

# Does the recruitment of a non-native mussel in native eelgrass habitat explain their disjunct adult distributions?

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## ABSTRACT

We studied variability in the abundance of small individuals of an invasive mussel (*Musculista senhousia*) across the depth distribution of a native marine angiosperm, eelgrass (*Zostera marina*). Adult mussels and eelgrass have a disjunct local distribution, each limiting the other in complex ways. To assess whether eelgrass also influenced the distribution of juvenile mussels, we sampled inside and outside eelgrass beds in one site in Mission Bay and two in San Diego Bay, California, USA. We sampled mussels in size classes 0.26–0.50 mm, 0.51–1.00 mm, 1.10–2.00 mm and > 2.00 mm from September 1997 to April 1999. We also monitored gonad development in larger mussels and in situ growth of mussels ≤ 2 mm tagged with the chemical marker calcein. Spatial and temporal variations in mussel abundances were high but seasonal patterns were roughly similar at San Diego Bay sites; very few mussels were found in Mission Bay. Mussels with full gonads were found year-round in San Diego Bay, as were mussels in the smallest size class (with a large peak in fall and a smaller secondary one in spring), suggesting that many of the smallest mussels represent recruitment. The observation that most, although not all, tagged mussels increased in size provides further support for recruitment. Some of the highest numbers of mussels in the smallest size class were found inside eelgrass beds, indicating that eelgrass does not restrict and may actually enhance the distribution of very small mussels. The disjunct distribution of adult mussels and eelgrass thus is apparently established primarily postrecruitment. *M. senhousia* is capable of year-round reproduction, recruitment and growth, and thus is poised to preempt space from eelgrass following any disturbance that results in eelgrass declines, such as habitat fragmentation, eutrophication, or disease.

## Keywords

Biological invasions, eelgrass, invasive mussel, *Musculista senhousia*, recruitment, *Zostera marina*.

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## INTRODUCTION

*Musculista senhousia* Benson is a highly successful invasive marine bivalve; native to east Asia, it has now spread to New Zealand, Australia, the Mediterranean and the Pacific coast of North America (reviewed in Crooks, 1996). A small mussel found in intertidal and subtidal habitats of protected bays and estuaries, *M. senhousia* can achieve adult densities of up to 170,000/m<sup>2</sup>, altering the local habitat through the formation of dense mats of coalesced byssal cocoons on the sediment surface (Morton, 1974; Crooks & Soule, 1999; Dexter & Crooks, 2000). Once established in non-native habitats, it can have profound effects on native marine communities. The mussel can inhibit

larger, and facilitate smaller, infaunal species (Willan, 1987; Creese *et al.*, 1997; Crooks, 1998; Crooks & Khim, 1999). The mussel also has largely negative effects on a dominant temperate marine angiosperm, eelgrass (*Zostera marina* L.) (Reusch & Williams, 1998). Eelgrass is widely distributed in coastal regions of the northern hemisphere and supports a highly productive and diverse community (Kikuchi, 1980).

In this study, we continue investigation of the negative correlation between the distribution and abundance of *M. senhousia* and *Z. marina* in San Diego, California (Reusch & Williams, 1998, 1999). High densities of adult mussels can limit eelgrass density and vegetative propagation, the most important mode of reproduction in local populations (Reusch & Williams, 1998). In

turn, dense eelgrass can limit the distribution of the mussel through food limitation; the eelgrass canopy reduces water flow speeds, thus decreasing the advection of phytoplankton food (Reusch & Williams, 1999; Allen & Williams, 2003). By changing water flow, eelgrass also can influence the distributions of benthic invertebrates by affecting their recruitment (reviewed in Williams & Heck, 2001). High densities of juvenile *M. senhousia* have been found on eelgrass, seaweeds, other molluscs and artificial substrata (Kikuchi & Pérèz, 1977; Kulikova, 1979). However, the extent to which the distribution pattern of adult mussels in the sediment is established by recruitment vs. postsettlement processes such as movement, predation or food limitation is poorly known (Sekiguchi *et al.*, 1995).

Previous studies reported that the distribution and abundance of *M. senhousia* fluctuate greatly in time in both native and non-native regions (Creese *et al.*, 1997; Dexter & Crooks, 2000; Miyawaki & Sekiguchi, 2000; Ishii *et al.*, 2001). Mussel larvae remain in the plankton up to 21 days and settle to the benthos when they are 0.23–0.28 mm shell length (Yoshida, 1937; Kulikova, 1978, 1979; Kimura & Sekiguchi, 1996). To date, reproduction and recruitment patterns in invaded habitats have been inferred primarily from changes in the population size structure of mussels at least 2 mm in length, with the reproductive peak inferred to occur in late summer (Crooks, 1996; Creese *et al.*, 1997). To evaluate whether variability in recruitment contributed in part to the observed disjunct distributions of adult mussels and eelgrass, we conducted a finer-scale study of variability in mussel recruitment at three sites in San Diego, California, focusing on the distribution, abundances and growth of mussels from 0.25 to 2 mm and directly assessing gonadal development in adult mussels.

## METHODS

We sampled *M. senhousia* at three sites with dense eelgrass beds: Coronado Island ('Coronado' hereafter) in San Diego Bay, California (32°41'13" N, 117°09'49" W), Harbor Island in San Diego Bay (32°43'25" N, 117°11'19" W) and Mariners Basin (32°47'26" N, 117°14'80" W) in Mission Bay, San Diego. The eelgrass beds at these sites had distinct upper and lower edges bounded by unvegetated sandflats. Sampling at each site was conducted weekly beginning 13 September 1997, except when prevented by weather or polluted waters. On 13 August 1998, sampling was reduced to once in every 3 weeks because of low mussel densities until a small recruitment spike on 24 September 1998, after which sampling was increased to every other week.

### Censusing *Musculista senhousia* in the sediments

Eight sampling stations were established along a transect placed perpendicular to shore across the depth gradient of each eelgrass bed: 4 m above the shallow edge of the eelgrass bed, 0.25 m above the shallow edge, 0.25 m inside the bed below the shallow edge, two stations near the centre of the bed (0.5 m above and below the centre of the bed), 0.25 m inside the bed above the deep edge,

0.25 m below the deep edge and 4 m below the deep edge. The average width of the eelgrass bed from shallow to deep edge was  $44.2 \text{ m} \pm 2.1 \text{ m SD}$  ( $n = 6$ ) at Coronado and  $25.4 \text{ m} \pm 5.1 \text{ SD}$  ( $n = 6$ ) at Harbor Island. The deep edge of eelgrass was 3.3–4 m water depth.

At each sampling location across the depth gradient, we removed duplicate sediment cores ( $47 \text{ cm}^2 \times 9 \text{ cm}$  long) from each sampling location taken at least 0.25 m apart. Transects were moved on each sampling date so that locations were not resampled.

After determining that negligible numbers of mussels were found below the top 2 cm of the sediment surface (12% of total number  $\pm 15\%$  SD,  $n = 33$  cores), we removed the upper 2 cm and sieved them through mesh sizes of 2.0 mm, 1.0 mm, 0.50 mm and 0.25 mm. The smallest individual we measured on the 0.25 mm sieve was 0.23 mm. We preserved the biota with 70% ethanol and sorted shells of *M. senhousia* under a dissection microscope, based on criteria in Yoshida (1937), Kimura and Sekiguchi (1994) and Kulikova (1978). Individuals with both valves intact and containing tissue were counted. Mussels retained by the 0.25 mm sieve included any putative recruits; shell length prior to metamorphosis is 0.25–0.28 mm (Kulikova, 1978; Kimura & Sekiguchi, 1996).

### Censusing *Musculista senhousia* on eelgrass leaves

To determine whether the smallest mussels occurred mostly in the sediments and not on eelgrass leaves, we collected five to nine leaf shoots from each of two  $25 \times 25 \text{ cm}$  quadrats haphazardly tossed onto the substratum at each sampling location in eelgrass along the transect at Coronado and Harbor Island in January 1998. Each shoot was enclosed in a bag of fine mesh plankton netting. The remaining shoots were counted and then a sediment core was taken inside each quadrat. We sieved contents of the bags and the sediments and counted the mussels retained by the 0.25 mm sieve under a dissection microscope. The surface area of each leaf shoot area was measured with a leaf area meter (Li-Cor, Model 2000; Lincoln, Nebraska) and mussel density was expressed per square metre of leaf area. Because the area of leaves per square metre of bottom is  $> 1 \text{ m}^2$ , we also calculated mussel density on the total leaf area per square metre of the bottom, estimated by multiplying the areal leaf shoot density by the average leaf area per shoot. Based on preliminary examination of the data, we pooled data from both sites for analysis.

### Assessing mussel gonad development

On each sampling date, we also haphazardly collected and preserved 50 adult mussels (8.6–30 mm shell length) below the eelgrass bed at each site to determine gonad development. We measured shell length to the nearest 0.1 mm and dissected each mussel to determine sex. Gonad status was categorized as full ( $\geq 40\%$  of total tissue mass), 'partial' and empty. Gonads representing 5% to  $< 40\%$  total body mass were classified as 'partial' (i.e. partially full). The empty classification represented no apparent gametic development (common in spring) or

only trace amounts of gonad apparently left over from spawning activity (more likely in summer and fall). In April and August 1998 and February 1999, we sampled at three to five additional sites in San Diego Bay to determine spatial variation in gonad development (Coronado Cays 32°37'13" N, 117°07'41" W; J Street 32°37'39" N, 117°06'32" W; Fish Pier, 32°42'16" N, 117°09'58" W; Zewicke 32°41'55" N, 117°10'02" W, Le Meridian 32°41'41" N, 117°09'52" W; Silver Strand 32°8'01" N, 117°08'03" W).

### Tagging mussels for growth measurements

To assess whether size was a reasonable proxy for age and thus, whether the smallest mussels represented recruits, we soaked intact sediment cores with mussels for 24 h in an aerated bath of calcein (125 mg/L, Reusch & Williams, 1999, Allen & Williams, 2003). Calcein is incorporated into the shells of growing mussels and later serves as a fluorescent marker for initial size under ultraviolet illumination. On the next day, we placed cores with their rims flush with surrounding sediments in the field. In June 1998, we tagged 40 cores and placed 10 each at 0.25 m above and below the shallow and deep edges of the eelgrass bed at Harbor Island, collecting them 21 days later. In February in Coronado, 12 tagged cores were situated in each of two rows 1 m apart in the middle of the eelgrass bed with another 24 placed 4 m below the deep edge of the eelgrass bed. We retrieved them 27 days later. After sieving and preserving mussels, we measured the initial size at tagging and final size under a dissecting scope with an ultraviolet light source.

### Statistical analyses

We analysed abundances of the smallest mussels (retained on the 0.25 mm sieve) at each site to determine temporal and spatial components of putative *M. senhousia* recruitment in relation to eelgrass. We compared the abundances of mussels in different transect locations through time with two-way analyses of variance (ANOVA). To allow for a statistical test of the location–time interaction, we grouped the data into seasons: fall (September, October, November), winter (December, January, February), spring (March, April, May) and summer (June, July, August) based on a priori information about the timing of mussel settlement in southern California. Preliminary inspection of the data suggested that grouping sampling dates this way was reasonable given the almost complete lack of location–time interactions within seasons. Although sampling dates within a season were random, we considered both season and location to be fixed factors given that we would choose the same classifications were we to repeat the study (p. 336, Sokal & Rohlf, 1995). Data were transformed with an  $\ln(x + 1)$  function to remove variance heterogeneity. Visual inspection of model residuals was done for every analysis. Following ANOVA, Tukey's HSD tests were used to identify significant differences among appropriate means. Mussel densities on leaves (averaged over leaf shoots collected) vs. in sediments were compared in paired (within quadrat) *t*-tests.

## RESULTS

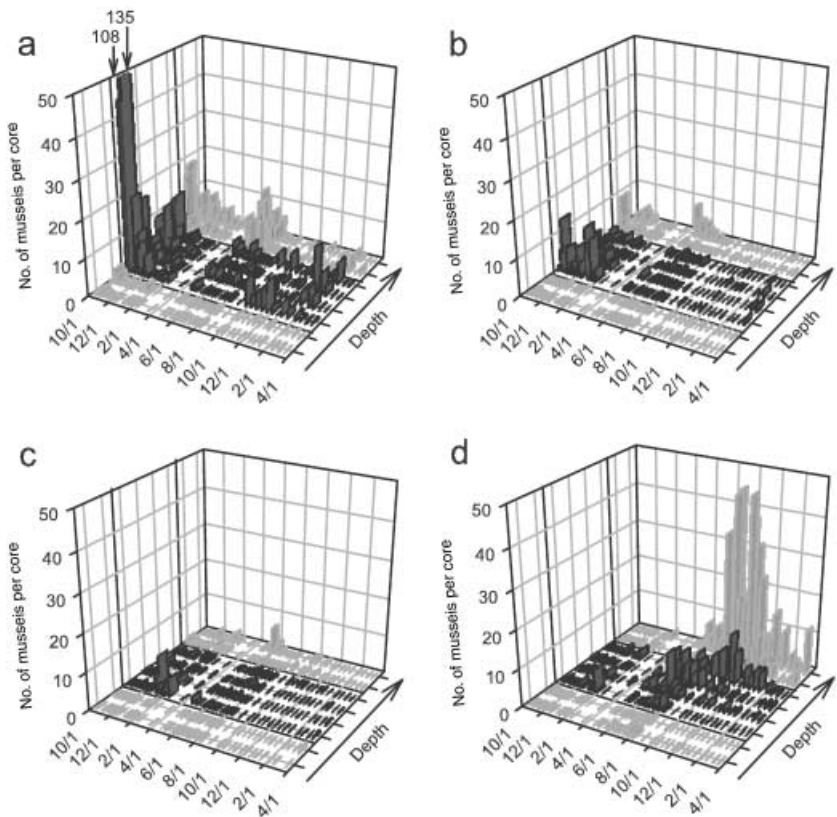
### *Musculista senhousia* in the sediments

As expected based on available life history information, *M. senhousia* retained by the 0.25 mm sieve were most numerous in the fall at both Coronado (Fig. 1) and Harbor Island (Fig. 2) in San Diego Bay. Densities of the smallest mussels were generally higher in Coronado, where the highest density in this study (30,500 m<sup>-2</sup>) was found during fall 1997. In addition, the smallest mussels were found during every sampling period and exhibited a much smaller secondary peak in abundance during spring 1998. Although *M. senhousia* is abundant in Mission Bay (Reusch & Williams, 1999; Dexter & Crooks, 2000) and occurred in the past in Mariners Basin, we found very few mussels of any size class there. The highest density of the smallest mussels (2340 m<sup>-2</sup>) in Mariners Basin occurred in September 1997. We will not discuss this site further, but it reinforces the pattern of high variability in abundances of the smallest *M. senhousia*.

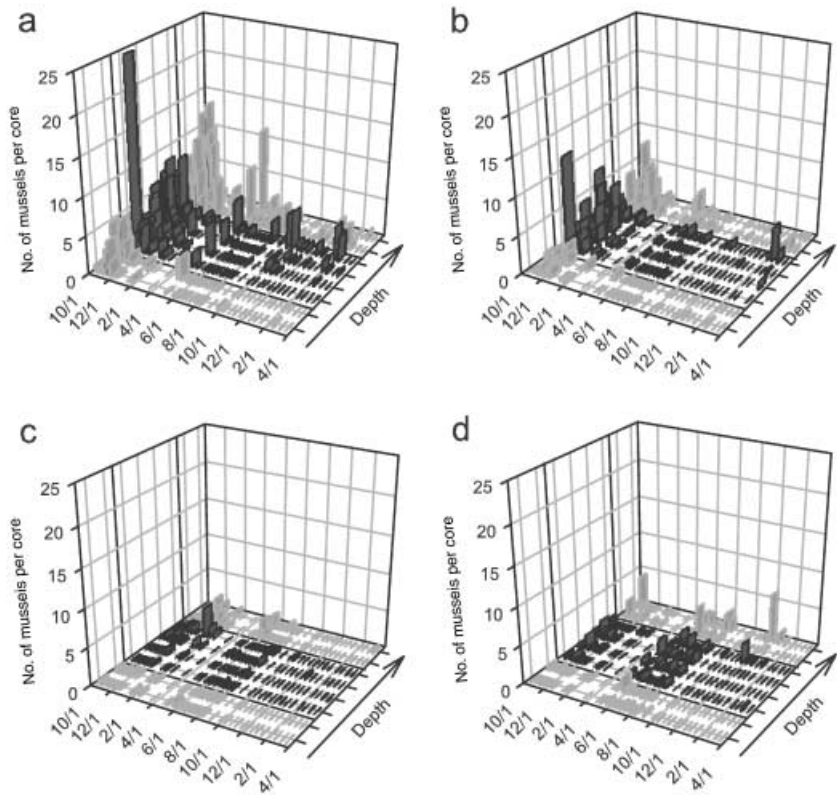
At Coronado, abundances of mussels retained on the 0.25 mm sieve were extremely variable in both space and time (location–season interaction  $F_{42,341} = 3.15$ ,  $P < 0.001$ ). Although much of this interaction effect is because of the fall 1997 data, the interaction was still significant following removal of this season from the analysis. Although testing main effects in the presence of a significant interaction is often considered to be uninformative, it may still be reasonable when overall patterns are clear (Sokal & Rohlf, 1995). In this case, both location and season were highly significant (location  $F_{7,341} = 12.27$ ,  $P < 0.001$ ; season  $F_{6,341} = 24.50$ ,  $P < 0.001$ ) and the results of the multiple comparisons tests were unambiguous; abundances of the smallest mussels were greatest in fall 1997 and were consistently lowest in the intertidal sandflat above the eelgrass bed. The density of mussels in the largest size class explained none of the variation in the smallest size class on a per core basis ( $r^2 = 0.0006$ ,  $P = 0.520$ ,  $n = 657$ ), suggesting that there are no notable adult–juvenile interactions.

With the exception of the peak recruitment event in fall 1997, juvenile mussels typically were distributed across the transect at Coronado in very low numbers in the shallow intertidal above the bed, intermediate numbers inside the bed, and high numbers 4 m below the deep edge of the eelgrass, where adults were most abundant. This spatial pattern changed in fall 1997 when the highest numbers of mussels were found just inside the shallow edge of the eelgrass bed.

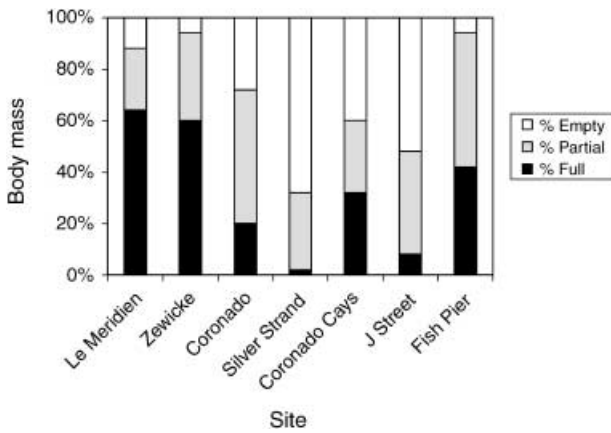
The abundances of mussels retained on the 0.25 mm sieve at Harbor Island (Fig. 2) exhibited a pattern similar to the Coronado pattern (Fig. 1). While there was no location–season interaction ( $F_{42,325} = 1.28$ ,  $P = 0.121$ ), both location and season were highly significant effects (location  $F_{7,325} = 6.48$ ,  $P < 0.001$ ; season  $F_{6,325} = 53.16$ ,  $P < 0.001$ ). As at Coronado, the clear results of the multiple comparison tests were that abundances of the smallest mussels were greatest in fall 1997 and were consistently lowest in the intertidal sandflat above the eelgrass bed. Again, with the exception of fall 1997, we found very low numbers of mussels in the shallow intertidal above the bed, intermediate numbers inside the bed, and high numbers 4 m below the deep edge of the eelgrass.



**Figure 1** Three-dimensional plots of the abundances of *Musculista senhousia* in different size classes across an eelgrass bed at Coronado Island, San Diego Bay, California through time. Size classes were defined as mussels retained on sieves of (a) 0.25 mm, (b) 0.50 mm, (c) 1 mm or (d) 2 mm mesh sizes. Bars are the mean number of mussels in two replicate cores taken *C.* 10 cm apart at each location on each sampling date. Sampling was done from October 1997 to April 1999. Dark grey bars represent samples taken from inside the eelgrass bed while light grey bars are for samples taken from the unvegetated sediments above and below the eelgrass. Note that actual sampling locations across the depth gradient were not equidistant to one another as implied in the figure (see text for details).



**Figure 2** Three-dimensional plots of the abundances of *Musculista senhousia* in different size classes across an eelgrass bed at Harbor Island, San Diego Bay, California through time. Size classes were defined as mussels retained on sieves of (a) 0.25 mm, (b) 0.50 mm, (c) 1 mm or (d) 2 mm mesh sizes. Bars are the mean number of mussels in two replicate cores taken *C.* 10 cm apart at each location on each sampling date. Sampling was done from October 1997 to April 1999. Dark grey bars represent samples taken from inside the eelgrass bed; light grey bars represent samples taken from the unvegetated sediments above and below the eelgrass. Actual sampling locations across depth were not equidistant to one another as implied in the figure (see text for details).



**Figure 3** Relative mean gonad development of adult *Musculista senhousia*. Sample size = 50 mussels from seven sites in San Diego Bay in August 1998, during peak reproductive season. Full (gonads  $\geq 40\%$  of total body mass); empty (no gonads or trace postspawning) and partial (gonads 5% to  $< 40\%$  total body mass).

***Musculista senhousia* on eelgrass leaves**

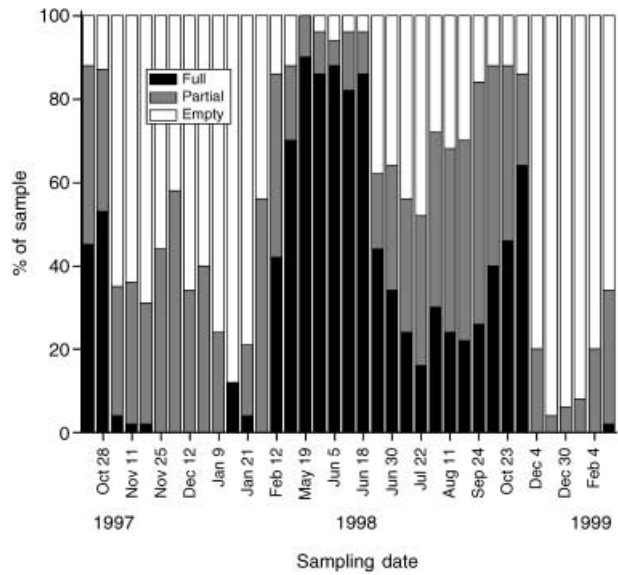
Very few of the smallest mussels (retained on the 0.25 mm sieve) were found on eelgrass leaves (80 average on leaves within 1 m<sup>2</sup> of substratum, ranging from 0 to 422). Despite the greater surface area for attachment afforded by the leaves (2.2–16.3 m<sup>2</sup> leaf area/square metre sediments) per unit area of bottom, more of the smallest mussels were found in the sediments (averaging 251/m<sup>2</sup>) than on eelgrass leaves on an areal basis (paired *t*-test, *P* = 0.0042, d.f. = 21). Also, significantly, more of the smallest mussels were found per square metre of sediments than per square metre of leaf (paired *t*-test, *P* = 0.0041, d.f. = 21).

**Mussel gonad development**

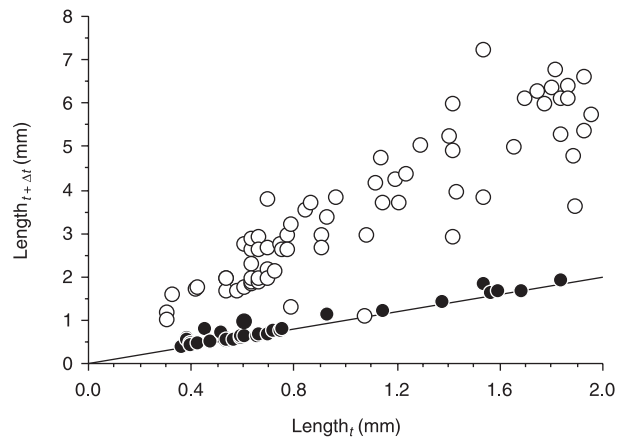
The sampled populations had approximately equal numbers of males and females. In the gonad survey, the smallest mussels collected (male: 8.6 mm; female: 9.4 mm) had full gonads. Variability in gonad development was high both within and between our sampling sites (Figs 3 & 4). Except for a few weeks during December to January, some individuals with full gonads were always present in San Diego Bay. From September 1997, over half of the mussels at Coronado had partially or fully developed gonads, whereas peak development occurred from May to June 1998 (Fig. 4). The pattern was similar at Harbor Island, except that from mid-November 1998 to February 1999, 50% to  $> 90\%$  of the individuals had fully developed gonads at a time when gonads were either undeveloped or spent at Coronado.

**Juvenile mussel growth**

There was considerable variation in the growth of tagged *M. senhousia* as a function of size (Fig. 5). The growth of mussels smaller than 2 mm varied up to sevenfold. Although most mussels increased in size, some did not, suggesting that the presence of mussels in the smallest size class cannot always be considered evidence for



**Figure 4** Relative gonad development of adult *Musculista senhousia* (*n* = 50 mussels) at Coronado Island, San Diego Bay through time. Full (gonads  $\geq 40\%$  of total body mass); empty (no gonads or trace sot-spawning) and partial (gonads 5% to  $< 40\%$  total body mass).



**Figure 5** Shell length at *t* +  $\Delta t$  as a function of size at marking with calcein (length at *t*) for *Musculista senhousia*; open circles  $\Delta t$  = 21 days from 3 to 24 June 1998 (at Harbor Island); filled circles  $\Delta t$  = 27 days 19 February–18 March 1999 (at Coronado). The line has a slope = 1, which is the line of zero growth.

recruitment. That said, additional support for recruitment comes from the progression of the putative fall 1997 cohort through the size classes over time (Panels b, c, d in Figs 1 & 2). The progression is most evident at the inside edge of the eelgrass bed.

**DISCUSSION**

Substantial spatial and temporal variabilities in recruitment densities are common among marine organisms with planktonic larvae (reviewed in Ólafsson *et al.*, 1994), and *M. senhousia* is no exception. Overall, there was large year-to-year variability in the

abundance of *M. senhousia* of the smallest sampled sizes, which in part can be considered recruits. *Musculista senhousia* individuals retained on the 0.25 mm sieve were collected year-round. Peaks in their abundance in fall undoubtedly represent recruitment, based on population size structure, available life history data and the growth of tagged mussels. The smaller secondary spring peak in abundance probably also indicates a previously undetected recruitment event. Our findings support the interpretation of Crooks (1996), that the high variance in the mean mussel length over a year of sampling at one site in Mission Bay, San Diego represented prolonged background recruitment. Although a summer peak in reproduction has been inferred (Kulikova, 1978, 1979; Crooks, 1996; Creese *et al.*, 1997), we found fully developed gonads nearly year-round, although we did not attempt spawning to verify reproductive potential. However, because some mussels smaller than 0.5 mm did not change size over a period of nearly a month, not all of the smallest mussels can be considered new recruits. Although the cause of the high variation in mussel growth is unknown, the long-term growth rates of juvenile mussels can be affected significantly by the early nutritional history of an individual (Phillips, 2002). The smallest mussels live well within the benthic boundary zone where food availability is reduced (Reusch & Williams, 1999), and water flow varies around seagrass leaf shoots on a scale that could also influence the delivery of food to small mussels (Nepf & Koch, 1999). Our ongoing analyses of a larger growth study reveal that the variation cannot be attributed simply to position across the depth gradient or seasons, despite the fact that the mussels tagged in Coronado in February grew slowly (Fig. 5). Whatever the cause of the variance in the relationship between size and growth, it will result in errors in population growth rates based on size structure data alone.

The spatial distribution of the smallest mussels with respect to the eelgrass beds appears to vary both within and among sites through time. In general, few mussels were found in the shallow intertidal, which was subjected to swash from boat wakes. We observed sediment resuspension from wakes, which eroded sediments around our site markers and around some cores we left in the sediments, and probably also around mussels. At these shallow locations, the new recruits experienced potentially stressful monthly exposure to air on the lowest tides. Mean numbers of mussels retained on the 0.25 mm sieve increased slightly across the eelgrass bed, and the highest numbers were found below the deep edges of the beds. The density of eelgrass also decreased across this gradient. The obvious exceptions to this pattern are recruitment events in both Coronado and Harbor Island in the fall 1997. In these cases, the highest densities of the smallest mussels occurred either just inside the shallow edge of the eelgrass bed, just inside the deep edge of the bed, or both. Overall, recruitment clearly was not limited by the presence of *Z. marina*. The smallest mussels were found on eelgrass but we did not observe a huge recruitment to eelgrass as observed occasionally by us and others (Kikuchi & Pérèz, 1977; Sewell, 1996). The observed patterns of distribution of the smallest mussels also did not correspond well to the distribution of adult mussels, which are densest outside eelgrass beds. Based on these data, the strikingly low abundances of adult mussels in eelgrass beds (Reusch &

Williams, 1998) seem determined primarily by postrecruitment processes such as juvenile emigration or mortality caused by factors such as predation and food limitation (Ólafsson *et al.*, 1994; Reusch & Williams, 1998; Allen & Williams, 2003).

Several of our findings have implications for the influence of *M. senhousia* on native eelgrass in San Diego. The incredibly fast growth of very small mussels verifies that *M. senhousia* can reach adult size within a single year. Along with some degree of year-round true recruitment and virtually year-round reproductive potential, *M. senhousia* seems poised to preempt habitat from eelgrass following disturbances, as *Z. marina* recruits very slowly (Thayer *et al.*, 1984). Eelgrass growth and density in San Diego decline seasonally in fall (Johnson *et al.*, 2003) during peak recruitment of *M. senhousia*, giving the mussel a good chance to establish. By the time eelgrass begins to recruit slowly from seedlings in January and to increase its leaf shoot density in spring, most *M. senhousia* have reached adult size.

Seagrass distributions are shrinking worldwide as a result of a multitude of disturbances (Short & Wyllie-Escheverria, 1996). Eelgrass in southern California is disturbed frequently through habitat destruction (Williams & Davis, 1996), in response to climate variability (Johnson *et al.*, 2003), and it is impacted by other invasive species (Williams & Heck, 2001; Williams & Grosholz, 2002). *M. senhousia* 'outbreaks' have been observed in recent times in native habitats that became polluted or eutrophic (Ishii *et al.*, 2001). *M. senhousia* also has been observed interfering with the restoration of *Z. marina* in Japan, where both species are native (S.L.W., pers. obs.). In San Diego bays, we have observed dense *M. senhousia* mats covering large areas otherwise suitable as eelgrass habitat, suggesting that more intense or frequent disturbances to eelgrass potentially could lead to a state-change in the benthos where *M. senhousia* completely replaces eelgrass. If this occurs, a mussel-dominated benthos is likely to persist, even if *M. senhousia* could be eradicated, because eelgrass lacks a seed bank from which to recolonize (Orth *et al.*, 2000). Given the extensive spread of *M. senhousia* to many areas throughout the present distribution of eelgrass, this scenario could play out elsewhere under the appropriate conditions.

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