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# Desiccation, predation, and mussel-barnacle interactions in the northern Gulf of California

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**Summary.** Field experiments were conducted in order to determine the potential for desiccation and predation to mediate the effect of mussels (*Brachidontes semilaevis*) on barnacles (*Chthamalus anisopoma*) in the highly seasonal northern Gulf of California. We did this by removing both mussels and a common mussel predator (*Morula ferruginosa*: Gastropoda) and by spraying selected sites with sea water during summertime spring low tides. We also determined the effect of crowding on resistance to desiccation in barnacles, and the effect of barnacles on colonization by mussels. The mussel-barnacle community was not affected by keeping experimental quadrats damp during daytime low tides throughout the summer. Exposure to summertime low tides, however, did affect the survivorship of isolated, but not crowded, barnacles; and barnacle clumps enhanced the recruitment of mussels. Hence crowding in barnacles had a positive effect on both barnacle survivorship and mussel recruitment. *Morula* had a negative effect on mussel density, and mussels had a negative effect on barnacle density. The effect of *Morula* on barnacle density was positive, presumably due to its selective removal of mussels. These results suggest an indirect mutualism between barnacles and the gastropod predator, because barnacles attract settlement or enhance the survival of mussels, and the predator reduces the competitive effect of mussels on barnacles.

**Key words:** Barnacles – Competition – Desiccation – Mussels – Predation

Studies of structure in marine, freshwater, and terrestrial communities have demonstrated that competition (reviews in Connell 1983; Schoener 1983), predation (e.g. Connell 1961; Paine 1966a, 1971, 1974; review in Sih et al. 1985), physical stress (e.g. Bertness 1981; Garrity and Levings 1981; review in Connell 1972), disturbance (e.g. Dayton 1971; Connell 1978; Sousa 1979; review in Sousa 1984) and recruitment patterns (e.g. Sale 1977; Connell 1985; Raimondi unpublished work) are all factors which contribute to the coexistence of multiple interacting species. A number of these studies have successfully combined the concomitant effects of several of these factors (e.g. Dayton 1971; Menge 1976, 1978a, b; Lubchenco 1978; Morin 1983; review in Sih et al. 1985), and some recent experiments have elucidated significant indirect effects among species, which result from interactions between competition and predation (e.g. Lubchenco 1978; Dethier and Duggins 1984; Davidson et al. 1984; Dungan 1986, 1987). In the present study, we evaluated the effects of competition, predation, and temporally variable physical stress on an intertidal mussel-barnacle community in the highly seasonal northern gulf of California.

The rocky intertidal region in the northern Gulf of California is unique in several interesting ways, which makes it an excellent place to test current generalizations regarding the mechanisms underlying the structure of such communities (see Underwood and Denley 1984). For example, the two major barnacle species are zoned "upside down"; that is the larger species (*Tetraclita*) is zoned above the smaller species (*Chthamalus*), rather than below as is usually the case (Dungan 1985). Similarly, the mid-intertidal mussel population (*Brachidontes semilaevis*) differs from the well-studied *Mytilus* populations of more temperate shores in several ways: (1) *Brachidontes* are small (< 10 mm); (2) they are distributed throughout the barnacle zone; and (3) they are generally somewhat rare (see also Menge and Lubchenco 1981). Observations of permanent quadrats between 1980 and 1986 indicated a trend for *Brachidontes* to undergo a recruitment pulse during the early summer, then die back during the late summer; a decrease in barnacle (*Chthamalus anisopoma*) densities corresponds with this early-summer increase by mussels (Lively, Raimondi and Delph, unpublished work). During a particularly large settlement in 1981, *Brachidontes* was observed at one site to go from being rare (< 5% cover) in the early summer to being abundant (> 70% cover) by mid summer, overgrowing the barnacle population in the process. By late summer the mussels had disappeared, leaving bare rock.

In the present study, we tested three hypotheses (in their null forms) regarding these observations: (1) mussels are killed in the late summer by desiccation; (2) the pulse in mussel settlement temporarily swamps the ability of a gastropod predator to harvest them; and (3) mussels outcompete barnacles in the absence of (a) predation and/or (b) desiccation. We also determined the effect of crowding in barnacles on their resistance to desiccation, and the presence of barnacles on settlement by mussels.

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*Study site and species descriptions*

The northern Gulf of California is a highly seasonal marine environment, a result of its shallowness and the influence of the surrounding Sonoran Desert (Hendrickson 1973; Brusca 1980). In addition, waves are generally small and the days clear, so there is little protection from stress imposed by the atmosphere during daytime low tides. Thomson and Lehner (1976) recorded air temperatures below 0° C in the winter and above 40° C in the summer (see also Hendrickson 1973), and we have recorded rock surface temperatures as high as 52° C during the summer.

*Chthamalus anisopoma* is a small acorn barnacle (maximum diameter 7 mm) that dominates space in the mid-intertidal throughout the Gulf of California, and commonly occurs in densely packed aggregations (Dungan 1985, 1986; Lively 1986a). Such aggregations reduce growth rates and enhance the probability of removal by wave action, but there is no significant adult mortality that results directly from crowding (Lively 1986b; see also Luckens 1975). The barnacle ranges from about 0–1.8 m above mean low water (MLW) in the northern Gulf of California (Dungan 1985).

*Brachidontes semilaevis* is a small intertidal mussel (maximum length approximately 10 mm) that overlaps with *Chthamalus*; and like the barnacle (see Malusa 1986; Dungan 1986), it shows a peak in recruitment during the summer months. It is the preferred prey of the small (approximately 12 mm) gastropod *Morula ferruginosa* (Raimondi, unpublished work). *Morula* forages when inundated and is less restricted to cracks and crevices than is *Acanthina* (Lively 1986a), which forages during periods of tidal exposure and specializes on barnacles (Paine 1966b; Dungan 1987).

The experiments that follow were conducted on rocky intertidal shores in the northern Gulf of California near the town of Puerto Peñasco (31°20′N, 113°40′W), Sonora, Mexico (see Malusa 1986 for a location map). The barnacle desiccation experiment was conducted at Playa Las Conchas (Shell Beach), a limestone reef with basalt boulders 5 km east of Puerto Peñasco. The remaining experiments were conducted at Punta Pelicano (Pelican Point), a granitic headland 10 km northwest of Puerto Peñasco. Both study sites were on horizontal shelves having direct exposure to wave action.

## Methods and materials

*Competition and desiccation.* In order to determine whether mussels are killed in the late summer by desiccation, and whether mussels outcompete barnacles in the absence of such stress, we established sixteen 10 × 10 cm quadrats (on 25 May 1982) at Pelican Point at each of two areas at site "A" (+1 m above MLW). The corners of the quadrats were marked using a marine epoxy, and the quadrats were randomly assigned to be one (of four) replicates of the following four treatments: (1) mussels removed (using tweezers), and the quadrat kept moist during spring low tides by periodically spraying with fresh seawater; (2) mussels removed, but the quadrat not sprayed during low tides; (3) quadrat sprayed, but mussels not removed; and (4) quadrats not sprayed, and mussels not removed (see Table 1). The quadrats were sampled after six and twelve wks by using a clear plexiglass plate with 100 randomly placed dots in a 10 cm × 10 cm area, and by counting the number of dots directly over barnacles and mussels in each quadrat, to give an estimate of the percentage of rock surface covered by each (after Connell 1970).

**Table 1.** The design of the competition, predation, and desiccation experiment, giving the number of quadrats in sites A and B for each of the four treatments in the predator removal and predator control areas

| Treatment | Predator removal area | Predator control area |
|---|---|---|
| Site A | | |
| 1. Mussel removal, spray | 4 | 4 |
| 2. Mussel removal, no spray | 4 | 4 |
| 3. Mussel control, spray | 4 | 4 |
| 4. Mussel control, no spray | 4 | 4 |
| Site B | | |
| 4. Mussel control, no spray | 4 | 4 |

We assessed the potential effect of natural wave splash on our quadrats by recording the time of inundation at site A and comparing this to the time of inundation at a protected site at the same tidal height. The difference between the two times served as an indication of the effect of natural wave action on reducing exposure time.

*Predation.* To determine the effect of predation by *Morula* on the mussel-barnacle community, we manually removed it from one (randomly selected) of the two areas at site A once each day during spring low tides. To replicate the *Morula* removal in space, we established another four quadrats on 7 July 1982 at each of two additional areas at a second site, site "B" (also +1 m above MLW), and we removed *Morula* from the vicinity of one of the areas (randomly selected); the quadrats at site B were sampled six wks later using the random-dot method described above. A third site ("C") was also established, but it was later abandoned because we were unable to decrease the densities of foraging *Morula* in the removal area.

Note that, unlike the mussel removal and spray treatments, the quadrats could not be randomly assigned with respect to the *Morula* removal treatment [We used manual removals instead of cages, because *Morula* are small enough to pass through standard mesh sizes large enough to prevent cage effects (personal observations)]. The layout of quadrats is summarized in Table 1.

We assessed the effectiveness of the *Morula* removals at site A three times during the course of the experiment by using snorkeling equipment. When the site was inundated by approximately 2 m of water, we dropped a stainless steel ring (diameter: 30.5 cm) from the surface onto the removal and control areas at site A, and we counted all *Morula* within the ring. A sample consisted of four replicates of this procedure within each area. A datum was considered to be the average of these four replicates. The mean density of *Morula* for the three samples in the control area was 105 $m^{-2}$ (SE = 20.52). This was significantly greater than the mean density ($\bar{x} = 1.13$; SE = 1.13) in the removal area (paired $t = 5.13$; d.f. = 2; $P < 0.025$). Hence, the manual removals of *Morula* were effective in reducing its densities during spring low tides. This predator, however, reinvaded the removal areas during neap tidal series; so we reduced, but did not eliminate the effects of predation.

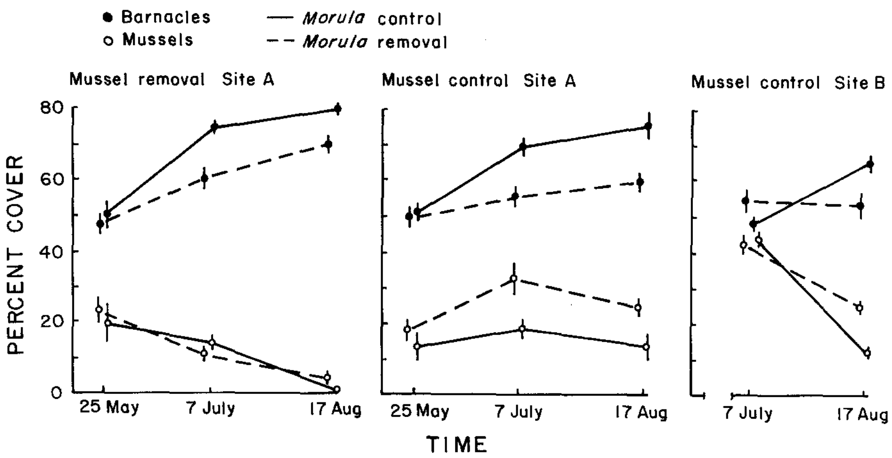


Fig. 1. Mean percentages of rock substrate covered by mussels and barnacles in the mussel and *Morula* removal treatments. Both sprayed and unsprayed quadrats at site A were included in the calculation of the means at site A, because the effects of spray were not significant ($P > 0.49$, Table 2). Vertical bars are ± SE

**Table 2.** ANOVA summary for the percentages of quadrats covered by mussels and barnacles at the end of the mussel removal/spray experiment. Data from site A

| Source | d.f. | Predator (*Morula*) removal area | | Predator (*Morula*) control area | |
|---|---|---|---|---|---|
| | | MS | *P* | MS | *P* |
| | | | Mussels | | |
| Main effects | | | | | |
| Spray | 1 | 5.06 | 0.748 | 36.06 | 0.495 |
| Mussel removals | 1 | 1743.06 | <0.001 | 588.06 | 0.012 |
| Interaction | 1 | 3.06 | 0.802 | 0.06 | 0.976 |
| Error | 12 | 46.65 | | 66.81 | |
| | | | Barnacles | | |
| Main effects | | | | | |
| Spray | 1 | 5.06 | 0.825 | 4.00 | 0.819 |
| Mussel removals | 1 | 390.06 | 0.071 | 72.25 | 0.340 |
| Interaction | 1 | 105.06 | 0.324 | 90.25 | 0.288 |
| Error | 12 | 99.19 | | 73.13 | |

*Crowding and desiccation in barnacles.* Keeping selected quadrats moist during low tides in the previous experiments had no effect on the mussel-barnacle community. This suggests the hypothesis that the closely-packed aggregations of barnacles (which characterized our study sites) might modify the environment in a way which is beneficial to both barnacles and mussels. To test the idea that crowded barnacles have a greater resistance to desiccation than isolated barnacles, we placed six basalt boulders having isolated *Chthamalus* together in the intertidal zone at Shell Beach. On each boulder, 15–20 individuals of comparable size were selected and marked by placing a dab of nail polish nearby on the boulder. All individuals selected were at least 1 cm from their nearest conspecific. A second set of six boulders was collected, which had clumps of individuals in direct contact. Two such clumps, with a minimum of 20 adults in each, were marked as above on all six boulders. One boulder from each of the two "treatments" was then randomly assigned one of the following times for inundation: 10:30, 11:00, 11:30, 12:00, 12:30, and 13:00 hours. Time at emersion was at about 06:00, so exposure time ranged from 4.5 to 7 h, which approximated the maximum summertime exposure period for 1983 (see Thomson 1983). Following inundation, which was simulated by dunking the boulders in a tidepool, the number of surviving barnacles was counted by recording the number of feeding individuals. Individuals that did not feed within 5 mins of inundation were counted as dead (a further check on one set of boulders after 24 h in natural conditions gave the same results as did the 5 min census). The experiment was conducted on 27 July and repeated on 12 August, 1983.

*Barnacles and mussel recruitment.* The association between barnacles and mussels might be due, in part, to higher recruitment of mussels into areas containing barnacles (see Dayton 1971; Paine 1974; Menge 1976). To test this hypothesis, we established eight replicates of each of the following four treatments at Pelican Point during the summer of 1984: (1) mussels removed, barnacles unmanipulated, (2) mussels removed, barnacles killed and their shells removed, (3) mussels removed, barnacles killed but their shells not removed, and (4) both mussels and barnacle unmanipulated. The treatments were performed on 5 × 5 cm quadrats, which were sampled every two wks using 25 random dots in the manner discussed above.

## Results

*Competition and desiccation.* The spray treatment had no significant effect on mussels or barnacles in either the predator removal area or the predator control area at site A (Table 2). There was also no significant spray × mussel-removal interaction effect in either area. Hence, desiccation would not appear to explain the late summer decline in mussels. In addition, there was no recruitment of algae to the quadrats which we kept moist during tidal exposure, suggesting the absence of algal spores during the summer or the requirement of shade for summertime colonization by algae.

The lack of response to the spray treatment would not appear to result from natural wetting due to wave action. The quadrats at site A were wetted by the incoming tide a mean of only 6.05 (SE = 4.73, $N = 39$) min before the protected site at the same tidal height. A mean air temperature of 32.51° C (SE = 0.43) was recorded just prior to inundation of site A, following morning spring low tides.

The removal of mussels, by contrast, had a marginally significant and positive effect on barnacles in the predator removal area at site A; but no such effect was observed in the predator control area (Fig. 1, Table 2).

**Table 3.** ANOVA summary and multiple range test for the desiccation experiment. Means are from untransformed data. Statistical analysis performed on transformed data (arcsine squareroot, see Zar 1974)

| Source | d.f. | MS | $P$ |
|---|---|---|---|
| Main effects | | | |
| Time | 5 | 301.07 | 0.010 |
| Isolation | 1 | 1633.50 | <0.001 |
| Interaction | 5 | 255.20 | 0.018 |
| Error | 12 | 59.92 | |

| Time of inundation | Means | |
|---|---|---|
| | Crowded | Isolated |
| 10:30 | 99[a] | 96.5[ab] |
| 11:00 | 100[a] | 96.5[ab] |
| 11:30 | 100[a] | 96.5[ab] |
| 12:00 | 100[a] | 97.5[ab] |
| 12:30 | 99[ab] | 54.0[c] |
| 13:00 | 100[a] | 66.0[bc] |

Means with the same superscript are not significantly different (i.e. $P>0.05$) by a least significant difference test

**Table 4.** ANOVA summary multiple range test for the percentages of quadrats covered by mussels in the mussel settlement experiment. Statistical tests performed on transformed data (arcsine squareroot); means are from untransformed data

| Source | d.f. | MS | $P$ |
|---|---|---|---|
| Treatment | 3 | 1346.89 | $\ll 0.001$ |
| Error | 24 | 23.14 | |

| Treatment (no) | $\bar{x} \pm$ Se | Grouping* |
|---|---|---|
| Dead barnacles (3) | $33.00 \pm 2.10$ | a |
| Live barnacles (1) | $20.00 \pm 1.85$ | b |
| Control (4) | $18.50 \pm 2.26$ | b |
| Bare rock (2) | $1.33 \pm 0.71$ | c |

* Means with the same letter are not significantly different by a least significant difference test

*Predation.* Mussels declined during the last twelve wks of the experiment at both sites A and B (Fig. 1), but there were significant differences between predator removal and predator control areas at both sites at the end of the experiment. At site A, for quadrats in which mussels were not removed, mussels were significantly more common ($t=2.37$, d.f. $=14$, $p=0.006$), and barnacles were significantly less common ($t=3.21$, d.f. $=14$, $P=0.006$), in the predator removal area. These differences did not exist at the beginning of the experiment (mussels: $t=0.74$, d.f. $=14$, $P=0.469$; barnacles: $t=0.36$, d.f. $=14$, $P=0.723$). The same result was observed at site B: mussels were significantly more common ($t=6.53$; d.f. $=6$, $P<0.001$), and barnacles were significantly less common ($t=2.49$; d.f. $=6$; $P=0.047$), in the predator removal area than in the predator control area. These differences between areas also did not exist at the beginning of the removal experiment (mussels: $t=0.29$, d.f. $=6$, $P=0.478$; barnacles: $t=1.78$, d.f. $=6$, $P=0.171$).

Note that these statistical comparisons are between removal and control areas, rather than between the treatments per se. Unfortunately, because we had only two removal and two control areas, we have very little power (sensu Cohen 1977) to detect differences between treatments. Surprisingly, the *Morula* removal treatment had a significantly negative effect on mussels nonetheless ($F_{1,1}=267$, $P=0.039$), and a positive but non-significant effect on barnacles ($F_{1,1}=33.14$, $P=0.109$) (see Fig. 1).

*Crowding and desiccation in barnacles.* Crowded barnacles showed no significant mortality in response to exposure period, but the survivorship of isolated barnacles was significantly reduced after 6.5 and 7 h of exposure (Table 3). Hence crowding in barnacles seems to have increased the resistance of barnacles to desiccation during summertime low tides.

*Barnacles and mussel recruitment.* The recruitment of mussels (i.e. the survivorship of colonists to a size observable by the naked eye) was positively affected by the presence of barnacles. Mussel recruitment was highest in treatment (3) where barnacles were killed but not removed (Table 4); this was because of recruitment into, as well as between, the dead barnacle shells. Virtually no mussel recruitment (or survival) was observed in the quadrats of treatment (2) where both barnacles and mussels had been removed (see also Menge 1976). The means of treatments (1) where only mussels were originally removed, and (4) where neither species was removed, were not significantly different from each other. These means, however, were significantly lower than the mean of treatment (3), and significantly higher than the mean of treatment (2).

## Discussion

The northern Gulf of California is unique in its strong seasonality and therefore useful for testing the generalizations regarding intertidal community structure that have come from less seasonal regions. The present study was concerned with contrasting the effects of desiccation and predation in mediating the effect of mussels on barnacles following an early summer pulse in mussel settlement.

Surprisingly, the results indicated no effect of exposure during summertime low tides on the mussel-barnacle community; quadrats that were kept continuously moist during daytime low tides did not differ significantly from untreated control sites. This result differs from some previous studies, in which the vertical ranges of species were increased by experimental trickles of water (Hatton 1938; Frank 1965). The absence of significant differences in our experiment is difficult to interpret with confidence, because it may simply be that we did not keep the experimental quadrats wet enough for colonization by species, which normally live lower in the intertidal; but it does suggest the possibility that such larvae (or spores) are absent during the summer or that they have the additional requirement of shade for summertime colonization.

In the spray experiment, we had expected mussels to survive through the summer in sprayed, but not in control, quadrats. The lack of response by mussels may have been due to the capacity of tightly packed barnacles (which characterized our sites) to modify the microenvironment. We found that individual barnacles living in contact with conspecifics had a greater (100%) survivorship during exposure by low tides than isolated barnacles. The mechanism for this is potentially two-fold: (1) clumps of barnacles tend to retain more moisture (personal observations), and (2) they are likely to reduce the thermal loading of the rock substrate. This positive effect of barnacles on barnacles is likely to be extended to mussels living within the barnacle clump. It may be for this reason that mussels either actively select barnacles for settlement, or that they have enhanced survivorship among barnacles as juveniles (Dayton 1971; Paine 1974; Menge 1976).

The results of the present study also suggest that *Morula* preys selectively on *Brachidontes*, and that this mussel has a negative effect on *Chthamalus* in the absence of such predation. Hence *Morula* would seem at least partially responsible for the late summer decline in mussels; and it appears to have had an indirect, positive effect on barnacles. In the *Morula* removal areas at both sites A and B (where mussels were not experimentally removed), mussels were significantly more common and barnacles were significantly less common than in the non-removal areas, differences that did not exist at the beginning of the experiment (Fig. 1). We wish to emphasize, nontheless, that the statistical tests in the *Morula* removal experiment are comparisons of physical locations, rather than treatments per se (see (Hurlbert 1984). We have made the connection between physical locations and treatments, because the removal areas diverged from the non-removal areas in both sites during the course of the experiment, and because, in our view, the simplest explanation for this divergence is that it is the result of removing the predator (see also Stewart-Oaten et al. 1986).

Independent evidence for a negative effect of mussels on barnacles in the absence of *Morula* comes from the experimental removal of mussels from randomly selected quadrats in the *Morula* removal area at site A. Barnacles were more abundant in the mussel removal quadrats (but the difference was only marginally significant; see Table 2). This result is consistent with previous studies on mussel-barnacle interactions, which have shown that mussels compete with barnacles in the absence of mussel predators (Dayton 1971; Luckens 1975; Paine 1966a, 1974).

Taken together, our results suggest that *Morula* and *Chthamalus* might be "indirect mutualists" (sensu Vandermeer 1980). *Morula* benefits from the presence of *Chthamalus* because the latter aids recruitment by mussels, and *Chthamalus* benefits from the presence of *Morula* because *Morula* selectively removes mussels. Whether they are, in fact, indirect mutualists depends on the direct effect of *Morula* on barnacles, especially during the fall through spring when mussels are rare. Raimondi (unpublished work) has recently shown that *Morula* is a switching predator (sensu Murdoch 1969) and that it will eat barnacles when mussels are rare or absent; so the effect of *Morula* on barnacles is likely to be seasonally dependent, with a variable net effect among years depending on the mussel recruitment. The indirect effects between *Morula* and the "barnacle specialist," *Acanthina angelica* (Paine 1966b) may also be seasonally dependent for the same reason.

In summary, the gastropod predator, *Morula ferruginosa*, specializes on mussels and this has an indirect and positive effect on barnacles. This is because barnacles facilitate recruitment by mussels, which overgrow them in the absence of such predation. Crowding by barnacles enhances their survivorship during the summer, but summertime temperature extremes appear to have no effect on the mussel-barnacle interaction.

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