

**THE EFFECTS OF THE INTRODUCED ASIAN MUSSEL *MUSCULISTA*
SENHOUSIA ON NATIVE BIVALVE GROWTH AND SURVIVAL IN
SOUTHERN CALIFORNIA**

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Thesis of Rachel B. Kushner:

Effects of the Introduced Asian Mussel *Musculista senhousia* on Native Bivalve

Growth and Survival in Southern California

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by

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DEDICATION

To my parents, Anita and Harvey Kushner, for their continual support, encouragement, and love that motivates me to accomplish my goals and to be happy

Wisdom is not a product of schooling but of the lifelong attempt to acquire it.

- Albert Einstein

ABSTRACT OF THE THESIS

Effects of the Introduced Asian Mussel *Musculista senhousia* on
Native Bivalve Growth and Survival in Southern California

by

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The frequency of marine introductions in coastal seas and estuaries has increased dramatically in the last several decades. Non-native species often degrade local communities by preying on native species, outcompeting natives for food or space, and modifying habitat. Non-native species also may positively influence native species, if, for example, an introduced species is preferred as prey by native predators. In the coastal waters of southern California, I experimentally tested the hypothesis that the abundant introduced Asian mussel *Musculista senhousia* competitively inhibits the growth of two native bivalve species, but enhances native bivalve survival by providing native predators with an alternative, highly palatable source of prey. To test this hypothesis, I (1) quantified the effect of *M. senhousia* on the growth and survivorship of two native bivalves, *Chione undatella* and *Laevicardium substriatum*, in the absence of predators; (2) quantified predator-induced proportional mortality of *C. undatella* and *L. substriatum* in the presence and absence of *M. senhousia*; and (3) determined if the functional response of an important native predator, the gastropod *Pteropurpura festiva*, to native bivalve density changes in the presence of *M. senhousia*. All experiments were conducted by transplanting Asian mussels and native bivalves to small artificial eelgrass (*Zostera marina*) plots embedded within naturally occurring eelgrass beds in San Diego Bay and Mission Bay.

I found no evidence that Asian mussels competitively reduce growth rates of either native species when predators were excluded from plots. However, survivorship of both species decreased as Asian mussel density increased in the absence of predators. When clams were exposed to predators in increasing Asian mussel densities, predators aggregated in plots of high mussel density, leading to low survival of the thin-shelled *Laevicardium substriatum* but not the thick-shelled *Chione undatella*. Predator foraging behavior also was altered by the presence of Asian mussels: *Pteropurpura festiva* exhibited a type II functional response to *L. substriatum* density in the absence of mussels but a type III functional response in the presence of mussels. Though this suggests that *L. substriatum* may have a refuge from predators in small, high density Asian mussel patches when predator abundance is low, predator aggregation in high mussel density patches results in high proportional mortality of *L. substriatum* at high densities of Asian mussels. In contrast, the thick shells of *Chione undatella* provide this native species with a refuge from predators regardless of Asian mussel density. Overall, my results suggest that Asian mussels reduce survival rates of *Chione undatella* due to competition, and reduced survival rates of *Laevicardium substriatum* due both to competition and predation. Though *M. senhousia* is heavily consumed by native predators in southern California, high densities of Asian mussels, which are common in soft

sediments in Mission Bay and San Diego Bay, appear to reduce the survival and abundance of native bivalves.

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INTRODUCTION

Species introductions have become a global concern among biologists because of their potential negative effects on native faunal and floral communities. Species introductions occur naturally at relatively slow rates due to the movement of organisms beyond home range boundaries. In the marine realm, however, exploration, shipping, travel, and trade of marine organisms have introduced thousands of species to many coastlines at vastly accelerated rates (Carlton and Geller 1993). Despite the increasing attention that marine invasions are receiving, our knowledge of how introduced species alter native communities and how these alterations can be slowed remains very limited (Lafferty and Kuris 1996).

Many introductions have small effects on native communities because non-native species are unable to persist or persist at undetectable numbers (Ruiz et al. 1997). However, some introduced species alter population dynamics and community structure by preying on native species (e.g., the European green crab *Carcinus maenas* reduces the densities of infaunal bivalves on the US west coast: Grosholz and Ruiz 1995), competitively excluding natives (e.g., the introduced snail *Batillaria attramentaria* may replace the native *Cerithidea californica* in Central California by inhibiting its growth and reproduction: Byers 2000), or by modifying habitat (e.g., grazing by periwinkles *Littorina littorea* alters soft sediment substrates: Bertness 1984; see also Carlton 1989, Crooks 2002). Activities of introduced species may harm some species but benefit others. Waterfowl in the Chesapeake Bay have benefited from the consumption of the introduced plant, *Hydrilla verticillata* (Perry 1996) and introduced clam, *Corbicula manilensis* (Perry 1981). Both non-native species now are consumed by waterfowl and their introduction is correlated with increased bird population sizes. The introduced anemone *Nematostella vectensis* reduces spionid polychaete abundance by consuming larvae, but also is heavily consumed by a native grass shrimp (Posey and Hines 1991). *Codium fragile* was introduced to rocky shores of New Zealand where it is consumed and preferred over native *Codium* by some native predators (Trowbridge 1995).

The Asian mussel *Musculista senhousia* is a small mytilid bivalve native to the West Pacific from Siberia to Singapore, but has been introduced to New Zealand, Australia and the southwestern coast of North America (Morton 1974). The Asian mussel that was first detected in southern California in the 1960s (Crooks 1996). Asian mussels anchor themselves to conspecifics with byssal threads and at high densities form a conspicuous byssal mat that may smother native bivalves (Creese et al. 1997, Crooks 1998) and alter seagrass habitat structure (Reusch and Williams 1999). Asian mussels may outcompete suspension feeders for food by reducing phytoplankton abundance in near-bottom waters. In southern California, the presence of *M. senhousia* decreased growth and survivorship of two native suspension-feeding clams, *Chione undatella* and *Chione fluctifraga* (Crooks 1998). In southern California, Asian mussels are found at densities $> 10,000 \text{ m}^{-2}$ in the surface sediments of San Diego Bay and Mission Bay and their presence has dramatically altered benthic habitat structure and community structure in many locations (Crooks and Khim 1999). Asian mussels may have positive and negative effects on the survival and density of native fauna and flora. Asian mussel byssal mats decrease the density of some taxa (specifically, planktonic-developing polychaetes), but increase the densities of other fauna by providing a structured habitat for settlement (Crooks and Khim 1999). Additionally, Asian mussels are consumed by native predators including birds, fish, crustaceans and gastropods in Mission Bay (Crooks 2002) and San Diego Bay (Reusch 1998). In some subtidal areas of southern California, the drilling gastropod *Pteropurpura festiva* (the “festive murex”) is the chief predator of Asian mussels (Reusch 1998, Kushner and Hovel in press). *Pteropurpura festiva* preferred *M. senhousia* to the native bivalve *Chione undatella*, perhaps because the thin shell of Asian mussels reduces handling time (Reusch 1998). Thus, in sites where Asian mussels are abundant, proportional mortality of native bivalves such as *C. undatella* may be reduced. However, any potential benefit of Asian mussel presence to native bivalves will depend on their relative palatability, relative densities, and on predator type and behavior. The overall goal of my study was to determine how Asian mussels influence the growth and survival of native bivalves in southern California. Specifically, I tested the hypothesis that there is a threshold density of Asian mussels above which growth and survivorship of native bivalves is reduced but survival of native bivalves upon exposure to predators is enhanced. To test this, I (1) measured the effects of varying levels of *M. senhousia* densities on growth

and survivorship of two native bivalve species, *Chione undatella* (Sowerby, 1835) and *Laevicardium substriatum* (Conrad, 1837) in the absence of predators; (2) tested how the presence of Asian mussels influences proportional mortality of these two species; and (3) tested the functional response of the predatory gastropod *Pteropurpura festiva* to the density of native *L. substriatum* in the presence and absence of Asian mussels.

METHODS

STUDY SITES

My experiments were conducted in San Diego Bay and Mission Bay, California, USA (Figure 1). San Diego Bay is a 22.5 km long crescent-shaped estuary adjacent to San Diego's downtown area and is heavily used for commercial, military and recreational purposes. Growth and survivorship of natives was investigated in a subtidal mudflat near the center of the bay where average salinity and temperature over the duration of the experiment were 35.2 psu and 19.5 °C respectively.

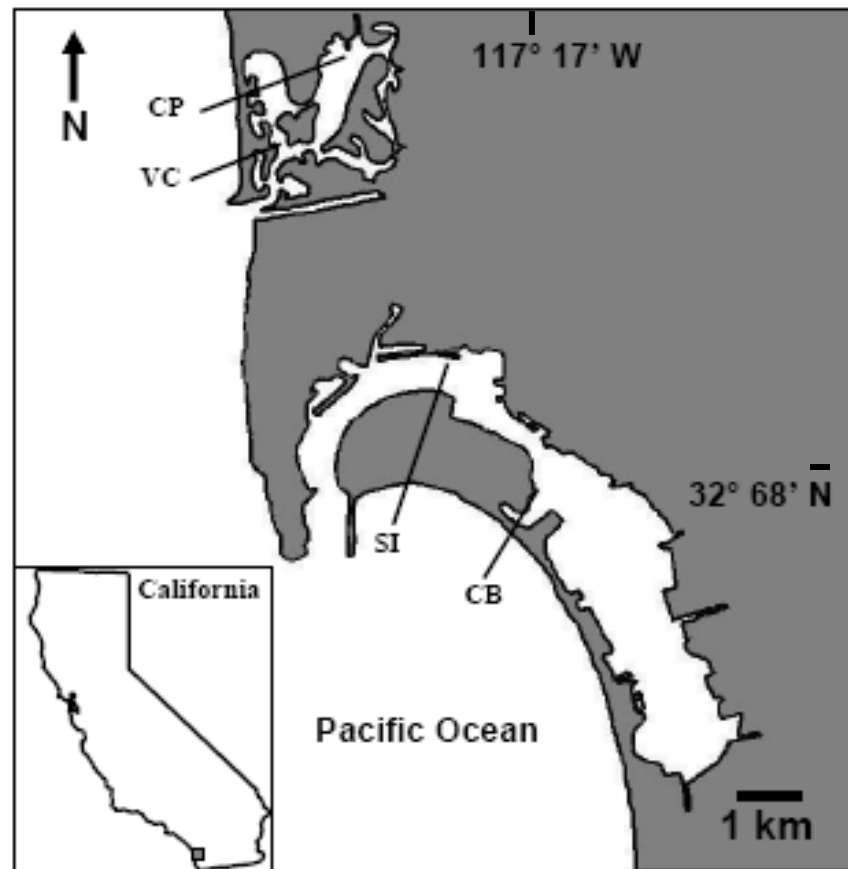


Figure 1. Maps of San Diego Bay and Mission Bay indicating the study and bivalve collection sites. CP=Crown Point; VC=Ventura Cove; SI=Shelter Island; CB=Coronado Bridge. CP and CB were collection sites for *M. senhousia*. SI was the collection site for *L. substriatum* and *C. undatella*. VC and CB were study sites.

Additional experiments were performed at a site near the mouth of Mission Bay, an urbanized and heavily modified 1862 ha coastal lagoon, presently forming the largest aquatic park on the west coast of the United States (Dexter and Crooks 2000). Mission Bay is seasonally hypersaline, with warmer waters and higher salinities in the back of the bay during summer months (Levin 1983). Over the course of the experiments average salinity and temperature were 34.6 psu and 20 °C respectively.

STUDY SPECIES

I used two native clam species in my experiments, the wavy cockle *Chione undatella* (Sowerby, 1835) and the egg cockle *Laevicardium substriatum* (Conrad, 1837). I chose these two species because their distribution, feeding behavior, and burrowing behavior are similar to Asian mussels, but they differ in shell thickness which may influence predation intensity and predator behavior. *Chione undatella* is a thick-shelled clam reaching sizes of ca. 60 mm shell length (SL) and typically is found just below the sediment surface in sand and mud flats near the mouth of bays in waters < 1 m to 50 m deep (Haderlie and Abbott 1980). Their thick shells may allow them to reach a size refuge from predators such as crustaceans, gastropods, birds, and octopuses. *Chione undatella* densities in Mission Bay and San Diego Bay generally are between 7 – 12 individuals per m² (Macdonald 1969; Kushner, unpublished data). *Laevicardium substriatum* is a thin-shelled clam reaching a SH of 37 mm and like *C. undatella* is found just beneath the sediment surface in sand and mud flats (Haderlie and Abbott 1980). *Laevicardium substriatum* densities in San Diego Bay typically are < 10 individuals m⁻² (Kushner, personal observation).

EXPERIMENT 1- CLAM GROWTH AND SURVIVORSHIP

To determine the effect of *M. senhousia* density on the growth and survivorship of native clams, I enclosed native clams and Asian mussels in caged, 0.016m² artificial seagrass units (ASUs) placed on a subtidal mudflat in San Diego Bay. ASUs consisted of a square PVC frame to which monofilament fishing line was strung to form attachment points for artificial seagrass, which consisted of 25 cm lengths of green polypropylene ribbon at a density of 1000 m⁻². Mesh window screening was attached to the bottom of each ASU, and ASUs were enclosed within 1 cm mesh galvanized steel cages to prevent predators from

accessing native clams and Asian mussels. ASUs were filled with sieved sediment to a depth of 7 cm. Each plot contained one native bivalve (either *C. undatella* or *L. substriatum*) and one of ten densities of Asian mussels (0, 125, 250, 500, 750, 1000, 1500, 2000, 3500, and 5000 mussels per m²; n = 12 plots each). Asian mussel densities were chosen to represent low to moderately high densities in San Diego Bay and Mission Bay.

Native clams and *Musculista senhousia* with intact byssal cocoons were collected from San Diego Bay and held in a recirculating seawater system at ambient water temperatures at San Diego State University. To aid in growth determination, native clams were bathed in Calcein, a phosphorescent tag (500 mg/L), for 24 h (Crooks 2001). Clam shell lengths (SL) were measured to the nearest 0.1 mm after tagging with Calcein and clams then were deployed in ASUs no less than 24 h and no more than 72 h later. Mean initial clam lengths (+ 1 SE) for *C. undatella* and *L. substriatum* were 23.0 + 1.0 mm and 12.6 + 0.2 mm respectively. I deployed 20 or 40 ASUs on each of four separate dates between 11 and 25 February 2005. Plots were placed 1 m apart along three 40 m transects parallel to the shoreline. Transect were 10 m apart, and water depth varied from 0.5 – 1 m below MLLW.

I scraped fouling organisms and algae from mesh cages weekly to reduce any caging effects on water flow and food delivery to bivalves. Soak time for plots varied from 61-78 d. Despite cages, some predators, including mud crabs (*Lophopenopus* spp.), spider crabs (*Pyromaia* spp.), and *Cancer* spp crabs were able to enter the plots. Upon completion of the experiment I counted any predators found in plots and categorized mussels and clams as being alive, dead from unknown causes, consumed by predators, or missing. Bivalves were categorized as consumed if at least one valve was crushed or damaged and their flesh was absent. Living clams were measured (SL) to the nearest mm. To determine if *M. senhousia* density affects native clam growth, I used separate multiple regressions (one for each species) with 10 d clam growth rate ($= ((\text{end size} - \text{start size}) / \text{exposure time}) * 10$) as the dependent variable, and mean mussel density and clam initial size as independent variables. During the experiment some Asian mussels died, and therefore Asian mussel density used in the analysis was computed as the mean of the densities at the start and end of the experiment. Clams missing or consumed were deleted from the growth analysis and therefore sample sizes differed between clam types and treatments. Assumptions of homoscedasticity and

normality were checked with Cochran's test and probability plots, respectively, and I transformed data when necessary for this and all subsequent analyses (Underwood 1997).

To determine if *M. senhousia* density affected the survivorship of native clams, I used logistic regression to test how clam status (alive vs. dead) varied with Asian mussel density. Missing and eaten clams were not included in the analysis. A separate test was performed for each species. Any model not meeting the goodness-of-fit criteria of Hosmer & Lemeshow (1989) was rejected in this and subsequent tests.

Despite the presence of predator exclusion cages, some predators were able to enter ASUs. Predators can affect the behavior of prey and influence growth. To determine if the abundance of predators was correlated with Asian mussel density I performed a linear regression to test if the total predator density at the end of the experiment was related to the mean density of Asian mussels.

EXPERIMENT 2 – PROPORTIONAL MORTALITY OF NATIVE BIVALVES

To determine how the proportional mortality of native bivalves may be influenced by Asian mussel density, I exposed native bivalves and Asian mussels to predators in 0.05 m² ASUs containing three levels of *M. senhousia* density: zero, low (160 m⁻²) and high (640 m⁻²). Each ASU contained eight individuals (160 m⁻²) of either *Chione undatella* (thick shell) or *Laevicardium substriatum* (thin shell). ASUs were placed in subtidal eelgrass habitat in Ventura Cove, a small embayment of Mission Bay (Figure 1). Bivalves were exposed to predators for 5 d in two replicate trials from 11 June to 30 June 2004. Ventura Cove has low densities of *M. senhousia* and *L. substriatum*, moderate densities of *C. undatella* and high densities of the predatory gastropod *P. festiva* (personal observation). Each trial consisted of 3 replicate ASUs of each Asian mussel density treatment plus two control ASUs for each of the two bivalve species (N = 3 ASUs/mussel density/species/trial * 3 mussel densities * 2 clam species * 2 trials = 36 experimental ASUs total). The eight control ASUs consisted of caged ASUs (1 cm mesh size) containing 32 Asian mussels (640 m⁻²) and eight natives (160 m⁻²) to test for effects of handling and non-predator induced mortality on native bivalve survival. Upon recovery of ASUs, Asian mussels and native bivalves were categorized as alive, consumed by gastropods (hole drilled in at least one

valve), consumed by crustaceans (one or both valves chipped or crushed), dead from unknown causes, or missing. Any potential predators found in ASUs were counted.

I used a two-way analysis of variance (ANOVA) to test if clam proportional mortality (= no. dead clams + no. consumed clams + no. missing/ no. at start of experiment) differed between clam species (independent variable) and *M. senhousia* density (independent variable). Separate ANOVAs were used for each species. If the ANOVA results provided strong evidence of an effect of Asian mussel density on clam proportional mortality, I performed LSD pairwise comparisons to determine which treatments differed. I also used ANOVAs to test how the proportion of clams consumed (no. consumed + no. missing/ no. clams at start of experiment) varied with Asian mussel density and clam species. Missing clams were considered consumed by predators because control plots had high survival and recovery for *C. undatella* (100% survival) and *L. substriatum* (91 % survival). I used a two-way, fixed factor ANOVA to investigate the effects of *M. senhousia* density and clam species (independent variables) on predator density (density of predators that colonized the plot and were present at the end of the experiment).

EXPERIMENT 3- ALTERNATIVE PREY AND FUNCTIONAL RESPONSE

To determine how the presence of Asian mussels may alter the response of predators to native clams, I experimentally tested the functional response of *Pteropurpura festiva* to *L. substriatum* density in the presence and absence of Asian mussels. First, in 0.05 m² cage-enclosed ASUs placed subtidally in Ventura Cove I measured *P. festiva* consumption rate of *L. substriatum* at six *L. substriatum* densities (40, 80, 160, 240, 320, and 400 m⁻²). I conducted two, 5 d trials with two ASUs per treatment in each trial from 13 August to 24 August 2004. In a second set of trials also in cage-enclosed ASUs in Ventura Cove, I varied the ratio of *M. senhousia* to *L. substriatum* while keeping the total density of prey constant among treatments (20 individuals/ plot). ASUs contained 10, 20, 30, 50, 70, or 100 % *L. substriatum*. I conducted two, 5 d trials with two ASUs per treatment in each trial from 20 September to 30 September 2004. Three controls consisted of plots containing eight *L. substriatum* (40%) and 12 *M. senhousia* (60%) without predators to test for secondary effects of handling on bivalve mortality.

Before beginning trials, clams collected from San Diego Bay were measured (SL) and randomly assigned to treatments. There was no significant difference in mean clam size among treatments (mean SL = 11.6 mm, SE = 0.3; ANOVA: df = 5,18, F = 0.35, P = 0.88). I collected *P. festiva* from Ventura Cove, held them in a recirculating seawater aquarium, and starved them for 48 h before experiments commenced. Each plot contained two *P. festiva* to maximize probability of consumption. Consumption rate was calculated by enumerating the number of individuals consumed for each prey type per predator per 5d trial.

To test how *P. festiva* consumption rate varied with *L. substriatum* density with and without Asian mussels, I began by linearly regressing the number of *L. substriatum* consumed per predator per ASU on *L. substriatum* density. Separate regressions were performed for ASUs with and without Asian mussels. If residuals from this regression were randomly distributed (as determined visually and with normal probability plots) and the relationship was significant, I considered the relationship linear (Type I functional response). If the linear regression was non-significant or residuals were non-random, I used the following model to distinguish hyperbolic curves (type II functional response) from sigmoid curves (type III functional response):

$$Y = AX^{\beta} / (B + X^{\beta})$$

where Y = proportional clam survival, X = clam density, A = asymptotic survival, B = the value of X at which Y = 0.5A, and β = the parameter associated with the form of the function. The functional response is sigmoid when $\beta > 1$, and hyperbolic when $\beta < 1$ but greater than zero (Real 1979, Lipcius et al. 1998).

The linear form of the above equation is:

$$\log(Y / [A - Y]) = \log(1/B) + \beta \log(X)$$

Thus, a linear regression of $\log(Y / [A - Y])$ on $\log(x)$ yields an estimate of β that can be tested against hypothetical values of 0 or 1 with standard t-tests (Chatterjee & Price 1991, Lipcius et al. 1998).

EXPERIMENT 4- MUSSEL PATCH SIZE

The effect of Asian mussels on relative rates of predation on native clams may depend on the size of the mussel patch in which clams are found. To determine the effects of

mussel patch size on native clam predator-induced mortality, I tethered *C. undatella* and *L. substriatum* in square patches of Asian mussels of three sizes; 0.016 m², 0.25m², and 1 m². Mussel density (= 250 m⁻²) and artificial seagrass shoot density (= 1000 m⁻²) were consistent among all plots. Clams were tethered by gluing a polypropylene ribbon onto one valve and tying the ribbon to the mesh portion in the middle of the ASU. Mussels were haphazardly placed in ASUs and partially buried in the sediment with siphons pointing up. To test the security of the tether and to test secondary effects of the glue on clam survival, four tethered *C. undatella* and three tethered *L. substriatum* were held in a recirculating seawater tank for six days. All native clams survived and were glued to tethers after six days. In the field, experimental plots were placed in a random order along a 20 m transect in a subtidal eelgrass bed in Mission Bay. Bivalves were exposed to predators for 6 d from 7 July to 20 July 2005. Two total trials were performed where each trial consisted of two replicates of each clam species for a total of four replicate patches of each size for each species. Upon completion of the experiment clams were categorized as alive, consumed, missing, or dead from unknown causes. I used a Chi-square test for independence to determine if clam survival (live vs. eaten: dependent variable) is independent of mussel patch size (independent variable) for *C. undatella* and *L. substriatum*.

RESULTS

EXPERIMENT 1: CLAM GROWTH AND SURVIVORSHIP

Clam growth. Due to rough weather conditions a total of four ASUs were lost (one *C. undatella* and three *L. substriatum* ASUs). Of the retrieved ASUs (= 116) a total of 11 clams were missing (three *C. undatella* and eight *L. substriatum*). Eighty four percent of *L. substriatum* and 100% of *C. undatella* survived in control plots.

Musculista senhousia density had no detectable effect on *C. undatella* or *L. substriatum* growth rates, but clam SL was inversely related to growth rate for both native clam species (Figure 2; Table 1). Only one *L. substriatum* survived mussel densities > 2500 m^{-2} (half the maximum mussel density they were exposed to), limiting the range of mussel densities available for analyses.

Clam survivorship. Survivorship of native clams, *C. undatella* and *L. substriatum* were reduced in plots of high *M. senhousia* densities (Table 2; Figure 3). In each case there was a significant inverse correlation between mussel density and survivorship of natives. Initial SL was not a significant factor for survivorship of either native clam ($P > 0.15$) and therefore dropped from the models.

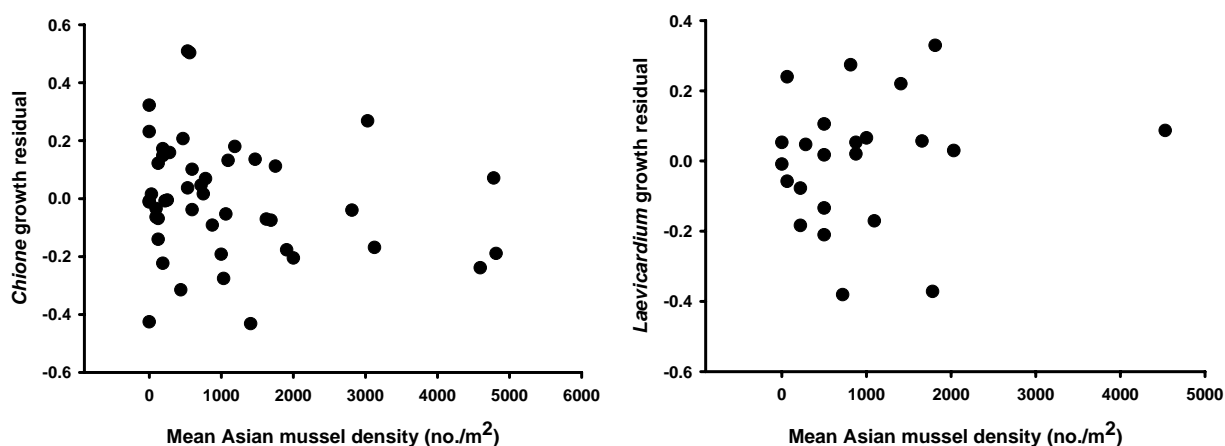


Figure 2. Clam growth. *Chione undatella* (N=46) and *L. substriatum* (N=23) growth as a function of Asian mussel density.

Table 1. Clam Growth. Results of Regression Analyses Investigating the Effects of *M. senhousia* Density and Initial Clam Shell Length (SL) on the Growth Rate of Native Clams, *C. undatella* (a.) and *L. substriatum* (b.)

a. *Chione undatella*

Source	Coefficient	St Error	Partial r ²	T	P
Constant	0.744	0.096	0.00	7.74	0.000
MMD	-0.000	0.000	0.04	-1.38	0.175
SL	-0.014	0.004	0.21	-3.38	0.002

	Df	MS	F	P
Regression	2	0.38	9.26	<0.001
Residual	43	0.04		

b. *Laevicardium substriatum*

Source	Coefficient	St Error	Partial r ²	T	P
Constant	0.658	0.127	0.00		0.000
MMD	0.000	0.000	0.00	0.99	0.864
SL	-0.043	0.010	0.48	0.99	0.000

	Df	MS	F	P
Regression	2	0.06	9.50	0.001
Residual	20	0.01		

Table 2. Clam Survivorship. Results of the Logistic Regression Determining the Effects of *M. senhousia* Density on the Survivorship of Native Clams, *C. undatella* and *L. substriatum*.

a. *Chione undatella*

Parameter	Estimate	dF	P	OR	Upper	Lower
Constant	2.290	1	<0.001			
MD	-0.000	1	0.031	1.64	2.56	1.05

b. *Laevicardium substriatum*

Parameter	Estimate	dF	P	OR	Upper	Lower
Constant	1.100	1	0.026			
MD	-0.000	1	0.019	1.91	3.29	1.11

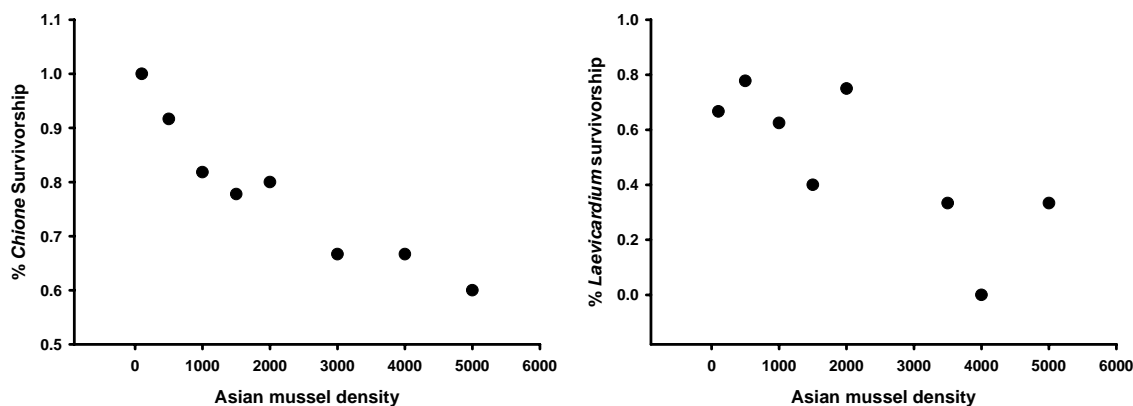


Figure 3. Clam survivorship. Survivorship of *C. undatella* and *L. substriatum* as a function of Asian mussel density. Percent clam survival was computed as the number dead / total number in that mussel density.

Predator able to enter ASUs and found at the end of the experiment were identified and enumerated. Predator density was not significantly affected by *M. senhousia* density in plots containing *C. undatella* or *L. substriatum* (Figure 4). However some clams were identified as consumed.

Overall *L. substriatum* had significantly higher mortality than *C. undatella* across mussel density treatments ($X^2 = 8.63$; $df = 1$, $P = 0.003$) resulting from consumption by

native predators and death from unknown causes (Table 3).

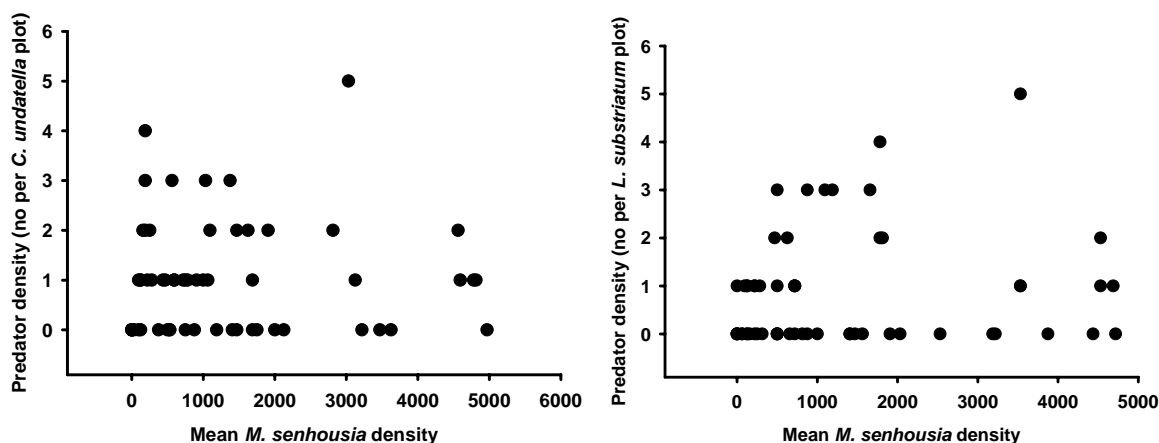


Figure 4. Predator density. Results from the growth experiment indicating predator density (no. per plot) as a function of Asian mussel density for *Chione undatella* and *Laevicardium substriatum*.

Table 3. Number of *C. undatella* and *L. substriatum* Found Alive, Dead from Unknown Causes, Crushed and Consumed, or Missing. *Laevicardium substriatum* had Significantly Higher Mortality and Higher Proportion Missing From ASUs than *C. undatella* ($X^2 = 20.7$; $P < 0.001$).

	Alive	Dead	Crushed	Missing	Total
<i>C. undatella</i>	46	10	0	4	60
<i>L. substriatum</i>	23	19	7	11	60
Total	69	29	7	15	120

EXPERIMENT 2: PROPORTIONAL MORTALITY OF NATIVE BIVALVES

In cage enclosed controls testing for secondary effects of handling and ASUs on clam mortality, *Chione undatella* and *Laevicardium substriatum* had 100% and 91% survival, respectively. *Chione undatella* had significantly lower total proportional mortality ($P < 0.001$) and proportion consumed by predators ($P < 0.001$) than *Laevicardium substriatum*. *Chione undatella* proportional mortality and proportion consumed were unaffected by *Musculista senhousia* density, and *C. undatella* generally had very high survival (>92%) over

the 5d experiment (Table 4; Figure 5). There was no significant effect of *M. senhousia* density on *Laevicardium substriatum* proportional mortality. However, there was significantly higher proportion of *L. substriatum* consumed in dense patches of the exotic mussel (Table 4; Figure 5). Mean *L. substriatum* consumed was significantly higher in the high than in the low mussel density treatment ($P=0.02$) and higher in the high than in the intermediate mussel density ($P=0.06$).

Table 4. Clam Predator-Induced Mortality. Results of a Two-way ANOVA Testing the Effects of *M. senhousia* Density (MD) and Clam Species (CS) on Total *C. undatella* and *L. substriatum* Proportional Mortality and the Proportion of Clams Consumed by Predators Including Crabs and the Native Gastropod *P. festiva*.

Source	Proportional Mortality				Proportion Consumed			
	dF	MS	F	P	dF	MS	F	P
<i>M. senhousia</i> density (MD)	2	0.10	3.78	0.034	2	0.05	5.79	0.007
Clam species (CS)	1	1.83	73.1	<0.01	1	0.10	11.1	0.002
MD X CS	2	0.04	1.57	0.224	2	0.03	2.82	0.075
Residual	30	0.03			30	0.01		

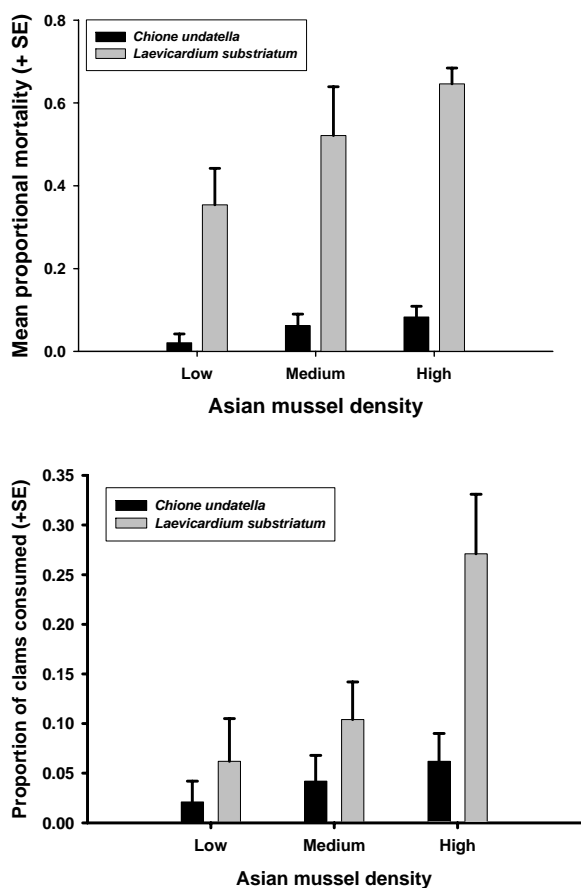


Figure 5. Clam proportional mortality. Mean proportional mortality and proportion consumed of *Chione undatella* and *Laevicardium substriatum* at low (0 m^{-2}), medium (160 m^{-2}), and high (640 m^{-2}) *M. senhousia* densities. Bars represent one standard error.

Several predators colonized ASUs including mud crabs (*Lophopenopeus* spp.), fish (bay blennies), and gastropods (*Pteropurpura festiva* and *Conus californicus*). *Pteropurpura festiva* was the most abundant of the predators to colonize ASUs and the predator responsible for the majority of bivalve consumption. This was evident by the presence of a conspicuous hole drilled by the gastropod into a valve of the clam or mussel. ASUs containing *Laevicardium substriatum* had significantly higher densities of predators at the end of the 5d experiment than the thick-shelled *Chione undatella* (Table 5; Figure 6).

Table 5. Predator Density. Results of a Two-way ANOVA Testing the Effects of *M. senhousia* Density and Native Clam Type on the Density of Predators in ASUs.

Source	dF	MS	F	P
<i>M. senhousia</i> density (MD)	2	127.58	51.61	<0.001
Clam (C)	1	12.25	4.96	0.034
MD X C	2	18.58	7.52	0.002
Residual	30	2.47		

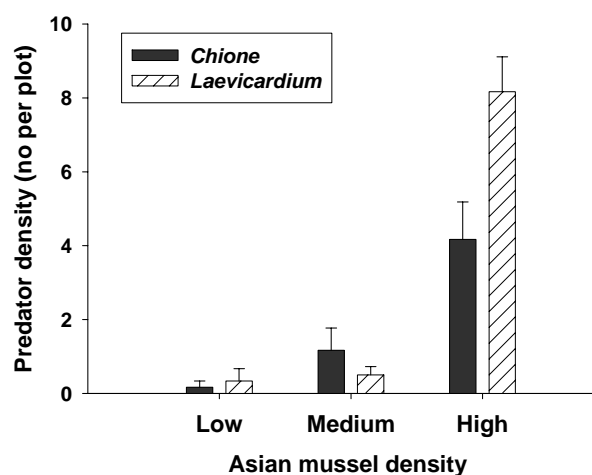


Figure 6. Predator density for ASUs containing *Chione undatella* and *Laevicardium substriatum* at low (0 m^{-2}), medium (160 m^{-2}), and high (640 m^{-2}) *M. senhousia* densities. Bars represent one standard error.

Predators aggregated to plots of high *M. senhousia* density where they consumed many (12 - 45%) of the available Asian mussels. Predators, although lower in numbers than in high density plots, consumed a higher proportion of mussels (37-62%) in intermediate mussel density treatments than in high density treatments. High mussel density treatments had significantly more predators than low ($P < 0.01$) and medium ($P < 0.01$) mussel density treatments for both native clam species. A significant interaction was detected between mussel density and native clam type due to a difference in slopes among species.

EXPERIMENT 3: ALTERNATIVE PREY AND FUNCTIONAL RESPONSE

To determine *Pteropurpura festiva* consumption of *L. substriatum* in the absence of Asian mussels a linear model was first fit to the data. However after close inspection of the linear curve and residuals it was apparent that assumptions of a linear model were not met (e.g. residuals were non-randomly distributed). Therefore I used the general functional response model to test whether the relationship could be considered hyperbolic (Type II) or sigmoid (Type III). A quantitative test of β values from the general functional response model (Lipcius and Hines 1986) indicates a hyperbolic curve ($\beta = 0.66$; $SE = 0.27$; Figure 7A). These results indicate a Type II functional response.

The functional response of *P. festiva* to *L. substriatum* density depended on whether *M. senhousia* was present. *P. festiva* exhibited a Type III functional response to *L. substriatum* in the presence of the introduced mussel ($r^2 = 0.92$; $P < 0.001$; Figure 7C). Both the qualitative comparison of model fit and the quantitative test for β indicate a Type III response ($\beta = 1.48$; $SE = 0.27$). Additionally my results indicate *P. festiva* exhibits a Type II functional response to *M. senhousia* in the presence of *L. substriatum* ($r^2 = 0.77$; $P < 0.001$) and without an alternative prey (Kushner and Hovel, in print).

EXPERIMENT 4: MUSSEL PATCH SIZE

I failed to detect an effect of mussel patch size on clam predator-induced mortality. A total of two out of twelve *C. undatella* were consumed, one in a small and one in medium size mussel patch. There was no significant difference in *C. undatella* mortality among patch sizes ($X^2 = 1.82$; $df = 2$; $P = 0.403$). A total of six *L. substriatum* were consumed, two in small, three in medium and one in a large mussel patch. Although more clams were consumed in small and medium patches than in large patches the difference was not significant ($X^2 = 2.09$; $df = 2$; $P = 0.351$).

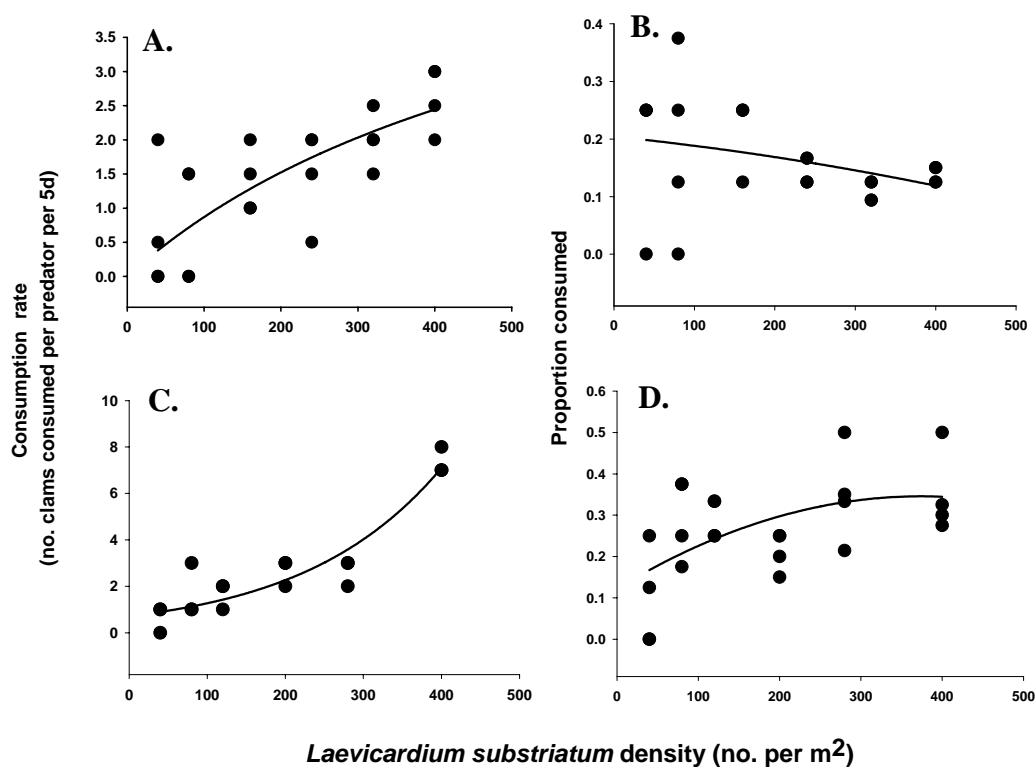


Figure 7. Results of the functional response of a native predator to the native egg cockle, *L. substriatum*. (A) *Pteropurpura festiva* consumption rate as a function of *Laevicardium substriatum* density in the absence of *M. Senhousia*. A hyperbolic model best fit the data ($r^2 = 0.71$). (B) *L. Substriatum* proportion consumed in the absence of *M. Senhousia*. (C) *Pteropurpura festiva* consumption rate as a function of *Laevicardium substriatum* density in the presence of *M. Senhousia*. An exponential curve best fit the data ($r^2 = 0.92$). (D) The proportion of *L. Substriatum* consumed in the presence of *M. Senhousia*.

DISCUSSION

In this study, I tested how the introduced Asian mussel *Musculista senhousia* influences the growth and survival of two native bivalve species in southern California. I hypothesized that high densities of Asian mussels reduce native clam growth and survivorship due to competition, but enhance survival of native bivalves exposed to predators if thin-shelled mussels divert predators from preying on natives. In contrast to previous studies, I found no evidence that Asian mussels competitively reduce growth rates of either native species. However, high densities of Asian mussels reduced survival rates of *Chione undatella* due to competition, and reduced survival rates of *Laevicardium substriatum* due both to competition and predation. Predators aggregated in plots of high mussel density, leading to low survival of the thin-shelled *Laevicardium substriatum* but not the thick-shelled *Chione undatella*. Predator foraging behavior also was altered by the presence of Asian mussels: *Pteropurpura festiva* exhibited a type II functional response to *L. substriatum* density in the absence of mussels but a type III functional response in the presence of mussels. Though this suggests that some refuge may be conferred upon native bivalves at high mussel densities when a single predator is present, the tendency for predators to aggregate in high mussel density patches (Kushner and Hovel, in press) results in low survival of native bivalves palatable to native predators. Overall, my results suggest that high densities of Asian mussels, which are common in soft sediments in Mission Bay and San Diego Bay, will reduce the survival of native bivalves.

EFFECTS OF ASIAN MUSSELS ON CLAM GROWTH AND SURVIVORSHIP

Both species of native clams in this study had decreased survivorship with increasing Asian mussel densities. *Chione undatella* and *L. substriatum* appear to have different tolerance levels for *M. senhousia*. Increases in Asian mussel density even at low levels of mussel density caused sharp declines in *C. undatella* survivorship, but some *C. undatella* were able to survive in the presence of very high mussel densities. In contrast, only one *L. substriatum* survived a mussel density greater than 2250 m⁻². Asian mussel density ranges from 0 to > 10,000 mussels m⁻² in Mission Bay and San Diego Bay (Reusch and Williams

1998; Dexter and Crooks 2000), and many sites consistently have mussel densities well beyond 2000 m^{-2} (Dexter & Crooks 2000, Kushner, unpublished data). Thus, the presence of Asian mussels may reduce native bivalve densities in many locations in southern California.

The significant effect of Asian mussel density on clam survivorship, but not on clam growth, suggests that the presence of Asian mussels negatively affects clams only beyond a threshold density of mussels. Asian mussels produce byssal threads and at high densities create dense mussel mats (Morton 1974) that may have smothered native clams in ASUs, interfering with their movement and ability to feed. In contrast to my study with *C. undatella* and *L. substriatum*, Asian mussel presence did not alter growth or survivorship of the native deposit feeder, *Macoma nasuta* possibly because of the different feeding modes and because *M. nasuta* lives deeper in the sediment than does *M. senhousia* (Crooks 2001). However, short-siphoned clams like *Chione undatella* are unable to alleviate interference competition with mussels by burrowing deeper in the sediment (Peterson 1985). A study on the competitive pressures of sponges reported several species of sponges are superior interference competitors and overgrow bivalves and barnacles preventing organisms from settlement or feeding causing high rates of mortality (Bell and Barnes 2003). Interference competition has been demonstrated in several marine studies and is not uncommon in soft-sediment communities (see review in Wilson 1990). Asian mussel mats may inhibit the settlement and survival of other macrofaunal invertebrate species (Creese et al. 1997). They have been correlated with low macrofaunal diversity in Mission Bay (Crooks and Khim 1999). Additionally, mussel mats inhibited the growth and survivorship of two clams, *C. undatella* and *C. fluctifraga* (Crooks 2001). In contrast, Mistri (2004) failed to detect an affect of Asian mussel mats on clam growth claiming that Asian mussels are selective filter-feeders which ingest active phytoplankton and clams are nonselective filter-feeders with a wider range of food types. Apparently because food types did not overlap there was no competitive pressure by Asian mussels on the clams investigated in Mistri's study.

Musculista senhousia deposit large amounts of pseudo-feces (Morton 1974) which may be toxic to native bivalves, clog their feeding mechanisms, alter sediment grain size characteristics, and alter the organic content of the sediment (Reusch and Williams 1998; Crooks and Khim 1999). I observed large amounts of pseudo-feces within high mussel density plots, which may have contributed to high clam mortality in my study. Habitat

characteristics such as sediment type have previously been shown to be important for clam growth (Peterson and Beal 1989). Sedimentation can also cause high clam mortality and induce density-dependent mortality in some clam species (Peterson 1985). I observed some sedimentation in ASUs, irrespective of mussel density treatment, which may also have contributed to clam mortality.

I found no evidence that Asian mussels affect native clam growth. However, effects of competitors on growth often are detected before effects on survivorship (Peterson 1982). It is possible that when effects are extreme (e.g. at high mussel densities), mortality can occur quickly and preclude the ability to find evidence for effects on bivalve growth. Although my study failed to detect an effect on clam growth, introduced species can inhibit bivalve growth by outcompeting natives for food. The introduced clam *Corbula gibba* had a negative impact on the size and growth of the native juvenile scallop *Pecten fumatus* in a south-east Australian bay (Talman and Keough 2001). Introduced suspension-feeders can deplete local phytoplankton biomass and limit food for native species (Alpine & Cloern 1992). If food limitation is severe bivalves can suffer high mortality rates. Food limitation has been observed for bivalves in seagrass beds (Allen and Williams 2003) and could have contributed to the observed mortality.

My experimental methodology also may have influenced my ability to detect effects of Asian mussels on clam growth. For instance, Crooks (2001) found significant affects on *Chione undatella* and *Chione fluctifraga* growth at high mussel densities ($\sim 5000 \text{ m}^{-2}$). I tested clam growth at densities $< 5000 \text{ m}^{-2}$ which may not have been high enough to influence growth. Additionally, site-specific hydrodynamic regimes, water temperatures, and food availability all may have contributed to the different results among studies. For instance, Crooks (2001) performed experiments in the fall season (August-December) and my study was conducted late winter into spring (February – April) when water temperatures are typically cooler and food availability lower (Mathews and Fairweather 2003). It is also possible that I may have detected effects on clam growth by using different measures of growth (e.g., flesh dry weight; Talman and Keough 2001). Finally, despite predator-exclusion cages, some predators were able to immigrate into plots. The presence of predators may have deterred clams from feeding and therefore my ability to detect differences in growth rates among treatments (see also Nakaoka 2000).

EFFECTS OF ASIAN MUSSELS ON NATIVE BIVALVE PREDATOR-INDUCED MORTALITY

The native gastropod *Pteropurpura festiva* is responsible for most Asian mussel predator-induced mortality in southern California (Reusch 1998) and aggregates in patches of high mussel density (Kushner and Hovel in press). I found that when *L. substriatum* are present in high density patches of Asian mussels they are more vulnerable to predation than in low and medium density patches, but that few *Chione undatella* were eaten regardless of mussel density. Additionally, predator density was substantially higher in plots with *Laevicardium substriatum* and high densities of Asian mussels than with *Chione undatella* and high densities of Asian mussels. I attribute the different vulnerabilities between the native clams at least partially to shell thickness. *Laevicardium substriatum* has a thin valve whereas *C. undatella* is relatively thick making it more difficult for a predator such as *P. festiva* to drill through to reach the flesh of the clam (Reusch 1998). Although *P. festiva* is the main predator of bivalves at this site, I also found crabs in plots and observed evidence of crab predation on *L. substriatum* and *M. senhousia*, but not on *C. undatella*, likely because crabs could not crush the valves of *C. undatella*.

A large discrepancy exists between the total proportional mortality and the proportion consumed for *L. substriatum*. The difference between the two explanatory variables is the number of clams dead from unknown causes, which was large for *L. substriatum*. However, in controls *L. substriatum* had relatively high survival. The high mortality from unknown causes may be due to predators which do not damage shells and leave no obvious evidence of consumption. For instance, an abundant predator at this site is the California cone snail, *Conus californicus*. These snails use a poisonous dart to harpoon their prey and subsequently consume them. Similarly, small octopuses recovered in ASUs may pry open bivalves without conspicuous damage to shells.

Relatively few marine studies have investigated the effects of relative prey density on predator choice of prey. Prey can have negative indirect interactions if a shared predator is present, defined as apparent competition (Holt 1977). Predators can aggregate to areas of high preferred prey density and consume secondary prey increasing mortality significantly. Much like my study, Schmitt (1987) demonstrated that predators of several types aggregate to areas where bivalve abundances are experimentally enhanced and consume the more

preferred prey (bivalves) and the less preferred gastropods. A shared predator can also induce positive indirect effects on prey. Fairweather (1985) demonstrated that when an alternative prey is present with a preferred prey at high densities, the secondary prey can have reduced mortality if the predator concentrates on the preferred prey.

My study demonstrates by evaluating the proportion of each prey consumed by *P. festiva* in plots with equal prey densities that Asian mussels are highly preferred over the thin-shelled native *L. substriatum*. *Pteropurpura festiva* always consumed more Asian mussels than natives and consumed on average 40% more of the introduced mussel ($t=6.64$; $df=5$, $P=0.001$). On average 8% of *L. substriatum* offered to predators were consumed in experimental plots. *Laevicardium substriatum* although less preferred is a secondary prey item for *P. festiva*.

The ability for predators to regulate prey populations is related to the manner in which predator consumption rates change with increasing prey density, which will be dictated by a combination of numerical and functional responses of predators to prey density. Holling (1959) identified three main types of functional responses by a predator. The simplest is linear (Type I) where consumption rate increases linearly with prey density. The second is described by a hyperbolic curve (Type II) whereby consumption rate increases in a decelerating manner and prey proportional mortality decreases as their density increases. The third type is described by an accelerating or sigmoidal curve (Type III). Type III functional responses indicate accelerating consumption rates as prey density increases over low to moderate prey densities, which may contribute to the ability of predators to regulate prey populations by causing positively density-dependent prey mortality.

Many studies of marine organisms have measured the functional response of a single predator to a single prey species (e.g. Eggleston 1990; Sponaugle and Lawton 1990; Anderson 2001). Fewer studies have evaluated the influence of multiple prey items on predator foraging behavior and predator functional responses (Holling 1965, 1966; Real 1979). My results indicate that *P. festiva* foraging behavior on a native bivalve changes in the presence of the introduced *M. senhousia*. When *P. festiva* was offered only the native clam *L. substriatum*, the gastropod's consumption rate increased to an upper asymptote best characterized by a hyperbolic curve. This response is typical of many invertebrate predators (Lipcius and Hines 1986). However when *P. festiva* was offered both *L. substriatum* and

Asian mussels, consumption rates accelerated with increasing *L. substriatum* density. This suggests that clams found in high density mussel patches may have a partial refuge from predation by *P. festiva* provided that the density of *P. festiva* is low. Nakaoka (2000) found that predation rates on clams were significantly lower at low clam densities compared with high dense areas. Clams appeared to have refuge from predators when kept at low densities. A low-density prey refuge has been demonstrated for marine invertebrates in complex habitats compared with homogeneous habitats (Sponaugle and Lawton 1990). Temperature can also be an important factor for predator behavior. Eggleston (1990) found low consumption rates by blue crabs (*Callinectes sapidus*) on juvenile American oysters (*Crassostrea virginica*) when oyster density and temperature was low.

Functional response equations have been described in a variety of ways. A general functional response model derived by Real (1977, 1979) states:

$$f = k * A^n / X + A^n$$

where f = the feeding rate, k = the maximum feeding rate (satiation), A = the initial prey density, X = the density of prey at which $A = 0.5k$, and n = the parameter associated with the form of the functional response curve. In ecological terms, the parameter k is related to the total resource use by predators, the parameter X is related to the affinity that a predator has for a particular prey species, and the parameter n is related to how predator detection of prey may change with prey density and learning (Real 1979). When $n = 1$ the curve is hyperbolic (Type II), and when $n > 1$ the curve is sigmoidal (Type III). Other forms of this equation include handling time as an additional parameter, which may influence predator choices among prey types (Lipcius and Hines 1986). The equation predicts that predator responses to target prey will change as the relative density of different prey species changes and as the relative palatability of prey species changes. Though some foragers simply pursue the more abundant prey when given two choices (Murdoch et al. 1975; Bergelson 1985), Akre and Johnson (1979) found that a damselfly exhibited a Type II functional response when one prey or two prey species of equal densities were present, but when the alternative prey was available in densities less than the principal prey, consumption rates for the principle prey accelerated, resulting in a Type III functional response. Murdoch (1969) demonstrated with marine invertebrates that the level of predator preference (strong versus weak) for its prey can alter the type of functional response. By training predatory gastropods they controlled

the magnitude of preference. When predators had a weak preference for prey item A versus B and were provided the two at unequal densities, switching among the prey items occurred resulting in population regulation (Type III functional response and density-dependent mortality). However when the preference for one prey species was strong, the distasteful prey was rarely if ever consumed, switching failed to occur and predators were unable to regulate the prey population. Finally, the deer mouse, *Peromyscus maniculatus bairdii*, had Type II functional response to the density of a “test” prey species (*Neodiprion sertifer*) when an alternative distasteful prey species was available, but exhibited a Type III response to test prey when the alternative prey species was highly palatable (Holling 1965). Real (1979) reviewed the data from this experiment and determined the presence of the distasteful prey resulted in an increase in predator search time and usage of other foods in the environment, evident by an increase in the parameter k and a decrease in X .

CAVEATS

My study addressed how Asian mussels influence the growth and survival of native bivalves in small patches of mussels. While the patch size experiment failed to detect differences in clam mortality between small patches and larger ones (up to 1 m²), far larger patches of Asian mussels are common in Mission Bay and San Diego Bay, and my results should be extrapolated to larger scales with caution. Predators may not aggregate at such high rates and consume as many clams in larger patches of Asian mussels as reported in this study. Additionally, I conducted my predator behavior and predator-induced mortality experiments at one site in Mission Bay that contains relatively high predator densities. My results may have been different if the experiments were conducted at other sites. Finally, in my experiments I used relatively high clam densities compared to typical densities in southern California sediments. Controls do not indicate evidence of intraspecific competition among clams, but it is possible that relatively high clam densities contributed to clam mortality.

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ABSTRACT OF THE THESIS

Effects of the Introduced Asian Mussel *Musculista senhousia* on
Native Bivalve Growth and Survival in Southern California

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The frequency of marine introductions in coastal seas and estuaries has increased dramatically in the last several decades. Non-native species often degrade local communities by preying on native species, outcompeting natives for food or space, and modifying habitat. Non-native species also may positively influence native species, if, for example, an introduced species is preferred as prey by native predators. In the coastal waters of southern California, I experimentally tested the hypothesis that the abundant introduced Asian mussel *Musculista senhousia* competitively inhibits the growth of two native bivalve species, but enhances native bivalve survival by providing native predators with an alternative, highly palatable source of prey. To test this hypothesis, I (1) quantified the effect of *M. senhousia* on the growth and survivorship of two native bivalves, *Chione undatella* and *Laevicardium substriatum*, in the absence of predators; (2) quantified predator-induced proportional mortality of *C. undatella* and *L. substriatum* in the presence and absence of *M. senhousia*; and (3) determined if the functional response of an important native predator, the gastropod *Pteropurpura festiva*, to native bivalve density changes in the presence of *M. senhousia*. All experiments were conducted by transplanting Asian mussels and native bivalves to small artificial eelgrass (*Zostera marina*) plots embedded within naturally occurring eelgrass beds in San Diego Bay and Mission Bay.

I found no evidence that Asian mussels competitively reduce growth rates of either native species when predators were excluded from plots. However, survivorship of both species decreased as Asian mussel density increased in the absence of predators. When clams were exposed to predators in increasing Asian mussel densities, predators aggregated in plots of high mussel density, leading to low survival of the thin-shelled *Laevicardium substriatum* but not the thick-shelled *Chione undatella*. Predator foraging behavior also was altered by the presence of Asian mussels: *Pteropurpura festiva* exhibited a type II functional response to *L. substriatum* density in the absence of mussels but a type III functional response in the presence of mussels. Though this suggests that *L. substriatum* may have a refuge from predators in small, high density Asian mussel patches when predator abundance is low, predator aggregation in high mussel density patches results in high proportional mortality of *L. substriatum* at high densities of Asian mussels. In contrast, the thick shells of *Chione undatella* provide this native species with a refuge from predators regardless of Asian mussel density. Overall, my results suggest that Asian mussels reduce survival rates of *Chione undatella* due to competition, and reduced survival rates of *Laevicardium substriatum* due both to competition and predation. Though *M. senhousia* is heavily consumed by native predators in southern California, high densities of Asian mussels, which are common in soft sediments in Mission Bay and San Diego Bay, appear to reduce the survival and abundance of native bivalves.