OBSERVATIONS ON THE INTERTIDAL BARNACLES (CIRRIPEDIA: BALANOMORPHA) AT FOSSIL ISLAND, TASMAN PENINSULA: PHYSICAL TOLERANCES, ORIENTATION AND FERTILISATION

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(with four tables and four text-figures)

Six species of barnacle are found intertidally at Fossil Island. Tolerances of the species to desiccation and temperature could be related to their position on the shore. The four common species all show significant orientation to water currents: in *Catomerus polymerus* the orientation is reversed lower on the shore. Strong evidence is presented that isolated *C. polymerus* individuals can self-fertilise.

INTRODUCTION

The rocky shores of Tasman Peninsula are typical of much of the east coast of Tasmania and are part of the Maugean sub-province (Bennett & Pope 1953, Dartnall 1974). The intertidal fauna is depauperate compared to the warmer provinces of mainland Australia but some species are confined to the region.

Tasman Peninsula was the site for several pioneering studies of the intertidal zone at Port Arthur (Cribb 1954) and at Eaglehawk Neck (Guiler 1952, Bennett & Pope 1960). Pirates Bay, at Eaglehawk Neck, provides a particularly valuable site because of the range of wave exposures found in various parts of the bay and headlands.

Recent studies at Fossil Island have centred on barnacles (Zacharin 1984, Fleming 1986) and ascidians (Ward 1985). This paper will report some preliminary findings on the barnacle fauna, particularly their distribution, tolerance of physical factors, orientation to water currents and reproductive biology.

THE BARNACLE FAUNA

Barnacles (Crustacea:Cirripedia) are strictly sessile and either free-living or parasitic invertebrates which, although found in estuaries and oceans at all depths, are especially characteristic of the rocky intertidal zone throughout the world. Sessility, while allowing the animal great economies and the advantage of heavy protection, brings with it a number of problems. Some of these are especially exaggerated for the barnacles since they belong to a group with a higher level of body organisation than the majority of sessile organisms. Sessile organisms do not have the capacity to respond to adverse physical conditions by movement. Thus they must be able to tolerate the complete range of conditions likely to be experienced at a given location. This problem is seen very clearly in the intertidal zone where fundamentally aquatic organisms face the problems of terrestrial life twice daily, as well as experiencing the wave action associated with tidal movements. Sessile animals cannot pursue their food and hence must develop some form of filter feeding. In the intertidal zone, this mode of feeding can be enhanced by the exploitation of water currents and barnacles can be expected to show orientation to the direction of water flow over the surfaces on which they live.

Although heavily protected by their shell plates, barnacles cannot escape predators by movement. Carnivorous molluscs with radulae adapted to bore through their plates can prey on them at will. To feed, barnacles must extend their unprotected cirri, and these form the food of some fish, such as blennies, e.g. *Parablennius tasmanianus tasmanianus*

(Richardson, 1849) (Cook 1986). The same fish are capable of removing smaller barnacles whole from the substrate.

Competition for the limited resource of space is another problem for sessile organisms, illustrated by the dense beds of barnacles seen at some sites. The mechanisms by which some barnacles settle close, but not too close, to conspecifics, and yet will smother another species, have been described by Crisp (1961). Not only other barnacles but other sessile species, such as mussels, and grazers, such as limpets, can affect the barnacles' ability to acquire and hold space.

Unlike many crustaceans, barnacles are hermaphrodites, but unlike most sessile animals, they retain internal cross-fertilisation, a process that presents obvious difficulties for a sessile organism. It means that inter-individual distances become critical, and raises an immediate question about the reproductive status of animals which are isolated. Self-fertilisation has been identified in some Northern Hemisphere barnacles (Barnes & Crisp 1955) and in New Zealand (Joll 1961) but does not appear to have been recorded in the Australian fauna.

Finally, dispersal and the selection of a settlement site by the larvae are obviously very important to all sessile organisms, including barnacles. Site selection and settlement behaviour have been studied extensively in Northern Hemisphere species, especially *Semibalanus balanoides* (e.g. Crisp 1961).

Members of both major suborders of the Cirripedia can be found on Tasmanian shores. The Lepadomorpha, or stalked barnacles, are represented by a single species *Ibla quadrivalvis* (Cuvier, 1817) which is found on the north and east coasts, often inconspicuously in crevices or amongst mussels. The Balanomorpha, or acorn barnacles, are represented by seven species intertidally: *Chthamalus antennatus* (Darwin, 1854), *Elminius modestus* (Darwin, 1854), *Chamaesipho columna* (Spengler, 1790), *Tetraclitella purpurascens* (Wood, 1815), *Catomerus polymerus* (Darwin, 1854), *Austromegabalanus nigrescens* (Lamark, 1818) and *Epopella simplex* (Darwin, 1854). None of these barnacles is endemic to Tasmania and most occur at lower densities here than on the shore of the Australian mainland.

On the intertidal rock platforms at Fossil Island, *Ibla quadrivalvis* is very scarce or absent, *Elminius modestus*, basically an estuarine and sheltered water species, is absent, and *Epopella simplex* is very scarce, being found only at the lowest tidal levels, often growing on the shell plates of *Austromegabalanus nigrescens*.

FOSSIL ISLAND

Forming the southern margin of Pirates Bay, Fossil Island is a small promontory, barely separated from the mainland by a small channel flooded only at the highest tides. The island is composed of sub-horizontally bedded Permian shales and sandstones; these have been differentially eroded to produce, especially on the eastern side, wide intertidal platforms which drop steeply immediately below the *Durvillaea* zone. Similar, but narrower platforms are present on the sheltered western side of the island. The eastern platforms are exposed to oceanic swells and may experience heavy wave action, i.e. sub-maximal on the scheme of Bennett & Pope (1960).

Mean maximum and minimum air temperatures range from 20–5°C; frost must be extremely rare in the intertidal zone, and highest maximum shade temperatures are unlikely to exceed 35°C. Sea temperatures range from 11–16°C (Wolfe 1965), although intertidal waters are likely to exceed this range. The tidal range is approximately 1.4 m. Salinity varies only slightly since there are no major freshwater discharges nearby. Ward (1985) recorded a range of 35–37% over an eight-month period, but Hoggins (1976) recorded a minimum of 34% after heavy September rains.

Offshore water movements are dominated by seasonal movements in the subantarctic and central Tasman currents. Thus, colder water moves northward in winter and warmer water southward in summer (Rochford 1957). The extent to which these offshore currents affect the movements of the reproductive products and larvae of intertidal organisms is unclear, but the general movement of beach sediments along the coast is northward (Davies 1973).

METHODS AND RESULTS

Distribution

Collections and observations of intertidal barnacles were made along the east coast of Tasmania from Swan Island to Maatsuyker Island and, indirectly, Pedra Branca. At Fossil Island, transects of the shore were examined and the zonation of species recorded in areas of different wave exposure.

It is clear that the Tasmanian barnacle fauna declines in diversity southwards and on the west coast (table 1). On the south coast, *Catomerus polymerus* and *Chamaesipho columna* are the only species present, but they extend to the offshore islands of Maatsuyker (Zacharin 1984, Fleming 1986) and Pedra

TABLE 1

The General Distribution of the Six Species of Balanomorph Barnacles found on Exposed Rocky Shores* in Tasmania

Species	Australian distribution	Tasmanian distribution			
		East coast	North coast	West coast	Far south & islands
Chthamalus antennatus	S Qld to SE Tas.	+	NW	–	–
Chamaesipho columna	N NSW to SE Tas.	+	+	+	inc. Maatsuyker & Pedra Branca
Tetraclitella purpurascens	Double Is. Pt, Qld, to SE Tas.	+	+	patchy	–
Catomerus polymerus	Morton Bay, Qld, to SE Tas.	+	?	patchy	inc. Maatsuyker & Pedra Branca
Austromegabalanus nigrescens	Double Is. Pt, Qld, to SE Tas. (Blackmans Bay)	+	–	–	–
Epopella simplex	Port Jackson, NSW, to E Tas.	Eaglehawk Neck	–	–	–

*One other species, *Elminius modestus,* is found on sheltered and estuarine shores. It is widely distributed in Tasmania and on mainland Australia.

Branca (on the basis of photographic evidence and specimens collected by N. Brothers, National Parks and Wildlife Service, Hobart: Fleming 1986). On the west coast, *Tetraclitella purpurascens* occurs sporadically in company with *Catomerus polymerus* and *Chaemosipho columna* (Edgar 1984a). The east coast clearly has the richest barnacle fauna.

The general intertidal zonation of the common barnacle species at Fossil Island is shown in figures 1 and 2, with the distributions of the other common organisms on the shore.

Physical Tolerances

Tolerance to high temperatures was assessed by placing barnacles in a small water bath at 12°C (the sea-surface temperature at the time of collection) and raising the temperature of the seawater by 0.5–1°C per minute until cirral activity ceased. Water temperature was monitored continuously and the water was stirred vigorously to stimulate cirral beating. Death was judged to have occurred if the animals failed to respond to mechanical stimulation of the opercular valve after 12 hours in flowing seawater at normal temperature.

Animals were also placed in water baths at 0 and -1°C. Samples were removed at hourly intervals and their viability checked as above. Further groups of animals were exposed in air to temperatures of 0, -2 and -10°C.

Figure 3 summarises the results of the temperature tolerance experiments. All species could maintain cirral activity between 5 and 30°C. Above that range cirral beats became irregular and the opercular plates were moved about before the animals became inactive. *Chamaesipho columna* could be revived after short exposure to 50°C and *Chthamalus antennatus* and *Tetraclitella purpurascens* could tolerate brief exposure to 45°C. The lower intertidal
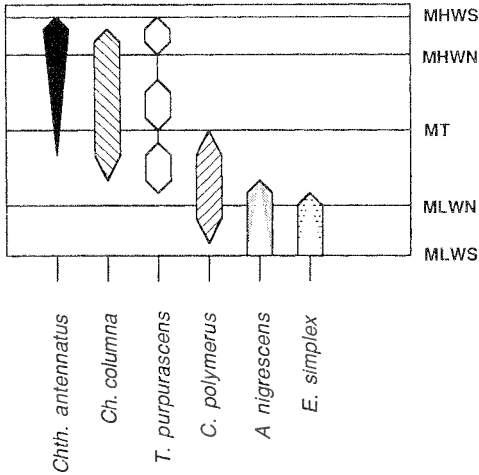
FIG. 1 — The generalised distribution of the six barnacle species found on the exposed intertidal rocky platforms at Fossil Island. Austromegabalanus nigrescens and Epopella simplex are much less abundant than the other species.

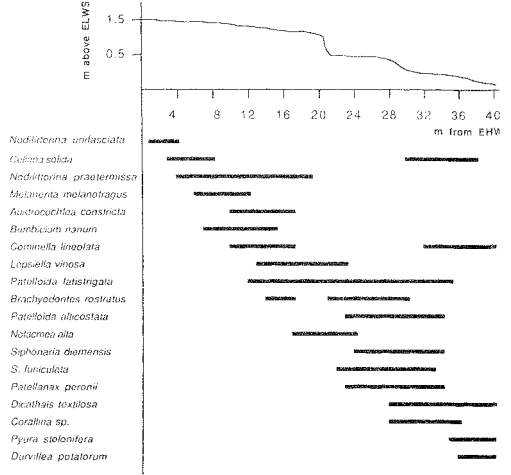
FIG.2 — The distribution of some of the more common organisms on a transect across the exposed intertidal rock platforms at Fossil Island.
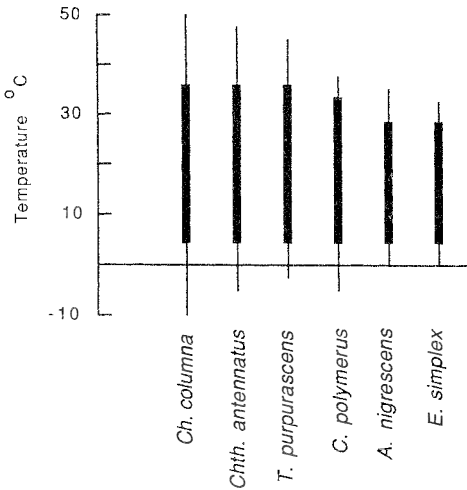

FIG. 3 — The temperature tolerance of six Tasmanian barnacle species. The thick bars represent the range over which cirral activity was maintained. The thinner bars show temperatures which the animals could tolerate for short periods.

species show a reduction in tolerance. All species were able to maintain cirral activity to 0°C and the upper shore species could be revived after two-day exposures to -2°C.

Desiccation

In order to compare their desiccation tolerances, barnacles were placed in desiccators over silica gel. Since the animals were collected on rocks, large amounts of water were present and the desiccant was changed frequently in the first four days of the observations. The animals' survival was checked daily, either by mechanical stimulation of the opercular plates or, if there was no response, they were removed to a flow tank of seawater. Failure to open after 12 hours in the flow tank was taken as evidence of death. Tolerances were tested at 10°C and 20°C.

To eliminate size effects, only adult animals were used, in the following size ranges: *Chamaesipho columna* 3–4 mm, *Chthamalus antennatus* 6–8 mm, *Catomerus polymerus* 9–10 mm, and *T. purpurascens* 8–10 mm (mean rostro-carinal diameter). Insufficient numbers of *Epopella simplex* or *Austromegabalanus nigrescens* were available to allow their inclusion.

To compare the desiccation tolerance of the four species, the mean life expectancy of individuals of each species at the two temperatures was calculated using the expression below:

$$e_x = 0.5 + \left(\sum_{i=x+1}^{w} l_i \right) / l_x$$

where x = time in days, w = total number of days lived by the group of l_i individuals from time x until death, and l_x = % survivorship.

Table 2 shows that life expectancy under these conditions declined with position on the shore (*Chamaesipho* > *Chthamalus* > *Tetraclitella* > *Catomerus*). Life expectancies of all species were reduced at the higher temperature.

It is hard to relate these data to desiccation tolerance in the field, since the experiments were carried out in still air (Foster 1971), but it seems probable that all species can resist more intense desiccation than they are likely to experience in the field.

Orientation

The Fossil Island rock platforms provide a useful site for the analysis of orientation of barnacle populations, because of their basically horizontal surfaces and the range of exposures available. Populations of the four major species were located in areas where the direction of water flow was consistent and could be measured at high tide. In a spatially-homogeneous area, the orientation of the carino–rostral axis of a sample of barnacles was measured by laying a transparent compass (Silva Type 3) over each animal. Only one suitable population of the shade-loving *T. purpurascens* could be located.

Table 3 shows the statistics calculated from each sample. In all cases there was a significant trend (or mean angle: Zar 1984) in orientation, i.e. none of the populations showed random orientation. In all but one sample, there was no significant deviation between the measured direction in which the water flowed over the animals and their mean angle.

Field observations of *A. nigrescens* suggest that it also orientates to the current. It is often found in crevices where the animal is orientated so that the cirral net faces the backwash of waves. In *C. polymerus* the same trend was noted in lower shore populations, where all the individuals faced up-shore, but those higher on the shore faced down-shore.

On vertical surfaces, *Chamaesipho columna* and *Catomerus polymerus* orientate vertically, with the rostral plate uppermost, but *T. purpurascens* takes up the reverse position, with the rostral plate facing away from the light.

Localised populations of *Chthamalus antennatus* were difficult to find and the larger variation about the mean angle seen in the samples of this species probably reflects the wider areas which had to be examined to collect sufficiently large samples. This must inevitably have increased the variation in direction of water flow over the area.

Fertilisation

Because the capacity of barnacles to cross-fertilise was of interest, animals were defined as being either isolated or contiguous, where isolation meant a distance of >50 mm from the nearest conspecific. This part of the study deals mostly with *Catomerus polymerus*, but information on *A. nigrescens* was collected from a dolerite shore at Boags Point, near Swansea, and *T. purpurascens* was sampled from Fossil Island in March and July 1985.

Twenty isolated and contiguous animals were collected from the Fossil Island rock platform from March through August 1985. These animals were returned intact to the laboratory for dissection to ascertain their reproductive status. Eggs and embryonic stages were divided into the classes described in table 4. The penises of all specimens were also measured by stretching them to full length with forceps and measuring from the tip to the distal end of the pedicel.

TABLE 2

Mean Life Expectancies (e_x) of Four Common Intertidal Barnacles at Two Temperatures at Very Low Humidity*

Species**	Life expectancy (days) at different temperatures	
	10°C	20°C
Chthamalus antennatus	10.5	8.5
Chamaesipho columna	15.9	13.7
Tetraclitella purpurascens	7.0	2.4
Catomerus polymerus	8.8	6.5

*   0-2% RH.
** Arranged in order of appearance from the high water mark.

TABLE 3

Orientation of Four Species of Barnacle at Fossil Island in Relation to Water Flow*

Species	Sample size (n)	Mean direction $(U_a)°$	Mean angle** ± confidence limits $(θ ± CL (99\%))$	Angular dispersion (S)
Chamaesipho columna	78	130	135±5.24	17.4
	70	140	136±8.02	25.24
	38	220	222±8.13	18.54
	65	132	134±6.42	19.46
Chthamalus antennatus	39	142	133±16.77	38.74
	20	145	150±18.43	28.97
Tetraclitella purpurascens	32	270	286±17.64	36.28
Catomerus polymerus	31	158	160±8.43	17.05
	82	47	89±15§	27.73
	28	64	68±6.01	11.95

* The direction of water flow over each position is given by U_a. If this angle falls within the range of confidence limits for the mean angle then there is no significant deviation between the mean orientation of the animals and the direction of water flow.
** All mean angles are significant.
§   Only significant deviation.

TABLE 4

Stages* used to describe the Eggs and developing Larvae of *Catomerus polymerus*

Stage	Description of embryo
1	Unsegmented egg in oval or pyriform case.
2	*From* two simple blastomeres *to* embryo divided by two or more constrictions between rudimentary swellings giving rise to the appendages.
3	*From* appendages clearly visible as short bifid swellings, setae absent or not evident *to* appendages with distinct setae; no eye visible.
4	*From* median eye red or poorly pigmented, mass of yolk cells present *to* eyes darkly pigmented, black or reddish brown; endoderm forming a clearly defined gut; hatching within a few minutes of being placed in seawater.

* Derived from Barnes & Barnes (1958).

Penis lengths of *C. polymerus* in isolated positions were significantly longer than those in contiguous groups (Students t_{215} = 3.54, P < 0.001), but this was associated with a significant increase in the size of isolated animals (Students t_{175} = 2.92, P < 0.01). However, the regression of penis length on barnacle volume (an efficient estimator of size: Fleming 1986) accounts for very little variation in penis length and hence the greater penis length of isolated individuals appears to be a real phenomenon. In *A. nigrescens* there was no difference in penis length between isolated and contiguous individuals. It is worth noting that the average penis length in *C. polymerus* samples (24.6–28.9 mm) exceeded, or at least equalled, that of the much larger *A. nigrescens* (25.7 mm). In *T. purpurascens* the penis is much smaller (mean = 12.7 mm, n = 90).

Very little difference was detected in the frequency of fertilised individuals (stages 2–4) between isolated and contiguous groups of animals. In April there were significantly more fertilised *C. polymerus* in contiguous groups (χ^2_1 = 4.51, P < 0.05), but no other monthly samples showed any difference.

The proportions of the four reproductive stages in *C. polymerus* and *A. nigrescens* are shown in

figure 4. The incidence of fertilised animals in
C. polymerus was highest in March and fell to a low
in June before increasing in July and August. In *A.
nigrescens*, fertilised animals were only observed in
March and April.

C. *polymerus,* collected at Maatsuyker Island
in April and June 1985, contained no reproductive
stages, but some specimens of the same species
collected from Pedra Branca in April 1986 had egg
masses in their mantle cavities.

DISCUSSION

Distribution

The decline in barnacle diversity southwards in
Tasmania certainly correlates with declining sea
temperatures, but the tolerances of adult barnacles at
least seem to be great enough to cope with these
lower temperatures in all the species studied. Cold
temperatures may decrease the fecundity and survival
of larvae (Crisp & Ritz 1967) and they also decrease
the rate of cirral beating and hence the rate of feeding
(Southward 1955). *Chamaesipho columna* appears to
settle lower on the shore on Maatsuyker Island
(Zacharin 1984), perhaps in order to reduce exposure
to cooler temperatures.

The reduced number of species on southern
shores may be due to the poor supply of larvae to
those shores. If water movements are contrary, or if
the larval stage is not long enough, species will not
be able to extend their range. There is insufficient
detailed information about inshore water movements
around the east coast of Tasmania to test this
suggestion, but it is known that the offshore currents
are primarily northerly in summer and southerly in
winter (Rochford 1974). If these currents are reflected
in the inshore water movements and if there are
substantial seasonal differences in the times at which
larvae are released then this may provide an
explanation for the disappearance of some species to
the south.

It is interesting to note that the range of at
least one barnacle appears to have extended
substantially and rapidly in recent years. Neither
Guiler (1952) nor Bennett & Pope (1960) make any
mention of *Austromegabalanus nigrescens* in their
papers on the Tasmanian intertidal biota. Since
A. nigrescens is such a large species it is fair to assume
that it was absent, or at extremely low numbers in
the 1950s. It was absent even as late as the 1970s on
Swan and Goose Islands in Bass Strait (King 1973),
although it was present at that time on Curtis and
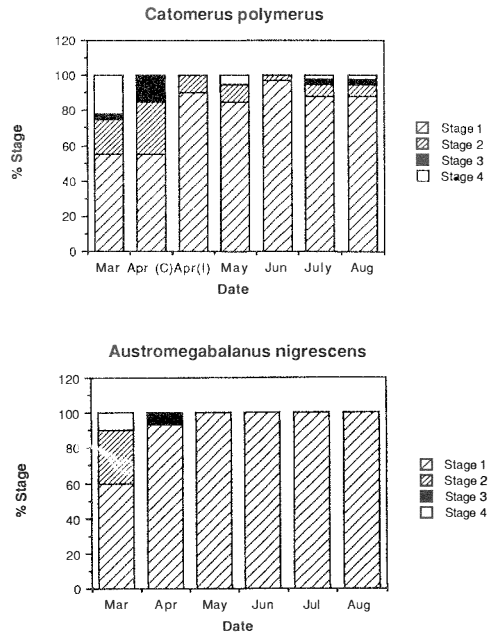Deal Islands, and it was collected from Rabbit Island

FIG. 4 — *The percentage occurrence of the four
reproductive stages, described in table 4, in*
Catomerus polymerus *at Fossil Island and*
Austromegabalanus nigrescens *at Boags Point,
near Swansea. C — contiguous animals,
I — isolated animals (for explanation see text).*

and North East River on Flinders Island in 1968
(G. Davis, pers. comm.). Specimens now in the
Tasmanian Museum were collected from the Iron Pot
at the mouth of the Derwent River as early as 1979.
Austromegabalanus nigrescens is now known from
the northeastern tip of the Tasmanian mainland to at
least as far south as Blackmans Bay at the mouth of
the Derwent River.

Earlier records deny the presence of barnacles
on Maatsuyker Island (Bennett & Pope 1960). It is
uncertain whether this was due to the difficult access
to the shore or represents a genuine absence at that
time.

These range extensions may reflect a warming
of sea temperatures in the last 30 years (Rochford
1981), and Edgar (1984b) suggests that other basically
Peronian species may be expected to appear, or at
least increase in abundance, on the east coast of
Tasmania.

Physical Tolerances

The general relationship between increasing tolerance to physical stresses and higher position on the shore is a predictable and well-known observation for barnacles world-wide (e.g. Foster 1971). It is not surprising that barnacles have tolerances which match the range of physical conditions which they experience, but it is of interest to know whether their distributions are limited by their tolerances. It is generally thought that the upper limits to the distributions of intertidal organisms are set by physical factors, while their lower limits are controlled by biological factors, i.e. predation and competition. In sessile species the upper limits may also be set by the time for which they are immersed and hence able to collect their food supply.

Foster (1971) has demonstrated in the field that temperature and desiccation can be responsible for the death of barnacles at high tidal levels, especially the more vulnerable small animals. Because of the lack of extended microclimate records, it is not possible to deduce from the results presented here whether the upper limits of any of these species are set by their tolerances. *Catomerus polymerus*, transferred from the lower shore into the *Chamaesipho* zone showed a 50% mortality after 94 days (Zacharin 1984), but this does not imply that physical factors set the exact upper limits to its distribution.

During emersion, the animal's needs to exchange gases with the atmosphere and yet retain water are clearly antagonistic (Barnes *et al.* 1963). This problem is minimised in some higher shore species by the tight closure of the opercular plates, which only open periodically to form a "micropylar" opening, or pneumostome, through which gases are exchanged, with the assistance of some movement of the cirri within the mantle cavity (Barnes *et al.* 1963, Grainger & Newell 1965). Low shore species may not have this ability; when emersed their opercular plates remain open and the cirri still protrude and beat irregularly. At Fossil Island, *Chamaesipho columna, Chthamalus antennatus* and *T. purpurascens* were observed to form micropylar openings, but *Catomerus polymerus* never did. This behavioural adaptation must contribute substantially to increased desiccation tolerance of the three species from the upper shore.

Predation and Competition

It seems likely that other factors affect the vertical distributions of the Fossil Island barnacles on the shore, but no detailed information has been collected in this study. Predation has been recognised as a significant factor in limiting barnacle distributions (e.g. Paine 1981). Zacharin (1984) assessed the preference of five potential predators (the gastropods *Dicathais textilosa, Lepsiella vinosa* and *Cominella lineolata*; the seastar *Pateriella calcar*; and the crab *Leptograpsus variegatus*) for two species of barnacle, *Chamaesipho columna* and *Catomerus polymerus*, as compared to mussels and limpets.

Dicathais textilosa proved to be the most important predator of barnacles, as are related species of *Dicathais* on the mainland (Phillips 1969, Laxton 1974), but it preferred small limpets (*Patelloida latistrigata*). Creese (1982) found that *Dicathais* prefers limpets when these are at high density, and Moran (1980) also found that *Morula marginalba*, a major predatory gastropod of the barnacle *Tesseropora rosea* in New South Wales, also prefers *Patelloida* to barnacles when the former is present at high densities. Since *P. latistrigata* occurs at higher density at Fossil Island than on mainland Australian shores, it seems likely that predation by *Dicathais* on barnacles in Tasmania is reduced in Tasmania.

The impact of other potential predators does not appear to be large because of their relatively low densities, restricted distributions and preference for other prey. *Pateriella calcar* is abundant in crevices on the rock platform, but its range is restricted by the need to return to the crevice during low tide. Barnacles are usually absent along the edges of these crevices, but this may be due to predation by *D. textilosa* , which also seeks refuge in them. *P. calcar* was only seen to attack small mussels in the laboratory.

Barnacles compete with mussels, algae and other non-sessile invertebrates for space, the major limiting resource in an intertidal community (Connell 1961a,b, Dayton 1971, Paine 1977, Underwood *et al.* 1983, Jernakoff 1983). Grazing of algal sporelings has a major effect in clearing space for barnacles (Denley & Underwood 1979, Underwood 1981, Jernakoff 1983). The main herbivores on the Fossil Island rock platforms are the limpets *Patelloida latistrigata, Patellanax peronii* and *Cellana solida*. Their effect is only beneficial to barnacles when the limpets are at low densities. At higher densities, settling barnacle spat are crushed or bulldozed from the platform (Creese 1982).

Densities of *Cellana solida* of up to 10 per 400 cm^2 were common on the upper part of the platform and, as Underwood *et al.* (1983) found, these were sufficient to prevent any settlement of barnacles. Where limpets densities were lower, further down the platform, algal growth became significant. In August and September 1984, the brown alga *Scytosiphon lomentaria* smothered settling *Catomerus*

polymerus in the lower midlittoral. Adults survived this growth but they often carried the green alga *Ulva* sp. on their opercular valves.

Mussels are the most important competitors with barnacles. The mussel *Brachyodontes rostratus* grows in small beds and clumps throughout the range of *C. polymerus*. In small crevices, *C. polymerus* and *T. purpurascens* may be overgrown and smothered. On the platform, *C. polymerus* in mussel beds grows very tall, up to three times its normal height. That the mussel beds come and go through the lifetime of *C. polymerus* is suggested by the presence of abnormally tall specimens in gaps within the mussel beds.

Competition between barnacle species was observed in the upper littoral where *Chamaesipho columna* was observed to undercut the shell plates of *Chthamalus antennatus* and thus dislodge them. Intraspecific competition occurs in *T. purpurascens* because of the lack of suitable shaded sites. Older individual are smothered by later settlers. The resulting mass has fragile foundations and clumps of animals may be broken off by wave action.

Orientation

There has been considerable interest in the ability of barnacles to orientate to water currents, and in understanding the mechanisms by which they achieve this. Moore (1933, 1935) first noted the ability of *Semibalanus balanoides* to respond to currents, and proposed that this came about firstly through forces acting on the cypris at settlement and then through differential growth. Crisp (1953) observed structural evidence for torsion during the growth of some species, but noted that light is the primary factor affecting the orientation of the cypris at settlement. Crisp & Stubbings (1957), working on barnacles in seawater conduits, or on barges and plates attached so that the water flowed unidirectionally over them, found that all species which they examined could orientate, but the cypris showed little or no response to water flow when settling. Thus they deduced that the orientation resulted from the animal's growth.

The Fossil Island species show very marked orientation. The increasing variation in orientation angle in the higher shore populations presumably reflects a greater variation in the direction of water currents at that level on the shore. Lower on the shore, the directional stimulus for the orientation of the growing barnacle is apparently very strong and their orientation shows little variation.

The reversed orientation of *Catomerus polymerus* at the edge of the horizontal platform is interesting. This may be an adaptation to reduce damage to the cirral net from water-borne particles such as sand grains. If such particles are deposited on the platform, the returning water will be less likely to damage the cirri. Alternatively there may be more food available in the backwash than in the wave advancing over the platform. How the growing *C. polymerus* is able to discriminate betweeen the advancing wave and the backwash is unclear, as only light and surface contour have been demonstrated to have an effect on initial settlement (Crisp & Stubbings 1957). Rotation after metamorphosis is possible, but only within limits which probably do not extend to a 180° turn (Crisp & Stubbings 1957, Crisp 1960), so it may be that *C. polymerus* larvae are able to respond to water movement at an earlier stage than has been recorded for other species.

Fertilisation

The lack of any significant difference in the proportion of fertilised individuals in the isolated and contiguous groups is strong circumstantial evidence that self-fertilisation is possible in the species studied here. However, the increased length of the penes of isolated *C. polymerus* suggests that cross-fertilisation is the preferred mode.

Although copulation was commonly seen, mutual cross-fertilisation was never observed in the field, which supports the view that these barnacles are functionally of a single sex. It also seems likely that water-borne cross-fertilisation does not occur. Emission of seminal fluid was never observed and Barnes & Crisp (1955) and Barnes *et al.* (1977) pointed out that there are several reasons why water-borne cross-fertilisation is unlikely. Firstly, the seminal fluid coagulates on contact with the seawater and thus would not disperse well. Secondly, if this mode of fertilisation were operating one would expect to see a decrease in the incidence of fertilisation with increasing isolation, but there was no evidence of this at Fossil Island (Fleming 1986). Further, copulation is the stimulus for ejaculation in most barnacles. There is also an enormous production of seminal fluid (about 50% of body weight in the annual breeders *Semibalanus balanoides* and *Balanus balanus*: Barnes 1962) which, Barnes *et al.* (1977) suggested, acts as the stimulus for the expulsion of eggs from the oviduct. In this study, unfertilised eggs were never found in the mantle cavity, supporting the idea that copulation and the presence of seminal fluid are a necessary stimulus.

This leads to the question of what stimulus produces oviposition in the self-fertilising members

of the population. In *Chthamalus stellatus*, Barnes & Crisp (1955) suggested that the continued presence of mature eggs in the ovary lowers the threshold for the oviposition stimulus to the point where the movement of the barnacle's own penis in the mantle cavity would produce the release of eggs and the simultaneous release of seminal fluid. In this study, the penes of sexually active animals were always found to contain seminal fluid. If the penis fails to contact a functional and receptive female, it is relaxed slightly and the tip is turned under to face the pedicel. The tip is then inserted between the cirri as the penis is repeatedly folded while becoming more flaccid towards its base. These movements could lead to the expulsion of seminal fluid in the mantle cavity providing a stimulus for egg release. For this mechanism to be effective then the animals must be capable of changing rapidly from one sex to the other.

Similar evidence, but for self-fertilisation in *Chamaesipho columna*, has been presented by Joll (1961) in New Zealand, but Miller (1976), working with *Chthamalus antennatus* in Queensland, concluded that obligatory cross-fertilisation was the rule. In Tasmania, at least, it seems highly likely that *A. nigrescens, Catomerus polymerus* and *T. purpurascens* are capable of self-fertilisation.

In the northern hemisphere, populations of *Semibalanus balanoides* at higher latitudes become fertilised later than those at lower latitudes (Crisp 1959). Wisely & Blick (1964) found that brooding specimens of *C. polymerus* could be found over an extended season, beginning in January and continuing until September, with peak brooding in March and April. At Phillip Island, Victoria, settlement occurs in all months, with peak brooding in January and February (J. Smissens, pers. comm.). Observations at Fossil Island extended only from March to August, but over that period brooding was highest in March, fell to a low of 10% in June and rose again in August.

No penis activity was observed at Fossil Island between March and July and there is some evidence to suggest that embryonic development was suspended during the months of May, June and July when water temperatures were low (Fleming 1986). However, the significant rise in the frequency of brooding animals in August must represent adaptations of the Tasmanian population to colder conditions, since the water temperatures in August do not rise above May–June–July levels. The presence of reproductive products in the mantle cavity of *C. polymerus* from Pedra Branca in April suggests that climatic differences between there and Tasman Peninsula are not significant to the barnacles.

The barnacle fauna of Tasman Peninsula is of interest for a number of reasons. Barnacles show well the ways in which the problems of sessility have been solved by animals from an otherwise active group with a high level of body organisation. Tasman Peninsula offers a range of habitats and is geographically placed so that it experiences seasonal and year to year variation in offshore waters and temperatures. Long-term studies of the barnacle communities of the peninsula will be of considerable interest.

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