

# Role of catastrophic disturbance in mediating *Nucella-Mytilus* interactions in the Alaskan rocky intertidal

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**ABSTRACT:** The mussel *Mytilus trossulus* is typically a dominant competitor and principal space-occupying species in the rocky mid-intertidal zone of south central Alaskan (USA). Its principal predator in the region is the whelk *Nucella lima*. We examined predator-prey interactions between *M. trossulus* and *N. lima* following a severe freeze which greatly reduced mussel abundance in the upper portion of their vertical range. *N. lima* in Kachemak Bay was locally abundant, but its spatial distribution was patchy, resulting in site-to-site variation in predation intensity. Following the freeze, mussel populations recovered to occupy 72% of primary space at a site where *N. lima* was rare. At sites where *N. lima* occurred in high densities ( $>100\text{ m}^{-2}$ ), mussel cover remained significantly lower. At the latter sites, up to 81% of mussel mortality was due to snail predation. In field trials, average densities of *N. lima* significantly reduced mussel cover within 2 wk. From published literature on *Nucella* sp. feeding rates and our data on *in situ* reductions in mussel beds, we estimate that *N. lima* can eliminate 60 to 90% of mussels at a given site in 1 season. In contrast to the general view that mussel recovery from disturbance is inevitable, our results indicate that local populations of young mussels were unable to increase space utilization because of intense *N. lima* predation. A stochastic, catastrophic disturbance event thus altered control of community structure by removing dense stands of large prey individuals that had grown to near-refuge size. This facilitated long-term *N. lima* control of what had been a mussel-dominated community by shifting the interaction toward smaller sized mussels that are susceptible to intense predation.

**KEY WORDS:** Alaska · Community structure · Disturbance · Indirect effects · Rocky intertidal · Predation · *Mytilus* · *Nucella*

## INTRODUCTION

Interspecific interactions occur within an environmental framework set by species' tolerances of the physical parameters characteristic of a particular habitat. Superimposed upon such characteristic patterns of environmental variability are episodic disturbance events (Connell 1978, Sousa 1979, 1984, Dethier 1984). At one end of a disturbance continuum are chronic, low-intensity, and relatively predictable events to which species may be able to adjust. At the other end

of the continuum are catastrophic events which are acute, rare, and unpredictable, and which affect many species, cause extensive mortality, and at least temporarily alter community structure (Harper 1977, Dethier 1984). Such stochastic disturbances may influence community structure directly via induced mortality and/or indirectly through alteration of interactions between component species (Knowlton et al. 1981, Menge 1995). Further, effects of disturbances may be exacerbated in species living in sub-optimal habitats at or near their limits of physiological tolerance (Bowman & Lewis 1977, Lewis et al. 1982, Sousa 1984).

Rocky intertidal habitats are particularly amenable to examining the influences of physically induced disturbances on species distributions and interactions

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because physical gradients are spatially compressed and often well defined. Also, many rocky intertidal species are sessile or have limited mobility, making them easy to observe and manipulate across gradients.

Mussels are common constituents of rocky intertidal communities throughout the world (Soot-Ryen 1955, Seed 1976, Suchanek 1986, Gosling 1992). The broad success of mytilids is due largely to their life-history characteristics. Mussels settle densely and grow quickly to reproductive size, often occupying 75 to 80% of the substratum soon after settlement to unoccupied space (Suchanek 1978). These characteristics, combined with their relative mobility compared to other space-occupying intertidal species, lead to the mussels' competitive superiority (Paine 1966, Menge 1976, Seed 1976, Lubchenco & Menge 1978), often resulting in extensive mussel bands on many rocky shorelines (Stephenson & Stephenson 1972, Ricketts et al. 1985, Suchanek 1986).

Mussels are preyed upon by a variety of invertebrate and vertebrate predators including snails, sea stars, crabs, fish, sea otters, sea birds and shore birds (Paine

1966, 1974, Suchanek 1986, Menge et al. 1994). Predation by sea stars and whelks in particular has been shown to set the lower extent of mussel distribution in intertidal habitats throughout the world (Seed 1969, Paine 1974, Suchanek 1986). Despite predation pressure, established mussel populations often persist on shorelines in a refuge zone above the level of greatest predator abundance. As a result, predator control of mussel populations over their entire vertical range on the shore is rare.

*Mytilus trossulus* Gould occurs on the west coast of North America from California, where it hybridizes with *M. galloprovincialis* Lamarck (McDonald & Koehn 1988, Koehn 1991, McDonald et al. 1991, review in Gosling 1992), to Alaska. At temperate latitudes, on exposed mid- to low intertidal sites, *M. trossulus* is competitively subordinate to *M. californianus* Conrad and is primarily restricted to disturbance-created refuges in *M. californianus* beds, and habitats less exposed to wave action (Suchanek 1978, 1979, 1981). In Alaska, however, *M. californianus* is not abundant and *M. trossulus* is the dominant band-forming mussel in the littoral zone (Feder et al. 1977, Feder & Keiser 1980, O'Clair & Zimmerman 1987, Seed & Suchanek 1992). The success of *M. trossulus* in occupying rocky intertidal space over large geographical areas is due, in part, to its tolerance of a wide range of environmental conditions including high and low temperatures (Seed 1969, Suchanek 1986, Seed & Suchanek 1992).

In Kachemak Bay, south central Alaska (Fig. 1), the principal predator on *Mytilus trossulus* is the predatory gastropod *Nucella lima* (Gmelin) (Kincaid 1964). *N. lima* occupies a broad vertical range in the mid-intertidal zone which overlaps that of *M. trossulus*. Other benthic predators occur in low densities or in low intertidal zones not overlapping with mussels (M. L. Carroll pers. obs.).

In January, 1989, an extended (3 wk) severe freeze occurred along the south central Alaskan coast, with recorded temperatures as low as  $-31^{\circ}\text{C}$  (NOAA 1994), and coincided with a spring low tide series (Fig. 2). The freeze was a large-scale disturbance event on the North American west coast, as its effects on intertidal mussel populations were noted several thousand km to the south of the study site (Seed & Suchanek 1992, Robles et al. 1995). This event substantially altered the structure of Alaskan rocky intertidal communities by causing

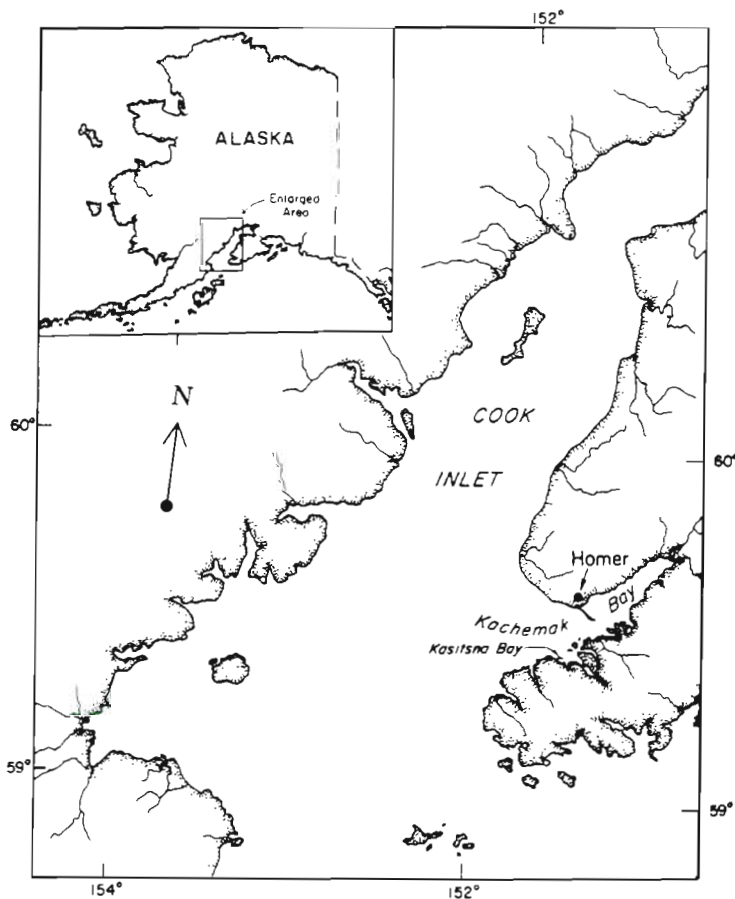


Fig. 1 Map showing location of Kachemak Bay in south central Alaska (USA)

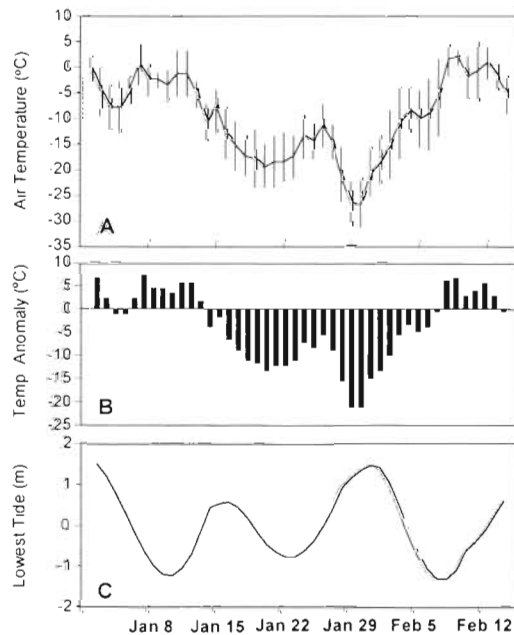


Fig. 2. Temperature and tide data from Homer, Alaska during January and February 1989: (A) daily average temperatures and temperature ranges (indicated by bars); (B) the deviation from historical average temperatures (a negative anomaly indicates colder than normal temperatures); and (C) the lowest daily tide level during that time period

extensive mortality of many resident species (Carroll 1994). *Mytilus trossulus* suffered nearly total mortality in the upper intertidal zone where it had previously dominated (R. C. Highsmith unpubl. data). *Nucella lima* was not as severely affected because it winters at lower levels in the intertidal (M. L. Carroll pers. obs.). Since the freeze, patterns of mussel recovery have been atypical compared to their usual recruitment patterns and growth characteristics. Although rates of recovery from disturbance in mussel beds vary, the process is thought to be deterministic (Suchanek 1986), with mussels predictably returning to dominance. However, more than 3 yr after large numbers of mussels were removed from the community, the characteristic mussel zone on shorelines of Kachemak Bay was rare and patchy.

In this paper, we report on observational and experimental field studies designed to reveal mechanisms responsible for the minimal post-disturbance recovery of mussel populations at many locations in Kachemak Bay. Specifically, we tested the hypothesis that intense predation by *Nucella lima* was responsible for the delayed recovery of *Mytilus trossulus* and its failure to regain spatial dominance. Further, we explore the indirect role of the disturbance event in influencing community structure through long-term alteration of predator-prey interactions between resident species.

## METHODS

**Density, cover, and size determinations.** Long-term trends in mussel cover were estimated from July 1989 through August 1992 by analyzing time-series photographs of permanent quadrats at 2 sites separated by 5 km: Kasitsna Bay and Hesketh Island (Carroll 1994).

*Nucella lima* abundance was determined monthly from April to July 1992 and again in December 1993. Initially, *N. lima* density was estimated in Kasitsna Bay, a small pocket embayment on the south shore of Kachemak Bay (Fig. 1), at 2 locations separated by approximately 200 m. *N. lima* densities were determined from 10 to 30 randomly located 0.25 m<sup>2</sup> quadrats which were cast blindly in the vertical zone of *N. lima*'s greatest occurrence (+1.5 to 3.5 m). The number of randomly located quadrats varied per census, but an equal number of quadrats were examined at each site during a given census. Snails in the quadrats were counted and measured to the nearest 1 mm. Snail size was measured as the length of the shell from the apex to the end of the siphonal canal (total length along the axis of coiling).

In July 1992, *Nucella lima* density was estimated using the procedure described above at both Kasitsna Bay and Nubble Point. Nubble Point is a semi-exposed rocky outcropping approximately 2 km from the Kasitsna Bay sites and is isolated from neighboring rocky intertidal habitats by several hundred meters of sand and gravel beaches. This buffer of highly mobile substrate effectively eliminates immigration from neighboring sites by species such as *N. lima* with non-dispersing larvae and crawl-away young. However, such a barrier does not affect species with dispersive larvae such as *Mytilus trossulus*.

In the same quadrats ( $n = 30$ ) that were censused for *Nucella lima* density, cover of *Mytilus trossulus* was estimated using a point frame method. A 0.25 m<sup>2</sup> frame with a grid of 81 evenly spaced points (every 5 cm on each axis) was placed over the quadrat and aligned with corner markers. Percent cover was determined as the number of points directly over mussels relative to the total number of points in the grid. All cover data were subjected to an arcsine square root transformation prior to analysis to normalize the distribution of percentages (Sokal & Rohlf 1981). Error intervals are presented as 1 standard error of the mean unless otherwise indicated.

**Causes of *Mytilus trossulus* mortality.** To estimate the proportion of mussel mortality attributable to *Nucella lima* predation versus other sources of mortality, the valves of dead mussel shells were examined at Kasitsna Bay and Nubble Point. *Nucella* spp. attack mussels by drilling a small hole through one of the valves (Carriker & van Zandt 1972); hence, mortality

resulting from *N. lima* predation is easily distinguishable from other mortality sources.

The first 100 empty *Mytilus trossulus* shells encountered in each of 2 size classes (<25 mm, >25 mm) at Kasitsna Bay and Nubble Point were inspected for drill holes caused by *Nucella lima* predation. Only shell remains with both valves present were included in the analysis because including shells with single valves would potentially bias the results.

**Effect of *Nucella lima* predation on *Mytilus trossulus*.** The role of *N. lima* in regulating mussel populations *in situ* was determined by experimentally manipulating the density of snails in mussel beds. Cages were used to maintain constant snail densities at test sites in mussel beds.

Cages (20 × 20 × 10 cm), made of 0.635 cm mesh galvanized steel hardware cloth, were placed in mussel beds at Kasitsna Bay where initial mussel cover exceeded 90%. Average sizes of mussels in beds where cages were placed ( $27.9 \pm 1.52$  mm;  $n = 40$ ) were consistent (ANOVA:  $df = 1, 78$ ,  $F = 1.49$ ,  $p = 0.23$ ) with the size of mussels outside cages ( $25.6 \pm 1.13$  mm;  $n = 40$ ). Each cage was randomly assigned 1 of 3 *Nucella lima* density treatments: normal density (5 snails), high density (10 snails), and a control which contained no snails. *N. lima* densities used in cages were based on the average density ( $131.6 \text{ m}^{-2}$ ) at that site. There were 8 replicates per treatment. The mean size of the snails ( $17.65 \pm 0.25$  mm;  $n = 120$ ) used in the cages was slightly smaller (ANOVA:  $df = 1, 452$ ,  $F = 9.69$ ,  $p = 0.0020$ ) than the size of the snails in the most recent census ( $19.26 \pm 0.49$  mm;  $n = 334$ ).

Mussel cover in the cages was estimated by overlaying a grid of 100 uniformly spaced points located on a clear acetate sheet atop the mussel bed within each cage, and determining the proportion of total points which were directly over mussels. Each cage was censused at the initiation of the experiment and every 2 wk during the 8 wk duration of the experiment.

## RESULTS

### Temporal trends in *Mytilus trossulus* and *Nucella lima* abundance and demography

In April 1989, less than 3 mo after the freeze, live mussels were rare in the mid-intertidal. Extensive stands of gaping mussel shells were still attached to rocks. Often, not a single live mussel was found in the shell beds. Also, conspicuous windrows of many thousands of mussel shells were commonly observed on beaches. By the summer of 1989, most of the dead mussel shells previously attached to rocks had fallen off or been washed away by wave action. Consequently, at

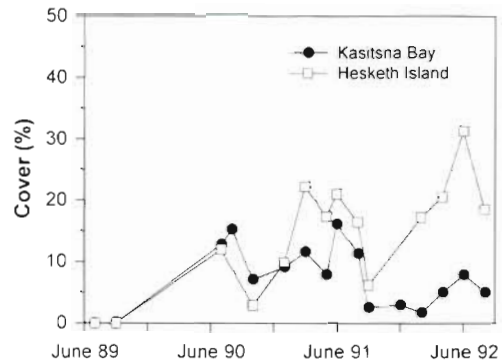


Fig. 3. Mean cover (%) of the mussel *Mytilus trossulus* at 2 sites in Kachemak Bay from 1989–1992.  $n = 3$  quadrats per site. Error bars are omitted for graphical clarity

the beginning of this study, live mussels occupied essentially no space in a zone where they are normally abundant (Fig. 3), underscoring the severity of the impact of the freeze on mussel populations.

An increase in mussel cover due to recruitment was evident in the vertical zone of greatest abundance (+1.5 to 3.0 m mean lower low water) during the summer following the freeze (Fig. 3), but their occupation of space did not increase rapidly through high recruitment and growth as would be expected from the literature (Seed 1976, Lubchenco & Menge 1978, Suchanek 1978). On the contrary, mussel cover decreased during the latter half of 1990 and through the spring of 1991. This pattern of moderate recruitment followed by a decline in cover was repeated in 1991 and 1992. As a result, more than 3.5 yr after the freeze, mussel cover had not increased appreciably at Kasitsna Bay, and had only modestly increased at Hesketh Island.

*Nucella lima* density varied between summer and winter. In winter, *N. lima* was scarce in the mid-intertidal at Kachemak Bay (December 1993:  $0.80 \pm 0.37 \text{ m}^{-2}$ ;  $n = 20$ ). The few snails found in the mid-intertidal were usually restricted to moist crevices and small tide pools. In April, *N. lima* density at both Kasitsna Bay sites (Fig. 4) was significantly less than during the 3 subsequent summer months (ANOVA, Site 1:  $df = 1, 48$ ,  $F = 81.89$ ,  $p < 0.0001$ ; Site 2:  $df = 1, 48$ ,  $F = 146.83$ ,  $p < 0.0001$ ), indicating a transition between winter and summer densities. By May, densities had increased about 3-fold (Fig. 4), then remained relatively constant through the remainder of the summer (ANOVA, Site 1:  $df = 2, 27$ ,  $F = 1.14$ ,  $P = 0.34$ ; Site 2:  $df = 2, 27$ ,  $F = 1.21$ ,  $p = 0.31$ ). *N. lima* size varied little through the study period, from  $19.02 \pm 0.37$  mm ( $n = 204$ ) in April to  $18.22 \pm 0.22$  mm ( $n = 455$ ) in July, indicating that the observed increase in density during the summer was primarily due to movement of established individuals into the mid-intertidal from below.

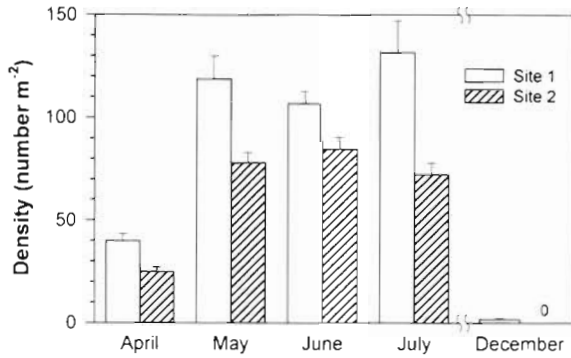


Fig. 4. Variation in *Nucella lima* density (+SE) at 2 locations in Kasitsna Bay during the spring and summer of 1992 and December 1993

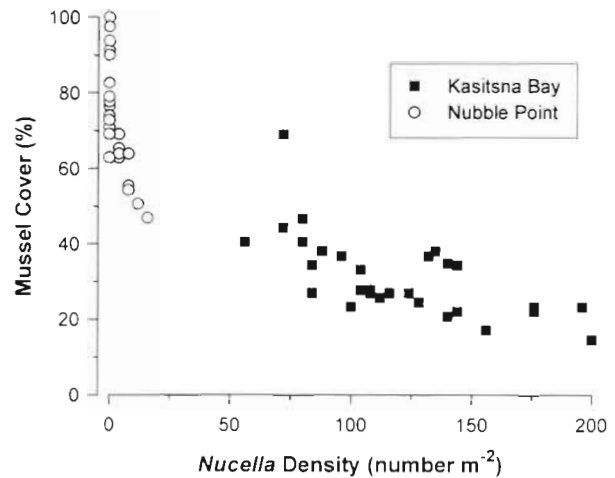


Fig. 6. Mussel cover relative to *Nucella lima* density at Kasitsna Bay and Nubble Point. The y-axis is slightly offset for graphical clarity

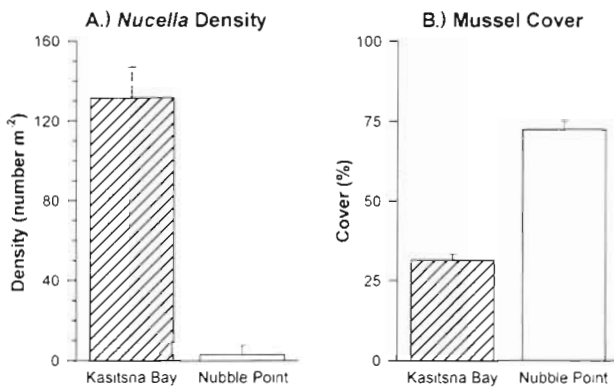


Fig. 5. (A) *Nucella lima* density and (B) *Mytilus trossulus* cover at Kasitsna Bay and Nubble Point in July 1992 (+SE)

Average mussel size at the Kasitsna Bay sites in early 1993 was  $26.7 \pm 0.95$  mm ( $n = 80$ ) and mean density was  $9460 \text{ m}^{-2}$  ( $n = 10$  quadrats). The only pre-freeze data available for comparison are from 1986, at which time the average length was 56.0 mm ( $n = 816$ ) and mean density was  $1900 \text{ m}^{-2}$  ( $n = 7$  quadrats) (R. C. Highsmith unpubl. data). Therefore, it appears that the demographic characteristics of the mussel population had changed from dominance by large individuals that filled the available space before the freeze to greater densities of small individuals since the freeze.

#### Site-to-site variation in *Nucella lima* and *Mytilus trossulus* abundance

In July 1992, mean *Nucella lima* density at Kasitsna Bay was high ( $131.6 \pm 15.6 \text{ m}^{-2}$ ; range = 56 to  $200 \text{ m}^{-2}$ ), while the density at Nubble Point, the isolated rocky outcropping 2 km distant, was significantly less ( $2.8 \pm 4.4 \text{ m}^{-2}$ ; range = 0 to  $16 \text{ m}^{-2}$ ) (ANOVA:  $df = 1, 38$ ,  $F = 211.8$ ,  $p < 0.0001$ ) (Fig. 5). This drastic difference in

predator density at sites separated by only a small distance underscores the physical barrier to immigration caused by highly mobile substrates like sand and gravel. In contrast to the site-to-site pattern of *N. lima*, mussel cover at Kasitsna Bay was less than half ( $31.4 \pm 2.0\%$ ) that at Nubble Point ( $72.4 \pm 2.5\%$ ) (ANOVA:  $df = 1, 58$ ,  $F = 127.7$ ,  $p < 0.0001$ ) (Fig. 5). This inverse pattern suggests that the presence of *N. lima* was negatively affecting mussel abundance. This hypothesis is further supported by the strong negative correlation between *N. lima* density and mussel cover in individual quadrats (Fig. 6).

#### Sources of mussel mortality

At the Kasitsna Bay site, *Nucella lima* predation is clearly a major source of mortality for mussels, with 73 to 81% of empty shells having drill holes (Table 1). In contrast to the large proportion of mussel mortality attributed to *N. lima* at Kasitsna Bay, the impact of *N. lima* predation was negligible at Nubble Point, with only 2 to 4% of empty mussel shells having been drilled (Table 1). This assessment method does not account for mortality sources, such as large waves or predation by gulls, ducks, or sea stars, which may remove mussel shells from the site. However, it is unlikely that such factors caused significant mortality at this site. Wave action, especially in summer, is minimal. Despite innumerable hours spent at the sites, avian predators were never observed removing mussels and the large tide range limits sea stars to levels on the shore that are well below the mussel distribution. There are potential limitations in inferring absolute mortality rates from dead shells; however, this method



Table 1. Proportion of small (<25 mm length) and large (>25 mm length) empty mussel shells at Kasitsna Bay and Nubble Point (Alaska, USA) whose mortality was attributed to *Nucella lima* predation. 'Drilled' shells exhibited a hole extending completely through the shell characteristic of gastropod predation, while no such hole existed in the 'Not drilled' class. Results are from observations on the first 100 empty shells in both size classes at each site

Shell condition	Kasitsna Bay		Nubble Point	
	<25 mm	>25 mm	<25 mm	>25 mm
Drilled	73	81	2	4
Not drilled	27	19	98	96

provides a useful measure of relative site-to-site variation in predation pressure when great differences exist between sites, such as in this study.

### Impact of *Nucella lima* on mussel beds

In the absence of *Nucella lima* predation, mussel cover in the cages remained essentially constant through the 8 wk duration of the field caging study (Fig. 7). In contrast, average densities of *N. lima* resulted in significant losses of cover by mussels, compared to control cages containing no snails, within 2 wk of the initiation of the experiment (Fig. 7). Due to

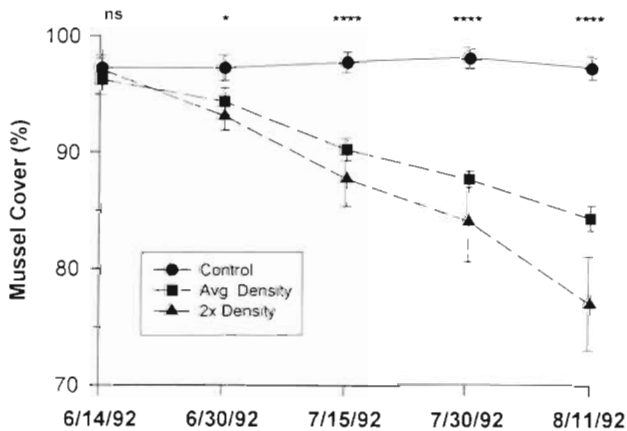


Fig. 7 Mussel cover ( $\pm 1$  SE) through time in caged arenas containing different densities of *Nucella lima* ( $n = 8$  replicates per treatment). After arcsine square root transformation, control (no snails) and average density (5 snails) treatments were compared using 1-way ANOVAs testing for the main effect of predator density on mussel cover on each sampling date. Because the high density treatment (10 snails per cage) contained twice the density naturally found at the site, it is plotted for informational purposes only, and was not included in the statistical analysis. Probability of significance of main effects is as follows: \* $p < 0.05$ ; \*\* $p < 0.01$ ; \*\*\* $p < 0.001$ ; \*\*\*\* $p < 0.0001$ ; ns = not significant

losses of cover of  $1.6\% \text{ wk}^{-1}$  by mussels in the average snail density treatment, the difference in cover between the 2 treatments steadily increased throughout the entire experiment. Although cages containing high densities of *N. lima* resulted in the greatest reductions of mussel cover of any of the treatments, the density of snails in the cages of that treatment was about twice that found naturally at the site. Therefore, the high density treatment was excluded from the statistical analysis contrasting the control and average density treatments but is also shown in Fig. 7.

The initial mussel cover in all the cages exceeded 90%. Consequently, snails sometimes became entrapped because mussels attached byssal threads to them. Entrapment can lead to starvation of *Nucella* spp. under some circumstances (Petraitis 1987, Day et al. 1991). Typically, these snails feed at the edge of mussel beds and are less likely to be captured by byssal threads. Trapped snails were freed during censuses but their overall feeding efficiency was reduced. Therefore, the reduction in mussel cover observed in the 2 predation treatments (Fig. 7) is probably conservative.

### DISCUSSION

The ability of an organism to respond to variation in its environment is of paramount importance to its success in a local community. The physiological resistance of mussels to sub-freezing temperatures allows them to withstand most freezing events encountered in temperate habitats (Williams 1970, Aarset 1982, Bourget 1983) and undoubtedly is a contributor to its persistence in such locations. However, the combination of a historic cold-snap, where the lowest temperature in over 70 yr was recorded in Homer, Alaska (NOAA 1994), and a spring low tide series resulted in extensive mortality of the local *Mytilus trossulus* population. Under the unusual circumstances dictated by this disturbance event, the behavioral adaptation of the *Nucella lima* to migrate into the subtidal zone during winter allowed it to largely escape the devastating mortality experienced by *M. trossulus*. The differential impact of the freeze event on these 2 species set the framework for a shift in the balance of their interaction.

The observational and experimental results of this study show an inverse correlation between predator density and prey abundance. Despite the ability of mussels to proliferate and occupy substrate via recruitment, growth, and immigration, predation by average *Nucella lima* densities in both manipulated and unmanipulated field experiments quickly resulted in significantly reduced mussel cover. Where snails are abundant (e.g. Kasitsna Bay), they are responsible for a large proportion of the mortality of their prey. At these

sites, mussel populations were unable to increase their spatial occupation despite annual recruitment events (Fig. 3). Conversely, at an isolated outcropping effectively isolated from immigration to *N. lima* (e.g. Nubble Point), the predator was rare and resulting predation pressure was low. At this site, mussels were a dominant spatial component of the community, demonstrating the ability of Alaskan mussels to successfully recover from a major disturbance when released from heavy predation pressure.

Seed (1976) reported laboratory consumption rates for adult *Nucella lapillus* feeding on *Mytilus edulis* (10 to 30 mm in length) of 2.17 mussels wk<sup>-1</sup>. Extrapolating Seed's data to the present study with predator densities at Kasitsna Bay of ~125 snails m<sup>-2</sup> and prey density of 9460 mussels m<sup>-2</sup>, *N. lima* could potentially consume 87% of the individuals in a continuous mussel bed in 30 weeks (the estimated mid-intertidal feeding season in south central Alaska). Based on the rate of reduction of mussel cover in the fenced feeding trials, the decline in mussel cover during a 30 wk period would be 58%. This is probably a conservative estimate because some of the fenced *N. lima* commonly became trapped among mussel byssal threads, reducing their feeding rates. In nature, snails do attack high-density populations of mussels, but they tend to do so from the edge of a patch so that they can retreat to a rock surface between feeding bouts. Even these conservative estimates of *N. lima* predation rates, however, demonstrate a strong inhibitory factor limiting recovery of the prey population.

Although mussel recovery rates may vary with several factors including timing of the disturbance and spatial extent of the disturbed patch, the recovery of mussels from disturbance is considered to be deterministic (Paine & Levin 1981, Suchanek 1981, 1986, Paine 1984, Seed & Suchanek 1992). For example, in New England (USA), Lubchenco & Menge (1978) demonstrated that mussel beds on exposed shores are extremely susceptible to removal by winter storms. However, settlement processes, fast growth rates, and superior competitive ability usually led to recovery and mussel dominance by the end of the summer following removal. This cycle of winter removal and summer recovery, they suggested, is more or less an annual event and emphasizes how rapidly mussels may recover from disturbance and monopolize large expanses of intertidal substrate. Furthermore, in Oregon (USA), Menge et al. (1994) documented the invasion of *Mytilus trossulus* to a disturbed site and observed spatial dominance of previously free space within 9 mo. In contrast to those systems, where rapid recovery of mussel populations was evident, recovery of mussels to spatial dominance did not occur during a period of more than 3 yr at sites with high *Nucella lima*

densities. Of course, other factors besides predation, such as insufficient numbers of surviving adults as a source population for larvae or lack of filamentous algae needed for primary plantigrade settlement, could have potentially contributed to the observed lack of recovery at Kasitsna Bay. However, the field data argues against these alternatives. Surviving adult populations in the extreme low intertidal zone and/or long-distance dispersal of larvae from other regions not as severely affected by the freeze were likely sources of the larval pool. Additionally, bare rock surface was rare during the recruitment season, and filamentous algae on which larvae attach was common (Carroll 1994). Further, it is improbable that the minimal mussel recovery was due to limited recruitment because moderate increases in cover attributable to mussel recruitment were evident early each summer at Kasitsna Bay and Hesketh Island (Fig. 3) before those gains disappeared later in the year. Growth rates of young mussels, while possibly reduced by the cold waters of south central Alaska, were clearly sufficient to allow the population at Nubble Point to dominate space in the absence of predation.

In addition to limited recovery of primary space, demographic characteristics of mussel populations where predators were abundant remained altered compared to pre-freeze levels. Mean mussel size during 1993 was less than half that in 1986 (26.7 vs 56.0 mm), indicating a shift in the size-structure in the prey population toward smaller mussels more vulnerable to predation.

The importance of physical forcing functions in affecting community structure through alteration of predator-prey interactions has been elegantly developed in a series of papers examining community structure in New England (Menge 1976, 1978a, b, 1983, Lubchenco & Menge 1978, Menge & Lubchenco 1981). At locations protected from heavy wave action, predators significantly influenced the lower limit of *Mytilus edulis* distribution. In locations exposed to heavy wave action, predator densities were reduced, making them ineffective at controlling mussel densities, so *M. edulis* achieved long-term spatial dominance. In New England, instead of a stochastic, severe disturbance event as in this study, the physical forcing function was relatively predictable and chronic and varied along a gradient (from low to high wave exposure).

Acute physical disturbances clearly have the potential to alter the structure of impacted communities. Ecologists have often been principally concerned with the immediately apparent and direct effects of disturbances. Indirect effects, such as mediation of species interactions, are more subtle but can be as important to long-term community structure as direct effects (Strauss 1991, Hughes 1994, Wootton 1994, Menge

1995). In the present study, a severe freeze altered pre-disturbance predator-prey interactions through differential mortality of the interactors. The ensuing shift in the dynamic relationship of predator-prey interactions resulted in an established *Nucella lima* population overwhelming annual *Mytilus trossulus* recruitment. Thus, predator control of mid-intertidal mussel populations was dictated by a catastrophic physical disturbance.

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