



Invasion resistance on rocky shores: direct and indirect effects of three native predators on an exotic and a native prey species

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ABSTRACT: Trophic relationships among native and exotic species produce novel direct and indirect interactions that can have wide-ranging community level effects and perhaps confer invasion resistance. We investigated whether native predators have the potential to directly limit the spread of the exotic mussel *Mytilus galloprovincialis* or mediate interactions among native and invasive mussels at a rocky intertidal invasion front in northern California. Lower survival of *M. galloprovincialis* in transplanted cultures exposed to predators indicated that the invader was more vulnerable to predators than the numerically dominant native *M. californianus*. Survival and per capita mortality rate in monocultures and polycultures did not vary for either *M. galloprovincialis* or *M. californianus*, suggesting that predator-mediated apparent competition and associational defense did not occur. Complementary laboratory feeding trials determined which among 3 intertidal predators preferred the exotic to 2 native species of mussel. The whelk *Nucella ostrina* was most selective, consuming the thinner shelled mussels (*M. galloprovincialis* and the native *M. trossulus*) rather than the thicker-shelled native species *M. californianus*. The crab *Cancer antennarius* and the sea star *Pisaster ochraceus* showed no preferences among mussel species. *N. ostrina* were commonly observed among field-transplanted mussels; thus whelk predation may be especially important in limiting the establishment of the invasive mussel. However, 15% of *M. galloprovincialis* remained intact in the field after 1 yr, suggesting that predation alone may not inhibit establishment of the invader. A tenuous balance between larval settlement and early post-settlement predation likely characterizes the invasion front.

KEY WORDS: Invasion · Resistance · Predation · Indirect effects · Rocky intertidal · Mussel · *Mytilus*

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INTRODUCTION

Invasions of non-native species are a worldwide epidemic, contributing to the biotic globalization of communities (Davis 2003). However, despite concerns over increased rates of introduction, as few as only 10% of exotic species become well established in endemic communities (Williamson 1994). Much research on invasive species has focused on the biotic resistance mounted by native competitors and their emergent effects on species diversity (Levine 2000, Stachowicz et al. 2002). More recently, investigators have targeted the important role that local predators can play in lim-

iting invasive species (Reusch 1998, Byers 2002, Ruesink 2007). Demographically, endemic predators can prevent the establishment of non-native species by consuming the invader at a rate greater than or equal to its rate of arrival. If predators are incapable of limiting establishment, they may still restrict the geographic extent of the spread of invaders (deRivera et al. 2005). Predation can also act in concert with other community level processes, such as immigration and resource availability, to limit invasions through density-mediated effects (Miller et al. 2002).

The indirect effects that native predators can have on a community during an invasion by an exotic spe-

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cies are not usually examined. For instance, local predators can facilitate invasion of the non-native species via consumption of native competitors if they fail to recognize a novel species as potential prey (Simoncini & Miller 2007). Alternatively, invasive species can release native species from natural enemies, if they are preferred by native predators (reviewed by Rodriguez 2006). If an invasive species is strongly preferred, then apparent competition may occur provided that predator density and predation rate on native prey increase with the growing prevalence of the invader (Noonburg & Byers 2005). Strong preferences for exotic prey also may produce novel responses, such as associational defenses that can occur when invasive prey are indirectly facilitated by living near or among non-preferred or unpalatable native species (reviewed by Wahl & Hay 1995).

Predation may be contributing to post-settlement mortality limiting the northward expansion of the Mediterranean mussel *Mytilus galloprovincialis* along the Pacific coast of the USA. An invasion front spanning approximately 560 km is located between Point Conception and Cape Mendocino, California, USA (Sanjuan et al. 1997). This cryptic invader has become well established in protected bays and harbors, but has had limited success in becoming established in wave-exposed rocky intertidal communities along the open coast in this region (Geller 1999, Rawson et al. 1999). *M. galloprovincialis* co-occurs with 2 native congeners, *M. trossulus* and *M. californianus*, within the invasion front. Larvae of all 3 species settle in open coast communities, but adult *M. californianus* are numerically dominant while *M. galloprovincialis* and *M. trossulus* are rare (Johnson & Geller 2006). Physiological limitations and competitive interactions among native and invasive mussels are not likely to restrict further invasion of *M. galloprovincialis*. Transplants of the invader experience high growth and survival rates in the absence of predators and are competitively robust among 2 native species of mussels on the open coast (Shinen & Morgan 2009). Moreover, *M. galloprovincialis* reduces growth and survival of *M. trossulus* (Shinen & Morgan 2009) and may be contributing to the decline of *M. trossulus* in the southern extent of its range (Geller 1999).

Native predators may be limiting the invasion success of *Mytilus galloprovincialis* via selective predation. Despite paradigmatic evidence of strong top-down control in rocky intertidal communities (Robles & Desharnais 2002), the role of predators in limiting the invasion success of *M. galloprovincialis* in the Pacific Northwest has not been examined. The shell of the invader is generally thinner than that of the more abundant native *M. californianus* (Landenberger 1968), making it potentially more vulnerable and pre-

ferred by certain intertidal predators. In addition to invasion resistance, selective predation on a competitively robust invasive like *M. galloprovincialis* can also lead to indirect effects that may promote coexistence among native and invasive prey (Griswold & Lounibos 2005). Moreover, the presence of the invader among native congeners may change the native predator-prey dynamics via apparent competition or associational defense (Menge 1995) and may even cause declines in native species via hyperpredation (Smith & Quin 1996).

To evaluate the importance of predation in limiting the establishment of *Mytilus galloprovincialis* in a rocky intertidal community within the invasion front, we experimentally determined both the direct impact of multiple native predators on the invader and indirect effects on native competitors. The relative vulnerability of native and invasive mussels to predators was determined in a caging study the field, and the prey preferences of 3 common intertidal predators were determined in the laboratory. The differential survival of native and invasive mussels outplanted in monoculture in the field indicated their relative vulnerability to predation. Differential survival among mussels outplanted in polyculture compared to monoculture would indicate the existence of predator-mediated apparent competition (greater per capita mortality rate of *M. californianus*) or associational defense (lower per capita mortality rate of *M. galloprovincialis*). The selectivity of different intertidal predators for native and invasive prey in the laboratory would suggest which among 3 key predators play an important role in invasion resistance and the dynamics among native and invasive mussels. Together, these results would reveal the effect of native predators on the invasion by *M. galloprovincialis* and indirect effects involving native mussels within an invasion front on the Pacific Northwest coast.

MATERIALS AND METHODS

Study site and species. All experiments were conducted at the Bodega Marine Reserve (BMR), approximately 100 km north of San Francisco, California, USA (38° 18' 18" N, 123° 3' 8" W). The region is characterized by mixed semidiurnal tides and strong oceanographic upwelling. All 3 species of mussels occur in the intertidal zone on the exposed rocky shores of BMR (Rawson et al. 1999).

All mussels used in this study were collected by hand from naturally occurring mid-intertidal mussel beds in April 2005. Small, newly settled 'bay mussels,' *Mytilus trossulus* and *M. galloprovincialis*, can be difficult to distinguish morphologically (Martel et al. 2000), and

therefore, larger juvenile mussels that are readily distinguishable (length 2 to 4 cm) were used in all experiments. To be further assured of mussel species identity, *M. trossulus* were collected from Strawberry Hill, Oregon (44° 15' 385" N, 124° 07' 594" W), north of the zone of sympatry of the 3 species of mussels. *M. galloprovincialis* were collected from Shell Beach in Tomales Bay, California (38° 06' 59.75" N, 122° 52' 23.93" W), where the population has historically comprised almost entirely *M. galloprovincialis* (Sarver & Foltz 1993, Suchanek et al. 1997). *M. californianus* were collected from BMR. Each mussel was individually inspected for diagnostic morphological features to further reduce the inadvertent inclusion of non-target species or hybrids (McDonald et al. 1991). Mussels that did not resemble the target population were eliminated from the experiment. All mussels were transported to Bodega Marine Laboratory and cleaned of epibionts. The 3 species of mussels were acclimated separately in sand-filtered, flow-through seawater containers for 1 mo.

Three common intertidal predators with different feeding modes were used in prey preference trials in the laboratory. The ochre sea star *Pisaster ochraceus* is widely regarded to be a keystone predator in rocky intertidal communities of the Pacific coast, where it preys heavily on the dominant space holders and frees space for a greater diversity of invertebrates and algae (Paine 1974). *P. ochraceus* uses tube feet to remove mussels from the substrate and pry open the shells of mussels. The stomach is then inserted to digest the soft tissue.

The second predator was the rock crab *Cancer antennarius*, which forages on invertebrate prey in submerged intertidal and shallow subtidal habitats. Mussels are eaten by breaking the shells of the bivalve prey with their claws. The effects of rock crab predation can be extremely variable in space and time, because they are highly mobile and often gregarious (Yamada & Boulding 1996). Nevertheless, they can limit distributions of a wide variety of marine species (Byers 2002, Siddon & Witman 2004).

Lastly, the dog whelk *Nucella ostrina* is small, inconspicuous, and abundant in the middle intertidal zone of rocky shores. Prey is consumed through a small hole created by a rasp-like radula. *N. ostrina* is a generalist predator, but individuals can have highly specialized diets, preferring a narrow range of available prey (West 1986). Direct and indirect effects of *N. ostrina* and other related *Nucella* spp. include changes to local species composition and diversity (Navarrete & Menge 1996), modification of the recovery rate of the community following a perturbation (Carroll & Highsmith 1996), and alteration of predicted succession patterns (Wootton 2002).

Predation rates on native and invasive mussels in the field. Predation rates on *Mytilus californianus* and *M. galloprovincialis* were determined by monitoring the survival of outplanted mussels on a rocky intertidal bench. The native species *M. trossulus* was not included. This species is in decline and is uncommon along the open coast in our study region. It is competitively inferior to *M. californianus* and *M. galloprovincialis* and suffers high mortality in culture with heterospecifics (Shinen & Morgan 2009). In May 2005, mussels were haphazardly assigned to 7 replicates of 3 experimental treatment types: *M. californianus* monoculture (n = 40), *M. galloprovincialis* monoculture (n = 40), and polyculture (n = 40; 20 *M. californianus* and 20 *M. galloprovincialis*). Mussels were transplanted to a 5 × 10 m² area of the middle intertidal zone at the BMR, within the foraging range of all 3 target predators. They were held close to the rock surface for 4 wk using flexible plastic mesh (7 × 7 mm) to facilitate reattachment of byssal threads. In June, the mesh was removed from half of the treatments to form spatially paired caged (approximately 20 × 20 cm) and uncaged cultures. Although the remaining mesh may have caused experimental artifacts that may affect mussel survival such as changes in flow or sedimentation, the experimental cultures were in an exposed, high flow area of the BMR, and we found no evidence of increased sedimentation inside caged cultures. After 2 d, waves dislodged less than 5% of the mussels across all treatments, and thereafter missing mussels were assumed to be removed by predation. Mussel survival was monitored periodically (approximately biweekly) in caged and uncaged cultures for 5 mo, and a final observation was made after 1 yr. The presence of predators and evidence of predation (drill holes, broken shells, and empty shells) were noted at each low-tide sampling period. Predator abundance was not directly assessed since both *Pisaster ochraceus* and *Cancer antennarius* are likely to be more abundant when the experimental plots were submerged. Furthermore, *Nucella ostrina* often forage in the interstices of mussels and cannot be assessed without destruction of the mussel bed. The abundance of predators within cultures was determined only at the end of the experiment when cultures were removed.

Cumulative, proportional survival and per capita mortality rates were calculated for each species for the first 5 mo. Predation was estimated by the difference in mortality observed in the paired predator-exclusion control (caged) cultures and predator-exposed cultures (see Menge et al. 2004 for general approach). Survival after 1 yr was estimated using only mussel counts in uncaged plots, because the cage controls no longer excluded small *Nucella ostrina* after 1 yr of exposure. All data were examined for deviations of statistical test as-

sumptions using Levene's test for variance homogeneity and visual inspection of the distribution of the residuals. The proportional survival of mussels after both 5 mo and 1 yr were compared using an analysis of variance (ANOVA) on arcsine square-root transformed data, with species and treatment type (monoculture versus polyculture) as factors. Species-specific per capita daily mortality rates in polycultures were averaged over each sampling interval. The number of mussels missing from plots for each species of mussel was divided by the total number of mussels in the plot at the previous time interval and the days between sampling intervals. To test for apparent competition or associational defense between the 2 species in polyculture, mortality rates were compared using an analysis of covariance (ANCOVA) with species as a factor and relative density of each species as a covariate (Schmidt & Whelan 1998). The abundance of *N. ostrina* was compared among cultures using a single-factor ANOVA followed by Tukey's HSD multiple comparison test.

Predator preferences for native and invasive mussels in the laboratory. Simultaneous feeding trials were conducted to determine the preferences of predators for native and invasive mussels. In May of 2006, *Mytilus californianus*, *M. galloprovincialis*, and *M. trossulus* were collected and marked with a small drop of nail polish on 1 valve to help distinguish species during feeding trials. Average-sized adult predators, *Pisaster ochraceus* (11.5 ± 1.4 cm radial arm length, $n = 35$), *Cancer antennarius* (6.1 ± 1.7 cm claw length, $n = 35$), and *Nucella ostrina* (1.9 ± 0.1 cm shell length, $n = 20$), were all hand-collected at BMR. The predators were held in flow-through seawater at ambient ocean temperature without food for 5 to 7 d to standardize hunger level for each species. In each feeding trial, a single predator was placed at 1 end of an aquarium ($42 \times 26 \times 17$ cm), and the 3 species of mussels were randomly and equidistantly arrayed at the opposite end. Aquaria were constantly inundated and supplied with sand-filtered, flow-through seawater at ambient ocean temperature (9.4 to 14.8°C). Predators were observed 2 to 3 times daily for up to 3 wk until a

mussel was eaten. Predators that did not eat or ate multiple prey before a primary choice was determined were excluded from analyses. Frequency of predation on each species of mussel was analyzed using Pearson's chi-squared test.

RESULTS

Predation rates on native and invasive mussels in the field

After 5 mo of exposure to predators, overall survival of *Mytilus galloprovincialis* was less than for the native mussel *M. californianus*, indicating that the invasive mussel was more vulnerable to predators (Fig. 1). Neither apparent competition nor associational defenses occurred, as indicated by the steady density-dependent mortality rates of *M. californianus* and *M. galloprovincialis* in polyculture (Table 1). After 1 yr, proportional survival remained lower for *M. galloprovincialis* than *M. californianus* and was similar in monocultures and polycultures (Fig. 2). Predatory whelks *Nucella ostrina* were observed within the experimental cultures at every sampling period and were often seen positioned over mussels, presumably engaged in predatory efforts. Other predators were observed near the experimental area, although none was noted within the cultures during low tide. Similarly, only shells that exhibited whelk drill holes were found. However, predation by non-whelk predators cannot be discounted, as any shells that may have been crushed

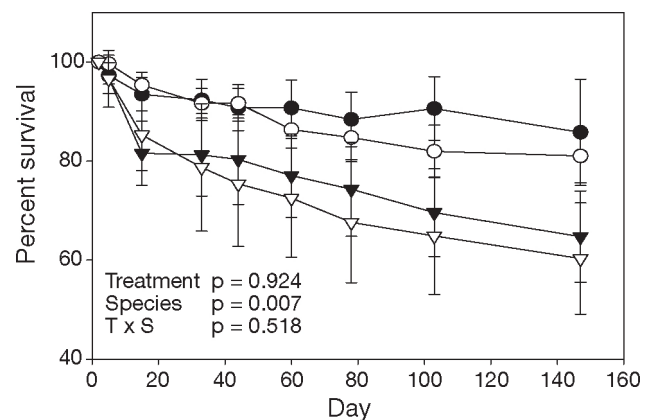


Fig. 1. *Mytilus californianus* and *M. galloprovincialis*. Mean \pm SE proportional survival of *M. californianus* (circles) and *M. galloprovincialis* (triangles) that were exposed to predators in experimental monocultures (shaded) and polycultures (unshaded) over 5 mo on the exposed rocky shores of the Bodega Marine Reserve, California, USA. Data were adjusted for mortality observed in paired predator-exclusion plots. Results include a 2-way ANOVA of survival (arcsine square-root transformed) of mussel species (species) and culture type (treatment)

Table 1. *Mytilus galloprovincialis* and *M. californianus*. ANCOVA of mean daily per capita mortality rate in polycultures over 5 mo of exposure to predators. Species-specific mortality rates were averaged over sampling intervals and were corrected for mussel mortality in paired predator-exclusion plots. The relative density of the 2 species of mussels was included as a covariate

Source	df	SS	F	p
Species	1	<0.001	0.096	0.757
Relative density	1	<0.001	0.051	0.821

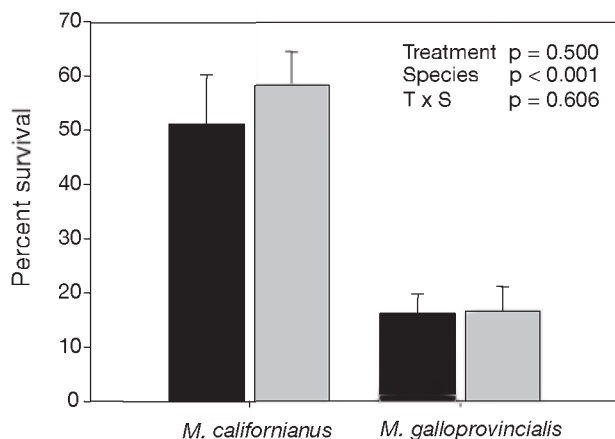


Fig. 2. *Mytilus californianus* and *M. galloprovincialis*. Mean \pm SE survival in experimental monocultures (shaded) and polycultures (unshaded) that were exposed to predators after 1 yr on the exposed rocky shores of the Bodega Marine Reserve, California, USA. Results include a 2-way ANOVA of survival (arcsine square-root transformed) of mussel species (species) and culture type (treatment)

or pried open were likely dislodged and removed by wave action. When the experiment was dismantled after 1 yr, *N. ostrina* were found in similar proportions in monocultures and polycultures of *M. galloprovincialis* and *M. californianus* ($F_{2,14} = 1.69$, $p = 0.22$). Removal of the experiment also revealed hundreds of 'bay' mussel recruits, either *M. galloprovincialis* or *M. trossulus*, among the byssal threads of mussels.

Predator preferences for native and invasive mussels in the laboratory

Of the 3 species of predators examined in the laboratory, the whelk *Nucella ostrina* was most selective in laboratory feeding trials (Fig. 3). *N. ostrina* preferentially consumed *Mytilus trossulus* over the other 2 mussel species ($\chi^2 = 14.00$, $p < 0.01$, $n = 16$). The crab *Cancer antennarius* and the sea star *Pisaster ochraceus* showed a similar tendency to reject *M. californianus*, but did not demonstrate significant preferences among the 3 species of mussels ($\chi^2 = 4.67$, $p = 0.10$, $n = 27$ and $\chi^2 = 3.00$, $p = 0.22$, $n = 24$, respectively).

DISCUSSION

The combined evidence from laboratory and field experiments suggests that predation may be contributing to the limited establishment of *Mytilus galloprovincialis*. In the field cultures exposed to predators, survival rates on the invader were consistently lower than those of *M. californianus*. Per capita mortality rates of

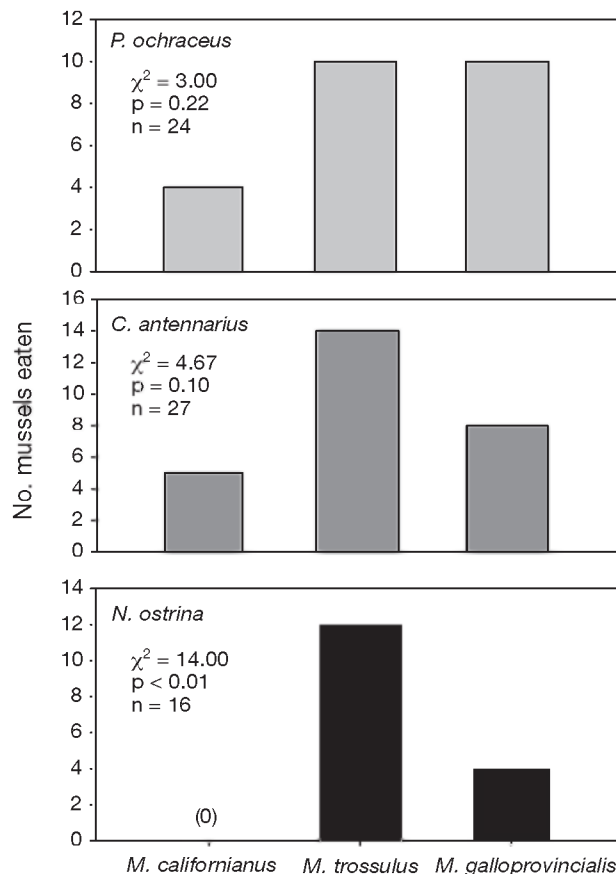


Fig. 3. Frequency of predation by *Pisaster ochraceus*, *Cancer antennarius*, and *Nucella ostrina* on native *Mytilus californianus* and *M. trossulus* and invasive *M. galloprovincialis* in the laboratory. Pearson's chi-squared statistics and probability values are shown

each mussel species were also consistent throughout the experiment, indicating that predator preference for the invader did not waiver even as mussel density declined. Furthermore, the 2 species of mussels were not likely interacting indirectly via apparent competition rather than through indirect facilitation or associational defense. The presence of novel prey could have attracted predators and may have led to switching among prey, but per capita mortality rates of the mussels did not decline with the decreasing proportions of the 2 species of mussels.

Nucella ostrina may be a key species limiting the establishment of *Mytilus galloprovincialis*. This mid-intertidal predator always occurred within our plots, where it preferred *M. galloprovincialis* to *M. californianus* and was often seen feeding on the invader. The preference for *M. galloprovincialis* is likely due to its thinner shell (Landenberger 1968), which would require less handling time for a drilling predator (Hart & Palmer 1987). The whelk also preferred *M. galloprovincialis* to *M. californianus* in the laboratory, but it preferred *M. trossulus* to

both of them. Like *M. galloprovincialis*, *M. trossulus* has a thin shell (Suchanek 1981), which explains why it was preferred to *M. californianus*. However, it cannot be ruled out that *M. trossulus* provides the greatest nutritional reward among the mussel species.

Strong prey preferences of *Nucella ostrina* may also influence competitive hierarchies among native and invasive mussels (Carroll & Highsmith 1996, Navarrete & Menge 1996) and may affect the decline of *Mytilus trossulus* and the invasion by *M. galloprovincialis*. *M. galloprovincialis* is competitively dominant over *M. trossulus* and is the fastest growing of the 3 species of mussels within the invasion front (Shinen & Morgan 2009). Because whelks prefer *M. trossulus* to *M. galloprovincialis*, predation by *N. ostrina* might have exacerbated the negative competitive effects of *M. galloprovincialis* on native mussels and contributed to the decline of the native species. Additionally, whelks strongly prefer *M. galloprovincialis* to *M. californianus*; thus predation on settlers likely promotes coexistence between the 2 species of mussels by slowing the advance of the invader. However, the direct and indirect effects of whelk predation on competition among the 3 mussels may vary over the range of the *M. galloprovincialis* invasion, because both prey preferences and predation rates of *Nucella* spp. can vary with prey availability (Wieters & Navarrete 1998) and across geographic regions (Dahlhoff et al. 2001, Hunt & Scheibling 2001, Sanford et al. 2003).

Crabs and seastars may play a lesser role in limiting the spread of *Mytilus galloprovincialis* than whelks. During low tide, we saw little conclusive evidence of predation (cracked, broken, or empty shells) by these predators in our experimental plots, but crabs and seastars generally forage in mussel beds during high tide, making them very difficult to observe. As a crushing predator, *Cancer antennarius* tended to avoid the thicker-shelled *M. californianus* in the laboratory, but significant preferences were not evident. Least selective, *Pisaster ochraceus* is a prying predator, needing only a 0.5 mm gap between mussel valves to insert its stomach and consume prey (Feder 1955). The lack of strong feeding preferences of *C. antennarius* and *P. ochraceus* suggests that any varying shell thickness or strength of the adductor muscles among experimental mussels was not sufficient to deter predation. Nevertheless, *C. antennarius* and *P. ochraceus* have the potential to help limit the expansion of *M. galloprovincialis*. Previous studies have shown that these mobile predators can limit the distribution of prey throughout the intertidal zone during high tide (Paine 1974, Robles 1987) and can quickly converge on abundant prey (Bomkamp et al. 2004).

In addition to feeding mode, differences in biogeography and life history may play critical roles in the

ability of native predators to limit the distribution of *Mytilus galloprovincialis*. Many predators, such as *Pisaster ochraceus* and *Cancer antennarius*, produce planktonic larvae that potentially disperse hundreds of kilometers, connecting populations throughout a species range (Kinlan & Gaines 2003). Wide diet breadth may be favored for predators with long larval dispersal due to the range of available prey at potential settlement sites (Beck & Kitching 2007). *C. antennarius* and *P. ochraceus* did not strongly prefer 1 species of mussel over another, especially between the thin-shelled *M. galloprovincialis* and *M. trossulus*. In contrast, highly selective *Nucella ostrina* develop directly into competent juveniles inside sessile eggs. Although the *N. ostrina* used in our study were all collected from a single site, our results were consistent with prey preferences of *N. ostrina* throughout the invasion front (Danner 1999, J. Shinen et al. unpubl. data). The ability of *N. ostrina* to limit the distribution of *M. galloprovincialis* may also be reflected by the inverse relationship between the predator and the prey along the invasion front. The invasive mussel is abundant only in protected bays and harbors (Braby & Somero 2006), where *N. ostrina* usually does not occur. Thus, on a regional scale crabs and seastars may be less likely to limit the establishment or spread of *M. galloprovincialis* than *N. ostrina* and may be more likely to promote coexistence among mussels (Shurin & Allen 2001).

Despite evidence from our field and laboratory studies demonstrating that *N. ostrina* may be limiting the invasion of *Mytilus galloprovincialis* in northern California, approximately 15% of the original *M. galloprovincialis* remained in the experimental plots after 1 yr (monocultures and polycultures combined). Although selective predation on *M. galloprovincialis* occurred, predators could not remove all of the established mussels in our plots. Furthermore, patches of *M. galloprovincialis* facilitated recruitment of 'bay' mussels, which previously have been shown to consist of far more *M. galloprovincialis* than *M. trossulus* within the invasion front (Braby & Somero 2006). The recruitment rates of *M. galloprovincialis* will likely increase, in part due to growing mariculture development in bays that likely serve as larval sources for open coast communities (FAO 2007). Although rapid predatory responses to stochastic high recruitment events have been documented for all 3 species of predators (Robles et al. 1995, Hunt & Scheibling 2001, Bomkamp et al. 2004), a large settlement event of *M. galloprovincialis* could swamp any biotic resistance (Hollebone & Hay 2007). For instance, along the west coast of South Africa where recruitment rates of *M. galloprovincialis* are extremely high, the invader has been an important trophic subsidy for many native preda-

tors, but their combined effect has not limited the establishment and spread of *M. galloprovincialis* (Griffiths et al. 1992).

Rocky shore predators create bare space on rocky shores that can be colonized by both native and introduced species. For the time being, predation appears to be contributing to the limitation of a northward expansion of *Mytilus galloprovincialis* on the exposed rocky coasts of northern California, but predicting its long-term effectiveness at slowing the invasion of *M. galloprovincialis* is complicated. *N. ostrina*, a key predator of *M. galloprovincialis*, is an intermediate predator in a complex interaction web that is subject to other biological and physical forces (Navarrete & Menge 1996, Dahlhoff et al. 2001). A recruitment failure or substantial post-settlement mortality event of 1 or several key predators within the invasion front may result in a substantial increase in cover of *M. galloprovincialis*. Additionally, further invasion success will likely have wide-ranging effects on intertidal community structure. Since *M. galloprovincialis* is competitively robust among native mussels (Shinen & Morgan 2009), the mussel bed community structure will change if native mussels decline. In particular, displacement of *M. californianus* by the smoother-shelled *M. galloprovincialis* may lead to declines in native epibiont species diversity and richness (J. Shinen & S. Morgan unpubl.).

In both marine and terrestrial systems, many invaders are successful because they escape a predator or other natural enemy when they are introduced outside of their natural range (Torchin et al. 2003). In contrast, rather than escaping a natural enemy, *Mytilus galloprovincialis* may be limited primarily by a native whelk that prefers it to the dominant native species of mussel (*M. californianus*) within the invasion front. Much attention has focused on the relative importance of native versus invasive predators on native prey (Salo et al. 2007), but more attention is needed to determine how native predators alter the dynamics between native and invasive prey (deRivera et al. 2005), particularly in systems that demonstrate strong top-down control. Moreover, the role that indirect effects play in native–invasive species interactions has been largely overlooked and is wholly lacking in the predictive framework of invasion ecology (White et al. 2006). Studies that examine a species invasion in the context of community ecology theory (Shea & Chesson 2002) are critical in developing a better understanding of the species interactions that generate biotic resistance to invaders. Identifying forces that facilitate or inhibit a species invasion can improve our ability to predict the success rate and likely impact of invasive species as well as foresee which native communities are most susceptible to invaders.

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