ATTACHMENT 14

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Variable responses of native eelgrass *Zostera marina* to a non-indigenous bivalve *Musculista senhousia*

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Abstract The transport and establishment of non-indigenous species in coastal marine environments are increasing worldwide, yet few studies have experimentally addressed the interactions between potentially dominant non-native species and native organisms. We studied the effects of the introduced mussel *Musculista senhousia* on leaf and rhizome growth and shoot density of eelgrass *Zostera marina* in San Diego Bay, California. We added *M. senhousia* over a natural range in biomass (0–1200 g dry mass/m^2) to eelgrass in transplanted and established beds. The effects of the non-indigenous mussel varied from facilitation to interference depending on time, the abundance of *M. senhousia*, and the response variable considered. Consistent results were that mussel additions linearly inhibited eelgrass rhizome elongation rates. With 800 g dry mass/m^2 of *M. senhousia*, eelgrass rhizomes grew 40% less than controls in two eelgrass transplantations and in one established eelgrass bed. These results indicate that *M. senhousia*, could both impair the success of transplantations of eelgrass, which spread vegetatively by rhizomes, and the spread of established *Z. marina* beds to areas inhabited by *M. senhousia*. Although effects on leaf growth were not always significant, in August in both eelgrass transplantations and established meadows leaf growth was fertilized by mussels, and showed a saturation-type relationship to sediment ammonium concentrations. Ammonium concentrations and sediment organic content were linear functions of mussel biomass. We found only small, non-consistent effects of *M. senhousia* on shoot density of eelgrass over 6-month periods. In established eelgrass beds, but not in transplanted eelgrass patches (≈0.8 m in diameter), added mussels suffered large declines. Hence, eelgrass is likely to be affected by *M. senhousia* primarily where *Z. marina* beds are patchy and sparse. Our study has management and conservation implications for eelgrass because many beds are already seriously degraded and limited in southern California where the mussel is very abundant.

Key words Biological invasion · Facilitation · Interference · *Musculista senhousia* · *Zostera marina*

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Introduction

In marine coastal environments, accidental species introductions are reaching an unprecedented scale. Although the magnitude and importance of introductions, in particular through ballast water, have been acknowledged (Carlton 1989; Carlton and Geller 1993), few studies have experimentally addressed how the newly arriving non-native species interact with indigenous ones (but see Brenchley and Carlton 1983; Posey 1988; Trowbridge 1995). In noting this striking lack of manipulative experiments, Kareiva (1996) pondered whether this gap had impeded progress in understanding the ecological effects of species invasions.

This study addresses the effects of the introduced mussel, *Musculista senhousia*, on native eelgrass, *Zostera marina*. *M. senhousia* was introduced from East Asia to the Pacific west coast of North America in the 1920s (Kincaid 1947) and arrived in southern California in the 1960s (MacDonald 1969). *M. senhousia* is an extraordinarily successful invasive species which has established populations in New Zealand (Willan 1985), Australia (Slack-Smith and Brearley 1987) and the Mediterranean Sea (Hoenselaar and Hoenselaar 1989; Lazzari 1994). *M. senhousia* occurs on intertidal mudflats (Crooks 1996a,b), in saltmarshes (Pacific Estuarine Research Laboratory 1994), and in deeper subtidal regions of estuaries (MacDonald et al. 1990). Although the mussel co-occurs with seagrasses *Zostera* spp. both in its indigenous habitat, which ranges from Siberia to the Red

Sea (Kikuchi and Pérez 1977), and in the invaded environments (Takahashi 1992; Sewell 1996; J.A. Crooks, personal communication), experimental information on the nature of the interaction between *M. senhousia* and eelgrass is lacking.

M. senhousia is a small (≤34 mm) mytilid bivalve with a short life-span (≤2 years), living endobenthically just below the sediment surface, where it filters particulate matter from the water column with a short (≤5 mm) siphon (Morton 1974). *M. senhousia* has the potential to profoundly alter the physico-chemical parameters of its habitat. In part, this is due to its numerical dominance. Dense beds of up to 15,000 adult *M. senhousia* individuals (≥5 mm in length) per square meter can be found in the shallow subtidal zone of San Diego Bay (T.B.H. Reusch and S.L. Williams, unpublished work). In addition, *M. senhousia* builds an encasing cocoon of byssus and sediments. When sufficient biomasses are attained, individual byssal cocoons of the mussel fuse to form continuous byssal carpets (Morton 1974; Crooks 1992; Crooks 1996a,b), which markedly increase sediment firmness (J.A. Crooks, personal communication). Also, the mussels deposit large amounts of organic matter in the sediment (Morton 1974) that possibly results in accumulation of toxic metabolites such as sulfide (Ito and Kajihara 1981). Although aquatic angiosperms seem adapted to the highly reducing sediments in which they are rooted (Crawford 1978; Penhale and Wetzel 1983), sulfide can have adverse effects on seagrass growth (Robblee et al. 1991; Carlson et al. 1994; Goodman et al. 1995). On the other hand, beds of co-occurring filter feeders may enhance angiosperm growth. Specifically, nutrient limitation of coastal marine macrophytes, including eelgrass, can be mitigated by the excretions of mytilid bivalves (Kautsky and Wallentinus 1980; Bertness 1984; Reusch et al. 1994).

The loss of eelgrass habitat is accelerating worldwide (Short and Wyllie-Escheverria 1996) such that only 10% of historical distributions remains in some locales, such as southern California (MacDonald et al. 1990). Several explanations have been invoked for the declines. The contribution of non-indigenous species to declines is poorly known (but see Posey 1988). Our research was motivated by reports that eelgrass transplantations in San Diego Bay, California, were unsuccessful when attempted where *M. senhousia* was abundant (M. Perdue, US Navy Southwest Division, and R. Hoffman, National Marine Fisheries Service, personal communication). This observation was of particular concern because *Musculista* may represent an additional threat to eelgrass restoration, acting in concert with other causes of failure which had resulted in a net loss of seagrass habitat in the past despite considerable restoration efforts (Fonseca et al. 1988).

We present a series of experiments designed to test the effects of *M. senhousia* on eelgrass abundance, leaf growth, and vegetative propagation in experimental eelgrass transplantations and natural beds.

Materials and methods

The experiments tested the responses of eelgrass to *M. senhousia* in both established eelgrass beds (three experiments) and eelgrass transplantations (two experiments) (Table 1). Two experiments in experimental eelgrass transplantations (*Musculista*-eelgrass transplantation experiments, METE) investigated whether the success of eelgrass transplantation is affected by *M. senhousia*. The other three experiments (established meadow experiments, EME) investigated how eelgrass leaf and rhizome growth and eelgrass shoot density are affected by *M. senhousia* (Table 1) within established eelgrass beds where the closed canopy creates a different environment and where eelgrass is less susceptible to disturbances.

Two established meadow and all eelgrass transplantation experiments were carried out at a sheltered site (wind fetch < 0.5 km) at Harbor Island, San Diego Bay (32°43′25″ N, 117°11′19″ W). Water temperatures ranged from 13 to 22°C (2-weekly measurements) and salinities from 34 to 35.5 g/kg (monthly measurements) during the study period. The site experienced vigorous tidal flushing because it was only ≈5 km to the mouth of the bay. Sediments were sandy (80% particles > 0.02 mm). A portion of the eelgrass meadow at Harbor Island was established by transplantation using nearby stands in 1988 to mitigate eelgrass loss at a marina next to the site. The original transplanted bed (0.1 ha) has since expanded to merge with the surrounding established eelgrass population and stretches from 0.8 m depth below mean low low water, MLLW, to a depth of 3 m (width of bed ≈20 m).

In urban San Diego Bay, where much subtidal habitat is restricted to military purposes or commercial port, choosing a site with suitable conditions for growth of eelgrass to perform a transplantation experiment is difficult because many potential sites already possess eelgrass. Clearing an area of established eelgrass to perform a transplantation experiment is not permissable in a region where a 90% decline in eelgrass has occurred. We planted in areas without eelgrass to simulate local transplantations. At a given site, the lack of eelgrass does not necessarily imply that it will not grow unless there is some obvious habitat unsuitability. We selected the site Harbor Island because in addition to a large established bed, there was an area without eelgrass >200 m^2 in the shallow subtidal zone (0.5–0.8 m depth below MLLW) that seemed suitable for transplantation, although during one transplantation experiment we realized that this area was devoid of eelgrass due to regular grazing by brant geese (*Branta bernicla*) in the winter months (December–February).

One established meadow experiment was performed in an eelgrass bed at Le Meridien (32°41′41″N, 117°09′52″W), located ≈2 km further into San Diego Bay. Although part of this extended meadow was the site of another mitigation project performed in 1990, our experiment was located away (>20 m) from the original mitigation site. Both sites are typical of steep-sided shores (slope 5–12°) inhabited by eelgrass in San Diego Bay and eelgrass abundance and shoot morphology is typical for subtidal beds in San Diego County (Ewanchuk 1995). Eelgrass beds at Harbor Island and Le Meridien have reduced genetic diversity compared to beds that have not been disturbed by dredging (Williams and Davis 1996) but in this regard they are representative of eelgrass habitat in urban bays in southern California (S.L. Williams, unpublished work).

Manipulation of *Musculista senhousia* abundance

All manipulations and measurements were made by SCUBA diving. In all experiments, we used the area of substratum inhabited by *M. senhousia* as a surrogate for mussel biomass because it was impractical to count the number required for each experiment (>25,000 mussels). A prospective donor mussel bed in which the mussels were densely aggregated in carpets was found within 5 m of the study eelgrass bed at Harbor Island. Here, mussel abundance was sufficiently homogeneous to use area as a surrogate for density. This was verified on two dates when we sampled randomly selected areas of 0.5 m^2 (n = 4,5 respectively) within the mussel donor bed

Table 1 Design of field experiments on effects of *Musculista senhousia* on eelgrass *Zostera marina*

Experiment/duration	Replication	Experimental factors (levels)	Response variable
Musculista-eelgrass transplantation experiments (METE)			
	Hypothesis: *M. senhousia* affects eelgrass transplantations in terms of shoot density, leaf and rhizome growth		
METE 1 30 Sep 94–10 Feb 95	5	*Musculista* (4 biomasses) Spatial blocking factor	Shoot density[a] (4-weekly) Rhizome growth (Nov 94)
METE 2 25 May–30 Nov 95	7	*Musculista* (4 biomasses) Water depth (2) Spatial blocking factor	Shoot density, rhizome Growth (Sep + Nov 95) Leaf growth (Aug + Oct 95) Porewater ammonium, sulfide (Aug/Oct 95)
Established meadow experiments (EME)			
	Hypothesis: *M. senhousia* affects established eelgrass beds in terms of shoot density, leaf and rhizome growth		
EME 1[b] 30 Sep 94–30 Jan 95	5	*Musculista* (4 biomasses) Spatial blocking factor	Shoot density (4-weekly) Rhizome growth (Nov 94)
EME 2 12 Feb–20 Jun 95	6	*Musculista* (4 biomasses Spatial blocking factor)	Shoot density (4-weekly) Leaf growth (Mar 95)
	Hypothesis: predators of *M. senhousia* indirectly affect eelgrass through consumption of mussels		
EME 3 15 May–20 Nov 95	5	*Musculista* (2 biomasses) × exclusion of predators Spatial blocking factor	Shoot density (6-weekly) Leaf growth (Aug 95)

[a] Leaf and reproductive shoots small experiments
[b] This experiment ran at station Le Meridien during the same time interval as METE 1

Table 2 Population parameters for *M. senhousia* in the donor bed used for all five experiments

M. senhousia	Date		
	Sep 1994	Feb 1995	May 1995
Biomass (dry mass/50 cm^2) ± SE ($n = 20$)	3.1 ± 0.19	2.3 ± 0.3	2.6 ± 0.18
Density (no./50 cm^2) ± SE ($n = 20$)	37 ± 4	23.7 ± 3.2	13.8 ± 2.3
Mean length (mm) ± SE ($n = 250$)	13 ± 0.5	14 ± 0.3	17.7 ± 0.4

with five replicate cores (50 cm^2, 6 cm deep). The cores were sifted through 1 mm mesh screen and mussels were measured to the nearest 1/10 mm with a vernier caliper (mussels < 5 mm in length were not considered). The size distribution of *M. senhousia* in the donor bed was approximately unimodal with few juvenile mussels present. The census revealed only small, non-significant differences in mussel biomass among replicate areas (maximal biomass difference among plots in February 1995: 0.7 g/50 cm^2, one-way ANOVA, $F_{3,16} = 1.45$, $P = 0.266$; maximal difference among plots in May 1995: 0.9 g/50 cm^2, $F_{4,20} = 1.30$, $P = 0.305$).

We collected a substratum area of 0.25, 0.5, and 1 m^2 in the mussel donor bed and added these doses to the circular experimental plots (0.5 m^2). Including a fourth treatment receiving no *M. senhousia* addition (0×), the *M. senhousia* treatments were thus an addition of 0×, 0.5×, 1× and 2× of the ambient biomass at Harbor Island sand flat. Treatment levels spanned 0–1100 g dry mass (tissue + shell, no cocoons)/m^2, corresponding to abundances between 0 and 14,000/m^2 (individuals ≥5 mm shell length). The same mussel donor bed was used for all experiments. Variations in treatment levels among experiments occurred because the donor bed changed its density and biomass over time (Table 2). The treatment levels represented the natural range of *M. senhousia* biomass in shallow subtidal areas of San Diego Bay (T.B.H. Reusch and S.L. Williams, unpublished work).

Prior to the addition, the *M. senhousia* carpets were washed in a mesh bag (mesh size 4 × 4 mm) in the field to remove sediment and other infauna. During this procedure, about half the mussels remained in byssal cocoons. The mussels were placed in the experimental plots and homogeneously spread by hand. In the 0×-addition plots, the sediment was disturbed to simulate mussel addition. By the next day, virtually all mussels re-established within the sediments, as they readily do upon disturbance.

We also assessed whether the disruption of the mussel carpets of *M. senhousia* caused a significant increase in mussel mortality caused by factors other than predation. For this purpose, we transplanted small (15 individuals) mussel populations (1) as a core of 50 cm^2 within their intact byssal carpet (2) as single individuals but within the byssal bag (3) as single individuals without byssal bag onto two habitats: (1) the shallow sand flat and (2) the established eelgrass at Harbor Island ($n = 3$). Mussels were planted in their natural position into completely buried vexar rings (18 cm in diameter, 8 cm height, mesh size 8 × 8 mm) to prevent migration. This experiment was conducted twice (August and October 1995); thus, the experiment had 12 treatments (3 transplantation procedures × 2 habitats × 2 dates). After 3 weeks, the mussels were retrieved, sifted through 1 mm and categorized as alive, dead and undamaged, and dead due to predation by whelks/crustaceans. We expressed the mortality due to unknown causes as the fraction of

the number of undamaged dead shells/number of transplanted individuals.

Musculista-eelgrass transplantation experiments (METE)

The first *Musculista*-eelgrass transplantation experiment (METE 1) was initiated in September 1994, and the second (METE 2) in May 1995 (Table 1). The eelgrass transplantations were performed in areas with moderate densities of *M. senhousia* (≈2.5 g dry mass/50 cm^2) which were situated shallower and deeper than the closed (100% cover) canopy at Harbor Island. Experimental plots were set up in a randomized block design with blocks ($n = 5$ in METE 1 and $n = 7$ in METE 2) arranged parallel to the shoreline and separated by ≈5 m. Each block had plots ($n = 4$) separated by ≈2 m. We blocked as a precaution for along-shore variation in currents and sediment characteristics. The plots of METE 1 were located on the sand flat shallower than the established eelgrass bed at 0.8 m below MLLW only. In METE 2, plots were located on the shallow sand flat and also at the depth limit for eelgrass distribution at the site to test for an interaction of *M. senhousia* addition with water depth. The deep plots were placed beyond the closed eelgrass canopy in natural clearings (each ≈4 m long and 2 m wide) among the scattered vegetated patches at 3–3.5 m depth. Only two *M. senhousia* levels (0× and 2×) were used at 3.5 m depth. We used a lower experimental effort for these treatments because there was insufficient space for more experimental units among the clearings.

M. senhousia in the surrounding substratum were first removed in an area of 0.5 m^2 around each plot (diameter 80 cm) by hand before adding the mussel treatment levels to the plots. The removal procedure only affected the superficial (5 cm) layer of the sediment. Eelgrass transplants were added to the experimental plots 1 week after removal of resident mussels and addition of *M. senhousia* treatment levels.

We used terminal leaf shoots of main rhizome branches attached to a 10-cm piece of rhizome (the typical morphology of local eelgrass), taken from the adjacent (< 5 m) eelgrass bed, as a transplant. Transplants were anchored with a metal staple (Fonseca et al. 1982) evenly in the central 0.25 m^2 portion of the plots. Each experimental plot received a total of 19 ramets (7 transplants bearing one, and 6 bearing two ramets, respectively, thus 13 transplants in total). One transplant was in the plot center, the other 12 were planted in two circles of 12 and 24 cm radius, respectively, around the plot center. In each circle, transplants bearing one and two leaf shoots alternated.

Established meadow experiments (EME)

The same experimental design as in the shallow plots of METE 1 and 2 was used in the first 2 established meadow experiments, EME 1 and 2, which were performed at 2 different sites (Table 1). EME 1 was situated within the center (mid-bed) of a continuous established eelgrass bed at Le Meridien at 0.5–1 m depth below MLLW. The bed was > 150 m long (along-shore) and 20 m wide. In November 1994, eelgrass shoot density was 128 ± 15/0.25 m^2 ($n = 10$) and mean shoot height (±SE) was 40 ± 4 cm ($n = 35$). At Harbor Island, EME 2 and 3 were situated in the center of a continuous eelgrass meadow ≈35 m long and 20 m wide at 1–1.8 m depth below MLLW. One month after the initiation of experiments eelgrass shoot densities/0.25 m^2 ± SE were 104 ± 9 and 100 ± 11 ($n = 10$), and mean shoot heights ± SE were 60 ± 4 cm and 57 ± 3 cm ($n = 30$) in EME 2 and EME 3, respectively. At both sites, mussels living in the eelgrass bed at the beginning of the experiment were not abundant enough (≤ 0.2 g dry mass/50 cm^2) to remove them before treatment mussels were added. EME 1 was executed identically and at the same time to METE 1 above, using the same donor mussel population.

A third established meadow experiment (EME 3) was conducted in May 1995 after aggregations of up to 30 individuals per experimental plot (0.5 m^2) of the predatory muricid snail, *Pteropurpura festiva*, had decimated *M. senhousia* additions in EME 2 at Harbor Island (Table 1). Within 4 months, snails consumed ≈90% of the transplanted mussels (T.B.H. Reusch, unpublished work). EME 3 thus was conducted to determine the effects of predators on *M. senhousia* and indirectly, through *M. senhousia* biomass alterations, on the eelgrass. The experiment was situated in 1–1.8 m depth below MLLW in the established bed. In a 2 × 2 factorial experiment, predators were either excluded from the experimental area of 0.5 m^2 by means of 25-cm-tall circular fences (mesh size 12 × 12 mm, upper 5 cm bent outwards) buried 5 cm into the sediment, or allowed access through three large (10 × 50 cm) openings at the base. Fences were ≈ half as tall as the eelgrass canopy (mean leaf height in June 95 ± 1 SE = 58 ± 1.6 cm, $n = 120$). Fencing was successful in excluding the snails. During 2- to 4-weekly inspections we found and removed only two snails inside the closed fences. In contrast to the other four experiments, we applied 1.5× ambient *M. senhousia*-addition and no addition fully crossed with complete fences/open fences. The replication was $n = 5$. Completely unfenced treatments served as controls for fence effects on eelgrass. Fouling organisms were removed after 3 months with a wire brush.

Response variables: mussel biomass, leaf and rhizome growth rates, leaf shoot abundance, sediments

In all experiments, *M. senhousia* biomass was monitored at the beginning of each experiment and then every 3 months by randomly taking three cores (depth 6 cm, area 50 cm^2) within each plot for a total sampling effort of 60–72 cores per sampling date per experiment. Mussels were sifted through 1 mm mesh screen and measured to the nearest 0.1 mm. The biomass was estimated using the following relationship, determined from a sample of $n = 40$ mussels collected in October 1994: dry mass = $0.0762 \times 10^{-3} \times \text{length (mm)}^{2.67}$. Holes left in the substratum were filled with ambient sediment to minimize disruption of the eelgrass rhizomes but mussels were not replaced. Sampling for biomass represented a maximal disruption of 6% of the experimental unit (2 × 3%) during each experiment. We also sampled the biomass and size distribution of *M. senhousia* every 3 months throughout the year in the donor bed to detect potential differences in mussel biomass among experiments and undisturbed *M. senhousia* beds.

In the METE, the eelgrass transplants quickly expanded through lateral growth and vegetative shoot recruitment beyond the initial planting area of 0.25 m^2. In these experiments as well as in the EME, all eelgrass response variables were measured only within the central 0.25 m^2 of the plots to avoid edge effects. We measured leaf growth on five plants per plot (thus a total of 100–140 plants) with a leaf puncture technique (Williams and Ruckelshaus 1993). After 3–7 days, we collected the tagged plants. On average, only 5% of the plants in the plots were harvested, and we assume that this did not lead to differences among treatments. In total, we performed five sets of leaf growth measurements in 1995. Leaf growth in EME 2 was measured on 4–10 March 1995 and in EME 3 on 8–11 August 1995. In METE 2, leaf growth was measured on 2–7 August, and 3–10 October 1995. In the deep plots of the METE 2, leaf growth was measured only once (20–26 October 1995).

Rhizome elongation rates were measured by tagging five vegetative shoots in each experimental plot (thus a total of 100–140 plants per measurement) with small flexible cable ties between the first and second root bundle. After 2–3 weeks the new rhizome produced was measured *in situ* with vernier calipers without collecting the plants. Three to five tagged plants could be recovered per plot as limited by complete burial of some tags. We performed four sets of rhizome growth measurements: November 1994 (METE 1 at Harbor Island, and EME 1 at Le Meridien), September 1995 (METE 2), and October/November 1995 (METE 2).

Eelgrass leaf + reproductive shoots were counted every 4–6 weeks during the experiments. Initial shoot counts were made 1–3 days after the mussels were added to the plots in all EME.

Biodeposition by *M. senhousia* hypothetically results in increased sediment porewater nutrients, which in turn can fertilize

leaf growth. To address this, we sampled porewater in the shallow plots of the METE 2 in August and November 1995. In each plot, duplicate samples were taken at random using methods in Williams and Ruckelshaus (1993). Due to time constraints, one block selected at random was deleted, leaving $n = 24$ experimental plots. We assumed *a priori* that phosphate would be of minor importance to eelgrass in the silicate sediment present at the site (Short 1987) and focused on nitrogen given demonstrated nitrogen limitation of Pacific coast eelgrass (Williams and Ruckelshaus 1993). In August, we determined the organic content of the sediment (upper 5 cm) in a random subsample of 20 out of 28 experimental plots as the loss of mass of the dried sediment (90°C to constant mass) in a muffle furnace at 550°C.

Because the buildup of hydrogen sulfide in the presence of mussel biodeposits might have negative effects on leaf growth, we measured free hydrogen sulfide in the sediment porewater. Sediment cores to a depth of 8 cm were taken with a modified 50-ml syringe and tightly closed with a rubber stopper. They were transferred in a cooler on ice in < 4 h to the laboratory where they were extruded quickly into N_2-purged, 50-ml centrifuge tubes, capped, and centrifuged. After centrifugation, 2 ml of porewater was immediately placed into test tubes with reagent. Sulfide was determined colorimetrically after Cline (1969), modified for a sample volume of 2 ml. In addition, samples were checked for sulfidic odor after opening the sampling syringes to ambient air.

Statistical analysis

We assessed the effects of the transplantation procedure on *M. senhousia* mortality through three-way factorial ANOVA, including the experimental factors eelgrass presence/absence, date, and transplantation procedure. In the METE 1 and 2, we compared the *M. senhousia* biomasses between the donor bed and the 1× ambient *M. senhousia* treatments of the experiments with *t*-tests to test for differences in population abundances over time, using the mean biomasses ($n = 3$) obtained within 0.5-m^2 areas ($n = 5$ to 7).

To determine the response function of eelgrass leaf and rhizome growth to *M. senhousia* biomass, we used the mussel biomasses determined within each plot instead of the categorical *M. senhousia* treatment levels as predictors for plant growth in a polynomial regression. Generally, there were ≤ 2 weeks between assessing *M. senhousia* biomass and eelgrass growth response except for October rhizome growth in METE 1 (5 weeks) and October leaf growth in METE 2 (4 weeks). In both METEs, however, our repeated sampling revealed that *M. senhousia* treatment levels were sufficiently stable to assume that no marked biomass changes occurred in the interim (see *Results*). The general linear model included the first and second-order polynomial and had the following form:

$$y_{ij} = ax_{ij}^2 + bx_{ij} + c + B_j + e_{ij}$$

where y_{ij} is the mean leaf or rhizome growth per plot, x_{ij} is the biomass of *M. senhousia* associated with each growth measurement, a, b and c are the coefficients for the polynomial regression, B_j is the effect of the jth block and e_{ij} is the random error associated with each mean. We hypothesized that under moderate mussel abundances, leaf growth is enhanced while under very high *M. senhousia* abundances, negative effects might prevail. Hence, we included the quadratic term to detect a potential dome-shaped function of maximum growth at intermediate mussel additions. Because no plot-specific mussel biomasses were available in the EME 1 at Le Meridien (see Results), rhizome growth data were analyzed using one-way ANOVA (with spatial blocking factor).

If eelgrass leaf growth were limited by sediment ammonium, it should follow a saturation-type response to ammonium concentration (Williams and Ruckelshaus 1993; Reusch et al. 1994). To assess this, we fitted data from the METE 2 to a hyperbolic tangent function of leaf growth vs. interstitial ammonium concentrations:

$$G = g_{max} \frac{C}{(C + K_M)}$$

where G is leaf growth, g_{max} is the maximal growth rate, C is the interstitial ammonium concentration and K_M is the half-saturation constant.

All ANOVAs and ANCOVAs for shoot densities included a spatial blocking factor. Shoot densities as a function of *M. senhousia* addition levels were analyzed with one-way ANOVA in METE 1 on each sampling date. In METE 2, we analyzed the data with a one-way ANOVA including only the shallow plots, and with a two-way ANOVA incorporating the 0× and 2× *Musculista*-addition plots at 0.8 m and 3.5 m depth. The initial shoot density in the EMEs varied considerably within blocks (coefficient of variation 16–22%). Therefore, we included the shoot densities counted 2–3 days after *M. senhousia* addition as covariate in an ANCOVA model. EME 3 was analyzed with a 2 × 2 ANCOVA with *M. senhousia* addition/no addition and predators absent/present as experimental factors.

Linear regressions of sediment parameters (organic content, sediment nutrients) as a function of mussel biomass were performed using the plot means.

Results

M. senhousia transplantation control

In the experimental tests for *M. senhousia* transplantation procedures, we recovered (live plus dead) an average of 14.2 animals/experimental unit (95%). Over 3 weeks, the mortality rate of *M. senhousia* due to unknown causes was not significantly different among individuals which were transplanted (1) within an intact byssal carpet, (2) as isolated individuals within their bag, or (3) as isolated individuals without byssal bag (Table 3). Thus, we found no evidence for increased *M. senhousia* mortality due to the transplantation procedures which involved disruption and sifting of the mussel mat through 4-mm-mesh screen. None of the other factors (date, presence of eelgrass) nor their interactions was significant (all $P > 0.2$).

Effects of *M. senhousia* on eelgrass transplantations

Eelgrass leaf growth

Leaf growth was not measured in the first experiment (METE 1). In METE 2, *M. senhousia* additions had a significant effect on leaf growth in August (Table 3). To

Table 3 Comparison of mortality rates of *M. senhousia* among different transplantation treatments ($n = 12$). Fifteen individuals were transplanted in August and October 1995 into the eelgrass *Z. marina* meadow and onto the sand flat. None of the differences are significant in a three-way factorial ANOVA ($P > 0.19$)

M. senhousia transplantation treatment	Mean fraction dead/total no. transplanted	SE
Intact byssal carpet	0.037	0.0121
Isolated, byssal bag	0.029	0.0172
Isolated, no byssal bag	0.054	0.0168

remove variation due to significant block effects in plots of leaf growth versus mussel biomass, we adjusted leaf growth by plotting the difference of each observation from the respective block mean. $\overline{B}_j - x_{ij}$. Leaf growth was a dome-shaped function of *M. senhousia* biomass in August, as indicated by the highly significant negative curvilinear component of the model ($P = 0.007$, Table 4). Eelgrass growth was enhanced with mussel densities up to ≈4 g/50 cm^2. With increasing mussel biomass (>5 g/50 cm^2), leaf growth tended to decline (Fig. 1a) to values similar to those with very few *M. senhousia* present. In October, mussel additions did not have a significant effect on leaf growth in the shallow or deep plots (Table 4, Fig. 1b,c). Because at that time, all *M. senhousia* biomasses had declined to <6 g dry mass/50 cm^2 in METE 2, the absence of a dome shaped function in October is not at odds with the August results.

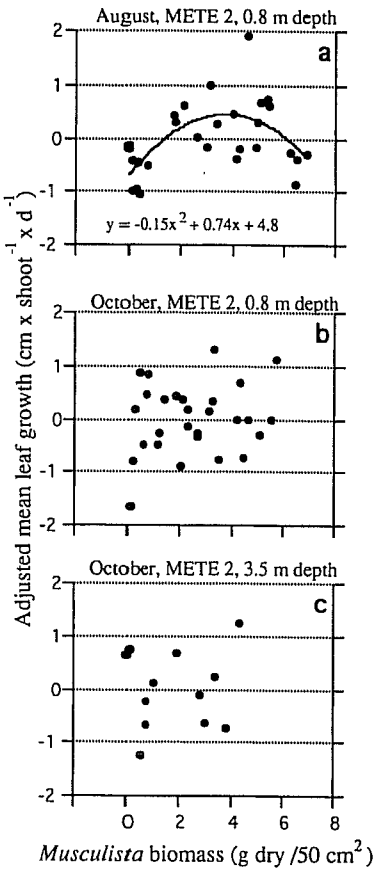

Fig. 1 Leaf growth rates of eelgrass (*Zostera marina*) adjusted by their associated spatial block mean ($\overline{B}_j - x_{ij}$) as a function of the co-occurring biomass of the mussel *Musculista senhousia* in the *Musculista*-eelgrass transplantation experiments (METE). Data are means of 5 leaf growth and 3 mussel biomass determinations per plot. The statistically significant equations of the general linear model are given. See Table 4 for statistical analysis

Eelgrass growth as function of porewater ammonium and M. senhousia effects on ammonium

In Fig. 2, we plotted August leaf growth as a hyperbolic tangent function of porewater ammonium concentration. The maximum leaf growth rate $g_{max}$was 7.8 cm shoot^{-1} day^{-1} attained at approximately 100 µM NH_4^+ in the porewater. The equation explained 44% of the variance in leaf growth and hence supports the hypothesis that nitrogen was limiting for eelgrass leaf growth. For the calculation of the model, we excluded three of the highest ammonium values (Fig. 2, open circles) because they were associated with declining leaf growth at *M. senhousia* biomass >6 g/50 cm^2 (Fig. 1a). Inclusion of these high NH_4^+ values was not justified because a hyperbolic tangent function only describes the limited and saturated range of nutrient concentrations, but not adverse effects at high nutrient doses.

It was not surprising that leaf growth was a significant function of both interstitial ammonium concentrations and mussel biomass because *M. senhousia* increased both the organic matter and the interstitial ammonium in the sediments in an approximately linear way (Fig. 3a, b). Because we detected no significant difference between slopes and intercepts of the August and October regressions (ANCOVA, interaction *M. senhousia* biomass × date, $P = 0.39$), we summarized both dates into one regression model. Presumably the organic enhancement resulted from the accumulation of *M. senhousia* pseudofeces and feces in the sediment.

Table 4 General linear model: effects of the mussel *M. senhousia* (dry biomass/50 cm^2) on eelgrass leaf growth (cm shoot^{-1} day^{-1}, means of 5 shoots per plot) in *Musculista*-eelgrass transplantation experiments. Interactions of the spatial blocking factor with mussel biomass were not significant in any analysis ($P > 0.3$). The quadratic effect of *M. senhousia* biomass was removed from the model if $P > 0.5$

Experiment, depth	Effect	*df*	MS	*F*	*P*
METE 2, 0.5–0.8 m August 1995	*Musculista* linear term	1	5.414	12.02	0.003**
	Musc. quadratic term	1	4.516	9.178	0.007**
	Block	6	2.437	9.935	0.001**
	Residual	19	0.390		
METE 2, 0.5–0.8 m October 1995	*Musculista* biomass	1	0.618	1.090	0.308ns
	Block	6	1.265	2.245	0.081ns
	Residual	20	0.563		
METE 2, 3.5 m October 1995	*Musculista* biomass	1	0.082	0.068	0.803ns
	Block	5	2.612	2.186	0.205ns
	Residual	5	5.972	1.194	

** $P \leq 0.01$, ns not significant

Despite the organic accumulation in sediments inhabited by *M. senhousia*, the hypothesis that such accumulation can lead to increased sulfide in the sediments was not supported. Surprisingly, we were unable to detect sulfide concentrations above the detection limit of the method (2 µM). Also, samples never smelled sulfidic to the several persons who sniffed the cores immediately after sampling. Sediments were reddish after combustion, suggesting that the sediments contained relatively high concentrations of iron which could have bound the sulfides.

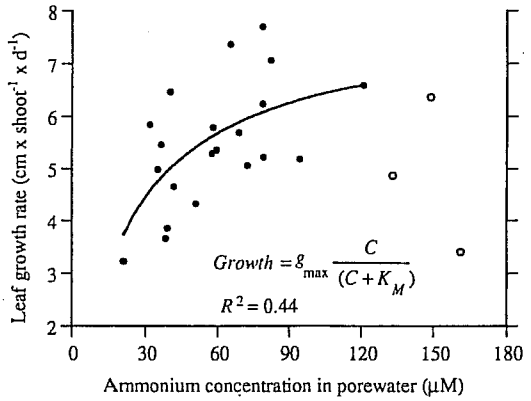

Fig. 2 Leaf growth of *Z. marina* as a function of the interstitial ammonium concentration in the eelgrass transplantation experiment METE 2 in August 1995. Each data point is the mean of 5 growth measurements and duplicate porewater determinations. The equation of a hyperbolic tangent function is given. C is interstitial ammonium concentration in the sediment, g_{max} is maximum growth rate and was 7.8 cm shoot^{-1} day^{-1}, K_M is the half-saturation constant and was 24 µMNH_4^+. The 3 *open circles* indicate data points which were excluded because they were associated with decreased growth rates at *M. senhousia* biomasses >6 g/50 cm^2 (Fig. 1a)

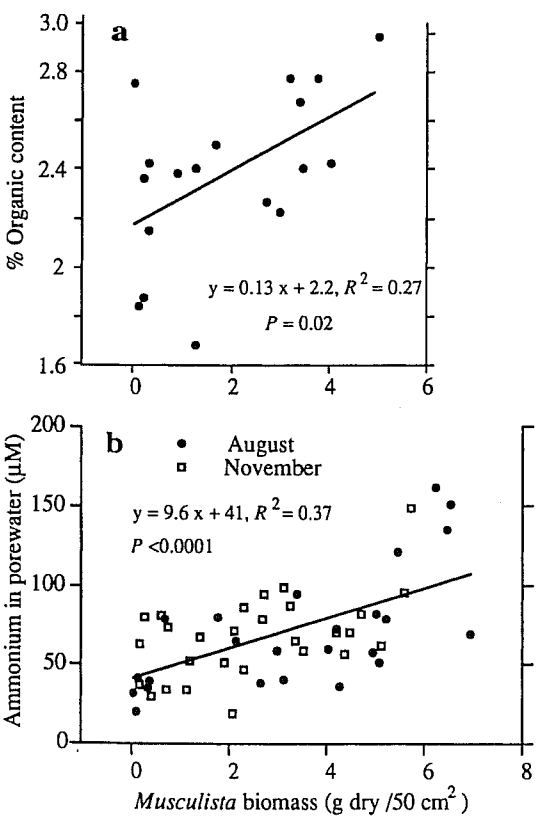

Fig. 3 **a** Organic content of the sediment (upper 5 cm) and **b** interstitial ammonium concentrations (mean of duplicate samples) as a function of *M. senhousia* biomass (mean of 3 cores of 50 cm^2). Samples were taken in the shallow plots of METE 2

Rhizome elongation rates

Rhizome elongation rates declined with increasing *M. senhousia* biomass in both experiments (all data included, Table 5, Fig. 4). Rhizome growth was up to 40% lower at *M. senhousia* biomass of 4 g/50 m^2 compared to mussel free treatments. In all experiments, it could be argued that the effects observed were due to organisms associated with *M. senhousia* or its byssal cocoons. While true, we inspected rhizomes and roots for signs of chewing or other damage and found none.

Leaf + flowering shoot abundance and M. senhousia *persistence*

Both shallow eelgrass transplantations did very well and shoot numbers increased exponentially during the first 3 mo (Figs. 5, 6) demonstrating that, except for brant grazing during 2.5 months in winter, all other environmental variables were suitable for eelgrass. At the end of the experiment, the transplanted eelgrass patches were 0.5–0.6 m and 0.8–0.92 m in diameter in METE 1 and 2, respectively. In general, we found only weak and non-significant effects of *M. senhousia* biomass on eelgrass shoot density. In METE 1, although the rate of shoot increase was slowest at the highest mussel treatment level, the only significant negative effect on shoot density occurred between 4 and 5 months in February 1995 (Fig. 5, one-way-ANOVA, P = 0.012). The plots of METE 1 were shallow enough to allow brant geese to graze on the eelgrass starting in late November 1994. By mid-February 1995, the geese had destroyed the entire experiment. Because of unidentified interactions between goose grazing and mussel additions, these results should be viewed with caution. In all other experiments we never observed interference by geese. In METE 2, mussel biomass as high as 7 g/50 cm^2 had only small, non-significant effects on shoot densities (Fig. 6a). Eelgrass transplantation success, measured as shoot density, was not more susceptible to high mussel biomass at the lower depth limit for eelgrass growth (3.5 m, Fig. 6b; two-way ANOVA, interaction depth × *M. senhousia*, P = 0.3).

M. senhousia biomass persisted at the original treatment levels, although at the end of METE 2, the differences among the levels became less pronounced (Fig. 6). The changes in mussel biomass in the experimental plots paralleled those in the donor mussel bed (Fig. 5, 6), demonstrating that the transplantation of

Table 5 General linear model: effects of the mussel *M. senhousia* (dry biomass/50 cm^2) on eelgrass rhizome growth (mm day^{-1}, mean of 5 shoots per plot). All interactions of the spatial blocking factor with *M. senhousia* biomass were deleted because they were not significant ($P > 0.5$)

Experiment	Effect	*df*	MS	*F*	P
METE 1 November 1994	*Musculista* biomass	1	1.1097	6.3565	0.0244*
	Block	4	0.2822	1.6163	0.2252
	Residual	14	0.1746		
METE 2 August 1995	*Musculista* biomass	1	3.142	5.867	0.025*
	Block	6	0.096	0.179	0.979
	Residual	20	0.535		
METE 2 November 1995	*Musculista* biomass	1	0.5201	5.3064	0.0321*
	Block	6	0.1010	1.0305	0.4347
	Residual	20	0.0980		

* $P \leq 0.05$

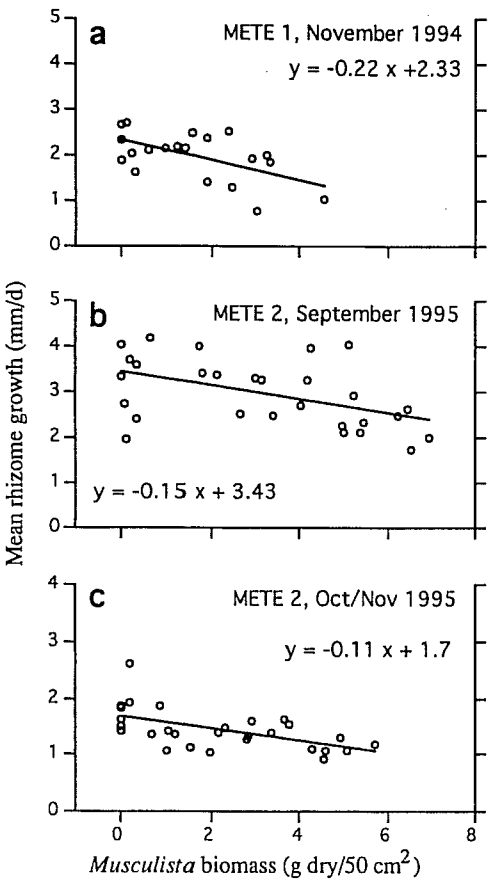

Fig. 4 Rhizome growth of *Z. marina* as a function of the *M. senhousia* biomass in 2 *Musculista*-eelgrass transplantation experiments (METE). The equations of the significant linear regressions are given. Each data point is the mean of 5 rhizome growth measurements and 3 mussel biomass determinations per plot

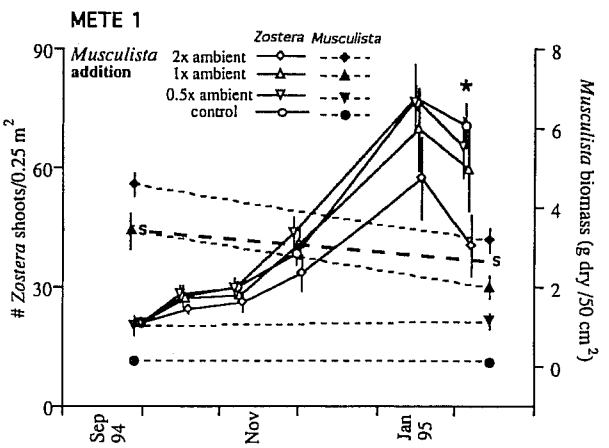

Fig. 5 Time courses of shoot densities in plots with 4 different *M. senhousia* additions in the *Musculista*-eelgrass transplantation experiment METE 1 with associated mussel treatment levels (± 1 SE). METE 1 was conducted in a single depth at 0.5–0.8 m below MLLW. Significant differences among treatments are indicated as follows * $0.05 > P \geq 0.01$ P, (*) $= 0.1 > P \geq 0.05$. The *dashed boldface line* denoted by *s* is the biomass in the source bed for *M. senhousia*

M. senhousia had little effect on mussel mortality. A statistical comparison of the *M. senhousia* biomass between the donor bed and the 1× ambient treatment in METE 1 after 4 months experimental duration revealed only small, non-significant differences (*t*-test, mean biomass of 3 determinations per plot, $n = 5$, $P = 0.14$). Likewise, after 3 months of experimental exposure in METE 2, only small, non-significant differences among the biomass of transplanted and non-transplanted *M. senhousia* were present (*t*-test, $n = 7$, $P = 0.6$). After 6 months, however, the biomass of *M. senhousia* was 27% lower in the 1× ambient treatment of the eelgrass transplantations compared to the adjacent mussel donor bed, a difference which was marginally significant (*t*-test, $n = 7$, $P = 0.06$).

Effects of *M. senhousia* on eelgrass in established meadows

Leaf growth was not measured in EME 1. In March 1995 in EME 2 there was no significant effect of *M. senhousia* on leaf growth (Table 6, Fig. 7a). In contrast, in August in EME 3, we found a significant positive effect of *M. senhousia* (Fig. 7b). Similar to the transplantations, leaf growth rates increased linearly with mussel biomass until approximately 4 g/50 cm^2. However, there was no parallel decline in leaf growth rates with high mussel biomass. At the time of leaf measurements, mussel biomass had declined to < 4 g/50 cm^2, below the level associated with declines in growth rates in the *Musculista*-eelgrass transplantation experiment 2 (Fig. 1a).

Rhizome elongation rates, measured at Le Meridien (EME 1), declined significantly with *M. senhousia* biomass (Table 7), similarly to the effect in the trans-

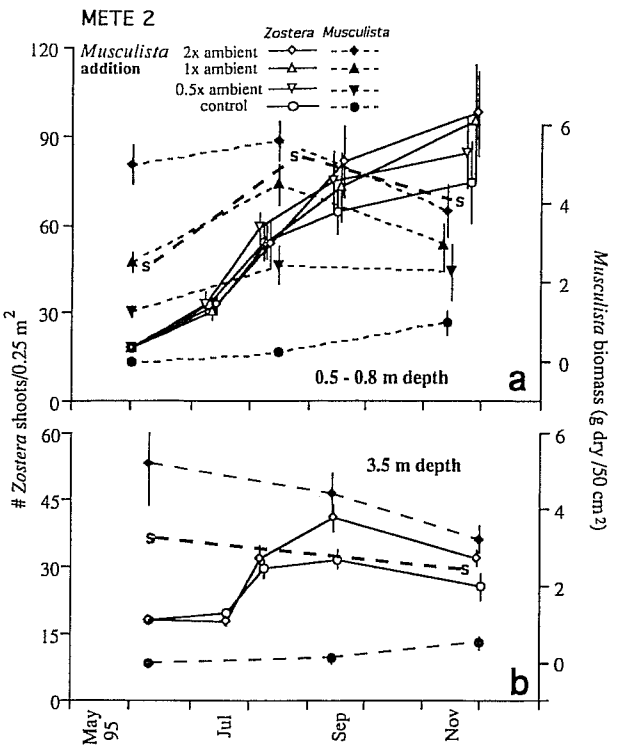

Fig. 6 a,b Time courses of shoot densities of plots with 4 different *M. senhousia* additions in the *Musculista*-eelgrass transplantation experiment METE 2 (±1 SE). Here, eelgrass was also transplanted to 3.5 m depth, the lower distribution limit of *Z. marina* at the site (**b**). The *dashed boldface* line denoted by *s* is the donor bed for *M. senhousia*

Table 6 General linear model: effects of the mussel *M. senhousia* (dry biomass/50 cm^2) on eelgrass leaf growth (cm shoot $^{-1}$ day^{-1}, means of 5 shoots per plot) in established meadow experiments. Interactions of factor "spatial block" with mussel biomass were not significant in any analysis ($P > 0.3$). The quadratic effect of *M. senhousia* biomass was removed from the model if $P > 0.5$

Experiment	Effect	*df*	MS	*F*	*P*
EME 2	*Musculista* biomass	1	2.237	2.987	0.102ns
March 1995	Block	5	0.961	1.283	0.317ns
	Residual	17	0.749		
EME 3	*Musculista* biomass	1	3.740	9.296	0.009**
August 1995	Block	4	0.622	1.546	0.243ns
	Residual	14	0.402		

** $P \leq 0.01$, ns not significant

Table 7 Rhizome growth of *Zostera marina* as a function of four different *Musculista senhousia* additions at Le Meridien (EME 1) in November 1994. Significant differences among treatment means ($n = 5$, Tukey-Kramer test) are indicated with different capital letters ($P \leq 0.05$)

Musculista biomass g dry mass ± SE	Rhizome growth (mm day^{-1}) ± SE
0.13 ± 0.05	1.16 ± 0.08 A
1.02 ± 0.31	1.22 ± 0.04 A
3.41 ± 0.30	0.89 ± 0.13 AB
4.59 ± 0.29	0.84 ± 0.08 B

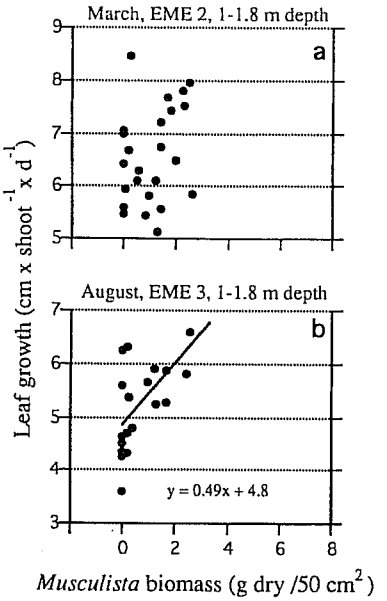

Fig. 7 a,b Leaf growth rates of eelgrass (*Z. marina*) as a function of the co-occurring biomass of the mussel *M. senhousia* in the established meadow experiments (EME). Leaf growth data are plotwise means (5 plants per experimental unit) and mussel biomasses are triplicate plotwise means. The statistically significant equation of the general linear model is given. See Table 6 for statistical analysis

plantations (ANOVA with spatial blocking factor, $MS_{error} = 0.425$, $F_{3,12} = 5.19$, $P = 0.0159$). At the time of rhizome measurements, *M. senhousia* was still abundant enough to form visible carpets.

A striking finding was that *M. senhousia* biomass added to 2 different established meadows declined to low levels in all three experiments (Figs. 8, 9), in contrast to population persistence when *M. senhousia* were added to the eelgrass transplantations (Figs. 5, 6). Therefore, it was not surprising there were few significant effects of *M. senhousia* on eelgrass shoot density in established beds. In EME 1, the only marginally significant or significant negative effects, respectively, of *M. senhousia* on eelgrass shoot density occurred at 5 and 9 weeks (Fig. 8a, ANCOVA, $P = 0.07$ at 5 weeks and $P = 0.02$ at 9 weeks). In EME 2, there were no significant effects on shoot density (all $P > 0.3$, Fig. 8b). In this experiment, *M. senhousia* was not protected from the predator *Pteropurpura festiva* and treatment levels of *M. senhousia* declined by roughly 50% within the first 6 weeks. After 5 months, less than 8% of the originally transplanted *M. senhousia* were alive (Fig. 8b).

Assuming that predation was the cause of the biomass decline at Harbor Island, EME 3 was designed with fences to maintain mussel treatment levels. Snail exclusion by fences did result in higher mussel biomass at the end of the experiment, but this effect of fencing was small (Fig. 9). The initial *M. senhousia* biomass still declined by 84% whereas the low unmanipulated *M. senhousia* abundances in the surrounding vegetated areas remained nearly constant (biomass 0.31 and 0.25/50 cm^2 in July and November 1995, respectively). We

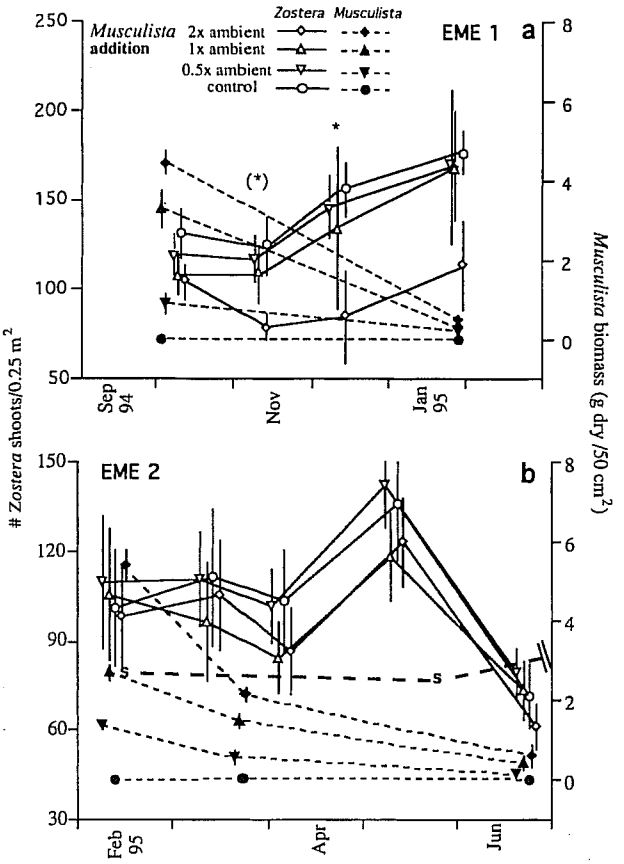

Fig. 8 a,b Time courses of eelgrass shoot densities and associated *M. senhousia* treatment levels in the established meadow experiment (±1 SE). **a** EME 1 at La Meridien ran during the same time interval as METE 1; **b** EME 2 was performed at Harbor Island. Both experiments used the same *M. senhousia* addition levels. Significant differences among treatment means are indicated as follows: * $0.05 > P \geq 0.01$ *P*, (*) $0.1 > P \geq 0.05$. The line denoted by *s* is the donor bed for *M. senhousia*

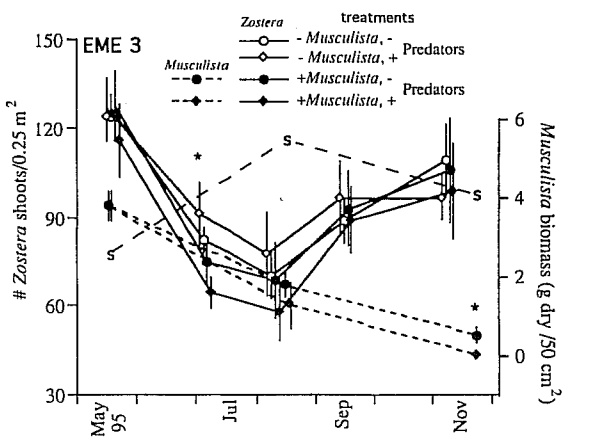

Fig. 9 Time courses of eelgrass shoot densities and *M. senhousia* treatment levels in the established meadow experiment EME 3 (±1 SE). In this experiment, based on the observations made in EME 2, predator presence/absence was an additional experimental factor fully crossed with 1.5 × ambient *M. senhousia* addition/no addition. Significant differences among treatments are indicated as follows: * $0.05 > P \geq 0.01$ *P*, (*) $0.1 > P \geq 0.05$. The line denoted by *s* is the donor bed for *M. senhousia*

detected no fence artifacts on eelgrass shoot density (paired *t*-test, partially fenced vs. unfenced treatments, $P = 0.4$). In the main experiment, most effects of *M. senhousia* on eelgrass shoot density in the EME 3 were statistically non-significant (all $P > 0.2$). In this experiment, only at 6 weeks (July 1995) was the main effect of mussel addition significant, resulting in 19% lower shoot density with *M. senhousia* (2-way ANOVA, main factor *M. senhousia*-addition, $P = 0.0041$).

Discussion

At natural abundances found in San Diego Bay, the non-indigenous mussel *M. senhousia* has negative, positive or no effects on native eelgrass depending on the *M. senhousia* biomass present and the response variable considered. *M. senhousia* and eelgrass interact in complex ways and our conclusions would have been incomplete if we had done a single experiment or had considered only eelgrass transplantations or only one response variable. In summary, *M. senhousia* (and perhaps associated organisms) had consistent negative effects on the asexual propagation of eelgrass (Fig. 4, Table 7), which is the most important mode of reproduction for population growth of this clonal angiosperm in southern California (Ewanchuk 1995). Leaf growth was either facilitated by mussels or not affected (Figs. 2, 7). In all experiments, the effects of *M. senhousia* on eelgrass shoot density were inconsistent and weak (Figs. 5, 6, 8, 9).

This study was devoted to determining the nature of a hypothetical eelgrass-*Musculista* interaction. Identification of the underlying mechanisms will require further research. As a starting point, several mechanisms can be hypothesized for the effects observed. Alleviation of nitrogen limitation is a reasonable mechanism underlying the enhancement of eelgrass leaf growth at low to moderate mussel densities in August (Figs. 1a, 7). Other studies also have demonstrated that biodeposition of feces and pseudofeces by bivalves can increase ammonium availability for rooted angiosperms (Bertness 1984; Reusch et al. 1994). The saturation-type growth response of leaf growth in August is similar to other eelgrass populations growing under nitrogen limitation. Eelgrass leaf growth was maximal at ≈100 μM NH_4^+ in the sediment porewater, a concentration that supports maximum leaf growth in other eelgrass beds (Dennison et al. 1987; Williams and Ruckelshaus 1993; Reusch et al. 1994). Less obvious is why there was no fertilization of leaf growth in March and October. Other studies have demonstrated that nitrogen limitation of eelgrass can be seasonal (Williams and Ruckelshaus 1993). Hence, it is reasonable to suggest that leaf growth was not affected by nitrogen availability in months when light is reduced (T.B.H. Reusch and S.L. Williams, unpublished work; Ewanchuk and Williams 1996; Sewell 1996).

We have no explanation for why leaf growth declined significantly at high mussel densities in METE 2. There was no evidence that sulfide reached toxic levels (Carlson et al. 1994; Goodman et al. 1995). We suggest that some attribute of mussel carpets is deleterious to eelgrass, but have only anecdotal observations to suggest a mechanism. Rhizomes, which unlike leaves and shoots, are in intimate contact with mussels in the sediments, consistently grew more slowly as mussel biomass increased. We found no evidence for physical damage of rhizome or root tissue that would indicate chewing by animals associated with the carpets. We did observe that the rhizomes of eelgrass plants often grew across the top of the carpets at high mussel biomass. Qualitatively, byssal carpets are much firmer than ambient sediment and can be rolled up intact. Because all *M. senhousia* live in the same sediment horizon just below the surface, it is reasonable to approximate the area occupied by the *M. senhousia* population as the sum of areas each individual occupies (shell + bag). If we do so, at carpet-forming biomasses (>3 g dry mass/50 cm^2), 65–100% of the topmost sediment layer consists of *M. senhousia* individuals including their byssal bag. Thus, in contrast to most other soft-bottom environments (Peterson 1979), spatial interference through *M. senhousia* may be an explanation for reduced eelgrass rhizome growth. To test whether rhizome elongation through the byssal mats was impeded, byssal carpet firmness must be measured in a way biologically relevant to rhizome elongation. Such research was beyond the scope of this study.

In all experiments, shoot densities were hardly affected by *M. senhousia*. Several hypotheses may account for this. First, in modular clonal plants like seagrasses, there can be significant lags between effects of environmental changes, such as fertilization or grazing, on different plant parts, e.g., fast-growing leaves, slow-growing rhizomes, and the production of new shoots, which depends upon both new leaf and rhizome production (Williams 1987). Although our experiments continued for 6 months, perhaps this was not long enough for *M. senhousia* effects on shoot density to be manifested.

In all established meadow experiments, we would not expect *M. senhousia* to affect eelgrass shoot density because the transplanted mussel population declined rapidly. This even applied to EME 3 where predatory snails were excluded (Figs. 9). In contrast, the mussel population in the eelgrass transplantation experiments persisted both shallower and deeper than the closed eelgrass canopy and their abundance remained similar to the mussel donor bed where there was no eelgrass (Figs. 5, 6). In particular at the onset of the experiments, the eelgrass transplantations had lower shoot densities compared to the established meadows at Le Meridien and Harbor Island (compare Figs. 5, 6 with Figs. 8, 9, respectively). We suggest that, besides predation, the cause of the *M. senhousia* die-off in the established beds was starvation. Probably within the denser, extended (>5 m diameter) eelgrass beds, the food supply to the filter-feeding mussels was markedly reduced due to reduced water flow in eelgrass canopies (Kerswill 1949; Gambi et al. 1990; Worcester 1995). Our observations differ from studies conducted in coastal waters of the Northwest Atlantic. Several authors have demonstrated an enhancement of bivalve growth and food availability to suspension feeders inside seagrass canopies compared to adjacent sand flats (e.g., Peterson et al. 1984; Peterson and Beal 1989; Irlandi and Peterson 1991; Judge et al. 1993; Irlandi 1996). However, it is likely that this enhancement does not apply to the subtidal eelgrass beds of San Diego Bay, based on research now underway. These ongoing experiments conducted at three sites revealed that *M. senhousia* grew at less than half the rate inside closed (100% cover) canopy eelgrass beds compared to adjacent sand flats (Reusch and Williams unpublished work). In contrast, mussels grew almost as well inside sparse eelgrass patches (0.8 m in diameter, shoot density 50–70/0.25 m^2) as on the adjacent sand flat. In addition, we found mussels living in extended eelgrass beds to have lower flesh to shell weight ratio indicating starvation. Moreover, food availability (chlorophyll *a*) to the mussels, sampled in a protocol that realistically simulates *M. senhousia* suspension feeding (siphon diameter, intake speed) was consistently lower inside the eelgrass bed compared to the adjacent sand flat (Reusch and Williams, in preparation), supporting the hypothesis that *M. senhousia* is food-limited inside the canopy.

Although the eelgrass transplantations were manipulations performed to address the critical conservation and management issues, they also mimic other conditions, increasingly common in disturbed eelgrass habitats, and thus provide insight to the importance of spatial heterogeneity. The response of the mussel populations was dramatically different between more dense established beds and sparse, small eelgrass transplantations. Consequently, eelgrass is likely to be affected by *M. senhousia* primarily where the eelgrass bed is sparse or fragmented, as in disturbed beds, at the lower distribution limit, or in recolonizing patches. Eelgrass shoot densities in the transplantations ≥3 months after planting ranged from 55–100/0.25 m^2, which falls within the range of 50% (5 out of 10 sites) of the eelgrass habitats in San Diego and Mission Bay we routinely censused from 1994 to 1997 (Table 8). In addition, eelgrass beds in San Diego and adjacent Mission Bay were either permanently patchy (<50% cover, $n = 2$), or suffered from die-offs which caused patchiness for periods of >8 months ($n = 2$, Table 8). Low shoot density or patchy eelgrass beds are also now common in San Francisco Bay (Zimmerman et al. 1995) where *M. senhousia* already occurs. Such conditions are also not unusual in regions where the mussel has not invaded, e.g., parts of Chesapeake Bay (Orth et al. 1995) or large areas of the Baltic Sea (Reusch et al. 1994). Likewise, the *M. senhousia* densities found at our study sites and applied in the experiments are within the range of other densities reported in the literature (Table 9).

Table 8 Range of eelgrass shoot densities at 5 sites in San Diego Bay and Mission Bay, San Diego, California. These data represent a subset of 10 sites censused from 1994 to 1997 (S.L. Williams and T.B.H. Reusch, unpublished work). 10–20 quadrats of 50 × 50 cm were placed at random parallel to the shore. Shoot densities refer to average counts in vegetated and unvegetated areas, and include vegetative and reproductive shoots. Patchy structure of eelgrass bed refers to ≤ 50% cover

Station	Position	Range of shoot densities no./0.25 m^2 ± SE	Structure of eelgrass bed	No. sampling dates
San Diego Bay				
Harbor Island	32°43′25″N 117°11′19″W	3 ± 1.5 – 35 ± 6[a]	Patchy below 3 m depth	4
Naval Training Center	32°44′31″N 117°12′56″W	15 ± 3 – 27 ± 7	Patchy	4
5th Street Fish Pier	32°42′26″N 117°09′97″W	7 ± 2 – 17 ± 4	Patchy	4
Mission Bay				
Kendall Frost	32°47′29″N 117°13′24″W	21 ± 7 – 62 ± 4	Patchy from April 1994 to Feb 96	6
Sail Bay	32°47′26″N 117°15′00″W	10 ± 3.5 – 65 ± 4	Patchy from June 96 to February 97	6

[a] Only the deep edge of the eelgrass bed (3–3.5 m depth) was censused

Table 9 Abundance of *M. senhousia* in its indigenous and new habitats

Location	Abundance individuals/m^2	Biomass g/m^2	Reference
Indigenous habitat			
Japan, Seto Inland Sea	28,650[a]		Kikuchi 1964; Kikuchi and Perez 1977
Yokosuka Harbor, Japan	10,000 400,000[a]	8,000 (fresh mass)	Ito and Kajihara 1981
Shitomo River, Japan	15,000		Kimura and Sekiguchi 1993
Tai Tam Bay, Hong Kong	2,500		Morton 1974
New habitat			
Whangarei Harbor, New Zealand	3,300		Willan 1987
Mission Bay, southern CA	200,000[a] 8,600	250 (dry mass)	Crooks 1996a, b
San Francisco Bay	2,000		Hopkins 1986
San Diego Bay, channel	12,370		MacDonald et al. 1990
San Diego Bay, shallow subtidal zone	15,000	1,200 (dry mass)	this study

[a] Including juvenile settlers

In addition to interactions of adult mussel populations with eelgrass, heavy mussel recruitment via pelagic settlers has the potential to rapidly change a site from eelgrass meadow to mussel carpet. In 1995 in nearby Mission Bay, San Diego, recruitment onto eelgrass leaves was intense enough to weigh down the leaf canopy (Sewell 1996). *Z. marina* beds in northern Europe apparently also can be changed within weeks to *Mytilus edulis* beds after heavy spatfall (Gründel 1980; Ruth 1991; T.B.H. Reusch, personal observations). Consequently, any changes that favor mussel growth and reproduction, e.g., increased phytoplankton availability or further reductions in eelgrass cover, could have future harmful effects on eelgrass. Non-indigenous species represent only one disturbance to eelgrass on heavily developed coastlines. Attributing the cumulative effects of, for example, non-native species, poor water quality, habitat loss, and reduced genetic diversity on eelgrass is a daunting problem for estuarine ecologists and managers (Short and Wyllie-Escheverria 1996; Williams and Davis 1996).

Until the ecological effects of marine non-indigenous species are known, both the rationale and the necessary scientific details for formulation of management plans are missing. This study revealed that *M. senhousia* is a problem for eelgrass habitat restoration because the mussel had negative effects on rhizome elongation that increased linearly with mussel biomass in all experiments. The area of substratum covered by eelgrass, which is the usual criterion for judging the success of a transplantation (Fonseca et al. 1988), obviously depends on rhizome elongation. We have found dry biomass of *M. senhousia* > 4 g/50 cm^2 (corresponding to >800 g/m^2) at 3 of 8 sites which we routinely census. Transplantation of eelgrass should be avoided in such areas unless the mussel carpet is thinned to moderate biomass (≤2 g/50 cm^2, corresponding to 400 g/m^2).

Non-indigenous species which alter the habitat through modifying the access to resources for other species (ecosystem engineers *sensu* Jones et al. 1994) are likely to strongly affect native species in the invaded environment. Gregarious filter feeders including

M. senhousia are a case in point. Other examples include the invasive freshwater bivalves *Dreissena polymorpha* (Hebert et al. 1991) and *Corbicula fluminea* (McMahon 1983), and the marine clam *Potamocorbula amurensis* (Kimmerer et al. 1994). Common to these bivalves is that they can have profound effects on the structure and function of the invaded ecosystems because they are very abundant, change the physico-chemical nature of the sediment they live on or in, and enhance the transport of carbon and nutrients from the pelagic zone to the benthos (see also Lenihan et al. 1996).

Not all non-indigenous species, even if they become dominant, will have negative effects on the native species of the invaded environments. For example, introductions of the non-native aquatic angiosperms *Zostera japonica* and *Hydrilla verticillata* resulted in increased faunal abundance and species numbers, similar to the effects of native macrophytes (Posey 1988; Posey et al. 1993; but see Harrison 1987). In the intertidal mudflats of Mission Bay, San Diego, *M. senhousia* enhances the abundance of many benthic invertebrate groups, except oligochaetes and larger bivalves which decreased in abundance, within dense mussel mats (Crooks 1996b; J.A. Crooks, personal communication).

Certainly, once established, some non-indigenous species can profoundly change the biodiversity and ecological function in their new environment. Little attention, however, has been paid to the complex range of responses of a single native species to non-indigenous organisms, which can vary from enhancement to interference, depending on the relative abundances of the two species, the season, and the attribute of the native target species considered (e.g., growth versus abundance). Partly, this gap is due to a surprising lack of experimental information on the quantitative effects of non-native species (Grosholz and Ruiz 1995; Kareiva 1996). Our study demonstrates that within a single native target species, eelgrass *Zostera marina*, all three principal outcomes of ecological species interactions (neutral, negative, positive) are possible. It is likely, that with an increasing number of experimental studies, other complex arrays of ecological effects of non-indigenous species will be revealed.

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