

COMPETITIVE GRAZERS AND THE PREDATORY WHELK
LEPSIELLA FLINDERSI (GASTROPODA: MURICIDAE)
STRUCTURE A MUSSEL BED (*XENOSTROBUS PULEX*)
ON A SOUTHWEST AUSTRALIAN SHORE

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ABSTRACT

On a southwest Australian exposed rocky shore within King George Sound, the predatory muricid *Dicathais orbita* was observed feeding non-selectively on an array of sessile prey, including *Austromegabalanus nigrescens*, *Galeolaria caespitosa*, *Patelloida nigrosulcata*, *Serpulorbis sipho*, *Siphonaria* sp. and the mussel *Xenostrobus pulex*.

On a more sheltered, contiguous, platform of the same shore, however, a mat of *Xenostrobus pulex* occurred which was being predated by another muricid, *Lepsiella flindersi*. *X. pulex* occupied a wide vertical range on this shore. Higher-zoned, supralittoral, individuals were small and occurred as clusters in crevices and pits in the rock. A mat of mussels in the lower eulittoral zone was heavily predated by the drilling *L. flindersi* which attacked selectively the largest individuals. Between, in the high eulittoral, the mussel bed was formed into patches which were isolated by the grazing activities of an array of herbivorous gastropods. Recruitment here by *X. pulex* was to the patch edges and the grazer's habits of clustering against them, further kept them discrete. Little predation by *L. flindersi* occurred at this shore level.

The *Xenostrobus pulex* community was, therefore, highly structured down the shore sequentially by: (a), physiological stresses; (b), competitive grazing pressures and (c), predation.

INTRODUCTION

Virtually world-wide, species of the bivalve Mytilidae colonize rocky intertidal shores, typically as a band which occupies much of the eulittoral zone. The ecologies of the European *Mytilus edulis* (Linnaeus) and American *Mytilus californianus* Conrad have been studied extensively (Gosling, 1992; Seed & Suchanek, 1992). Other mytilids from different genera, for example, *Septifer virgatus* (Wiegmann) on

Hong Kong shores, have also been studied to obtain a picture of their biology, ecology and role in structuring the associated eulittoral community (Morton & Ong Che, 1992; Liu & Morton, 1994; Morton, 1995).

On sheltered shores in southwest Australia, for example, Princess Royal Harbour in King George Sound, the mussel *Brachidontes erosus* (Lamarck) forms a typical band on rocks, but also extends onto sand flats where its range is greatly expanded (Morton, 1990). At this location, a second mytilid, *Xenostrobus pulex* (Lamarck) (Wilson, 1967), occurs as small, scattered, individuals as it does on shores experiencing higher degrees of exposure to wave action. Such a shore is present at Whaling Cove, also within King George Sound but, on its flanks where intermediate levels of exposure are encountered and a near horizontal platform is created in the eulittoral, *X. pulex* occurs as a typical mussel bed. This bed is the subject of this study.

The upper distributional limits of mussel colonization on rocky shores are usually thought to be determined by extreme physical forces, such as temperature and desiccation. Soaring rock temperatures (to 50°C) in summer in Hong Kong (Liu & Morton, 1994) control the mussel *Septifer virgatus* whereas winter freezes lower the upper limit of *Mytilus californianus* in North America (Suchanek, 1985). Grazing pressure from either limpets or a suite of other, usually molluscan, herbivores may also limit the upper level of mussel distribution (Seed, 1969).

The lower limits of mussel bed development can be similarly controlled by either physical factors, such as sand burial (Daly & Mathieson, 1977) or competitors, *Mytilus californianus* dominating *Mytilus edulis* on most exposed rocky shores in North America (Suchanek, 1978).

The most well-known controls are, however, imposed by predators and on temperate rocky shores the starfish *Asterias rubens* Linnaeus has been studied with regard to its role (and that of *Nucella lapillus* (Linnaeus)) in structuring a *M. edulis* community on the east coast of England (Seed, 1969). In Ireland, the same mussel is controlled by *Nucella*, the asteroid *Marthasterias glacialis* Linnaeus and crabs, such as *Carcinus maenas* (Linnaeus) (Kitching & Ebling, 1967). The researches of Paine (1971, 1974) and Paine *et al.* (1985) have shown how in New Zealand, the U.S.A. and Chile, starfish control the lower limits of mussel distribution.

Another group of predators, the numerous species of the gastropod family Muricidae, are also common on both temperate and tropical rocky shores, and are significant predators of mussels (Navarette, 1996). On temperate shores, for example, in Europe and eastern North America, only *Nucella lapillus* is generally present and may consume, rather monotonically, barnacles and mussels (Hughes & Dunkin, 1984a, b; Hughes & Drewett, 1985), selecting optimally-sized individuals and modifying its foraging behaviour, in terms of prey choice and method of attack, over time. On tropical rocky shores, a greater range of predator species is present and these exploit a similarly wider range of prey (Taylor, 1980; Taylor & Morton, 1996). Methods of attack vary according to the prey chosen; some are drilled, others are chipped marginally and yet others are attacked aperturally. Such behavioural flexibility has been recognised for other muricids, notably on Australian shores (Moran *et al.* 1984; Fairweather, 1985; Morton & Britton, 1993; Taylor & Glover, 1999).

On southwest Australian shores, the common predatory muricid is *Dicathais orbita* (Gmelin), which drills limpets (Black, 1978) but can also consume a wide range of prey, including carrion (Phillips, 1969) as, for example, on the limestone platforms of Rottnest Island, off the coast from Perth, Western Australia (Morton & Britton, 1993; Taylor & Glover, 1999). This species was also present, albeit in reduced numbers, on the shore at Whaling Cove and an examination of its prey provides, herein, further information on this little-studied predator. On the *Xenostrobus pulex* mussel beds in deeper shelter, however, occurred another muricid predator, *Lepsiella flindersi* (Adams & Angas), about which little is known.

It has been reported from South Australia that *Lepsiella vinosa* (Lamarck) is an intertidal predator. In a South Australian mangrove, *L.*

vinosa feeds on barnacles (Bayliss, 1982), whilst on a rocky shore, *Nodilittorina unifasciata* (Gray) recognises *L. vinosa* as a predator and avoids it (McKillup, 1982). The occurrence within Whaling Cove of a little studied mussel and an even less studied predator gave the opportunity to consider how such communities of related species are structured, as compared with the well-studied species of *Mytilus* in the northern hemisphere. An initial study of the potential role of a suite of grazers in creating and regulating mussel patch patterns was also made.

MATERIALS AND METHODS

During December 1996, a research visit was paid to King George Sound, Western Australia. At Whaling Cove, on the eastern shoreline of the Quaranup Peninsula (Figs. 1A & 2A), a rocky intertidal community experiencing various degrees of exposure to wave action was identified. Two transects were established on the exposed (Site A) and semi-sheltered faces (Site B) of a rocky outcrop at Whaling Cove (Fig. 1B) and which extended between the approximate positions of extreme high and extreme low water spring tide. At every one metre interval down the transects, five 10 × 10 cm random quadrats were examined and counts made of the numbers of the common intertidal organisms present. These observations were not meant to constitute a detailed inventory of all species present but, rather, to provide a broad picture of the distribution of key zoning organisms, possible prey and predators on the shores and to serve as a comparison of the two exposure profiles for subsequent studies of the community interactions occurring on them.

Because of the different degrees of exposure experienced by the two selected areas of shore, the mytilid *Xenostrobus pulex* was present to differing extents. On the more exposed shore (Site A), *X. pulex* occurred as small clusters of small individuals in the supralittoral at between +0.8–1.0 m C.D. and was typically associated with crevices and pits in the rock. On the more sheltered shore (Site B), *X. pulex* also occurred in the supralittoral at between +0.8–1.5 m C.D., i.e. with a higher vertical range of ~0.5 m, and as small clusters of small individuals. At both sites, ten random quadrats of 10 × 10 cm² were examined at this level and counts made of the *X. pulex* individuals present in each. The sampled individuals were also removed and measured along their greatest shell lengths to the nearest 1 mm using vernier calipers. On the more exposed Site A, *X. pulex* was present only as solitary individuals lower on the shore throughout the eulittoral at between +.5–0.8 m C.D. A sample of such individuals was also obtained, counted and measured. On the less exposed shore (Site B), throughout the eulittoral, at between +0.25–0.70 m C.D., *X. pulex* was present as a mat (Fig. 2B). The upper eulittoral extent of the mat (+0.50–0.70 m C.D.), for

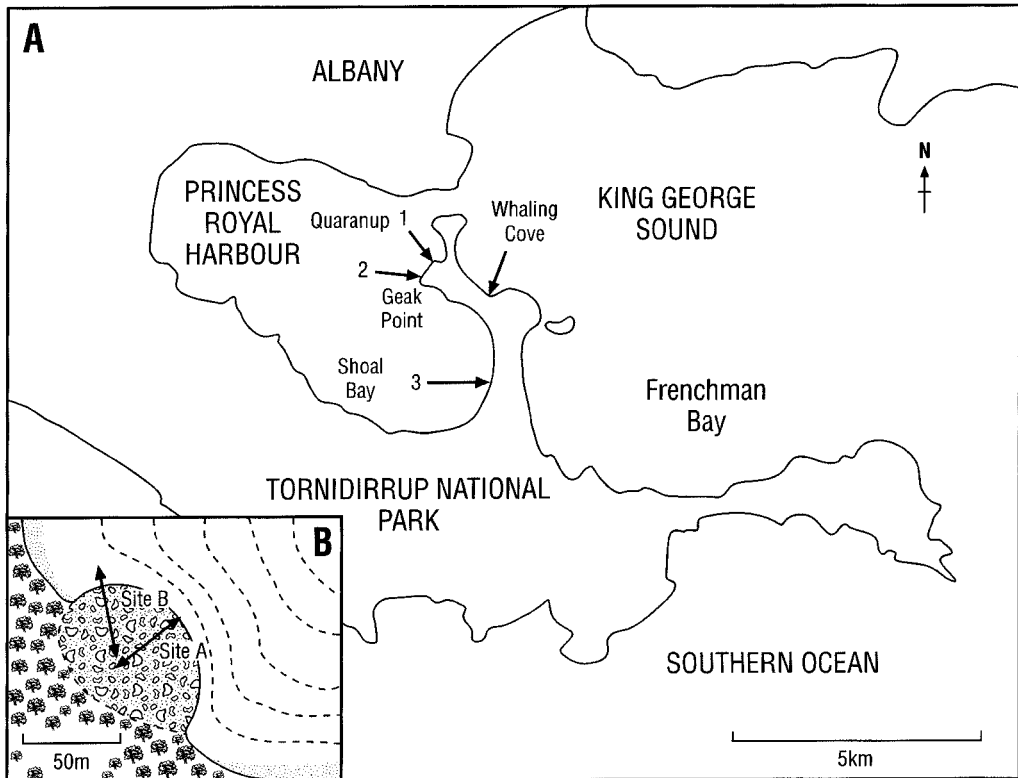


Figure 1. **A**, A map of Princess Royal Harbour and King George Sound, Albany, Western Australia, showing the position of the study site at Whaling Cove. The numbers 1, 2 and 3 refer to sites investigated earlier by Morton (1990) and discussed in the text. **B**, A simplified map of the study area site at Whaling Cove showing the exposed Site A and sheltered Site B.

about 2 m near-horizontal distance, comprised mussel patches (Fig. 2C). In this area, ten patches were analysed, again using random 10×10 cm² quadrats and by taking five 2.5×2.5 cm² samples of the mussels from both patch edges and centres. Every individual in these samples was counted, measured (again along the greatest length) and living animals separated from empty shells which were also inspected for signs of predation. At this same level also, five random 1×1 m² quadrats were examined and all the gastropods (and chitons) within them removed. These were identified to species, counted, measured along their greatest heights (or lengths) and then returned to the same shore position, alive.

Lower on the more sheltered shore (Site B), at between $+0.25$ – 0.5 m C.D., i.e. the lower eulittoral, *Xenostrobus pulex* formed a dense, uniform mat of individuals bound together by byssal threads. The mat's cohesion was also sustained by algal filaments of various species and the predatory gastropod *Lepsiella flindersi* was present in large numbers (Fig. 2D). At this level, five random quadrats of 10×10 cm² was examined and every individual mussel

within them removed and their length measured to the nearest 1 mm. The mussels were separated into living and empty individuals. For the latter, each intact shell and valve was inspected for signs of predation. Here, *L. flindersi* feeds on *X. pulex* by shell drilling and, accordingly, every drilled individual was also isolated from the total number of empty valves, counted and measured. In addition, the position of each drill hole was recorded on five master diagrams of a *X. pulex* shell, representing the five random quadrats, to determine if there was any site selection in terms of attack position.

Ten larger quadrats (25×25 cm²) were thrown randomly onto the *Xenostrobus pulex* mat in the lower eulittoral and every individual gastropod in them was collected and recorded. Only *Lepsiella flindersi* was obtained and each was measured along its maximum shell height to the nearest 1 mm and returned to the same shore position alive.

Lepsiella flindersi was only encountered twice on the exposed shore (Site A), the dominant predator here being *Dicathais orbita*. The full vertical and horizontal extent of the shore, i.e. approximately 10×100

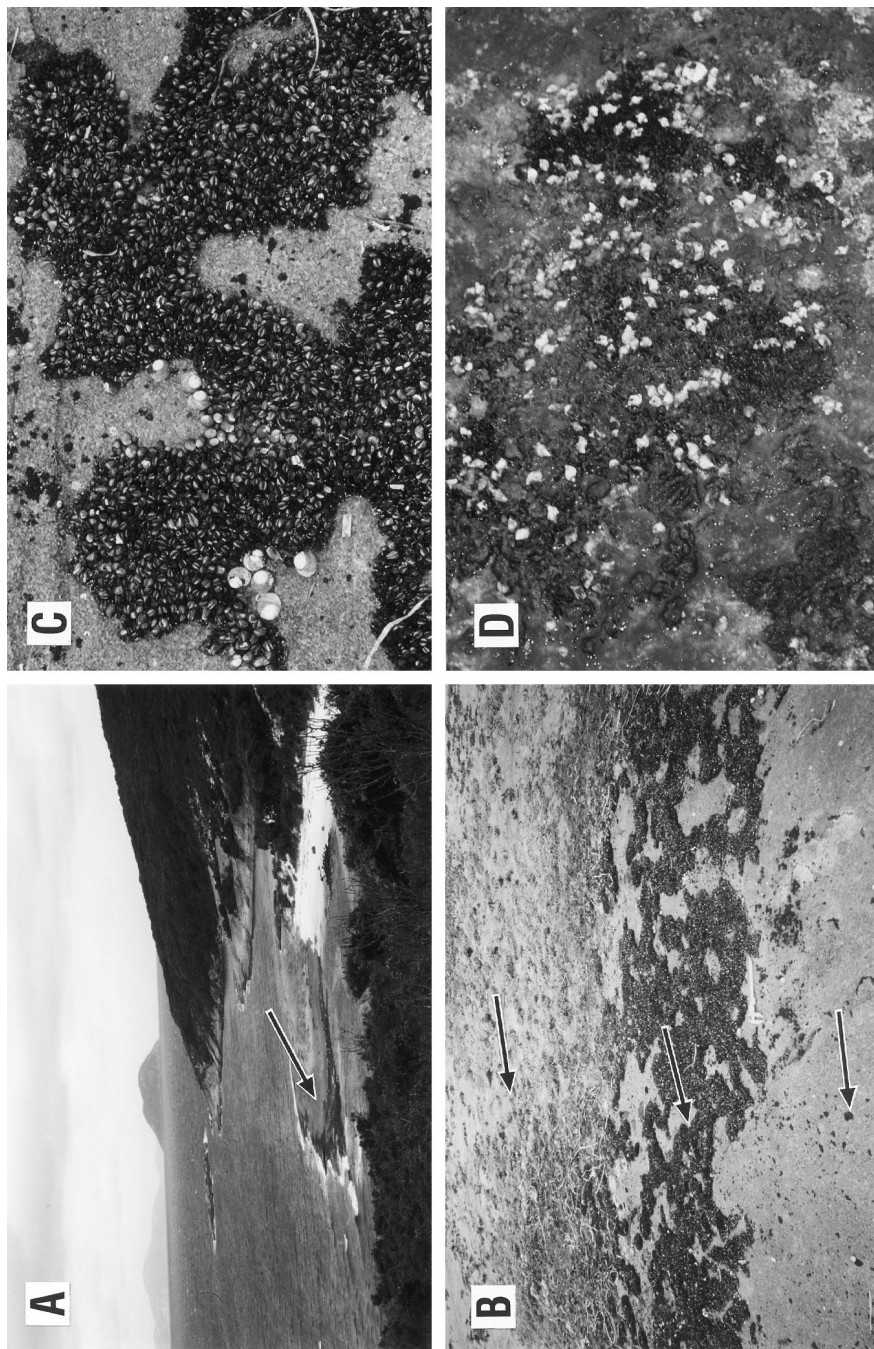


Figure 2. **A,** A general view of the rocky shore outcrop at Whaling Cove showing nearest the front left (arrowed) the sheltered Site B. **B,** A photograph taken looking down the shore at Whaling Cove (Site B) showing, in the foreground (arrowed), scattered individuals of *Xenostrobus pulex* in the supralittoral, patches of *X. pulex* in the upper eulittoral (arrowed) and, furthest away, the mat of *X. pulex* (arrowed) in the lower eulittoral. **C,** A view of the *Xenostrobus pulex* patches in the upper eulittoral of the shore at Site B with individuals of *Austrocochlea concamerata* and *Nerita atramentosa* clustered around them. **D,** An impression of the densities of *Lepsiella flindersi* with the *Xenostrobus pulex* mat on the lower eulittoral.

metres, at Site A was searched for *D. orbita* for a total of ten days, following the general pattern used successfully by Taylor & Morton (1996) to study predatory muricids on a Hong Kong shore. Every individual of *D. orbita* encountered was examined and measured along its greatest shell height to the nearest 1 mm. The prey of every feeding individual was also recorded, measured along either its greatest shell length (Bivalvia; Serpulidae) or height (Gastropoda; Cirripedia) and the method of attack determined.

Data analysis

The differences in the mean shell lengths of *Xenostrobus pulex* between all quadrat samples were compared using ANOVA (Analysis of Variance) (at the $p = 0.05$ significance level), the data having earlier been tested for normality using the Shapiro-Wilk test and the assumption of homogeneity of variance (homoscedasticity) examined by Bartlett's test (Bartlett, 1937; Sokal and Rohlf, 1995). When assumptions of ANOVA were violated and could not be rectified by transformations, *X. pulex* median shell lengths were compared using the non-parametric Kruskal-Wallis test or the Wilcoxon rank-sum test (both tests at the $p = 0.05$ significance level). In this connection, shell lengths of *X. pulex* above the eulittoral zone at Sites A and B on the rocky shore at Whaling Cove were also compared using the Kruskal-Wallis test. The same test was used to compare shell lengths of *X. pulex* at the patch edges and centres and the shell lengths of the living, dead and bored individuals between the upper and lower eulittoral zone at Site B.

In the upper eulittoral, the numbers and shell heights or lengths of grazers associated with the *Xenostrobus pulex* patches were compared using a Student-Newman-Kuels test ($p = 0.05$), after the ANOVA test, on non-transformed and transformed (for *Austrocochlea concamerata*) data.

Shell heights of feeding *Dicathais orbita* from Site A and either the shell lengths or heights (Cirripedia) of their identified prey were compared using Pearson correlations to provide r^2 values for the predator and its prey category, i.e. Cirripedia, Serpulidae, Gastropoda and Bivalvia, and significance values for the regressions so obtained.

RESULTS

The shore at Whaling Cove

The rocky shore at Whaling Cove (Figs. 1A & 2A) comprises a smoothly and gently-sloped granite outcrop with a typical Western Australian coastal scrub behind. Figure 3 shows schematic belt transect illustrations of the exposed Site A (left) and sheltered Site B (right) and their contained intertidal flora and fauna.

At Site A, the splash zone and supralittoral shore levels were the habitat of two littorinids, *Nodilittorina unifasciata* and, at a somewhat lower level, *Bembicium auratum* (Quoy & Gaimard). At +1.2 m C.D., there was a steeply-sided pool which marked, approximately, the lower margin of the upper shore and contained limpets, *Patelloida alticostata* (Angas), the serpulid polychaete *Galeolaria caespitosa* (Savigny) and was rimmed by *Hormosira banksii*. A few *Dicathais orbita* occurred in the pool. The eulittoral, or middle shore, was demarcated landward by a few large barnacles, *Austromegabalanus nigrescens*, accompanied by a scattering, in crevices, of small *Xenostrobus pulex*. The algal film here was grazed by limpets, e.g. *Patelloida alticostata*, *Nerita atramentosa* Reeve and *Austrocochlea concamerata* (Wood). Here too *G. caespitosa* and scattered plants of *Laurencia* sp. occurred. The lower margin of the eulittoral was demarcated by a fringe of *Cystophora paniculata*. The lower shore, or sublittoral fringe, from +0.5 cm C.D. downwards was covered by an algal mat, the main component of which was a species of *Cladophora* gradually merging with a littoral fringe of *Corallina* turf. This contained numerous limpets, including the large *Patella latcostata* Blainville, the small *Patelloida nigrosulcata* (Reeve), a species of *Siphonaria* and the chiton *Clavarezona hirtosa* (Blainville). *Dicathais orbita* was also here but ranged upwards into the higher eulittoral zone.

High on the less exposed shore at Site B were *Nodilittorina unifasciata* and *Bembicium auratum*. Here, *Xenostrobus pulex* occurred much higher up to +1.5 m C.D. in the supralittoral and, as on the exposed shore, was present as small clusters of small individuals within crevices. The littorinids ranged down the eulittoral to a thin band of the alga *Colpomenia sinuosa* (Roth) Derbes et Solier and were replaced by the grazers *Nerita atramentosa*, *Austrocochlea concamerata* and a few *Patelloida alticostata*. As will be seen, these grazers abutted patches of *Xenostrobus pulex* surrounded by superficially bare rock. From +0.5 m C.D. down, the shore was dominated by a dense mat of *X. pulex* intermingled with *Cladophora* sp. and *Hormosira banksii* which gradually thickened seawards, terminating at the lower limit of the eulittoral. The lower shore and sub-littoral fringe was, on the exposed component of the shore, marked by a community based on a mat of *Cladophora* sp. grading into a *Corallina* turf. *Lepsiella flindersi* was abundant on the *X. pulex* mat.

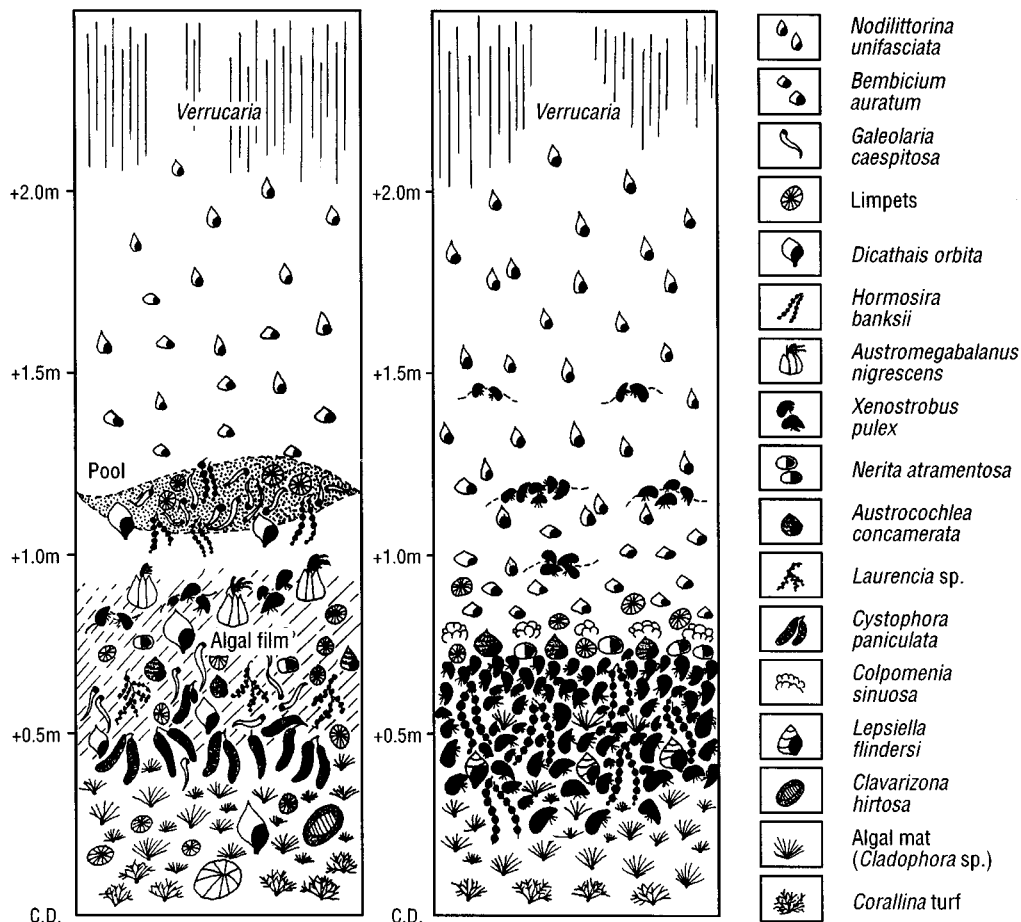


Figure 3. Belt transect illustrations of the shores and their communities at Sites A (left) and B (right) in Whaling Cove.

High-zoned *Xenostrobus pulex*

At Sites A and B, *Xenostrobus pulex* occupied the upper part of the eulittoral but also ranged higher into the supralittoral (to +1.5 m C.D.). An analysis of ten random samples of *X. pulex* from the supralittoral at Site A (Table 1) showed the mussel to occur in clusters with a mean number of 9 individuals·100 cm² and to have a mean shell length of 5.6 mm. At Site B, at the same shore level, the species occurred in greater densities (Table 1) at a mean of 53.2 individuals·100 cm² and with a mean shell length of 4.7 mm. The two median shell length values obtained for *X. pulex* at Sites A and B were also significantly different from each other (Kruskal-Wallis test, $p < 0.05$). The size distributions of *X. pulex* in the pooled quadrat data

from the supralittoral at Sites A and B were significantly different from each other (Wilcoxon rank-sum test, $P < 0.05$) and both were shown to have unimodal population structures (Shapiro-Wilk test; $p < 0.05$) (Fig. 4).

Most *Xenostrobus pulex* (98.2%) were alive, but, in four quadrats, a few were dead, i.e. with an average of 1.2 individuals·100 cm², or 1.8% of the samples (Table 1). The mean shell length of the dead individuals was 5.3 mm but these did not show any sign of predation. The median shell lengths of living and dead individuals were not significantly different from each other (Kruskal-Wallis test, $p > 0.05$) (Table 1).

A comparison of the living high-zoned, supralittoral, individuals of *Xenostrobus pulex* at Sites A and B showed them to be less dense (9.0 vs. 53.2·100 cm²) at the former site and to be

Table 1. *Xenostrobus pulex*. The mean numbers and mean shell lengths of living and dead individuals collected from ten random quadrat samples above the eulittoral zone at Sites A and B on the rocky shore at Whaling Cove, Albany, Western Australia. (Quadrat dimensions were $10 \times 10 \text{ cm}^2$).

	Mean no. <i>X. pulex</i> per quadrat	Mean no. living <i>X. pulex</i> per quadrat ¹	Mean shell length (mm) ²	Shell length range (mm)	Mean no. of dead <i>X. pulex</i> per quadrat ¹	Mean shell length (mm)	Shell length range (mm)
Site A	9.0	9.0 (100)	5.6 (± 2.20)	2.2–9.8	0	0	0
Site B	53.2	52.0 (98.2)	4.7 (± 1.9)	0.7–9.4	1.2 (1.8)	5.3	3.5–7.6

¹ Values in parentheses represent the mean percentage of individuals per quadrat.

² Values in parentheses represent standard deviations.

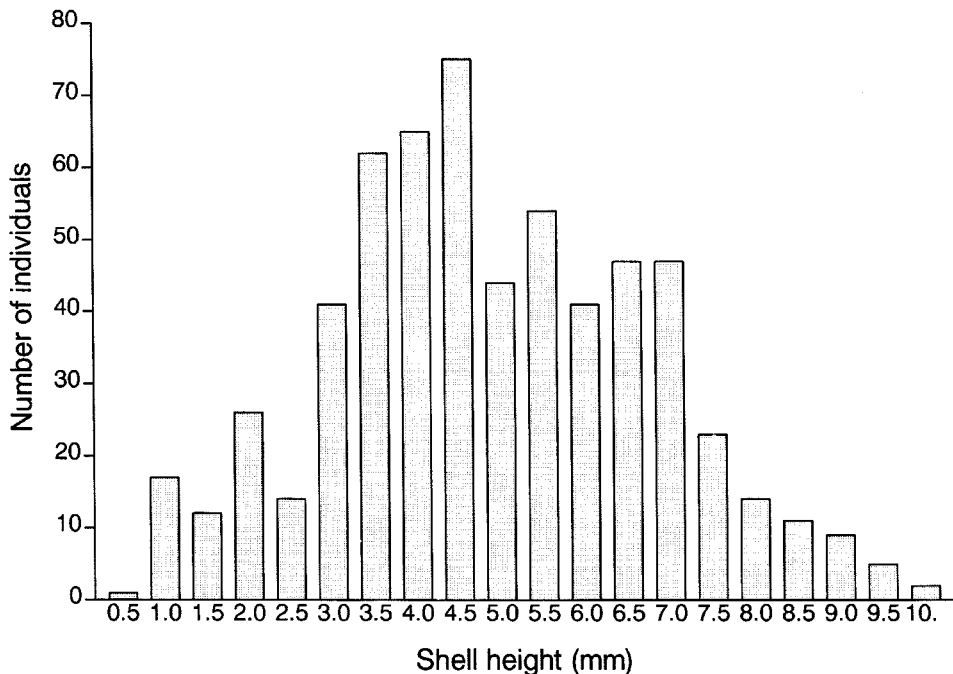


Figure 4. *Xenostrobus pulex*. Pooled data of shell lengths for all samples obtained from the upper eulittoral at Sites A and B on the rocky shore at Whaling Cove.

significantly larger (5.6 mm vs. 4.7 mm) (Kruskal-Wallis test, $p < 0.05$).

Upper eulittoral *Xenostrobus pulex*

Samples of *Xenostrobus pulex* from the upper eulittoral at Site B were analyzed (Table 2). In

the patches there was a mean of 224.8 individuals-100 cm^2 . Most of these (93.3%) were alive (Table 2A) and had a mean shell length of 13.4 mm. The median inter-sample shell length values were, however, significantly different from each other (Kruskal-Wallis test, $p < 0.05$). The dead individuals could be divided into two groups, drilled and non-drilled. The latter

Table 2. *Xenostrobus pulex*. The mean numbers and mean shell lengths of individuals collected from five 10 × 10 cm² random quadrats from the upper eulittoral zone at Site B on the rocky shore at Whaling Cove, Albany, Western Australia. (A). Living. (B). Dead and non-drilled individuals. (C). Dead drilled individuals.

(A).				
Mean no. of <i>X. pulex</i> per quadrat	Mean no. of living individuals per quadrat ¹	Mean shell length (mm) ²	Shell length range (mm)	Mean no. of dead individuals per quadrat ¹
224.8	209.8 (93.3)	13.44 (±3.96)	1.0–20.0	15 (6.7)
(B).				
Mean no. non-drilled <i>X. pulex</i> per quadrat ¹	Percentage of non-drilled individuals to all dead individuals	Mean shell length of non-drilled individuals (mm) ²	Shell length range (mm) ²	
118 (4.0)	80.5	13.42 (±2.8)	4.0 (±17.5)	
(C).				
Mean no. drilled <i>X. pulex</i> per quadrat ¹	Percentage of drilled individuals to all dead individuals	Mean shell length of drilled individuals (mm) ²	Shell length range (mm)	
3.2 (1.4)	19.5	14.19 (±1.7)	10.5–16.5	

¹ Values in parentheses represent the mean percentage of individuals per quadrat.

² Values in parentheses represent standard deviations.

constituted 80.5% of all the dead individuals, with a mean shell length of 13.42 mm (Table 2B). The median inter-sample shell length values of the dead individuals were not significantly different from each other (Kruskal-Wallis test, $p > 0.05$) and were very similar to the living individuals (Table 2A).

Drilled individuals made up 19.5% of the dead *Xenostrobus pulex* in the upper eulittoral mussel patches. With a mean shell length of 14.2 mm, they were approximately 0.8 mm longer than both living and dead, non-drilled, individuals (Table 2C). The drilled individuals in the five samples were not, moreover, significantly different from each other in terms of median shell length (Kruskal-Wallis test, $p > 0.05$). There was, thus, only a small level of predation upon the *X. pulex* at this upper eulittoral level, i.e. a mean of 3.2 individuals/100 cm², in a mean living population of 224.8 individuals/100 cm², and with the largest mussels only being drilled.

The patches of *Xenostrobus pulex* at Site B were analyzed in another way. Five 2.5 × 2.5 cm² samples were taken from both patch edges and centres (Table 3). At the patch edges, there

was a mean of 57 individuals/6.25 cm², most of which were alive (99%) and non-drilled. The mean shell length of such individuals was 8.8 mm. The median shell lengths of *X. pulex* in the five samples were not significantly different from each other (Kruskal-Wallis test, $p > 0.05$). The few dead individuals were not-drilled and had a mean shell length of 9.6 mm. In the patch centres (Table 3), there was a mean of 32.6 individuals/6.25 cm² with a mean shell length of 12.99 mm. Of these, 94.2% were alive. Of the dead individuals, i.e. 1.8/6.25 cm², none was drilled and the mean shell length was 15.3 mm. The median shell lengths of *X. pulex* in the five samples were not significantly different from each other (Kruskal-Wallis test, $p > 0.05$).

There were thus more living individuals of *Xenostrobus pulex* at the patch edges than the centres and those at the former were also significantly smaller than those in the latter, i.e. a mean of 8.8 mm vs. 13.0 mm shell length. There were only a few dead individuals in both situations, i.e. a mean of 2 vs. 9/6.25 cm² at the edges and centres, respectively, and those at the former were smaller than those at the latter, i.e. a mean of 9.6 mm vs. 15.3 mm shell length.

Table 3. *Xenostrobus pulex*. The mean numbers and shell lengths of living and dead individuals collected from five random quadrat samples (2.5×2.5 cm) from patch edges and centres in the upper eulittoral zone at Site B on the rocky shore at Whaling Cove, Albany, Western Australia.

	Mean no. of <i>X. pulex</i> per quadrat	Mean no. of living <i>X. pulex</i> per quadrat ¹	Mean shell length (mm) ²	Shell length range (mm)	Mean no. of dead <i>X. pulex</i> per quadrat ¹	Mean shell length (mm) ²	Shell length range (mm)
Patch edges	57.0	56.6 (99.0)	8.78 (\pm 3.30)	0.6–17.1	0.4 (1.0)	9.6 (\pm 7.35)	4.4–14.8
Patch centres	32.6	30.8 (94.2)	12.99 (\pm 5.35)	1.0–22.0	1.8 (1.8)	15.3 9 \pm 8.51)	4.6–18.4

¹ Values in parentheses represent the mean percentage of individuals per quadrat.

² Values in parentheses represent standard deviations.

Table 4. The mean numbers and mean shell heights or lengths of grazing herbivores in five random quadrats (1×1 m²) from the upper eulittoral zone at Site B on the rocky shore at Whaling Cove, Albany, Western Australia.

	Mean no. of individuals per quadrat	Mean shell height or length ¹ + SD (mm)	Shell height or length range (mm)
<i>Nerita atramentosa</i>	39.8	5.5 (\pm 1.63)	2.2–8.5
<i>Austocochlea concamerata</i>	6.8	18.8 (\pm 3.28)	13.8–28.5
<i>Clavarizona hirsuta</i>	2.3	19.9 (\pm 5.21)	10.1–24.4
<i>Patella nigrosulcata</i>	2.5	8.2 (\pm 4.27)	3.3–14.1

¹ Values in parentheses represent standard deviations.

Herbivores occurring with Xenostrobus pulex in the upper eulittoral

Around the edges of the *Xenostrobus pulex* patches at Site B, *Nerita atramentosa* occurred at an average density of 39.8 individuals·m⁻² and with an average shell height of 5.5 mm (Table 4). *Austocochlea concamerata* occurred at an average density of 6.8 individuals·m⁻² with a mean shell height of 18.84 mm (Table 4). The chiton *Clavarizona hirtosa* occurred in only three of the five random quadrats from the *X. pulex* patches at Site B, at a mean of 2.3 individuals·m⁻² and a mean body length of 19.9 mm (Table 4). The limpet *Patelloida nigrosulcata* only occurred in two of the quadrats on the *X. pulex* patches with a mean of 2.5 individuals·m⁻² and a mean shell length of 8.2 mm (Table 4).

Lower eulittoral Xenostrobus pulex

The numbers of individuals occurring in the *Xenostrobus pulex* mat in the lower eulittoral were estimated using five 100 cm² random quadrats. Individuals were measured and living and dead, either drilled or non-drilled, shells isolated (Table 5). The positions of the drill

holes in mussels from the five samples were identified on five master diagrams (Fig. 5 A–E). The numbers of living individuals occurred at a mean density of 281.4·100 cm² with a mean shell length of 9.9 mm (Table 5). Median shell length values were, however, significantly different from each other (Kruskal-Wallis test, $p < 0.05$). Living individuals accounted for a mean of 75.3% of all those collected. There was a mean of 66.2 dead individuals·100 cm², i.e. 24.7% of the shells collected (Table 5A). The mean number of non-drilled individuals was 35.2·100 cm², or 52.3% of all dead individuals, and these had a mean shell length of 12.1 mm (Table 5B). The mean number of drilled individuals was 31·100 cm², or 47.7% of all dead individuals, and these had a mean shell length of 14.5 mm (Table 5C). The median shell lengths of the non-drilled and drilled individuals in the five samples were not, moreover, significantly different from each other (Kruskal-Wallis test, $p > 0.05$).

Comparison of the upper and lower eulittoral Xenostrobus pulex

Of the totals of 1124 and 1407 individuals of *Xenostrobus pulex* collected from the upper and lower eulittoral at Site B, 1049 (93.3%) and

Table 5. *Xenostrobus pulex*. The mean numbers and mean shell lengths of individuals collected from five 10 × 10 cm² random quadrat samples from the lower eulittoral zone at Site B on the rocky shore at Whaling Cove, Albany, Western Australia. (A). Living individuals. (B). Dead and non-drilled individuals. (C). Dead and drilled individuals.

(A).				
Mean no. of <i>X. pulex</i> per quadrat	Mean no. of living individuals per quadrat ¹	Mean shell length of living individuals (mm) ²	Shell length range (mm)	Mean no. of dead individuals per quadrat ¹
281.4	215.2 (75.3)	9.96 (±3.90)	0.5–19.5	66.2 (24.7)
(B).				
Mean no. of dead (non-drilled) <i>X. pulex</i> per quadrat ¹	Percentage of non-drilled individuals to all dead individuals	Mean shell length of non-drilled individuals (mm) ²	Shell length range (mm)	
35.2 (13.2)	52.3	12.07 (±4.04)	1.0–18.5	
(C).				
Mean no. of dead (drilled) <i>X. pulex</i> per quadrat ¹	Percentage of drilled individuals to all dead individuals	Mean shell length of drilled individuals (mm) ²	Shell length range (mm)	
31.0 (11.6)	47.7	14.48 (±2.38)	6.0–18.0	

¹ Values in parentheses represent the mean percentage of individuals per quadrat.

² Values in parentheses represent standard deviations.

1076 (76.5%) were alive with mean shell lengths of 13.4 mm and 10.0 mm, respectively (Table 6A). The living individuals at the two shore levels were significantly different in size (Kruskal-Wallis test, $p < 0.05$), i.e. although densities were the same at the two levels, individuals from higher on the shore were longer, by some 3.5 mm, and fewer of them were dead.

Of the totals of 75 and 331 dead individuals collected from the upper and lower eulittoral levels at Site B, (Table 6A), 59 (78.7%) and 176 (53.2%) were not drilled, with mean shell lengths of 13.4 mm and 12.1 mm, (Table 6B). Median shell length values were not significantly different from each other (Kruskal-Wallis Test, $p > 0.05$).

The totals of 16 (21.3%) and 155 (46.8%) drilled individuals of *Xenostrobus pulex* collected from the upper and lower levels of the eulittoral zone at Site B had mean shell lengths of 14.2 mm and 14.6 mm (Table 6C). Median shell lengths of the two groups of drilled individuals were, moreover, not significantly different (Kruskal-Wallis test, $p > 0.05$). That is, although there was greater level of predator activity in the lower eulittoral, drilled individuals at the two levels were of the same size sug-

gesting that, regardless of tidal height, *Lepsiella flindersi* always prefers larger mussels.

The distribution of drillholes in 155 *Xenostrobus pulex* collected from the five random quadrats in the lower eulittoral at Site B in Whaling Cove are illustrated in Figure 4 A–E. There was no significant difference between left and right valves, i.e. no preference was shown for attacks on either valve by *Lepsiella flindersi*. It is clear, however, that the posterior half of the shell was attacked preferentially which relates to the vertical disposition of *Xenostrobus pulex* in its mat, that is, individuals are vertically oriented and attached to each other by a matrix of byssal threads, leaving only the posterior available as a drilling site.

Lepsiella flindersi

On the lower eulittoral mat of *Xenostrobus pulex* at Site B, the only predator present was *Lepsiella flindersi* at a mean density of 6.4 individuals·100 cm². *L. flindersi* here had a mean shell height of 19.1 mm and many were observed to be actively feeding, by drilling, on *X. pulex*.

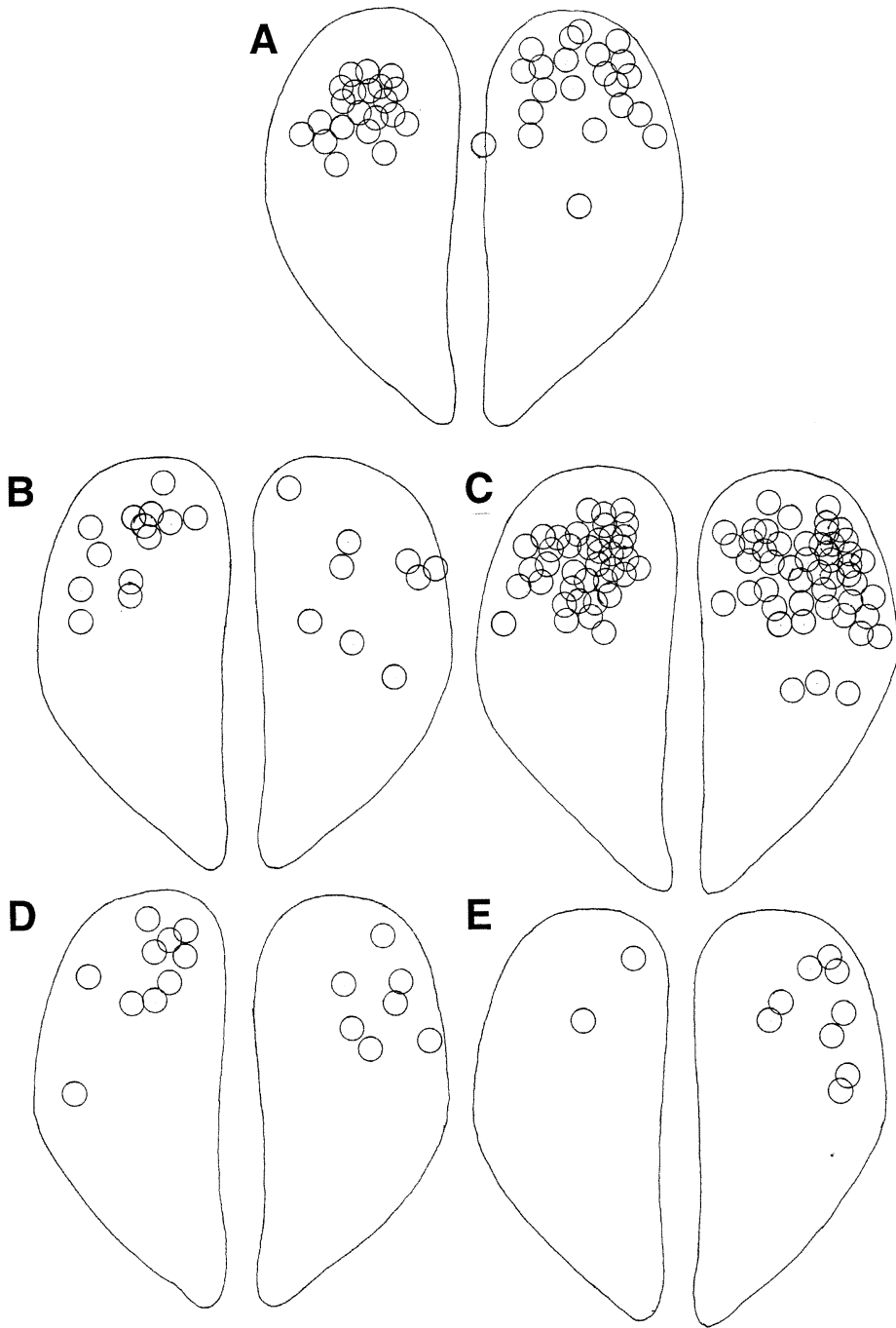


Figure 5. Master diagrams of the right and left shell valves of *Xenostrobus pulex* and the numbers and positions of drill-holes made by *Lepsiella flindersi* in five samples of the mussels (A–E) from the lower eulittoral shore at Site B in Whaling Cove.

Table 6. *Xenostrobus pulex*. A comparison of the mean numbers and shell lengths of individuals obtained in samples collected from the upper and lower eulittoral zone at Site B on the rocky shore at Whaling Cove, Albany, Western Australia. (A). Living individuals. (B). Dead and non-drilled individuals. (C). Dead and drilled individuals.

(A).					
	Total no of <i>X. pulex</i>	Total no. of living individuals	Mean shell length (mm)	Shell length range (mm)	Total no. of dead individuals
Upper eulittoral	1124	1049	13.44	1.0–20.0	75
Lower eulittoral	1407	1076	9.96	0.5–19.5	331
(B).					
	Total no. of non-drilled <i>X. pulex</i>	Mean shell length of non-drilled individuals (mm)	Shell length range (mm)		
Upper eulittoral	59	13.42	4.0–17.5		
Lower eulittoral	176	12.07	1.0–18.5		
(C).					
	Total no. of drilled <i>X. pulex</i>	Mean shell length of drilled individuals (mm)	Shell length range (mm)		
Upper eulittoral	16	14.19	10.5–16.5		
Lower eulittoral	155	14.57	6.0–18.00		

The diet of Dicathais orbita on the shore at Whaling Cove

On the exposed shore (Site A), over a period of ten days two individuals of *Lepsiella flindersi* were observed feeding, one upon crab carrion, the other, apparently, attacking at 16.8 mm long serpulid, *Galeolaria caespitosa* via the aperture (Table 7).

On the exposed shore, *Dicathais orbita* was much more numerous in the pool, the eulittoral and sub-littoral fringe (Table 7). Twenty-nine feeding records were obtained. Of these, three *D. orbita* were attacking, not by drilling, but through the aperture, the higher-zoned *Austromegabalanus nigrescens*. The apertures of the barnacles eaten by the whelk were covered in a blue mucous secretion.

All other records of *Dicathais orbita* predation were from lower on the shore with prey falling into the sequence: Gastropoda (mostly limpets) (12), Serpulidae (all *Galeolaria caespitosa*) (7), Bivalvia (mostly *Xenostrobus pulex*) (7). Of the attacks on gastropods, most were *Siphonaria* sp. Two of the latter were attacked by marginal drilling but most by simple engulf-

ment. A single *Serpulorbis siphon* (Lamarck) was seen being attacked via the aperture and two *Patelloida nigrosulcata* were attacked, one by drilling, the other by engulfment. All the *Galeolaria caespitosa* were attacked via the aperture and all the bivalves (six *Xenostrobus pulex* and one *Lasaea australis* (Lamarck)), were engulfed. The significance of this latter observation is that *Dicathais orbita* does not, here, drill its *X. pulex* prey.

The predator vs. prey size relationships for *Dicathais orbita* and four categories of common dietary items, i.e. Cirripedia (*Austromegabalanus nigrescens*), limpets (*Patelloida nigrosulcata* and *Siphonaria* sp.), Serpulidae (*Galeolaria caespitosa*) and bivalves (*Xenostrobus pulex*), are illustrated in Figure 6. Although there could be drawn a positive relationship between *D. orbita* and all prey ($r^2 = 0.457$; $p = 0.0145$) (Fig. 6A), taken individually, the four prey categories showed no such significant correlation, i.e.: Cirripedia $r^2 = 0.495$; $p = 0.5030$, limpets ($r^2 = 0.001$; $p = 0.8904$), Serpulidae ($r^2 = 0.331$; $p = 0.1765$), *Xenostrobus pulex* ($r^2 = 0.178$; $p = 0.4051$) (Fig. 6B).

Table 7. The shell heights and observed prey (with sizes) of *Lepsiella flindersi* and *Dicathais orbita* at Site A on the rocky shore at Whaling Cove, Albany, Western Australia. (An * indicates the individual was being drilled.)

Predator	Shell height (mm)	Prey	Shell length or height (mm)
<i>Lepsiella flindersi</i>	14.9	Serpulidae <i>Galeolaria caespitosa</i>	16.8
	19.1	Decapoda <i>Leptograpsus</i> sp.	(carrion)
<i>Dicathais orbita</i>	24.1	Cirripedia <i>Austromegabalanus nigrescens</i>	17.6 (height)
	20.4	<i>Austromegabalanus nigrescens</i>	16.8 (height)
	19.6	<i>Austromegabalanus nigrescens</i>	9.5 (height)
	22.6	Gastropoda <i>Siphonaria</i> sp.	3.2
	12.5	<i>Siphonaria</i> sp.	5.5
	19.6	<i>Siphonaria</i> sp.	5.8
	19.9	<i>Siphonaria</i> sp.	3.4
	30.8	<i>Siphonaria</i> sp.	4.4
	11.7	<i>Siphonaria</i> sp.	4.4
	10.3	<i>Siphonaria</i> sp.*	4.0
	25.2	<i>Siphonaria</i> sp.	3.3
	17.0	<i>Siphonaria</i> sp.*	4.0
	23.2	<i>Serpulorbis siph</i>	21.7 (diameter)
	13.4	<i>Patelloida nigrosulcata</i> *	16.4
	10.4	<i>Patelloida nigrosulcata</i>	4.2
	12.8	Serpulidae <i>Galeolaria caespitosa</i>	12.5
	20.6	<i>Galeolaria caespitosa</i>	20.6
	23.2	<i>Galeolaria caespitosa</i>	23.2
	27.3	<i>Galeolaria caespitosa</i>	18.9
	28.5	<i>Galeolaria caespitosa</i>	20.3
15.8	<i>Galeolaria caespitosa</i>	19.6	
16.3	<i>Galeolaria caespitosa</i>	5.5	
10.3	Bivalvia <i>Xenostrobus pulex</i>	2.7	
11.2	<i>Xenostrobus pulex</i>	5.3	
10.0	<i>Xenostrobus pulex</i>	2.9	
11.4	<i>Xenostrobus pulex</i>	3.1	
11.6	<i>Xenostrobus pulex</i>	2.8	
9.9	<i>Xenostrobus pulex</i>	9.6	
11.7	<i>Lasaea australis</i>	2.1	

DISCUSSION

The rocky shore at Whaling Cove is interesting because of the variation in the degree of exposure it experiences over a short distance. On the central, exposed, part of the shore, the dominant gastropod predator is *Dicathais orbita*, as it is on most southerly Western Australian shores. Here it was feeding on a range of sessile prey all of which are significant components of the inter-

tidal fauna. On a rocky platform on Rottnest Island, Western Australia, *D. orbita* consumed a wide range of prey (Morton & Britton, 1993), engulfing most, marginally chipping *Septifer bilocularis* (Linnaeus) and even consuming carrion and juvenile conspecifics. Also on Rottnest Shores, Taylor & Glover (1999) described *D. orbita* engulfing and attacking the apertures of gastropods but also drilling the thick, calcified, operculum of the turbinid

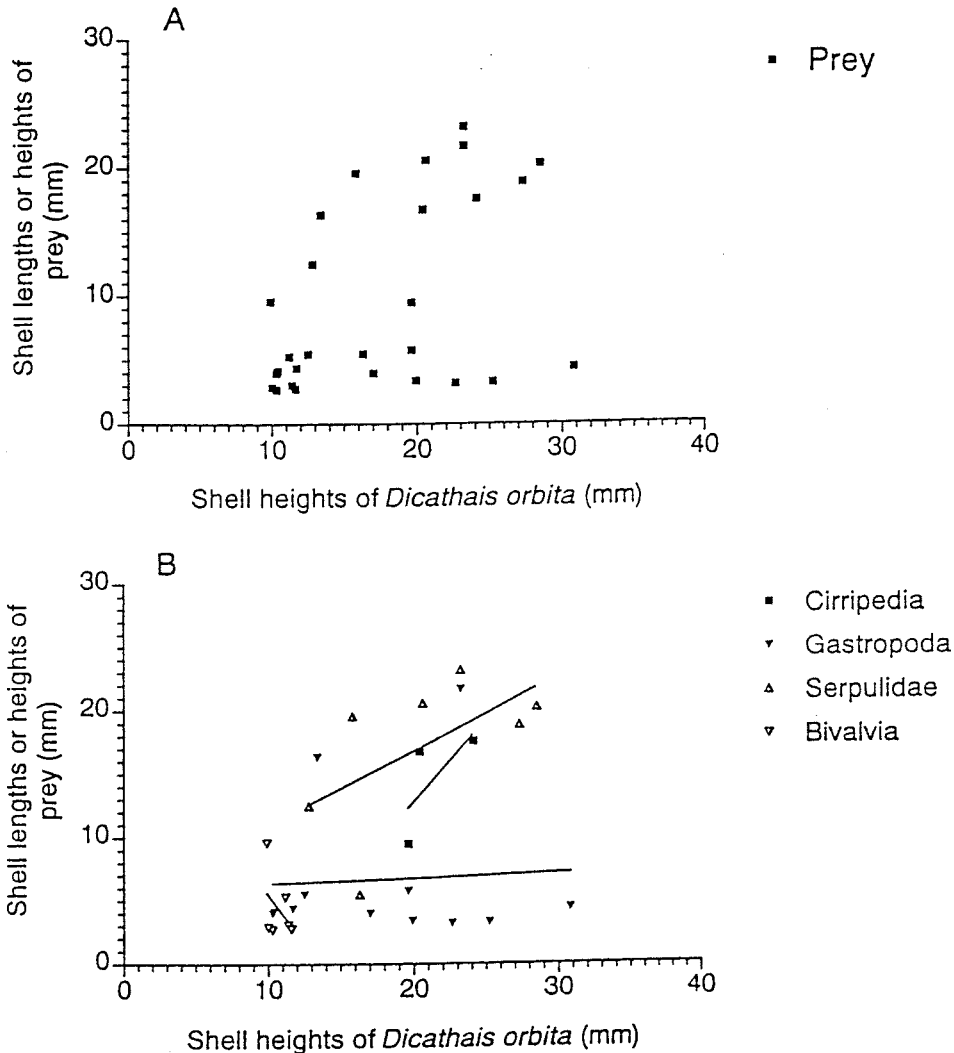


Figure 6. *Dicathais orbita*. A correlation between prey and predator size at Site A on the rocky shore at Whaling Cove, Western Australia. A, prey; B, prey items by category (■ = *Austromegabalanus nigrescens*; ▼ = limpets; △ = *Galeolaria caespitosa*; ▽ = *Xenostrobus pulex*).

Ninella torquata (Gmelin). Black (1978) records *D. orbita* as drilling limpets and although this was not seen by Morton & Britton (1993) and rarely by Taylor & Glover (1999), this ability is confirmed here. *Dicathais orbita* also consumes barnacles, for example *Austromegabalanus nigrescens* at Whaling Cove, anaesthetizing them with a blue secretion, presumably from the hypobranchial gland (Roseghini *et al.*, 1996). Throughout its range, therefore, *D. orbita* can employ a suite of attack methods in order to predate the numerous species with

which share its highly variable habitat. The feeding records of *D. orbita* at Whaling Cove showed no significant positive correlation between predator and prey size for any of the four categories of prey, but a significant positive correlation was obtained for all the prey, collectively assessed. As on Rottneest Island shores (Morton & Britton, 1993), therefore, *D. orbita* appears to be an opportunistic predator, bigger individuals generally able to handle bigger prey but, in the field, attacking almost anything available. A positive correlation between

predator and prey sizes has been demonstrated for a number of muricids (Palmer, 1984), e.g. *Acanthina punctulata* (Menge, 1974), *Nucella dubia* (McQuaid, 1985) and *Thais mutabilis* (Ekaratne & Goonewardena, 1994), all of which seem to have more specialised diets. The opportunism of *D. orbita*, like its ecological counterpart, *Thais clavigera* (Küster), on Hong Kong shores (Taylor & Morton, 1996) is becoming better appreciated.

Unlike the growing literature on *Dicathais orbita*, virtually nothing is known of *Lepsiella flindersi*, also a member of the Muricidae. In New Zealand, *Lepsiella scobina* is known as the 'oyster borer' (Gardner, 1978) while on southern Australian shores, *Lepsiella vinosa* is known to feed on barnacles, *Elminius modestus* Darwin and *Balanus amphitrite* (Darwin), in mangroves (Bayliss, 1982) and *Nodilittorina unifasciata* on rocky shores (McKillup, 1982). *N. unifasciata* and *Littorina cincta* are also eaten by *Lepsiella scobina* in New Zealand (McKillup, 1981). In Victoria, Australia, *L. vinosa* feeds on barnacles (*Chthamalus*), bivalves (*Brachidontes rostratus*, *Xenostrobus pulex*, *Lasaea australis*) and littorines (Ward & Quinn, 1988). Nothing is written about the prey of *Lepsiella flindersi*. Here, it is recorded as a carrion feeder and to attack, through the aperture, *Galeolaria caespitosa* on exposed shores—not its favoured habitat. On the sheltered shores of Whaling Cove, Western Australia, however, *L. flindersi* is the major predator of *X. pulex*, and here drills the largest individuals as does *Nucella lapillus* when feeding on *Mytilus edulis* (Burrows & Hughes, 1991). *L. flindersi* might, therefore, structure the lower eulittoral mat of *X. pulex* not only by making space available for new recruits but by keeping its profile low.

The shore at Whaling Cove is of further interest with regard to *Xenostrobus pulex*. On the exposed Site A, the mussel occurred as scattered individuals with *Megabalanus nigrescens* in the upper eulittoral and supralittoral. Here, the mussels were of 5.6 mm mean shell length (Table 1) and of the same size range, i.e. 2.2–9.8 mm, as the *X. pulex* prey of *Dicathais orbita* in the lower eulittoral (Table 7). That is, *X. pulex* is here a supralittoral and eulittoral species, of small overall size, and is restricted to crevices higher on the shore where it is not predated but is a favoured prey of *D. orbita* lower down. This is somewhat similar to the situation in Princess Royal Harbour where at Quararup (Fig. 1A, Sites 1 & 2), *X. pulex* was present on the high shore in small clusters, but still between the

higher-zoned littorines, *Nodilittorina unifasciata* and *Bembicium auratum*, and *Austrocochlea concamerata* lower down. At Quararup it was possibly excluded from the lower eulittoral by a dense mat of the larger mytilid *Brachidontes erosus* (Morton, 1990).

On the sheltered Site B at Whaling Cove, the situation was quite different. Here *Xenostrobus pulex* survives over a wider range of vertical shore heights. In the supralittoral, the species was similar to its conspecifics on the exposed shore, i.e. it lived in crevices and was small. Here, however, it occurred in six times the numbers, with only two of 100 individuals collected dead but not drilled. Here too, therefore, it escapes the attention of *Dicathais orbita* (and *Lepsiella flindersi*).

On the lower eulittoral at Site B, the mat of mussels was heavily predated by *Lepsiella flindersi*. Between the two extremes, in the upper eulittoral, another situation occurred, where patches of *Xenostrobus pulex* were surrounded by areas of superficially bare rock and with numerous grazing gastropods present. Although a few *L. flindersi* (and even one or two *Dicathais orbita*—but significantly not lower down) occurred at this height, there was little evidence of *X. pulex* predation (<1.0% of individuals had been so killed). The *X. pulex* patch centres were densely occupied (32.6 individuals·6.25 cm²) by longer (13.00 mm mean shell length) individuals whereas patch edges were more densely occupied (57·6.25 cm²) by smaller ones (8.8 mm mean shell length). That is, the patches seemed to attract recruits at the edges, on the cleared rocks, but were constrained from continuous enlargement by the activities of a surrounding array of grazers. *X. pulex* can, therefore, occupy supralittoral levels but is presumably constrained to crevices by physiological hardships, whereas on the upper eulittoral, patches are created and maintained by the actions of grazers. On the lower eulittoral, the almost monospecific mat of *X. pulex* is heavily-influenced by *L. flindersi* predation.

Patchiness is a feature of many rocky shore communities (Paine & Levin, 1981; Sousa, 1984; Hartnoll & Hawkins, 1985; Vadas, 1992; Sgrott Sauer Machado *et al.*, 1992). In the upper eulittoral of Whaling Cove, recruitment into the *Xenostrobus pulex* patches occurred mostly at the edges and they were, apparently, being maintained not only by surrounding grazing pressure but also by the additional behaviour of the herbivore's repose against the mussels, presumably as a means of reducing desiccation stress. McMahon (1990) has shown that the

major grazers co-occurring with *X. pulex*, i.e. *Austrocochlea concamerata* and *Nerita atramentosa*, experience evaporative water loss during periods of emersion which results in evaporative cooling that, in turn, enables them to remain active for only about 2.5 hours at 40°C. This, on the shores of King George Sound where the tidal range is only 1.3 metres, is a very short time and prolonged emersion results in inactivity against the mussel patches. It is not known, however, how stable the *X. pulex* patches at Whaling Cove are over time.

In the lower eulittoral of the same shore there is a uniform mat of *Xenostrobus pulex* and here large individuals are the prey of *Lepsiella flindersi*. Ward & Quinn (1988) have shown that on a exposed rocky shore in Victoria, Australia, *Lepsiella vinosa* feeds on a variety of intertidal prey items, including barnacles, gastropods, bivalves and serpulid polychaetes, by drilling and, further, that *X. pulex* constituted only 10% of its diet. At Whaling Cove, the same mussel apparently constituted 100% of the diet of *L. flindersi*. Interestingly, no predator-induced patches were present, probably because here *L. flindersi* was eating larger individual mussels thereby allowing recruitment into the spaces created. Indeed, smaller living *X. pulex* were often collected from within the valves of larger, bored, conspecifics. McMahon (1990) has shown for *L. vinosa* that emersion at high temperatures results in the gastropod sealing its aperture with the operculum, preventing water loss and becoming inactive. If *L. flindersi* has a similar physiology, this difference between it and the more sustained activity of the higher-zoned grazers, i.e. *Austrocochlea concamerata* and *Nerita atramentosa*, under the same conditions, explains why the muricid cannot colonize the higher eulittoral, why so few bored *X. pulex* were obtained from here and why, therefore, it plays no role in the dynamics of the mussel patches.

It is often stated that muricids play a role in the structuring of major space-occupying organisms such as mussels and barnacles on rocky shores (Navarette, 1996; Taylor, 1998). At Whaling Cove and, at the time of this study, *Xenostrobus pulex* was only influenced by *Lepsiella flindersi* in the lower eulittoral. It may, however, at times of enhanced wave action, occur higher on the shore to influence the dynamics of the *X. pulex* patches and this is suggested by the presence here of a few drilled individuals, but no *L. flindersi*. A natural cycle of foraging and sheltering, in relation to changing weather conditions and, thus, wave action,

has been demonstrated for *Nucella lapillus* (Burrows & Hughes, 1989) and it would, in Whaling Cove, be interesting to see if *L. flindersi* functions in the same way, as this study suggests it might. Hughes & Burrows (1991), for example, showed that under favourable, low wave, conditions, *N. lapillus* fed on larger prey. In Whaling Cove too, *L. flindersi* was feeding on large *X. pulex* on the studied calm days.

All work on mussel-patch dynamics has been performed upon species of *Mytilus* on north-temperate shores (Suchanek, 1978). This is the first study of a southern temperate species, *Xenostrobus pulex*, which is a significant space occupier of semi-protected shores in King George Sound. Formerly thought to be a specialist limpet driller (Black, 1978), the predatory muricid *Dicathais orbita* is now known to be a generalist predator employing an array of attack procedures to gain access to many different prey items (Morton & Britton, 1993; Taylor & Glover, 1999), but does not drill *X. pulex*, at least on the exposed part of this study site. Here, it engulfs small mussels. This initial study of *L. flindersi*, however, has shown it to feed, apparently monotonically, on *X. pulex* on the more sheltered component of the shore and this predator is, thus, different from the opportunistic *D. orbita*.

There is an array of predatory muricids in Australia (Wilson, 1994) about most of which little is known regarding diets and attack methods and little, therefore, of their role in structuring shore ecology. Exceptions to this include *Morula marginalba* Blainville on New South Wales shores (Moran *et al.*, 1984; Moran, 1985; Fairweather, 1985) and, more recently, *Dicathais orbita* on Western Australian shores (Black, 1978; Morton & Britton, 1993; Taylor & Glover, 1999). On the Great Barrier Reef, *Thais tuberosa* (Röding) attacks the trochid *Trochus niloticus* Linnaeus through the aperture without boring (Castell & Sweatman, 1997).

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