

# Preliminary investigations of predation by the whelk *Morula marginalba*

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**ABSTRACT:** Three short-term experiments (6 mo to 1 yr) were done in a preliminary attempt to determine the importance of predation by the muricid whelk *Morula marginalba* Blainville in rocky intertidal communities in New South Wales (Australia). In 2 experiments, whelks were manually removed from some sites, leaving control sites undisturbed. In the third experiment, crevices were filled with concrete, thus removing shelters needed by the whelks and therefore reducing the density of predators. The predators were shown to affect the structure of the community on each shore, but the effects varied considerably among the experiments. Highly preferred prey – oysters and the limpet *Patelloida latistrigata* (Angas) – were eliminated by whelks. Less-preferred species – such as the barnacle *Chamaesipho columna* Spengler – were reduced in density where the alternative prey were also less preferred. When other, more favoured prey were present, species low in the preference rankings were ignored by the whelks. The interpretation of simple removals of predators from intertidal systems are made difficult by the patterns of preference for different species by the predator, and by temporal and spatial variations in the availability of these species.

## INTRODUCTION

The intertidal muricid whelk *Morula marginalba* Blainville is very abundant on some shores in New South Wales (Australia), although it is patchy in its distribution (Moran, 1980). *M. marginalba* eats a diverse range of prey (Fairweather and Underwood, 1983; Moran et al., 1984) and is known to influence some interspecific interactions on local shores (Underwood et al., 1983). Because predation is often considered to be one of the most important processes organizing the structure of rocky intertidal communities (Connell, 1975; Menge and Sutherland, 1976; Paine, 1977, 1980) we wished to determine the importance of predation by *M. marginalba* for local communities. The effects of intertidal predators may be direct, for example by reducing the vertical distribution of populations of prey (e.g. Connell, 1970; Paine, 1974), or indirect, for example by reducing the intensity of competitive interactions or by modifying other interactions among prey species (e.g. Paine, 1966, 1974, 1980; Lubchenco, 1978; Garrity and Levings, 1981; Underwood et al., 1983).

Most studies of intertidal predators have concentrated on the slower moving whelks and starfish, although some experimental evidence exists about the important roles played by more active crabs and fish (Kitching et al., 1966; Menge and Lubchenco, 1981). In general, 2 major experimental procedures have been used to elucidate the role of predators in the structure of intertidal communities. Both methods involve the continued removal of predators with the aim of keeping their density at or near zero. By comparison with undisturbed control areas, the effects of removal of the predator may, in theory, be measured.

The first method is the simple manual removal of all predators from an area. This is usually repeated at regular intervals throughout the experiments, and the predators are released elsewhere (e.g. Paine, 1966, 1971, 1974; Dayton, 1971; Garrity and Levings, 1981). Because of subsequent immigration of predators into the experimental area, frequent monitoring is required. Often a 'buffer' zone around the experimental area is created (i.e. an area from which predators are also removed, but in which changes in distribution or abundance of prey are not recorded). Manual removal from experimental plots has also been used to examine competition among such predators (Menge, 1972b).

The second method is to exclude predators from

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small areas of the shore by experimental installations. Such barriers to immigration of predators include cages (Connell, 1961, 1970; Dayton, 1971; Menge, 1976; Lubchenco and Menge, 1978; Peterson, 1979; Menge and Lubchenco, 1981), fences (Underwood et al., 1983) and rooves (Dayton, 1971; Menge and Lubchenco, 1981). Such installations have the disadvantage that they may introduce artefacts due to fouling, shade or other causes (Underwood and Denley, 1984). These may be difficult to detect, and may require complex controls to ensure that the experimental results are reliable. The second method has the advantage, however, that immigration of predators is prevented, and densities of predators inside the enclosures may be kept constant at the desired experimental levels throughout the entire experiments without frequent monitoring.

Before a complete understanding of predation in local intertidal communities can be possible, information about spatial variations in abundances of prey and in the foraging of *Morula marginalba* is needed. Accordingly, we designed several short-term exploratory experimental removals of *M. marginalba* from shores dominated by different types of prey. In this paper, we describe 3 such experiments as a preliminary attempt to determine the importance of predation by *M. marginalba*. These whelks aggregate in large numbers during low tide in crevices and depressions in the substratum, apparently to avoid the effects of harsh weather during low tide both in periods of hot sunny weather during summer, and during heavy storms (Moran, 1980; see also Feare, 1971; Menge, 1978a, b for aggregating behaviour of other intertidal whelks). Because of this pattern of distribution during many low tides, we also investigated the effectiveness of the whelks when crevices were not available. We achieved this, in one experimental area, by filling all the crevices so that there were no longer any suitable shelters for the whelks.

## MATERIAL AND METHODS

Different designs were used for 3 experimental removals of *Morula marginalba* but all 3 were attempts to remove or exclude the whelks from experimental areas without using cages or fences. Each will be considered separately, and, for heuristic worth, the experiments will be described in order of increasing complexity, rather than in the chronological order of their execution. All study sites were relatively sheltered shores, and were chosen primarily because whelks were relatively abundant.

The simplest experiment was to investigate the

effects of predation by *Morula marginalba* on several species of prey at different heights on the shore. The shore chosen for investigation was a broad, gently and evenly sloping platform of mudstone at Ulladulla Harbour (N. S. W., 200 km south of Sydney). The shore is criss-crossed by parallel cracks some 0.5 to 1.5 m apart, providing readily available shelters for whelks so that they are not subject to much stress during long periods of emersion or during low-tides at mid-day (Moran, 1980). Because of the abundance of crevices, no place on the rock-platform was very far from a crevice. Two adjacent platforms, separated by a deep surge channel, but with similar amounts of crevices were sampled. Preliminary transects revealed that the 2 areas had similar covers of the barnacle *Chthamalus antennatus* (Darwin) at the top of the shore, and *Chamaesipho columna* Spengler at the top and extending to lower levels (see Dakin, 1950; Underwood, 1981, for descriptions of the usual patterns of vertical distribution of these barnacles). In addition, there were several species of gastropods present. *M. marginalba* were often seen eating barnacles and the juveniles of one species of snail – *Bembicium nanum* (Lamarck) – but rarely the juveniles or adults of other species. In January 1979, all *M. marginalba* were removed from the northern study area, leaving the southern one as a control. The manual removal was fairly successful, but some *M. marginalba* were found on the edges of the cleared area during subsequent visits, especially at the lowest level on the shore. Densities of *M. marginalba* and all prey species were recorded at 3 heights on each area at 5 times during the next 6 mo. At the uppermost height, there were *C. antennatus* and adult *C. columna*; the latter, but not the former, were also found at the middle height. At the lowest level (just below mid-tidal height), the only barnacles were juvenile *C. columna*. Barnacles were counted in 4 marked quadrats (2.5 × 4 cm) at each height. Gastropods were counted in 10 0.25 m<sup>2</sup> quadrats arranged contiguously to form a 1 × 2.5 m rectangle in the middle of the study area at each height. Rates of mortality of prey were calculated as the slope of the regression of log density on time (Underwood, 1975).

The second experiment investigated the effects of height on the shore and distance from the nearest crevice on predation by *Morula marginalba* of a highly-preferred species of prey, the oyster *Saccostrea commercialis* (Iredale & Roughley) (see Moran, 1980; Moran et al., 1984). This experiment preceded the one described above and was also done at Ulladulla harbour. Prior to the anticipated settlement of oysters, all crevices in a 25 m wide strip down a section of the shore dominated by *Chamaesipho columna* were filled with quick-setting concrete, in August 1977. All gastropods in the crevices (including *M. marginalba*) were

previously removed with a knife. The concrete prevented the subsequent use of the crevices by whelks, although about 10 % of crevices had to be refilled with concrete every few months. The experimental, and adjacent control areas were sampled at 3 heights every 2 mo for 1 yr. The 3 heights corresponded to those described for the earlier experiment (i.e. the top, middle and bottom of the zone occupied by the barnacle *C. columna*). At each height, the numbers of whelks and oysters were counted in 3 replicate quadrats at different distances from crevices. Control quadrats were sampled some 1.5 m outside and on each side of the crevice-free area; these were within 1 m of natural crevices. Inside the experimental area, quadrats were sampled 1, 6 and 12 m from the nearest crevices. The 1 m distance should also represent natural conditions on this shore, differing from the controls only in the fact that it was in an area with concreted crevices. There were no natural areas of the shore at 6 m or greater distances from crevices.

The third experiment was done on sandstone shores at Gibbon Beach (Port Hacking, N. S. W., 23 km south of Sydney). The shores were of different horizontal steps separated by gently sloping areas dominated by gastropods (see Underwood et al., 1983 for descriptions of gastropod areas). The horizontal areas had a cover of the barnacle *Tesseropora rosea* (Krauss), amongst which there were limpets *Patelloida latistrigata* (Angas) (see Creese, 1982), and snails *Littorina unifasciata* Gray (see Jernakoff, 1983). At the upper levels there were also *Chthamalus antennatus* and *Chamaesipho columna*. The most abundant gastropods in the intervening gastropod areas were limpets, *Cel-lana tramoserica* (Sowerby). In December 1978, some months after a very heavy settlement of *T. rosea*, all *Morula marginalba* were removed from two 10 m wide strips of shore, separated by about 100 m. These are referred to as the North and South areas; nearby 10 m wide strips of shore served as a control for each removal area. This experiment therefore allowed estimation of spatial variation (over 100 m of shore) in the effect of predation by *M. marginalba* on a number of species of prey at different heights on the shore. All *M. marginalba* found on the experimental plots at fortnightly intervals after the beginning of the experiment were removed. At 4 times during the year after the experiment started, photographs were taken of 4 10 × 10 cm marked areas in the centre of each of the removal and control areas at different heights. All organisms were counted in the field, or from these photographs. The densities of *C. tramoserica* were recorded from somewhat larger quadrats and adjusted to densities per 0.25 m<sup>2</sup>. Where possible the numbers of adults and juveniles of each species were recorded separately.

The effects of predation on any interaction between the 2 major space-occupying barnacles, *Tesseropora rosea* and *Chamaesipho columna*, were also examined. All *T. rosea* (the larger species) were removed using a screwdriver from some 10 × 10 cm quadrats near the other sample areas. The numbers of *C. columna* could subsequently be compared in the presence or absence of the larger barnacle, and with and without predation by the whelks.

At the end of this experiment, *Morula marginalba* rapidly reinvaded the experimental removal areas. On the southern removal area, we examined the preferences shown by *M. marginalba* among the now diverse assemblage of prey. Randomly-chosen quadrats (25 cm<sup>2</sup>) were examined in areas where whelks were feeding and where only 2 types of prey were present. In each quadrat, the numbers of each prey, and the numbers of whelks feeding on each prey were recorded. These results are presented graphically as crude estimates of preference; no attempt was made to fit empirical measures of preference to the data (see Chesson, 1978; Cock, 1978).

## RESULTS

### Removal of *Morula marginalba* from a shore at Ulladulla

Densities of *Morula marginalba* during the first experiment were less in the removal area than in the control for each height at each time (Table 1). There were significantly less *M. marginalba* at the top of the shore than lower, where rankings between middle and bottom areas varied through time, so that generally there was no real difference in the abundance of whelks between the 2 lower levels (analysis of variance and Student-Newman-Keuls tests of the data summarized in Table 1).

Juvenile *Chthamalus antennatus* were in small densities at high levels on the shore and showed decreased survival on the control shore compared with that on the shore where *Morula marginalba* were removed (trends throughout experiments are illustrated in Fig. 1). At the end of the experiment (July 1979), the proportional survival in areas without whelks was considerably greater (mean of 4 replicates = 0.91) compared with plots with whelks (mean = 0.50;  $\chi^2 = 4.90$ , 1 df,  $P < 0.05$ ).

The smaller, more dense *Chamaesipho columna* also survived better in areas without whelks (Fig. 1;  $\chi^2$  tests, 1 df, on proportional survival = 10.3, 6.4, 7.4 for top, middle and bottom levels, respectively; all  $P < 0.025$ ). Proportional survival increased with increasing height

Table 1. *Morula marginalba*. Densities in control and removal areas during the first experiment at Ulladulla. Mean number (S.E.) per 0.25 m<sup>2</sup> quadrat; n = 10 for each sample

| Height:    | Control   |            |            | Removal   |           |           |
|------------|-----------|------------|------------|-----------|-----------|-----------|
|            | Top       | Middle     | Bottom     | Top       | Middle    | Bottom    |
| 6 Jan 1979 | 0.2 (0.2) | 10.2 (0.8) | 9.5 (0.8)  | 0         | 0         | 0         |
| 22 Feb     | 0.8 (0.4) | 15.1 (1.4) | 11.2 (1.1) | 0         | 4.1 (0.7) | 0.9 (0.4) |
| 22 Mar     | 0.8 (0.4) | 14.7 (0.8) | 9.8 (0.7)  | 0         | 1.6 (0.4) | 2.5 (0.5) |
| 21 Apr     | 4.7 (0.6) | 14.8 (1.0) | 21.3 (1.2) | 0         | 4.8 (0.6) | 2.2 (0.4) |
| 10 Jul     | 8.1 (0.8) | 19.5 (0.6) | 11.7 (1.0) | 0.2 (0.2) | 3.9 (0.8) | 1.3 (0.4) |

on the shore both in the presence of whelks (mean proportional survival was 0.58, 0.73, 0.89 for bottom, middle and top levels, respectively;  $\chi^2$ , 2 df = 17.1,  $P < 0.01$ ) and where whelks were removed (mean proportional survival was 0.81, 0.89, 0.99 for bottom, middle and top, respectively;  $\chi^2$ , 2 df = 23.3,  $P < 0.01$ ). The effectiveness of whelks also increased towards the bottom of the shore (note the differences between sur-

vival with and without whelks at each level in the above data and in Fig. 1).

Prior to the start of the experiment, the gastropod *Bembicium nanum* had settled on the shore in large numbers (forming a distinct juvenile cohort; Fig. 2).

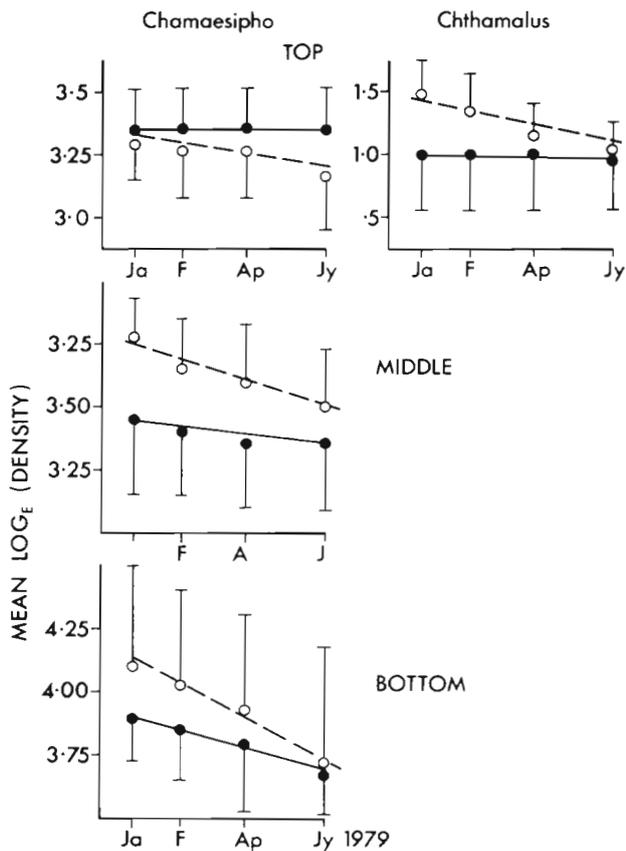


Fig. 1. Survival of barnacles in areas with and without whelks during the first experiment at Ulladulla. Rate of mortality of barnacles of each species at 3 heights on the shore is indicated by the slope of the regression line through log density. Data are means ( $\pm$  S. E.) of 4 quadrats (10 cm<sup>2</sup>) at each time of sampling.  $\circ$  controls (with *Morula marginalba*);  $\bullet$  whelks removed

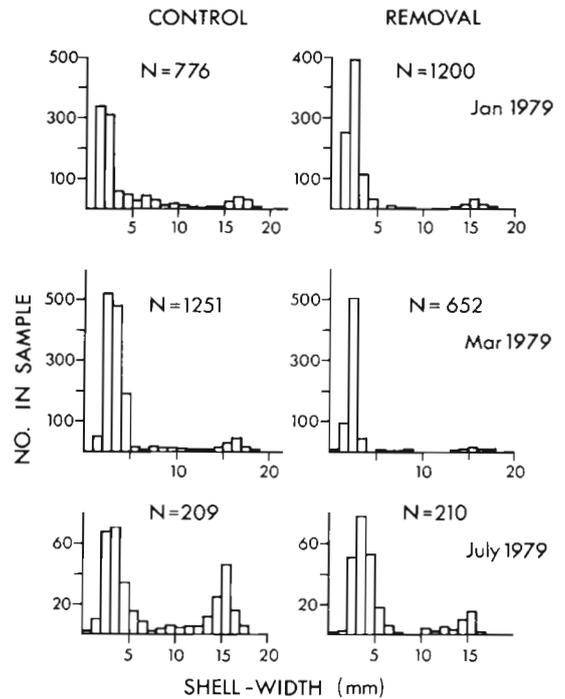


Fig. 2. *Bembicium nanum*. Size-frequency distributions in areas with (control) and without (removal) whelks during the first experiment at Ulladulla (sizes of samples indicated with each histogram)

The recruitment of small snails had apparently finished by February 1979; thereafter densities of juveniles began to decline and very few or no very small *B. nanum* were found on subsequent visits. The mortality of these snails was estimated separately for juveniles and adults but, because gastropods can move from one level of the shore to another, the data were pooled over all 3 heights. The mortality of juvenile

snails was estimated from February onwards because of the increasing numbers until recruitment had ceased. Neither size-class showed decreased survivorship on the shore where whelks were present compared with the removal area (analysis of covariance of slopes of regressions in Fig. 3;  $P > 0.2$ ). Adults sur-

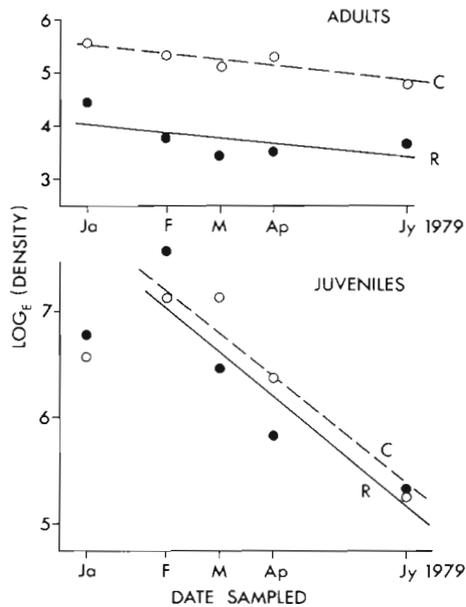


Fig. 3. *Bembicium nanum*. Survival in areas with (C) and without (R) whelks during the first experiment at Ulladulla. Rates of mortality indicated by slopes of regression lines through log density. Data analysed separately for adult and juvenile snails (< 10 mm and > 10 mm shell width, respectively; see histograms in Fig. 2)

vived better than juveniles on both shores (analyses of covariance,  $P < 0.05$ ), as described by Underwood (1975).

There was no discernible effect of *Morula marginalba* on the densities or size-frequencies of the snail *Nerita atramentosa* (Fig. 4). There is no obvious method for statistical comparison of these size-frequency distributions from one time to another in the presence and absence of whelks. Recruitment of small *N. atramentosa* into each area and great differences in the numbers of adults present at the start of the experiment confound any comparison between the beginning and the end of the experiment. Similar numbers of small snails appeared in control and removal areas during the course of the experiments (there were 42 and 48 snails smaller than 10 mm in the samples from removal and control areas, respectively, in July 1979; Fig. 4). Throughout the study, as at the beginning, there were more *N. atramentosa* in the control area. Recruitment of the trochid *Austrocochlea constricta* was virtually continuous throughout the year (Underwood, 1974; Creese and Underwood, 1976). For this reason, the size-frequency distributions are presented for each month of the experiment (Fig. 5). In all months except March 1979, there were more small snails (i.e. less than 10 mm shell width) in the control areas (where whelks were present) than in the areas without *M. marginalba* (Fig. 5). In both areas, however, there was an increase in overall density of *A. constricta* during the experiments. This was largely due to the immigration of adults into the experimental areas (note the increased frequencies of adults between the beginning and end of the experiment in Fig. 5). Note particularly the marked increase in total numbers in both areas between February and March 1979. There was a slightly greater increase in density in the removal area than in the area where whelks were active. This is unlikely to be a result of the absence of whelks and was mostly attributable to greater immigration of adult

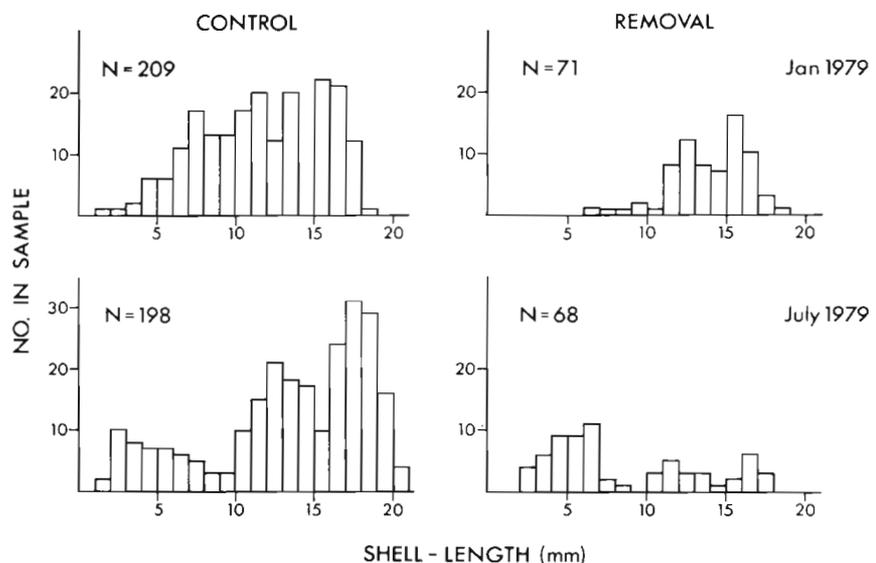


Fig. 4. *Nerita atramentosa*. Size-frequency distributions in areas with (control) and without (removal) whelks at beginning and end of the first experiment at Ulladulla (sizes of samples indicated with each histogram)

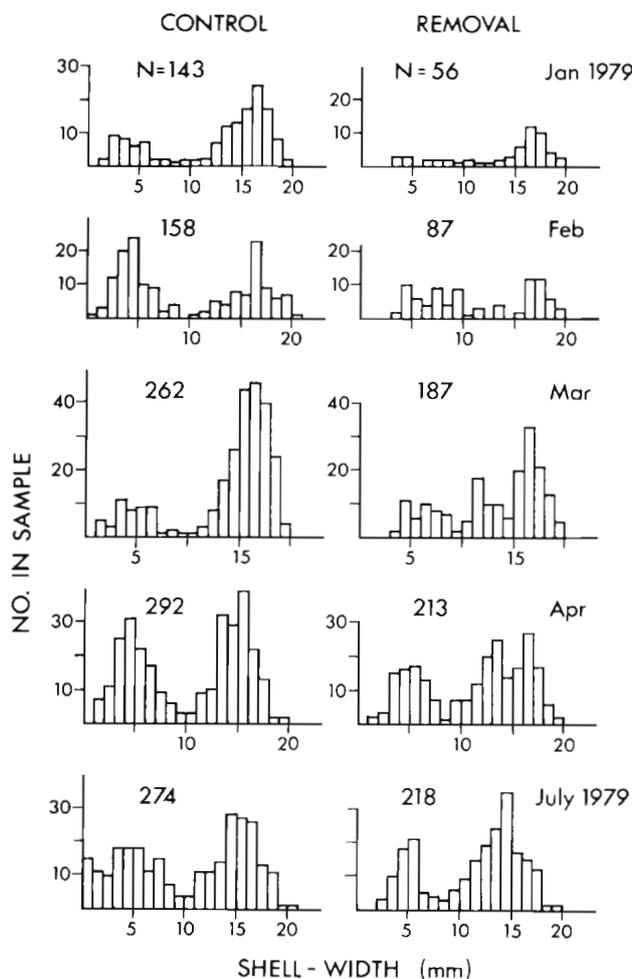


Fig. 5. *Austrocochlea constricta*. Size-frequency distributions in areas with (control) and without (removal) whelks during the first experiment at Ulladulla (sizes of samples indicated with each histogram)

snails into the removal areas between February and March.

#### Effects of crevices on predation by *Morula marginalba*

In the second experiment, where crevices were filled with concrete at Ulladulla, the mean density of whelks varied with time of sampling, height on the shore, and distance from the nearest crevice and there were complex interactions among these variables (analysis of variance of data in Fig. 6;  $P < 0.01$ ). In general, however, densities of whelks decreased with increasing height on the shore and at increasing distances from crevices. There was never any difference among mean densities in the control areas and those at 1 m distance from experimentally filled crevices (SNK tests,  $P > 0.05$ ). The densities at 6 and 12 m from crevices

were always less, except at the highest levels on the shore, where there were few *Morula marginalba* at any distance from crevices. At most times of sampling, and at the 2 lower levels, the densities of whelks 6 and 12 m from crevices did not differ. Throughout the experiment, the densities at different locations varied independently of one another, but with a maximum in June (Fig. 6).

Densities of oyster spat also varied with time of sampling, height on the shore and distance from crevices (Fig. 6). Densities increased as settlement occurred (October–December), and subsequently declined as predation and other agents of mortality became important. Maximal densities were reached mid-way during the experiment, at the highest level on the shore, and at the greatest distance from crevices. There were, however, very few oysters low on the shore. Near crevices there were many whelks and few oysters; far from crevices (6 and 12 m), there were few whelks and many oysters, at least for short periods. As the oysters grew, they apparently grew over some *Chamaesipho columna* (the other prey species present); the barnacles were not seen being eaten by whelks, but the potential outcome of this overgrowth was not examined experimentally. There was a non-linear, negative relation between mean density of whelks and that of oysters (Spearman's rank correlation coefficient =  $-0.77$ ,  $P < 0.01$ , 13 df for the data from the middle of the experiment in February 1978; Fig. 6). At the end of the experiment (October 1978), there were virtually no oysters in the experimental area; thus, height on the shore and distance from crevices ultimately made no difference to the survival of the oysters.

#### Removal of *Morula marginalba* from shores at Jibbon

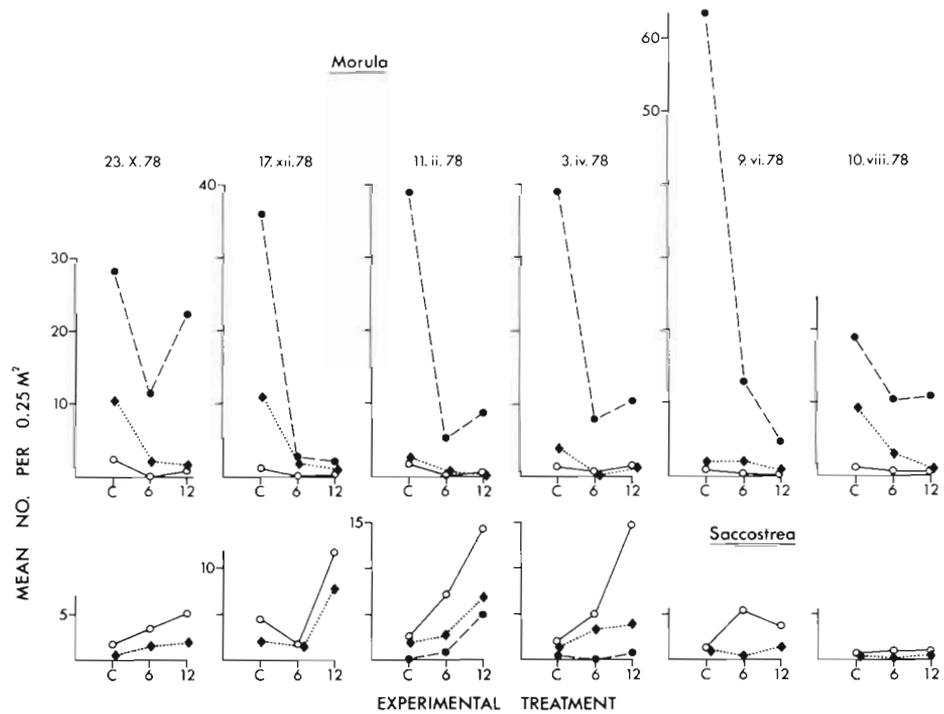
During the third experiment, densities of whelks were successfully kept at smaller numbers in the experimental areas than on corresponding control areas (Table 2). The whelks, however, showed spatial variation in that the densities in the northern areas were less than those in the southern control areas. The data presented are for the whole experimental transects. In fact, whelks were only found near the edges of removal (experimental) areas, and no *Morula marginalba* were found on the removal plots where prey were sampled.

In general, although the densities of various prey differed significantly between the 2 replicate study sites (100 m apart), the proportional survival was not different at this spatial scale (Fig. 7; Tables 2 and 3; analyses of variance of the ratios of densities January/December showed no significant differences from site to site within control and removal treatments;  $P > 0.20$

Table 2. Densities of species in areas with (Control) and without (Removal) whelks at beginning and end of third experiment at Jibbon. Mean (and S.E.) numbers 100 cm<sup>-2</sup> in 4 replicate quadrats except where stated, and the ratio of final to initial numbers

|  | Removal |       |       |       | Control |        |       |        |
|--|---------|-------|-------|-------|---------|--------|-------|--------|
|  | North   |       | South |       | North   |        | South |        |
| <i>Tesseropora rosea</i>   |         |       |       |       |         |        |       |        |
| Dec 1978   | 52      | (7)   | 89    | (7)   | 89      | (18)   | 87    | (17)   |
| Jan 1980   | 41      | (6)   | 68    | (5)   | 0       |        | 0     |        |
| Ratio Jan/Dec  | .79     | (.06) | .78   | (.05) | 0       |        | 0     |        |
| <i>Cellana tramoserica</i> (n = 6 quadrats; 0.25 m <sup>2</sup> )  |         |       |       |       |         |        |       |        |
| Dec 1978   | 12.3    | (1.9) | 18.9  | (5.5) | 42.5    | (12.9) | 11.3  | (4.6)  |
| Jan 1980   | 6.6     | (1.5) | 5.1   | (2.3) | 45.3    | (5.5)  | 9.8   | (6.1)  |
| Ratio Jan/Dec  | .54     | (.09) | .27   | (.11) | 1.06    | (.11)  | .87   | (.10)  |
| <i>Chamaesipho columna</i> (n = 8 quadrats)  |         |       |       |       |         |        |       |        |
| Dec 1978   | 432     | (27)  | 408   | (17)  | 310     | (28)   | 370   | (21)   |
| Jan 1980   | 370     | (21)  | 373   | (28)  | 273     | (33)   | 306   | (25)   |
| Ratio Jan/Dec  | .87     | (.06) | .91   | (.04) | .88     | (.07)  | .83   | (.05)  |
| <i>Chthamalus antennatus</i>   |         |       |       |       |         |        |       |        |
| Dec 1978   | 7.3     | (1.1) | 16.5  | (4.8) | 8.0     | (2.3)  | 9.5   | (2.3)  |
| Jan 1980   | 11.5    | (2.7) | 27.5  | (7.4) | 0       |        | 1.0   | (0.6)  |
| Ratio Jan/Dec  | 1.55    | (.19) | 1.97  | (.35) | 0       |        | .18   | (.12)  |
| <i>Patelloida latistrigata</i>   |         |       |       |       |         |        |       |        |
| Dec 1978   | 0       |       | 0     |       | 0       |        | 0     |        |
| Jan 1980   | 8.3     | (1.4) | 8.0   | (2.3) | 0       |        | 0.3   | (0.3)  |
| <i>Littorina unifasciata</i>   |         |       |       |       |         |        |       |        |
| Dec 1978   | 2.3     | (0.3) | 16.5  | (6.0) | 4.8     | (1.7)  | 54.3  | (17.1) |
| Jan 1980   | 18.5    | (5.2) | 19.0  | (4.7) | 0       |        | 15.0  | (9.3)  |
| Ratio Jan/Dec  | 8.0     | (1.9) | 1.7   | (0.5) | 0       |        | .24   | (.14)  |
| <i>Morula marginalba</i> : Mean from several times of sampling (n = 15 quadrats of 0.25 m <sup>2</sup> ) |         |       |       |       |         |        |       |        |
|  | 0.2     | (0.2) | 1.7   | (1.0) | 2.6     | (0.9)  | 7.5   | (3.6)  |

Fig. 6. Densities of *Morula marginalba* and oysters *Saccostrea commercialis* at 3 heights on the shore and at different distances from crevices during the second experiment at Ulladulla. C = control; data pooled from control quadrats and those within 1 m of experimentally filled crevices (n = 9 quadrats of 0.25 m<sup>2</sup>); 6 and 12 indicate the means of 3 quadrats at 6 and 12 m from crevices. ● low-shore; ◆ mid-shore; ○ high-shore



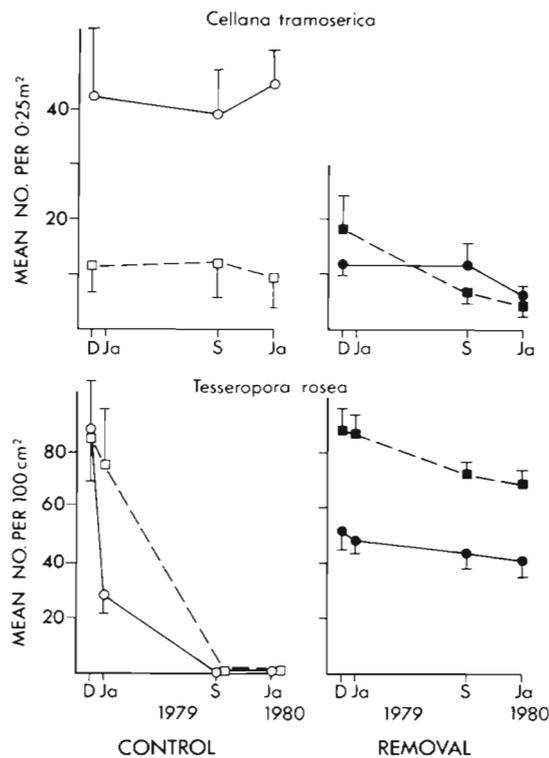


Fig. 7. Densities of limpet *Cellana tramoserica* and barnacle *Tesseropora rosea* in replicate areas with (control) and without (removal) whelks during the third experiment at Jibbon. Means (and S.E.) from 6 and 4 replicate quadrats for *C. tramoserica* and *T. rosea* respectively. ● ○ northern areas; ■ □ southern areas

in all analyses). The only exception was *Littorina unifasciata* which is discussed later. Thus, the 2 removal areas and the 2 control areas were generally similar to each other in terms of survival of prey. Most types of prey nevertheless showed marked decreases in the control areas where whelks were active. For example, the barnacle *Tesseropora rosea*

declined at different rates in the 2 control areas, but all were gone by September 1979 in both areas. Most were still alive at this time in the 2 areas where whelks were removed (Fig. 7). Where whelks were present, the limpet *Cellana tramoserica* maintained its densities, yet, even though there were differences in starting density, the numbers of limpets declined in both removal areas (Fig. 7) (see also Underwood et al., 1983).

The smaller limpet *Patelloida latistrigata* was absent from all 4 plots at the start of the experiment. There was, however, successful recruitment and survival of this limpet in the areas from which whelks were removed (Table 2), but very few or no limpets where whelks were present.

In the control plots, *Chthamalus antennatus* were decimated, yet in plots where *Morula marginalba* were removed, the densities increased because of survival of the original barnacles and recruitment (Table 2). Densities of *Chamaesipho columna* slightly decreased in numbers in all plots, indicating no effect of *M. marginalba* on survivorship in this experiment (Table 2). Similarly, there was no effect of whelks on survival of adult *C. columna* in plots where *Tesseropora rosea* had been removed, nor any direct effect on the smaller barnacles due to the *T. rosea* themselves (analysis of variance of proportional mortalities of adults,  $P > 0.05$ ; Table 3). The numbers of juvenile *C. columna* that had recruited and survived to the end of the experiment were greater in areas with *M. marginalba* than where the whelks were absent and were generally greater in the northern experimental areas than in the southern ones (analysis of variance of data in Table 3). The greater numbers of *C. columna* recruiting to the areas where whelks were active are attributable to the indirect effect of the whelks preventing pre-emption of the space by removing the larger *T. rosea*. Thus, where *T. rosea* continued to be abundant and to occupy space (in the removal areas),

Table 3. *Chamaesipho columna*. Densities (mean  $\pm$  S.E.) of adults and juveniles in areas with and without *Tesseropora rosea* and *Morula marginalba* at end of third experiment in January 1980 ( $n = 4$  replicate 100 cm<sup>2</sup> quadrats). Proportional mortality of juveniles not calculated because numbers of juveniles could not be counted reliably in photographs taken at start of experiment

| Species                            | Removal |       |       |       | Control |       |       |       |
|------------------------------------|---------|-------|-------|-------|---------|-------|-------|-------|
|                                    | North   |       | South |       | North   |       | South |       |
| Juvenile <i>C. columna</i> density |         |       |       |       |         |       |       |       |
| + <i>T. rosea</i>                  | 4.8     | (2.8) | 0     |       | 16.3    | (4.3) | 6.3   | (1.8) |
| - <i>T. rosea</i>                  | 6.5     | (3.8) | 1.3   | (1.3) | 21.0    | (2.3) | 8.3   | (1.4) |
| Adult <i>C. columna</i> density    |         |       |       |       |         |       |       |       |
| + <i>T. rosea</i>                  | 349     | (31)  | 351   | (43)  | 266     | (33)  | 319   | (18)  |
| - <i>T. rosea</i>                  | 391     | (29)  | 417   | (32)  | 280     | (64)  | 293   | (49)  |
| Proportional mortality of adults   |         |       |       |       |         |       |       |       |
| + <i>T. rosea</i>                  | 0.77    | (.07) | 0.88  | (.08) | 0.92    | (.11) | 0.82  | (.04) |
| - <i>T. rosea</i>                  | 0.98    | (.07) | 0.94  | (.03) | 0.85    | (.11) | 0.84  | (.10) |

fewer *C. columna* could settle. Where *M. marginalba* removed many of the *T. rosea*, there was more bare rock for settlement of *C. columna*.

Density of the highly mobile gastropod *Littorina*

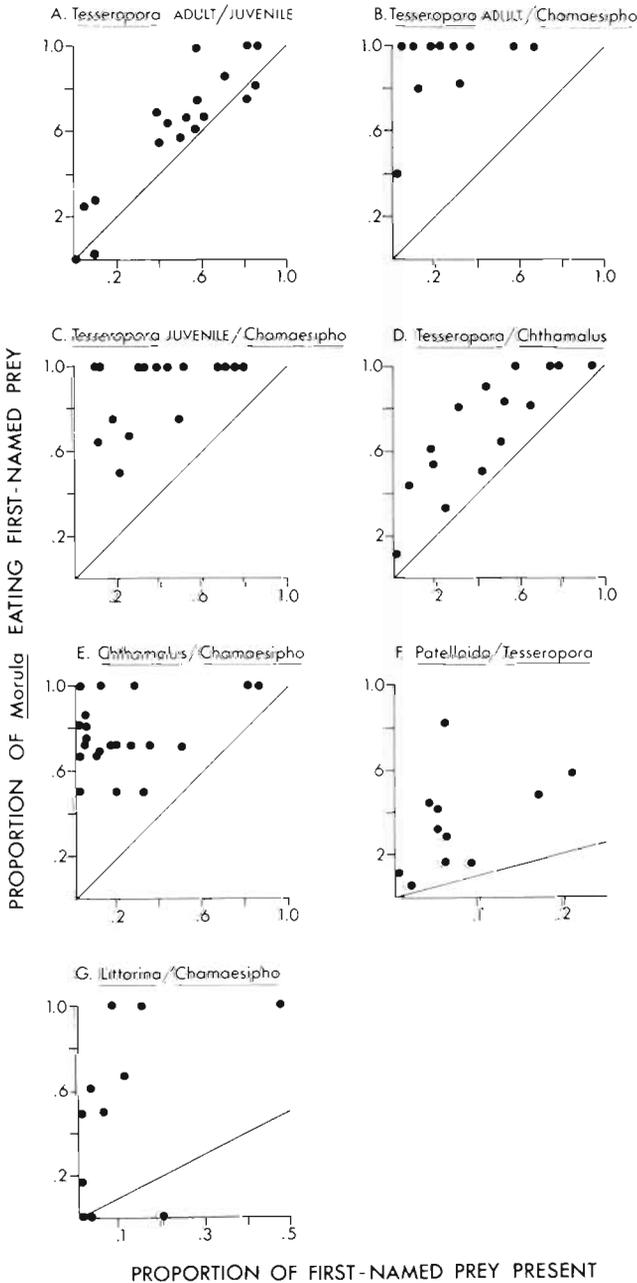


Fig. 8. *Morula marginalba*. Preferences for different types of prey. In each graph, data are presented as the proportion of whelks eating the first-named of a pair of prey plotted against the proportion of that prey in a quadrat. Each point represents a single quadrat ( $1/16 \text{ m}^2$ ) containing only the 2 indicated species or types of prey. Where this proportion for any quadrat is less than unity, the other whelks were eating the second-named prey in that quadrat. Quadrats were sampled after the end of the third experiment at Jibbon

*unifasciata* showed temporal and spatial variation (Table 2). Densities declined in areas with whelks, and increased where whelks had been removed. The only other species present was *Bembicium nanum*, which occurred patchily in sparse densities, and could not therefore be meaningfully analysed.

*Morula marginalba* exhibited strong preferences for particular prey when 2 prey species were found together, as indicated by the proportion of various prey consumed, relative to their availability (Fig. 8). The pairs of prey described represent common natural associations at certain heights on the shore. Some species were clearly preferred over others (e.g. *Tesseropora rosea* was preferred over *Chthamalus antennatus*; Fig. 8). The consumption of oysters, which co-existed in experimental plots with *Chamaesipho columna*, is not illustrated, because the preference for oysters by *M. marginalba* was absolute. Even though in very small relative abundances (0.04 to 0.1 % of all prey), all oysters were consumed by whelks, and the *C. columna* were untouched. Some species of prey were not eaten by whelks (e.g. *Cellana tramoserica*). *C. columna*, in particular, was not eaten, even though the barnacles were very abundant.

Such data suggest a hierarchy of preferences by the whelks. Oysters, *Patelloida latistrigata* and adult *Tesseropora rosea* were apparently very highly preferred; *Chthamalus antennatus*, *Littorina unifasciata* and juvenile *T. rosea* were consumed less, but were still highly preferred. In contrast, *Chamaesipho columna* and *Cellana tramoserica* ranked very low in the preferences shown by *Morula marginalba*.

## DISCUSSION

In the first experiment, the greatest mortality due to predation was sustained by the highly-preferred prey, the barnacle *Chthamalus antennatus*, then by the more abundant and widely distributed, but less-preferred *Chamaesipho columna* (Fig. 1 and 8 E). The decline in rates of mortality due to predation of *C. columna* with increasing height on the shore was probably due to the smaller density of the whelks at the higher levels, and decreased time available for foraging by these whelks during high tide. Rates of mortality of the 3 species of abundant gastropod were independent of the presence or absence of whelks. It is not clear why there was no measurable predation on juvenile *Bembicium nanum*, because whelks had been seen eating these snails. Most attacks by *Morula marginalba* on *B. nanum* were reliably observed (Fairweather and Underwood, 1983). Presumably the observations on predation tended to

overestimate its actual importance, or there was greater recruitment during the experiment into areas where whelks were present, so that juvenile snails were replaced as fast as they were consumed. The latter is an improbable explanation.

It is also possible that the differences in rates of mortality of prey between removal and control areas were not due to predation. By itself, this experiment cannot falsify the alternative hypothesis that the results were due to environmental differences between the 2 areas. Without replicate experimental and control areas, the removal of predators from a single area will always be confounded with any intrinsic variations between experimental and control sites. More extensive experimentation is required with adequate replication. This point is discussed later.

In the second experiment, filling in crevices reduced the density of *Morula marginalba*. This, in turn, affected the rate of extinction of newly settled oyster spat from this shore. The settlement of oysters was, however, eventually unsuccessful, and no oysters survived even in areas where crevices were filled, because this experimental treatment does not remove all of the predators. Perhaps experimental cages that totally exclude the whelks would have allowed the survival of some of the oysters. Note also that no part of the experimental area on this shore was further than 12 m from a crevice. It is probable that filling the crevices over a wider area would cause much greater reductions in the rate and intensity of predation because *M. marginalba* often forage over relatively short distances from their crevices (Moran, 1980).

Throughout the experiment, there was evidence that oysters, once settled in an area, would overgrow the smaller barnacles. There was no recruitment of oysters in the year following the experiment, and no attempts have yet been made to test whether oysters and *Chamaesipho columna* would compete for eventual domination of the space on the shore. It is possible that the dominance of *C. columna* observed on similar shores is brought about by the selective predation of the oysters by *Morula marginalba* (see other examples in Underwood et al., 1983). Settlement of oysters is, however, very patchy in space and time (unpubl. own observations); it is unlikely that competitive elimination of *C. columna* by oysters would occur very often, even if whelks were absent.

Again, the results of the second experiment confirmed the effects of predation with those due to individual environmental characteristics of the unreplicated control and experimental areas. The nature of the results, and comparison with the trends during the first experiments strongly support the interpretation that the results were, in fact, due to predation.

Dead oysters with drill-holes characteristic of

*Morula marginalba* in their upper valves were found at all times during the experiment at all levels on the shore. Thus, many oysters were eaten within a very short period after settlement. The actual number settling is thus vastly underestimated in our data, due to the rapid early mortality (Keough and Downes, 1982). No *Chamaesipho columna* were seen being eaten, and there was no evidence of predation on these barnacles during this second experiment.

The data presented suggest that predation by *Morula marginalba* was more intense on oysters at lower levels on the shore (Fig. 6). Because of the relatively long period between samples, and the apparently rapid predation of the oysters where whelks were abundant, oysters could have settled low on the shore, or near crevices and been consumed before they were recorded. Alternatively, the decreased densities of oysters could be due to decreased settlement at lower levels on the shore. This second suggestion is supported by the fact that more small oysters have been found at high levels than at low levels in areas where whelks were naturally absent. The potential differences in recruitment at different heights need further investigation (see also Underwood and Denley, 1984).

Although the effect of height on the shore could be interpreted as merely a gradient in the intensity of settlement of the oysters, the effects of distance from a crevice are unlikely to be. Predation on these oysters was observed in the field, and the pattern of mortality must be interpreted as a combination of the rates of settlement and the effects of the whelks. Higher and further from crevices, cumulative spatfall was eventually greater than cumulative predation as the period of settlement progressed (October to December). After settlement ceased, however, the density of oysters declined because of predation. There was, however, some other unknown factor involved in the decline of oysters. Note that the oysters disappeared after April 1978 most quickly from the areas where whelks were in very small numbers (i.e. high on the shore and 12 m from crevices; Fig. 6). We can offer no particular explanation for non-predatory sources of mortality of these oysters, but desiccation and other factors associated with prolonged periods of emersion are possible causes of death. This phenomenon requires further study.

In the third experiment at Jibbon, the highly preferred prey (*Patelloida latistrigata*, *Tesseropora rosea*, *Chthamalus antennatus*) were heavily affected by whelks while others not so preferred (e.g. *Chamaesipho columna* and *Cellana tramoserica*; Fig. 8; Fairweather and Underwood, 1983; Underwood et al., 1983) were unaffected by the presence of *Morula marginalba*. The increase numbers of *C. tramoserica* in

areas where whelks were present are attributable to the predatory removal of the barnacles, thus freeing bare rock over which the limpets could graze (see the detailed experiments and observations of this phenomenon in Underwood et al., 1983). It is notable that recruitment of *C. columna* was variable, and differed significantly between the northern and southern study sites (Table 3).

In this experiment, all decreases in mortality in removal areas can be reliably interpreted as being due to the removal of whelks, because significant results were obtained despite heterogeneity between the replicate areas. In our first 2 experiments, and in many published accounts of experimental manipulations of predators, no replication of study sites was included in the design of the experiments. Thus, no unequivocal conclusions may be reached about the importance of predation because alternative sources of mortality of prey may differ markedly between a single control and a single experimental site. We overcame this problem in our third experiment, and obtained results that support the conclusions reached from our earlier 2, weaker experiments. This has sadly not been the general rule for this type of investigation (see for example Paine, 1966, 1974; Garrity and Levings, 1981).

Where experimental installations are used to exclude predators from small replicated plots within a single study site (e.g. Connell, 1970), comparison with unmanipulated small plots in the same site allows estimation of the role of predators. Because of the lack of spatial replication from one study site to any others, such results cannot serve as the basis for broad generalizations about the effects of predators.

The results for *Littorina unifasciata* were ambiguous in that the increased densities in the northern area where whelks were absent (compared with the control area) and the decrease in the southern area where whelks were present could have been caused by several different processes. These include: (a) a true effect of predation (i.e. the *L. unifasciata* declined in numbers because they were eaten by whelks) but only in the southern area; (b) greater immigration of snails into the northern area where whelks had been removed (but not into the southern area); (c) a similarly discrepant difference in the numbers of recruiting small snails into the 2 areas. Another possibility is avoidance behaviour by the littorinids in some areas to escape from contact with the whelks (this has been observed in the field by Fairweather, unpubl.; see also McKillup, 1982). Few littorinids were seen being eaten by whelks during the experiments, but this is unreliable evidence for the importance of predation (Fairweather and Underwood, 1983). No clear explanation can be offered for the results for this snail without more frequent sampling and observation in larger plots dur-

ing the experiment, and without proper estimation of the diets of the whelks in the various areas (as discussed by Fairweather and Underwood, 1983). These data are unavailable for the present series of experiments, and the various competing hypotheses cannot be distinguished.

The trends in density of *Patelloida latistrigata* at Jibbon during the third experiment could possibly also be explained by greater intensity of settlement of these limpets in areas without whelks. Newly settled *P. latistrigata* were not counted; this is extremely difficult because the limpets cannot be identified until they reach some 2 mm shell length (Creese, 1982). Numerous observations of *Morula marginalba* eating very small *P. latistrigata* have, however, been made, and the difference in density between control and experimental areas was almost certainly due to predation. This is entirely consistent with other accounts of the interaction between *M. marginalba* and *P. latistrigata* (Creese, 1982; Fairweather and Underwood, 1983; Underwood et al., 1983; Fairweather, in prep.).

The measures of preference among prey by *Morula marginalba* are crude (Fig. 8), but these agree with subsequently obtained more extensive analyses (Fairweather, unpubl.). Any bias in the sampling of whelks eating the different species, because of differences in the handling times of the various prey (Fairweather and Underwood, 1983), would cause underestimation of the preference by whelks for *Patelloida latistrigata* and *Littorina unifasciata* (the prey with the shortest handling times). *M. marginalba* take a similar amount of time to handle individuals of all the other species (Fairweather and Underwood, 1983; Fairweather, unpubl.). Hence bias for other species is minimal, and the suggested preference rankings by the whelks are probably more accurate. The results of the various removal experiments can be understood more completely in the light of the hierarchy of preference for the different types of prey. For example, the lack of predation on *Chamaesipho columna* in the third experiment, in contrast to the situation during the first experiment at Ulladulla, can probably be explained in terms of the other types of prey available during the 2 experiments. During the third experiment, there were numerous alternative and more highly preferred species on the shore, compared with the situation during the first experiment. Thus, whelks concentrated on other prey (juvenile or adult *Tesseropora rosea*, *Chthamalus antennatus*, or *L. unifasciata*; Fig. 8 B, C, E, G) so that relatively few *C. columna* were eaten in comparison to their relative abundance in the experimental quadrats. Note, however, that there was still no evidence for any competitive interference between *T. rosea* and *C. columna*. The presence of *T. rosea* made no difference to the survival of *C. columna*. The

only interaction between these 2 species was that of pre-emption of space by the larger *T. rosea* in the third experiment, thus influencing the recruitment of the smaller *C. columna*.

Thus, there was no evidence in any of the 3 experiments of a 'keystone' effect of the whelks (Paine, 1969). This is presumably because of the lack of intense competition between highly preferred prey (such as *Tesseropora rosea*) and prey that are consumed much less readily (such as *Chamaesipho columna*). The only possibility for such competitive interactions was the observation of overgrowth of *C. columna* by oysters during the second experiment at Ulladulla. Clearly, the effects of predation revealed by the present introductory experiments varied with location. Although much of this could be attributable to the different unmeasured environmental regimes at the various sites and during the different periods investigated, it is also partially a function of the differences in availability of prey in the different experiments. Within a shore, the distributions of prey, and the effects of predators were not even (see particularly the differences at different heights in the first 2 experiments). Much of the variations in results can probably be explained by patterns of recruitment as well as patterns of predation (Underwood and Denley, 1984; Underwood et al., 1983).

The spatial and temporal variations in effects of intertidal predators have not received much attention. Menge (1976) and Lubchenco and Menge (1978), however, demonstrated that the effect of *Thais lapillus* varied considerably over a number of shores. This was attributed to a combination of various factors (particularly wave-action) that modified the voracity and foraging of the whelks (Menge, 1978a, b, 1983). In his study sites on the east coast of the USA, only 2 species of prey (1 barnacle and 1 mussel) were present. The present studies on relatively sheltered shores suggest that future experimentation should also consider another source of variation among sites – the spatial differences in availability of different species of prey. In other studies, Menge (1972a) showed that the foraging strategy of a predatory starfish responded to the predictability of the availability of prey. Apparently *Morula marginalba* shows responses to large, unpredictable variations in recruitment of a number of types of prey (Underwood and Denley, 1984; Underwood et al., 1983; Fairweather, in prep.). In contrast, Dayton (1971) and Paine (1974) documented no, and relatively little variation in the effect of a predatory starfish and various whelks, respectively, in the Pacific Northwest.

The temporal variations in densities of *Morula marginalba* at Ulladulla (Fig. 6) are consistent with movements of the whelks from crevices in search of food (Moran, 1980). Crevices are clearly important for some

intertidal grazers and predators. For example, Levings and Garrity (1983) used concrete and urethane to fill crevices to exclude the herbivore *Nerita funiculata*. The grazing activities of this snail varied with distance from the crevices. The present experiments demonstrate the importance to *Morula marginalba* of crevices for shelter, and suggest that the availability of crevices is an important factor in experiments on the effects of intertidal predators (see also Menge, 1978a, b; Garrity and Levings, 1981; Underwood and Denley, 1984).

The present experiments also revealed that manual removals of *Morula marginalba* were reasonably effective: densities of whelks indicated a reduction of 85 to 90 % in removal areas (Tables 1 and 2). We conclude that this technique is preferable to the use of experimental installations, because manual removal of predators does not cause any of the potential artefacts associated with the commonly-used installations (Underwood and Denley, 1984; Underwood et al., 1983). The manual removals at Jibbon were most effective, suggesting a need for monitoring the experimental areas every 2 weeks to remove *M. marginalba* that had immigrated since the last removal.

In the experiment at Jibbon, we obtained, for different species of prey, several of a potential range of possible results (i.e. no effect of predators through to elimination of some or all species of prey on the shore). We did not observe elimination by predators of any species in the first experiment at Ulladulla, probably because lesser preferred prey were the only ones available. In contrast, when a highly preferred prey (oysters) settled in relatively small numbers during the second experiment on nearby shores, they were rapidly eliminated within a few months of recruitment.

Predation in this community thus appears very dynamic, and not as static as the picture painted for other communities in some recent literature (e.g. Connell, 1961, 1970; Paine, 1974; Menge, 1976). The case of *Chamaesipho columna* indicates that at different places (Ulladulla and Jibbon) and at different times (1977 and 1979 at Ulladulla), a species of prey may suffer no predation, or may incur heavy losses. In all cases, predators were foraging. What appeared to be of great importance for the interpretation of the effects of these predators on the prey was the availability of other, more highly preferred prey (such as *Saccostrea commercialis*, *Patelloida latistrigata*, *Tesseropora rosea*). The role of preferences by the predator, and differences in abundances or sizes of different species of prey on shores in New South Wales will be investigated elsewhere. In addition, the indirect effects of predation (such as the reduced rates of grazing where *Morula marginalba* consume *Littorina unifasciata* and *P. latistrigata*) have not yet been fully investigated for this system (see the experimental work of Jernakoff,

1983). Previous investigations of the structure of local communities indicate strong interactions between species of prey (Underwood et al., 1983). In cases where density, growth and life-history of the predator also vary in accordance with the availability of different types of prey (Moran et al., 1984), the analysis of predation becomes even more complex. Preliminary studies such as those described here, and the detailed analyses provided by Menge (1983), should, however, allow a considerably better understanding of the predatory interactions to enable meaningful future experimentation.

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#### LITERATURE CITED

- Chesson, J. (1978). Measuring preference in selective predation. *Ecology* 59: 211–215
- Cock, M. J. W. (1978). The assessment of preference. *J. Anim. Ecol.* 47: 805–816
- Connell, J. H. (1961). The effect of competition, predation by *Thais lapillus* and other factors on natural populations of the barnacle *Balanus balanoides*. *Ecol. Monogr.* 31: 61–104
- Connell, J. H. (1970). A predator-prey system in the marine intertidal region. I. *Balanus glandula* and several predatory species of *Thais*. *Ecol. Monogr.* 40: 49–78
- Connell, J. H. (1975). Some mechanisms producing structure in natural communities: a model and evidence from field experiments. In: Cody, M. L., Diamond, J. M. (ed.) *Ecology and evolution of communities*. Harvard University Press, Cambridge, p. 460–490
- Creese, R. G. (1982). Distribution and abundance of the acmaeid limpet *Patelloida latistrigata*, and its interaction with barnacles. *Oecologia (Berl.)* 52: 85–96
- Creese, R. G., Underwood, A. J. (1976). Observations on the biology of the trochid gastropod *Austrocochlea constricta* (Lamarck) (Prosobranchia). I. Factors affecting shell-banding. *J. exp. mar. Biol. Ecol.* 23: 211–228
- Dakin, W. J. (1950). *Australian seashores*. Angus & Robertson, Sydney
- Dayton, P. K. (1971). Competition, disturbance and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecol. Monogr.* 41: 351–389
- Fairweather, P. G., Underwood, A. J. (1983). The apparent diet of predators and biases due to different handling times of their prey. *Oecologia (Berl.)* 56: 169–179
- Feare, C. J. (1971). The adaptive significance of aggregation behaviour in the dogwhelk *Nucella lapillus* (L.). *Oecologia (Berl.)* 7: 117–126
- Garrity, S. D., Levings, S. C. (1981). A predator-prey interaction between two physically and biologically constrained tropical rocky shore gastropods – direct, indirect and community effects. *Ecol. Monogr.* 51: 267–286
- Jernakoff, P. (1983). Factors affecting the recruitment of algae in a midshore region dominated by barnacles. *J. exp. mar. Biol. Ecol.* 67: 17–31
- Keough, M. J., Downes, B. J. (1982). Recruitment of marine invertebrates: the role of active choices and early mortality. *Oecologia (Berl.)* 54: 348–352
- Kitching, J. A., Muntz, L., Ebling, F. J. (1966). The ecology of Lough Ine: XV. The ecological significance of shell and body forms in *Nucella*. *J. Anim. Ecol.* 35: 113–136
- Levings, S. C., Garrity, S. D. (1983). Diel and tidal movement of two co-occurring neritid snails: differences in grazing patterns on a tropical rocky shore. *J. exp. mar. Biol. Ecol.* 67: 261–278
- Lubchenco, J. (1978). Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. *Am. Nat.* 112: 23–29
- Lubchenco, J., Menge, B. A. (1978). Community development and persistence in a low rocky intertidal zone. *Ecol. Monogr.* 48: 67–94
- McKillup, S. C. (1982). The selective advantage of avoidance of the predatory whelk *Lepsiella vinosa* (Lamarck) by *Littorina unifasciata* (Phillippi). *J. exp. mar. Biol. Ecol.* 63: 59–66
- Menge, B. A. (1972a). Foraging strategy of a starfish in relation to actual prey availability and environmental predictability. *Ecol. Monogr.* 42: 25–50
- Menge, B. A. (1972b). Competition for food between two intertidal starfish species and its effect on body size and feeding. *Ecology* 63: 635–644
- Menge, B. A. (1976). Organization of the New England rocky intertidal community: role of predation, competition and environmental heterogeneity. *Ecol. Monogr.* 46: 355–393
- Menge, B. A. (1978a). Predation intensity in a rocky intertidal community. Relation between predator foraging activity and environmental harshness. *Oecologia (Berl.)* 34: 1–16
- Menge, B. A. (1978b). Predation intensity in a rocky intertidal community. Effect of an algal canopy, wave action and desiccation on predator feeding rates. *Oecologia (Berl.)* 34: 17–35
- Menge, B. A. (1983). Components of predation intensity in the low zone of the New England rocky intertidal region. *Oecologia (Berl.)* 58: 141–155
- Menge, B. A., Lubchenco, J. (1981). Community organization in temperate and tropical rocky intertidal habitats – prey refuges in relation to consumer pressure gradients. *Ecol. Monogr.* 51: 429–450
- Menge, B. A., Sutherland, J. P. (1976). Species diversity gradients: synthesis of the roles of predation, competition, and temporal heterogeneity. *Am. Nat.* 110: 351–369
- Moran, M. J. (1980). Ecology and effects on its prey of the intertidal predatory whelk *Morula marginalba* Blainville. Unpublished Ph. D. thesis, University of Sydney
- Moran, M. J., Fairweather, P. G., Underwood, A. J. (1984). Growth and mortality of the predatory intertidal gastropod *Morula marginalba* Blainville (Muricidae): the effects of different species of prey. *J. exp. mar. Biol. Ecol.* 75: 1–17
- Paine, R. T. (1966). Food web complexity and species diversity. *Am. Nat.* 100: 65–75
- Paine, R. T. (1969). The *Pisaster-Tegula* interaction: prey patches, predator food preference, and intertidal community structure. *Ecology* 50: 950–962
- Paine, R. T. (1971). A short-term experimental investigation of resource partitioning in a New Zealand intertidal habitat. *Ecology* 52: 1096–1106

- Paine, R. T. (1974). Intertidal community structure. Experimental studies on the relationship between a dominant competitor and its principal predator. *Oecologia (Berl.)* 15: 93-120
- Paine, R. T. (1977). Controlled manipulations in the marine intertidal zone, and their contributions to ecological theory. In: *The changing scenes in natural sciences, 1776-1976*. Acad. Nat. Sci. Special Publication 12: 245-270
- Paine, R. T. (1980). Food webs: linkage, interaction strength and community infrastructure. *J. Anim. Ecol.* 49: 667-685
- Peterson, C. H. (1979). The importance of predation and competition in organizing the epifaunal communities of Barnegat Inlet, New Jersey. *Oecologia (Berl.)* 39: 1-24
- Underwood, A. J. (1974). The reproductive cycles and geographical distribution of some common Eastern Australian prosobranchs (Mollusca: Gastropoda). *Aust. J. mar. Freshwat. Res.* 25: 63-88
- Underwood, A. J. (1975). Comparative studies on the biology of *Nerita atramentosa* Reeve, *Bembicium nanum* (Lamarck) and *Cellana tramoserica* (Sowerby) (Gastropoda: Prosobranchia) in S. E. Australia. *J. exp. mar. Biol. Ecol.* 19: 153-172
- Underwood, A. J. (1981). Structure of a rocky intertidal community in New South Wales: patterns of vertical distribution and seasonal changes. *J. exp. mar. Biol. Ecol.* 51-85
- Underwood, A. J., Denley, E. J. (1984). Paradigms, explanations and generalizations in models for the structure of intertidal communities on rocky shores. In: Strong, D. R., Simberloff, D. S., Abele, L. G., Thistle, A. B. (ed.) *Ecological communities: conceptual issues and the evidence*. Princeton University (in press)
- Underwood, A. J., Denley, E. J., Moran, M. J. (1983). Experimental analysis of the structure and dynamics of mid-shore rocky intertidal communities in New South Wales. *Oecologia (Berl.)* 56: 202-219

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