

Comparison of Early Life History of Native and Exotic Mytilids, *Musculista senhousia* and *Xenostrobus securis*, in the Brackish Lake Hamana, Japan

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Abstract: During the period 1991–1992, we examined temporal fluctuations in densities of the native and exotic mytilids *Musculista senhousia* and *Xenostrobus securis* in the brackish Lake Hamana on the Pacific coast of central Japan, using cohort separation of planktonic stages and benthic stages (*i.e.*, new settlers and small individuals). Temporal fluctuations in densities of both planktonic and benthic stages were similar between the two species. However, the densities of benthic stages were much higher for *M. senhousia* than for *X. securis*. There was a similar trend of variation in densities of benthic stages among sampling sites for each mytilid. This suggests that microhabitat separation of large individuals (≥ 1.0 mm in shell length) between these two species may be determined at the post-recruitment stage, when *X. securis* individuals with shell lengths of ≥ 2.0 mm probably immigrate into the study area from other areas.

Keywords: Mytilidae, *Xenostrobus securis*, *Musculista senhousia*, recruitment, larval supply, settlement

Introduction

Although estuarine and coastal ecosystems are the most heavily invaded systems in the world, the study of exotic species in these ecosystems has historically lagged behind that of terrestrial and freshwater ecosystems (Sakai *et al.*, 2001; Grosholz, 2002). Ecological interactions between native and exotic species may be direct (*e.g.*, predation, competition, mutualism) or indirect (*e.g.*, habitat alteration, habitat separation, cascading trophic interactions). Human-mediated introduction of exotic species, changes in habitat quality, and a broadened range of traits that lead to successful establishment may result in changes to the population and community structure of native ecosystems (Sakai *et al.*, 2001). In particular, invasions of dreissenid and mytilid bivalves have had serious impacts on native freshwater and estuarine/coastal ecosystems as well as commercial industries in many countries (see Gosling, 1992; Nalepa & Schloesser, 1992).

Most studies of these invasive bivalves have focused on competitive exclusion of native species (*e.g.*, Dexter & Crooks, 2000; Williams *et al.*, 2005). However, there have been few studies of the coexistence mechanisms of native and exotic bivalves sharing similar guilds, and little comparison of their ecological traits (Kennedy, 1976; Safriel & Sasson-Frostig, 1988; Braby & Somero, 2006; Fields *et al.*, 2006; Bownes & McQuaid, 2006, 2009).

Several studies have examined the co-existence of native and exotic mytilids. For example, in the waters of California in North America the exotic mussel *Mytilus galloprovincialis* is confined to more sheltered shores, where it has replaced the native mussel *M. trossulus*. However, the introduced species has not displaced another native, *M. californianus*, which is predominant on

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wave-exposed shores (Martel *et al.*, 1999; Braby & Somero, 2006; Fields *et al.*, 2006). Most studies have examined habitat separation of juveniles and adults comparing native and exotic mytilids from a physiological perspective (Kennedy, 1976; Braby & Somero, 2006; Fields *et al.*, 2006). There are few studies comparing the early life history of native and exotic mytilids (see Grosholz, 2002), although Bownes & McQuaid (2006, 2009) recently detailed the larval recruitment processes for the native and exotic mytilids *M. galloprovincialis* and *Perna perna* on the South African coast.

In the brackish Lake Hamana, located on the Pacific coast of central Japan, *M. senhousia* was the dominant organism on tidal flats, as well as on artificial hard substrates, when *Xenostrobus securis* was introduced in the late 1970s (Kajihara *et al.*, 1976; Kimura, 1994). Since then, these two mytilids have predominated on tidal flats and artificial hard substrates (Kajihara *et al.*, 1976; Abdel-Razek *et al.*, 1993a, b; Kimura, 1994).

The mytilid *M. senhousia* is native to coastal waters from southern Siberia through mainland China and Japan to southeastern Asia (Morton, 1974; Kimura & Sekiguchi, 1993). Individuals that were introduced to the Mediterranean, the Pacific coast of North America, and Australasia have established permanent populations that have had profound impacts on native ecosystems (Crooks, 1998). In Japan, *M. senhousia* is abundant in eutrophicated bays and estuaries along the coast from Hokkaido (northern Japan) to Kyushu (southern Japan). Another mytilid, *X. securis*, is exotic to Japanese coasts. It was probably introduced from Australia and/or New Zealand in the 1970s, but was initially erroneously identified as *Limnoperna fortunei kikuchii* (Kimura *et al.*, 1999). *Xenostrobus securis* was also introduced to Italy in the 1990s and to Spain and Korea in the 2000s (Lazzari & Rinaldi, 1994; Garci *et al.*, 2007; Kimura & Sekiguchi, 2009). *Xenostrobus securis* is now common and abundant alongside the native *M. senhousia* in eutrophicated bays and estuaries along Japanese coasts (Kimura *et al.*, 1999). These two mytilids are classified as obligate suspension filter feeders and are usually found on muddy sediments, where they often form characteristically large colonies or mats (Kimura, 1994).

Based on spatio-temporal fluctuations in densities of large individuals of *M. senhousia* and *X. securis* in Lake Hamana, Kimura & Sekiguchi (2009) found similarities in their life histories in the post-recruitment period (*e.g.*, the number, occurrence, and duration of benthic cohorts). However, they detected a microhabitat separation between large individuals of the two species on tidal flats, with *M. senhousia* found on muddy sediment and *X. securis* on hard substrates. Differences in microhabitat may allow the two mytilids to avoid ecological interactions during the benthic stages, thus allowing their coexistence on local spatial scales such as in Inohana Inlet within Lake Hamana.

Kimura & Sekiguchi (1994, 1996a) succeeded in culturing larval and post-larval stages of *M. senhousia* and *X. securis* in the laboratory, and they revealed marked differences in the morphology and early life histories (*e.g.*, larval growth, planktonic life period, and size at larval settlement and metamorphosis) of the two species. Therefore, by examining temporal fluctuations in the densities of different life stages (planktonic larvae, new settlers, and small and large benthic individuals) through frequent sampling and cohort separation, we can trace the early life history of the two species in the field. In particular we can investigate the roles that their larval recruitment processes (including larval settlement and post-settlement processes) play in establishing the microhabitat separation of large individuals of the two species.

Materials and Methods

Study area

The brackish Lake Hamana is located on the Pacific coast of central Japan (Fig. 1), covering a surface area of 74 km² with a mean depth of 7.2 m in the north and 2.5 m in the south. The lake

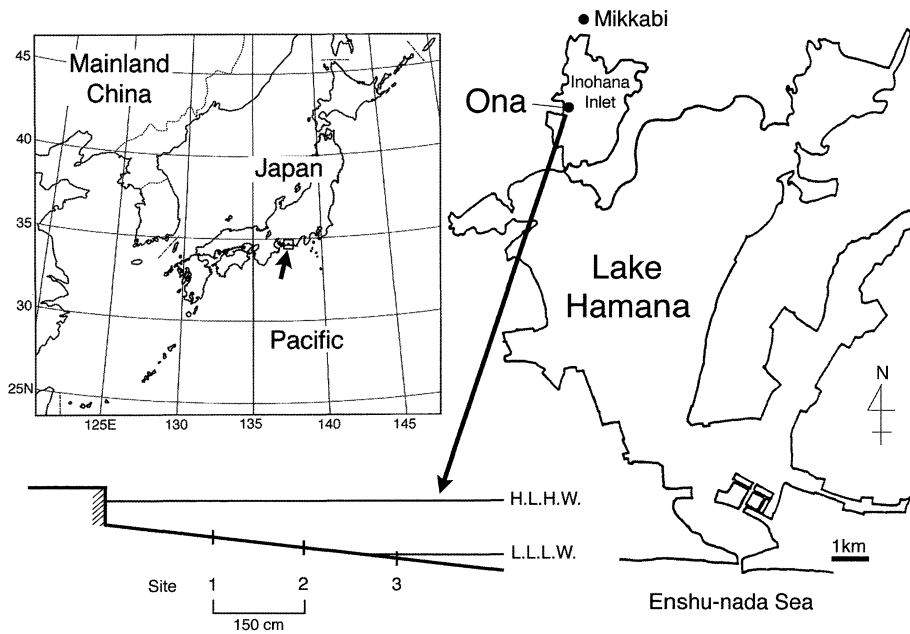


Fig. 1. Study area and sampling location within Inohana Inlet of Lake Hamana along the Pacific coast of central Japan.

is connected to the Enshu-nada Sea (north of the Kuroshio Current) through a passage 200 m wide and 3 m deep. The study area is located in the intertidal to subtidal zones of the Ona area within Inohana Inlet (one of several inlets within Lake Hamana) covering a surface area of 6.9 km² with an average depth of 5 m in the centre (34°78'N, 137°55'E). This inlet is located in the innermost part of Lake Hamana, and is connected with the other parts of the lake by a passage 100 m wide and more than 12 m deep (Fig. 1: Mazda, 1982; Fujimura & Mazda, 1983). A considerable area of Lake Hamana is occupied by floating cage systems for the cultivation of oysters, and the lake is also well-known for its clam fisheries (including *Ruditapes philippinarum*). However, eutrophication resulting from frequent discharges of towns around the semi-enclosed lake has caused the brackish water in the lake, including Inohana inlet, to become turbid. Red tides and oxygen-poor water just above the lake bottom have often been observed, particularly during the summer (Okamoto, 1995; Kimura & Sekiguchi, 1996b).

Our previous surveys of the spatial distribution of certain benthic individuals (the “large” cohort, defined as having shell lengths ≥ 1.0 mm) of *M. senhousia* and *X. securis* in the intertidal zone of Inohana Inlet (Kimura, 1994) revealed a high abundance of the two mytilids, which were the dominant benthic invertebrates. Relative abundance of *X. securis* varied considerably between sampling areas, although *M. senhousia* was much more abundant than *X. securis* within the present study area (*i.e.*, the Ona area). However, it was difficult to find any benthic organisms within the subtidal zone on the muddy sediment (which was often covered with oxygen-poor water) except within scattered wild oyster beds on the sediment (Kimura & Sekiguchi, 1996b).

To sample the benthic stages of the bivalves, we established sampling sites along a fixed transect line from the intertidal zone down to the upper subtidal zone within the Ona area. Site 1 was located in the upper intertidal zone (from H.L.H.W. to L.L.L.W.), Site 2 in the lower intertidal zone, and Site 3 in the subtidal zone (below L.L.L.W.) (Fig. 1). These sites have benthic sediments composed of fine sand/mud mixed-sediment gravels.

Sampling planktonic larvae and benthic stages of bivalves

We collected planktonic bivalve larvae in the intertidal to subtidal zones within the Ona area along the western coast of Inohana Inlet (Fig. 1) during low tide once a week from July 1991 to August 1993. A 100 L sample of surface shallow water was obtained to be filtered with a plankton net (with a mesh opening size of 0.044 mm). Samples were immediately fixed with 3% neutralized formalin-seawater and were kept in a refrigerator until microscopic examination. Bivalve larvae were identified at a species level according to the guidelines of Sakai & Sekiguchi (1992), Kimura & Sekiguchi (1994) and Kimura *et al.* (2004).

To sample the benthic stages of the bivalves, we set up three sampling sites (Sites 1 to 3) at intervals of 150 cm on a fixed transect extending from the intertidal zone down to the subtidal zone within the Ona area (Fig. 1). Once a week from July 1991 to August 1993, two samples of surface sediments were collected using a core sampler (covering a surface area of 9.6 cm², and a depth of 1.0 cm). Surface sediments were collected because both *M. senhousia* and *X. securis* dwell mainly on the sediment surface throughout their benthic stages. After filtering the sediments with a coarse mesh (1.0 mm mesh opening size) and then a fine mesh (0.125 mm mesh opening size), samples were fixed with 3% neutralized formalin-seawater mixed with Rose Bengal. All bivalve specimens remaining on the fine mesh were sorted under a stereomicroscope following Sakai & Sekiguchi (1990), and then identified at a species level according to Sakai & Sekiguchi (1992), Kimura & Sekiguchi (1994) and Kimura *et al.* (2004). Shell lengths of benthic individuals (see below for classification guidelines) of *M. senhousia* and *X. securis* were measured to the nearest 0.01 mm with a micrometer under a stereomicroscope.

Terminology

According to laboratory rearing experiments (Kimura & Sekiguchi, 1996a), planktonic larvae of *M. senhousia* and *X. securis* pass through trochophore and veliger larval stages (D-shaped larvae in the earlier period, and umboned larvae in the latter period) and settle at shell lengths of *ca.* 0.24–0.30 mm for *M. senhousia* and *ca.* 0.25–0.75 mm for *X. securis*. Larvae and new settlers of *M. senhousia* are clearly distinguishable from those of *X. securis* using several morphological characteristics. Following Miyawaki & Sekiguchi (1999) and Ishii *et al.* (2001a), we defined “planktonic larvae” as umboned larvae with shell lengths of greater than 0.15 mm but less than 0.25 mm (larvae with shell lengths of 0.3–0.75 mm were not detected in plankton samples), “new settlers” as benthic individuals with shell lengths of greater than 0.25 mm but less than 0.3 mm, “small individuals” as benthic individuals with shell lengths of greater than 0.3 mm but less than 1.0 mm, and “large individuals” as benthic individuals with shell lengths of greater than 1.0 mm. We also define “larval recruitment” to be when average shell lengths of individuals have reached greater than 1.0 mm, for each cohort.

Data analysis

We found similar trends in the densities of new settlers and small individuals of *M. senhousia* and *X. securis* between the two samples collected at each site, as well as among the three individual sampling sites, so these densities were averaged among the six samples. Using the above density data for the two groups (new settlers and small individuals) of the two species, we examined temporal fluctuations in their densities. We did not include the data for the densities of large individuals, due to the low numbers obtained in the samples, although we did use this data later for cohort separation. To account for the temporal fluctuations in their densities, we made the data sets including all density data of both new settlers and small individuals for six samples collected at three sampling sites on the same day, although density data were used for samples collected during the period of July to December (corresponding to the main spawning and recruitment season). Then, based on a general linear mixed model (GLMM) with a Poisson

distribution using the above data sets, we compared densities of new settlers as well as small individuals between the two mytilids, and also compared the densities of new settlers as well as small individuals between the two sampling years. Days and sites were incorporated as random variables, and species and years as fixed variables. The *lme4* libraries within the statistical software program R (version 2.8.1) were used for GLMM analyses, so that we could detect significant treatment differences ($P = 0.05$) for all models.

We examined differences in environmental conditions between the two years using a Wilcoxon signed rank test (StatView for Macintosh: version 5.0 in Japanese: HULINKS, Tokyo, Japan, significance level $P = 0.05$). In the present study, “Year 1991” indicates the period from July 1991 to June 1992, while “Year 1992” is from July 1992 to June 1993.

We compiled all shell length data of two groups (new settlers to small individuals, and large individuals) at the three sites for each species. On the basis of these shell length frequency histograms, we identified different cohorts according to the guidelines of Akamine (1985) and Aizawa & Takiguchi (1999), who separated polymodal distributions into multiple normal distributions to calculate the mean shell length and standard deviation of each cohort using MS Excel 4.0 for Macintosh. We estimated the growth curve of each cohort based on temporal changes in its average shell length.

Environmental conditions

We measured water temperature, salinity, and chlorophyll-a concentration in the surface water during low tide in the daytime once a week from July 1991 to August 1993, simultaneously with plankton sampling. Salinity was measured with a salinometer (TSK, Tsurumi Seiki Ltd., Yokohama, Japan). We measured the chlorophyll-a concentration ($\mu\text{g L}^{-1}$) following the procedure given by the Oceanographic Society of Japan (1990), after filtering 0.5 to 1.0 L surface water with a Whatman GF/C filter (mean pore size: 1.0 μm). Weekly rainfall data (mm week^{-1}) around the Ona area were obtained from the Mikkabi Weather Observatory in Hamamatsu City, located close to Lake Hamana (see Fig. 1 for location).

Results

Temporal fluctuation in environmental conditions

Temporal fluctuations in environmental conditions are shown in Fig. 2. Water temperature increased to $> 30^\circ\text{C}$ (with a recorded maximum of 33.6°C) from January to August, and then decreased to $< 10^\circ\text{C}$ (minimum of 6.9°C) toward February. Salinity ranged from 2.6 to 31.3; marked decreases in salinity were observed during and after rainfall exceeding 100 mm week^{-1} in spring and autumn, whereas salinity was almost stable in winter when rainfall was low. Seasonal and monthly fluctuations of chlorophyll-a concentration did not reflect changes in water temperature. Concentrations were very high, except for the period from March to June. Extraordinarily high concentrations exceeding $15 \mu\text{g L}^{-1}$ (usually defined as a red tide) were often detected from July to December, indicating severe eutrophication in the Inohana inlet.

Throughout the two year survey, mean environmental conditions and the range of 95% of all data were as follows: water temperature ($^\circ\text{C}$) 19.4, 7.7–31.7; salinity 21.7, 3.5–31.1; rainfall (mm week^{-1}) 46, 0–158; and chlorophyll-a concentration 7.5, 0.0–41.6 $\mu\text{g L}^{-1}$. There was no significant difference in any of these environmental conditions between the two years of the study (Wilcoxon signed rank test, $P > 0.05$).

Temporal fluctuation in densities of planktonic larvae and benthic stages of *Musculista senhousia* and *Xenostrobus securis*

Planktonic larvae: Larvae of *M. senhousia* were collected throughout the year from 1991 to

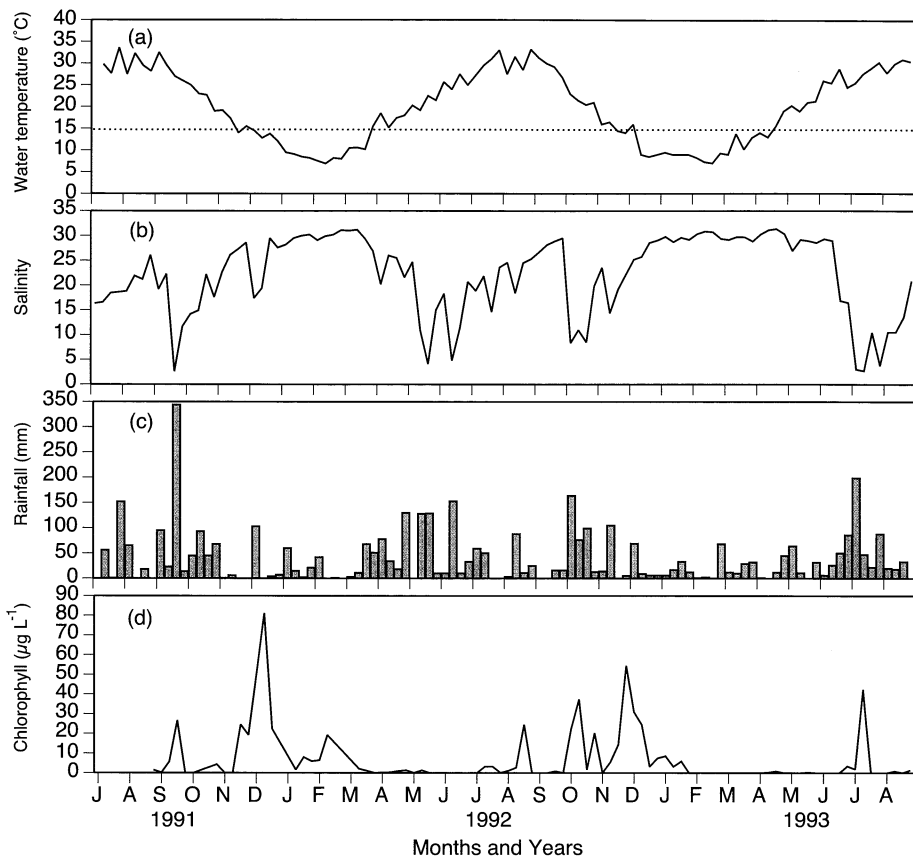


Fig. 2. Seasonal and inter-annual fluctuations in environmental conditions in Inohana Inlet, Lake Hamana: (a) water temperature, (b) salinity, (c) total rainfall per week, (d) chlorophyll-a concentration. The dotted horizontal line in the upper figure indicates 15°C; below this temperature, planktonic larvae of *Musculista senhousia* and *Xenostrobus securis* may not successfully settle (Kimura & Sekiguchi 1996a).

1992, except in February 1992 and January–May 1993 (Fig. 3). Pulse-like peaks of larval density were often detected in July to August each year; densities exceeding 100 ind. 100 L⁻¹ were detected from July to December 1991 and from July to August 1992, with the highest density observed in July 1991 (783 ind. 100 L⁻¹) and August 1992 (330 ind. 100 L⁻¹). This indicates that larvae with higher densities experienced water temperatures of 15–30°C and salinity of 2.6 to 30, often together with red tides. On days when a drastic decrease in salinity (< 10) was detected following higher rainfall, extremely low densities of larvae were collected. Furthermore, higher densities were detected over much shorter periods in 1992 than in 1991.

Seasonal and inter-annual fluctuations in the larval density of *X. securis* were similar to those of *M. senhousia*. Larvae of *X. securis* were collected from July 1991 to January 1992, from March to April 1992, and from July to December 1992 (Fig. 3). Pulse-like peaks of larval density were often detected during the above periods. Densities exceeding 100 ind. 100 L⁻¹ were detected from July to December 1991 and in July 1992, with the highest density in September 1991 (883 ind. 100 L⁻¹) and July 1992 (104 ind. 100 L⁻¹). These higher densities were detected over a much shorter period in 1992 than in 1991.

Pulse-like peaks of larval density of *X. securis* corresponded with those of *M. senhousia* (Fig. 3). There were significant differences in the larval density of both species between the two years

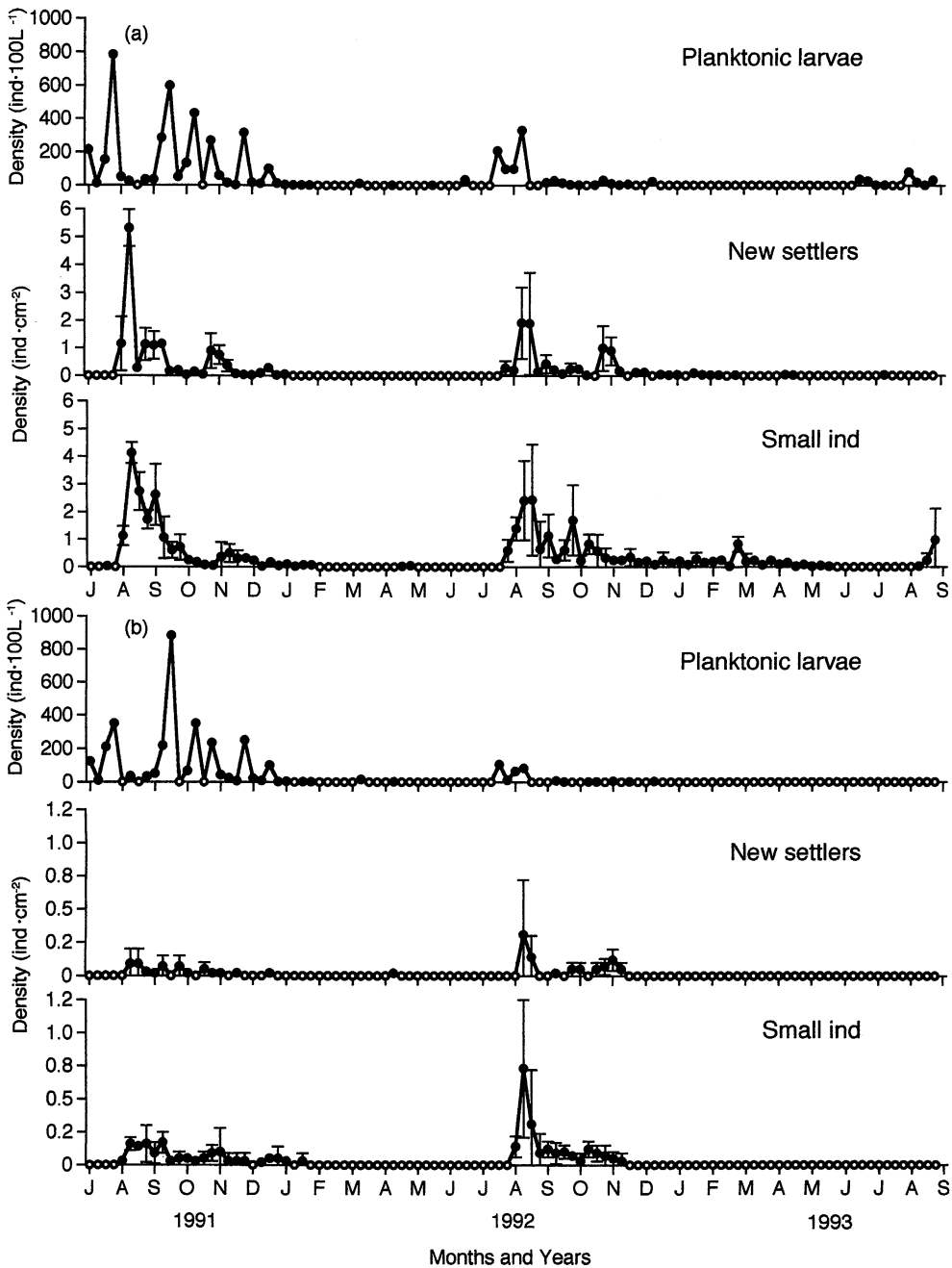


Fig. 3. Seasonal and inter-annual fluctuations in densities of planktonic larvae and benthic stages (*i.e.*, new settlers and small individuals) of (a) *Musculista senhousia* and (b) *Xenostrobus securis* in Inohana Inlet, Lake Hamana. Closed circles with vertical lines indicate the mean with standard deviation. Open circles indicate that no cohort individuals could be found for that month.

(GLMM, $P < 0.001$; Fig. 4): mean densities in 1991 were 4 times higher than those in 1992. On the other hand, significant differences were also detected in larval density between the two species (GLMM, $P < 0.0001$; Fig. 4). Mean densities of larvae of *M. senhousia* were 1.2 and 3 times than

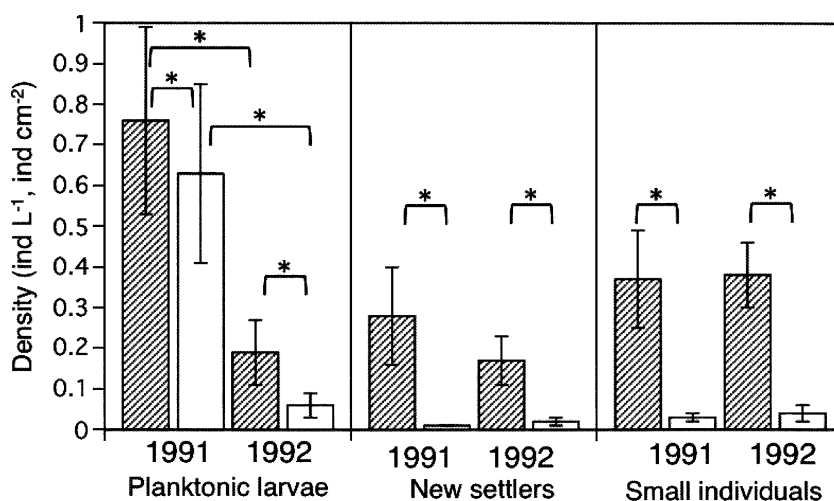


Fig. 4. Comparison of *Musculista senhousia* and *Xenostrobus securis* densities in Inohana Inlet, Lake Hamana during 1991–1992. Open and shaded columns indicate *M. senhousia* and *X. securis*, respectively. Columns with vertical line indicate the mean with standard error. An asterisk (*) indicates a significant difference ($P < 0.05$, GLMM).

those of *X. securis* in 1991 and 1992, respectively. There was a significant interaction between year and species (GLMM, $P < 0.0001$).

Benthic stages: New settlers of *M. senhousia* were collected throughout the year, except in July 1991 and from February to June 1992 (Fig. 3). Densities exceeding 1.0 ind. cm^{-2} (i.e., at the surface) were detected from August to September 1991 and in August 1992, although the highest density (1.9 to 5.3 ind. cm^{-2}) occurred in August of each year. Temporal fluctuation in the density of new settlers was similar to that of larval density (Fig. 3), but in contrast, densities of new settlers were much higher early in the main spawning season in 1991 and 1992. The situation was similar for small individuals (Fig. 3).

Seasonal and inter-annual fluctuations in new settler densities of *X. securis* differed from those of *M. senhousia*. New settlers were collected from August to December 1991 and from August to November 1992, with the highest density (0.09 to $0.31 \text{ ind. cm}^{-2}$) being in August each year (Fig. 3). Temporal fluctuation in the density of new settlers was similar to that of larval density (Fig. 3). However, the density of new settlers was extremely low, making it difficult to detect temporal trends. The situation was similar for small individuals (Fig. 3).

In contrast to the case of planktonic larvae, no significant differences were detected in the density of new settlers and small individuals of each species between the two years (GLMM, $P > 0.05$ and 0.05 , Fig. 4). However, there were significant differences in the densities of both new settlers and small individuals between two species (GLMM, $P < 0.0001$ and 0.0001 ; Fig. 4): the mean density of new settlers of *M. senhousia* was more than 15 times higher than that of *X. securis*, while the mean density of small individuals of *M. senhousia* was more than 10 times higher than that of *X. securis*. There was a significant interaction between year and species for both new settlers and small individuals for each species ($P < 0.0001$ and 0.0001).

Cohort separation of benthic stages of *Musculista senhousia* and *Xenostrobus securis*

For benthic individuals of *M. senhousia*, we identified 12 cohorts for 1991 and 10 for 1992 (Fig. 5). Based on survival and growth curves of the different cohorts, we found that half of the cohorts of both small and large individuals were not successful in larval recruitment through the

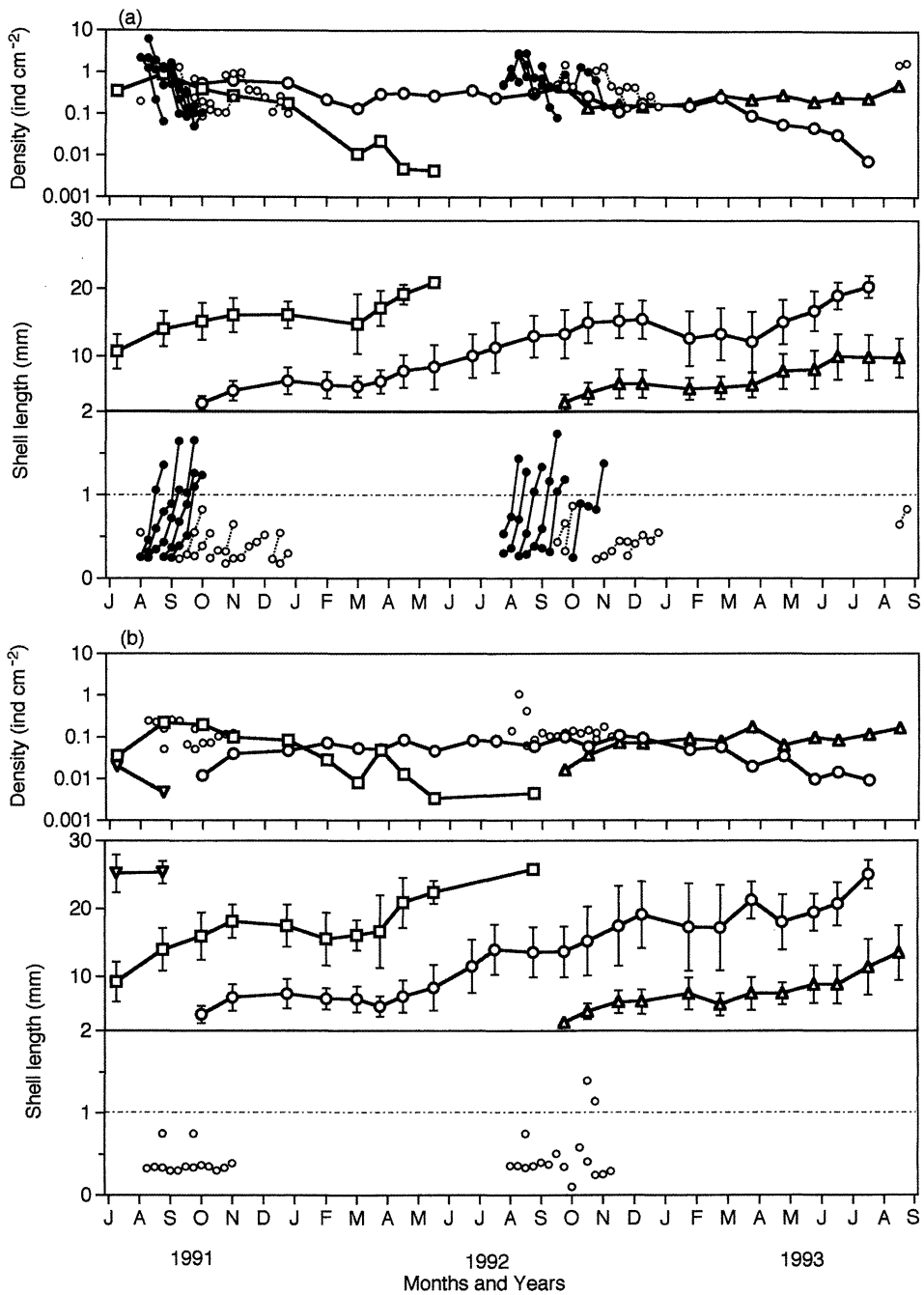


Fig. 5. Cohort separation and survival curves of (a) *Musculista senhousia* and (b) *Xenostrobus securis* benthic individuals in Inohana Inlet, Lake Hamana. Upper figures: survival curves of different cohorts with a logarithmic vertical axis. Lower figures: cohorts separated based on shell length frequency histograms, incorporating the data of post-settlement individuals with shell lengths ≥ 0.25 mm by Kimura & Sekiguchi (2009). Solid and open circles for individuals with shell lengths ≤ 2.0 mm indicate cohorts with and without successful larval recruitment, respectively. Symbols with vertical lines indicate the mean with standard deviation. Dotted horizontal lines indicate successful recruitment of different cohorts attaining 1.0 mm or more. Note the difference in the length scale of the vertical axis.

spawning period, as deduced from the occurrence of planktonic larvae. It is not immediately apparent why these cohorts experienced unsuccessful larval recruitment. New settlers and small individuals collected early in the main spawning season (August to September 1991 and July to September 1992) were successful in larval recruitment for both 1991 and 1992. From the growth curves of those cohorts successful in larval recruitment, we deduced that they reached an average shell length of ~1.0 mm a month after settlement. Based on the cohort separation illustrated in Fig. 5, few of those identified earlier as successful cohorts continued on to establish permanent populations. This was the case even for large individuals with shell lengths of 2.0 mm or more, although we detected one cohort each year of these large individuals. In *X. securis*, we failed to separate cohorts of benthic individuals because of their low densities.

Discussion

We collected larvae of *M. senhousia* at high densities (or with pulse-like peaks of density) from Lake Hamana mainly in summer to autumn, although they were also present throughout the study except in February 1992 and January to May 1993. Similar results were obtained for *M. senhousia* both in Ise Bay along the Pacific coast of central Japan and in the Ariake Sound in southern Japan (Kimura & Sekiguchi, 1993; Miyawaki & Sekiguchi, 1999; Ishii *et al.*, 2001b). However, new benthic cohorts of *M. senhousia* were established during the earlier spawning period when the water temperature was at 15°C or more (Fig. 5). This may be explained by the fact that these larvae have an optimum water temperature for growth during the early period of the main spawning season. According to Kimura & Sekiguchi (1996a), larvae of *M. senhousia* kept alive at 25°C or more grew fast and were successful in settlement/metamorphosis, whereas those kept at 15°C or less postponed metamorphosis, making it difficult to get successful recruitment. It is apparent that fluctuations in salinity and chlorophyll-a concentration did not synchronize with larval recruitment of *M. senhousia*, as we did not detect any correlation between environmental conditions and larval recruitment (see Figs. 2 and 5). However, the influence of environmental conditions on larval recruitment in *X. securis* is still uncertain.

For *M. senhousia*, as well as *X. securis*, it is interesting that the mean density of new settlers was lower than the density of small individuals each year (Fig. 4). No changes according to year in fluctuations in the density of either new settlers or small individuals of either species were detected. This trend of higher densities of small individuals than of new settlers may be due in part to our definition of new settlers and small individuals: the probability of sampling new settlers would be much lower than the probability of sampling small individuals, as the latter have a much longer benthic period.

Kimura & Sekiguchi (2009) found similarities in the life histories of *M. senhousia* and *X. securis* post-recruitment (*e.g.*, the number, occurrence, and duration of cohorts), yet they detected a microhabitat separation between large individuals of these two mytilids. Differences in microhabitat use may contribute to the avoidance of interspecific interactions during the benthic stages, thus allowing coexistence at a local spatial scale. In the present study, larval density was not markedly different between *M. senhousia* and *X. securis*, whereas the densities of their new settlers and small individuals differed greatly. This suggests that these mytilids may each have distinctive larval recruitment processes. Mean densities of new settlers and small individuals of *M. senhousia* were nearly 15 and 10 times higher, respectively, than the densities of new settlers and small individuals of *X. securis*.

Several alternative scenarios may explain the similar larval densities but much lower densities of new settlers and small individuals of *X. securis* compared with *M. senhousia*: (1) mortality rates at larval settlement were much higher for *X. securis*, and (2) larvae of *X. securis* delayed or canceled settling within the area sampled by the present study, perhaps due to it being unavailable,

preferring to disperse into other areas, while larvae of *M. senhousia* settled in the area sampled. It is not immediately apparent which scenario is more likely.

Unlike in the case of *M. senhousia*, we failed to separate cohorts of benthic individuals of *X. securis* because of their low densities. However, it is interesting that large individuals of *X. securis* with shell lengths ≥ 2.0 mm established benthic cohorts similar to those of *M. senhousia* in terms of number, occurrence and duration (Fig. 5), as indicated previously in Kimura & Sekiguchi (2009). Judging from the near absence of large individuals of *X. securis* with shell lengths of 1.0–2.0 mm (Fig. 5), new settlers and small individuals did not contribute to establishing permanent populations composed of large individuals with shell lengths ≥ 2.0 mm. This suggests that new settlers and small individuals either die without growing into large individuals or emigrate out of our study's sampled area.

Kimura & Sekiguchi (2009) found new cohorts of large individuals of *X. securis* (with shell lengths ≥ 2.0 mm) rather than new settlers to be abundant on artificial rock in our study area, whereas new settlers to large individuals of *M. senhousia* were found to be abundant on muddy sediment. Therefore, large individuals of *X. securis* may originate from other areas where they settled first, and then immigrate into the study area by drifting with byssus threads (e.g., Sigurdsson *et al.*, 1976; Lane *et al.*, 1985); this may be regarded as secondary settlement (Bownes & McQuaid, 2009). A different situation has been reported from the southern coasts of South Africa, where the exotic mussel *M. galloprovincialis* replaces the native *P. perna*: local coexistence of these two mytilids is due to differing importance of pre- and post-recruitment factors for each species (Bownes & McQuaid, 2006, 2009). Although secondary settlement does not occur in every bivalve species, or even in all members of the same species (see Seed & Suchanek, 1992), new settlers of most estuarine and coastal bivalves may pass through a secondary pelagic phase, also called the byssus drifting phase, during which time they detach from the original settlement substrate and may subsequently select sites of permanent attachment on adult beds (e.g., Sigurdsson *et al.*, 1976; Lane *et al.*, 1985).

In Inohana Inlet, *M. senhousia* and *X. securis* mainly inhabit the intertidal zone and, less frequently, the natural oyster reefs in the subtidal zone. In addition, there is an intensive system of oyster cultivation in operation, which uses floating structures between the sea surface and mid-water depths. Juveniles or adults of these two mytilids can easily colonize these floating systems and become abundant there as fouling organisms. Accordingly, there are three larval sources for these mytilids within Inohana Inlet: (1) from individuals living on tidal flats, (2) from individuals living on the floating oyster culture systems, and (3) through water exchange via the passage that links Inohana Inlet with the other parts of Lake Hamana. This situation will influence the sustainability and coexistence of the benthic populations of these two mytilids within the intertidal zone of Inohana Inlet.

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浜名湖における在来種ホトトギスガイと外来種コウロエンカワヒバリガイの 初期生活史の比較

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要 約

日本太平洋岸の汽水湖である浜名湖において、在来種ホトトギスガイと外来種コウロエンカワヒバリガイの浮遊幼生と着底稚貝の2年間にわたる高頻度の定量調査とコホート分析を行い、時間的変動を調査した。その結果、時間的変動傾向は浮遊幼生、着底稚貝とも2種間で類似していた。一方、密度は着底稚貝では大きな差がみられた。調査地点間では両種とも着底稚貝の密度は類似した傾向にあることから、2種の微小生息域の違いは加入以降に決定されると考えられた。また、コウロエンカワヒバリガイは大型個体の加入は見られているのにも関わらず、着底稚貝がほとんど観察されなかったことから、おそらく別の場所で2 mm以上の殻長に成長した後、調査地内に移動したと推察された。