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The Population Ecology of an Exotic Mussel, *Musculista senhousia,* in a Southern California Bay

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ABSTRACT: *Musculista senhousia* is a small, infaunal mussel native to Asia. Over the last 75 yrs, humans have unintentionally introduced it to various parts of the world, including the Mediterranean, Australasia, and North America. Recently, *M. senhousia* has become abundant in Mission Bay, San Diego, California. Here, the mussel exhibits many traits typical of opportunistic species. It is small, only attaining a maximum length of about 32 mm, and is capable of rapid growth, reaching up to 25 mm after 1 yr. In San Diego, there was a major peak of recruitment during the late fall of 1990, and low levels of background recruitment throughout much of the year. Although the maximum life span of *M. senhousia* is approximately 2 yr, mortality is high and most of the population are only annuals. Overall, *M. senhousia* appears to display similar life-history characteristics both in this invaded system and within its native range.

Introduction

The Asian mussel, *Musculista senhousia* (Benson 1842), is an exotic organism that recently has become abundant in Mission Bay, San Diego, California. This small, thin-shelled mytilid is a suspension-feeder that lives in the intertidal and subtidal soft sediments of bays and estuaries, where it constructs a nest or "cocoon" by binding sediment with its byssal threads. Where the mussel lives in high densities, these nests can be woven together to create a byssal mat, thereby altering the nature of the habitat (Morton 1974; Crooks 1992).

Musculista senhousia is native to Asia, where it is found from the Siberian coast (Kulikova 1978, 1979), around the Malay Peninsula (Chuang 1961), and into the Red Sea (Barash and Danin 1971, 1972; Hoenselaar and Hoenselaar 1989). Within the last 70 yrs, *M. senhousia* has invaded various parts of the world, including Australia and New Zealand (Willan 1985; Hutchings et al. 1986; Slack-Smith and Brearley 1987), the eastern Mediterranean via the Suez Canal (Barash and Danin 1971, 1972), and the south of France (Hoenselaar and Hoenselaar 1989). *Musculista senhousia* was first found in North America in 1924 in Japanese oyster beds in Samish Bay, Washington (Kincaid 1947). In the 1940s *M. senhousia* was reported from central California (Carlton 1979), and in the mid 1960s it was found in southern California (MacDonald 1969; MacDonald et al. 1990). Although

the mussel has been continuously present in Mission Bay since this time (Dexter 1983), its abundance has increased dramatically within the last decade. The mode of introduction of *M. senhousia* to southern California is unknown, although it is probable that larvae were carried in the ballast water of ships arriving from either the Orient or from other North American ports, perhaps due to the increased vessel traffic due to the Vietnam War (Carlton 1979).

Although the mussel is relatively widespread on the Pacific Coast of North America (Carlton 1979), it has been little studied in this region. Thus, the primary purpose of this research was to document the growth, mortality, longevity, and recruitment patterns of the population of *M. senhousia* in Mission Bay to better understand some life-history characteristics of this successful invader. This purpose was accomplished by analyzing the size structure and length-weight relationships of the population over a period of 14 mo. The data from Mission Bay were then compared to the information available on *M. senhousia* within its native range.

Methods

Mission Bay is a highly modified, shallow lagoon 21 km north of the United States-Mexico border (Fig. 1). The temperature of the bay typically ranges between 12°C and 26°C, and its salinity is usually near that of full seawater (Levin 1982). Freshwater input into the bay is limited, mostly in the form of organic-rich urban run-off (California Regional Water Quality Control Board 1977; Marcus 1989),

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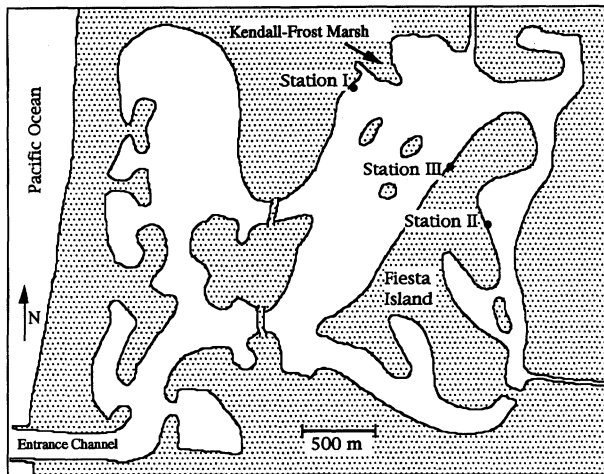
Fig. 1. Mission Bay, San Diego, California. The positions of the three study stations are indicated.

the majority of which is received in areas of limited circulation. This can result in considerable organic enrichment.

Three intertidal stations were established in the back of Mission Bay: two on Fiesta Island, and one adjacent to the Kendall-Frost salt marsh (Fig. 1). All three stations were on sandy-mud beaches, with the lower and upper boundaries of each station approximately 0.3 m below and 0.5 m above MLLW. Eelgrass (*Zostera marina*) was present in the lowest parts of the stations. Sampling was done on 10 dates between December 1989 and February 1991. On each date, cores with a surface area of 0.02 m² were taken to a depth of 10 cm at 10 different sites at each station. The cores were randomly selected and located by stepping off positions on an imaginary Cartesian coordinate system. After coring, sediment was sieved through 1.6-mm mesh, and all material retained was preserved in formalin. In the laboratory, samples were sorted visually and any mussels were removed, preserved in formalin, and transferred to 70% alcohol. All mussels were counted and measured, with length determined as the maximum distance from the anterior margin to the posterior margin as measured with an analog caliper. Data for mussels over 4 mm (the smallest size consistently retained) were used to construct size-frequency histograms and to determine population densities, number of new recruits, and mean lengths of the mussels.

The spatial distribution of the *M. senhousia* was examined using an index developed by Morisita (1964), and reviewed by Hurlbert (1990). The sample estimator, $\hat{I}_M$ of this index is

$$\hat{I}_m = \left(\frac{s^2 - m}{m^2 - (s^2/Q_s)} \right) + 1 \qquad (1)$$

where s^2 and m are the sample estimates of the variance and mean, respectively, and Q_s is the number of cores taken at the station. This index measures how many times more likely it is that two randomly selected individuals from the station are from the same core than would be expected if all the individuals at the station were randomly distributed among cores. For example, a value of 1.75 indicates that the chance that two randomly selected individuals are from the same core is 75% greater than if all the individuals at the station were randomly distributed. For the purpose of this analysis, only individuals in the lower two-thirds of each station were considered (below approximately 0.3 m above MLLW), because at higher tidal levels *M. senhousia* was scarce. Also, no values were calculated for the last sample date (February 1991), because too few mussels were collected.

Dry weights of *M. senhousia* were determined to evaluate length-weight relationships. No weights were obtained from the first sampling date (December 1989) because of improper sample preservation. For the remaining dates, subsamples from the entire sample were taken so as to ensure that mussels from a range of sizes were represented. When possible, at least 20 mussels per station were weighed. The selected mussels were measured to the nearest 0.1 mm with a digital caliper, their flesh was separated from the shell, and the shell and flesh were allowed to completely dry overnight in an oven maintained at 70°C. The dry flesh weight, dry shell weight, and dry weight of the whole organism (shell plus flesh) were then determined to the nearest 1 mg. To construct length-weight regressions, the dry weights were natural log-transformed and combined across all dates to obtain length-flesh weight, length-shell weight, and length-whole organism weight relationships. These relationships, combined with the length-frequency distributions, were then used to estimate biomass of the mussels.

Annual mortality rates of the mussel were determined by two different methods. Z, the mortality coefficient in the equation (Beverton and Holt 1957):

$$N_t = N_0 e^{-zt} \qquad (2)$$

was calculated using the observed decreases in abundances from December to the following August. For interpretive purposes, Z is related to annual mortality, q_x by the equation:

$$q_x = 1 - e^{-z} \qquad (3)$$

Mortality was also estimated using an iterative, nonlinear regression technique and the mean lengths of the mussel (Ebert 1987). This technique allows for the estimation of up to four parameters: Z, K
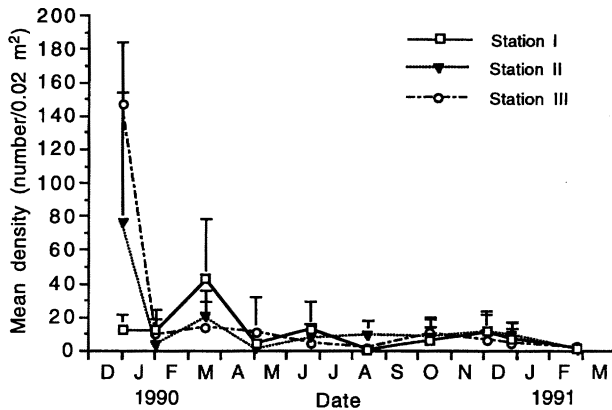
Fig. 2. Mean densities of *Musculista senhousia* in the lower intertidal sites (+1 SE).
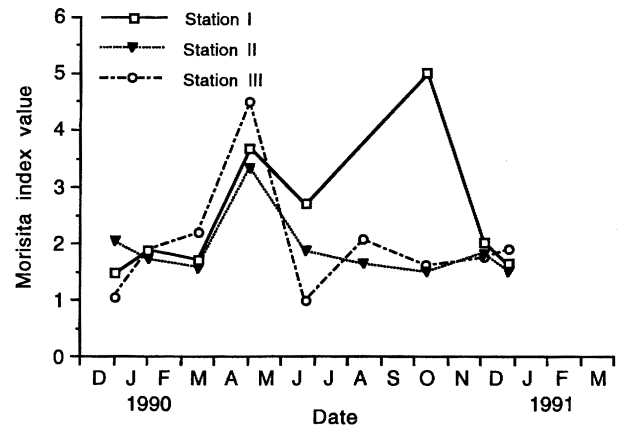

Fig. 3. Morisita index values for *Musculista senhousia* in the lower intertidal sites.

(a growth rate constant indicating how quickly organisms grow toward asymptotic size), S_0 (size at recruitment), and S_∞ (asymptotic size). For the regression, any of the four parameters can be constant or estimated. For the calculations of mortality, Z and K were estimated, and S_0 and S_∞ were set equal to 4 mm (the size of the smallest individuals collected) and 30 mm (approximately asymptotic size), respectively.

The growth rate constant, K, was also estimated in two ways. The first, described above, was using the regression technique in estimating both K and Z. The second method also involved using the regression technique, except that Z was set constant at the value obtained using Eq. 2. Thus only K was estimated. For these analyses, a Brody-Bertalanffy growth model was used (see Ricker 1975). The equation for this model is

$$S_t = S_\infty(1 - be^{-Kt}) \tag{4}$$

where S_0 and S_∞ are defined as above, b is $(S_\infty - S_0)/S_\infty$, and S_t is the size at time t. The mean lengths from the first six sampling dates from the lower intertidal sites, representing the growth of the 1989 cohort, were used in these analyses.

Results

POPULATION STRUCTURE

The highest mean densities of the mussels (Fig. 2), calculated only for the lower intertidal sites, were observed in December 1989, with an average density per core at station III of 150 mussels (7,500 m^{-2}). For the next 12 mo, densities decreased, leveling off at approximately 10 mussels per core at all stations. In addition, the mussels almost always exhibited a patchy distribution (Fig. 3), sometimes strongly so (e.g., April 1990).

Recruitment to the population was defined as the presence of individuals in the smallest sampled

size class (4 mm). Because *M. senhousia* settles at a length of about 0.25 mm, after spending two to three weeks in the plankton (Uchida 1965; Chiba 1977; Kulikova 1978), the smallest individuals in this study were probably already approximately two months old (discussed in more detail later). The most obvious recruitment event was in the fall of 1990 (Fig. 4). In October, 1990, at Station I, over half of the individuals were in the smallest size class. At the other two stations, a distinct shift in the mode toward the smaller size classes also appeared. This suggests that a major recruitment event occurred some time before October 1990. Recruitment continued throughout much of the following year as evidenced by the continued presence of individuals in the smallest size classes.

Despite this apparent background recruitment, it is possible to recognize somewhat distinct cohorts. In December 1989 there were unimodal distributions at all three stations. At stations I and II during the winter and early spring months the modal length increased relatively slowly. In the late spring and summer, however, the mussels grew more rapidly. This same trend was not as apparent at station III. By August 1990, at approximately one year of age, the mode had shifted to about 23 mm at stations I and III and to 17 mm at station II, suggesting average growth of 17 mm to 23 mm in 1 yr. The largest mussel ever measured from Mission Bay was 32 mm, indicating that *M. senhousia* can reach approximately two-thirds of its maximum size in its first year.

The size structure of the population and its change over time can also be assessed by examining the mean lengths of the entire population of mussels at each date (Fig. 5). Under conditions of a single pulse of recruitment followed by growth of individuals, the mean lengths of the population over time would show a saw-tooth pattern, with
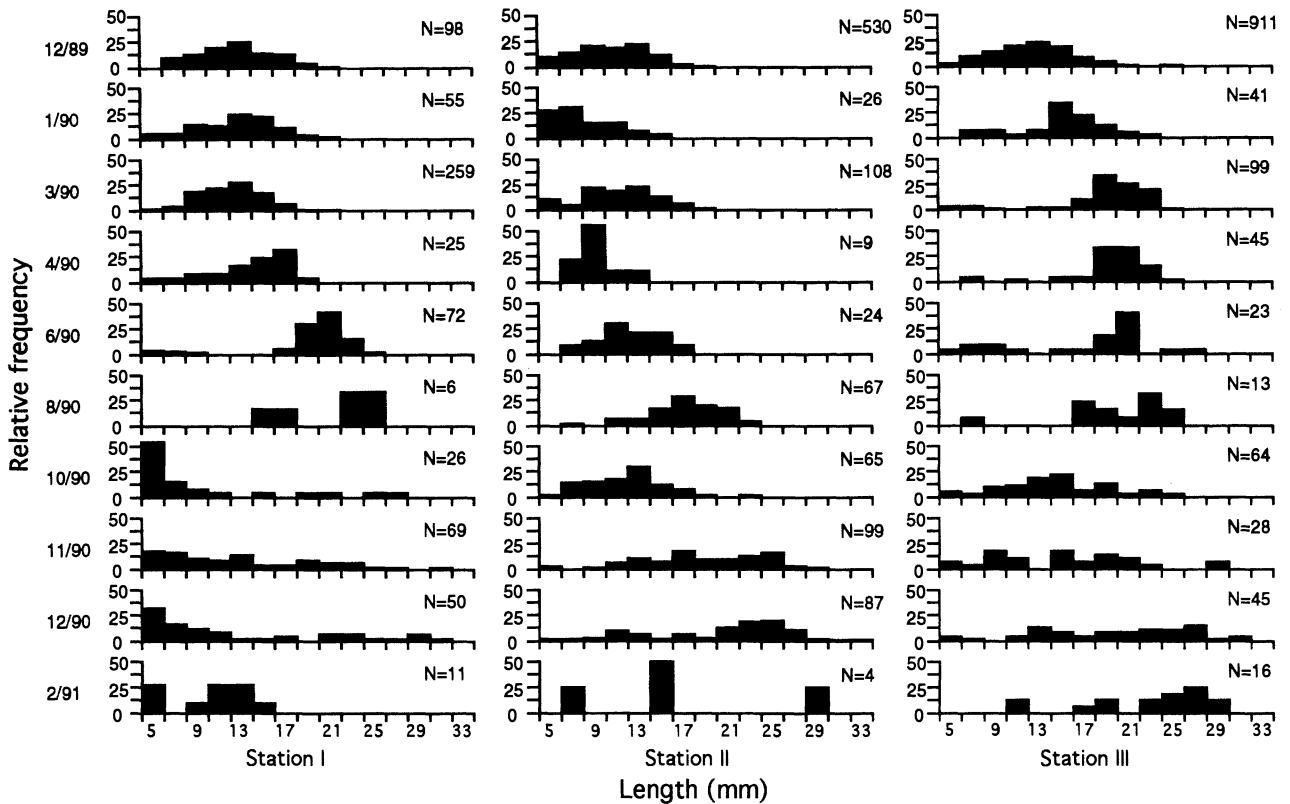
Fig. 4. Length-frequency distributions for *Musculista senhousia*. N is the number of individuals in the samples. The mid-points of the size classes are shown along the x-axis.

smallest values at the time of recruitment followed by ever-increasing values until recruitment the following year. In the Mission Bay population, there was a discernible increase in mean lengths from February to August 1990. Thereafter, the mean lengths show decreases as a result of the influx of small individuals recruiting to the population. There were, however, erratic curves and relatively large standard errors associated with these mean

Fig. 5. Mean lengths of *Musculista senhousia* (±1 SE).

lengths. These can be partially explained by two factors: the prolonged background recruitment of small individuals and sampling difficulties caused by the patchy distribution of the mussel (Fig. 3).

The K coefficients, indicating how fast the mussels reach asymptotic size, are shown in Table 1. These were as high as 0.9 (at station III) using the fixed mortality coefficient (Z) calculated from Eq. 2, and 0.77 when both K and Z were estimated. The mortality estimates (Table 1) for organisms over 4 mm were close to 100% when Z was calculated using Eq. 2 but were lower when both Z and K were estimated.

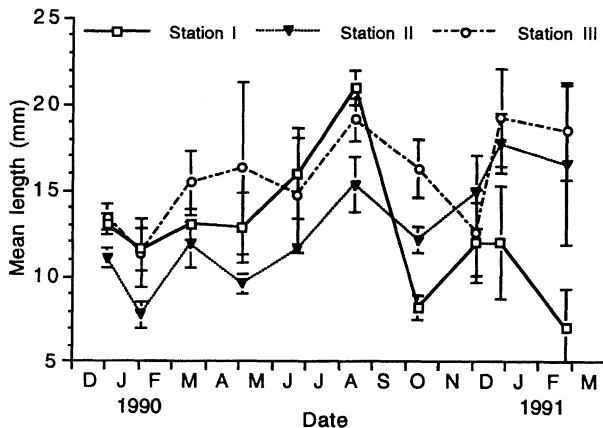A length versus age curve (Fig. 6), constructed

TABLE 1. Mortality (Z) and growth rate (K) coefficients for *Musculista senhousia* over 4 mm in length. Z was obtained both by using Eq. 2 (calculated Z) and by the nonlinear regression technique (estimated Z). Percent (%) equals annual mortality (from Eq. 3). K was calculated by the nonlinear regression technique, using both values of Z.

	Station					
	I		II		III	
	Z (%)	K	Z (%)	K	Z (%)	K
Calculated Z	4.6 (99)	0.88	3.4 (97)	0.52	7.3 (100)	0.9
Estimated Z	2.1 (88)	0.77	1.4 (75)	0.38	1.1 (67)	0.62

using the Brody-Bertalanffy model (Eq. 4) and an average K value of 0.77 (Table 1), demonstrates the hypothetical increase in shell length of an individual mussel. This curve was also extended backward beyond the size at recruitment (4 mm) to a length of 0 mm to obtain a better estimate of how old recruiting individuals in this study may be. This resulted in an age of approximately 2 mo for the new recruits, suggesting that the recruits present in December 1989 and October 1990 were probably the result of a late summer spawning event.

Longevity of *M. senhousia* was estimated by examining the length-frequency histograms (Fig. 4). From these it can be seen that in December 1989 there was one distinct, small-sized cohort and no large individuals. This suggests that the previous year's cohort died after giving rise to the observed recruits, at an age of not much greater than 1 yr (up to perhaps 17 mo). Also, if the 1989 year-class is followed, there were very few large individuals left on the last sampling date (February 1991). It is likely that those remaining died soon thereafter, at an age of 1.5 yr to at most 2 yr.

LENGTH–WEIGHT RELATIONSHIPS

The common length–weight regressions for the mussel yielded the equations:

$$\ln(\text{dry flesh weight})$$
$$= -4.13 + 2.54 \ln(\text{length})$$
$$(R^2 = 0.93) \tag{5}$$

$$\ln(\text{dry shell weight})$$
$$= -3.03 + 2.73 \ln(\text{length})$$
$$(R^2 = 0.98) \tag{6}$$

$$\ln(\text{dry whole mussel weight})$$
$$= -2.68 + 2.67 \ln(\text{length})$$
$$(R^2 = 0.98). \tag{7}$$

Equation 5 was used to calculate the total dry flesh weights (dfw) of all *M. senhousia* collected (10 cores at 0.02 m^2 core^{-1}) at each station at each date. Maximum values were 2.59 g dfw 0.2 m^{-2}, 4.03 g dfw 0.2 m^{-2}, and 10.01 g dfw 0.2 m^{-2} at stations I, II, and III respectively. Average values ($\pm$ 1 se) across all months were 0.96 ($\pm$ 0.28), 1.44 ($\pm$ 0.49), and 2.06 ($\pm$ 0.92) g dfw 0.02 m^{-2} at the three stations. Also, the increase in individual weight over time, calculated using Eq. 5 and the lengths obtained from the Brody-Bertalanffy model, is shown in Fig. 6. It should be noted that these weights may represent underestimates, as dry weight were taken on preserved individuals (Dare 1976 for *Mytilus edulis*).
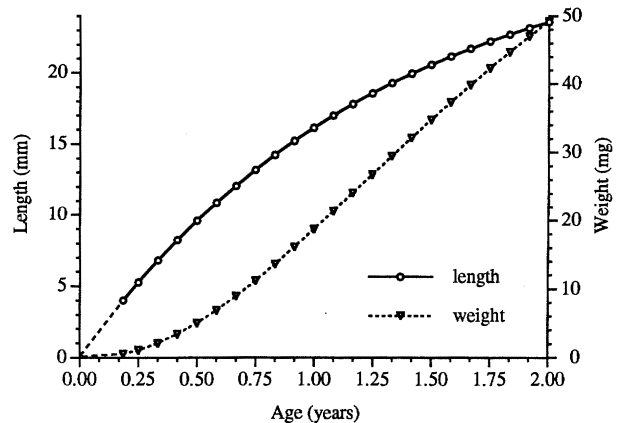

Fig. 6.   Calculated shell lengths and soft-tissue biomass versus age for the *Musculista senhousia* population. The dashed lines without symbols represent extrapolation beyond the size of recruitment (4 mm) to size at birth (0 mm).

Discussion

GROWTH

Musculista senhousia in Mission Bay attains a maximum length of about 32 mm in less than 2 yr, although some individuals in the population may grow at least 25 mm in their first year. Fast growth has also been measured for *M. senhousia* in India (George and Nair 1974), China (Morton 1974; Guan et al. 1989), and Japan (Tanaka and Kikuchi 1978).

The Brody-Bertalanffy analyses of growth in the Mission Bay populations yielded growth rate coefficients (K) ranging from 0.38 to 0.90. Other K values calculated for *M. senhousia* include 0.75 and 0.76 from San Diego Bay (Takahashi 1992) and 1.56 from India (from mean lengths presented in George and Nair 1974 in Crooks 1992). Studies of the confamilial blue mussel, *Mytilus edulis*, often considered to be a fast-growing species, yielded K constants ranging from 0.02 to 1.14 (Seed 1976), with most being lower than the values calculated for the Mission Bay populations of *Musculista senhousia*. These observations further support the notion that *M. senhousia* is a fast-growing species. The K values calculated for *M. senhousia* in Mission Bay, however, may be underestimates in that background recruitment throughout the year tended to decrease the mean lengths of the populations, and thus reduced estimates of growth below that exhibited by the primary cohort. That the K values are underestimates is also supported by comparing the growth curve (Fig. 6) with the length-frequency distributions (Fig. 4). In August, 1990, the modal size of one year olds at stations I and III is about 23 mm. However, the size of a one year old taken from the growth curve is 18 mm. This length is

similar to the modal length of mussels at station II, the station with the slowest observed growth (Fig. 4 and Table 1). This slow growth may be a result of the poor water quality at station II, resulting from sluggish flushing and heavy winter inputs of organic pollution in the form of urban run-off and sewage (California Regional Water Quality Control Board 1977).

The seasonal effect on growth of *M. senhousia* in Mission Bay appears to be moderate. At stations I and II, modal lengths increased more slowly during the winter of 1990 than during the following spring and summer (Fig. 4). The reverse pattern was observed at station II, however. Slower growth during winter months may be related to factors other than solely temperature, as Thompson and Nichols (1988) have demonstrated that winter growth of *Macoma balthica* in San Francisco Bay may actually be food limited.

MORTALITY AND LONGEVITY

The high yearly mortality rates of *M. senhousia* (over 4 mm in length) in Mission Bay (Table 1) agree reasonably well with the yearly mortality values of 97% and 69% for two populations of *M. senhousia* in San Diego Bay (Takahashi 1992). Yearly mortality rates of 80% to 90% have also been reported in Asia (Anonymous 1965; Uchida 1965). *Musculista senhousia* in Mission Bay lives at most two years. Similar life spans are reported for this species in Hong Kong (Morton 1974) and Japan (Tanaka and Kikuchi 1978). Researchers in China and India concluded that there the mussels live no longer than 18 mo (George and Nair 1974; Guan et al. 1989).

DENSITY, DISTRIBUTION, AND BIOMASS

The distribution and abundance of the mussel in subtidal sites of Mission Bay over the last 15 yr has been calculated by D. Dexter (in Crooks 1992). These reveal the highly erratic nature of *M. senhousia* populations over time. In some years *M. senhousia* was numerous (up to 8,600 m^{-2}), while in others it was almost absent. This pattern seems to be a distinguishing feature of the species, and is also true in San Diego Bay (MacDonald et al. 1990) and Asia (Morton 1974; Mukai 1974; Tanaka and Kikuchi 1978). Such dramatic population fluctuations exhibited by *M. senhousia* are typical of many opportunistic species (Pianka 1970; Levinton 1972).

Within its native range, densities of *M. senhousia* can exceed several thousand m^{-2} (Kawaguchi and Shirai 1944; Morton 1974; Kulikova 1978; Tanaka and Kikuchi 1978; Sun and Tang 1989). Juveniles have been reported in very high numbers, ranging from 28,650 m^{-2} on eelgrass blades (Kikuchi and

Peres 1977) to 126,000 m^{-2} on synthetic filament line (Kulikova 1978). Where *M. senhousia* has been introduced, it is also quite abundant. They have been reported in densities of 3,300 m^{-2} in New Zealand (Willan 1987), 2,000 m^{-2} in San Francisco Bay (Hopkins 1986), 12,370 m^{-2} in San Diego Bay (MacDonald et al. 1990), and 8,600 m^{-2} in Mission Bay (Crooks 1992). However, none of these studies include densities of newly settled individuals.

Musculista senhousia is often patchily distributed on the spatial scales examined in this study, as evidenced by Morisita index values as high as 5 for the Mission Bay populations. In Japan, Tanaka and Kikuchi (1978) report index values as high as 14, but more often they were between 2 and 10 (using samples from a somewhat larger area). It is not yet clear whether this contagious distribution results from preferential settlement with conspecifics, or results from factors such as the physical nature of the substrate, small-scale hydrodynamics, or the high predation risk of individuals that are not in clumps (e.g., Woodin 1976; Eckman 1983; Butman 1987). Regardless, it has been suggested that a survivorship advantage may be afforded to those organisms living in aggregations (Bertness and Grosholz 1985; Lin 1991). Given the ability of *M. senhousia* to modify the environment in which it is found (Morton 1974; Crooks 1992), its aggregations are likely to create habitat mosaics of the sort which have been found to be important in structuring other benthic communities (e.g., Hall et al. 1994).

The biomass estimates of *M. senhousia* in Mission Bay appear to be on the same order of magnitude as those reported for the mussel in Japan (Tanaka and Kikuchi 1978), although the maximum value of 50 g dfw m^{-2} in Mission Bay is higher than the highest value reported value for the mussel within its native range (14 g dfw m^{-2}). The relatively large standard errors associated with the average biomass at a station over time are caused by the biomass being dependent on both the number and size of individuals present (which are themselves variable) as well as on the patchy distribution of the mussel.

RECRUITMENT

The spawning and recruitment patterns of *M. senhousia* both in Asia and San Diego (Table 2) appear to be markedly inconsistent. In some places spawning and recruitment occurs during a short time span, while in others it is protracted (it should be noted that Kawahara and Katou (1970) suggest that the larvae observed by Yamashiro and Kato (1961; in Kawahara and Katou 1970) were actually not only those of *M. senhousia,* and that the actual spawning season may be more restricted). Further-

TABLE 2. Timing of reproduction and recruitment in *Musculista senhousia*. The methods used to determine this information are also provided. These include the presence of larvae identified as *M. senhousia* in the water column, the presence of settled juveniles (and the smallest size detected), and induced spawning of adults.

Location	Time of Year	Methods	Source
Russia	July–September	Planktonic larvae	Kulikova 1978, 1979
Japan	May–November; July and August maximum	Induced spawning	Kawahara and Katou 1970
Japan	Fall	Planktonic larvae	Taki 1952 (in Kawahara and Katou 1970)
Japan	March–January; October maximum	Planktonic larvae	Kato and Akiyama 1959
Japan	September–November	Planktonic larvae	Yoshida 1937
	October	Settlers (? mm)	
Japan	January–April; some in summer	Settlers (? mm)	Kikuchi 1964
Japan	July–November, August and September maximum	Settlers (2–3 mm)	Uchida 1965
Japan	June–October; August and September maximum	Settlers (2–3 mm)	Anonymous 1965
Japan	June–November; July and August maximum	Settlers (? mm)	Chiba and Oshima 1976 (in Chiba 1977)
Japan	January–May	Settlers (2 mm)	Tanaka and Kikuchi 1978
Japan	June–December	Settlers (? mm)	Kawahara et al. 1979
South Korea	All year[a]; fall and summer maximum	Planktonic larvae	Yamashiro and Kato 1961 (in Kawahara and Katou 1970)
Hong Kong	January	Settlers (3 mm)	Morton 1974
India	Prolonged; May–October maximum	Settlers (5 mm)	George and Nair 1974
San Diego	Prolonged; fall maximum	Settlers (4 mm)	This study

[a] May represent an overestimation, see text for details.

more, the timing of the spawning and recruitment events also varies widely from place to place, with peaks occurring throughout the year. As was seen in Mission Bay (Fig. 4), the magnitude of recruitment events can vary substantially from year to year and on relatively small spatial scales (i.e., between the three stations). Such variability also exists in the *M. senhousia* populations living subtidally in Mission Bay (in Crooks 1992). The relationship between the subtidal and intertidal stocks should be noted as the long planktonic period of the mussel means that organisms living in one area may contribute recruits to the other.

The source of variability in reproduction and recruitment patterns is difficult to understand but has been reported for other bivalves (Seed 1976; Sastry 1979; Strathmann 1987) and marine invertebrates in general (Dayton 1984). To better establish the reproductive characteristics of *M. senhousia*, future studies should incorporate use of smaller mesh sizes to collect newly settled individuals as well as direct measurements of gonad weight and/ or histological analyses of gonadal material.

Musculista senhousia as a Successful Invader

There has been much debate on the life-history characteristics that make a successful invader. Some studies find that exotics are "typical" opportunistic species, while others state that there are just as many exceptions to this generalization as there are examples supporting it (Lodge 1993 and references therein). Many end up concluding that the question lies unresolved. This and other research on *M. senhousia*, however, suggest that this species fits the classical concept of an opportunist.

In both its native range and in San Diego, this mussel is short-lived, suffers high mortality, can experience very high, but often variable population sizes, is small in body size, grows quickly, and has a long planktonic dispersal stage. Other opportunistic features, such as high fecundity, have been qualitatively assessed (Kulikova 1978). One particularly interesting aspect of the life history of *M. senhousia* is its life span; although most individuals are annuals, some small fraction of the population lives perhaps up to 2 yr. Morton (1989) concluded, in the consideration of other bivalve species, that this overstepping of generations is an adaptation for the continued survival of population in a variable environment. Even in the case of massive mortality of the newest year-class, some of the older individuals would survive and reproduce.

Clearly, adaptations other than those affecting life-history traits are also important in allowing an organism to successfully invade an ecosystem. *M. senhousia*, a suspension-feeder, possesses a suite of characteristics that allow it to thrive in the fine-sediment habitat typical of the back of estuaries. These include a style sac separate from the gut, which facilitates the processing of turbid water, and large labial palps and powerful rejectory currents, which aid in the removal of sediment (Morton 1974).

The thin shell of *M. senhousia*, which has been suggested to be an adaptation for fast growth in other bivalves (Palmer 1981; Heller 1990), allows the mussel to inhabit the surface of soft sediments. Furthermore, *M. senhousia* decreases the relative density of its shell as it grows, as the slope of ln length versus ln shell weight regression is only 2.7 (from Eq. 6), less than the value of 3 that would

be obtained if the same density is maintained throughout growth (Thayer 1975). To protect this thin shell, *M. senhousia* constructs byssal nests or cocoons. These important structures also stabilize the sediment around the mussel and serve as an anchor (Morton 1974). When the mussel occurs in high densities, these byssal nests can become woven together and form a mat, thus profoundly affecting the nature of the sediment (Morton 1974; Crooks 1992).

The results of this study demonstrate that *M. senhousia* possesses similar, opportunistic characteristics in both its native range and San Diego, and knowledge of the basic life-history traits of this organism provides a foundation upon which further research on the impacts of this exotic species can be based. *M. senhousia* has already been suggested to have important consequences for benthic fauna (Crooks unpublished data) and flora (Reusch personal communication), which are related to the mussel's high densities and alteration of benthic habitat. Given that *M. senhousia* is but one of a large number of non-indigenous species that are now present in the bays and estuaries of the Pacific Coast of North America (Carlton and Geller 1993), it is surprising to realize how little is known about the effects of these organisms on native species. Continued research on organisms such as *M. senhousia* can therefore lend insight into the role of exotic species in invaded ecosystems.

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