Native eelgrass *Zostera marina* controls growth and reproduction of an invasive mussel through food limitation

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ABSTRACT: In southern California, native eelgrass *Zostera marina* L. and the invasive non-native mussel *Musculista senhousia* have dynamic complex interactions. Although high densities of *M. senhousia* inhibit the growth of eelgrass, mussel survival and growth decline with increasing eelgrass shoot density and patch size. The correlation of these eelgrass attributes with local concentrations of chlorophyll *a* and water flow speeds suggested that the mussels, which feed on phytoplankton delivered by water currents, might suffer food limitation inside large eelgrass beds. By supplementing phytoplankton to *M. senhousia* living in eelgrass, we confirmed this hypothesis: mussels grew 50% faster when food availability was enhanced. Lab and field experiments investigating the effects of food limitation on growth and reproduction of *M. senhousia* showed that mussels respond by reducing shell growth, and subsequently fecundity. We found no evidence that mussels reallocated resources preferentially to reproduction when food was limited. Our results highlight how the effects of anthropogenic perturbations that currently threaten eelgrass populations directly could be magnified by interactions with a non-native species. Eelgrass habitat fragmentation and increasingly frequent phytoplankton blooms resulting from coastal development and eutrophication have well-described direct negative effects on eelgrass. By increasing phytoplankton availability to *M. senhousia*, such perturbations also indirectly affect eelgrass by acting to enhance mussel survival and growth, magnifying the negative effects of the mussel on *Z. marina*.

KEY WORDS: *Musculista senhousia* · Food limitation · Resource allocation · Non-native species · *Zostera marina* · Multiple perturbations

INTRODUCTION

Estuaries are ecologically and economically important ecosystems that support a myriad of commercial, recreational, and military activities. Many estuarine habitats are exhibiting marked changes in community structure and function as a result of multiple anthropogenic perturbations, superimposed on natural change (NRC [National Research Council] 1995, Short & Neckles 1999). Of particular concern are perturbations to productive estuarine wetlands such as sea-grasses and salt marshes (Dennison et al. 1993, Short & Wyllie-Echeverria 1996). Seagrasses are marine flowering plants that form extensive meadows in shallow waters, providing ecologically important functions including primary production, filtration of land runoff, sediment stabilization, and nursery habitat for many fisheries species (McRoy & Helfferich 1977, Phillips & McRoy 1980, Williams & Heck 2001). Seagrass habitat consequently is protected under the US Coastal Zone Management Act and the Clean Water Act. Nevertheless, loss of such habitat is accelerating in the USA and

worldwide, due to eutrophication and subsequent algal blooms, disease, physical disturbance, and interactions with non-native species (Peterson et al. 1987, Short & Neckles 1999, Hauxwell et al. 2001, Williams & Heck 2001).

In San Diego Bay, a highly disturbed urban estuary in southern California, USA, a native seagrass, *Zostera marina* L. (eelgrass), is conditionally threatened by the invasive marine bivalve *Musculista senhousia* (Benson 1842). At high densities, *M. senhousia* interferes with eelgrass vegetative growth (Reusch & Williams 1998), the most important mode of reproduction in local *Z. marina* populations (Ewanchuk 1995). *M. senhousia* is a small mytilid mussel native to east Asia that has successfully spread to New Zealand, Australia, the Mediterranean, and the Pacific coast of North America (reviewed in Crooks 1996). First reported in southern California in the mid-1960s (MacDonald 1969), the abundance of *M. senhousia* has increased dramatically in the past decade (Crooks 1996) such that the mussel is now the most abundant macroinvertebrate in terms of biomass at many sites, occurring at densities as high as $15\,000$ m^{-2} (Reusch 1998). Like other mytilid mussels, *M. senhousia* feeds by filtering phytoplankton from the water column, and has high fecundity and a planktonic larval stage lasting several weeks (Kulikova 1978, Crooks 1996). Unlike most mussels, *M. senhousia* lives entirely within the sediments, surrounded by a bag of byssal threads (Morton 1974). At mussel densities >1500 m^{-2}, individual byssal bags coalesce to form a continuous mat or carpet on the sediment surface (Reusch & Williams 1999). The presence of mussel mats dramatically alters the natural benthic habitat, changing both the local physical environment and the resident macroinvertebrate assemblage (Morton 1974, Crooks 1998, Crooks & Khim 1999). Although the creation of new habitat structure associated with high densities of mussels can result in increased species richness and abundances of some infaunal taxa (Crooks 1998, Crooks & Khim 1999), mussel mats reduce the densities of many common native bivalves and the growth of nearby eelgrass (possibly due to spatial interference) (Crooks 1992, Reusch & Williams 1998).

The interactions between *Musculista senhousia* and *Zostera marina* are complex, however, and in southern California *M. senhousia* is found at mat-forming densities only in areas where eelgrass beds are fragmented and sparsely vegetated or absent (Reusch & Williams 1998, 1999). Where eelgrass is dense, the growth and survival of *M. senhousia* are poor (Reusch & Williams 1998, 1999). Mussel growth rates are highest outside of *Z. marina* beds and decrease with increasing eelgrass patch size and distance from the edge of the leaf canopy. This inverse pattern of eelgrass versus mussel distribution and growth also correlates well with water flow speeds (Reusch & Williams 1999), which are highest outside eelgrass beds but slow within the canopy as momentum is extracted through friction along the leaf surfaces (reviewed in Koch 2001). These observations provide a mechanism by which eelgrass could influence mussel growth and distribution. Dependent on water flow for delivery of their phytoplankton food, mussels living in dense eelgrass or deep within a large eelgrass patch might be severely food-limited as an indirect consequence of eelgrass effectively blocking water flow through its leaf canopy. The expectation that mussels within eelgrass beds have less food is supported by observations of lower concentrations of chlorophyll *a* (chl *a*) in the feeding ambit of mussels inside eelgrass patches compared to in nearby unvegetated areas (Reusch & Williams 1999). Reduced water flow and local depletion of suspended particles has been implicated in food limitation of other suspension-feeding organisms (Wildish & Kristmanson 1984, Fréchette et al. 1989, Butman et al. 1994), and there is compelling indirect evidence that bivalve growth can be limited by food availability (Kautsky 1982, Peterson 1982, Bertness & Grosholz 1985, Fréchette & Bourget 1985, Peterson & Black 1987). This hypothesis has not, however, been tested directly in the field.

For many marine invertebrates, an inevitable consequence of limited food availability is a reduction in individual growth and fecundity (reviewed in Ólafsson et al. 1994). A prediction of the hypothesis that *Musculista senhousia* in eelgrass are food-limited is that growth and fecundity will be reduced relative to mussels living outside *Zostera marina* beds. Some organisms, however, can maintain a relatively high level of fecundity even when food is limited by reallocating available resources to reproduction at the expense of growth (a trade-off) (Bayne 1976, reviewed for bivalves in Griffiths & Griffiths 1987, Thompson & MacDonald 1991). Populations of *M. senhousia* at sites in southern California are often short-lived, suggesting that the mussel is highly dependent on successful reproduction and dispersal for persistence (Crooks 1996, T. A. Ebert & S. L. Williams unpubl. data). When resources are limited, the ability to preferentially allocate those available to the production of gametes might therefore be adaptive.

The purpose of our study was to (1) provide a direct test of whether *Musculista senhousia* is food-limited in *Zostera marina* by experimentally supplementing the phytoplankton available to mussels living in a natural eelgrass bed, (2) quantify the effects of food limitation on relative growth and fecundity of *M. senhousia* in the laboratory, and (3) compare relative growth and fecundity of *M. senhousia* inside of and outside a natural eelgrass bed.

MATERIALS AND METHODS

Experimental manipulations were done at Silver Strand (32° 38′ 01″ N, 117° 08′ 03″ W) and Harbor Island (32° 43′ 25″ N, 117° 11′ 19″ W), San Diego Bay, California, USA. Both are sheltered subtidal sites with *Zostera marina* leaf shoot densities and heights typical of other local eelgrass beds. *Musculista senhousia* is commonly found at mat-forming densities in the adjacent un-vegetated sand flats, although the abundance of the mussel varies considerably in space and time. All observations and experimental manipulations were accomplished by SCUBA.

***In situ* food addition to mussels.** Mussels were collected from a sand flat adjacent to the eelgrass bed at Silver Strand in June 1998, and tagged in an aerated solution of calcein in seawater (100 mg l⁻¹) for 24 h. Calcein is a fluorescent dye that is incorporated into the shells of growing mussels as a marker for initial size (Wilson et al. 1987, Kaehler & McQuaid 1999). Individual growth was measured later under a micro-scope with an ultraviolet epi-illuminator as the dis-tance from the tag to the shell margin. Tagging effi-ciency was 100% (50/50 mussels examined), and previous work has demonstrated that there are no negative effects of tagging on growth or survival of molluscs (Kaehler & McQuaid 1999, Moran 2000). We deliberately chose small mussels for this experiment (5 to 12 mm shell length; n = 225) because *Musculista senhousia* of this size range exhibit the fastest growth (T. A. Ebert & S. L. Williams unpubl. data).

Following tagging, mussels were transplanted at mat-forming densities (n = 75 mussels) into 24 plots (100 cm⁻²) within the eelgrass bed (20 to 30 m from the edge). All resident mussels were removed from the experimental plots prior to the beginning of the experi-ment. Although each plot was bounded by a buried ring of polyethylene mesh (15 cm diameter; 6 mm mesh size) to facilitate mussel recovery at the end of the experiment, the transplanted mussels tended to remain clumped together in the middle of the plot for the duration of the experiment. Each plot was sepa-rated from the others by at least 3 m. Eelgrass leaf shoot density was 314 ± 23 shoots m⁻² (mean ± 1 SE, n = 24, 50 × 50 cm quadrats) and leaf height was 63 ± 5 cm (tallest leaf of n = 5 shoots quadrat⁻¹).

Replicated plots (n = 6) received 1 of 4 treatments: (1) laboratory-cultured phytoplankton added to the water above the mussels, (2) unmanipulated ambient conditions, (3) culture medium but no additional phytoplankton added to the water above the mussels, and (4) the presence of a non-operating delivery system. *Musculista senhousia* readily consumed the phytoplankton *Tetraselmis* sp. (10⁴–10⁵ cells ml⁻¹) and *Nannochloropsis* sp. (10⁵–10⁶ cells ml⁻¹) cultured in

nutrient-enriched natural seawater (Strathmann 1987) during a preliminary experiment (authors' unpubl. data). Microscopic analyses of the gut contents of mus-sels verified that *M. senhousia* in San Diego Bay eel-grass beds feeds primarily on small (~5 μm diameter) phytoplankton (authors' unpubl. data), rather than on benthic microalgae that might represent an important source of food to other bivalves living in seagrasses (e.g. Judge et al. 1993). Fresh culture medium ± phyto-plankton was delivered from 20 l soft plastic containers placed close to each plot daily for 28 d (1 container per plot). A small weight (1.4 kg) on top of each container forced the culture medium through a flexible tube into the water column 1 cm above the mussels, delivering approximately 10 l over a 6 h period (09:00 to 15:00 h daily). The flow of culture medium from storage con-tainers to the water above experimental plots was visually inspected using fluorescein dye.

To test the efficacy of the phytoplankton treatment, food availability (concentration of chl *a*) above the experimental plots was measured weekly (n = 4 sam-pling dates). On each sampling date, immediately prior to the addition of culture medium ± phytoplankton and hourly for 6 h thereafter, duplicate seawater samples were collected at a distance of 1 cm above the mussels in each plot using 60 ml syringes. Water samples were taken from the middle of each plot (approximately 10 cm from the phytoplankton discharge tube). Water was withdrawn at a rate of 20 ml min⁻¹ to mimic active filtering by mussels (Judge et al. 1993). The samples were immediately filtered through 1.2 μm mesh glass-fiber filters (Watson GF/C), and extracted with 90% acetone in the dark for 24 h. Concentrations of chl *a* were determined fluorometrically according to Parsons et al. (1984). Because the phytoplankton medium was fertilized with ammonium which could be harmful to molluscs, we measured ammonium concentrations in duplicate samples of water taken above each plot 1 h after the start of the treatments, filtering and adding reagents immediately (Koroleff 1976). Ammonium concentrations in the plots receiving culture medium ± phytoplankton were higher than in the ambient or delivery system control plots, but the elevated concen-trations of 8.9 ± 2.4 μmol l⁻¹ (mean ± 1 SE, n = 24) were within the natural range of values which occur locally, and well below concentrations which are harmful to other bivalves (Nalepa & Schloesser 1993, Sewell 1996).

After 28 d, the sediment inside each plot (to a depth of ~8 cm) was sieved through 1 mm mesh screen. Mus-sels were collected, preserved in 70% ethyl alcohol, and 25 individuals were randomly selected per plot. Mussel shell length and growth were measured to the nearest 0.1 mm with a digital caliper and ocular micrometer, and tissue mass to the nearest 0.1 mg after

drying until constant mass at 70°C. Mussels were identified as experimentally transplanted by the presence of a calcein tag. Survival in each plot was estimated as the number of tagged/number of transplanted mussels.

Effects of food limitation in the laboratory. To assess the effects of food limitation on growth and reproduction of *Musculista senhousia* under controlled conditions in the laboratory, adult mussels (8 to 28 mm in length) were collected from outside the eelgrass bed at Harbor Island in June 1997 and immediately tagged with calcein. After tagging, mussels were evenly distributed across a shallow flow-through water table (length 2.5 m, width 1.0 m, water depth 10 cm) filled with 10 cm of washed sand from San Diego Bay to form a dense assemblage of individuals (1650 ± 290 ind. m^{-2}; mean ± 1 SD, assessed with 20 haphazardly placed cores of 50 cm^2). Seawater pumped directly from San Diego Bay flowed uni-directionally across the length of the experimental mussel bed (inflow of approximately 4 l min^{-1}). *M. senhousia* at this density can reduce near-bottom food resources by up to 70% compared with ambient seawater (Reusch & Williams 1999). The experimental mussel bed provided for an assessment of mussel response along a gradient of decreasing food availability (from a maximum of ambient at the inflow pipe).

Mussels were held under conditions of ambient light and water temperature (22.1 to 25.2°C) for the duration of the experiment. Food availability to mussels along the length of the water table was measured weekly (n = 8 sampling dates) as the local concentration of chl *a*. On each sampling date, duplicate seawater samples were collected 1 cm above the mussels at 0.00, 0.75, 1.50, and 2.25 m downstream of the inflow pipe. On 3 sampling dates, ammonium concentration, dissolved oxygen concentration, and pH were also measured at the inflow and outflow pipes to assess water quality for mussel growth. Dissolved oxygen concentrations were measured using a YSI oxygen meter (Model 53), and pH using a Beckman pH meter (Model 32).

In southern California, *Musculista senhousia* spawns primarily in the late summer and early fall (Crooks 1996, authors' unpubl. data). Beginning in January 1997, monthly assessments of the color, texture, and thickness of mantle tissues from the Harbor Island mussel population were made to ensure the experiment began prior to significant gametogenesis. Like other mytilid mussels (Seed & Suchanek 1992), the gonad of *M. senhousia* is typically orange in females and white in males, while the mantle tissues of non-reproductive mussels are relatively thin and transparent. With the exception of a few hermaphrodites, *M. senhousia* populations in southern California have approximately equal numbers of males and females (authors' unpubl. data).

The reproductive status of mussels (n = 20) was assessed weekly so that the experiment could be ended before the mussels spawned. After 54 d, mussels were collected from the water table at 0.00, 0.75, 1.50, and 2.25 m from the inflow pipe, using haphazardly placed cores of 50 cm^2 (n = 6 cores location^{-1}). Shell length and growth, and gonad and somatic tissue dry mass of 30 randomly selected mussels per location were measured. To assess relative fecundity, a gonad index was calculated for each mussel as the ratio of gonad dry mass to total tissue dry mass (the sexes were not considered separately, as gonad index values were similar for male and female mussels).

Effects of an eelgrass bed. To assess the effects of an eelgrass bed on the growth and reproduction of *Musculista senhousia*, a field experiment was conducted concurrently with the laboratory food limitation experiment. Tagged mussels from the same Harbor Island collection (n = 50 mussels 100 cm^{-2}) were transplanted into 12 plots inside the dense eelgrass bed at Harbor Island (5 to 10 m from the edge), and 12 plots in the adjacent unvegetated sand flat. All resident mussels were removed before introduction of the tagged mussels. Plots were bounded by a buried ring of polyethylene mesh, and were separated by at least 3 m. Half of the plots in each location (n = 6) were caged to protect the mussels from predators. Predation on *M. senhousia* in San Diego Bay is variable among sites and habitats, but mussel mortality due to predation (primarily by the muricid snail *Pteropurpura festiva*) can be high at times in the eelgrass bed at Harbor Island (Reusch 1998, Reusch & Williams 1998). Cages were circular (diameter = 20 cm), constructed of polyethylene mesh (11 mm mesh size), and buried in the sediments to a depth of 8 cm. Each cage extended 15 cm into the water column, and had a conical roof to shed eelgrass litter. Previous studies have demonstrated that experimental artifacts of this type of cage on *M. senhousia* growth at this site are minimal (Reusch 1998, Reusch & Williams 1999). Plots were checked weekly for *P. festiva*, and snails found feeding in the experimental plots were counted and removed.

Eelgrass leaf shoot density was 232 ± 41 shoots m^{-2} (mean ± 1 SE, n = 12, 50 × 50 cm quadrats), and leaf height was 76 ± 8 cm (tallest leaf of n = 5 shoots quadrat^{-1}). After 54 d, the sediment inside each plot was sieved, and the surviving mussels preserved in alcohol. Shell growth and tissue mass were measured for 20 randomly chosen mussels per plot, and a gonad index calculated as in the laboratory experiment. Mussel survival per plot was calculated as in the *in situ* food addition experiment.

Statistical analyses. Chl *a* concentrations were compared among treatments (fixed) and sampling times

(random) using 2-way mixed model analysis of variance (ANOVA). Mussel shell growth and tissue mass are functions of individual size. Consequently, mean shell growth among treatments (fixed) was compared using analysis of covariance (ANCOVA), with initial shell length as the covariate, and plots (random, nested within treatment) as the error component (Sokal & Rohlf 1995). Differences in mean mussel tissue mass were evaluated using ANCOVA with final shell length as the covariate. Mean values of the gonad index and survival were compared among treatments using ANOVA with plots (random, nested within treatment) as the error component.

Visual inspection of model residuals was done for every analysis. Where variances showed significant heterogeneity, the data were transformed using a $\ln(x+1)$ function. Gonad index and survival data were transformed using an arcsine ($\sqrt{x}$) function to meet distributional assumptions of normality (Sokal & Rohlf 1995). Following ANOVA or ANCOVA, Tukey's HSD tests were used to identify significant differences among appropriate means.

RESULTS

In situ food addition to mussels

Food availability in the experimental plots was 3 to 4 times higher than in the ambient and control plots following the addition of phytoplankton (Fig. 1). Despite significant temporal variation, the direction and magnitude of these differences were comparable on all 4 sampling dates, as evidenced by a non-significant treatment × sampling date interaction (Table 1). Chl *a* concentrations in the ambient plots were consistent with other measurements taken in San Diego Bay during summer months (Reusch & Williams 1999, authors' unpubl. data). Fluorescein-dyed medium flowed from the storage containers to the water directly overlying the mussels and remained there as a discernable water mass (~30 cm diameter) for at least 6 h.

Mussels given supplemental phytoplankton grew 40% more than mussels under ambient conditions (Fig. 2A) supporting the hypothesis that food is a limiting resource for *Musculista senhousia* in eelgrass. In addition to the statistically significant treatment effect, there was also a significant plot effect for mussel shell growth (p = 0.024, Table 1). This is due entirely to variability among plots within the plankton addition treatment, presumably because the efficacy of our treatment application (although successful overall) was variable among plots. Although mussels in the food addition treatment were larger at the end of the experiment, mean dry tissue mass of individu-
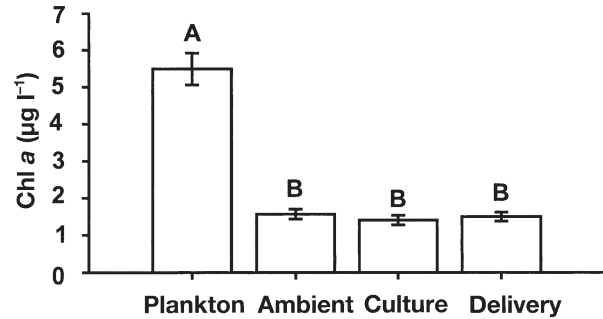

Fig. 1. Chl *a* concentrations (mean ± SE, n = 24) among treatments in the *in situ* food addition experiment in the eelgrass bed at Silver Strand, San Diego Bay. Water samples were taken 1 cm above mussels *Musculista senhousia* in each plot. Data were pooled over 4 sampling dates because the interaction treatment × sampling date was not significant (Table 1; Winer et al. 1991). Differing letters indicate significant differences among treatments (p < 0.05, Tukey's HSD multiple-comparison method)

als did not differ among treatments when adjusted for differences in final size (Table 1, Fig. 2B). This suggests that the increased shell growth of mussels in the plankton addition plots cannot be explained by the utilization of stored energy reserves. Survival was high in all plots (79 to 100% tagged mussel recovery) and did not differ among treatments (ANOVA, $F_{3,20}$ = 1.28, p = 0.308).

Table 1. Analyses of effects of treatments (plankton addition, and ambient, culture medium and delivery system controls) on chl *a* concentration (ANOVA), and mussel *Musculista senhousia* shell growth and dry tissue mass (ANCOVA) in the *in situ* food addition experiment. Adjusted plot means for shell growth and dry tissue mass were used to test for effects of treatments. Data were transformed using a $\ln(x + 1)$ function to remove variance heterogeneity (chl *a*, shell length and tissue mass). Assumption of homogeneity of slopes was tested prior to ANCOVAs

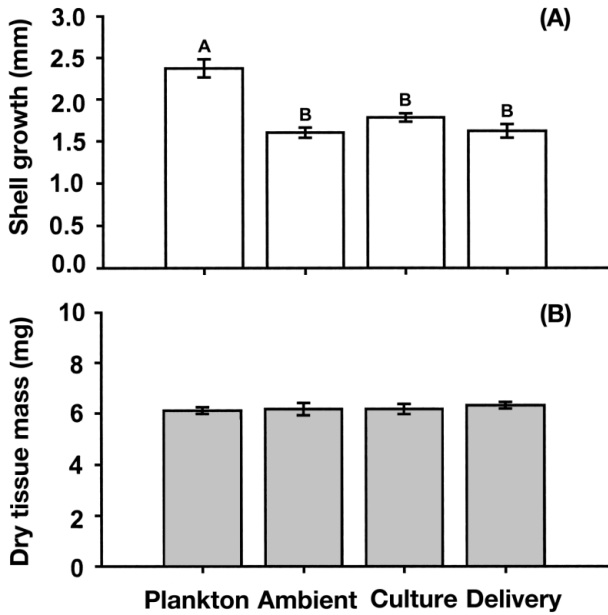| Source	df	MS	*F*	p
Chl *a* concentration				
Treatment	3	5.166	77.10	<0.001
Sampling date	3	0.435	5.95	0.001
Treatment × sampling date	9	0.067	0.92	0.510
Error	80	0.073		
Shell growth				
Treatment	3	2.163	19.48	<0.001
Initial shell length	1	1.155	18.13	<0.001
Plot (treatment)	20	0.111	1.74	0.024
Error	575	0.064		
Dry tissue mass				
Treatment	3	0.022	1.35	0.286
Final shell length	1	69.596	2425.37	<0.001
Plot (treatment)	20	0.016	0.55	0.945
Error	575	0.029		

Fig. 2. *Musculista senhousia.* Shell growth (A, white bars) and dry tissue mass (B, gray bars) of mussels among treatments in the *in situ* food addition experiment in the eelgrass bed at Silver Strand, San Diego Bay (adjusted mean ± SE, n = 6 plots). Differing letters indicate significant differences among treatments (p < 0.05, Tukey's HSD multiple-comparison method)

Effects of food limitation in the laboratory

Food availability across the length of the experimental mussel bed declined monotonically with increasing distance from the inflow pipe (Fig. 3). The reduction in chl *a* concentrations from the inflow pipe to the 0.75 m sampling location (~25%) was comparable to the reduction in chl *a* concentrations measured inside (~1 m from edge) versus outside eelgrass beds in San Diego Bay (Reusch & Williams 1999). No other measures of water quality differed significantly between inflow and outflow pipes (all p > 0.210).

Mussel shell growth was correlated with chl *a* concentrations, also decreasing with increasing distance downstream of the inflow pipe (Table 2, Fig. 4A). The downstream reduction in shell growth across the mussel bed was mirrored by a reduction in mean dry tissue mass (adjusted for differences in final mussel size) (Table 2, Fig. 4B), suggesting that mussels farther downstream were possibly using stored energy reserves to a greater degree than those near the inflow pipe (under ambient levels of food availability). The observation that mussels with access to the least amount of food continued to increase in shell length (although at a much reduced rate) despite losing a significant proportion of soft tissue mass has been seen in

other marine mussels, and may be due to the relative energetic costs of production of shell versus other tissues (Hawkins & Bayne 1992).

Mean gonad index (gonad dry mass/total tissue dry mass) was ~0.43 for mussels at the 2 upstream locations, and ~0.08 for mussels farther downstream (Fig. 4C). Among mussels that produced gonad, variation in individual size explained very little of the variation in gonad index values (R^2 = 0.01). There appears to be a threshold of food availability below which little or no gonad is produced, a result that has been found in other studies of bivalve reproduction (Bayne et al. 1982, Newell et al. 1982). The importance of this threshold to *Musculista senhousia* in southern California may be limited, however, as mussels at multiple sites are generally observed to produce gonad (authors' unpubl. data).

Effects of an eelgrass bed

Mussels living inside dense eelgrass canopy exhibited growth and reproductive responses similar to those of food-limited mussels in the experimental mussel bed. Shell growth of individuals inside the eelgrass bed was reduced by 50% relative to mussels in the adjacent unvegetated sand flat (Table 3, Fig. 5A). As predicted, cage effects were small relative to treatment effects, and were not statistically significant (maximum of 9% different, all p ≥ 0.148). More importantly, the interaction between caging and habitat was also not significant (all p ≥ 0.533), suggesting that cage effects were similar in the eelgrass bed and the sand flat. Survival was high in all caged plots (74 to 92% tagged mussel recovery) and did not differ between habitats
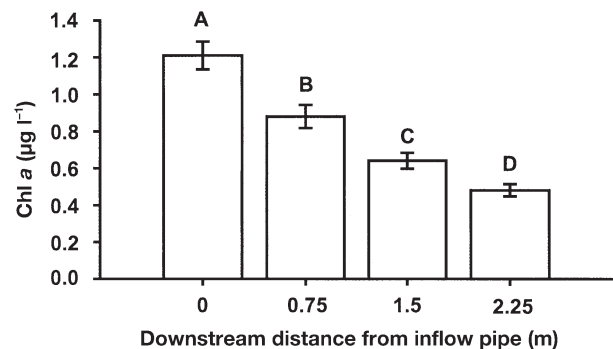

Fig. 3. Chl *a* concentrations (mean ± SE, n = 16) downstream of the water table inflow of the laboratory mussel bed experiment. Data were pooled over 8 sampling dates because the interaction treatment × sampling date was not significant (Table 3; Winer et al. 1991). Differing letters indicate significant differences among treatments (p < 0.05, Tukey's HSD multiple-comparison method)

Table 2. Analyses of effects of downstream distance (0.00, 0.75, 1.50, and 2.25 m) on chl *a* concentration (ANOVA), mussel *Musculista senhousia* shell growth and dry tissue mass (ANCOVA) and mussel gonad index (ANOVA) in the laboratory mussel bed experiment. Data were transformed with a ln(*x* + 1) function to remove variance heterogeneity (chl *a*, shell length and tissue mass), and an arcsine($\sqrt{x}$) function to meet assumptions of normality (gonad index). Assumption of homogeneity of slopes was tested prior to ANCOVAs

Source	df	MS	*F*	p
Chl *a* concentration				
Treatment	3	0.474	59.27	<0.001
Sampling date	7	0.052	6.74	<0.001
Treatment × sampling date	21	0.008	1.01	0.483
Error	32	0.008		
Shell growth				
Treatment	3	4.424	39.60	<0.001
Initial shell length	1	4.992	44.69	<0.001
Error	115	0.112		
Dry tissue mass				
Treatment	3	2.905	146.15	<0.001
Final shell length	1	31.719	1595.68	<0.001
Error	115	0.020		
Gonad index				
Treatment	3	11018.060	86.20	<0.001
Error	116	127.814		

(ANOVA, $F_{1,10}$ = 2.278, p = 0.162). Although predation mortality was higher in the uncaged plots (particularly in the eelgrass bed), with the exception of 1 plot, mortality never exceeded 60 %. In contrast to other studies at this site (e.g. Reusch 1998), few *Pteropurpura festiva* were found feeding in experimental plots during the course of the experiment. There is no evidence that non-lethal interference by predators affects *Musculista senhousia* growth in San Diego Bay, and manipulative experiments have shown that mussels will continue to feed even as nearby individuals are eaten by snails (Reusch 1998, Reusch & Williams 1998). This experiment (like the *in situ* food addition experiment) was probably too short to detect any effects of *Zostera marina* (not due to predation) on mussel survival (Reusch & Williams 1999). Studies of longer duration have documented significantly reduced survival of *M. senhousia* inside eelgrass beds relative to unvegetated habitat in San Diego Bay (Reusch & Williams 1998, 1999).

Like shell growth, the size-specific mean dry tissue mass of mussels in the eelgrass bed was significantly reduced compared to individuals from the sand flat (Fig. 5B). Mean gonad index, however, was similar in both treatments (Fig. 5C). As in the laboratory experiment, gonad index values were not related to mussel size (R^2 = 0.05).

DISCUSSION

Our demonstration that the non-native mussel *Musculista senhousia* is limited by the availability of its phytoplankton food provides 1 mechanism for the resistance of dense continuous eelgrass beds to the formation of mussel mats, and the deleterious effects of such mats on eelgrass (Reusch & Williams 1998, 1999). This result is accordant with those of other experimental manipulations showing that growth and survival of *M. senhousia* are consistently reduced inside eelgrass beds across a variety of spatial and temporal scales in southern California (Reusch & Williams 1998, 1999). Water flow speeds are slower inside eelgrass beds than in adjacent unvegetated areas (Reusch & Williams 1999), presumably reducing the flux of food particles to resident mussels and increasing the likelihood that the
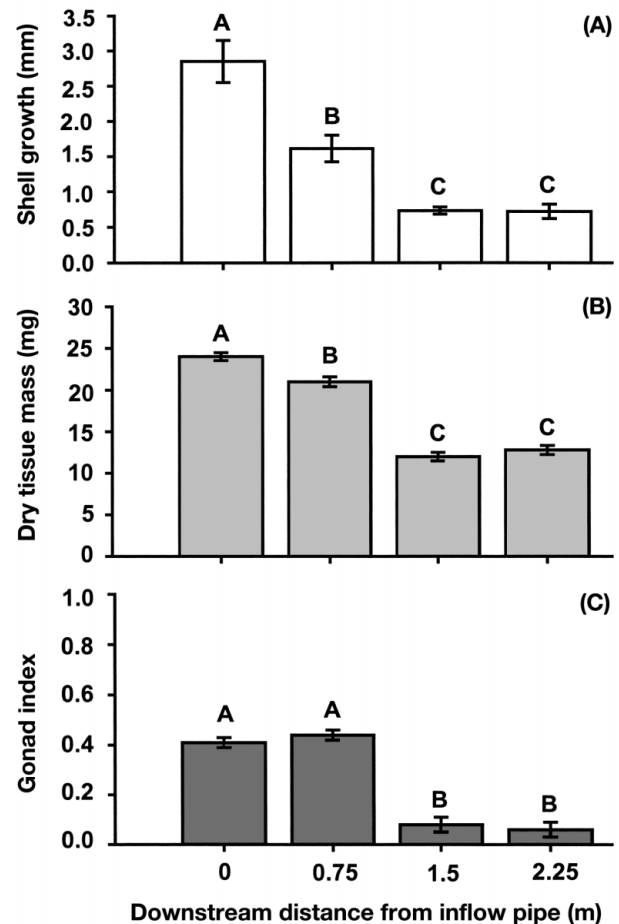

Fig. 4. *Musculista senhousia.* Shell growth (A, white bars) and dry tissue mass (B, light gray bars), and gonad index (C, dark gray bars) of mussels downstream of the water table inflow of the laboratory mussel bed experiment (A&B: adjusted means ± SE; C: means ± SE; n = 30). Differing letters indicate significant differences among treatments (p < 0.05, Tukey's HSD multiple-comparison method)

Table 3. Analyses of effects of habitat (*Zostera marina* bed vs sandflat) on mussel *Musculista senhousia* shell growth and dry tissue mass (ANCOVA), and mussel gonad index (ANOVA) in the Harbor Island transplantation experiment. Adjusted plot means for shell growth and dry tissue mass were used to test for effects of habitat. Data were transformed with a $\ln(x+1)$ function to remove variance heterogeneity (shell length and tissue mass), and an $\arcsin(\sqrt{x})$ function to meet assumptions of normality (gonad index). Assumption of homogeneity of slopes was tested prior to ANCOVAs

Source	df	MS	*F*	p
Shell growth				
Treatment	1	25.205	381.89	<0.001
Initial shell length	1	46.824	479.92	<0.001
Plot (treatment)	22	0.066	0.68	0.861
Error	454	0.098		
Dry tissue mass				
Treatment	1	3.292	205.78	<0.001
Final shell length	1	143.320	5857.59	<0.001
Plot (treatment)	22	0.016	0.67	0.869
Error	454	0.024		
Gonad index				
Treatment	1	30.046	1.52	0.231
Plot (treatment)	22	19.815	0.93	0.551
Error	455	21.243		

near-bottom water will be depleted of food when mussel densities are high (Wildish & Kristmanson 1984, Fréchette et al. 1989, Butman et al. 1994).

Fecundity is highly correlated with individual size in bivalves, such that marked reductions in shell growth (as observed in our study) will result in substantial decreases in fecundity unless offset by a reallocation of resources. Our results show that *Musculista senhousia* responds to moderate reductions in food availability by reducing shell growth, but continues to allocate a constant proportion of resources to reproduction. There is no evidence of a trade-off in favor of reproduction when food is limited. *M. senhousia* has a very short life span of only 1 to 2 yr, and many individuals reproduce only once (Morton 1974, Crooks 1996). Mussels may consequently always be allocating the maximum possible amount of resources to reproduction, regardless of local environmental conditions. Such an expectation is consistent with predictions of life history theory for semelparous organisms (Stearns 1992). If *M. senhousia* reproduce only once, reductions in fecundity such as those we observed can be related directly to reductions in mussel fitness and possibly population growth.

The fact that *Musculista senhousia* in southern California is food-limited carries a significant implication for local eelgrass populations. Any increase in phytoplankton food supply to *M. senhousia* is likely to increase the population growth rate of the mussel, magnifying negative effects of the mussel on eelgrass.

Phytoplankton blooms resulting from nitrogen loading and subsequent eutrophication of estuaries are increasingly common (Paerl 1997, Cloern 2001), and could release *M. senhousia* from food limitation. Such blooms also directly affect *Zostera marina* by reducing the transmittance of light critical for eelgrass growth and distribution (Dennison & Alberte 1985, Zimmerman et al. 1991, Moore et al. 1996, Bricelj & Lonsdale 1997), and have been implicated in numerous seagrass declines around the world (Dennison et al. 1993, Short & Wyllie-Echeverria 1996, Paerl 1997). Increases in the frequency and duration of blooms in southern California could act synergistically with *M. senhousia* to com-
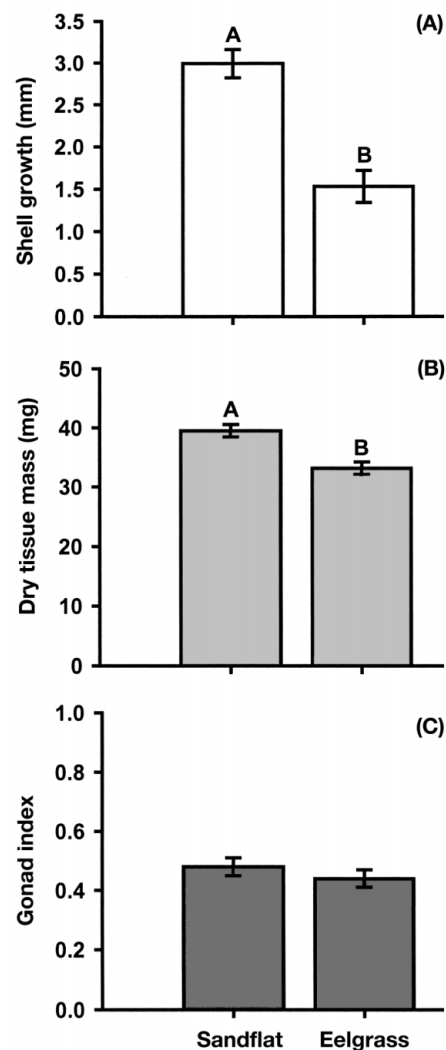

Fig. 5. *Musculista senhousia.* Shell growth (A, white bars) and dry tissue mass (B, light gray bars), and gonad index (C, dark gray bars) of mussels in the eelgrass bed and adjacent unvegetated sand flat at Harbor Island, San Diego Bay (A & B: adjusted means ± SE; C: means ± SE; n = 6 plots). Differing letters indicate significant differences among treatments (p < 0.05, Tukey's HSD multiple-comparison method)

promise eelgrass populations in the region. Although increases in water clarity associated with the introduction of bivalves (e.g. *Dreissena polymorpha* and *Potamocorbula amurensis*) into other systems have been demonstrated or hypothesized (Alpine & Cloern 1992, Padilla et al. 1996, Karatayev et al. 1997), there are no historical data to assess whether *M. senhousia* has had a similar effect. Nevertheless, given the observation that mussel mats apparently interfere spatially with rhizome extension by eelgrass, it is hard to imagine that the net effect of mussels on eelgrass population growth will be positive even if they do increase water clarity through their filtration activities.

The consistent negative effects of *Musculista senhousia* on asexual propagation of eelgrass in southern California are undoubtedly exacerbated by eelgrass decline due to other factors, which include sedimentation due to storm water runoff, heat stress in summer and interactions with other marine organisms (Sewell 1996, Williams 2001). Fragmentation of eelgrass beds through human activities such as boating, dredging, marine construction, and subsequent mitigation activities also favors *M. senhousia* over *Zostera marina* in several ways. Growth and abundance of the mussel are negatively correlated with eelgrass patch size, so reductions in patch size should result in better conditions for the mussel. *M. senhousia* also recruits into open space much more readily than eelgrass. The short life span (1 to 2 yr) and planktonic larval stage of *M. senhousia* effectively uncouples mussel population persistence from local environmental conditions. In an extreme example, populations in frequently disturbed areas could be maintained entirely by the recruitment of mussels from other locations. In contrast, eelgrass relies primarily upon the vegetative growth of nearby plants for recolonization (Thayer et al. 1984). Seeds of *Z. marina* rarely disperse more than a few centimeters to meters (Orth et al. 1994), and successful re-establishment of vegetative fragments is uncommon (Ewanchuk & Williams 1996). Without nearby established patches, eelgrass is unlikely to recover even in areas previously vegetated (Thayer et al. 1984).

Reduced growth of bivalves in seagrass beds is not necessarily a general phenomenon, and the direction of the growth response depends on factors linked to water flow (e.g. eelgrass patch size and leaf shoot density), local production and resuspension of benthic microalgae, bivalve density, and in some cases disturbance of bivalve feeding by predators (reviewed in Williams & Heck 2001). Although our results are currently limited to eelgrass beds similar to those in southern California, identification of the mechanism underlying poor growth and hypothetically survival of *Musculista senhousia* in these beds should foster increased attention to the ecological effects of multiple

disturbances to eelgrass, including but not limited to non-native species, eutrophication and increasing algal blooms, and population fragmentation. On the Pacific coast of the USA *M. senhousia* is now common from San Diego north to British Columbia (Carlton 1992), and its global distribution overlaps extensively with that of *Zostera marina* and other seagrasses, including Europe, Asia, and Australia and New Zealand in addition to North America (den Hartog 1970, Crooks 1996).

Ecologically significant changes resulting from multiple perturbations acting in combination, synergistically, or occurring at a rate faster than that of ecosystem recovery are occurring in other estuaries (NRC 1995, Paine et al. 1998). For example, the invasion of San Francisco Bay, California, by the Asian clam *Potamocorbula amurensis* was apparently facilitated by extreme climatic events that displaced the resident benthic community long enough for *P. amurensis* to establish successfully (Carlton et al. 1990, Nichols et al. 1990). The invasive clam has persisted in spite of the return of normal environmental conditions, and has dramatically altered the trophic webs and community structure in the estuary (Alpine & Cloern 1992, Kimmerer et al. 1994). In San Diego Bay, we have observed mussel mats covering large areas of the substratum otherwise suitable as eelgrass habitat, and it is conceivable that the ecological perturbations described above could promote a transition from eelgrass beds to mats of *Musculista senhousia* (Peterson et al. 1987). Replacement of eelgrass with mussels would have dramatic and long-lasting effects on the structure and function of the local estuarine ecosystem. Benthic primary production would decrease, as would the abundances of common native bivalves and eelgrass-dependent species such as the California halibut and the brant goose (Kramer 1991, Crooks 1998, Reusch & Williams 1998, Crooks & Khim 1999, Valle et al. 1999). As with *P. amurensis* in San Francisco Bay, and the zebra mussel *Dreissena polymorpha* in the Hudson River, New York (Baker et al. 1998), large numbers of actively filtering *M. senhousia* also have the potential to alter the abundance and distribution of the local plankton assemblage. The future management and conservation of ecologically valuable estuarine resources such as *Z. marina* requires a greater understanding of how multiple perturbations interact, and the relative importance of direct versus indirect effects (Menge 1997). Given the demonstrated negative effects of *M. senhousia* on eelgrass in southern California (Reusch & Williams 1998), our study clearly points out that preventing further eelgrass habitat fragmentation and developing and enforcing water quality standards will be critical not just in and of themselves, but also because they could mitigate effects of this non-native mussel on native seagrass.

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