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

I. ZONATION, MOVEMENTS AND FEEDING

G. M. BRANCH
Department of Zoology, University of Cape Town

INTRODUCTION

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 The paper includes information drawn from various sources, particularly from the unpublished projects of Mr.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

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

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

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

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

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

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

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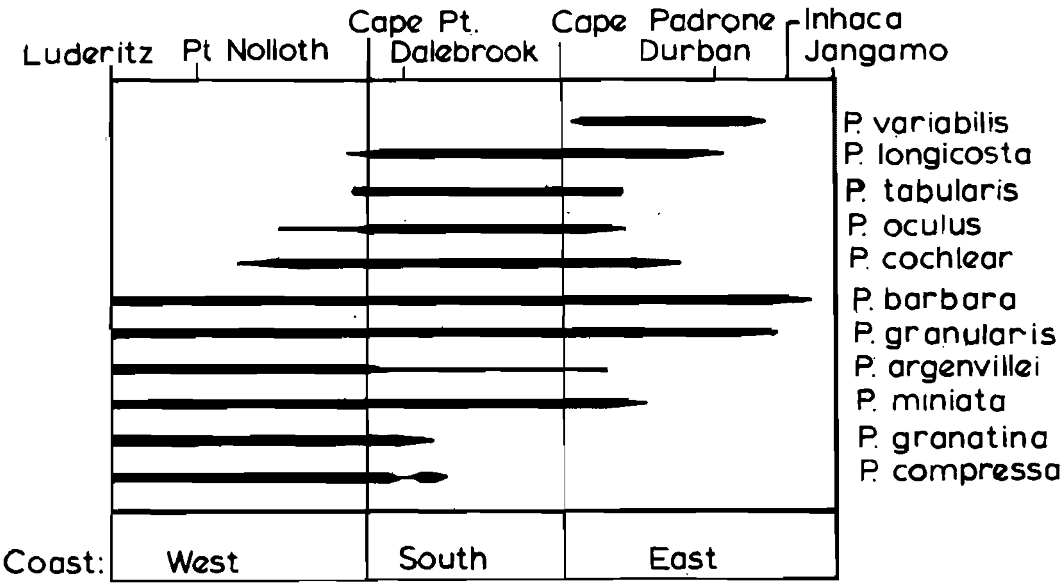

Figure 1a
Distribution of *Patella* spp. around the coast of southern Africa.

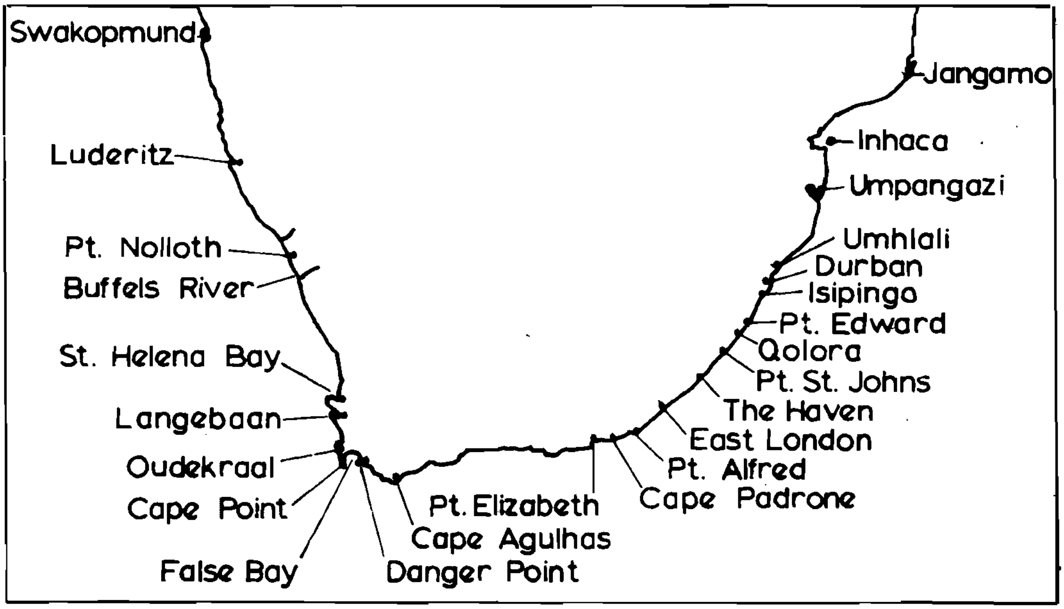

Figure 1b
Localities in southern Africa referred to in the text.

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

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

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

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

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

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

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

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

MATERIAL AND METHODS

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

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

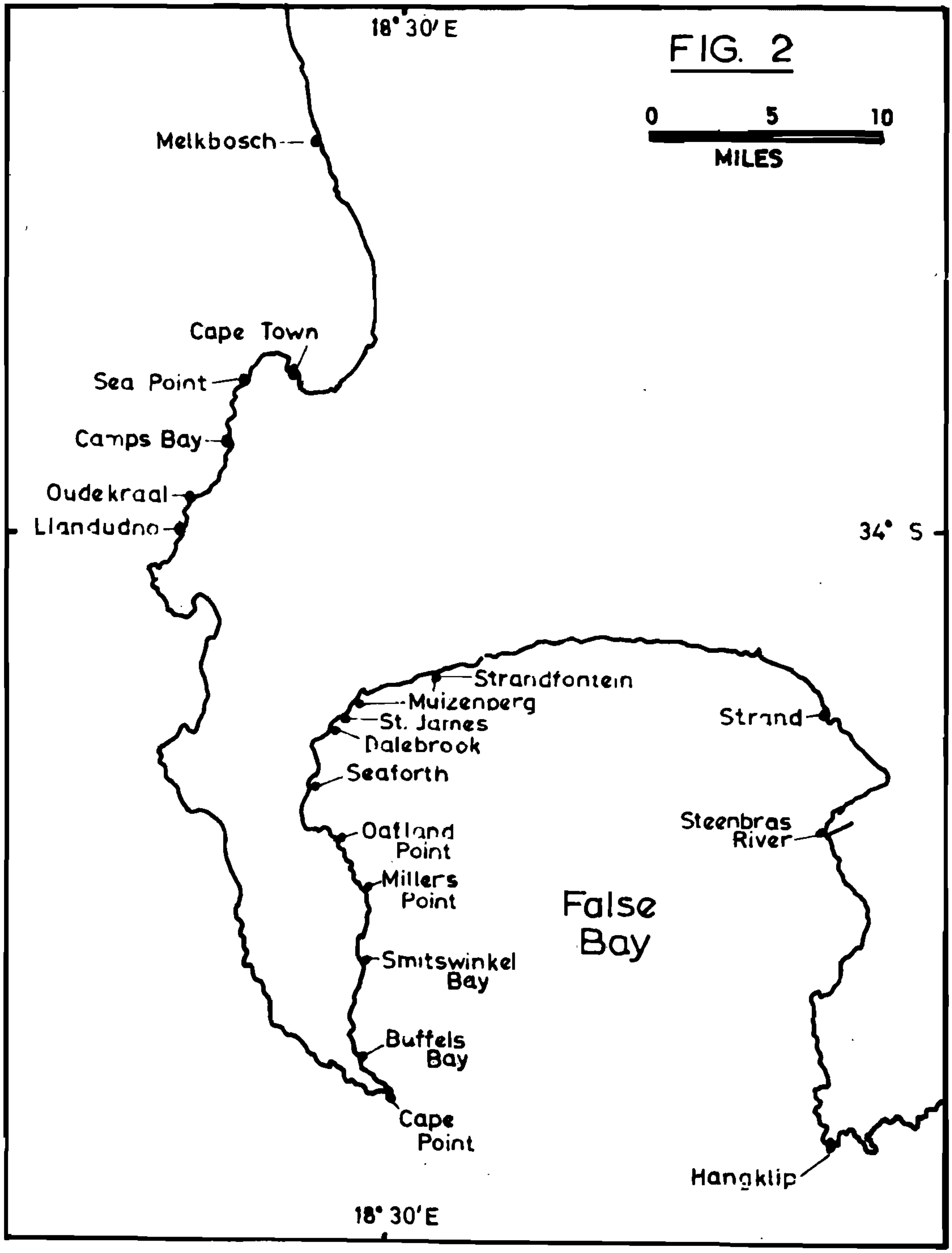

FIGURE 2
Map of the Cape Peninsula, showing areas surveyed and referred to in the text.

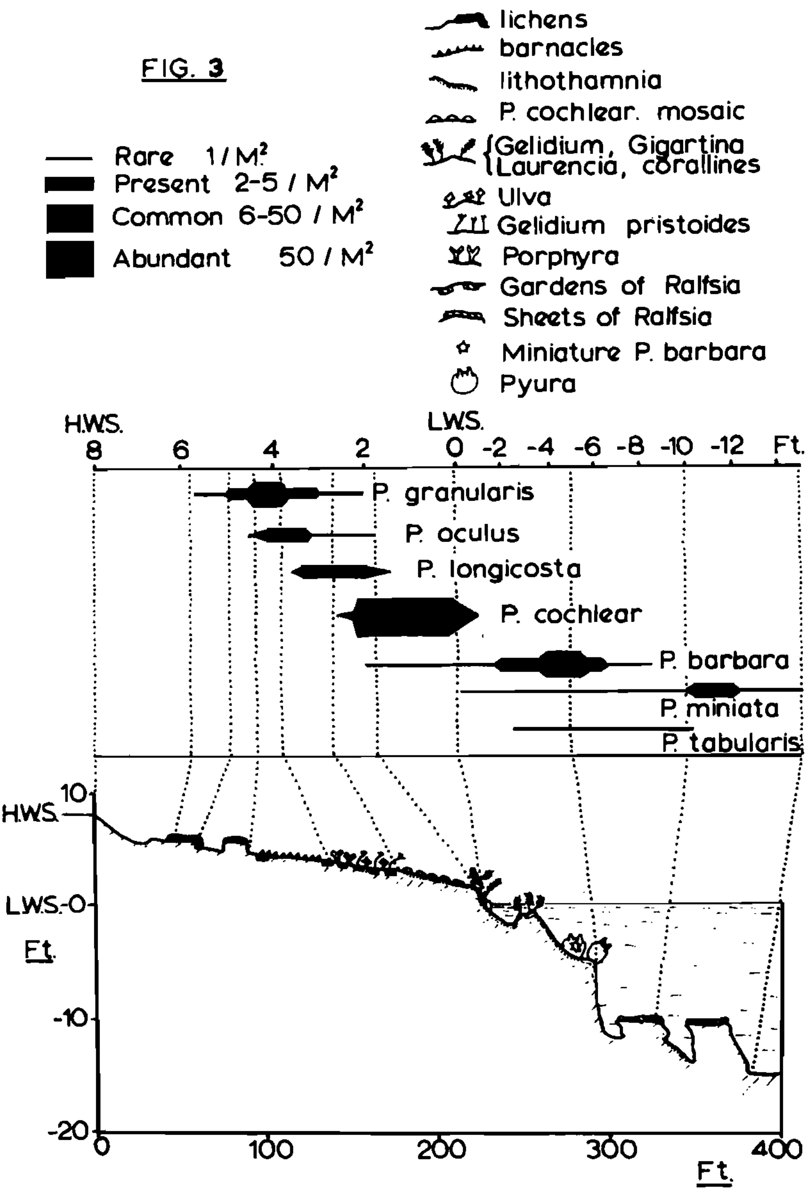

FIGURE 3

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

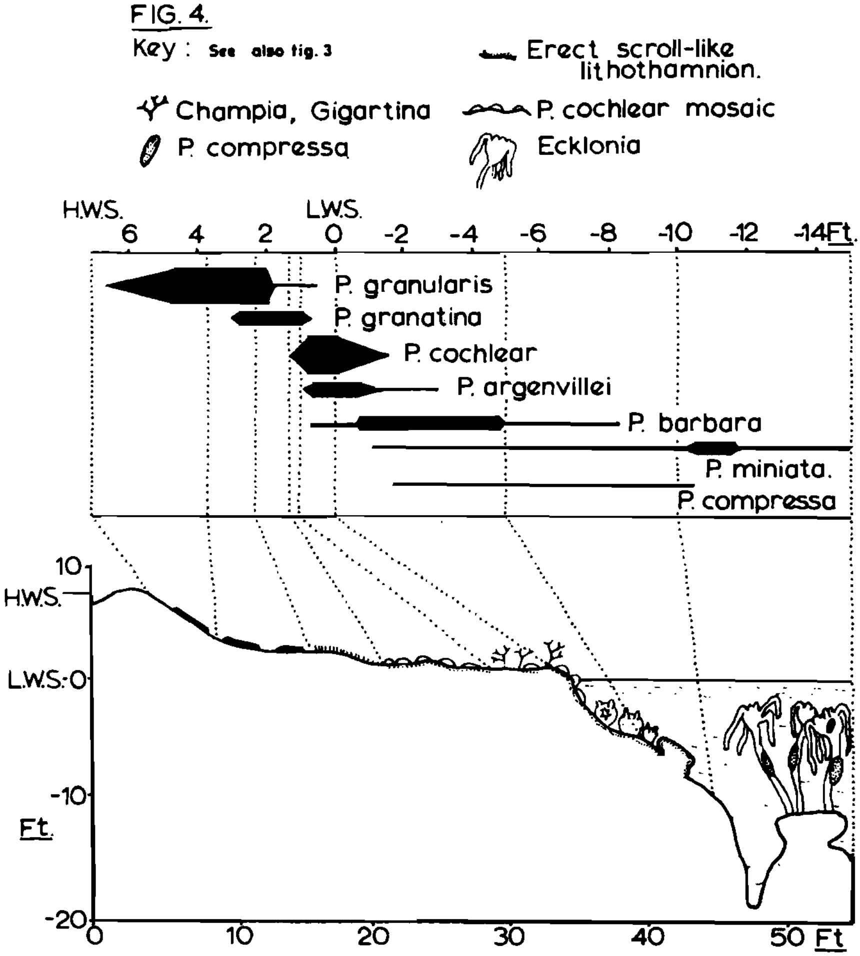

FIGURE 4

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

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

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

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

ZONATION FEEDING AND MOVEMENT

P. granularis

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

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

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

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

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

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

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

TABLE 1

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

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

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

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

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

P. oculus

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

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

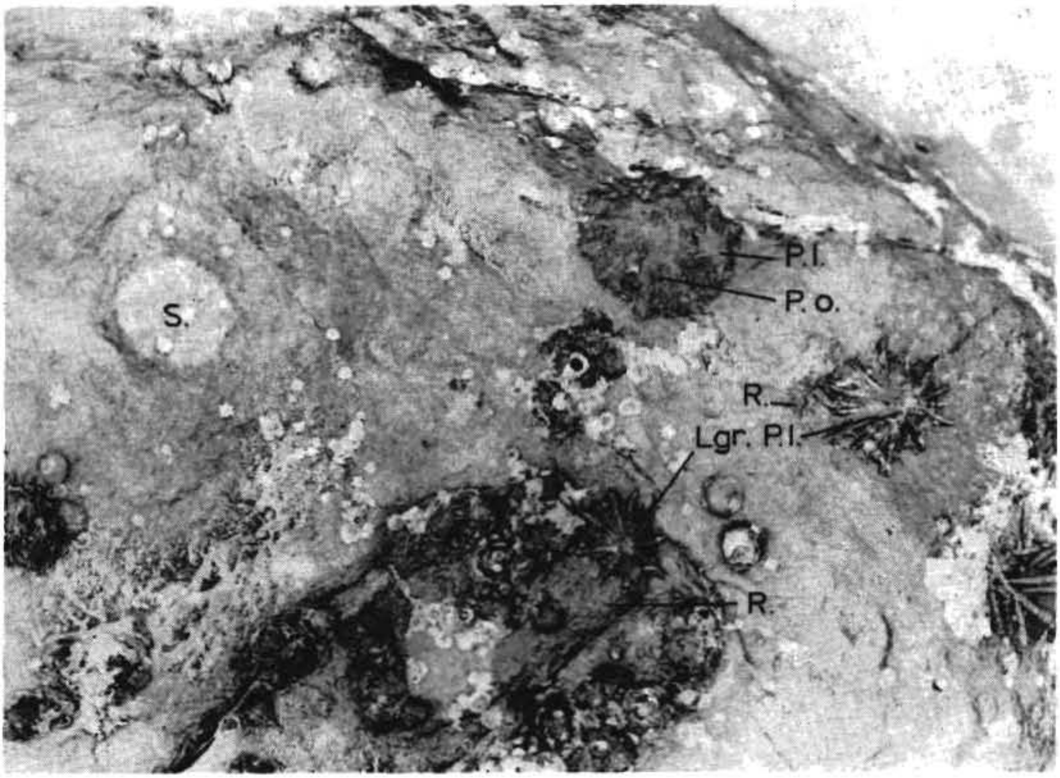

PLATE 1
Movement of *P. oculus* from scar. P.l.: Small *P. longicosta* situated on shell of *P. oculus*. Lgr. P.l.: Larger *P. longicosta* on *Ralfsia*. P.O.: *P. oculus*. R.: *Ralfsia expansa*. S.: *P. oculus* scar.

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

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

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

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

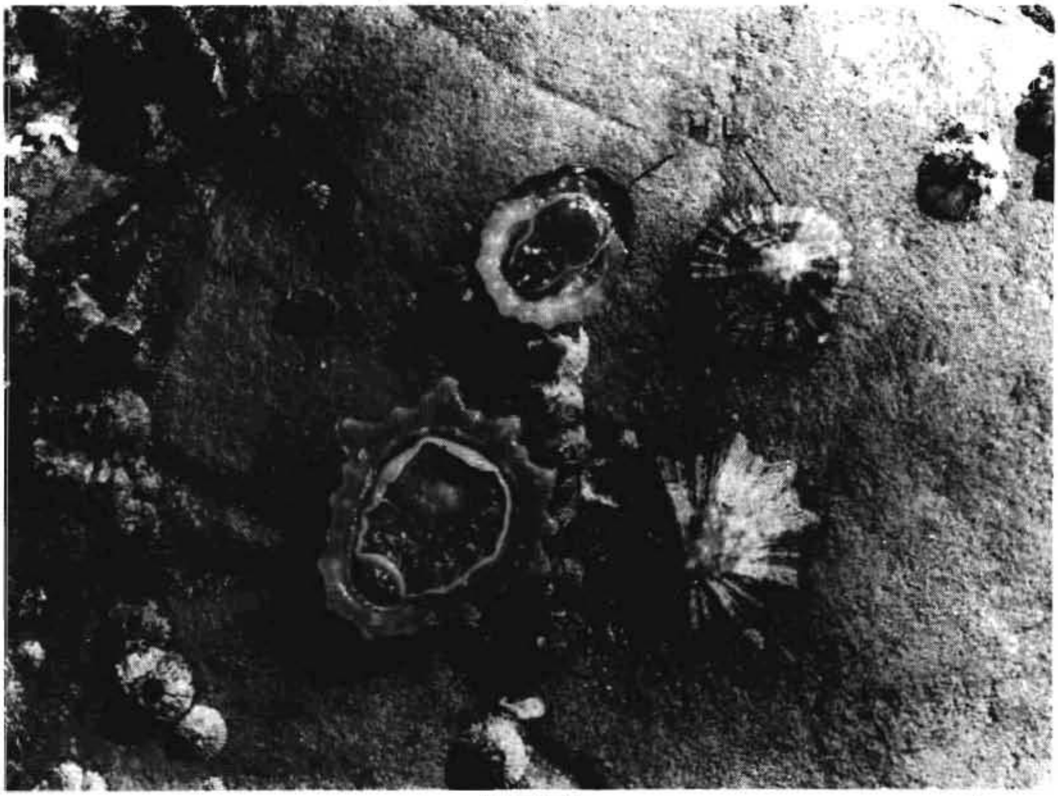

PLATE 2
P. oculus. H.L.: High level specimens. L.L.: Low level specimens. Np.: *Notoplana*—commensal with *P. oculus*.

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

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

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

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

TABLE 2

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

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

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

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

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

P. granatina

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

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

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

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

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

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

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

P. longicosta

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

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

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

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

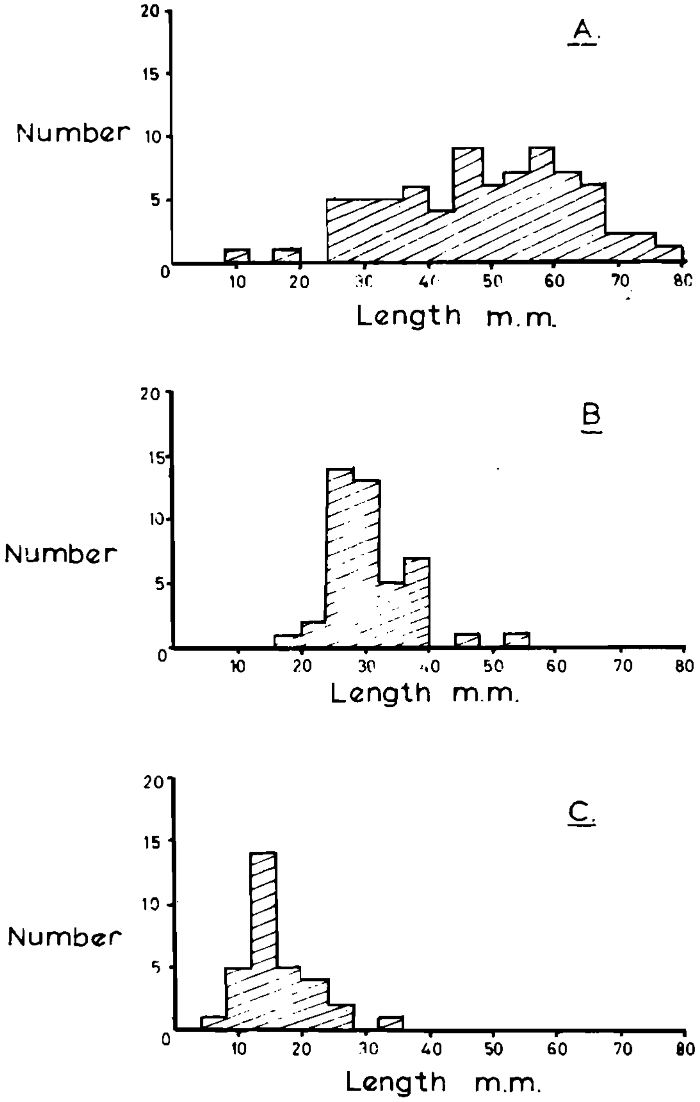

FIGURE 5
Size of *P. longicosta* in relation to substrate. A. On *Ralfsia* gardens. B. On lithothamnion. C. With *Ralfsia* on shells of other molluscs.

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

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

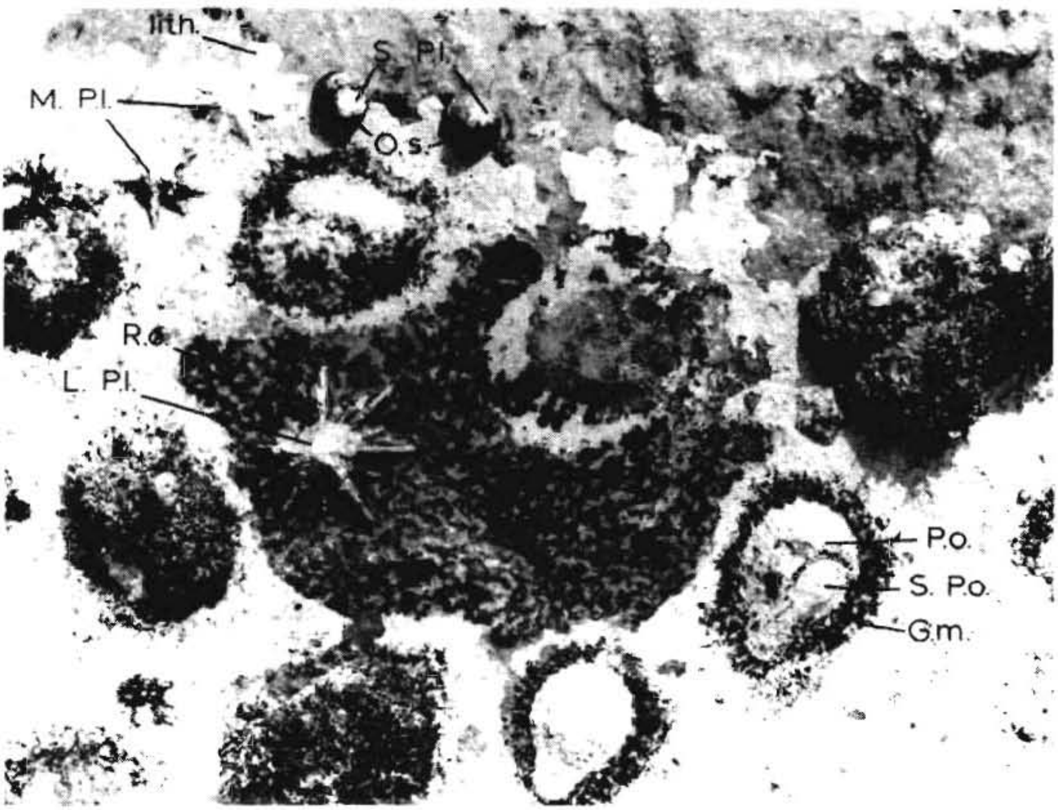

PLATE 3

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

TABLE 3

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

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

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

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

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

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

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

TABLE 4

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

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

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

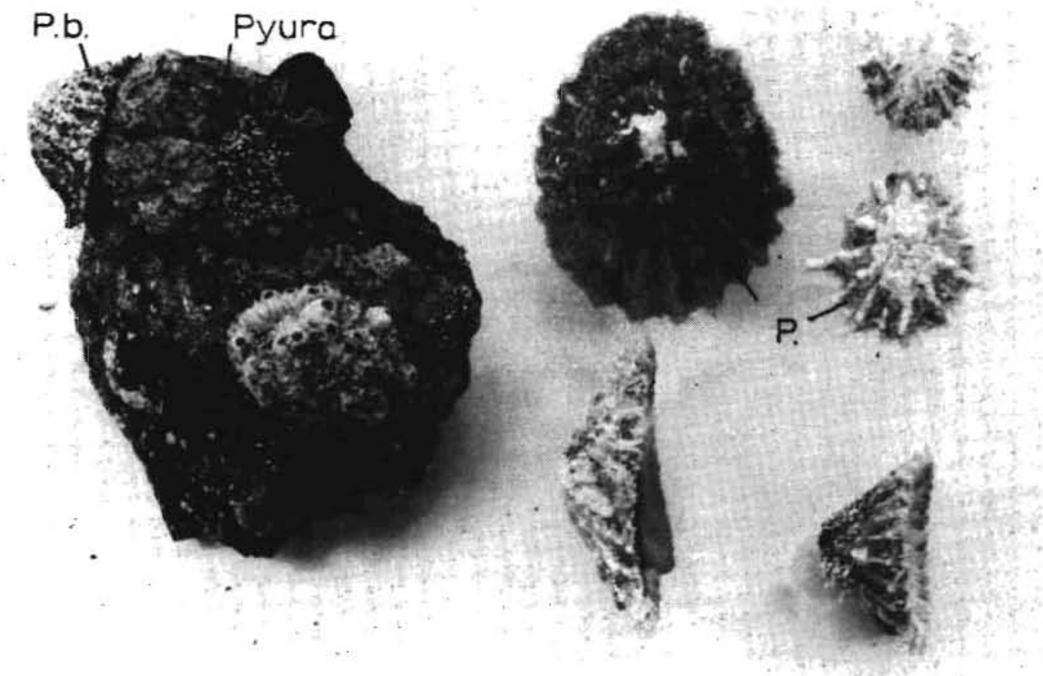

PLATE 4
P. barbara. Pyura with *P. barbara* (P.b.); Normal *P. barbara* in centre and miniature concave specimens on right. Note growth of ?*Pantoneura* (P.) on all.

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

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

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

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

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

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

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

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

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

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

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

P. cochlear

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

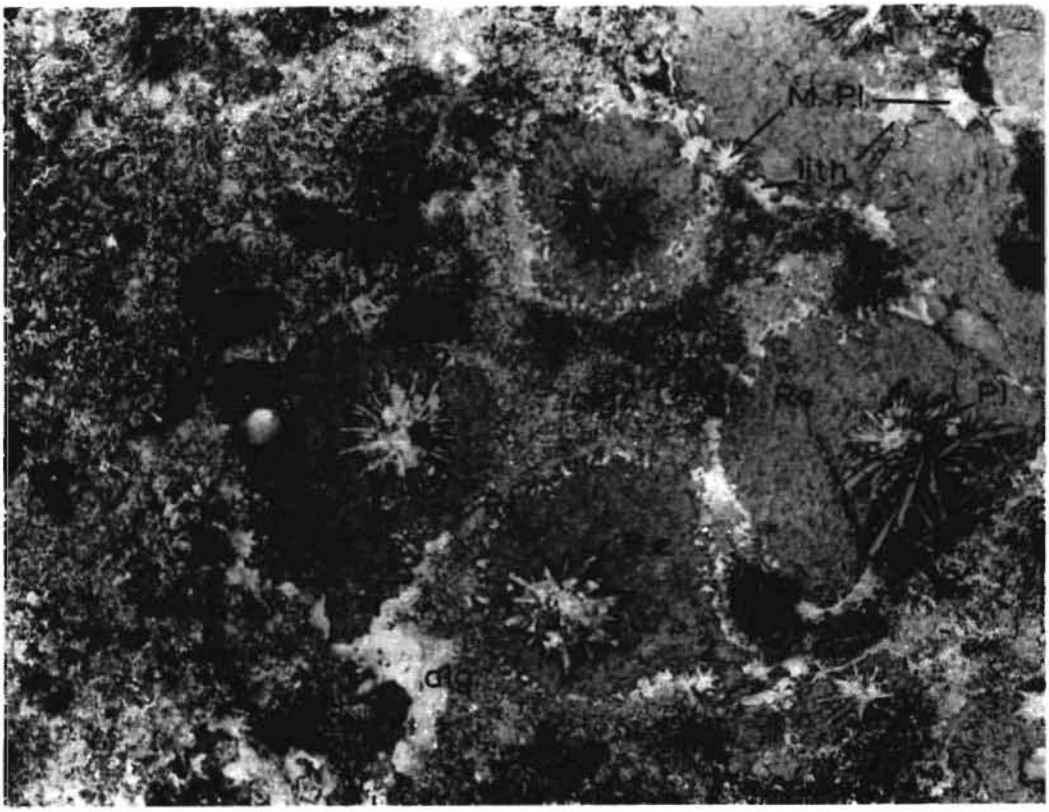

PLATE 5
P. longicosta (P.l.) on gardens of *Ralfsia expansa* (R.e.). The surrounding algal turf (Alg.) is cropped back. Medium *P. longicosta* (M.P.l.) situated on the peripheral lithothamnion (lith.).

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

TABLE 5

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

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

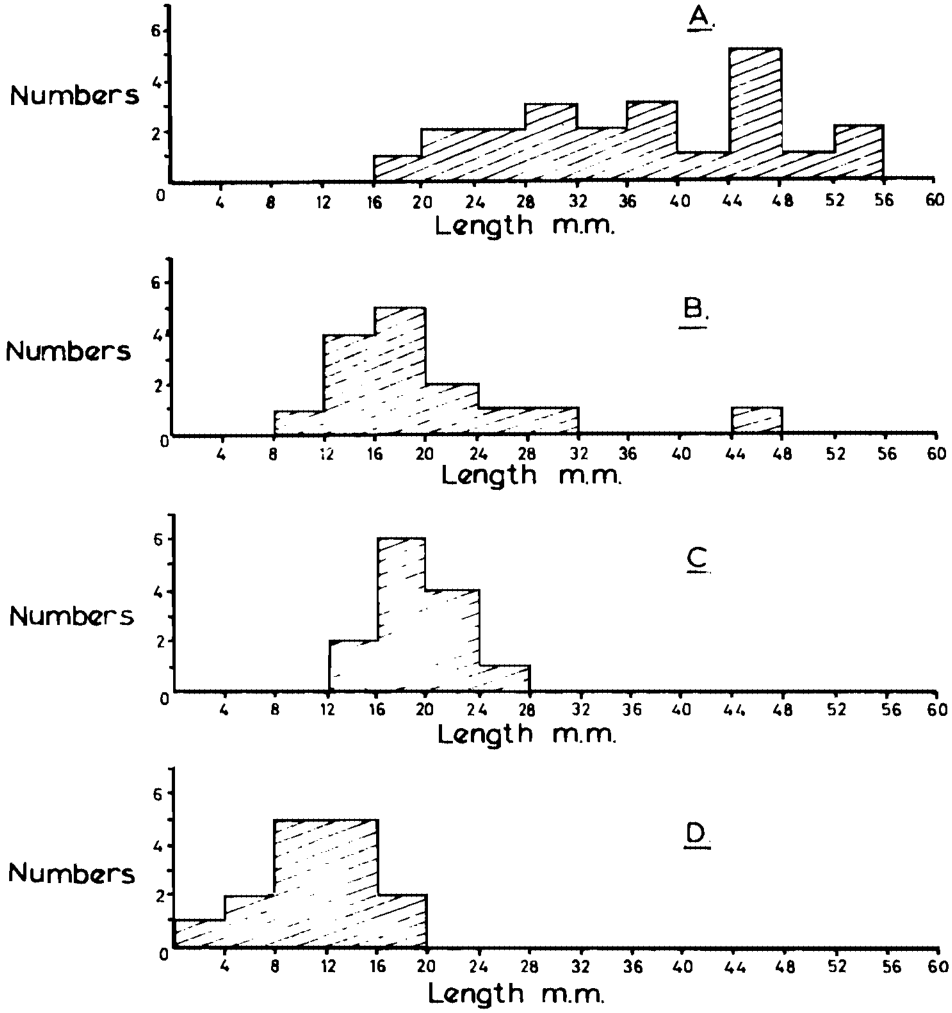

FIGURE 6

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

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

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

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

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

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

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

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

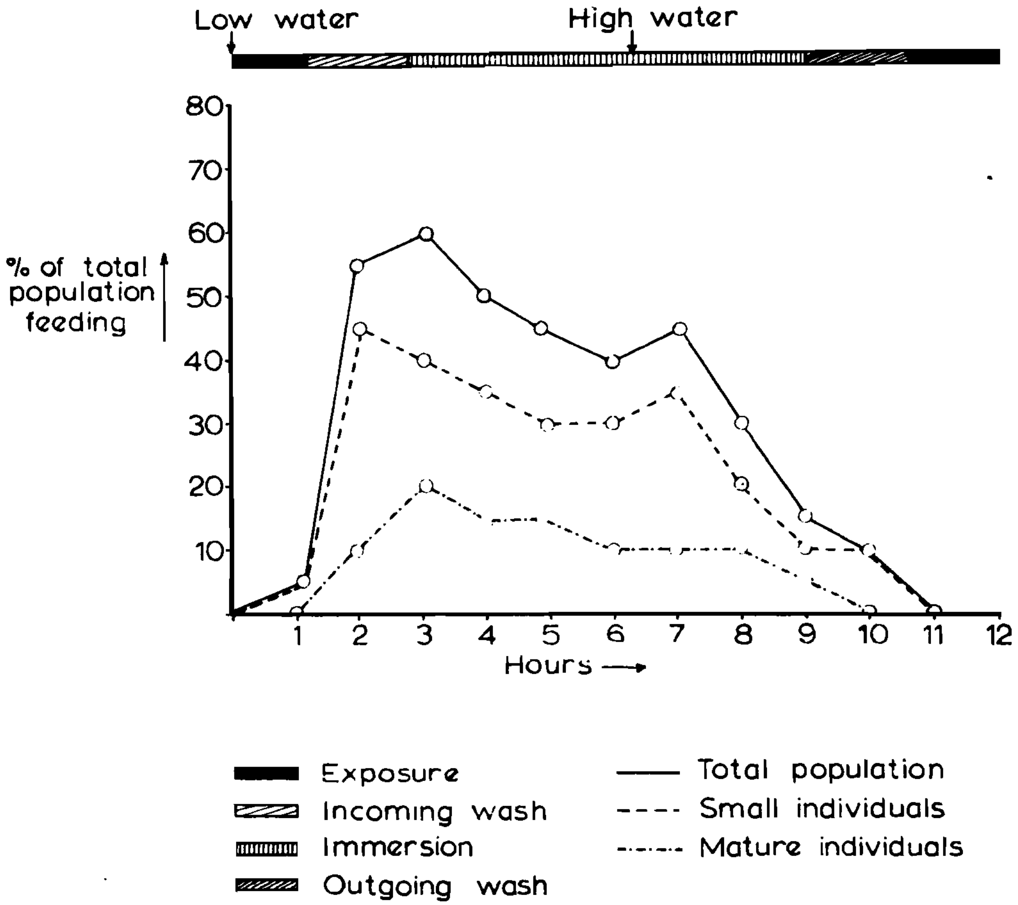

FIGURE 7
Feeding in *P. cochlear* relative to tidal rhythm. Counts taken at hourly intervals of the population in a fixed square metre at Dalebrook. Figures expressed to the nearest 5%.

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

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

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

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

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

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

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

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

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

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

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

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

P. argenvillei

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

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

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

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

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

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

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

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

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

P. barbara

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

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

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

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

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

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

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

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

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

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

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

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

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

P. miniata

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

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

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

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

P. tabularis

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

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

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

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

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

P. compressa

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

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

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

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

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

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

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

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

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

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

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

DISCUSSION

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

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

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

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

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

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

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

FACTORS EFFECTING ZONATION

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

Food

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

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

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

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

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

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

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

Salinity

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

Desiccation

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

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

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

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

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

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

Wave Action

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

Light

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

Substrate

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

Temperature

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

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

Larval Behaviour

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

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

Acclimation

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

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

BIOTIC RELATIONSHIPS

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

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

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

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drawn from his own experience and records, and for allowing me to quote the distribution records of this department.

SUMMARY

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

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

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

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

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

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

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

REFERENCES

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

ADDENDUM

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