Effects of native predators and eelgrass habitat structure on the introduced Asian mussel *Musculista senhousia* (Benson in Cantor) in southern California

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Abstract

The ability of predators to control the abundance of non-native species has been little explored in marine systems. Native predators may be used to control non-native species or may confer invasion resistance to communities if predation rates on invaders are density-dependent. We studied the response of southern California native predators to the density of *Musculista senhousia* (Benson in Cantor, 1842), a small, fast growing mussel that has been introduced from Japan to several coastlines worldwide. We performed field experiments to determine if *M. senhousia* proportional mortality is density-dependent and if eelgrass *Zostera marina* L. habitat structure influenced mussel density-dependent mortality. We also evaluated the effect of seagrass habitat structure on the aggregative and functional responses of the predatory gastropod *Pteropurpura festiva* (Hinds, 1844) to Asian mussel density. In the summer of 2002, *P. festiva* aggregated in plots with high mussel density and was responsible for nearly all predation on *M. senhousia*. However, *M. senhousia* proportional mortality was inversely density-dependent at all levels of eelgrass above-ground and below-ground habitat structure. Asian mussel proportional mortality also was inversely density-dependent and was not influenced by eelgrass habitat structure in the spring of 2004 when wading birds were the chief predator of mussels. In contrast to results for mussel proportional mortality, the aggregative and functional responses of *P. festiva* varied with seagrass habitat structure. *P. festiva* density increased with Asian mussel density in plots with low simulated habitat structure, but the relationship between *P. festiva* density and Asian mussel density was parabolic at zero, intermediate and high levels of habitat structure. In field enclosures, *P. festiva* exhibited a Type I (linear) functional response to Asian mussel density at low levels of eelgrass structure, and a Type II (hyperbolic) functional response to mussel density at high levels of eelgrass structure. Our results and those of others suggest that the degree to which local benthic communities in southern California are resistant to Asian mussel invasion depends on habitat structure, mussel settlement rates, and the density and diversity of predators.
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1. Introduction

Introduced species pose a substantial threat to marine biodiversity worldwide (Vitousek et al., 1997; Bax et al., 2001). Non-native species may outcompete native species for food or space, leading to rapid growth

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of an introduced population that substantially alters local community structure. Well-known examples include the introduction of the Asian clam *Potamocorbula amurensis* to San Francisco Bay sediments (Carlton et al., 1990) and the European periwinkle *Littorina littorea* to shorelines of North America (Race, 1982). Introduced species also may threaten biodiversity by altering habitat structure (e.g., the introduction of kelp-consuming sea urchins *Strongylocentrotus* spp. to US coasts: Ebeling et al., 1985), by consuming native species (e.g., introduction of the predatory European green crab *Carcinus maenus* to the US West Coast and to New England: Cohen et al., 1995; Grosholz et al., 2000), and by acting as new vectors for disease (Vitousek et al., 1996).

Efforts to prevent invasions or to control the abundance of invaders after they have established are increasing, but control of introduced marine species is still in its early stages (Lafferty and Kuris, 1996; Bax et al., 2001). Top-down control ("biocontrol") of invaders may be feasible for some introduced species by introducing predators from the invader's native range. More appealing is biocontrol via a native predator that learns to consume the invader, which eliminates the risk of unforeseen consequences for local species and communities that may arise from introducing a non-native predator (Pemberton and Strong, 2000).

In this study we tested the response of native predators to an invasive marine bivalve, the Asian mussel *Musculista senhousia* (Mollusca: Bivalvia: Mytilidae). The Asian mussel is native to the West Pacific from Siberia to Singapore, but has been introduced to New Zealand, Australia, the Mediterranean Sea, and to the southwestern coast of North America (Morton, 1974). *M. senhousia* was first recorded in southern California in the 1960s and mussel densities now exceed 10,000 m^{-2} in portions of San Diego Bay and Mission Bay (Crooks and Khim, 1999; Dexter and Crooks, 2000). Asian mussels inhabit the top 15–25 mm of sediment and are most abundant in eelgrass *Zostera marina* beds where they anchor themselves to eelgrass rhizomes. *M. senhousia* reduces eelgrass leaf and rhizome elongation rates by depositing feces and pseudofeces (Morton, 1974) and by forming a conspicuous byssal mat when densities exceed ca. 1500 m^{-2} (Reusch, 1998). Both eelgrass loss and byssal mat formation alter native community structure in southern California (Crooks and Khim, 1999).

Several predators native to southern California consume Asian mussels, including the festive murex *Pteropurpura festiva* (a muricid gastropod; Reusch, 1998), fishes such as yellowfin croaker (*Umbrina roncador*),

spotfin croaker (*Roncador stearnsii*), and sargo (*Anisotrmus davidsonii*) (Crooks, 2002), the California spiny lobster *Panulirus interruptus* (Reusch, 1998), and wading birds such as the willet (*Catoptrophorus semipalmatus*) and marbled godwit (*Limosa fedoa*) (Crooks, 2002). The gastropod *P. festiva* likely is the dominant predator of Asian mussels in southern California's subtidal waters: up to 65% of Asian mussels transplanted to San Diego Bay were consumed by *P. festiva* within 2 wk (Reusch, 1998). Relative predation rates on mussels by this drilling snail were higher in eelgrass habitat than outside of eelgrass, and *P. festiva* aggregated in areas of high mussel density and preferred Asian mussels to the native bivalve *Chione undatella* (Reusch, 1998). In the intertidal zone, wading birds rapidly decimated experimental Asian mussel patches in Mission Bay (Crooks, 2002). Thus, on a local scale native predators may confer invasion resistance to *M. senhousia* on southern California communities (Reusch, 1998). However, it is unknown whether Asian mussel proportional mortality in southern California is density-dependent and whether variability in eelgrass structural complexity influences the responses of native predators to this invasive species. This information is important to determine the conditions under which local communities may be able to resist Asian mussel invasion and for investigating the feasibility of using native predators to regulate local Asian mussel populations.

We conducted field experiments in shallow eelgrass beds to determine if Asian mussel proportional mortality is density-dependent, and whether increasing levels of eelgrass above-ground and below-ground structure influence Asian mussel proportional mortality at a single site in Mission Bay, California in which *P. festiva* is abundant. Because *P. festiva* accounted for nearly all mussel mortality in most of our experiments, we also examined the influence of eelgrass structure on the functional and aggregative response of *P. festiva* to *M. senhousia*.

2. Methods

Field experiments were conducted from July 2002–March 2004 in eelgrass beds at Ventura Cove, a small embayment in Mission Bay, San Diego, California, USA (Fig. 1). Water temperatures during the experiments ranged from 17 to 21 °C, salinity was ca. 34 psu, and water depths ranged from 0–1.5 m. *M. senhousia* are rare in Ventura Cove, with densities ranging from 0 to 50 m^{-2} (versus densities of >10,000 m^{-2} in other Mission Bay eelgrass beds; Kushner and Hovel, unpub-
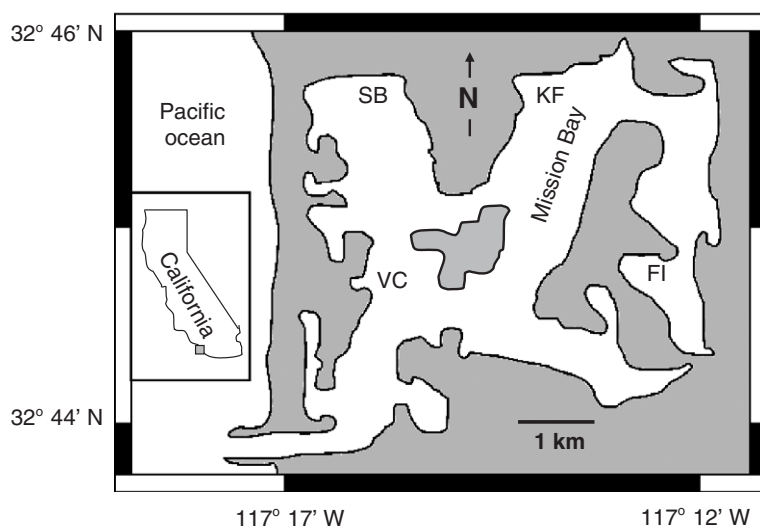
Fig. 1. Map of Mission Bay, California, USA. All *Musculista senhousia* mortality experiments were conducted in Ventura Cove (VC). Mussels for experiments were collected near the Kendall–Frost marine reserve (KF), and pilot experiments on Asian mussel mortality were conducted at Sail Bay (SB) and Fiesta Island (FI).

lished data). Ventura Cove features a rock jetty that acts as a source of *P. festiva* to the neighboring eelgrass bed in which we conducted our experiments.

We collected Asian mussels for experiments from the eelgrass bed adjacent to the Kendall–Frost Marine Reserve in Mission Bay (ca. 3 km from Ventura Cove; Fig. 1) using SCUBA and a PVC suction dredge. Mean shell height (SH) of *M. senhousia* used in experiments was 16.4 mm+0.16 SE. Juvenile mussels (<10.0 mm SH) were relatively rare in collections, and therefore were not used in our experiments.

2.1. Effects of mussel density and eelgrass shoot density on mussel proportional mortality

We tested whether Asian mussel proportional mortality is density-dependent at Ventura Cove and whether eelgrass shoot density influences the relationship between mussel density and mussel proportional mortality by exposing mussels to predators in small (25 cm diameter × 2 cm high) circular artificial seagrass units (ASUs). Small ASUs were used to simulate small, isolated patches of mussels that were found in Ventura Cove upon initial sampling of the eelgrass bed (Kushner, unpublished data). ASUs were made of PVC rings to which 36 kg test monofilament fishing line was strung in a criss-cross fashion to simulate eelgrass rhizomes. Fiberglass mesh was secured to the bottom of each plot with a stainless steel hose clamp. We then tied green polypropylene ribbon to the fishing line to simulate eelgrass shoots. Each shoot had 2 simulated

blades that were 25 cm long, which approximated mean shoot lengths in Ventura Cove in spring 2004 ($=30.1+11.0$ cm SE, $n=24$ core samples). Mussels were exposed to predators in plots containing 0, 15, 30, and 90 simulated shoots with equivalent densities of 0, 300, 600, and 1800 shoots m^{-2}, which encompassed the range of shoot densities found in Mission Bay in spring 2004 (range$=235$–1700 shoots m^{-2}, mean$=1098+73$ shoots m^{-2} SE, $n=24$ core samples: Hovel, unpublished data). Within each shoot density treatment, we exposed mussels to predators at six levels of mussel density: 40, 80, 160, 320, 640, 1280 mussels m^{-2} (2, 4, 8, 16, 32, and 64 mussels per plot, respectively). Each experimental trial consisted of 24 experimental plots (four shoot densities × six mussel densities) and 4 predator-exclusion (caged) plots containing 32 mussels to control for mussel mortality due to handling and sources other than predation. We conducted four trials of the experiment in summer (July–September) 2002, for a total of $n=112$ plots.

For each trial we filled plots with sediment from Ventura Cove (a mixture of ca. 75% sand and 25% mud) and placed mussels into plots by haphazardly inserting then into the sediment vertically until the anterior lip of the shell was 1 mm above the sediment surface (Reusch, 1998). Sediment was sieved through a 5 mm mesh screen before placing it into plots to remove naturally occurring prey and detritus. For each trial, ASUs were laid out 2 m apart within the eelgrass bed in random order along a 60 m transect parallel to, and ca. 10 m from the rock jetty. We placed

plots along a transect to standardize the distance to the rock jetty, which was the primary source of *P. festiva*. In pilot experiments in which Asian mussels were exposed to predators in plots for 7–10 d, nearly all Asian mussels (>95%) in Ventura Cove were eaten by predators, with *P. festiva* accounting for ca. 90% of mussel mortality. We therefore allowed predators to consume Asian mussels for 48 h to generate mortality levels meaningful for analysis. After 48 h, plots were retrieved and mussels were scored as: alive, crushed (dead with part or all of one or both valves broken), drilled (dead with a small round hole in one valve), dead but intact, or missing. Crushed valves are indicative of predation due to crustaceans, and drilled valves indicate predation by *P. festiva* (Reusch, 1998). We also measured the aggregative response of *P. festiva* to *M. senhousia* density by counting the number of *P. festiva* found within each plot when plots were retrieved. The presence of other potential predators in plots also was noted.

An additional two trials of this experiment were conducted by a marine ecology class at San Diego State University in March 2004. Methodology was identical to that described above, except that two shoot densities (0 and 600 shoots m^{-2}) were used rather than four shoot density treatments. Thus there were two replicate plots for each combination of mussel density (6 levels) and shoot density (2 levels) in each trial, plus 6 control (=caged) plots in each trial. The tidal range for spring 2004 experiments was much greater than for summer 2002 experiments, such that experimental and control plots in spring 2004 were emersed for several hours over the course of each trial. In contrast, plots used in summer 2002 remained at least 0.25 m underwater for the duration of each trial. We did not statistically compare results from 2002 and 2004 due to confounding between tidal range and time.

We calculated mussel proportional mortality by summing the number of crushed, drilled, and missing mussels in each plot and dividing this by the starting density in the plot. Dead but intact mussels, killed by unknown causes, accounted for <5% of mussel deaths and were eliminated from the analysis. We considered missing mussels as being eaten by predators because very few mussels were missing from control plots, and because predators such as fishes, crustaceans, and birds can carry off mussels when consuming them (Crooks, 2002). Inclusion or exclusion of missing mussels from analyses did not change the results. We used an analysis of covariance (ANCOVA) to test whether Asian mussel proportional mortality varied with simulated eelgrass shoot density (factor) and with mussel

density (covariate). Cochran's test was used to test for heterogeneous variances (Underwood, 1997) in this and all subsequent analyses, and data were log transformed when necessary to meet the assumptions of ANCOVA. We also used ANCOVA to determine how the number of *P. festiva* varied with simulated shoot density and mussel density. When *P. festiva* density and mussel density were significantly correlated, we performed linear regressions and visually evaluated the residuals for randomness, and fit non-linear (quadratic) models to our data if residuals appeared non-random (Chatterjee et al., 2000).

2.2. Effects of mussel density and simulated eelgrass rhizome density on mussel proportional mortality

Asian mussels anchor themselves to each other and to the base of eelgrass shoots. Therefore, eelgrass below-ground habitat structure may influence predation rates on mussels. To more completely determine how *Z. marina* habitat structure may influence mussel proportional mortality, we tested how simulated below-ground eelgrass habitat structure influences Asian mussel proportional mortality by exposing mussels to predators in the same ASUs described above, but to which were affixed two levels of simulated rhizome density. We strung extra monofilament fishing line within plots to create an additional treatment in which simulated rhizome density was ca. two times the level used in the simulated shoot density experiment described above. For this experiment, simulated shoot density was standardized among all plots at 1000 m^{-2}. Though the three dimensional nature of the eelgrass rhizome mat made it difficulty to relate simulated rhizome density to naturally occurring levels, to determine if the two simulated rhizome density levels likely provided meaningfully different conditions within plots, we measured the size of the spaces (longest linear dimension) that were formed between the criss-crossed monofilament ($n=10$ measurements per plot × 3 plots per treatment=30 measurements per treatment). Space sizes averaged 2.73+0.11 cm and 1.66+0.09 cm SE in the low and high rhizome density treatments, respectively, which were significantly different in an ANOVA ($df=1$, $F=41.56$, $P<0.001$). Four trials of this experiment were conducted between March and April 2003 for a total of 48 experimental plots (2 simulated rhizome densities × 6 mussel densities × 4 trials=48 plots). Asian mussel proportional mortality and *P. festiva* aggregation were quantified as in the simulated shoot density experiment. We used ANCOVA to test how mussel proportional mortality varied with simulated rhizome density and mussel density.

2.3. Functional response of P. festiva to Asian mussel density

P. festiva were by far the most important predator of Asian mussels in most of our experiments. We therefore tested the functional response of P. festiva to Asian mussel density in two levels of simulated eelgrass habitat structure by caging two P. festiva in plots containing 2, 4, 8, 16, 24, or 32 mussels (40, 80, 160, 320, 480, and 640 mussels m^{-2}, respectively). Plots contained either 300 or 1800 shoots m^{-2}. P. festiva used in this experiment were held in laboratory aquaria with recirculating seawater and fed Asian mussels ad libitum until 48 h before their use in the field. In the field, P. festiva were allowed to eat Asian mussels for 48 h and plots then were retrieved and the number of live, dead and drilled mussels were counted as described above. An additional 6 caged control plots (three at 300 shoots m^{-2} and three at 1800 shoots m^{-2}) containing 32 mussels and no predators were included in each trial. We conducted 5 trials of this experiment from May to June 2003, for a total of $n=60$ experimental plots (6 mussel densities $\times$ 2 shoot densities $\times$ 5 trials = 60 plots).

To determine which of three common functional response models (linear [Type I], hyperbolic [Type II], or sigmoid [Type III]) provided the best fit to the data, we used a general functional response model (Real, 1979; Lipcius and Hines, 1986; Mistri, 2003):

$$N_a = KN^\beta / X + N^\beta$$

where N_a=number of prey eaten, K=maximum feeding rate, N=initial prey density, X=the density of prey at which $N_a=0.5K$, and β=the parameter associated with the form of the functional response curve (Real, 1979; Lipcius and Hines, 1986). The curve is linear when $\beta=0$, hyperbolic when $\beta=1$, and sigmoidal when $\beta>1$. Estimates of β were derived for each shoot density by performing a linear regression on a log transformation

Table 1a
Analysis of covariance (ANCOVA) for the effects of Asian mussel Musculista senhousia density and simulated eelgrass shoot density on Asian mussel proportional mortality in summer 2002

(A)				
Source	df	MS	F	P
Mussel density (MD)	1	2.04	24.0	<0.001
Shoot density (SD)	3	0.09	1.08	0.36
MD × SD	3	0.09	1.07	0.37
Residual	88	0.08		
Total	95			

Table 1b
Analysis of covariance (ANCOVA) for the effects of Asian mussel Musculista senhousia density on Asian mussel proportional mortality in summer 2002

(B)				
Source	df	MS	F	P
Mussel density (MD)	1	0.22	7.56	0.01
Rhizome density (RD)	1	0.03	1.07	0.31
MD × RD	1	0.01	0.43	0.52
Residual	44	0.03		
Total	47			

of the general functional response model (Real, 1979), and these estimates were tested against 0 and 1 with standard t-tests (Lipcius and Hines, 1986; Lipcius et al., 1998; Chatterjee et al., 2000; Mistri, 2003).

3. Results

3.1. Overall Asian mussel mortality rates

In our experiments exposing Asian mussels to predators in the summer of 2002, mean proportional mussel mortality in experimental plots after 48 h was 56% (+0.03 SE), with ca. 48% of all mussels showing evidence of being eaten by P. festiva. A total of ca. 1% of mussels were crushed (evidence of crustacean or fish predation), 4% were dead but intact (i.e., died of unknown causes), and 15% were missing. In control plots, a total of 95% of mussels were alive, 2% were missing, and 3% died of unknown causes. When mussels were exposed to predators in the spring of 2004, 7% of mussels showed evidence of being preyed upon by P. festiva, 1% of mussels were crushed, and 2% died of unknown causes. Fifty seven percent of all Asian mussels were missing from experimental plots after 48 h, whereas only 5% were missing from caged control plots. The predominant mussel predators in spring 2004 trials likely were wading birds, many of which were observed foraging in experimental plots at low tide. We assumed that bird predation was responsible for missing mussels in experimental plots, because birds were common at our site, they typically consume mussels whole (Crooks, 2002), and because control plots had high mussel survival (95% of all mussels in control plots were alive after 48 h).

3.2. Effects of Asian mussel density and eelgrass structure on mussel proportional mortality

In summer 2002, Asian mussel proportional mortality did not vary significantly among simulated eelgrass shoot density treatments, but proportional
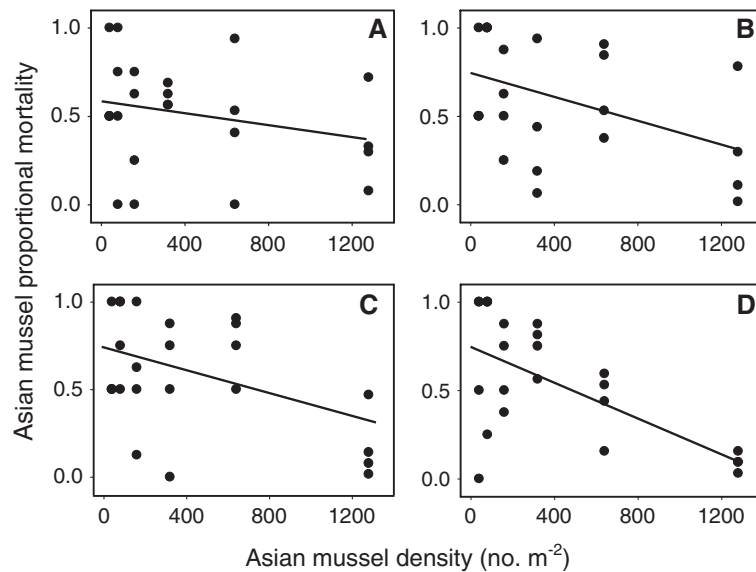
Fig. 2. *Musculista senhousia* proportional mortality vs. *M. senhousia* density for four levels of simulated *Zostera marina* shoot density (A=0, B=300, C=600, and D=1800 shoots m^{-2}). Best-fit lines were generated by linear regression following a significant effect of Asian mussel density on mussel proportional mortality in an ANCOVA.

mortality decreased with mussel density and there was no interactive effect of shoot density and mussel density on mussel proportional mortality (Table 1a, Fig. 2). Similarly, in experiments testing the effect of simulated rhizome density on Asian mussel proportional mortality, mussel proportional mortality did not vary among levels of simulated structure, but proportional mortality decreased with mussel density and there was no interactive effect of rhizome density and mussel density on mussel proportional mortality (Table 1b, Fig. 3A).

In March 2004, Asian mussel proportional mortality did not differ among the two levels of simulated shoot density, but there was a weak inverse correlation between mussel proportional mortality and mussel density, and there was no interactive effect of shoot density and mussel density on mussel proportional mortality (ANCOVA: shoot density: $F_{1,44}=0.6$, $P=0.45$; mussel density: $F_{1,44}=4.7$, $P=0.04$; shoot density × mussel density: $F_{1,44}=0.4$; $P=0.52$; Fig. 3B).

3.3. Aggregative response of P. festiva to Asian mussel density

There was a significant interactive effect of simulated shoot density and mussel density on the density of *P. festiva* in experimental plots (Table 2a) suggesting that the relationship between predator density and mussel density differs as a function of shoot density. We therefore performed separate regressions of *P. festiva* density
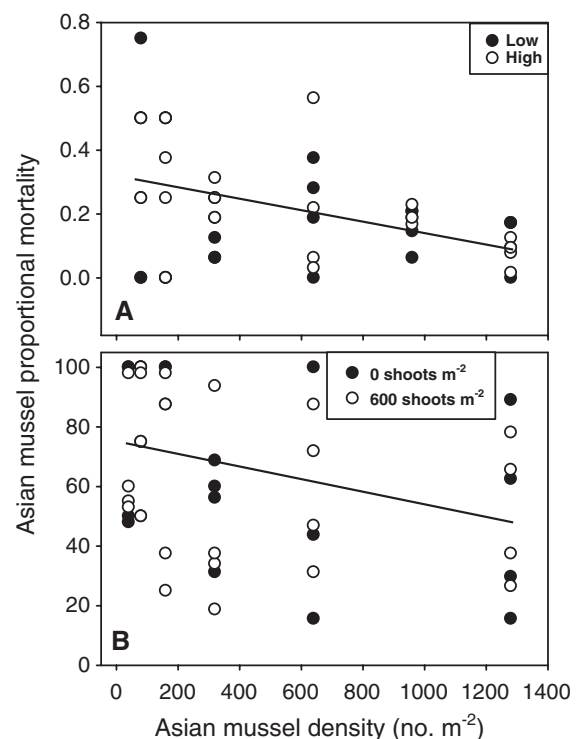

Fig. 3. (A) *Musculista senhousia* proportional mortality vs. *M. senhousia* density for (A) two levels of simulated *Zostera marina* rhizome density (summer 2002), and (B) two levels of simulated *Z. marina* shoot density (spring 2004). Best-fit lines were generated by linear regression for all data in graphs following a significant effect of Asian mussel density on mussel proportional mortality in an ANCOVA.

Table 2a

Analysis of covariance (ANCOVA) for the effects of Asian mussel *Musculista senhousia* density and simulated eelgrass shoot density on the density of the predatory snail *Pteropurpura festiva* in summer 2002

(A)

Source	df	MS	F	P
Mussel density (MD)	1	1225.1	36.9	<0.001
Shoot density (SD)	3	22.8	0.69	0.56
MD × SD	3	119.9	3.6	0.02
Residual	88	33.2		
Total	92			

Table 2b

Results of linear and quadratic regressions of *P. festiva* density on Asian mussel density for four levels of simulated eelgrass shoot density in summer 2002

(B)

Shoot density (no. m^{-2})	F	P	r^2	Model
0	10.6	<0.01	0.29	Quadratic
300	21.4	<0.001	0.47	Linear
600	11.6	<0.01	0.32	Quadratic
1800	19.9	<0.001	0.45	Quadratic

Model=best fit model based on analysis of residuals and coefficient of determination.

on mussel density for each level of shoot density (Fig. 4). There was a significant linear relationship between *P. festiva* density and Asian mussel density when shoot densities were 300 m^{-2}. However, for all other levels of shoot density, residuals from linear regressions were non-random. Quadratic models provided significant fits to these data, generated random residuals, and generated higher r^2 values than did linear models (Table 2b, Fig. 4B–D). Curves generated by quadratic models were parabolic, indicating that the number of *P. festiva* in plots was maximal at an intermediate mussel density, and therefore that the ratio of *P. festiva* to *M. senhousia* decreased from intermediate to high levels of mussel density. In plots in which we varied simulated rhizome density, there was a significant effect of mussel density on the density of *P. festiva* in experimental plots, but no

effect of simulated rhizome density on *P. festiva* density was detected and there was no interaction (ANCOVA: mussel density: $F_{1,44}=24.0$, $P<0.001$; rhizome density: $F_{1,44}=0.5$, $P=0.48$; rhizome density × mussel density: $F_{1,44}=0.4$; $P=0.53$). A quadratic model (=parabolic curve) best fit the relationship between *P. festiva* density and Asian mussel density (Fig. 5).

3.4. Functional response of P. festiva to Asian mussel density

In plots containing simulated shoot densities of 300 m^{-2}, β was 0.3, which was not significantly different than 0, but was significantly <1, indicating that the functional response of *P. festiva* to Asian mussel density at relatively low shoot density levels
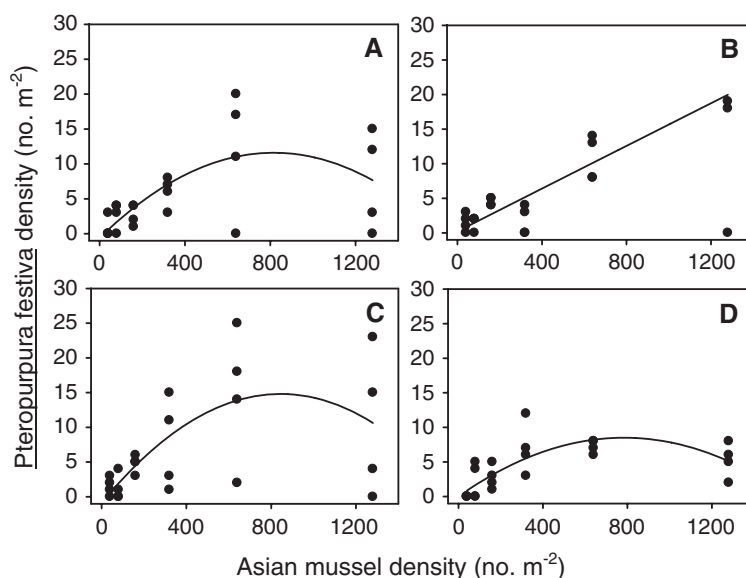

Fig. 4. *Pteropurpura festiva* density vs. *Musculista senhousia* density for four levels of simulated *Zostera marina* shoot density in summer 2002 (A=0, B=300, C=600, and D=1800 shoots m^{-2}). Best-fit lines were generated by linear or non-linear regression following a significant interactive effect of Asian mussel density and simulated shoot density on *P. festiva* density in an ANCOVA.
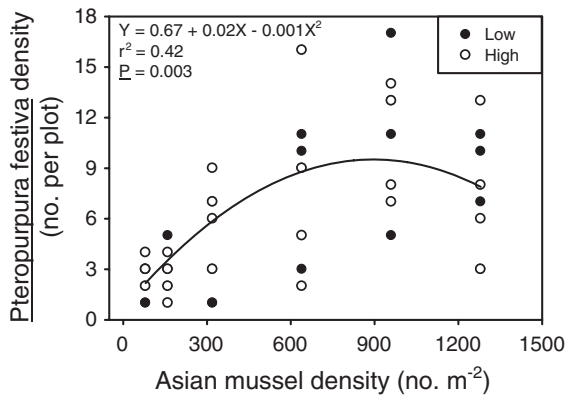
Fig. 5. *Pteropurpura festiva* density vs. *Musculista senhousia* density for two levels of simulated *Zostera marina* rhizome density in summer 2002 (black circles=low, white circles=high). Best-fit line was generated by non-linear regression following a significant effect of Asian mussel density on *P. festiva* density in an ANCOVA.

is linear (Fig. 6A). However, when plot shoot densities were 1800 m^{-2}, β was 0.9, which was significantly greater than 0, but not significantly different than 1, indicating a type II (hyperbolic) functional response of *P. festiva* to Asian mussel density at relatively high levels of shoot density (Fig. 6B).

4. Discussion

The Asian mussel *M. senhousia* has been introduced to several coastlines worldwide and is now a conspicuous, habitat-altering member of the benthic community in southern California. In this study we determined (i) whether *M. senhousia* proportional mortality depends on mussel density, and (ii) whether simulated eelgrass habitat structure influences this relationship and influences the behavioral response of a native gastropod predator to mussels in Mission Bay, California. We found that Asian mussel proportional mortality is inversely density-dependent and that this relationship does not vary with the amount of eelgrass aboveground or below-ground structure. However, simulated eelgrass habitat structure influenced the functional and aggregative response of the gastropod predator *P. festiva* to mussels. *P. festiva* density increased with Asian mussel density in plots with low simulated habitat structure, but the relationship between *P. festiva* density and Asian mussel density was parabolic at zero, intermediate and high levels of habitat structure. Additionally, *P. festiva* exhibited a type I (linear) functional response to Asian mussels at low levels of simulated habitat structure, and a type II (hyperbolic) functional response to Asian mussels at high levels of structure. Asian mussels may experience extremely high mortal-

ity rates due to native predators in the subtidal and intertidal zone of Mission Bay. However, our results suggest that over short time scales, Asian mussel proportional mortality decreases with mussel density and that increasing eelgrass habitat structure alters the behavioral response of native predators to Asian mussels. Whether local communities may be able to resist Asian mussel invasions will depend on the interactive effects of predator density and diversity, *M. senhousia* settlement and growth rates, and eelgrass habitat structure.

4.1. Asian mussel proportional mortality and eelgrass habitat structure

The presence of structure in marine habitats such as kelp forests (Anderson, 2001), seagrass beds (Pile et al., 1996; Hovel and Lipcius, 2001), coral reefs (Hixon and Carr, 1997; Forrester and Steele, 2004), and oyster reefs (Grabowski, 2004) typically results in reduced prey mortality because structural elements interfere with predator search and capture of prey. Habitat structure also may alter the relationship between prey density and prey proportional mortality. For instance, kelp perch proportional mortality was inversely density-dependent
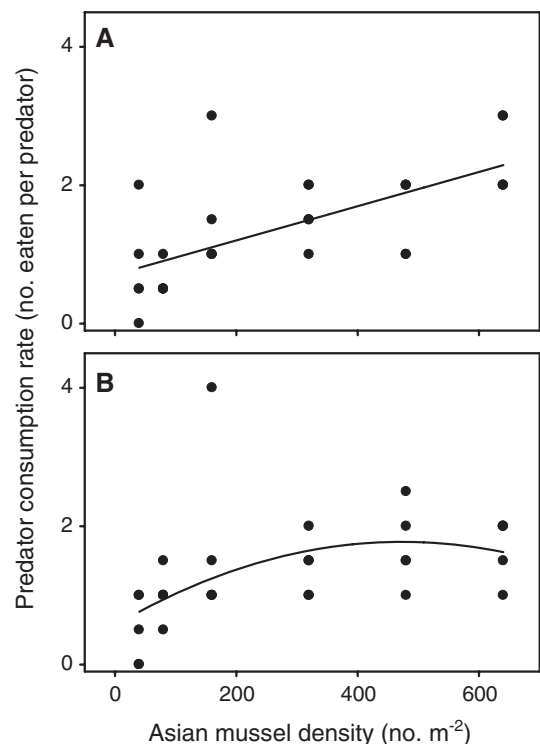

Fig. 6. Functional response of *Pteropurpura festiva* to *Musculista senhousia* density for two levels of simulated *Zostera marina* shoot density in summer 2002 (A=300, B=1800 shoots m^{-2}).

in experimental arenas with low levels of kelp structure, but was density-independent in arenas with high levels of kelp structure (Anderson, 2001). Proportional mortality of the bridled goby *Coryphopterus glaucofraenum* was density-dependent in areas with little coral shelter, but was density-independent in areas with abundant shelter (Forrester and Steele, 2004). In these studies, the addition of habitat structure resulted in additional refuge for prey and altered proportional prey mortality at low or high levels of prey density. In our study, Asian mussel proportional mortality was unaffected by variation in simulated eelgrass shoot density despite the fact that shoot densities ranged from 0–1800 shoots m^{-2}, and Asian mussel proportional mortality was inversely density-dependent at all levels of eelgrass structure. The lack of an effect of habitat structure on mussel mortality in part may be explained by the foraging strategy of *P. festiva*, which accounted for the majority of mussel deaths in summer 2002. These gastropod predators likely seek out prey via chemical and tactile cues, rather than by visual cues, and their relatively small shell height (ca. 2.5–4.5 cm) may allow them to easily move through dense eelgrass. Reusch (1998) found that predation rates of *P. festiva* on Asian mussels were higher in eelgrass habitat than in areas of unvegetated sediment, possibly because *P. festiva* prefer to forage in eelgrass for protection from higher-order predators. Though predation rates on Asian mussels in our experiments were not reduced in the absence of simulated eelgrass shoots, gaps in eelgrass habitat created by our unvegetated plots, which were 0.05 m^2 in size, may have been too small to deter *P. festiva* and other predators from entering the plots.

Mussel proportional mortality also was inversely density-dependent and was unaffected by simulated eelgrass structure in spring 2004 experiments in which wading birds such as willets and godwits likely were the chief predator of mussels (authors' personal observation). Though we could not definitely determine that bird predation caused a large fraction of mussels to be missing from plots after 48 h, birds swallow mussels whole and leave few shell fragments on the sediment (Crooks, 2002), and our caged control plots had close to 100% mussel survival. Wading birds appeared to forage on mussels when plots were emersed, and apparently the naturally occurring and simulated *Z. marina* shoots that lay over our plots at low tide did not provide additional refuge to Asian mussels.

Below-ground habitat structure and the physical structure of sediments may alter predation rates on bivalves (Blundon and Kennedy, 1982; Peterson, 1982) as well as relationships between bivalve density

and proportional mortality (Lipcius and Hines, 1986). Blue crabs *Callinectes sapidus* displayed a density-dependent, type III functional response to soft-shelled clams *Mya arenaria* in sand, and an inversely density-dependent (type II) functional response to *M. arenaria* in mud (Lipcius and Hines, 1986). Sandy sediment likely reduced encounter rates between foraging crabs and clams because crabs could not easily penetrate sand with their walking legs to search for clams. In our experiments, mussel proportional mortality rates were similar and were inversely density-dependent at two levels of simulated below-ground structure, perhaps because *P. festiva* can use their long proboscis to attack bivalves through small spaces. Eelgrass below-ground structure likely does not deter predation on Asian mussels in naturally occurring *Z. marina* beds, because Asian mussels do not burrow deeply to avoid predators but instead inhabit the upper sediment layer where they attach themselves to the base of eelgrass shoots with byssal threads (Reusch, 1998). It is also possible that we did not vary simulated rhizome density over a sufficient range to detect effects of below-ground structure on mussel mortality, though our artificial plots appeared to be reasonable approximations of sparse and dense levels of below-ground eelgrass structure in southern California.

4.2. P. festiva behavior and eelgrass habitat structure

Quantifying predator numerical and functional responses to prey density is an important step in determining if predators can regulate populations. Population growth of prey may be regulated if predator consumption rates are density-dependent (Murdoch, 1969; Lafferty and Kuris, 1996). The functional response describes a predator's consumption rate as a function of prey density over relatively short time scales (Holling, 1959). A type III functional response is potentially regulating at low to intermediate prey densities (i.e., prey densities under the accelerating portion of the curve). The type II, or decelerating functional response of predators to prey also is common and does not result in prey population regulation. However, predator aggregation at areas of high prey density may result in density-dependent mortality of prey, even if per-predator rates of consumption do not accelerate as prey density increases (e.g., Anderson, 2001).

We found that *P. festiva* aggregated in plots of high mussel density but that the rate at which individual *P. festiva* consumed Asian mussels did not accelerate with mussel density. Additionally, the aggregative and functional responses of *P. festiva* to Asian mussel density

varied with levels of simulated eelgrass structure. *P. festiva* density peaked at intermediate levels of mussel density at zero, intermediate, and high levels of simulated structure, but the density of this predator increased linearly with mussel density at low levels of structure. Explanations for this result are not immediately obvious. *P. festiva* density may be reduced at high levels of Asian mussel density if aggregations of *P. festiva* attract higher-order predators that consume gastropods. Potential predators of gastropods include spiny lobsters, wading birds, crabs, octopuses, and large fishes, all of which were found at our site (authors' unpublished data). Mutual interference among *P. festiva* also may result in a non-linear aggregative response of predators to prey. Additional experiments examining *P. festiva* behavior will be necessary to determine how these patterns may be established and if they are consistent.

We found that the functional response of *P. festiva* to Asian mussel density was linear (Type I) in low shoot density plots, but was hyperbolic (Type II) in high shoot density plots. Thus, the proportion of Asian mussels eaten per plot did not change with mussel density at low levels of simulated eelgrass habitat structure, but decreased with mussel density at high levels of structure. These results contrast those of Anderson (2001) who found that the proportion of kelp perch *Brachyistius frenatus* consumed by kelp bass *Paralabrax clathratus* in experimental pools decreased with perch density at low levels of kelp structure, but did not change with perch density at higher levels of kelp structure. Kelp perch were able to reduce per capita mortality at high perch density by schooling, but experienced high per capita mortality at low perch densities unless enough kelp habitat structure was present to serve as a refuge (Anderson, 2001). We hypothesized that results would be similar in our experiments if dense seagrass interfered with *P. festiva* movement and detection of prey. However, increases in seagrass structure did not reduce the number of mussels eaten per predator. One possible explanation is that *P. festiva* movement rates, and consequently the rates at which they encounter prey, are higher in dense seagrass because dense seagrass confers protection to *P. festiva* from higher-order predators (see also Reusch, 1998). We speculate that predators such as birds, fishes, crabs, lobsters and octopuses, all of which are found at our site, may forage on gastropods efficiently when shoot densities are low, but not at high levels of habitat structure. Thus, *P. festiva* may have been more willing to move around plots and search for prey under the cover of dense seagrass shoots, such that per capita mortality

rates of mussels were high at low mussel densities only when many simulated shoots were present.

4.3. Invasion resistance and biocontrol of M. senhousia

Previous studies in marine systems have found that dominant predators can regulate the abundance of native fish (Hixon and Carr, 1997; Steele, 1997) and invertebrate (Lipcius and Hines, 1986; Eggleston et al., 1992) prey, by aggregating at areas of high prey density (Hassell and May, 1974; Anderson, 2001) or by accelerating per-predator consumption rates with prey density (e.g., Wright et al., 1993; Forrester and Steele, 2004). Despite the prevalence of marine invasions, far fewer studies have explored the ability of predators, particularly native predators, to regulate the abundance of non-native prey (Lafferty and Kuris, 1996). Predators can be used to control non-native pests in two ways: (i) predators may be introduced, or their densities may be enhanced, to control established pest populations (Sheldon and Creed, 1995; Settle et al., 1996); or (ii) their presence may confer "invasion resistance" on native communities (Baltz and Moyle, 1993; Reusch, 1998). Though the scope of our study was too limited to suggest whether Asian mussel populations can be regulated by native predators, our results and those of others suggest that, for the introduced pest *M. senhousia* in southern California, native predators may be able to confer invasion resistance to local communities (Reusch, 1998), but are unlikely to be able to control large, established *M. senhousia* populations. We found that proportional mortality of Asian mussels was inversely density-dependent at a site that probably contains the highest densities of *P. festiva*, the mussel's chief predator, in Mission Bay. Additionally, per capita mortality rates of Asian mussels exposed to *P. festiva* did not increase with mussel density (i.e., a potentially regulating, Type III functional response was not observed). We also have measured *M. senhousia* proportional mortality in artificial seagrass plots at several other sites in Mission Bay where mussel densities average 5000–10,000 m^{-2} (Kushner, unpublished data; Fig. 1) and found <5% mussel mortality after 14 d. These results suggest that *M. senhousia* per capita mortality rates will be low where mussel densities are high, and that Asian mussels may exist at high densities in part to reduce mortality rates in the absence of other defenses such as hard shells or predator-avoidance strategies such as burrowing. At high densities Asian mussels secrete and live within a byssal mat that may confer additional protection from predators, though the pres-

ence of a byssal mat did not reduce mussel mortality rates in field experiments (Reusch, 1998).

In experiments with Asian mussels in laboratory aquaria, Mistri (2003) found that *M. senhousia* mortality rates were reduced when predatory Mediterranean shore crab *Carcinus aestuarii* density was high, presumably due to mutual interference among crabs. Predatory crabs also exhibited a type II functional response to Asian mussels. In our experiments, *P. festiva* density generally increased with Asian mussel density, but the resulting increase in predation pressure on mussels apparently was swamped by mussel density. Given that our highest experimental mussel density (1280 m^{-2}) was an order of magnitude below mussel densities commonly found in Mission Bay sediments, predators such as *P. festiva* are unlikely to be able to substantially reduce established, high density *M. senhousia* populations in southern California so long as mussel recruitment to those populations continues. In contrast, diving duck *Aythya* spp. predation resulted in local extinctions of Asian mussels in a Japanese lagoon, likely due to high seasonal bird abundance and feeding rates (Yamamuro et al., 1998).

Several pieces of evidence suggest that native species may be able to prevent *M. senhousia* invasions at local scales. Our preliminary experiments in Ventura Cove revealed that nearly 100% of Asian mussels placed in plots were eaten by *P. festiva* and other predators after 7–10 d. Reusch (1998) found that up to 65% of Asian mussels transplanted to subtidal areas of San Diego Bay were consumed by *P. festiva* within 14 d. In experimental plots in the intertidal zone of Mission Bay, bird predation reduced Asian mussel density 35 fold compared to caged control plots (Crooks, 2002). One caveat in all of these experiments is that mussels were exposed to predators in small patches at densities substantially less than those found in most locations in southern California, and that predator responses to mussels may differ between small experimental patches and larger, denser mussel aggregations. Though we also exposed Asian mussels to predators in small patches, our approach revealed that mussel proportional mortality rates depend strongly on mussel density. Further experiments are needed to determine how the interaction of mussel patch size and mussel density influence *M. senhousia* mortality rates.

For native predators to be successful at controlling an introduced species, they must learn to consume the introduced species, should prefer the introduced species to native prey, and should increase their feeding rates with density of the introduced prey (Trowbridge, 1995; Lafferty and Kuris, 1996). Even if native predators display these characteristics, many introduced species have extremely high recruitment and growth rates that may allow them to swamp predators. We found that native predators can quickly aggregate to dense Asian mussel patches, and several studies have shown that predation rates on Asian mussels can be extremely high in subtidal and intertidal areas of southern California. However, *M. senhousia* proportional mortality rates were inversely density-dependent and consumption rates of a chief native predator of *M. senhousia* did not accelerate with mussel density. Overall, intertidal or subtidal areas with high seagrass cover and high predator abundance may be resistant to invasion by Asian mussels, but the likelihood that a population of *M. senhousia* will become established will depend on the relative densities of predator and prey, *M. senhousia* settlement and growth rates, and the spatial and temporal scale being considered.

References

Anderson, T.W., 2001. Predator responses, prey refuges, and density-dependent mortality of a marine fish. Ecology 82, 245–257.

Baltz, D.M., Moyle, P.B., 1993. Invasion resistance to introduced species by a native assemblage of California stream fishes. Ecol. Appl. 3, 246–255.

Bax, N., Carlton, J.T., Mathews-Amos, A., Haedrich, R.L., Howarth, F.G., Purcell, J.E., Rieser, A., Gray, A., 2001. The control of biological invasions in the world's oceans. Conserv. Biol. 15, 1234–1246.

Blundon, J.A., Kennedy, V.S., 1982. Refuges for infaunal bivalves from blue crab, *Callinectes sapidus* (Rathbun), predation in Chesapeake Bay. J. Exp. Mar. Biol. Ecol. 65, 67–81.

Carlton, J.T., Thompson, J.K., Schemel, L.E., Nichols, F.H., 1990. Remarkable invasion of San Francisco Bay (California, USA), by the Asian clam *Potamocorbula amurensis*. I. Introduction and dispersal. Mar. Ecol. Prog. Ser. 66, 81–94.

Chatterjee, S., Hadi, A.S., Price, B., 2000. Regression Analysis by Example, 3rd edn. Wiley, New York.

Cohen, A.N., Carlton, J.T., Fountain, M.C., 1995. Introduction, dispersal and potential impacts of the green crab *Carcinus maenas* in San Francisco Bay, California. Mar. Biol. 122, 225–237.

Crooks, J.A., 2002. Predators of the invasive mussel *Musculista senhousia* (Mollusca: Mytilidae). Pac. Sci. 56, 49–56.

Crooks, J.A., Khim, H.S., 1999. Architectural vs. biological effects of a habitat-altering, exotic mussel, *Musculista senhousia*. J. Exp. Mar. Biol. Ecol. 240, 53–75.

Dexter, D.M., Crooks, J.A., 2000. Benthic communities and the invasion of an exotic mussel in Mission Bay, San Diego: a long-term history. Bull. South. Calif. Acad. Sci. 99, 128–146.

Ebeling, A.W., Laur, D.R., Rowley, R.J., 1985. Severe storm disturbances and reversal of community structure in a southern California kelp forest. Mar. Biol. 84, 287–294.

Eggleston, D.B., Lipcius, R.N., Hines, A.H., 1992. Density-dependent predation by blue crabs upon infaunal clam species with contrasting distribution and abundance patterns. Mar. Ecol. Prog. Ser. 85, 55–68.

Forrester, G.E., Steele, M.A., 2004. Predators, prey refuges, and the spatial scaling of density-dependent prey mortality. Ecology 85, 1332–1342.

Grabowski, J.H., 2004. Habitat complexity disrupts predator–prey interactions but not the trophic cascade on oyster reefs. Ecology 85, 995–1004.

Grosholz, E.D., Ruiz, G.M., Dean, C.A., Shirley, K.A., Maron, J.L., Connors, P.G., 2000. The impacts of a nonindigenous marine predator in a California bay. Ecology 81, 1206–1224.

Hassell, M.P., May, R.M., 1974. Aggregation of predators and insect parasites and its effect on stability. J. Anim. Ecol. 43, 567–594.

Hixon, M.A., Carr, M.H., 1997. Synergistic predation, density dependence, and population regulation in marine fish. Science 277, 946–949.

Holling, C.S., 1959. The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. Can. Entomol. 91, 293–320.

Hovel, K.A., Lipcius, R.N., 2001. Habitat fragmentation in a seagrass landscape: patch size and complexity control blue crab survival. Ecology 82, 1814–1829.

Lafferty, K.D., Kuris, A.M., 1996. Biological control of marine pests. Ecology 77, 1989–2000.

Lipcius, R.N., Hines, A.H., 1986. Variable functional responses of a marine predator in dissimilar homogeneous microhabitats. Ecology 67, 1361–1371.

Lipcius, R.N., Eggleston, D.B., Miller, D.L., Luhrs, T.C., 1998. The habitat–survival function for Caribbean spiny lobster: an inverted size effect and non-linearity in mixed algal and seagrass habitats. Mar. Freshw. Res. 49, 807–816.

Mistri, M., 2003. Foraging behaviour and mutual interference in the Mediterranean shore crab, *Carcinus aestuarii*, preying upon the immigrant mussel *Musculista senhousia*. Estuar. Coast. Shelf Sci. 56, 155–160.

Morton, B., 1974. Some aspects of the biology, population dynamics, and functional morphology of *Musculista senhousia* Benson (*Bivalvia, Mytilidae*). Pac. Sci. 28, 19–33.

Murdoch, W.W., 1969. Switching in general predators: experiments on predator specificity and stability of prey populations. Ecol. Monogr. 39, 335–354.

Pemberton, R.W., Strong, D.R., 2000. Safety data crucial for biological control of insect agents. Science 290, 1895.

Peterson, C.H., 1982. The importance of predation and intra- and interspecific competition in the population biology of two infaunal suspension-feeding bivalves, *Protothaca staminea* and *Chione undatella*. Ecol. Monogr. 52, 437–475.

Pile, A.J., Lipcius, R.N., van Montfrans, J., Orth, R.J., 1996. Density-dependent settler–recruit–juvenile relationships in blue crabs. Ecol. Monogr. 66, 277–300.

Race, M.S., 1982. Competitive displacement and predation between introduced and native mud snails. Oecologia 54, 337–347.

Real, L.A., 1979. Ecological determinants of functional response. Ecology 60, 481–485.

Reusch, T.B.H., 1998. Native predators contribute to invasion resistance to non-indigenous bivalve *Musculista senhousia* in southern California, USA. Mar. Ecol. Prog. Ser. 170, 159–168.

Settle, W.H., Ariawan, H., Astuti, E.T., Cahyana, W., Lukman Hakim, A., Hindayana, D., Lestari, A.S., Pajarningsih, S., 1996. Managing tropical rice pests through conservation of generalist natural enemies and alternative prey. Ecology 77, 1975–1988.

Sheldon, S.P., Creed, R.P., 1995. Use of a native insect as a biological control for an introduced weed. Ecol. Appl. 5, 1122–1132.

Steele, M.A., 1997. Population regulation by post-settlement mortality in two temperate reef fishes. Oecologia 112, 64–74.

Trowbridge, C.D., 1995. Establishment of the green alga *Codium fragile* ssp. *tomentosoides* on New Zealand rocky shores: current distribution and invertebrate grazers. J. Ecol. 83, 949.

Underwood, A.J., 1997. Experiments in Ecology: Their Logical Design and Interpretation Using Analysis of Variance. Cambridge University Press, Cambridge [England]; New York, p. xviii, 504.

Vitousek, P.M., Antonio, C.M., Loope, L.L., Westbrooks, R., 1996. Biological invasions as global environmental change–redistribution of species threatens ecosystems, human health and economies. Am. Sci. 84, 468–478.

Vitousek, P.M., D'Antonio, C.M., Loope, L.L., Rejmanek, M., 1997. Introduced species: a significant component of human-caused global change. N.Z. J. Ecol. 21, 1.

Wright, R.A., Crowder, L.B., Martin, T.H., 1993. The effects of predation on the survival and size-distribution of estuarine fishes: an experimental approach. Environ. Biol. Fish. 36, 291–300.

Yamamuro, M., Oka, N., Hiratsuka, J., 1998. Predation by diving ducks on the biofouling mussel *Musculista senhousia* in a eutrophic estuarine lagoon. Mar. Ecol. Prog. Ser. 174, 101–106.