Ecology and environmental impact of Musculista senhousia (Moilusca: Bivalvia: Mytilidae) in Tamaki Estuary, Auckland, New Zealand

Robert Creese , Simon Hooker , Sharon de Luca & Yvette Wharton

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ROBERT CREESE

SIMON HOOKER

SHARON DE LUCA

YVETTE WHARTON

Leigh Marine Laboratory & School of
    Environmental and Marine Sciences
University of Auckland
Private Bag 92019
Auckland, New Zealand

Abstract The introduced, mytilid bivalve *Musculista senhousia* (Asian date mussel) occurs on the east coast of New Zealand in the Auckland region. Eighteen sites were searched within the Tamaki Estuary: six had extensive mats of mussels and three contained small, isolated clumps. Core samples were taken monthly during 1994/95 from two of the mat-forming populations. Densities reached 16 000 m^{-2} at Bucklands Beach and 5000 m^{-2} at Farm Cove. Both populations were dominated by a single cohort of mussels. Mussels grew to about 20 mm in 12 months, after which growth virtually ceased. Recruitment was sporadic into existing mats, but occurred adjacent to the monitored mat at Bucklands Beach in April 1995. The area occupied by the initial mussel bed at this site decreased by 60% over 1 year. Further core sampling revealed significantly fewer macrofaunal invertebrates under mussel mats compared to control samples taken from areas of beach without mussels. Infaunal bivalves were most adversely affected by *M. senhousia*, showing an 8-fold decrease in abundance within mats compared to cores in the control area. Our results reveal that *M. senhousia* in the Auckland area has similar life history features to those reported from populations

outside New Zealand. We suggest that any adverse environmental effects caused by *M. senhousia* are likely to be local and short-lived.

INTRODUCTION

Bivalves are often successfully introduced, usually accidentally, into marine and freshwater environments. Several international examples have been documented recently: the American razor clam *Ensis directus* into parts of Western Europe (Beukema & Dekker 1995), the South American edible brown mussel *Perna perna* into Texas (Hicks & Tunnell 1993), the Asian clam *Potamocorbula amurensis* into California (Carlton et al. 1990; Nichols et al. 1990), and the zebra mussel *Dreissena polymorpha* into the Great Lakes and associated waterways of North America (Ludyanskiy et al. 1993). There is a growing body of evidence that transoceanic shipping activity is the major vector for the unintentional introductions of these and other so-called "invaders" (Carlton 1985, 1987). Sheltered coastal bays and estuaries near major ports are most likely to receive marine invaders, and severe ecological impacts may occur in these areas. A frequently cited example is Lake Merritt (a brackish water extension of San Francisco Bay, California) where 37 of the 46 recorded invertebrate species are exotic (Carlton 1989; Carlton & Geller 1993).

The introduction of zebra mussels to North America, usually attributed to ballast water released in Lake St Clair (Hebert et al. 1989), has resulted in major ecological damage, notably serious reductions in the abundances of some rare native, unionid bivalves (French 1990; Schloesser & Nalepa 1994), as well as having social and economic impacts (Roberts 1990; Ludyanskiy et al.

1993). The zebra mussel reaches a size of 30 mm, grows rapidly and has high fecundity (Hebert et al. 1991). The damage it causes results in part from its ability to form compact mats over the substratum (Ahlstedt 1994). Another invasive mussel, the Asian date mussel *Musculista senhousia* (Benson *in* Cantor, 1842) shares many of these features. Over the past 70 years, *M. senhousia* has been introduced from Asia to the west coast of the United States (Kincaid 1947; Carlton 1979; Dexter 1983), southern France (Hoenselaar & Hoenselaar 1989), Western Australia (Slack-Smith & Brearley 1987; Willan 1987), and New Zealand (Willan 1985, 1987). Because it has been a successful invader of many parts of the world and because its life history and ecological characteristics predispose it to spread rapidly and form large mats on the seabed, *M. senhousia* has the potential to cause adverse ecological effects (Crooks 1996).

In recent years there has been considerable public and media attention in New Zealand on the threats of invading marine species, especially in relation to ballast water discharges (see examples in: The Royal Society of New Zealand 1995). This has lead to a desire to better understand the nature of invasive species which have appeared around the coastline of New Zealand (Dromgoole & Foster 1983). The Asian date mussel is one of several bivalve species to become widely established around Auckland Harbour in recent years (B. W. Hayward pers. comm. 1996). In particular, the Tamaki Estuary (see Fig. 1), where *M. senhousia* was first detected, still has large populations of mussels (Creese & Hooker 1996). By monitoring populations of *M. senhousia* over time, our work provides preliminary information on the population dynamics and life history of *M. senhousia* in the Auckland region. We also assess the range of impacts that this species might have on coastal habitats in New Zealand.

METHODS

A detailed search of 18 stretches of foreshore of the Tamaki Estuary was undertaken in June/July 1995 to document the occurrence of *Musculista senhousia*. This search covered virtually all available intertidal habitat that was unvegetated (i.e., did not support mangrove forests: Fig. 1). Where *M. senhousia* was encountered, its presence was recorded as either "mat-forming" (large numbers of individuals bound together in a
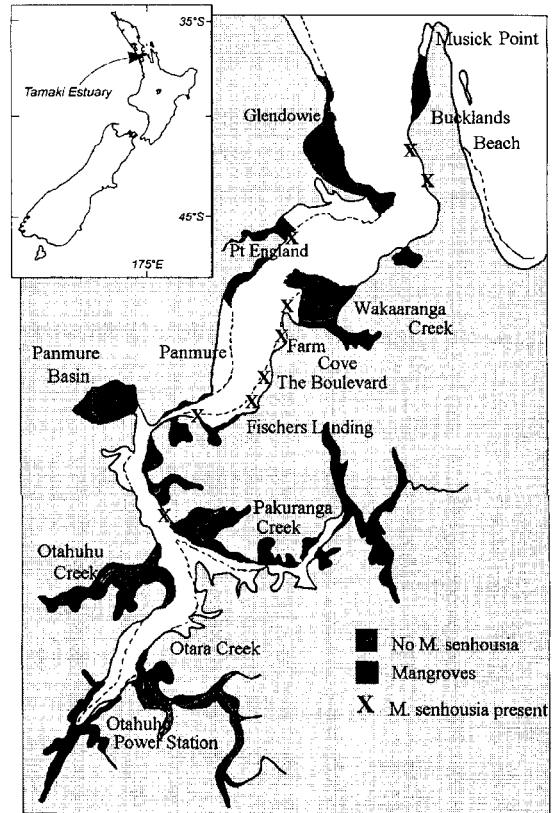

Fig. 1 Distribution of *M. senhousia* in the Tamaki Estuary, Auckland. Records are for 1995.

continuous bed of several square metres) or "isolated groups" (small clumps containing fewer than 100 mussels). Subtidal searches were also carried out in the subtidal channels.

Two intertidal beds of mussels (at Bucklands Beach and Farm Cove: Fig. 1) were selected for detailed ecological studies on the basis of a known long history of occurrence (M. Morley unpubl. data) and ease of access. The first site had an extensive mat of mussels that had first been noted in mid 1994, and the second a more diffuse mat of unknown age. The two beds were sampled at approximately monthly intervals between November 1994 and November 1995. At each site, nine replicate core samples of sediment were taken from randomly selected positions on the surface of the mussel bed to a depth of 20 cm, using a 6.6 cm diam. circular plastic pipe. Each sample was washed through a 1-mm mesh sieve, the material retained on the sieve was sorted, and all macrofauna present were

identified and counted. Numbers of *M. senhousia* per core were converted into densities per square metre to allow comparison with other published studies. The shell length of each individual mussel was measured using Vernier calipers, and analysis of the resulting length-frequency histograms was performed using the computer software package "Elefan" (Pauly et al. 1995).

. Nine additional replicate core samples were taken from the same level of the shore but in areas without mussel mats (i.e., control sites). These additional samples were collected monthly between November 1994 and January 1995 at Bucklands Beach, but on only one occasion at Farm Cove (December 1994). The samples were processed as described above. Data from within the mats and from the control sites were used to calculate mean macrofaunal abundances and mean species richness (excluding *M. senhousia*). The faunal composition of the samples was compared further by dividing the macrofaunal individuals into three arbitrary groups (worms, bivalve molluscs, and other organisms) as casual observation suggested that worms and bivalves differed the most in a comparison between mussel mats and adjacent sediment.

To document any changes in the size or shape of the mussel mat at the Bucklands Beach site, a plot (30 m long × 16 m down the shore) was positioned on the shore to include the entire bed. The plot was set up in November 1994 and remapped on three occasions during 1995. The lower edge of the plot corresponded approximately to mean low tide level, and the entire plot was divided into 2 m × 2 m grid squares. Qualitative, hand-drawn maps of the outline of the mussel mat were drawn for each grid square and then transposed onto graph paper, to produce a map of the entire 480 m² plot and allow calculation of the area occupied by mussel mat. Changes in the shape of the bed were determined by qualitative assessment of these maps.

One mechanism by which new patches of mussels could become established is if fragments of existing beds were torn off (e.g., by large waves), transported to a new location, and then were able to reattach. An attempt was made to determine the viability of dislodged portions of mussel mat by removing three 25 cm diam. circles of mussel mat from Bucklands Beach (well away from the standard sampling area) and transferring them to a similar intertidal habitat at the other end of the beach. Markers were placed next to each transplanted segment of mat and observations made 3 days later. The holes in the main mat created by the removal of the transplanted circles were checked for 2 months following removal to ascertain whether mussels had recolonised the free space.

RESULTS

Distribution

During the period 1985–94, populations of *M. senhousia* have appeared throughout the Tamaki Estuary (Morley 1988, unpubl. data). They have occurred as far up stream as Otara Creek (Fig. 1) but have been most abundant on eastern shores. In our intertidal survey in 1995, populations of *M. senhousia* were found in many of these same areas. The most densely populated areas were on the eastern shores, especially on Bucklands Beach and the stretch of foreshore between Wakaaranga Creek and Fischers Landing (Fig. 1). Only one small population was found on the western shore (at Point England), and there was no longer a population at the entrance to Otara Creek. *M. senhousia* were found in 9 of the 18 intertidal sites searched. At 6 of these sites, mussels formed continuous beds, covering tens to hundreds of square metres. At the remaining three sites, mussels occurred as small clumps up to 5 cm in diameter, each containing fewer than 10 mussels. *M. senhousia* were most often found at mid- to low-tidal levels in sheltered- to semi-exposed localities on firm mud or medium to coarse sand. In many areas, fragments of cockle or other shells were present in the substratum, which may aid the initial attachment of recruiting juveniles. Many of the beds were found in the vicinity of small, freshwater rivulets or run-off.

Surveys along subtidal transects positioned across the main channel of the Tamaki Estuary in February 1995 revealed no trace of *M. senhousia* immediately adjacent to the Bucklands Beach site where they had previously been recorded (Morley 1988).

Population ecology

The Bucklands Beach population had significantly higher densities of *M. senhousia* than the Farm Cove population over the entire period of sampling (Fig. 2). There was a trend of decreasing density with time at both sites. Density at Bucklands Beach declined from 16 000 m^{-2} in November 1994, to 5500 m^{-2} in November 1995 (Fig. 2). A notable increase in density occurred in May 1995 as a result
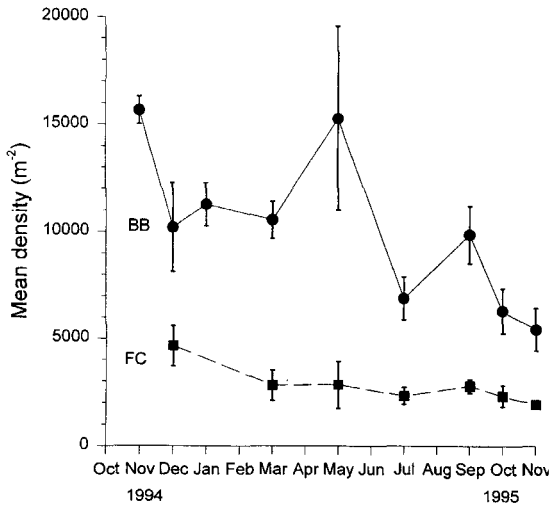
Fig. 2 Mean densities (± SE) of *M. senhousia* at two sites in the Tamaki Estuary over a 12-month period.

of recruitment of juveniles into the population (see Fig. 3). A smaller increase occurred in September 1995 but this was not related to a recruitment event (Fig. 3). The variability among replicate core samples was highest during the period of

recruitment in May 1995. The density of *M. senhousia* at Farm Cove declined from a high of 4 600 m^{-2} in December 1994 to a low of 2000 m^{-2} in November 1995 (Fig. 2).

Length-frequency histograms for the population of *M. senhousia* at Bucklands Beach showed a bimodal structure for the initial sample in November 1994 (Fig. 3), with mean sizes of 7.4 mm and 13.3 mm (Table 1). However, this bimodality had disappeared by January 1995 because Cohorts A and B had merged (Table 1). The average size of this combined adult cohort increased from January 1995 (14.4 mm shell length) to July 1995 (20.1 mm shell length), a growth rate of about 1 mm per month from summer to mid winter. Juvenile *M. senhousia* recruited into this site between March and May 1995 (Fig. 3), the new cohort (Cohort C: Table 1) having a mean shell length of 4.5 mm. This cohort was still visible in July with a greatly increased mean size of 10.2 mm (Table 1) but many fewer individuals (Fig. 3). Few juveniles were sampled in September and the computer analysis could only identify one juvenile cohort which had a mean size of 3.1 mm. This was tentatively labelled Cohort D (Table 1), but its numbers were so small (Fig. 3) that it probably was not a new cohort of recruits. Both Cohorts C and D appeared to be present in

Table 1 Cohort structure derived from length-frequency analysis using the software package "Elefan" (Pauly et al. 1995) for samples of *M. senhousia* at Bucklands Beach obtained on nine occasions, and Farm Cove obtained on eight occasions.

Date	Bucklands Beach		Farm Cove	
	Mean ± SD	Cohort	Mean ± SD	Cohort
Nov 1994	7.4 ± 1.6	B		
	13.3 ± 2.2	A		
Dec 1994	11.1 ± 2.1	B	7.8 ± 0.7	B
	15.4 ± 1.8	A	13.7 ± 1.8	A
Jan 1995	14.4 ± 2.0	A+B	8.5 ± 0.9	B
			15.7 ± 2.1	A
Mar 1995	17.1 ± 1.6	A+B	3.5 ± 2.7	C
			20.3 ± 1.6	A+B
May 1995	4.5 ± 1.3	C	8.0 ± 0.8	C
	18.8 ± 2.8	A+B	21.4 ± 1.1	A+B
Jul 1995	2.7 ± 2.1	D	21.4 ± 1.4	A+B
	10.2 ± 1.9	C		
	20.1 ± 1.6	A+B		
Sep 1995	3.1 ± 1.3	D	22.4 ± 2.0	A+B
	20.0 ± 2.1	A + B		
Oct 1995	3.8 ± 1.2	D	22.2 ± 1.4	A+B
	11.5 ± 2.7	C		
	21.2 ± 2.3	A+B		
Nov 1995	19.6 ± 1.6	A+B	21.1 ± 1.2	A+B

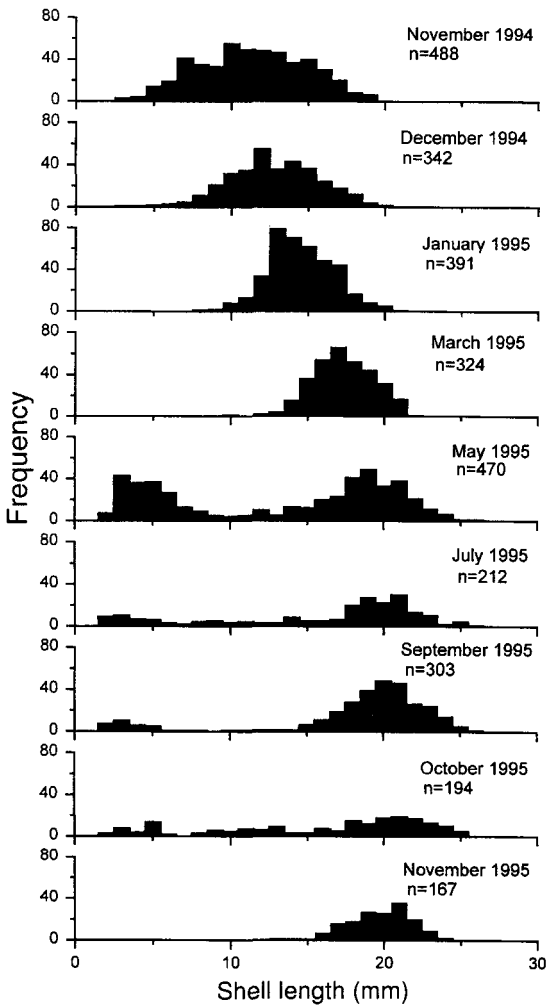**Fig. 3** Population size structure of *M. senhousia* over 13 months at Bucklands Beach, Tamaki Estuary.

Fig. 4 Population size structure of *M. senhousia* over 12 months at Farm Cove, Tamaki Estuary.

October but again at very low numbers, and there were only three juvenile mussels in the final sample in November 1995. The mean size of the adult cohort (A+B) at this site increased only marginally between July and November 1995 (Table 1, Fig. 3), suggesting negligible growth. The largest mussel encountered had a shell length of 26 mm, but the largest individuals in a sample were usually between 21 and 24 mm. The size structure at the end of the sampling period was quite different to what it had been a year earlier; initially there were rapidly growing smaller individuals ranging in size from 3 mm to 19 mm, but at the end the population was
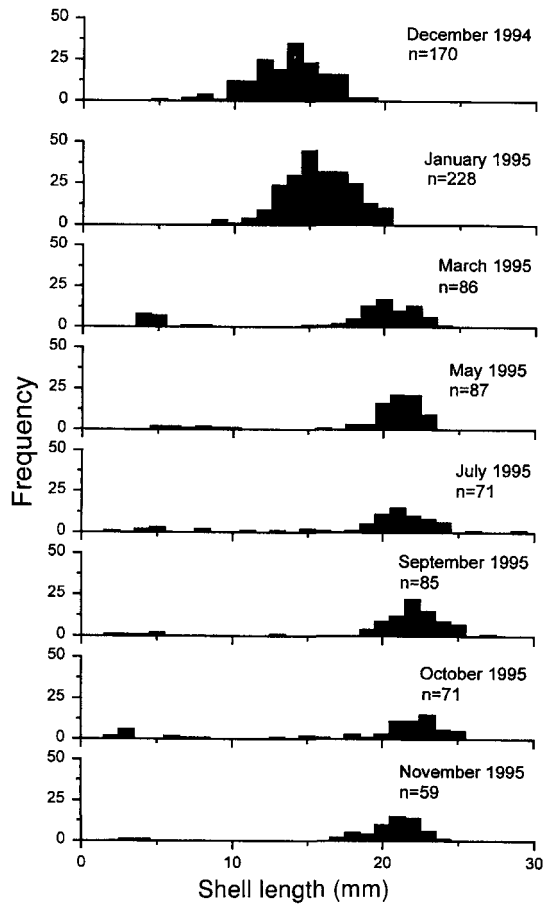
numerically dominated by large, slow-growing adults between 16 mm and 24 mm.

Population size structure at Farm Cove was similar to that at Bucklands Beach (Fig. 4) over the survey period. The population was numerically dominated in December 1994 by medium-sized mussels (mean size 13.7 mm; Cohort A in Table 1). The mean shell length of this cohort had increased by 2 mm by January 1995, after which it was joined by the numerically much less abundant Cohort B. The shell length of this combined adult cohort (A+B) continued to grow at 2 mm per month, reaching a mean of 21.4 mm in May 1995, after which it remained approximately constant at 21.1–22.4 mm until the end of the study. The largest sampled individual measured 29 mm but, as at Bucklands Beach, most adult mussels were below

25 mm in shell length. Recruitment at this site was not as clearly defined as at Bucklands Beach. There was a small pulse of recruitment into this population in March 1995 (Fig. 4) giving a new cohort with a mean shell length of 3.5 mm (Cohort C in Table 1). This cohort was barely recognisable in May, after which only very low numbers of small animals (< 10 mm) were found in each monthly sample.

The mortality rate of *M. senhousia* was high at both sites, indicated by the continuous loss of mussels from the adult cohorts at all times except the initial period of November 1994 to January 1995 (Fig. 3 and 4). From this analysis, and given a calculated annual growth rate from recruitment of 15–20 mm, the estimated longevity of mussels in the Tamaki Estuary is 1–2 years.

Bed dynamics

The mussel bed mapped at Bucklands Beach occupied 170 m² between November and December 1994, about 40% of the mapped plot. This decreased to 115 m² in February 1995, and shrank further to 90 m² in August 1995. The greatest loss was in the central part of the plot where a small freshwater rivulet flowed. This rivulet eroded away large areas of the byssal mat together with any resident mussels. Further loss continued after August in that area and along the seaward edge. The original bed disappeared completely by June 1996, about 2 years after its establishment.

Initially there were isolated clumps of *M. senhousia* adjacent to the main bed at Bucklands Beach. By May 1995, a new extension to the bed had formed in this region: it completely filled that section of the plot and extended both along- and down-shore for tens of metres. The mussels in this new extension were < 10 mm in shell length, indicating that they were juvenile recruits. The timing of their appearance coincided with the pulse of recruits found in the original bed (Fig. 3). The new extension covered an additional 200 m² by August 1995 and continued to expand both within the mapped plot and outside it. By November 1995 it was barely possible to separate the new extension from the remains of the original mat.

The circles of mat that were moved to the other end of Bucklands Beach were checked 3 days after transplantation. The tags placed next to the circles were still in place. There was no trace of the transplanted sections of mat, however, suggesting that sections of mat of this size are unlikely to reattach themselves to the substratum if transported

to a new location. The holes left in the main bed showed no re-colonisation by *M. senhousia* over the following 2 months and they rapidly filled in with fine mud. There was no evidence of any erosion of the mat around the edges of the cleared circles.

Environmental impact

During the study, the original bed at Bucklands Beach accumulated fine, muddy and eventually, anoxic sediments. Immediately underneath the layer of living mussels (at c. 3 cm depth), the substratum was black and contained few living organisms. The bed was raised above the surrounding beach, often by as much as 8–10 cm, suggesting that considerable amounts of new material had been accumulated. Within 3 months of its first appearance in May 1995, the extension to the original mat had a noticeable covering of fine silt, and by April 1996 it was raised c. 5 cm above the surrounding beach.

Thirty-five macrofaunal species were found in core samples collected over the summer of 1994/95 (Table 2). The greatest species richness was found in samples from the control substratum at Bucklands Beach, with 37.5% more macrofaunal species outside the mussel mat than inside it (Fig. 5A). Although the magnitude of the difference was not as great at Farm Cove, the effect was similar with 36.4% fewer macrofaunal species within mussel mats (Fig. 5A). In December 1994, when both sites were sampled, the mean number of species per core was lower in samples taken from within mats compared to samples taken outside the mussel mats (Fig. 5B) but the differences were not statistically significant at either site (*t*-tests, $P > 0.1$).

In December 1994, the mean number of individuals per sample was also greater in cores from control areas compared with cores from the mussel mat (Fig. 6). This effect was most pronounced at Bucklands Beach, where there was an average of 9 macrofaunal individuals per core outside the mussel mat but only 2.1 per core within the mat. This pattern was consistent for the samples taken in each of the 3 months at Bucklands Beach (Fig. 7).

Polychaete worms and bivalves dominated the core samples (Table 2). Bivalves (excluding *M. senhousia*) were on average 8 times more abundant in control cores than in cores taken from within the mats (Fig. 8). Species most affected were suspension feeders such as pipi (*Paphies australis*),

cockles (*Austrovenus stutchburyi*), and black mussels (*Xenostrobus pulex*). Numbers of worms per core were similar for the two treatments (Fig. 8).

DISCUSSION

Population ecology

Populations of *Musculista senhousia* at both sites were numerically dominated by a single cohort of individuals for most of the year. The mean size of this cohort rapidly increased to 20 mm, after which growth slowed considerably and mussels rarely grew larger than 25 mm. Recruitment to established

beds was sporadic and at low levels, although occasional small pulses were encountered (e.g., at Bucklands Beach in April 1995). These features suggest that existing beds are not the primary site for new recruitment, and that the two monitored beds were largely the result of a single recruitment and colonisation event that occurred just before our study started. Observations by M. Morley (pers. comm.) support our contention that the monitored bed at Bucklands Beach appeared between April and October 1994. Older animals in a mat appear to senesce and die in their second year and the mat subsequently disintegrates. Instead of being self-perpetuating, the mats are therefore best considered

Table 2 List of species encountered during core sampling at Bucklands Beach (BB, sampled three times between November 1994 and January 1995) and Farm Cove (FC, sampled once in December 1994). Samples are from within mussel mats (in) and from control samples taken outside mats (out). Y indicates presence; — indicates absence.

| Group	Species	BB out	BB in	FC out	FC in
Anemone	*Actinothoe albocincta*	Y	—	—	—
	Anthopleura aureoradiata	—	Y	Y	Y
Chiton	*Amaurochiton glaucus*	Y	—	—	—
	Chiton pelliserpentis	Y	—	—	—
Gastropod	*Notoacmea daedala*	Y	—	—	—
	Haminoea zelandica	—	—	—	Y
Bivalve	*Austrovenus stutchburyi*	Y	—	Y	Y
	Corbula zelandica	Y	—	—	—
	Felaniella zelandica	Y	Y	—	—
	Macomona liliana	—	—	Y	—
	Musculista senhousia	—	Y	—	Y
	Nucula hartvigiana	Y	Y	Y	Y
	Paphies australis	Y	—	—	—
	Tawera spissa	Y	—	—	—
	Xenostrobus pulex	Y	—	—	Y
Crab	*Helice crassa*	—	Y	Y	Y
	Hemigrapsus crenulatus	Y	Y	—	—
	H. edwardsii	Y	—	—	—
	Hemipodus sp.	—	Y	—	—
	Hymenicus cooki	—	—	Y	—
Barnacle	*Elminius modestus*	Y	—	—	—
Caddis fly	*Philanisus plebius*	Y	—	—	—
Holothurian	*Trochodota* sp.	Y	Y	—	—
Polychaete	*Clymene insecta*	Y	—	—	—
	Clymene sp.	—	Y	—	—
	Glycera americana	Y	Y	Y	—
	G. lamellopoda	Y	—	—	—
	Goniada sp.	Y	—	—	—
	Unidentified maldanid	—	Y	—	—
	Macroclymenella stewartiensis	Y	Y	Y	—
	Notomastus zeylanicus	Y	Y	Y	—
	Owenia fusiformis	Y	—	—	—
	Paraphoxus sp.	Y	—	—	—
	Perinereis nuntia	—	Y	Y	Y
Nemertean	Unidentified sp.	—	Y	—	—
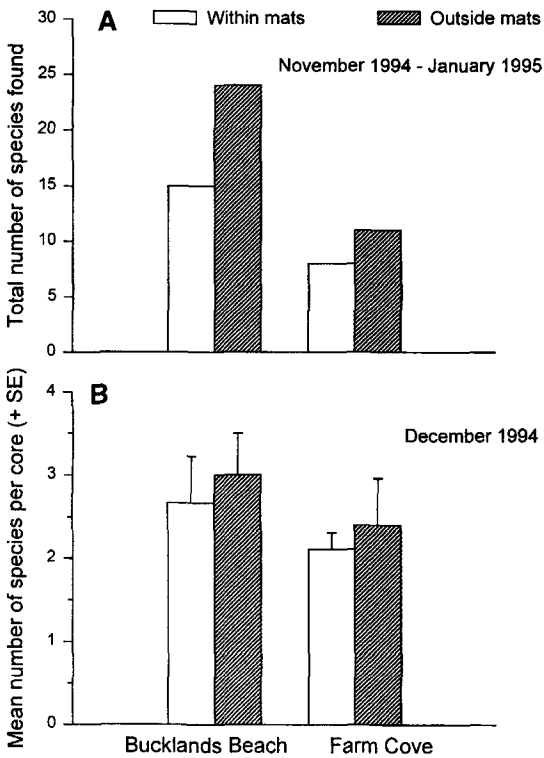
Fig. 5 Species richness of macrofauna (excluding *M. senhousia*) at two sites in the Tamaki Estuary. **A**, Total numbers of species found inside the mussel mats ("within") and adjacent to the mussel mats ("outside"); **B**, mean number of species per core inside and outside mussel mats; *n* = 9 cores.

Fig. 6 Average abundances of macrofauna (excluding *M. senhousia*) in core samples taken inside and outside the mussel mats at two sites in the Tamaki Estuary in December 1994.

ephemeral. The existing area of mussel mat within the mapped plot at Bucklands Beach demonstrated this pattern: about 60% of the original bed was eroded away over a 12-month period, and the entire mat disappeared after about 2 years. Similarly, checks at Cheltenham Beach on Auckland's north shore, where the mussel was abundant in 1992/93 (Gardner 1993), revealed no live mussels in December 1994 (Hooker & Creese 1995).

We conclude that *M. senhousia* typically colonises an area as larvae, that an extensive byssal mat is formed as these densely-packed juvenile mussels grow, and that the life-span of the mat is determined by the longevity of the mussels (1–2 years). Beds do not appear to be maintained by subsequent recruitment into existing mats. These population characteristics are consistent with previously published accounts. *M. senhousia* has
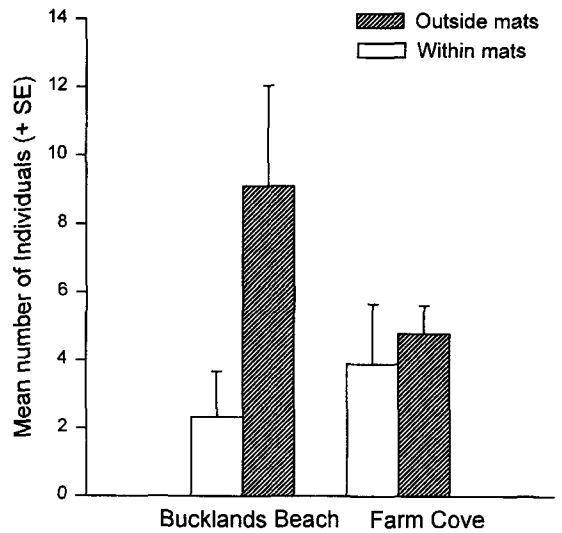
high fecundity, rapid growth, short life span, and good dispersal ability in both its native region (Morton 1974; Tanaka & Kikuchi 1978) and in regions to which it has been introduced (Willan 1987; Crooks 1996). For example, in Mission Bay, southern California, mussels spawned all year round, grew rapidly to a maximum shell length of 32 mm, lived for only 2 years, and showed erratic recruitment (Crooks 1996).

To offset the high mortality of adults and the consequent rapid demise of established beds (in the absence of significant levels of new recruitment), formation of new mats must be frequent. This would require high fecundity, resulting in a large pool of planktonic larvae which then settle gregariously— features that have been demonstrated for populations in other countries (Yoshida 1937; Kawahara & Katou 1970; Kulikova 1979; Crooks 1992, 1996). A high-density patch of new recruits was encountered in the mapped plot at Bucklands Beach, and such patches have been previously reported at Beachlands in the nearby Tamaki Strait (Willan 1987) and in other countries (Kikuchi & Tanaka 1978; Kulikova 1978; Crooks 1996). If survival of these gregarious settlers is good, a large, dense mat will be formed. Densities of *M. senhousia* beds often reach several thousand per square metre (Crooks 1996), with an exceptionally high density
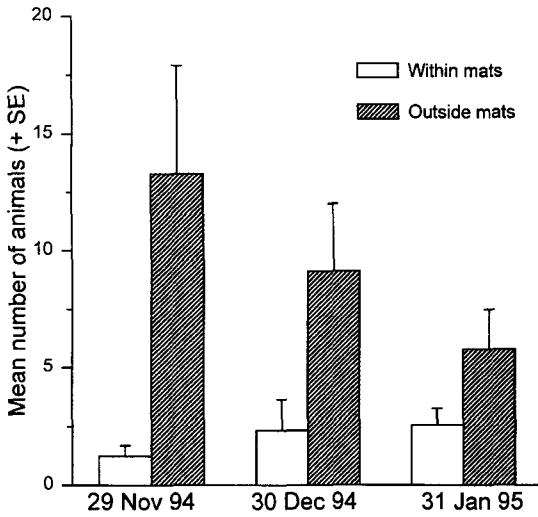
Fig. 7 Average abundances of macrofauna (excluding *M. senhousia*) in core samples taken inside and outside mussel mats at Bucklands Beach, Tamaki Estuary, in three consecutive months.
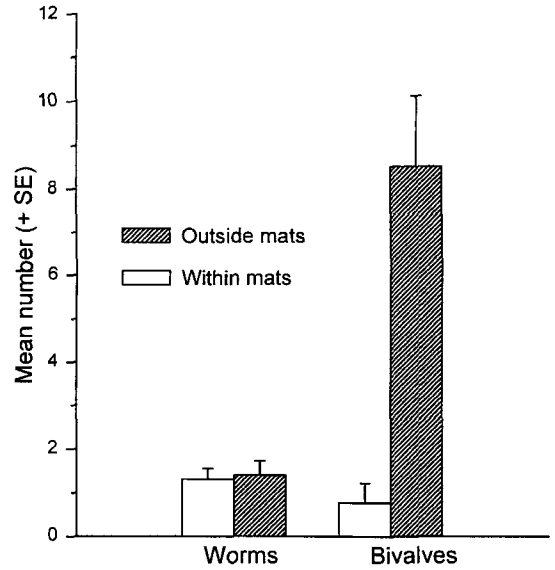

Fig. 8 Average abundances of two groups of macrofauna (excluding *M. senhousia*) in core samples taken inside and outside mussel mats at Bucklands Beach, Tamaki Estuary. Data are pooled for the three samples taken monthly between November 1994 and January 1995.

of 28 650 m^{-2} being reported from a Japanese population (Kikuchi & Tanaka 1978).

If recruitment is not heavy, small clumps of mussels may form rather than continuous beds. This was observed at Farm Cove during the course of our study. Clumps of mussels may also result from the disintegration of an existing mat. The development of hillocks in some areas of the mat at Bucklands Beach during December 1994 may be related to the observed decrease in coverage of the mat, and may represent an intermediate stage in its break-up. Either process may have caused the observed clumping at the three sites in the Tamaki Estuary during the general survey. Ducks and oyster catchers were often observed feeding at the edges of the mussel mat. If ducks are predators on *M. senhousia* (as has been reported for zebra mussels in the United States by Hamilton et al. 1994), they may be responsible for some of the observed changes to the shape of mussel mats. Patchy predation, however, is unlikely to cause major disruption to existing mats, as our small removal experiment did not result in appreciable changes to the surrounding mat. A larger disturbance would be necessary to cause the mat to disintegrate.

If biotic or abiotic disturbance does cause the mat to break into small pieces, it appears unlikely that resultant fragments could be transported and form new mats elsewhere. Our pilot experiment suggested that even quite large fragments would be readily swept away. The well-documented gregarious settlement and recruitment behaviour of *M. senhousia* is the more likely mechanism for the establishment of new beds. Because of the short lifespan of individual beds, this can only occur in areas with enough breeding adults to provide a sizeable pool of larvae.

Environmental impact

Previous authors have claimed that mussel mats suppress growth of other benthic animals in the same habitat and can exclude all underlying biota (Morton 1974; Willan 1987). Kikuchi & Tanaka (1978) found that high densities of *M. senhousia* corresponded to a drop in the number of infaunal species and Crooks (1992) reviewed several other Japanese studies which have noted the smothering effect of mussel mats. None of these studies, however, used quantitative comparisons between mussel mats and adjacent control areas. Our sampling showed a small but consistent effect on species richness and a much greater effect on species abundances (Fig. 5–7).

The existence of significantly more macrofaunal invertebrates outside mussel mats may be related to space or food. Because mussels are so dense within the mats, there is little physical space for other species to inhabit and only smaller species or those which are able to readily move through the byssal threads (e.g., errant polychaetes) can live in the habitat created by *M. senhousia*. In addition, the anoxic sediment trapped in or under mussel mats may not be a suitable environment for other animals. Small deposit feeders such as *Nucula hartvigiana* may be able to survive well in these conditions (Willan 1987; present study) but suspension feeders are not likely to fare so well. It may be impossible for most suspension-feeding bivalves to extend their siphons above the dense mats to feed (Chiba 1977), thus affecting their survival. Crooks (1992) experimentally demonstrated an adverse effect of *M. senhousia* on co-occurring suspension-feeding bivalves and he cites several Japanese studies that purportedly show similar effects. Our preliminary sampling showed fewer bivalves within mussel mats (Fig. 8), and Willan (1987) documented a reduction in abundance of *Xenostrobus pulex* in plots which *M. senhousia* had invaded.

Range expansion

Several marine organisms including *M. senhousia* are postulated to have arrived in New Zealand in ballast water (Nelson 1995). The Asian date mussel is a native of Japan, and shipping movements between Japanese ports and Auckland have increased markedly since 1970 (Nelson 1995). It is a well-known fouling organism in its native habitat, and has all the life history features that would predispose it to transoceanic dispersal in ballast water (Crooks 1996). It is now firmly established in the Auckland area (Creese & Hooker 1996; B. W. Hayward pers. comm.), and is likely to persist in this region although populations at specific sites may be quite ephemeral.

We postulate that the continued presence of *M. senhousia* in a region is dependent on the production of a large larval pool. *M. senhousia* spread rapidly in the Hauraki Gulf (Willan 1985, 1987), probably owing to the dispersal of larvae within the relatively enclosed waters of the Gulf. No persistent populations have become established outside the Auckland area in the past 15 years (Creese & Hooker 1996), and we contend that large, self-perpetuating populations are unlikely to spread to intertidal regions beyond Auckland. Although we failed to find subtidal populations in the channels of the Tamaki Estuary, subtidal populations have been recorded at depths to 8 m at other localities both within New Zealand (Willan 1987; Hooker & Creese 1995) and in other countries (Crooks 1992). It is possible that extensive populations exist subtidally; such populations could continue to provide the larvae required to establish new intertidal beds.

Where *M. senhousia* does occur intertidally, it has a detrimental effect on the existing sediment and infaunal assemblages (Morton 1974; Crooks 1992, 1996; present study). This effect is very localised, however, and only occurs when extensive beds are formed. Given the ephemeral nature of these beds, the environmental effects at any particular site are likely to be short-lived. Although the accumulated muddy sediments may persist for some time after the mussels have died, they too will eventually be washed away by tidal currents, as occurred at Cheltenham Beach. We conclude that *M. senhousia* will remain in the Auckland area. Its environmental effects, however, are likely to be local and short-lived rather than long-term and chronic, and the dramatic impacts caused by the ecologically similar zebra mussel in freshwater habitats in the United States are unlikely to occur in coastal habitats of New Zealand.

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