THE RESPONSES OF SOUTH AFRICAN PATELLID LIMPETS TO INVERTEBRATE PREDATORS

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ABSTRACT

The starfish *Marthasterias glacialis* is a generalized predator, feeding particularly on *Choromytilus meridionalis*, but also on several limpets, notably *Patella longicosta. Thais dubia* (Gastropoda) feeds mainly on barnacles, mussels, and *Patella granularis.* The gastropods *Burnupena delalandii* and *B. cincta* are principally scavengers, feeding on damaged or dead animals. The responses of *Patella* spp. to these predators are described. *P. granularis, P. concolor, P. compressa* and *P. miniata* all retreat rapidly on contact. Small *P. granatina* and *P. oculus* respond similarly, but larger specimens react aggressively, smashing their shells downwards and often damaging the predator. The territorial species (*P. longicosta, P. cochlear* and *P. tabularis*) all retreat to their scars and remain clamped there. *P. argenvillei* and *P. tabularis* are usually unresponsive, possibly because they are too large to fall prey. *Cellana capensis* rolls its mantle upwards to cover the shell, preventing predators from attaching. The responses and their effectiveness are discussed in relation to other behavioural patterns displayed by limpets. There is no correlation between the intensity of a prey's response to a predator and the degree of contact between the two in the field.

INTRODUCTION

A variety of limpet predators has been recorded. Several birds attack limpets by knocking them off the rock, and either picking out the flesh or consuming the whole limpet and regurgitating the shell: oyster catchers (*Haematopus* spp.), various gulls (*Larus* spp.) and the sheathbill (*Chionus alba*) (Test 1945; Feare 1971; Walker 1972). In Britain large numbers of *Patella vulgata* and *P. aspersa* are attacked by *Haematopus ostralegus, P. aspersa* being more susceptible (Feare 1971). In South Africa *Haematopus moquini* also feeds on limpets, particularly *P. granularis*, each bird consuming up to 12 limpets per hour (Puttick pers. comm.). The turnstone (*Arenaria interpres*) also eats small *P. granularis.*

In California, rodents occasionally eat *Acmaea* spp., although Frank (1965) suggests this only occurs if the limpets are weakened by desiccation. Feral rats on South African coastal islands feed on intertidal molluscs, including *P. granularis.* In South Africa baboons (*Papio ursinus*) have been recorded feeding on *Patella* (Hall 1962) but this is probably a local occurrence. Middens in caves near the sea testify to the large numbers of limpets and mussels eaten by "hunter-gatherers", and there is evidence that this has substantially reduced the mean size of limpets (Parkington 1977). Crabs feed on *Acmaea*, crushing the shell with their chelipeds or prising them off the substrate (Chapin 1968).

Fish are also common predators of limpets (Test 1945; Walker 1972) and in South Africa the suckerfish (*Chorisochismus dentex*) often contains *Patella* shells in its gut, the largest recorded being an 80 mm *P. oculus* shell in a fish 200 mm long.

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In South Africa, two major predators are the starfish *Marthasterias glacialis* and the gastropod *Thais dubia.* The five *Burnupena* spp. are all scavengers, but are rapidly attracted to any damaged animal, voraciously devouring it while it is still alive. In a few instances they have also been seen attacking healthy limpets and are thus partly predatory.

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

The present work records the relative importance of the various prey species to *Marthasterias* and to *Thais dubia.* Briefer consideration is also given to the *Burnupena* spp. In addition, the reactions of *Patella* spp. to these predators have been tested. South African *Patellas* have been grouped according to their behaviour, and two extremes recognized: "migratory" species which move progressively up the shore from the site of settlement, and "non-migratory" species which remain in a narrow habitat throughout their lives. (Trends associated with these groups are summarized in Branch 1975, Fig. 16; and 1976, Fig. 18). It was thus of interest whether their reactions to predators are similarly divisible.

MATERIAL AND METHODS

Intermittent records were kept over seven years of the prey of *Marthasterias glacialis* and *Thais dubia,* mainly within the Cape Peninsula. In addition systematic surveys of *M. glacialis* and its prey were made at Sunny Cove, Fish Hoek, Kalk Bay, Seaforth, Buffels Bay, Simonstown and Oatland Point (all on the eastern coast of the Cape Peninsula).

The reaction of a limpet to a predator was established by staging contacts between the two in the field. Contacts with the non-predatory *Asterina exigua* and *Oxystele sinensis* were used as controls and in all cases failed to evoke a response.

RESULTS

Incidence of predation

Marthasterias glacialis occurs subtidally at densities of about $0{,}5/\mathrm{m}^2$, reaching local maxima of up to 35 per m^2.

Figure 1 summarizes the prey species of *M. glacialis* at various sites. *Choromytilus meridionalis* is the preferred prey, but if it is rare or absent, a wider range of species is eaten. more or less in relation to their abundance in the field. *Oxystele sinensis* is the commonest prey when *C. meridionalis* is not available. The large numbers of *O. sinensis* are interesting because this winkle has a strongly developed escape response to *M. glacialis*, can perceive it at a distance, and will migrate out to pools or aquaria if the starfish is introduced (Pitt-Kennedy 1968).

Several predators and scavengers were included in the diet of *Marthasterias* such as *Thais squamosa* and *Burnupena* spp. Of the limpets, *P. longicosta* is a frequent food item and *P. barbara* and *P. miniata* are occasionally eaten, while *P. tabularis* is probably immune to attack because of its size (up to 150 mm in length). *P. cochlear* is of interest, for despite its great abundance, only four specimens have been found eaten by *Marthasterias*. This is partly because it predominates in wave-lashed areas avoided by *Marthasterias*, but even under calm conditions it was not eaten. The mid-shore *P. oculus* hardly overlaps with the starfish

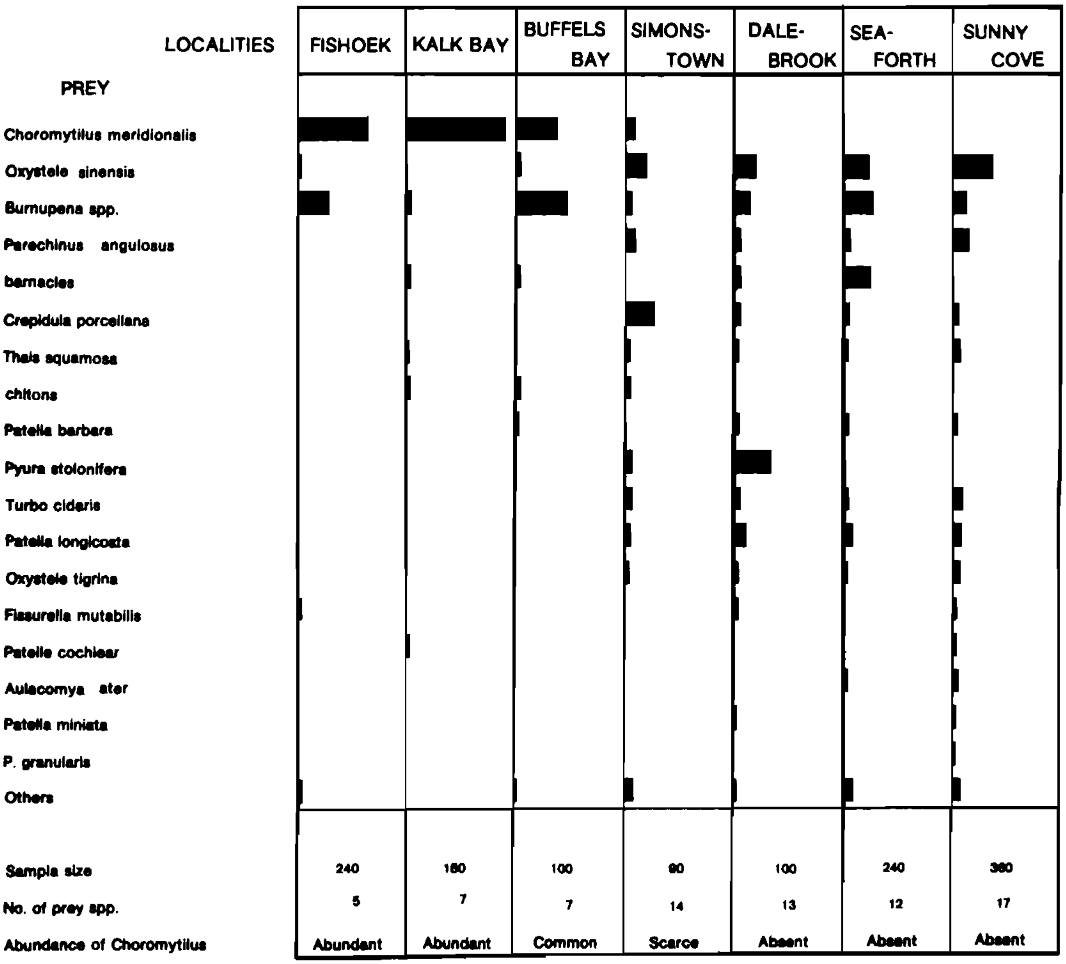

FIGURE 1.

The percentage of *Marthasterias glacialis* feeding on various prey species, at seven sites in the Cape Peninsula. Sites are ranked in order of the natural abundance of *Choromytilus meridionalis*.

but isolated specimens are eaten.

Thais dubia is an intertidal species occurring commonly in the upper balanoid zone and reaching densities of up to 150/m^2. It feeds predominantly on *Chthamalus dentatus* (42%), *Tetraclita serrata* (16%), *Littorina knysnaensis* (10%), *Octomeris angulosus* (9%) and *P. granularis* (18%), while other barnacles, *Aulacomya ater*, *P. granatina* and *P. oculus* make up the rest of its diet. At times *Littorina knysnaensis* aggregates in clumps of 50 or more, presumably to breed, and *T. dubia* converges on these clumps, paticularly in cool wet weather when *Thais* is active during low tide.

T. dubia drills into barnacles, usually by way of the operculum, and into mussels. The thinner walled *Chthamalus* is particularly vulnerable. Limpets are not usually attacked by drilling, but by insertion of the siphon under the shell.

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

Burnupena spp. occur in large numbers in the lower intertidal zone and subtidally. They are scavengers, but rapidly detect and feed avidly on any damaged living animal. *P. cochlear* which was weakened by oil pollution in False Bay was also eaten by *Burnupena delalandii*. *Burnupena* is exceptionally responsive to damaged animals, and within minutes it gathers in large numbers: it is even responsive to the filings from a limpet's shell. This avid response to damaged animals may account for the large numbers of *Burnupena* which fall prey to *Marthasterias*; attracted to *Marthasterias* prey, they may themselves be eaten.

Occasional observations were made of predation or attempted predation by *Burnupena delalandii*. One was seen thrusting its proboscis under the shell of a *P. longicosta*, but it withdrew after the limpet clamped down on its proboscis. Another group were found feeding on an apparently healthy and live *P. longicosta*. Predation on healthy animals is however exceptional. In aquaria they feed on live *P. granatina* and *P. granularis*, although preferring dead or damaged specimens.

Responses of Patella *spp. to predators*

P. granularis.

Contact with *Thais dubia* is almost invariably followed by an elevation of the shell away from the point of contact ("mushrooming") and protrusion of all the pallial tentacles. Within seconds the limpet swings away from the point of contact and glides rapidly in the opposite direction (Figure 2). After the initial flight the limpets often swing around and migrate up the shore for a few centimetres before stopping. This geotaxis is interesting in the light of the progressive migration which *P. granularis* undertakes up the shore (Branch 1975).

Flight will be repeated successively if contact with a predator is repeated, but becomes less marked and may eventually cease altogether. This suggests a conditioning or fatigue of receptors, and may be important in allowing capture of *P. granularis* by the slow-moving *Thais*. Occasionally *Thais* managed to mount the shell of *P. granularis*, but the latter responded by twisting the shell from side to side and often shook the predator off.

Escape responses often fail to occur in limpets which are dry due to exposure at low tide, but *Thais* is also inactive during exposure and retreats into crevices or under algae. *Thais* will however remain feeding while exposed, if it has captured a *P. granularis* during high tide. Both species are active during exposure if humidity is high, and at night.

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

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

P. concolor.

Occurring only on the east coast of South Africa, this limpet was only briefly examined. Its responses to three predatory gastropods (*Thais dubia, T. capensis* and *Morula granulata*) and to *Burnupena* spp. were very similar to those of *P. granularis:* mushrooming, extension of pallial tentacles, and rapid retreat. Identical reactions occur in *Helcion pruinosus* and *H. dunkeri.*

FIGURE 2.

Response of *P. granularis* to *Thais dubia:* "mushrooming", extension of pallial tentacles, and rapid flight.

Cellana capensis.

This limpet has a reaction unique among the patellids, for the mantle edge is rolled over the edge of the shell and expands upwards to form a thin layer which covers the whole of the external surface of the shell. None of the predatory gastropods tested (*Thais dubia*, *T. capensis* and *Urosalpinx heptagonalis*) could maintain a grip on the mantle-covered shell and the limpet then rapidly retreated. A very similar mantle response is recorded for the fissurelid *Diodora aperta* (Margolin 1964*a*).

P. oculus and *P. granatina.*

These two species react in a similar way to predators, described elsewhere in more detail (Branch in press *a*) and recapitulated here. Small *P. oculus* (less than 30 mm in length) react to *Thais dubia* by mushrooming of the shell away from the predator, followed by an extremely rapid retreat. Larger animals react quite differently by elevating the shell and then crunching it down on the foot or shell of the *Thais*, sometimes cutting off part of the propodium. The whelk retreats into its shell and usually rolls out of reach.

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

Marthasterias induces flight in most specimens of *P. oculus.* Much larger animals (over 50 mm) may display weaker flight or slight aggression, but none were strongly aggressive. Larger specimens of *P. oculus* were often unresponsive to either predator if the staged encounter occurred while the limpet was exposed on a dry rock.

P. granatina parallels the response of *P. oculus*, except that aggression to *Thais dubia* only begins in slightly larger animals (50–60 mm). Still larger specimens of *P. granatina* (63–90 mm) are aggressive towards *Marthasterias.* As in *P. oculus*, smaller specimens flee from both predators.

The different responses to *Thais* and *Marthasterias* indicate recognition of different predators and have clear survival value; aggression may be effective against *Thais*, but flight is more likely to be effective against *Marthasterias* unless the limpet is considerably larger.

P. miniata.

In response to *Thais*, small specimens of *P. miniata* retreat rapidly, while larger animals usually lift their shells aggressively and scrape them down on the predator's foot. The response is similar to that of the two preceding species. On the other hand, *P. miniata* of all sizes took rapid flight from *Marthasterias.* This may be because the zonation of the latter two overlaps considerably, both species predominating in the infratidal zone. *P. miniata* also responds more quickly and moves further after contact with *Marthasterias* than with *Thais.*

P. compressa.

Living on the stipes of *Ecklonia maxima*, *P. compressa* will not normally come into contact with predatory molluscs or echinoderms, but despite this it reacts strongly to *Burnupena papyracea* and to *Marthasterias*, moving rapidly away from the point of contact. Movement stops after a few centimetres, but is repeated after further contact. Occasional specimens of *Octopus* sp. were observed clinging to kelp and feeding on this limpet.

P. barbara.

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

P. longicosta.

Reaction to predators was quite different in *P. longicosta.* As previously described, juveniles of this limpet are found on the shells of other molluscs, particularly *Oxystele sinensis.* Subsequently they move onto lithothamnion-covered rock, until they establish territorial patches of the alga *Ralfsia expansa,* where they remain for the rest of their lives (Branch 1971: Plate 3). Juveniles lack any response to the three predators, remaining clamped onto their host shell. As they have well-defined scars and their shells fit these closely, the negative response may simply be due to a lack of direct contact with the predator during experimental encounters. The association with the highly responsive *Oxystele sinensis* may be of fortuitous survival value.

P. longicosta on lithothamnion moves around considerably (Branch 1974) and often lacks well-defined scars. If it encounters a *Thais* while moving around feeding, it immediately clamps down and tests the predator by extending pallial tentacles from the tips of the long shell costae. If the *Thais* is applied persistently, the limpet violently rotates its shell from side to side through an arc of about 110°, striking the *Thais* in the process. If this is still not successful the limpet retreats to its scar.

Adult specimens of *P. longicosta* have well-defined scars in the centre of *Ralfsia* patches. While the limpet is feeding, staged encounters with *Thais* result in immediate retreat to the scar, where the limpet clamps down. Persistent application of the *Thais* may result in shell rotation. This action is particularly characteristic of *P. longicosta* and may explain the survival value of long shell costae. Adults which are on their scars at the time of contact with a predator, simply clamp down and usually react no further, except for periodic extension of pallial tentacles to test if the predator is still present.

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

P. cochlear.

Irrespective of the predator encountered, *P. cochlear* simply clamps firmly onto its scar and remains there. No tentacle-testing or movements occur. If the limpet is off its scar when it contacts a predator, it moves slowly but directly back to its scar, orientates on it and clamps down. Larger specimens remain on their scars when feeding, rotating around the scar. Any contact with a predator at this stage results in rotation to the original position and clamping. Juveniles may move some distance from the scar when feeding, but migrate back to their scar in an almost straight line if a predator is met, even to the extent of shovelling the predator aside if it lies in this path. The shell is kept low, and there is never any "mushrooming" as in most other limpets.

The predominant feature of *P. cochlear* was its persistent clamping to the scar when in contact with a predator.

P. tabularis and *P. argenvillei.*

Neither of these species is responsive to predators, apart from a withdrawal of the mantle. A single *P. tabularis*, which was feeding when it encountered a *Marthasterias*, retreated to its scar and clamped there, but all others seemed to ignore the starfish if they were on their scars. Possibly reaction is similar to that of *P. longicosta* and clamping on the scar is the most effective means of defence. No offensive action was ever seen.

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

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

DISCUSSION

Marthasterias is an important predator of *P. longicosta* and to a lesser extent of *P. barbara* and *P. miniata. P. cochlear, P. granularis* and *P. oculus* are eaten in smaller numbers. *Thais dubia* is one of the major invertebrate predators on *P. granularis. P. oculus* and *P. granatina* are less often eaten by *T. dubia. P. tabularis* and *P. argenvillei* probably escape most predators because of their size, and *P. compressa* because of its specialized habitat on *Ecklonia.*

Bullock (1953) has suggested that reaction to a predator is only evolved if there is an ecological overlap between predator and prey, so that the two often come into contact. Both his data and those of Margolin (1964*b*) on *Acmaea* spp. support this idea, but Clark (1958) and Feder (1972) give examples of prey species which are highly responsive to predators they never naturally meet.

The zonation of *Patella* spp. has already been described (Branch 1971), but can be summarized here in relation to that of *M. glacialis* and *T. dubia* (Figure 3). Clearly there are several species which do not encounter predators to which they are responsive. *P. miniata* does not come in contact with *T. dubia* but reacts strongly to it. Perhaps this can be explained by the evolution of responses to allied species such as *T. squamosa*, which occurs subtidally with *P. miniata.* However, mid-shore *P. granatina* and *P. oculus* respond to the predominantly subtidal *M. glacialis*, and *P. compressa* is strongly responsive to both this starfish and *Burnupena*, although it never comes in contact with either. *Patina pellucida* (which occurs on kelp in Europe) is usually strongly reactive to *M. glacialis*, although at Plymouth it is unresponsive (Feder 1967).

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

This may be explained by the nature of the stimulus inducing escape. In several species, predators can be perceived at a distance. *Tegula* spp. (Bullock 1953) and *Oxystele* spp. have already been mentioned. Limpets usually require actual contact with the predator which is not surprising considering the turbulence of the intertidal zone. In either case chemoreception is implicated because of the specificity of the response, and because mechanical stimulus alone fails to elicit an escape response. Steroid glycosides isolated from *M. glacialis* and non-ionic surface-active agents induce escape reactions in various animals including *P. vulgata* (Mackie 1970, 1972). Both the glycosides and the surface-active agents produce fatigue in the chemoreceptors of the foot if they are applied for any length of time, and this may explain the "conditioning" of *P. granularis* to *T. dubia.*

Metabolites of a similar nature are likely to be widespread in predatory starfish. Feder (1972) suggests that they may occur in small quantities in non-predatory echinoderms. Responses to non-overlapping predators and even occasionally to non-predatory echinoderms may thus be explained.

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

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

All of the reactions to predators are totally different from the reactions evoked by intra- and interspecific meeting between limpets (Branch 1975, 1976). *P. granularis* and *P. granatina* may form aggregates of their own species, but flee from predators or aggressively repulse them. *P. compressa* (and probably *P. miniata*) is aggressive to its own species but takes flight from predators. *P. longicosta* and *P. tabularis* defend their territories against other limpets, but clamp on their scars in response to predators. *P. cochlear* is dispersive and moves away after contact with another *P. cochlear*, but clamps on its scar in the face of predation.

These responses to predators are basically of three kinds: rapid flight, aggressive defence and clamping down on a scar (Figure 3). Possibly the large species should be considered separately because they remain inert; and *Cellana capensis* has its specialized response of rolling the mantle over the shell.

The relative effectiveness of these responses is difficult to gauge, because of different degrees of habitat overlap, and possible food preferences. However, very few *P. oculus* and *P. granatina* are eaten by *T. dubia* while *P. granularis* often falls prey to it. *P. longicosta* is often eaten by *Marthasterias* (more than any other *Patella*), perhaps because it fails to escape, remaining clamped on its scar. *Acmaea scabra* also clamps down in response to predatory starfish and is eaten more often than other *Acmaea* spp. (Feder 1963). Such behaviour will only be effective against starfish if the shell seals onto the rock, excluding the digestive juices from the starfish stomach. In *P. longicosta* this is not so, for there are slender channels along the costae of the shell, through which the pallial tentacles project.

P. cochlear also clamps down on its scar in response to predators, but is rarely eaten by *M. glacialis.* By contrast with *P. longicosta*, its shell fits the substrate exactly and its power of adhesion is higher than in any of the other limpets. Only four *P. cochlear* were found being eaten by *M. glacialis*, despite it being the most abundant of the limpets.

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

The "migratory" group of limpets (including *P. granularis, P. granatina, P. concolor* and *P. oculus*) comprises species which progressively migrate up the shore, and have generalized diets and flexible behaviour; homing behaviour varies according to conditions and scars are never permanent; territorial behaviour is absent. Conversely species of the "non-migratory" group occupy the same habitat throughout life and have specialized feeding habits often

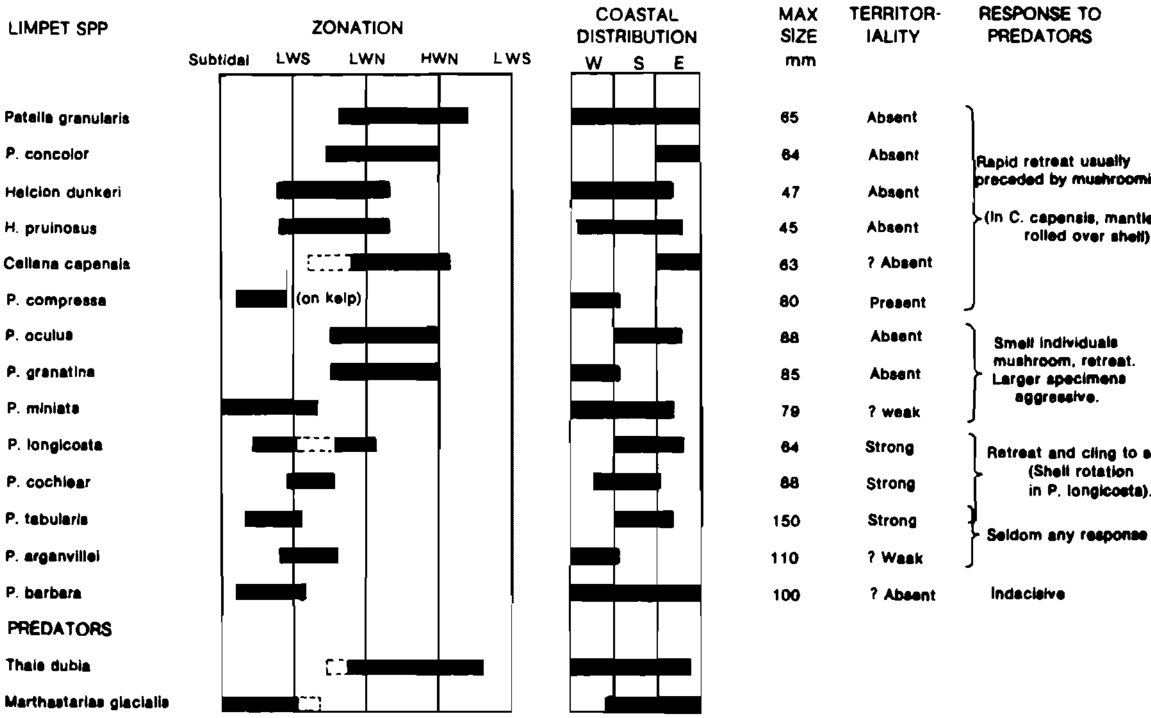

FIGURE 3.

Synopsis of the characteristics of *Patella* spp., their responses to predators, and their relative distribution and zonation.

associated with territorial defence, a narrow niche, and rigid behaviour patterns (Branch 1975, 1976).

In relation to this, the migratory species all have strong escape responses or react aggressively to predators, but have no tendency to remain on a scar (Figure 3). The behaviour is flexible, and modified according to the size of the limpet, and according to the predator involved: smaller species and individuals rapidly retreat, larger individuals act aggressively (Figure 3).

Conversely the more extreme non-migratory species (*P. tabularis, P. longicosta* and *P. cochlear*) clamp onto their scars in response to a predator and make no attempt at flight, and only occasionally (in *P. longicosta*) show aggression. Responses are inflexible and stereotyped, irrespective of the predator encountered. This is logical in species where territories have obvious advantages, and survival is high once they are established (Branch 1974, 1975). It may however make *P. longicosta* vulnerable to *Marthasterias.* Perhaps in this case the overall advantages of the territory as a source of food, and the scar as a protection against other predators (such as fish), are greater than the disadvantage of not fleeing from *Marthasterias.*

The migratory species also have low powers of adhesion and high speeds of movement in comparison with the territorial non-migratory species (Branch in press *b*), and this too correlates with their divergent strategies of predator avoidance.

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REFERENCES

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

BRANCH, G M 1974. The ecology of *Patella* Linnaeus from the Cape Peninsula, South Africa. 3. Growth rates. *Trans. R. Soc. S. Afr.* 41: 161–193.

BRANCH, G M 1975. Mechanisms reducing intraspecific competition in *Patella* spp.: migration, differentiation, and territorial behaviour. *J. anim. Ecol.* 44: 575–600.

BRANCH, G M 1976. Interspecific competition experienced by *Patella* spp. *J. anim. Ecol.* 45: 507–529.

BRANCH, G M In press *a*.An aggressive response of limpets to invertebrate predators. *Anim. Behaviour.*

BRANCH, G M In press *b*. Limpet adhesion and shell shape: adaptive features. *J. exp. mar. Biol. Ecol.*

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

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

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

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

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

FEDER, H M 1967. Organisms responsive to predatory starfish. *Sarsia* 29: 371–394.

FEDER, H M 1972. Escape responses in marine invertebrates. *Scient. Am.* 227: 92–100.

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

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

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

MACKIE, A M 1972. The escape reactions of marine invertebrates to predatory starfish. *Eur. Mar. Biol. Symp.* 5: 269–274.

MARGOLIN, A S 1964*a*. The mantle response of *Diodora aspersa. Anim. Behav.* 12: 187–194.

MARGOLIN, A S 1964*b*. A running response of *Acmaea* to sea stars. *Ecology, N.Y.* 45: 191–193.

MAUZEY, K P 1966. Feeding behaviour and reproductive cycles in *Pisaster ochraceous. Biol. Bull. mar. biol. Lab. Woods Hole* 131: 127–144.

PARKINGTON, J 1977. Coastal settlement between the mouths of the Berg and Olifants Rivers, Cape Province. *S. Afr. archaeol. Bull.* 31: 127–140.

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

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

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

WALKER, A J M 1972. An introduction to the ecology of the Antarctic limpet *Patinigera polaris* (Hombron and Jacquinot) at Signy Island, South Orkney Islands *Bull. Br. Antarct. Surv.* 28: 49–69.