

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

5. COMMENSALISM

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ABSTRACT

Forty-six species were recorded in association with *Patella* spp., but most of these are casual associates, seeking temporary shelter. The shell surface offers an important substrate for algae.

The amphipod *Hyale grandicornis* is often associated with *Patella*, particularly in the juvenile stages. It is a facultative inquilin which vacates its hosts at high tide. The isopods *Dynamenella australis* and *D. scabricula* are predominantly associated with limpets and complete their life cycles under limpets. Choice chamber experiments demonstrate their preference for sheltering under limpets. The copepod *Scutellidium patellarum* is similar, but the association is more marked.

Calliopiella michaelsoni (Amphipoda) is commensal and show a preference for certain limpet species. Its colour changes in relation to the host species. Feeding occurs on limpet faeces and algal fragments. The life cycle is completed under the limpet, two reproductive peaks occurring each year. Adults usually occur in pairs and there is a positive correlation between host and amphipod size. Juveniles remain with their parents initially, and then disperse to other limpets. Adult pairs may defend their host, excluding other amphipods. *Calliopiella* is strongly photonegative and thigmotactic.

The turbellarian *Notoplana patellarum* is preferentially commensal with *Patella oculus*. This can be experimentally demonstrated. It feeds on small crustacea, including *Scutellidium*.

INTRODUCTION

The occurrence of various organisms associated with *Patella* Linnaeus spp. in South Africa is well known and has been recorded by Koch (1949). The present paper describes some aspects of the biology of these commensals: particularly the nature of the association and the behaviour of the associates.

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

An entirely different group of organisms is associated with limpet shells: algae are often confined there because the limpets graze the surrounding rocks. Some invertebrates are similarly restricted to limpet shells.

Such relationships with limpets have been recorded from many parts of the world. Cheng

TABLE 1

Animals associated with *Patella* spp. Data are pooled from 12 monthly collections at Kommetjie and Kalk Bay. Numbers have been scaled to represent the number of associates per 100 limpets.

Tidal level	Number of associates per 100 limpets per year										Number of associates per 100 limpets	
	High			Low				Subtidal			Sample at low tide (0900 h)	Sample at high tide (1500 h)
<i>Patella</i> sp.	P. granularis	P. granatina	P. oculus	P. longicosta	P. cochlear	P. argenvillei	P. barbara	P. miniata	P. tabularis	P. compressa		
Number sampled	310	311	300	300	346	284	302	286	142	82	90	90
AMPHIPODA												
* <i>Calliopiella michaelsoni</i>	20	174	140	4	5	8	27	73	48	162	72	78
* <i>Hyale grandicornis</i>	27	2	3	7	13	24	1	1	0	8	52	10
<i>Jassa falcata</i>	0	0	0	0	1	4	0	0	0	0	4	0
<i>Paramoera capensis</i>	0	0	0	14	2	1	2	0	0	0	7	10
Caprellids	0	0	0	1	1	2	2	0	0	0	7	0
Others	0	0	1	1	1	1	2	0	0	1	3	0
ISOPODA												
<i>Paridotea rubra</i> & <i>P. ungulata</i>	0	0	0	0	0	1	2	0	0	0	0	0
<i>Exosphaeroma</i> spp.	0	1	1	4	1	5	5	0	0	1	7	0
<i>Parisocladus perforatus</i>	0	0	8	1	0	0	2	0	0	0	3	0

<i>P. stimpsoni</i>	1	0	0	0	0	0	0	0	0	0	1	0
<i>Dynamenella huttoni</i>	0	1	0	1	1	4	1	0	0	0	4	0
* <i>D. scabricula</i>	35	21	4	1	3	6	2	0	0	5	62	48
* <i>D. australis</i>	6	1	0	0	141	440	2	0	0	0	146	171
COPEPODA												
* <i>Scutellidium</i> sp.	0	2	1	5	>3000	>3000	3	71	71	0	—	—
<i>Pelteutha</i> sp.	0	0	0	1	9	9	3	0	0	0	—	—
<i>Harpacticus</i> sp.	0	0	0	0	7	5	9	0	0	0	—	—
TANAIDACEA												
<i>Tanais philataerus</i>	0	0	1	1	1	5	2	0	0	0	3	0
INSECTA												
<i>Aponogeton</i> sp.	0	0	5	1	0	5	0	0	0	0	1	0
POLYCHAETA												
<i>Pseudonereis variegata</i>	0	1	1	0	0	2	2	0	0	0	1	0
<i>Syllis</i> sp.	0	0	2	0	0	2	1	0	0	0	—	—
Others	0	0	0	0	0	2	2	0	0	0	—	—
TURBELLARIA												
* <i>Notoplana patellarum</i>	5	1	307	20	3	2	20	0	0	0	180	198

* Indicates commensal and associated species.

(1967) has given a general account of the various associations involving molluscs, and Vader (1972) has recently reviewed the records of amphipods associated with molluscs.

MATERIAL AND METHODS

Samples of all *Patella* spp. were collected monthly from Kommetjie and Kalk Bay in the Cape Peninsula. A minimum of 30 specimens of each species was collected, superficially examined for associates and preserved in 7% formalin for microscopic examination.

Distribution patterns were determined from collections ranging from Lamberts Bay on the west coast to Lwandile (31°53'S/29°15'E) on the east coast. Line and quadrat transects were undertaken to assess zonation and density of commensals and hosts, at Dalebrook, Kalk Bay, Kommetjie and Camps Bay.

Commensals were maintained in marine aquaria at temperatures comparable to field conditions to assess their relationship with the hosts. Experiments conducted to elucidate the relationships are described below under the relevant sections. Light intensities were measured in lux, using a solenium light meter kindly loaned by the Botany Department, University of Cape Town.

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

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

CASUAL ASSOCIATION

Most animals found under limpets are casual associates seeking temporary shelter from desiccation. Forty-six species have been recorded in this work. The more important species are summarized in Table 1, which gives the cumulative totals from 12 monthly samples from Kommetjie and Kalk Bay. Seasonal and distributional trends for the more important associates are discussed in the text. Comparative figures are also given for collections made at low tide and high tide, on a single occasion, collecting 10 of each *Patella* species.

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

ASSOCIATES ON THE SHELL

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

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

The polychaete *Polydora capensis* bores into mollusc shells and is frequently found on *P. argenvillei*, *P. cochlear* and *P. barbara* in the cochlear zone. Shells of old limpets are often riddled by the polychaete, and become fragile. Penetration through the shell seldom occurs, as fresh nacreous layers are deposited internally to cover the polychaete tubes. Densities of up to 725 *Polydora capensis* per shell have been recorded. The worms appear to be gregarious in their settling pattern, as large numbers are usually found on a few shells while surrounding shells are free of them. Haigler (1969) has described how the larvae of *Polydora websteri* select a calcareous substrate when settling, and bore into the shell by a chemical secretion. Blake and Evans (1973) have recently reviewed *Polydora* and related genera, and show that 26 of the 65 species are confined to a calcareous substrate: mainly in the form of mollusc shells or calcareous algae.

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

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

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

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

The lack of specificity in these associations does not detract from the importance of the shell as a niche. Table 2 illustrates this quantitatively for some of the predominant organisms. Korrington (1951) has described how the shells of *Ostrea edulis* provide a similar substrate for many organisms.

TABLE 2

Organisms associated with *Patella* shells. (N=4 for all samples, 95% confidence limits indicated in parenthesis.) Material collected from Kommetjie (K), Dalebrook (D) and Bloubergstrand (B).

Species	Biomass (dry weight: g/m ²)		Zone	Patella spp.
	On shells	On rock		
1. Algae				
<i>Gelidium pristoides</i>	18,2 (± 4,2)	4,2 (± 2,4)	Cochlear (D)	<i>P. cochlear</i>
	62,6 (±17,2)	40,2 (±10,2)	Low balanoid (D)	<i>P. longicosta</i>
	14,2 (±12,0)	0,2 (± 0,1)	Mid balanoid (D)	<i>P. oculus</i>
<i>Laurencia glomerata</i>	9,6 (± 6,2)	1,2 (± 1,0)	Cochlear (D)	<i>P. cochlear</i>
	22,4 (±14,1)	26,2 (±16,1)	Low balanoid (D)	<i>P. longicosta</i>
<i>Cheilosporium</i> sp.	26,2 (±14,2)	3,1 (± 1,6)	Cochlear (D)	<i>P. cochlear</i> , <i>P. barbara</i>
<i>Pterosiphonia cloiophylla</i>	19,2 (± 6,2)	3,0 (± 1,1)	subtidal (D)	<i>P. miniata</i>
	25,3 (± 9,1)	1,2 (± 0,6)	subtidal (D)	<i>P. tabularis</i>
	42,6 (±20,1)	4,2 (± 1,2)	Cochlear (B)	<i>P. cochlear</i>
<i>Gigartina stiriata</i>	5,8 (± 5,0)	9,2 (± 2,4)	subtidal (B)	<i>P. miniata</i>
	6,2 (± 1,0)	12,2 (± 9,2)	Cochlear (B)	<i>P. cochlear</i>
<i>Champia lumbricalis</i>	5,2 (± 2,1)	0,4 (± 0,3)	subtidal (D)	<i>P. miniata</i>
<i>Hypnea spicifera</i>	22,1 (±10,0)	72,6 (±15,1)	subtidal (D)	<i>P. tabularis</i>
<i>Ulva</i> sp.	106,7 (±12,2)	3,2 (± 3,0)	Low balanoid (K)	<i>P. granatina</i>
Numbers per 0,5 m²				
2. Animals				
<i>Spirorbis levinseni</i>	122 (± 92)	42 (±27)	} Intertidal pools, Cochlear to subtidal	} <i>P. miniata</i> , <i>P. longicosta</i> <i>P. cochlear</i> , <i>P. argenvillei</i> and <i>P. barbara</i>
<i>Vermetus corallinaceus</i>	1 460 (±106)	692 (±16)		
<i>Polydora capensis</i>	622 (±242)	0		

Calliopiella michaelseni (Amphipoda)

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

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

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

The colour variations and percentage specificity relating to different hosts, is summarized in Table 3.

TABLE 3
Host specificity and colour variation in *C. michaelseni*.

Host	% Specificity	Colour of <i>Calliopiella</i>
<i>P. granularis</i>	3,6	Uniform pale green-brown. Gut dark brown. Eyes red-brown
<i>P. granatina</i>	26,4	Uniform dark khaki. Gut darker.
<i>P. oculus</i>	18,0	Paler khaki. Gut green to khaki.
<i>P. longicosta</i>	0,9	Pale blue-green. Gut green to reddish brown.
<i>P. cochlear</i>	0,9	Pale brown-green. Gut whitish.
<i>P. argenvillei</i>	4,5	Variable, usually whitish-brown. Gut green. Mid-dorsal stripe Eyes bright red.
<i>P. barbara</i>	5,4	Pale green-brown.
<i>P. miniata</i>	13,8	Delicate blue, pink tinges, mid-dorsal red stripe.
<i>P. tabularis</i>	10,8	As for <i>P. miniata</i> but paler blue.
<i>P. compressa</i>	15,4	Dorsally deep purple, fading to blue-pink. Gut brown. Eyes orange with brown mosaic.

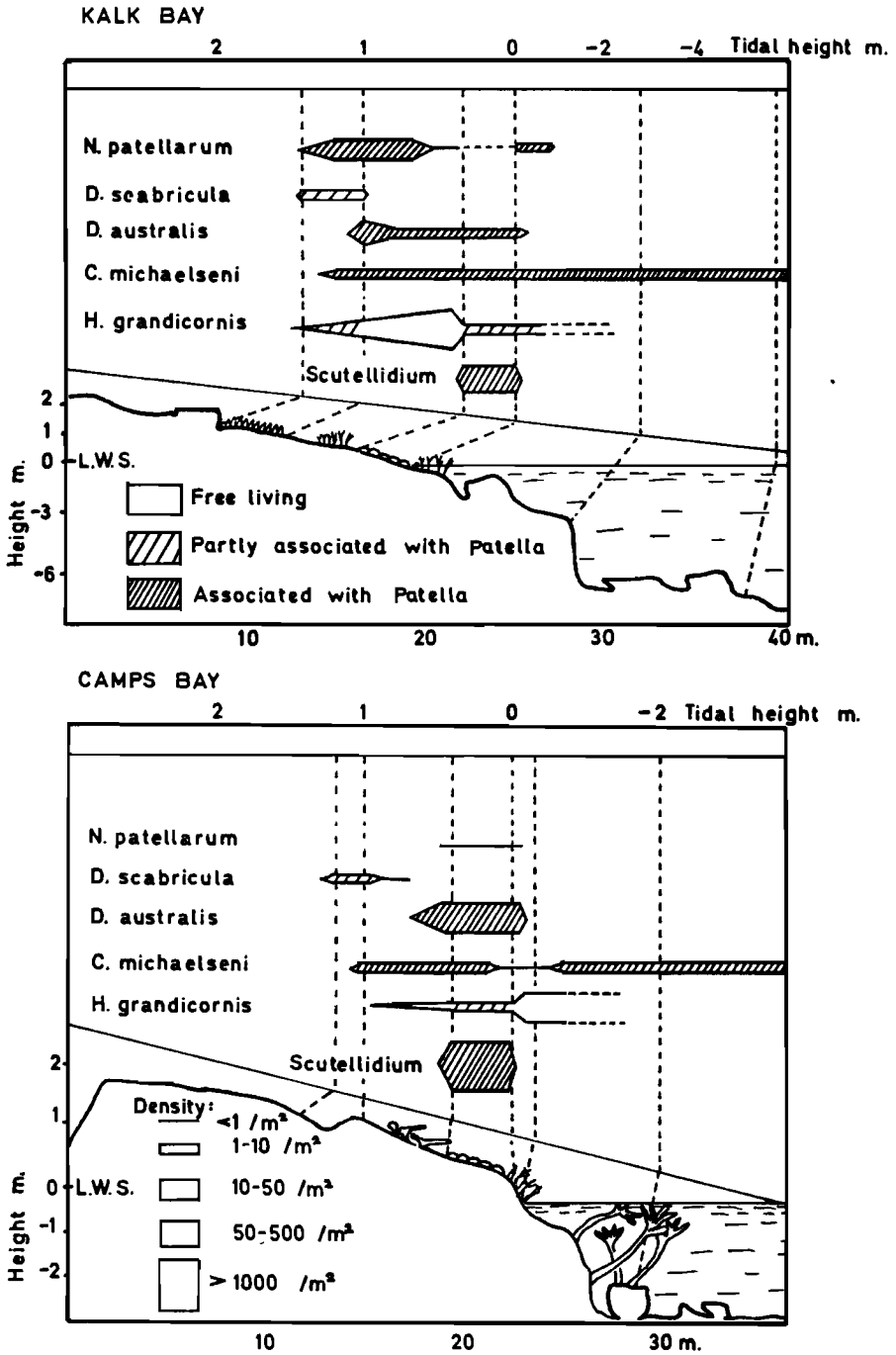


FIGURE 1

Transects at Kalk Bay and Camps Bay showing zonation of species associated with *Patella* spp.

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A certain amount of morphological variability occurs in *C. michaelsoni*, due partly to age and partly to zonation. Some variations fall outside the accepted definition of the species as discussed by Griffiths (1974:181). Specimens found high in the intertidal zone are smaller at maturity (6–11 mm) than subtidal specimens (8–14 mm).

Specimens of *C. michaelsoni* and its host were maintained in the laboratory for examination. To simulate tidal exposure and submergence, 10 *P. oculus* housing 15 amphipods were subjected to cyclic removal and replacement of water, using a simplified version of the tidal machine described by Underwood (1972). After an initial 10-hour period, none of the amphipods left their hosts during three successive 10-hour 'tidal' cycles. The amphipods lie in the pallial or mantle cavity, periodically moving around between the gills. Feeding, mating, moulting and emergence of the young were all observed to occur under the limpets.

The faeces of *Calliopiella* comprise a wide variety of algal fragments, but were constant within specimens taken from each host species. *Calliopiella* were observed feeding on the faeces of their hosts while in the mantle cavity and pallial groove. Isolated specimens would also feed readily on the faeces of *P. compressa*. In the cases of *P. compressa*, *P. longicosta* and *P. tabularis*, the host faeces and amphipod faeces were very similar in composition. The amphipods probably also feed on algal scrapings left behind while the host is feeding. These methods of feeding may in part explain the host preferences, as *P. cochlear* feeds predominantly on *Lithothamnion* and its faeces must have a low nutritive value. The colour of amphipod guts (Table 3) may similarly be explained by this diet. On one occasion a specimen was found feeding on the mucus deposited

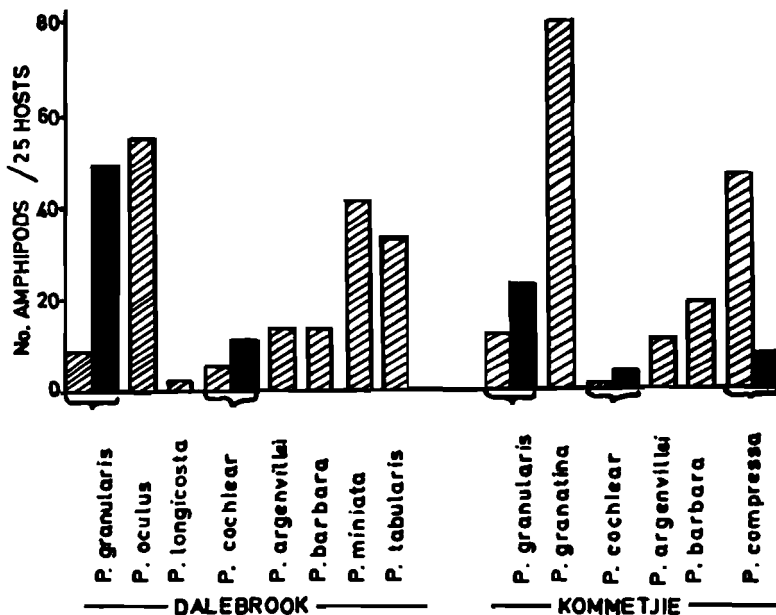


FIGURE 2

Numbers of amphipods associated with *Patella*. Black: *Hyale grandicornis*. Hatched: *Calliopiella michaelsoni*.

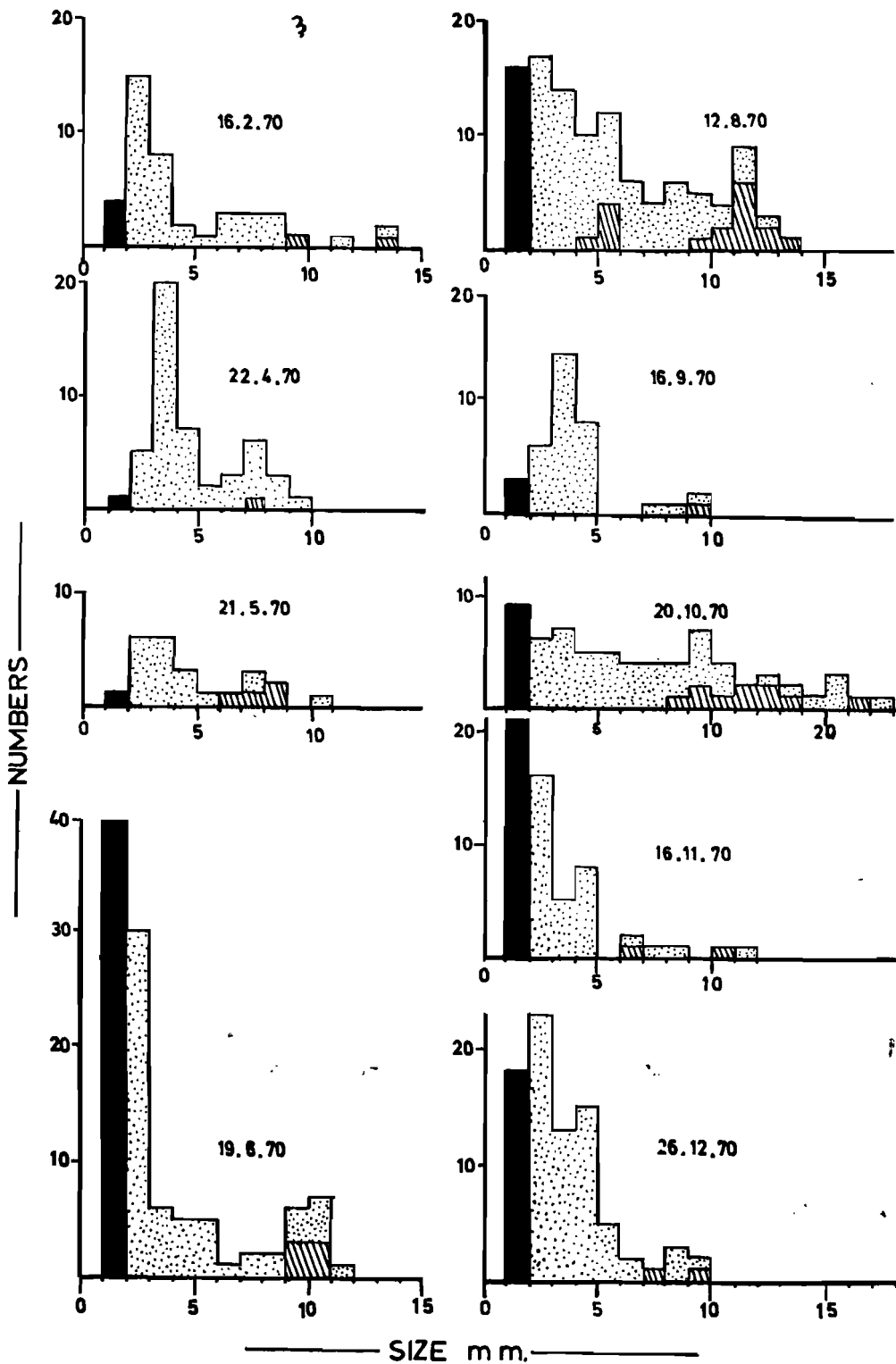


FIGURE 3

Monthly size distribution of *Calliopiella michaelseni* from Kommetjie. Small juveniles are shown in black, and ovigerous females are cross-hatched.

by a *P. oculus*, but this did not seem to be a regular occurrence.

Analysis of monthly samples of *Calliopiella* from Kommetjie, for size distribution, number of juveniles and ovigerous females, indicates that reproduction occurs throughout the year. However, there are two marked peaks of activity in June (Winter) and November (Spring) when large numbers of juveniles appear (Figure 3). This is similar to the condition found in *Neohausorius schmitzi* and *Austrochiltonia subtenius*, recorded by Dexter (1971) and Lim & Williams (1971). Between two and four age groups are apparent in most populations. The growth of each age group indicates a longevity of about 12 months and a deduced growth rate of 8 mm in six months. Most ovigerous females fall into a size range of 8–12 mm although a few specimens of 5 mm were recorded.

The reaction of *Calliopiella* to light was demonstrated by a series of choice chamber experiments. Circular glass dishes of 10 cm diameter were used, dividing each to allow the animals a choice of two alternatives. At least four trials of ten minutes were run for each experiment and each independently statistically tested. Table 4 gives the cumulative results for each experiment. These demonstrate a strong and sensitive photonegative reaction, similar to that displayed by *Lystriella clymenellae*, which is commensal in the tubes of the polychaete *Clymenella torquata* (Batcheller & Mills 1965).

An interesting positive correlation exists between the size of a host limpet and the size of its commensal amphipods (Figure 4), excluding newly emerged juveniles, which before dispersal remain with their parents and are thus associated with large limpets. With *P. oculus*, *P. granatina* and *P. compressa*, correlations of respectively 0,73; 0,90 and 0,78 were obtained: all significant at $P < 0,001$. These correlations suggest the selection of hosts according to size. Furthermore, a high percentage of large limpets contain a pair of *Calliopiella* (one of each sex) or a pair of adults and a number of offspring. In the case of smaller limpets (less than 50 mm), most lack amphipods or contain only a single specimen (Figure 5).

The dispersal of *Calliopiella* can be interpreted in the light of these observations. Mature males and females almost always occur in pairs, one per limpet, and are found only under large limpets. After reproduction, the offspring remain with their parents until they are about 4 mm in length (about two months growth). Dispersal then occurs, and the juveniles are subsequently found, usually singly, under small limpets (Figures 4 and 5). Heavy mortality occurs during dispersal, as is apparent from the size of the population age groups (Figure 3).

Large amphipods may select large limpets, while smaller amphipods are distributed among the remaining limpets, thus giving an illusion that they select small limpets.

The rate of growth in some limpets is such that not more than one change of host would be necessary to explain the correlation between amphipod and host size. Two of the preferred hosts, *P. granatina* and *P. oculus*, have growth rates in the order of 18 to 25 mm per year, respectively (Branch 1974a). Movement from one host to another must presumably occur with pairing (although this has not been observed) and 'selection' of a larger limpet may occur in the process.

As never more than one pair of adult *Calliopiella* is associated with each limpet, some mechanism must operate to exclude additional amphipods. Whether an 'occupied' limpet is rejected by incoming amphipods, or the resident pair actively excludes further amphipods, is not known. Some form of territorial behaviour is implied. Connell (1963) has demonstrated territorial defense in the tubicolous amphipod *Erichthonius braziliensis*. When twenty *Calli-*

TABLE 4

Choice chamber experiments: the responses of *Calliopiella*, *Hyale* and *Notoplana* to light. Each result is the sum of five trials. I = incident light, R = reflected light, measured at 10 cm from the surface.

	Choice				Species					
	Lighting	Background	I (lux)	R (lux)	Calliopiella	p	Hyale	p	Notoplana	p
1.	Direct	Black	10 000	650	3	<0,001	9	<0,01	7	<0,001
	Darkness	Black	14	8	73		31		89	
2.	Direct	Black	10 000	650	4	<0,001	—	—	40	>0,1
	Diffuse	Black	430	150	28		—		56	
3.	Direct	White	10 000	3 600	8	<0,001	10	<0,02	42	>0,1
	Direct	Black	10 000	650	46		24		54	

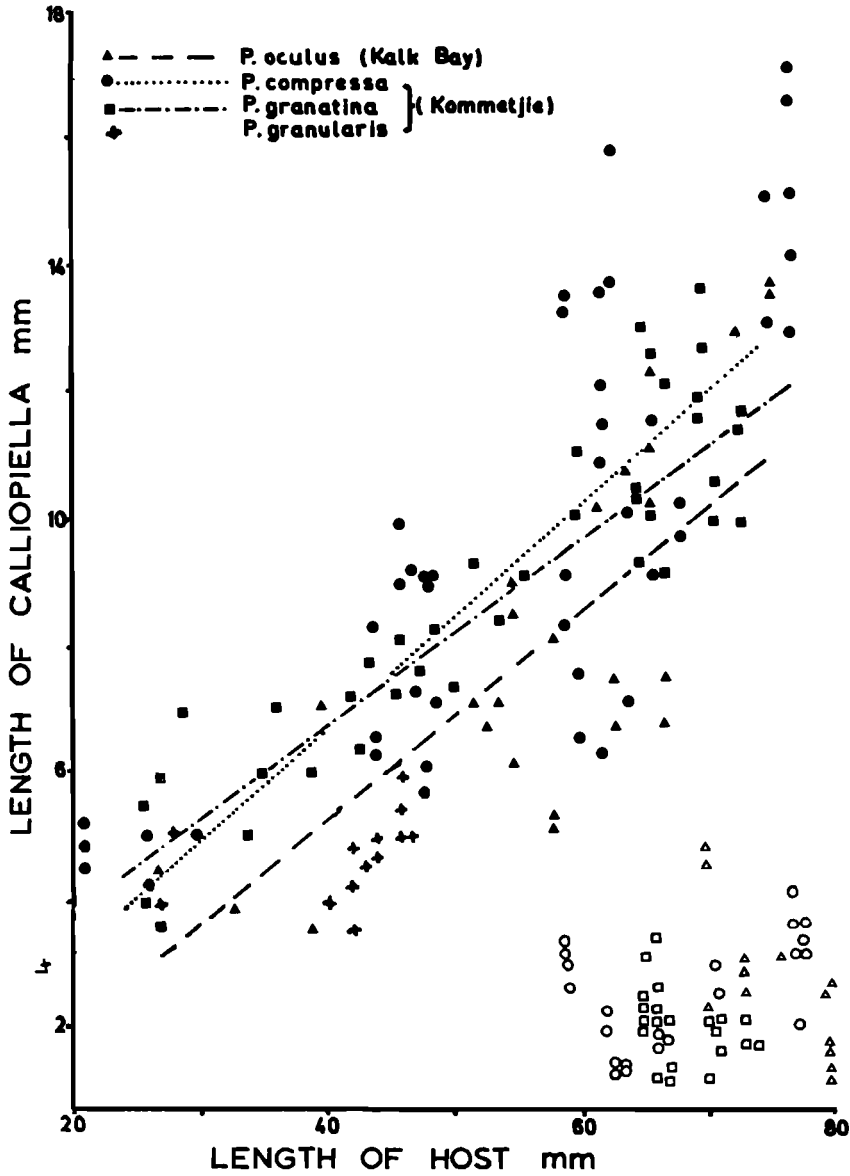


FIGURE 4

Lengths of *Calliopiella michaelseni* in relation to host length. Open symbols indicate juveniles still associated with their parents, and which are excluded from the regressions. No regression has been drawn for specimens associated with *P. granularis*.

opiella were introduced into an aquarium under a single *P. oculus*, they dispersed within three days to other (unoccupied) limpets in the aquarium. This situation is similar to the case described by Dimock (1971) for the symbiotic polychaete *Arctonoe pulchra*, which occurs with the limpet *Megathura crenulata* and the holothurian *Stichopus parvimensis*. Small worms occur together, but larger individuals become aggressive, disperse, and are found singly under their hosts.

Whilst the mechanism of dispersion in *Calliopiella* is not known, the advantage is obvious: only a limited amount of food will be available under each limpet. Similar advantage results from the size correlation between host and amphipod.

The amphipod *Hyale grandicornis* was never found under limpets housing *Calliopiella* adults.

The initial attraction of *C. michaelsoni* to a limpet may be phototactic as the amphipods are strongly photonegative, and crawl readily under any shell. This is not adequate to explain the attraction; some form of chemical attraction is also probable. In aquaria initial escape under dark objects is always followed later by rejection of the object in favour of a limpet (if available). The attractive factor occurs only in living limpets, and dead limpets repel the amphipods, even

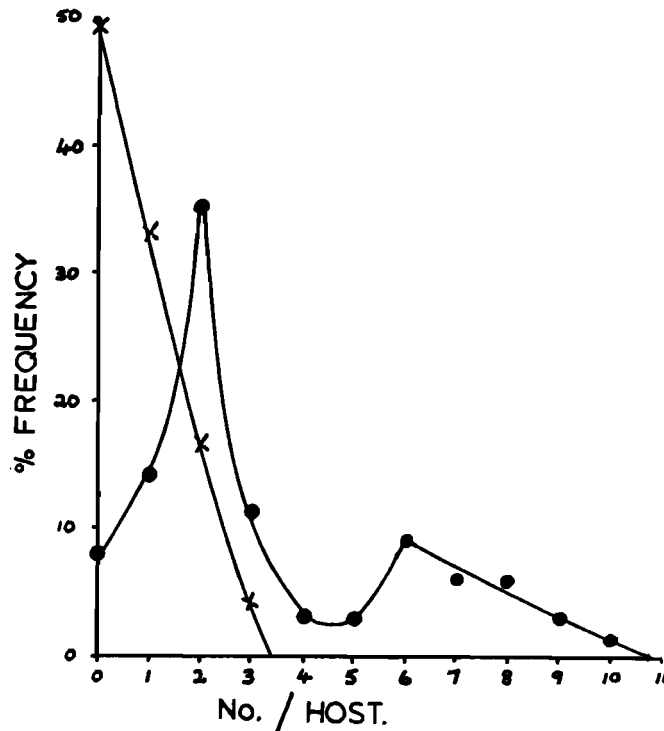


FIGURE 5

Number of *Calliopiella* per host. Circles indicate hosts of over 50 mm in length, and crosses indicate those under 50 mm.

if they have only recently been killed. (See results of experiments summarized in Table 5.)

Calliopiella is also strongly thigmotactic. When specimens are liberated in a round smooth glass container in which little contact with the substrate is possible, they clump together in small groups. The clumping effect only occurs if the background is dark or the light intensity low; in the presence of strong light or a white background the effect is abolished and the animals swim rapidly around trying to avoid the light.

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

Hyale grandicornis (Amphipoda)

H. grandicornis is a widely distributed and common species, recorded from the Californian coast of America (J. L. Barnard 1969) in association with *Acmaea* spp. (Johnson 1968), and in

TABLE 5
Choice chamber experiments with *C. michaelsoni*.

Number tested	Choice			Time per trial (hours)	Conditions	Significance of difference
	2 live <i>P. oculus</i>	2 empty <i>P. oculus</i> shells	Free swimming			
14	8	6	0	0,1	Diffuse light	p > 0,05
14	7	7	0			p > 0,05
14	9	5	0			p > 0,05
14	9	5	0			p > 0,05
18	16	1	1	12,0	Diffuse light	p < 0,001
16	16	0	0			p < 0,001
16	14	2	0			p < 0,001
14	14	0	0	12,0	Total darkness	p < 0,001
14	12	1	1			p < 0,001
14	14	4	0			p < 0,01
		2 recently killed <i>P. oculus</i>	Free swimming			
16	16	0	0	12,0	Diffuse light	p < 0,001
14	12	0	2			p < 0,001
14	12	0	2			p < 0,001

association with *P. vulgata* in Europe (Vader, personal communication). In South Africa it is ubiquitous and has been recorded from Luderitz to Durban. Its zonation extends from the upper balanoid to the sublittoral (Figure 1). Densities of up to 4 212 per m² were recorded.

H. grandicornis is found under all *Patella* spp., but almost all are associated with *P. cochlear* (30%) and *P. granularis* (62%) (Figure 2). Large numbers are also found free-living in algal tufts. The 'preference' for *P. cochlear* and *P. granularis* is explicable by the distribution of algal cover from the encrusting lithothamnion. Similarly, the Upper Balanoid is high on the shore and characterized by a lack of algae. *P. cochlear* and *P. granularis* respectively predominate in these zones and provide a logical shelter at low tide, in the absence of algae. Empty barnacle shells are also utilized.

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

Spooner (1957) has similarly described how juveniles of *H. perieri* are found under *P. vulgata*. Juveniles of *H. nilssonii* are also associated with this limpet (Vader 1972) and with *Nucella lapillus* (Brattegard 1963).

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

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

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

In the laboratory *H. grandicornis* is photonegative and reacts positively to a dark substrate, as shown by the results of choice chamber experiments (Table 4). The amphipods were liberated into circular chambers, one half of which was darkened, the other in the light. Similarly, choices of black or white backgrounds (both in light) were offered. Ten minutes were allowed for each trial.

Under water, *H. grandicornis* is attracted to dark shells and remains on (but not under) them. Feeding on algae was observed. If the water is drained off, the amphipods crawl under the limpet shell or into any niche where water has accumulated. With the addition of further water, they emerge and swim actively around and onto the shell surface again. If algal tufts are available, they too may be settled on. Quantitatively this is shown by the results in Table 6 obtained by liberating *H. grandicornis* into an aquarium with four intact *P. oculus* and four empty *P. oculus* shells.

Observations in the field confirm this behaviour. As the tide washes over the rocks, large numbers of *H. grandicornis* emerge from under limpets or other niches, and actively swim or

jump over the substrate. With the receding tide they again retreat into shelters, reacting photo-negatively.

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

Allorchestes inquiridens has recently been sunk in *H. grandicornis* (Griffiths 1975).

Dynamenella spp (Isopoda)

Several species of isopod have been recorded as commensals (Glynn 1968; Brattegard 1968). The relationship between *Dynamenella perforata* and *Acanthopleura granulata* has been analyzed in some detail by Glynn (1968). In South Africa a large variety of isopods is common intertidally, but only *D. scabricula* and *D. australis* are regularly associated with *Patella*, with respectively 85% and 96% association. *D. scabricula* is distributed from Luderitz to Hermanus (Day 1969) and occurs predominantly in the balanoid zone at about mid-tide level. *D. australis* ranges from Luderitz to Hermanus, principally in the cochlear zone, but extending into the lower Balanoid (Figure 1). Related to these zonation patterns, *D. scabricula* is mainly associated with *P. granularis* and *P. granatina*, while *D. australis* is found under *P. cochlear* and *P. argenvillei* (Table 1).

Analysis of the relative zonation and density of all common intertidal isopods at Dalebrook, Kalk Bay and Camps Bay show that these two species are the only regular isopod associates found under *Patella*. *D. huttoni* is probably the commonest isopod at these sites but is seldom found under limpets. Similarly, *Parisocladius* spp. and *Exosphaeroma* spp. are abundant in tufts of sea-weed but only occasionally occur under limpets (Table 7). *D. huttoni* is found abundantly in beds of *Bifurcaria brassicaeformis* as well as on *Gelidium pristoides*, *Gigartina stiriata* and other

TABLE 6

Niche selection by *Hyale grandicornis*.

Conditions	Time (minutes)	Number under living <i>P. oculus</i>	Number under empty shell	Number on top of shells	Number free swimming	Total
Under water	1	0	0	7	1	8
	10	0	0	7	1	8
Water drained off	10	4	3	3	0	10
	30	5	3	1	0	9
	30	5	3	2	0	10

algae. Small specimens are commoner in tufts of *Cladophora* spp. Faecal contents indicate that *D. huttoni* feeds entirely on the alga to which it is clinging.

Field & McFarlane (1968) have shown that *D. australis* and *D. scabricula* are associated with shores with strong wave action, while *D. huttoni* occurs over a much wider range of wave

TABLE 7

Intertidal distribution of the isopod genera *Dynamenella*, *Exosphaeroma*, and *Parisocladius*. Figures for Dalebrook are from Fuhr (1970 unpublished), obtained accumulatively from three samples of approximately 5 000 cm². Densities for Kalk Bay and Camps Bay are from duplicate 400 cm² samples. All figures have been scaled to represent density per m². Figures in italics represent numbers associated with *Patella*.

<i>Species</i>	<i>Upper balanoid</i>	<i>Lower balanoid</i>	<i>- Cochlear</i>	<i>Sub-tidal</i>	<i>Locality</i>
<i>D. australis</i>	0	0	0+9	4	
<i>D. scabricula</i>	0+6	0	0	0	
<i>D. dioxus</i>	0	0	6	0	
<i>D. macrocephala</i>	0	12	90	0	
<i>D. huttoni</i>	0	96	888	96	Dalebrook
<i>E. truncatitelson</i>	12	6	0	0	
<i>E. planum</i>	6	12	24	0	
<i>E. kraussi</i>	84	12	0	0	
<i>P. stimpsoni</i>	78+3	6	0	0	
<i>P. perforatus</i>	12	1 584	18	0	
<i>D. australis</i>	22+40	10+127	10+170	—	
<i>D. scabricula</i>	34+60	0	0	—	
<i>D. huttoni</i>	0	340	620	—	Kalk Bay
<i>E. porrectum</i>	0	0	20	—	
<i>E. kraussi</i>	25	0	0	—	
<i>P. perforatus</i>	6	270	0	—	
<i>D. australis</i>	10	22+504	42+ 2 016	46+1 512	
<i>D. scabricula</i>	1+27	0+17	0	0	
<i>D. huttoni</i>	10	120	1 252+12	626	
<i>E. kraussi</i>	26	0	0	0	Camps Bay
<i>E. laeviusculum</i>	6	0	0	0	
<i>P. perforatus</i>	6	26	0	0	
<i>Paridotea rubra</i>	0	0	3	3	

conditions. It is significant that *P. cochlear* and *P. argenvillei* also predominate in areas of strong wave action.

The reactions of *D. huttoni* and *D. australis* were tested by randomly releasing 26 of each into an aquarium containing two *P. argenvillei*, eight small *P. cochlear* (on the shells of *P. argenvillei*) and an equivalent amount of *Bifurcaria brassicaeformis*. The specimens were maintained in sea-water at 16° for 24 hours. The water was then slowly siphoned off to simulate low tide conditions and then poured back after three hours. Isopod distribution was determined periodically throughout the experimental period of 28 hours.

The results are given in Figure 6 and clearly indicate the preference the associate *D. australis* has for limpets, while the free living *D. huttoni* attaches onto the algae. During exposure, a few *D. huttoni* may crawl under limpets, but most bury themselves in the holdfast of the alga. *D. australis* rapidly crawl under (or onto) a *Patella*, and remain there even when the limpets are

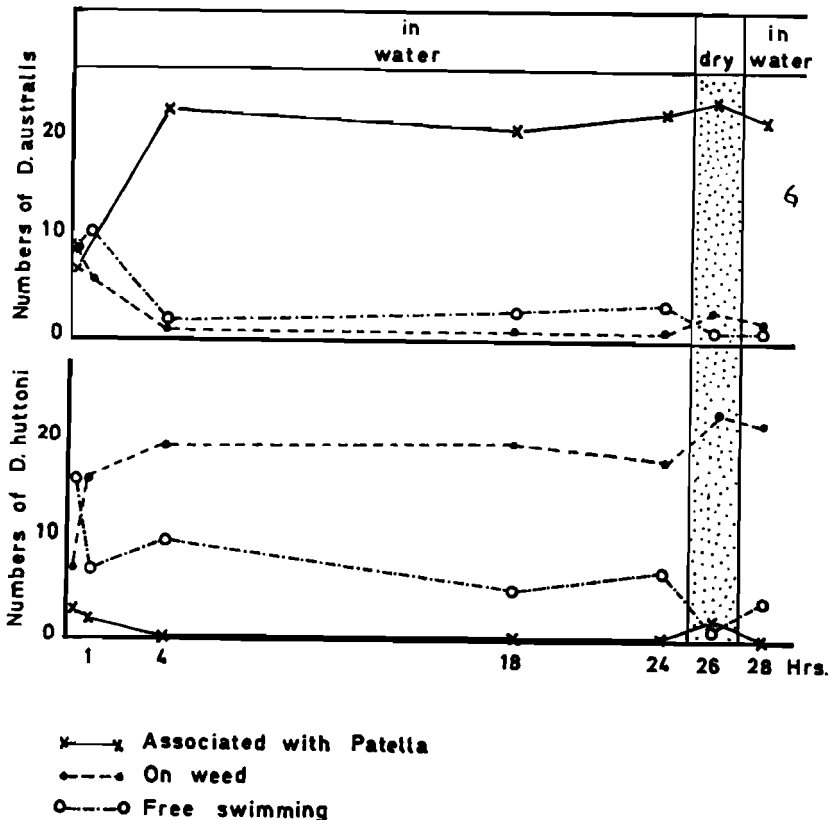


FIGURE 6

Substrate selection by *Dynamenella australis* and *D. huttoni*.

moving. If the limpet crawls away, the isopods rapidly follow it until they can move under the shell. Moulting and mating of *D. australis* have both been observed in the pallial groove of a limpet.

Under the limpet, *D. australis* lies in the pallial groove or on the mantle edge. Often it is orientated with its head buried between the gills. Glynn (1968) has observed that *D. perforata* adopts a similar position in the pallial groove of *Acanthopleura granulata*, and suggests that it is feeding on algal fragments left by the rasping of the chiton, and swept back in the respiratory current of *Acanthopleura*. *D. australis* may also feed on these algal particles, but was also seen emerging from under the limpet and eating alga on the edge of the shell. Some *D. australis* crawl over the shell, but never attempt to leave the limpet.

D. scabricula is not as common as *D. australis*, and occurs higher up the shore. While its relationship with *Patella* seems similar to that of *D. australis*, the association is less marked. In surveys (Table 7) most *D. scabricula* are found under limpets (85% association), but in aquaria about 40% cling to algae and 50% select limpets. Adults are often too large to lie in the pallial groove of *P. granularis*, and the limpet completely covers the isopod with its foot, so that it is firmly trapped to the substrate. This has no effect on the isopod, which is liberated when the limpet moves off to feed.

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

Scutellidium spp (Copepoda, Harpacticoidea)

Scutellidium patellarum was found in large numbers associated with *Patella*. A separate description of the species and its life cycle has been published (Branch 1974b). The known distribution of the species extends from Lamberts Bay (west coast) to Hangklip (False Bay), but this range will probably be extended with further work. At present it is suggestive of a cold water distribution. The species has a restricted zonation, being confined almost entirely to the Cochlear zone (Figure 1).

There is a marked correlation between the host size and the number of copepods (Figure 7), which together with the restricted zonation, probably explains the apparent preference of *Scutellidium* for *P. argenvillei*. About 80% are found associated with this limpet and the remainder are almost all limited to *P. cochlear*. Occasional specimens are found under other limpets but have not been found on any other hosts. An interesting negative correlation exists between the number of *Scutellidium* on a limpet, and the numbers of *Notoplana patellarum* (Figure 8). It is unlikely that a direct cause-and-effect relationship exists between the two distributions. Nevertheless, the reduction of contact is certainly of survival value to the copepods, as most polyclad turbellarians feed on small crustaceans (Hyman 1951) and the occasional *Notoplana* found on *P. argenvillei* fed readily on *Scutellidium*.

Scutellidium appears to be a scavenger and the limpets are unaffected by the relationship. In aquaria the copepods run continually over the pallial cavity and gills and even occasionally on

the external surface of the shell. Specimens have been kept alive for three weeks without their hosts, fed on dry shavings of *Ecklonia maxima* and small amounts of wet algae. During this time they produced larvae. It seems probable that they normally scavenge on the limpet faeces as well as algal fragments and possibly mucus produced by the limpets. Other members of the genus are free-living and usually found on littoral algae (Lang 1948; Wells 1967). *S. ringueleti* and *S. macrosetum* were found on algae adjacent to the limpets, but never associated with the limpets (Branch 1975).

Ovigerous females and larval stages can be found throughout the year and no marked peaks of reproduction have yet been detected. A marked sexual disparity exists and about 95% of adults are female. It is interesting that all of the larval stages are found under limpets suggesting that planktonic dispersal is minimal. Up to 200 specimens have been found on a large *P. argenvillei*, and due to the high density of limpets in the cochlear zone, dispersal could occur by direct transfer from limpet to limpet. All stages of the life cycle cling strongly to the host: the adult and copepodites have strong raptorial setae and sucktorial setal pads while the nauplii have a large central sucktorial membrane. Specimens cling tenaciously to the host when water movement occurs and even violent currents are incapable of dislodging them.

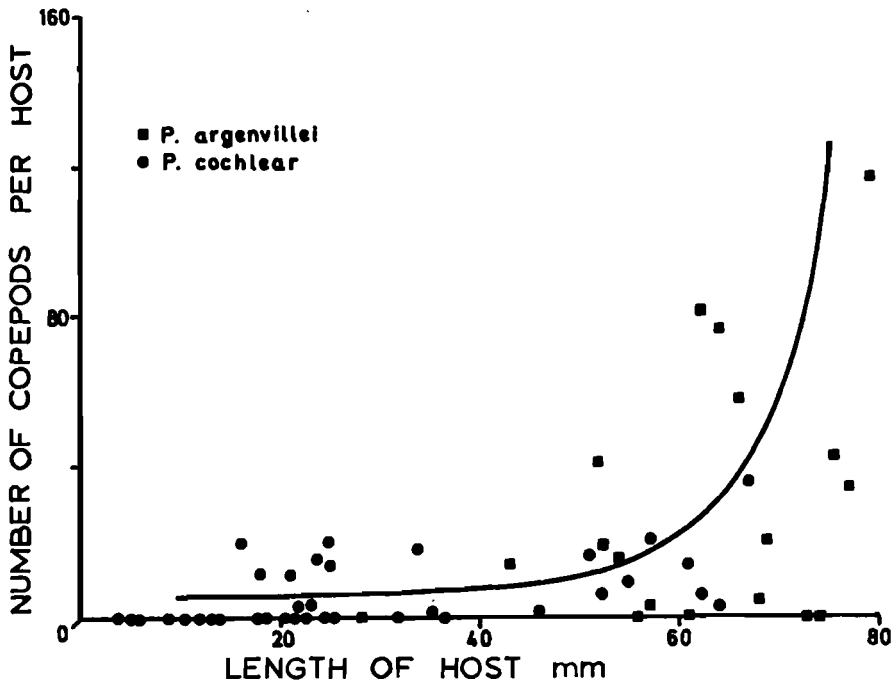


FIGURE 7
Number of *Scutellidium patellarum* in relation to host size.

Of incidental interest is the regular occurrence of two suctorian species and a peritrich ciliate on the body of *S. patellarum*. One of the suctorians (an ophryodendrid) is found only on the basal segments of the first antenna – a situation similar to the suctorian *Spathocyamus caridina* found on the antenna of the shrimp *Caridina* sp. (Nie & Lue 1945). Presumably the swimming action of the antenna assists the feeding mechanism of the suctorian.

Notoplana patellarum (Turbellaria, Polycladida)

The association between *N. patellarum* and *Patella* has long been known (Stephenson 1939; Koch 1949). In the present work 98,5% association was recorded, 78% being specific to *P. oculus*. The remainder are mainly associated with *P. longicosta* and *P. barbara* and to a lesser extent *P. cochlear*, although individuals have been found under all of the intertidal limpets. The distribution of the turbellarian was obtained by counting the number that could be found in one hour's examination of all the limpets in the given area. This correlates almost exactly with the numerical distribution of *P. oculus* obtained by using Stephenson's (1939) method of counting the number of *P. oculus* that could be identified in one hour without removing the limpets from the rocks (Figure 9).

N. patellarum occurs predominantly in the balanoid zone, occasionally being found subtidally (Figure 1). This pattern coincides with the zonation of *P. oculus*, except that small populations of *P. oculus* sometimes occur above their optimal range (Branch 1971) and these usually lack *N. patellarum*.

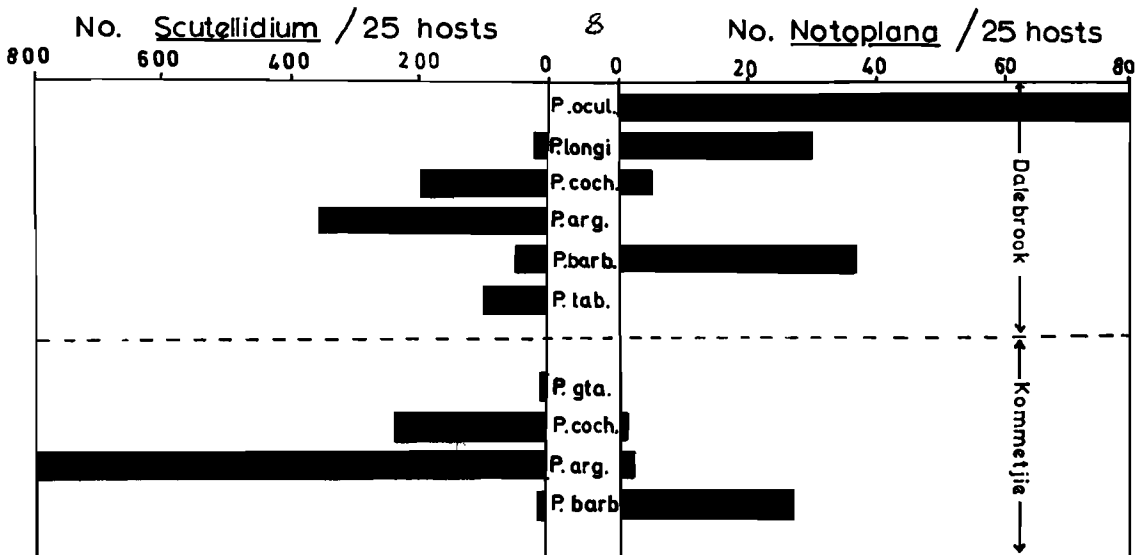


FIGURE 8

The relative numbers of *Scutellidium patellarum* and *Notoplana* associated with different *Patella* spp.

Although a marked preference for *P. oculus* is obvious, *N. patellarum* is also found associated with *P. longicosta* and *P. barbara*. On the west coast of South Africa where *P. oculus* and *P. longicosta* are absent or uncommon, the flatworm occurs in limited numbers, almost always

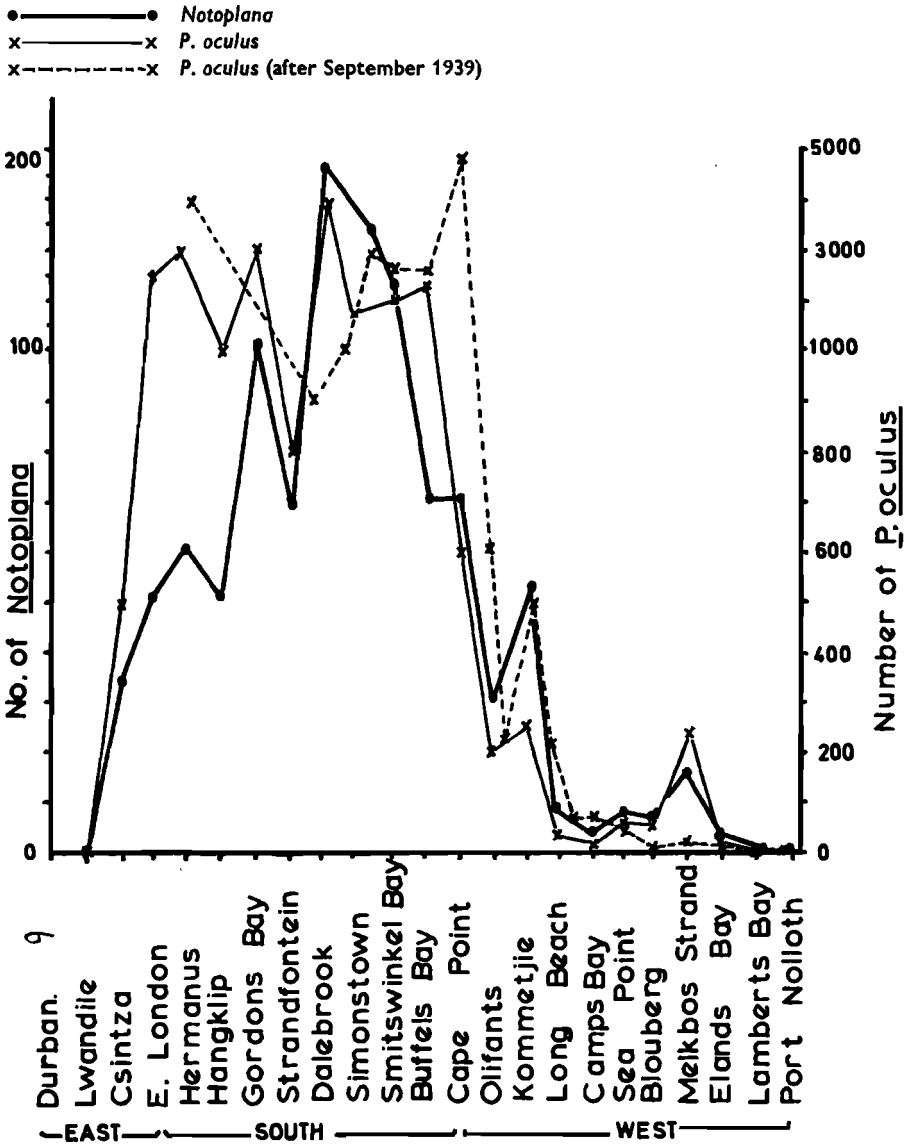


FIGURE 9
 Relative abundance and distribution of *Patella oculus* and *Notoplana patellarum*.

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associated with *P. barbara* or *P. cochlear*.

At Langebaan and St Helena Bay where there are sheltered and localized warm patches of water on the west coast, *P. oculus* is locally common. It is interesting that *Notoplana* too becomes common at Langebaan. Counts have not been made at St Helena Bay.

A positive correlation exists between host size and the number of *Notoplana* carried, but again *P. oculus* always has more *Notoplana* than either *P. longicosta* or *P. barbara* of comparable size (Figure 10). Isolated specimens are also found under other limpets (Figure 8). Host size alone cannot explain specificity.

The zonation of *N. patellarum* is also not a factor which can explain the specificity as *P. oculus* and *P. granatina* occupy comparable positions on the shore, and yet the latter very seldom houses the turbellarian. This is strikingly demonstrated in areas where both *P. oculus* and *P. granatina* occur. Counts taken at Melkbos Strand illustrate this. Despite the numerical domination of the lower balanoid by *P. granatina*, almost all *N. patellarum* were found with *P. oculus* (Figure 11).

The reaction of *N. patellarum* to light, limpets, and limpet shells was tested using choice

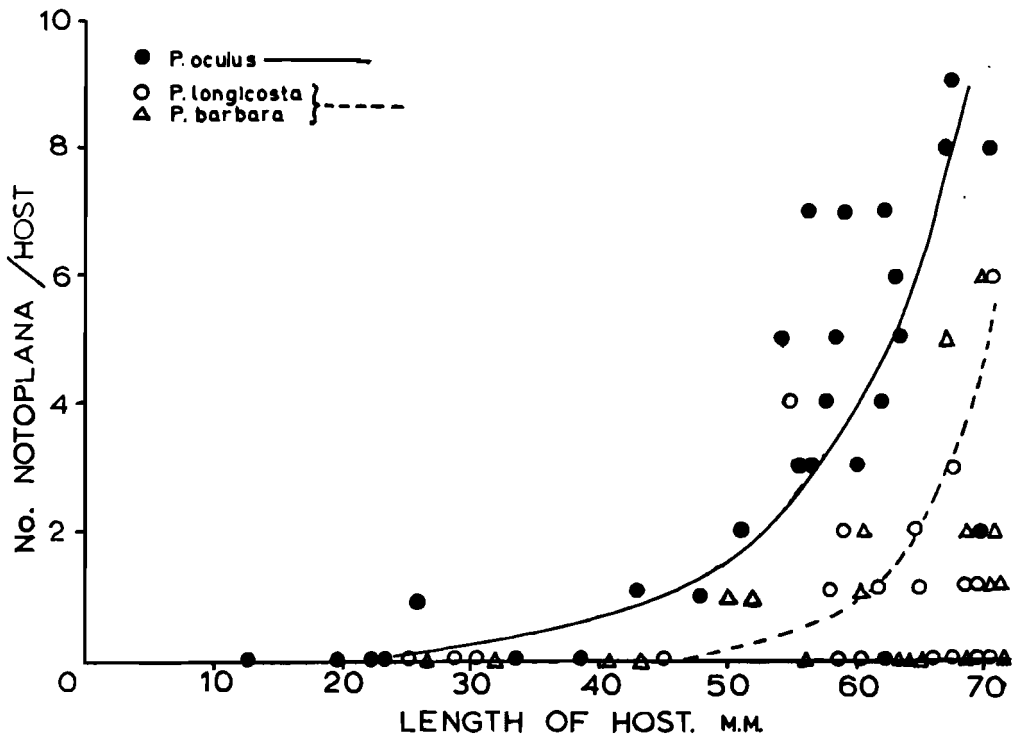


FIGURE 10

Numbers of *Notoplana patellarum* relative to host species and size, at Dalebrook.

chambers. The choices offered and the results obtained are summarized in Tables 4 and 8.

Although a photonegative response is apparent from the results (Table 4), the sensitivity is low, as indicated by the limited distinction between direct and diffuse light, and between black and white backgrounds. In the choice between intact *P. oculus* and fresh empty shells of this limpet, a strong attraction to the live limpet was apparent (Table 8). Initial reaction was random, and the *Notoplana* moved around and under the limpets or shells in an irregular manner: many crawled under one of the limpets and then out again almost immediately. This random pattern disappeared progressively, and within 12 hours almost all were confined to the live *P. oculus*.

Host specificity was strikingly demonstrated by introducing 27 *Notoplana* into the centre of a round aquarium containing two specimens each of *P. oculus*, *P. cochlear*, *P. longicosta* and *P. granularis* arranged equidistantly around the periphery. Results are shown in Table 9, and indicated marked preference for live *P. oculus* ($\chi^2, p < 0,001$). Some form of chemical attraction must exist to explain the marked specificity. The attraction ceases with death or mutilation of the *P. oculus* and the limpets are rejected ($\chi^2, p < 0,001$). This is similar to the situation recorded by Davenport & Hickok (1951) for the polychaete *Arctonoë fragilis* which is commensal with *Evasterias troschelii*.

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

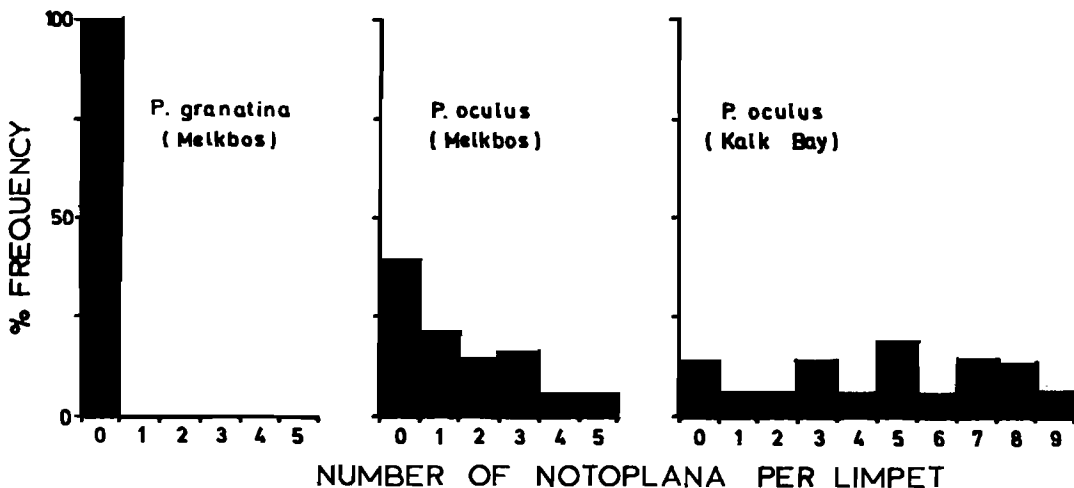


FIGURE 11

Relative numbers of *Notoplana patellarum* associated with *Patella granatina* and *P. oculus*.

TABLE 8

Choice chamber experiments with *N. patellarum*.

Number tested	Choice			Conditions	Significance of difference
	2 living <i>P. oculus</i>	2 empty shells	Free swimming		
26	6	7	13	} 10 minutes in light	p < 0,1
26	8	5	13		p < 0,1
26	26	0	0	} 12 hours in light	p < 0,001
26	24	2	0		p < 0,001
26	20	6	0		p < 0,01
26	24	1	1	12 hours in dark	p < 0,001
26	25	0	1	12 hours alternating light and dark	p < 0,001

TABLE 9

Selection of different *Patella* spp. by *N. patellarum*.

Conditions	Number under limpets								Number not under limpets	Total
	<i>P. oculus</i>		<i>P. longicosta</i>		<i>P. granularis</i>		<i>P. cochlear</i>			
	1	2	1	2	1	2	1	2		
14 hours in light All limpets alive	8	8	1	1	4	0	0	0	5	27
5 hours in dark All limpets alive	18	2	0	4	0	2	0	0	1	27
6 hours in light Limpets died after 3 hours	2	0	0	0	0	0	0	0	24	26
6 hours in light Limpets mutilated but alive	2	0	1	0	0	0	0	0	23	26

DISCUSSION

The retention of water in the pallial cavity of limpets makes them a logical shelter for small intertidal organisms during low tide. This niche is exploited by a large number of species, but in most cases the association is casual and temporary. Forty-six species have been recorded under limpets, but only six occur sufficiently often to be considered associates or commensals. Among the 46 species, almost every group of intertidal animals is represented, including fish, nemertines, polychaetes, crustaceans and molluscs, but amphipods and isopods predominate.

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

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

In the case of *Scutellidium patellarum* and *Dynamenella australis* (and to a lesser extent *D. scabricula*) a greater degree of association occurs. Even at high tide these animals remain under their hosts, or undertake only short excursions and then return. Fewer are found free-living. The complete life-cycle may occur under the limpets. Feeding on algal fragments has been observed, and the radular movements of the limpet may leave small algal particles on which these animals can feed. Specificity is still low, for although all three are confined to a few *Patella* spp., this is probably due to their zonation patterns rather than a true specificity. *Scutellidium*, *D. australis* and *D. scabricula* are probably facultative inquilines. In both genera there are other intertidal species which are entirely free-living. In such cases speciation may have followed a behavioural mutation which led to commensalism: the consequent isolation from free-living counterparts would allow further divergence and eventually the formation of separate species, in a manner similar to that suggested by Meadows & Campbell (1972).

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

Turbellarians are mainly cryptic animals, a habit which leads naturally to inquilinism and commensalism. Smith (1961) has described a case of inquilinism in which *Hoploplana luracola* occurs in the mantle cavity of *Nerita scabricosta* but probably feeds elsewhere. Several of the Leptoplanidae (to which *Notoplana* belongs) are commensal. *Hoploplana inquilina* is found in the mantle cavity of several whelks (Hyman 1967). *Stylochoplana inquilina* is associated with a hermit crab – anemone complex (Hyman 1950). *S. pusilla* occurs in the mantle cavity of *Monodonta labis*, and *S. parasitica* in the pallial groove of the chiton *Liolophura japonica tessell-*

lata (Kato 1934; 1935). *Notoplana* is a widely distributed genus, and common on rocky shores (Hyman 1951) so that the development of commensalism in *N. patellarum* is not surprising. *N. patellarum* is specific to a limited number of limpets and shows a marked preference for *P. oculus*.

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

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