although this movement is somewhat restricted. Fusion has occurred between the hypohyal and the ceratohyoid, and the epihyal is apparently absent.

All the branchial arches are reduced to a certain extent, and are delicate slender structures. The first two bear their full complement of elements, except for the basibranchials which are missing. The copula communis links the hypobranchials of the first branchial arch, while those of the second arch extend ventrally to meet one another. Elongate pharyngobranchials pass over the top of the arch and link the first two arches together. The third arch has lost its pharyngobranchial, and the fourth lacks both pharyngobranchial and epibranchial. Of the fifth arch, only a rudimentary element remains, which Kindred (1924) maintains is the hypobranchial.

The ceratobranchials pass around the pharynx in an anteroventral direction, and provide the anterior support for each of the four gill slits.

None of the branchial arch elements bear teeth, but the endothelium covering the ceratobranchials—and thus bordering the gill slits—is thrown into papillae which project across the gill slit and prevent food from entering the branchial chamber.

FIG. 3

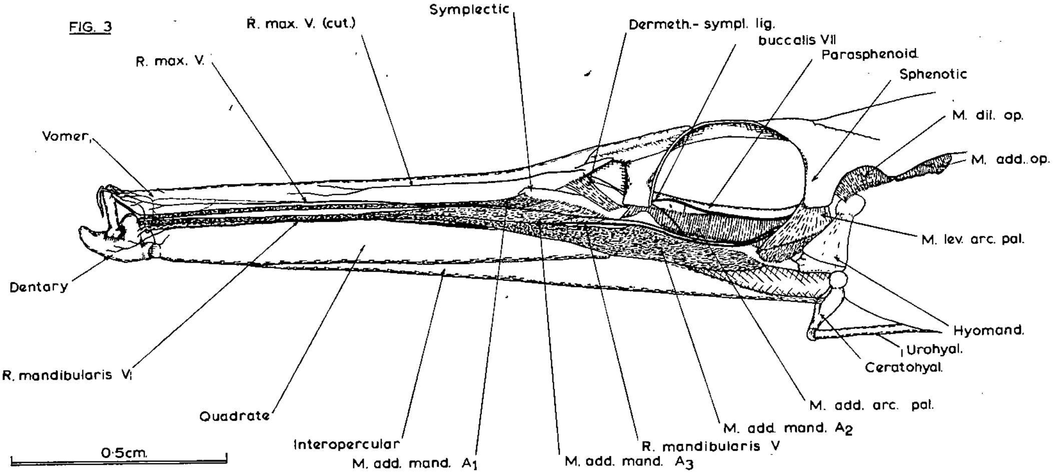


Fig. 3 *Syngnathus acus.* Dissection of cranial region to show muscles.

| | |
|---|---|
| Dermeth.-sympl. lig. | Dermethmoido-symplectic ligament |
| Hyomand. | Hyomandibula |
| M. add. arc. pal. | Musculus adductor arcus palatini |
| M. add. mand. A1, A2 & A3. | M. adductor mandibulae A1, A2 & A3 |
| M. add. op. | M. adductor operculi |
| M. dil. op. | M. dilatator operculi |
| M. Lev. arc. pal. | M. levator arcus palatini |
| R. max. V. | R. maxillaris V |
| R. max. V (cut). | R. maxillaris V (cutaneous) |

*Homologies of the Bones*

Most of the bones in the skull, although extensively modified in some cases, have obvious counterparts in the skulls of other fishes. However, the homology of some remains uncertain.

Working on the allied genera *Phyllopteryx* and *Solenostomus*, Gregory (1933) and Jungersen (1910) conclude that the two bones encasing the quadrate in the snout region are metapterygoid bones, which have presumably ossified in two portions in the former case; and that the lacrimal and suborbital bones have been lost. Gregory maintains that these bones are specialisations of the Syngnathid skull, and with reference to *Phyllopteryx*, states that it has "leading specialisations . . . of its own, notably the presence of a row of 'antorbital plates' on the sides of the oral tube . . ." (p. 226).

The present author contends that these antorbital plates are not in fact metapterygoid bones, but a lacrimal and a suborbital that have been carried forward with the elongation of the snout into an oral cone.

It seems very likely that the antorbital plates are of dermal origin, in contrast with the cartilaginous origin of the metapterygoid. They are finely sculptured and pitted in a manner that is characteristic of dermal bone. Sections cut of a young fish failed to show any cartilage in these bones, although it was obvious in all the recognised cartilage bones.

Although Kindred (1921 and 1924) has proved by embryological studies that the antorbital plates of *Syngnathus fuscus* are not cartilaginous in origin, he still regards the anterior of the two plates as the metapterygoid. His views are based largely on the relative position of this bone, for he states "I have regarded it as the homologue of the metapterygoid in other teleosts because it lies posterior to the pterygoid bone, postero-dorsal to the quadrate, postero-ventral to the short metapterygoid process of the pterygoquadrate cartilage, and in the position of the posterior flange in other teleosts". (1924, p. 427.)

The posterior of the two antorbital plates Kindred terms the infraorbital bone, which he and Swinnerton (1902) homologise with the anterior bones of the suborbitalia in *Gasterosteus.*

Further evidence that the antorbital plates are lacrimal and suborbital bones comes from a study of allied but less specialised forms included by Gregory in his order Thoracostei. According to Gregory (1933, p. 228) "in a general way, the gasterosteoids, the hemibranchs, and the lophobranchs form successive grades of organisation". Consequently it is reasonable to examine the less specialised gasterosteoids in an attempt to determine which bones are likely to form the antorbital plates.

*Gasterosteus aculeatus* represents the primitive stage in this group, showing no elongation of the front part of the skull: but it does have a large lacrimal and a prominent ring of suborbital bones (Gregory 1933, Fig. 102).

*Gasterosteus spinachia* has a partially elongated snout, and it is the lacrimal and first suborbital which extend forward over the snout, partially covering the quadrate (Gregory 1933, Fig. 103).

If this trend is continued further, it is easy to visualise how the long snout of *Syngnathus* can be formed, and how the lacrimal and suborbital could be carried forward from the margin of the orbit to form antorbital plates.

The condition of these plates in the Thoracostei lends further evidence for the phylogeny of the group, and this is discussed below (p. 88).

If these bones are the lacrimal and suborbital, it is difficult to say which bone is homologous with the metapterygoid. Starks (1902) states that the "pterygoid" bone becomes fused with the quadrate in *Fistularia.* In *S. acus* there is an upward extension of the anterior region of the quadrate (Figs. 2 and 3) which may be a fused "pterygoid". As the endopterygoid and the ectopterygoid are distinct and separate, this could be the metapterygoid. However, Starks has shown that the pterygoid of *Fistularia* can be separated from the quadrate by prolonged maceration: this is not the case in *S. acus.* Even after prolonged maceration this expansion of the quadrate remains attached, and there is no sign of a suture between it and the quadrate.

The fact that the metapterygoid is part of the mandibular arch supports the theory that the metapterygoid is fused to the quadrate.

The alternative is that the metapterygoid may have become fused to the symplectic, to form the upper limb of this bone—or at least part of it (Fig. 2). There is no dividing suture

FIG. 4

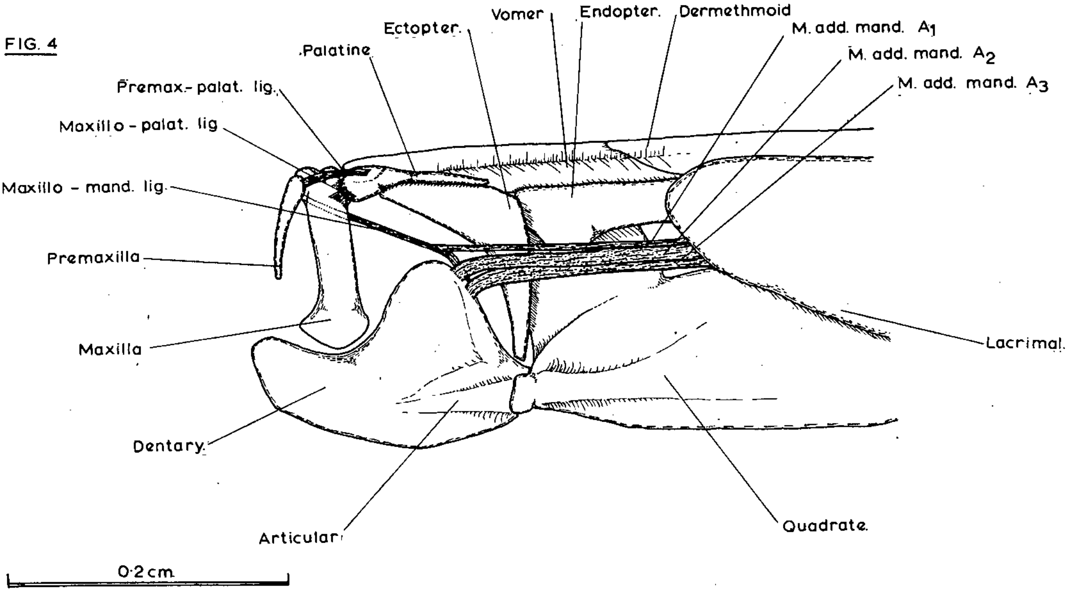


Fig. 4 *Syngnathus acus*. Left lateral view of mouth region, showing muscles and ligaments.

Ectopter. : Ectopterygoid
Endopter. : Endopterygoid
M. add. mand. A1, A2 & A3 : Musculus adductor mandibulae A1, A2 & A3
Maxillo-mand. lig. : Maxillo-mandibular ligament
Maxillo-palat. lig. : Maxillo-palatine ligament
Premax.-palat. lig. : Premaxillo-palatine ligament

here, nor can one be demonstrated by maceration, although the metapterygoid normally occupies such a position.

Finally, it is possible that the metapterygoid may have been lost, for most of the palatal bones are reduced in size.

## MUSCLES

### 1. *Adductor mandibulae*

Three sections of the adductor are present, extending from beneath the orbit to their insertion on the lower jaw. They pass over the quadrate but lie beneath the antorbital plates (Figs. 3 and 4). This constitutes further evidence that these are lacrimal and suborbital bones, for it is unlikely that the adductor muscles would pass medial to the metapterygoid.

With the development of an elongate snout, the tendons of the adductor sections have elongated. The body of the muscle lies beneath and in front of the orbit, while the long tendons stretch along the snout to their insertion on the jaws.

Adductor $A_1$ originates on the upper limb of the symplectic (Fig. 3) and passes forwards to its insertion on the maxillo-mandibular ligament (Fig. 4). The insertion is characteristic of this muscle, but its origin has shifted from its more normal position on the preopercular and metapterygoid, to the symplectic. Contraction exerts a tension on the maxillo-mandibular ligament, so that the maxilla and lower jaw are drawn backwards and inwards. Due to the connective tissue between the maxilla and the premaxilla, the latter is also pulled back. The mandible pivots at its articulation with the quadrate, and swings upwards and backwards, closing the mouth.

Sections $A_2$ and $A_3$ originate on the symplectic behind $A_1$ and extend to their insertion on the dentary. $A_3$ originates antero-dorsally to $A_2$, and then crosses under the latter half-way along the snout, to insert on the mandible ventrally to the insertion of $A_2$ (Fig. 3). The action of both these sections is to close the mouth by retracting the mandibles. The ligament between the maxilla and the mandible ensures a simultaneous retraction of the maxilla and the mandible.

The trigeminal nerve arises from the brain near to the facial nerve, and the two run together for a distance before diverging. The trigeminal divides into three principal rami. The superior ophthalmic passes forward over the orbit to supply the skin. The maxillary branch divides near the front of the orbit, one branch supplying the dorsal skin, and the other passing forwards to the mouth (Fig. 3).

The mandibular branch of the trigeminal nerve passes over $A_3$ and along its surface, under $A_2$, and after supplying twigs to the adductor, dives down to the lower jaw.

The position of this nerve in *S. acus* would thus support Kesteven's (1943) division of the muscle into a temperomasseteric group including $A_1$ and $A_2$, and situated superficial to the nerve, and a pterygoid group including $A_3$ situated medial to the nerve.

2. *Muscles of the palate*

(i) *Adductor arcus palatini.* Originating on the parasphenoid, this muscle passes downwards and outwards to its insertion on the symplectic (Figs. 3 and 5). It forms a thin sheet of short transverse fibres, which pass under the eye, bordering the orbit.

The action of the adductor arcus palatini is to pull the symplectic up and in, thus narrowing the buccal cavity. This movement is possible, as the symplectic can shift in the groove of the quadrate, and its posterior end is only loosely held to the hyomandibula.

From the back of the orbit the facial nerve gives off a thick branch, the buccalis, which passes along the parasphenoid, giving off very obvious twigs to the adductor arcus palatini. This is unusual, for the buccalis is usually a sensory somatic nerve and does not supply muscles.

(ii) *Levator arcus palatini.* This muscle originates from the inner surface of the sphenotic, and is inserted on the inside of the hyomandibula and the preopercular. As these bones are situated more medial than the sphenotic, the levator arcus palatini pulls the hyomandibula and preopercular outwards. Because the latter forms part of the snout rather than being associated with the operculum, its outward movement (and that of the hyomandibula) enlarges the buccal cavity. The action of the levator arcus palatini is therefore antagonistic to that of the adductor arcus palatini.

The mandibularis nerve of the trigeminal gives off a small twig at the back of the orbit, which innervates the levator arcus palatini.

FIG. 5

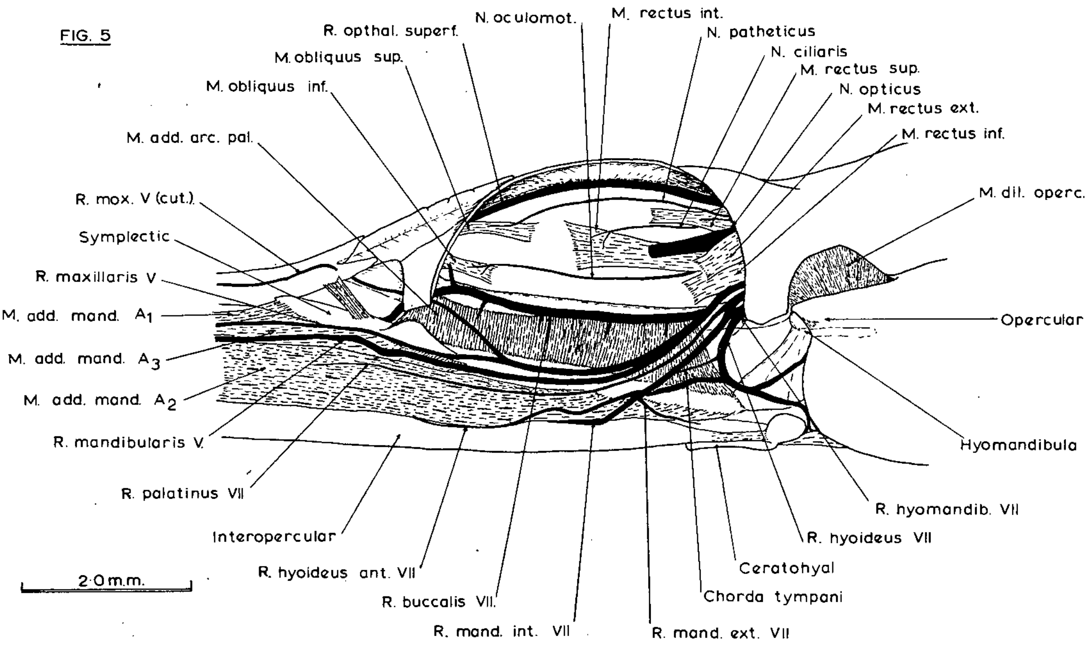


Fig. 5 *Syngnathus acus*. Muscles and nerves of the orbital region. Left lateral view.

| | |
|---|---|
| M. add. arc. pal. | Musculus adductor arcus palatini |
| M. add mand. A1 A2 & A3 | M. adductor mandibulae A1, A2 & A3 |
| M. dil. operc. | M. dilatator operculi |
| M. obliquus inf. | M. obliquus inferioris |
| M. obliquus sup. | M. obliquus superioris |
| M. rectus ext. | M. rectus externus |
| M. rectus inf. | M. rectus inferioris |
| M. rectus int. | M. rectus internus |
| M. rectus sup. | M. rectus superioris |
| N. oculomot. | Nervus oculomotorius |
| R. hyoideus ant. VII | Ramus hyoideus anterioris VII |
| R. hyomandib. VII | R. hyomandibularis VII |
| R. mand. ext. VII | R. mandibularis externus VII |
| R. mand. int. VII | R. mandibularis internus VII |
| R. max. V (cut.) | R. maxillaris V (cutaneous) |
| R. ophthal. superf. | R. ophthalmicus superficialis |

3. *Muscles of the ventral surface*

(i) *Rectus cervicis*. This muscle originates from the cleithrum and is inserted on the long urohyal, and its origin is partially confluent with the body muscles (Fig. 6). Contraction of the muscle pulls the urohyal back, rotating the hyoid arch backwards, so that instead of

FIG. 6

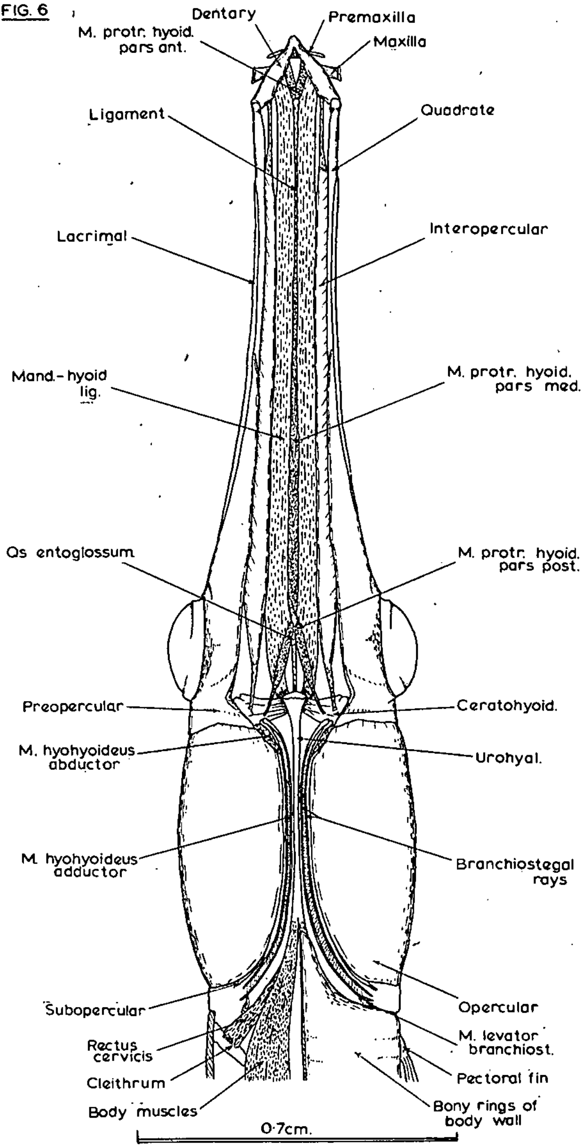


Fig. 6 *Syngnathus acus.* Ventral view of head dissected to show muscles. Bony, rings of body wall removed on left.

Mand.-hyoid lig. : Mandibulo-hyoid ligament
M. levator branchiost : Musculus levator branchiostegalium
M. protr. hyoid. pars ant. : M. protractor hyoidei pars anterioris
M. protr. hyoid. pars med. : M. protractor hyoidei pars medialis
M. protr. hyoid. pars post. : M. protractor hyoidei pars posterioris

FIG. 7

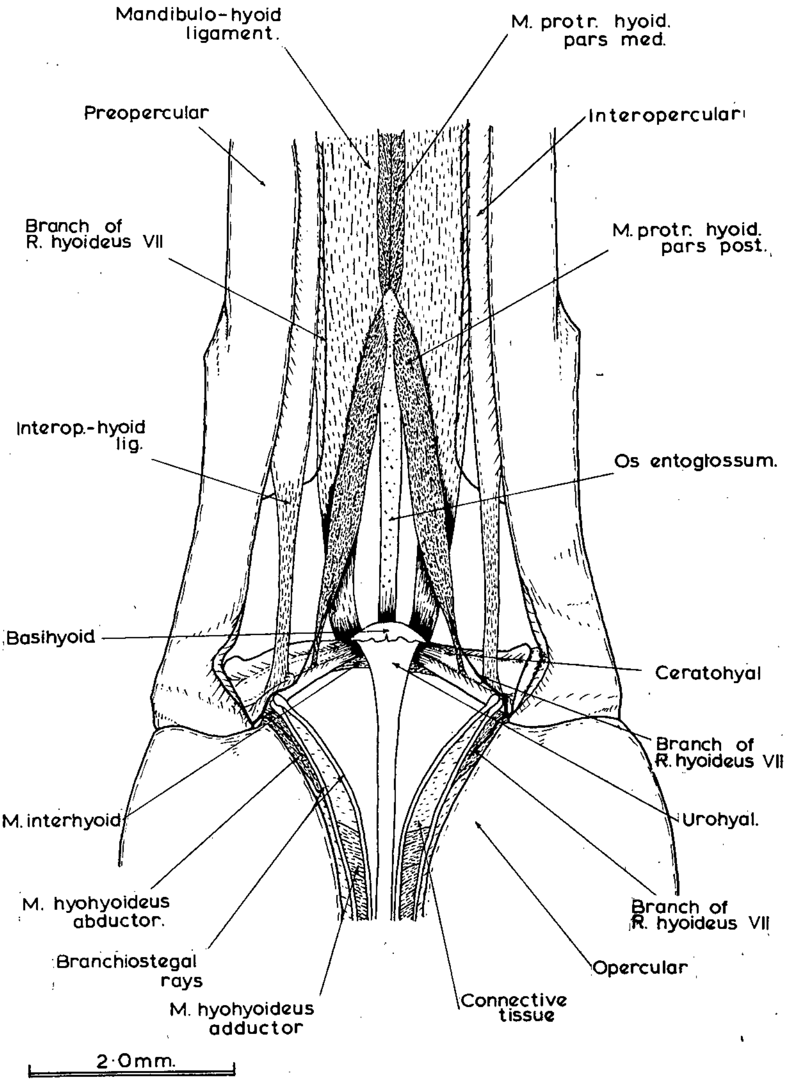


Fig. 7 *Syngnathus acus*. Ventral view of the orbital region, dissected to show the muscles and their innervation.

| | |
|---|---|
| Interop.-hyoid lig. | Interoperculo-hyoid ligament |
| M. interhyoid. | Musculus interhyoideus |
| M. protr. hyoid. pars med. | M. protractor hyoidei pars medialis |
| M. protr. hyoid. pars post. | M. protractor hyoidei pars posterioris |
| Branch of R. hyoideus VII | Branch of ramus hyoideus VII |

lying flat against the skull, the arch is rotated through about 65° to lie at an angle to the skull (Fig. 3).

The rectus cervicis is a hypobranchial muscle and is therefore innervated by spinal nerves.

(ii) *Protractor hyoidei.* The protractor hyoidei is a compound muscle extending from the mandibles to the hyoid arch. It lies between the interopercular bones (Fig. 6) and is covered by a loose and extensible layer of skin (Fig. 10).

The formation of this muscle is described by Edgeworth (1935) and summarised by Millard (1966) in the introduction to this series. The muscle is compounded of a posterior slip of the intermandibularis, and the interhyoideus which extends forwards. The two are associated more or less intimately to form a single muscle system.

In *S. acus* the interhyoideus apparently divides into two portions. A deep portion extends forward from the inner surface of the ceratohyoid (Fig. 7), to insert on the dentary. In this portion the contractile tissue is replaced by a tendinous connective tissue, forming the mandibulo-hyoid ligament (Figs. 6 and 8).

A superficial and more ventral portion of the interhyoideus extends forwards and is associated with the intermandibularis posterior to form the protractor hyoidei muscle (Figs. 6 and 10). A slip of the interhyoideus retains its position between the ceratohyoids (Fig. 7). Its function appears to be largely connective, and it is reduced in size and incapable of pulling the two ceratohyoids together.

The embryonic copula communis develops for the attachment of muscles, and forms the os entoglossum of the adult (Figs. 6 and 7). In *S. acus* the intermandibularis posterior and the superficial interhyoideus form part of the same functional muscle system—the protractor hyoidei—but they are not fused together. The superficial interhyoideus extends from the outer surface of the ceratohyoid to the os entoglossum (Fig. 7), thus forming the protractor hyoidei pars posterioris (Fig. 6). The intermandibularis posterior originates on the tip of the os entoglossum (Fig. 7), and inserts on the mandible, superficial to the mandibulo-hyoid ligament (Fig. 8). This muscle tends to be replaced by ligamentous tissue, so that the muscle is split into two contractile units, the protractor hyoidei pars anterioris, and the protractor hyoidei pars medialis (Fig. 6).

In *S. acus* the superficial portion of the protractor hyoidei is in a maximal state of contraction when the jaws are closed, indicating that it is more likely to effect adduction of the hyoid arch than abduction of the jaws. Cutting of the protractor hyoidei of a dead fish had no effect on the opening of the jaw, for this occurred automatically when the rectus cervicis was pulled, whether or not the protractor hyoidei was cut. The indication is that the jaw opening is effected by way of the mandibulo-hyoid ligament and the interopercular ligaments, and that the action of the protractor hyoidei is unnecessary. On the other hand, when the jaws were forcibly closed, the mandibulo-hyoid ligament caused only partial protraction of the hyoid arch if the protractor hyoidei was cut. It seems that this muscle is needed for complete protraction of the hyoid arch.

The strong development of the mandibulo-hyoid ligament must partially take over the function of the protractor hyoidei, accounting for the poor development of the latter.

Having components of both mandibular and hyoid arch origin, the protractor hyoidei is normally innervated by both facial and trigeminal nerves.

An anterior branch of the mandibularis V normally dives down to supply those parts of the protractor hyoidei which are of mandibular arch origin (Kesteven 1943), but no such nerve was found in *S. acus*. The hyoideus VII divides off from the hyomandibularis nerve, near the point where the latter energes from the back of the orbit, and gives off two branches. The hyoideus anterioris supplies the mandibulo-hyoid ligament, while the hyoideus posterioris passes back to the protractor hyoidei posterioris and the hyohyoideus muscles (Figs. 5 and 7).

(iii) *Intermandibularis anterioris*. Transverse fibres of this muscle stretch between the mandibles, and these hold the mandibles together (Figs. 8 and 9). When contraction occurs the mandibles are pulled together. The muscle is innervated by a small anterior branch of the mandibularis V.

### 4. *Muscles of the Operculum*

(i) *Dilatator operculi*. From its origin on the pterotic, the dilatator operculi passes over the articulation of the opercular with the hyomandibula, and inserts on the upper external surface of the opercular. Contraction enlarges the opercular chamber.

A fine posterior branch of the mandibularis V (which supplies the levator arcus palatini) gives off a twig innervating the dilatator operculi.

(ii) *Adductor operculi*. The adductor operculi originates from the pterotic underneath the opercular bone, and inserts on the inside of the latter. Its action is antagonistic to the dilatator operculi, and it pulls the opercular inwards, decreasing the volume of the branchial chamber.

Innervation is by the hyohyoideus posterioris, which gives off a twig passing up to the adductor operculi.

In *S. acus* no separate levator operculi can be distinguished.

### 5. *Muscles of the Branchiostegal Rays*

(i) *Hyohyoideus abductor*. This originates on either side from the base of the ceratohyoids, and passes back to be inserted on the outermost of the two pairs of branchiostegal rays (Fig. 7). The muscle is relatively small, and its function likely to be reduced. It pulls the branchiostegal ray nearer to the operculum, and as the second ray is pulled with it by the connective tissue, the rays of opposite sides are pulled apart. In conjunction with the expansion of the operculum, this aids in enlarging the branchial chamber.

(ii) *Hyohyoideus adductor*. This is a thin sheet of muscle stretched obliquely between the branchiostegal rays. The fibres are delicate and mixed with connective tissue (Figs. 6 and 7). Functionally this muscle is antagonistic to the abductor, for its contraction pulls the branchiostegal rays together, making the branchial chamber smaller.

Both hyohyoideus muscles are innervated by a posterior branch of the hyoideus VII (Fig. 7).

(iii) *Levator branchiostegalium*. This is the name applied to a small slip of muscle originating on the superficial fascia, medial and dorsal to the cleithrum, and inserting on the inner branchiostegal ray (Fig. 6). Its action is to pull the rays outwards, expanding the gill chamber.

FIG. 8

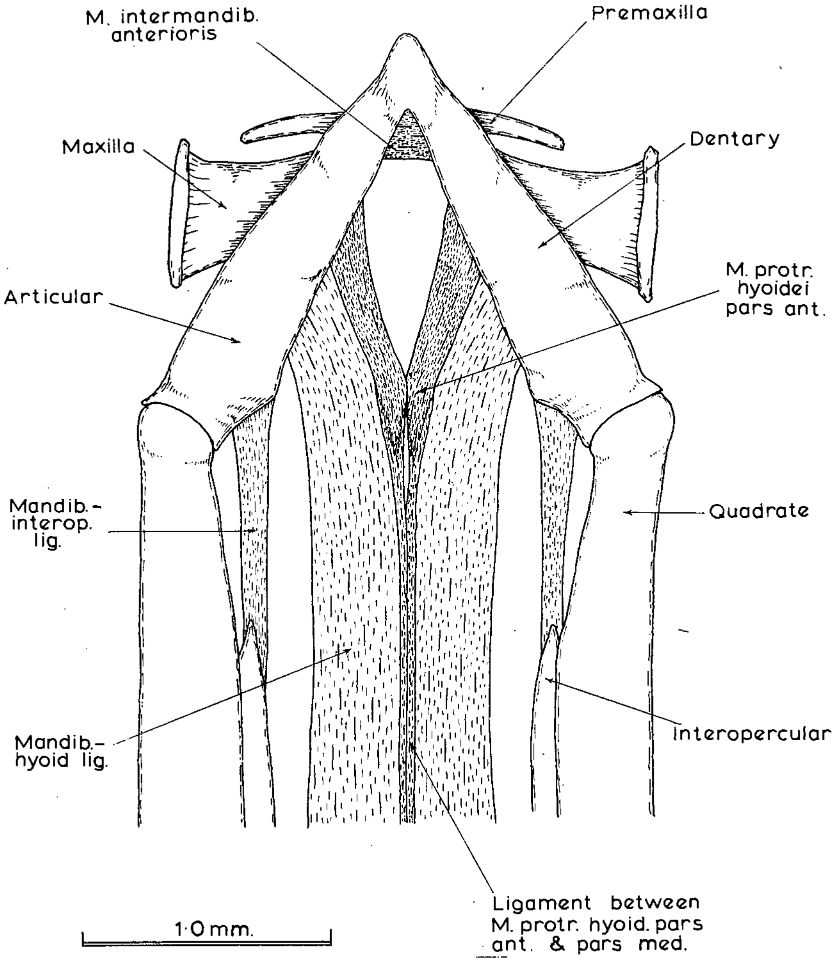


Fig. 8 *Syngnathus acus*. Ventral view of jaws, revealing muscles and ligaments.

Mandib.-hyoid lig. : Mandibulo-hyoid ligament
Mandib.-interop. lig. : Mandibulo-interopercular ligament
M. intermandib. anterioris : Musculus intermandibularis anterioris
M. protr. hyoid. pars ant. & pars med. : M. protractor hyoidei pars anterioris & pars medi

The levator occupies a similar position to the hyohyoideus dorsalis of Kesteven (1943), but is innervated by a spinal nerve and cannot therefore be considered one of the hyohyoideus group. There does not appear to be any homologous muscle in fishes described by other authors.

## DISCUSSION

### 1. *Method of feeding*

From observation of aquarium specimens, *S. acus* is known to feed on small crustaceans, and will even accept fresh-water forms like *Daphnia.* Examination of the stomach contents of several specimens revealed little except a few unidentifiable fragments of crustacean limbs. Serial sections of one fish did, however, reveal two complete copepods in the stomach. As these were intact, it seems unlikely that the fish breaks up the prey in any way before swallowing it.

*S. acus* seems to depend largely on its sense of sight to detect its food, for its large protruding eyes are sensitive to any movement. The fish approaches a small crustacean slowly and then sucks the animal in by drawing a swift current of water into the mouth. In this way the fish is capable of capturing crustacea over a centimeter from its mouth.

### 2. *Muscle action during feeding*

In most teleosts, ligaments between the hyoid arch and the interopercular and between this and the retroarticular process of the jaw, transmit the movement of the hyoid arch and operculum to the lower jaw. Consequently the lower jaw is abducted when contraction of the rectus cervicis rotates the hyoid arch backwards (Holmqvist 1910; van Dobben 1935 and Ballintijn and Hughes 1965).

In *S. acus* the mandibulo-hyoid ligament is of far more importance than the mandibulo-interopercular ligament in transmitting the movement of the hyoid arch to the lower jaw. Ligaments are also present which suspend the interopercular between the hyoid arch and the mandible, and these also convey movement of the hyoid arch to the mandible. Cutting of the interopercular ligaments and the mandibulo-hyoid ligament respectively, indicates that the latter is of far more importance in lowering the mandible than are the former.

The pull of the mandibulo-hyoid ligament on the lower jaw has a strong backward component, but also a weaker outward component. As the mandibles are loosely joined together, this outward component causes them to swing apart at their articulation with the quadrate bones, thus widening the gape. The quadrate bones are in turn pushed apart, so that the whole snout is widened.

The downward swing of the mandible rotates the maxilla and premaxilla forwards to increase the gape. There is no real protrusion of the upper jaw, but the ligamentous connection between the jaw bones and the snout allow some degree of movement.

During respiration, water is drawn into the buccal cavity by contraction of the levator arcus palatini, which pulls the hyomandibula outwards, and contraction of the rectus cervicis which rotates the hyoid arch downwards. This increases the volume of the buccal cavity; the consequent decrease of pressure results in water being sucked in. The effect is aided by the widening of the snout as described above. Subsequently the water is directed into the branchial chamber by mutual action of the opercular and buccal muscles.

FIG. 9

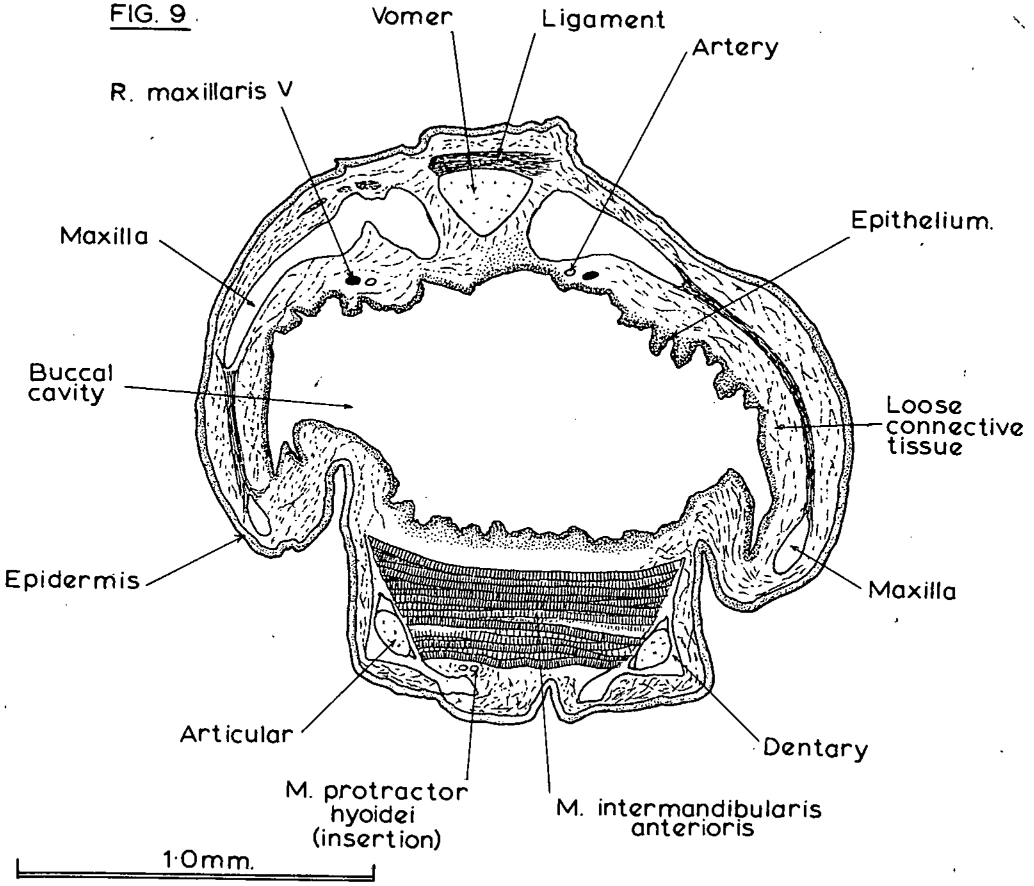


Fig. 9 *Syngnathus acus.* Transverse secton through jaws.

The dilatator operculi, hyohyoideus abductor, and levator branchiostegalium lift the operculum outwards and spread the branchiostegal rays. The branchial chamber is consequently enlarged and the water passes through the gill slits and into the gill chamber. The branchial aperture acts as a valve, preventing water from entering through it, but allowing deoxygenated water to be forced out.

The mouth is then closed by the action of the adductor mandibulae. Contraction of the intermandibularis, which narrows the mouth and the snout, and the action of the adductor arcus palatini, decrease the volume of the buccal cavity. Retraction of the hyoid apparatus by the protractor hyoidei and the mandibulo-hyoid ligament occurs simultaneously, and the remaining water is forced from the buccal cavity into the branchial chamber.

The function of the protractor hyoidei is partially replaced by the mandibulo-hyoid ligament, which transmits the movement of the upper jaw to the hyoid apparatus, thus aiding protraction of the hyoid arch when the jaws close. This explains the poor development of this muscle in *S. acus*. Partial protraction of the hyoid arch is therefore effected by the mandibulo-hyoid ligament, and the process supplemented by contraction of the protractor hyoidei muscle.

Evacuation of the gill chamber is brought about by contraction of the adductor operculi, and the hyohyoideus adductor, which pull the operculum inwards and the branchiostegal rays together respectively. The consequent decrease in volume forces the water out of the branchial aperture.

The action of the buccal cavity and the operculum can be likened to an interplay between a buccal pressure pump and an opercular suction pump. In the majority of teleosts it is the former which plays the predominant part (Saunders 1961), but in *S. acus* the reverse is true (Hughes 1960). This is principally due to the enlarged opercular cavity and the rigidity of the snout, for the former will increase the effectiveness of the opercular pump, while the latter inhibits the buccal pump. In addition, the opercular pump is aided by the almost complete closure of the opercular valve, which opens only at a small dorsal aperture.

The opercular pump is regulated by the opercular muscles and the branchiostegal muscles. In *S. acus* the branchiostegal muscles are of little importance; so much so that Hughes (1960, p. 42) states "there is no branchiostegal apparatus in this group". The branchiostegal apparatus is, however, present in *S. acus*, although admittedly it is relatively ineffective.

As these respiratory movements are continually performed without nearby particles of food being engulfed, it is obvious that the normal respiratory mechanism is inadequate for feeding. The additional suction necessary to engulf a crustacean is provided by the action of the rectus cervicis. This muscle normally pulls the hyoid arch backwards so that it rotates around at its articulation with the hyomandibula, and lies at an angle of about 65° to the skull, instead of flat against it. During prey capture the hyoid arch rotates even further, so that it lies almost perpendicular to the skull. This is presumably due to stronger contraction of the rectus cervicis than is normally experienced during respiration. Superimposed on the additional backwards rotation, the hyoid arch also twists outwards, forcing the hyomandibula bones apart. The net result is that the buccal and branchial chambers are expanded more than usual, creating sufficient suction to draw the prey in.

After the prey has been drawn into the mouth, the accompanying water is forced into the gill chamber by the usual expiratory muscles. Endothelial papillae stretch across the gill slits, and these act like a sieve, retaining any food. The food thus remains in the pharynx, and is passed down into the oesophagus.

The whole action of suction feeding is extremely rapid, and the fish must discriminate between desirable and undesirable objects before sucking anything into the snout. Food in the pharynx passes into the oesophagus, presumably forced there by a subsequent influx of water. The anterior end of the oesophagus and stomach is lined by a striated muscle, the sphincter oesophagi. Apparently it is not usual for striped fibres to extend over the stomach of fishes (Barrington 1957). Passage of the food into the oesophagus is aided by contraction of the pharynx while the sphincter oesophagi relaxes (Matthes 1963).

FIG. 10

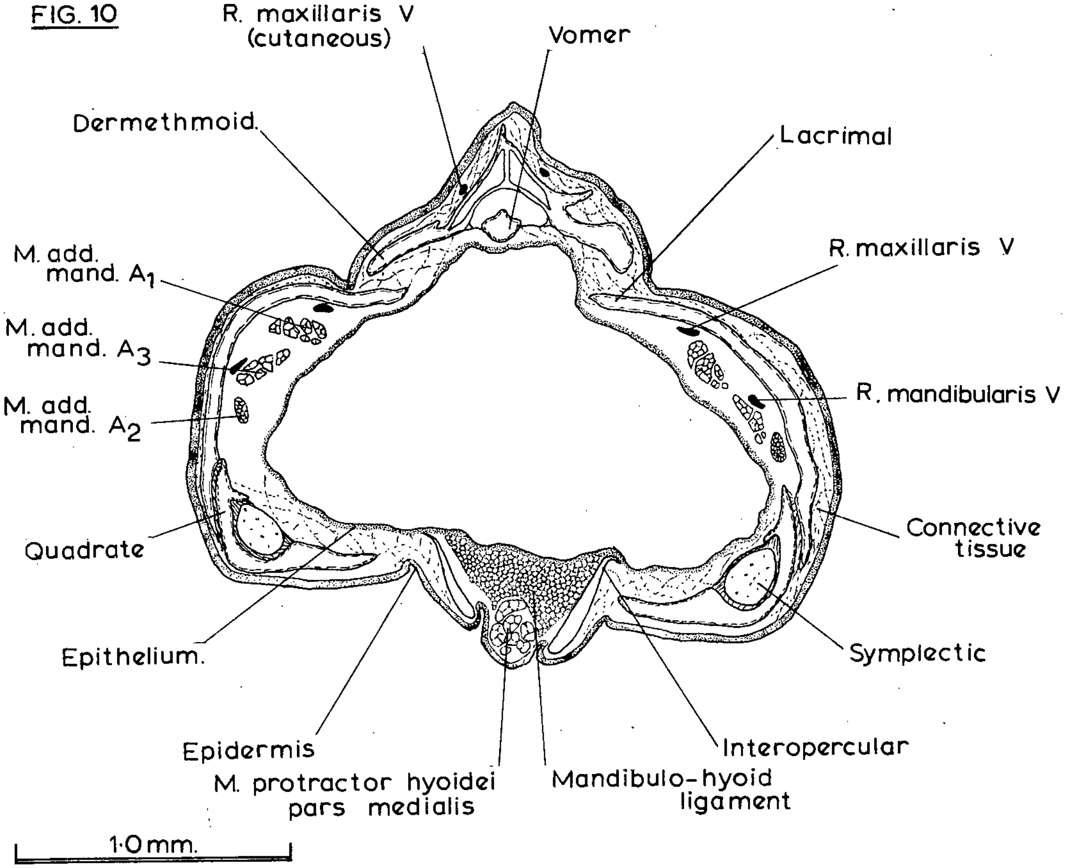


Fig. 10 *Syngnathus acus*. Transverse section through mid-region of snout.
M. add. mand. A1 A2 & A3 : Musculus adductor mandibulae A1 A2 & A3

### 3. *Adaptations of the head for feeding*

Judging from the method of feeding in this fish, it is likely that the snout has been developed in association with the sucking mechanism employed. An elongate and narrow snout with a small mouth not only increases the speed with which water can be sucked in, but also makes it possible for the fish to be more selective about what it sucks in.

The relative rigidity of the buccal cavity reduces the action of the buccal pump, but this is compensated for by the large branchial chamber, which enables a predominance of the opercular pump and increases the suction possible.

With the elongation of the snout, it is necessary for the muscles to shift their origins and become longer. In *S. acus* some of the muscles have changed their origins, such as the three sections of the adductor mandibulae. Increase of the length of the muscles is due to the development of long tendons in those muscles which lie longitudinally. The adductor mandibulae has extremely long tendons, and the protractor hyoidei is partially replaced by tendinous tissue.

Elongation of the fibres of longitudinal muscles will increase the speed of their contraction, a factor which is of some importance in this type of sucking mechanism.

The lack of teeth on the jaws and branchial arches is a reflection on the type of feeding habits, for the prey is swallowed whole. The filtering action of the branchial arches is aided by the development of epithelial papillae on the arches.

Selection of food before feeding seems to be of importance, for *S. acus* is very specific in the choice of particles that it swallows. Towards this end, the eyes are well developed. The nasal sacs are large and lined with a well developed epithelium, and it seems that both optic and olfactory senses play a part in food selection.

Many of the modifications of the head are therefore primarily aids to the method of feeding.

### 4. *Phylogenetic significance of the cranial anatomy*

As has been outlined in the introduction (Millard 1966), Eaton (1935) has suggested that the phylogeny of fishes is indicated by the arrangement of their cranial muscles, and the type of protractile mechanism which they possess. Four basic types of protractile mechanism are distinguished:

1. The non-protrusible mechanism of the Isospondyli.
2. The acanthopteran (Perciform) type where protrusion is controlled by crossed ligaments.
3. The cyprinodont type. The maxilla bears an internal hook which inserts into a socket on the premaxilla. Depression of the lower jaw twists the maxilla on its axis, driving the premaxilla forwards. No specialised ligaments are developed to control the movement.
4. The condition found in the Ostariophysi, of a single median ligament restricting the premaxilla.

Examination of the jaws of *S. acus* seems to indicate that the Syngnathidae are related to fishes of the cyprinodont type (Microcyprini of Regan, Cyprinodontiformes of Berg). *S. acus* is admittedly a highly specialised fish, and the mechanism of protrusion is absent, but certain generalisations can be made which support this relationship.

Despite the fact that the upper jaw is supported by many small ligaments, none of these are well developed, nor are they arranged as the typical perciform crossed ligaments; and there is no median rostral ligament as in the Ostariophysi. The lack of specialised ligaments in the upper jaw indicates closer affinity with the cyprinodont type than with any other type.

The presence of a rudimentary hook on the inside of each maxilla is further indication that the Syngnathidae are close to the cyprinodont type.

The usual systematic procedure is to place the sticklebacks, tube-mouths, and sea-horses in three groups, namely the Gasterosteoidea, Hemibranchii, and Lophobranchii; the last including the Syngnathidae. The three groups are associated in various ways by various authors.

Gregory (1933) includes all three as suborders of the Thoracostei. Regan (1929) associates the hemibranch and lophobranch fish in the order Solenichthyes, and considers the gasterosteoids to be a separate and unallied order—a view which is supported by the work of Starks (1902) on the hemibranch shoulder girdle. Berg (1947) places the Syngnathidae in the Syngnathiformes, allied to the hemibranch fishes (which he terms the Aulostomiformes). Smith (1950) also places the pipefish in a separate order, Lophobranchii, associated with the Aulostomi, but distinct from the gasterosteoids.

The present work indicates that the Syngnathidae (and their allied family, the Solenostomidae), differ markedly from the Hemibranchii in the development of antorbital plates. The view has already been put forward that these are lacrimal and suborbital bones, and the development or loss of these is indicative that there is a deep gap between the Lophobranchii and the Hemibranchii.

It is suggested that these two groups have evolved from the same ancestors, but that the elongate snouts of both are similar due only to parallel evolution; and it is further suggested that due to the retention of the lacrimal and suborbital, the Lophobranchii are more closely allied to the Gasterosteoidea than are the Hemibranchii.

## SUMMARY

1. The osteology of the skull of *Syngnathus acus* is described, with particular reference to the snout and jaws.
2. The homology of the antorbital plates is discussed, and evidence put forward that they represent lacrimal and suborbital bones.
3. The anatomy of the cranial muscles is described.
4. Based on the anatomical investigation and observation of the live animals, suggestions are put forward as to the method of feeding in *S. acus*. It is concluded that the animal captures food by a sucking mechanism, and the structure of the skull and muscles is discussed in this light.
5. Possibly phylogenetic affinities of the Syngnathidae and allied groups are put forward. It is suggested that the snouts of the Syngnathidae and the Hemibranchii are similar due only to parallel evolution.

## ACKNOWLEDGEMENTS

My thanks must be most sincerely extended to Dr. N. A. H. Millard, under whose guidance this work was performed; and to Mr. N. Fuller for maintaining aquarium specimens for my observations on the live fish. This paper was published with the aid of a grant from the University of Cape Town.

## REFERENCES

BALLINTIJN, C. M. and HUGHES, G. M. 1965. The muscular basis of the respiratory pumps in the trout. *J. exp. Biol.* 43: 349–362.

BARRINGTON, E. J. W. 1957. The alimentary canal and digestion. Chap. 5 in "The Physiology of Fishes". (Ed. Brown, M. E.). Academic Press, New York.

BERG, L. 1947. Classification of Fishes both Recent and Fossil. J. W. Edwards, Ann Arbor.

EATON, T. H. 1935. Evolution of the upper jaw mechanism in teleost fish. *J. Morph.* 58 (1): 157–173.

EDGEWORTH, F. H. 1935. The Cranial Muscles of Vertebrates. Cambridge Univ. Press.

GREGORY, W. K. 1933. Fish Skulls. A Study of the Evolution of Natural Mechanisms. *Trans. Amer. phil. Soc.* 23: 75–481.

HOLMQVIST, O. 1910. Der Musculus Protractor Hyoidei (Geniohyoideus auctt) und der Sekungsmechanismus des Unterkiefers bei den Knochenfischen. Zugleich ein Beitrag zur Kenntnis der Atembewegung. *Lund Univ. Arsskr.* (2) 6 (6): 1–24.

HUGHES, G. M. 1960. A comparative study of gill ventilation in marine teleosts. *J. exp. Biol.* 37 (1): 28–45.

JUNGERSEN, H. F. E. 1910. Ichthyotomical contributions II: the structure of the Aulostomidae, Syngnathidae, and Solenostomidae. *Dansk. vidensk. Naturv.* 8 (7): 268–364.

KESTEVEN, H. L. 1943. The evolution of the skull and cephalic muscles. I. The fishes. *Mem. Aust. Mus.* 8 (2): 63–132.

KINDRED, J. E. 1921. The chondrocranium of *Syngnathus fuscus*. *J. Morph.* 35 (2): 425–456.

KINDRED, J. E. 1924. An intermediate stage in the development of the skull of *Syngnathus fuscus*. *Amer. J. Anat.* 33 (3): 421–448.

MATTHES, H. 1963. A comparative study of the feeding mechanisms of some African Cyprinidae (Pisces Cypriniformes). *Bijdr. Dierk.* 33: 3–35.

MCMURRICH, J. P. 1883. On the osteology and development of *Syngnathus peckianus*. *Quart. J. micr. Sci.* 23: 623–652.

MILLARD, N. A. H. 1966. Contributions to the functional morphology of fishes. Part I. Introduction. *Zool. Afr.* 2: 31-43.

PUSEY, H. K. 1939. Methods of reconstruction from microscopic sections. *J. R. micr. Soc.* 59: 232–244.

REGAN, C. T. 1929. Fishes. *Encycl. Brit.* (14), 9: 305–328.

SAUNDERS, R. L. 1961. The irrigation of the gills in fishes. I. Studies of the mechanism of branchial irrigation. *Canad. J. Zool.* 39: 637–653.

SMITH, J. L. B. 1949. *Sea Fishes of Southern Africa.* Central News Agency, Cape Town.

SMITH, J. L. B. 1963. Fishes of the family Syngnathidae from the Red Sea and the Western Indian Ocean. *Ichthyological Bulletin* 27. Rhodes Univ., Grahamstown.

STARKS, E. C. 1902. The shoulder girdle and characteristic osteology of the Hemibranchiate fishes. *Proc. U.S. Nat. Mus.* 25: 619–634.

SWINNERTON, H. H. 1902. A contribution to the morphology of the teleostean head skeleton. *Quart. J. micr. Sci.* 45: 503–593.

VAN DOBBEN, W. K. 1935. Ueber den Kiefermechanismus der Knochenfische. *Arch. néerl. Zool.* 2: 1–72.