Spatial, temporal and vertical variation of distribution and major habitats in Asian mussel (Arcuatula senhousia) in a brackish river along Sea of Japan

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Abstract: Spatial, temporal and vertical variation of distribution in Asian mussels (Arcuatula senhousia) were described via belt transect observations by scuba diving, and the mussel bed coverage in a brackish river was observed over a 3-year period (2012–2014). The spatial changes in the mussel bed distribution showed a similar pattern over the 3-year period: the mussel bed spread from the deeper part of the river toward the shallow part of the river. Temporal changes in the mussel bed distribution followed two patterns: one was expansion from spring to summer and retreat during autumn, and the other was expansion from late autumn to the following summer and retreat during autumn. The relationship between the mussel bed coverage and environmental parameters (salinity, dissolved oxygen, water temperature, and water depth) was determined using Pearson’s correlation analysis. To identify the major habitat of the mussels, the median values of environmental parameters were compared with six levels of biomass categories of the mussel bed coverage, by the Steel–Dwass test. We presumed that major habitats are found in areas with a salinity of 9.2–17.3. This result was obtained from continuous field data (e.g., mussel distribution, water environments, and depth) indicating that caused by the patchy spatial and temporal distribution of the mussel.

Key words: Arcuatula senhousia, major habitat, mussel bed coverage, water environment

Introduction

The Asian mussel, Arcuatula senhousia (Benson, 1842), is a small mytilid bivalve with a thin shell that is native to Asia and distributed in the western Pacific, i.e., China, Singapore, Korea, Japan, and the Kurile Islands (Yoshida 1937, Morton 1974, Chiba 1977). This mussel is a highly invasive species that has recently successfully colonized numerous areas in the world, e.g., Oceania, western North America, Northern Atlantic, and Mediterranean Sea (Wyllan 1985, 1987, Hoenselaar & Hoenselaar 1989, Charles 2007, Crooks 1996, Lazzari & Rinaldi 1994, Mistri 2002, 2003, Mastrootaro et al. 2004, Mistri et al. 2004, Munari 2008, Despalatović 2013). The mussels inhabit intertidal and shallow subtidal soft or hard substrata of estuaries and sheltered bays (Morton 1974, Slack-Smith & Brearley 1987) and form nests with their byssal threads. As they multiply, they weave themselves together and construct a mussel bed (Morton 1974; Crooks 1996). The sediment beneath the mussel bed is muddy due to the accumulation of the mussel excrement (Morton 1974, Ito & Kajihara 1981). Shallow-burrowing bivalves (e.g., Chione spp. and Macraa veneriformis) are more sensitive (with respect to growth and mortality) to changes in mussel beds than are the deep-burrowing bivalves (e.g., Macoma nasuta and Ruditas philippinarum) (Crooks 2001, Mistri 2003, 2004, Tsutsumi et al. 2013). The populations of commercially important clams, such as R. philippinarum, Scapharca kagoshimensis, Meretrix lusoria, and Corbicula japonica

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have decreased significantly due to choking when dense mussel beds cover the bottom substratum (Uchida 1965, Chiba 1977, Miura et al. 2002). Miura et al. (2002) were concerned that occasional outbreaks of *A. senhousia* caused serious damage to *C. japonica* because of the difficulty in predicting the mussel distribution in upstream reaches of the Ohashi River.

Further study of the major habitats of *A. senhousia* is required to predict mussel outbreaks and take appropriate measures before other species are affected. Inglis et al. (2006) created a habitat suitability index (HSI) model of *A. senhousia* to speed up the discovery of its invasion and to predict its distribution. Their method was not successful because the distribution of the mussels was both spatially and temporally patchy. The errors caused by the spatially patchy distribution of this mussel were also reported by Hosozawa et al. (2015). Based on these studies, it is clear that patchy distribution of the mussel is a central problem that must be overcome in order to accurately compare with the mussel distribution and environmental parameters. Therefore, it is necessary to obtain both spatially and temporally continuous field data (e.g., mussel distribution, water environments, and depth) to understand the major habitats of the mussel.

The Ohashi River is a brackish river located in southwest Japan on the coast of the Sea of Japan; it links the upper oligohaline Lake Shinji to the lower polyhaline Lake Nakaumi. The river has a small tidal range, and the tidal flats are very narrow. Although the mussels habitats are limited to subtidal riverbeds, the population density of mussels in the Ohashi River is greater than that in other areas (e.g., Hosozawa et al. 2015, Takenaka et al. 2016, Kurata et al. 2018), and the river exhibits large fluctuations in water environments (salinity and dissolved oxygen) and mussel distribution (Hosozawa et al. 2015). Thus, the Ohashi River is ideal for studying the relationships between water environments and mussel population dynamics.

In this study, the belt transect was performed by scuba diving in order to describe spatial and temporal changes in the distribution of *A. senhousia* and the mussel bed coverage was categorized using quadrats. Quadrat methods, such as Braun-Blanquet cover-abundance scale method, have been widely employed for vegetation analysis on land (e.g., Douglas et al. 1978, Rossen et al. 2009). However, quadrat sampling was not carried out in this study because of the large amount of effort required for continuous quadrat sampling both on spatial and temporal scales for a long period. Data of the distribution of *A. senhousia* were continually obtained via belt transects, and the relationship between their coverage and environmental parameters was analyzed to determine the major habitats of *A. senhousia*.

**Materials and Methods**

**Study site**

This study was carried out in the Ohashi River, a brackish river in Southwest Japan. The river is 7.6 km long and ~170 m wide. It links the upper oligohaline Lake Shinji to the lower polyhaline Lake Nakaumi (Fig. 1). Waters from the upper and lower lakes mix in the Ohashi River under

![Fig. 1](#) Location of the Ohashi River and study sites. Two cross sections, Line A and Line B, were located approximately 6.8 km and 4.1 km from the river mouth, respectively. Two observation stations were located near the two cross sections in the upstream (6.8 km from the river mouth) and middle-section sections of the river (3.8 km from the river mouth).
the influence of wind, runoff, tides, and internal oscillations. Water from the middle part of Lake Nakaumi generally flows toward the Ohashi River; however, in summer, highly saline and hypoxic water in deeper parts of Lake Nakaumi frequently flows toward the Ohashi River (Fujii et al. 2006, Izumo River Office 2009). Salinity, water temperature, and dissolved oxygen are automatically measured at 15-min intervals at several depths in three stations along the river that are maintained by the Izumo River Office of the Ministry of Land, Infrastructure, Transport, and Tourism of Japan (MLIT). The average salinity of Lake Nakaumi is 24.8 in the lower layer (ranging between 13.3 and 31.8) and 15.2 in the upper layer (ranging between 2.0 and 25.2) (Izumo River Office 2009).

Field observations

To examine the spatial and temporal changes in mussel bed coverage, two cross sections, Line A and Line B, were randomly selected close to the observation stations of water environments along the Ohashi River (Fig. 1). Line A was in the upstream part of the river, and Line B was in the middle part of the river. The belt transect was performed by scuba diving to obtain spatially continuous data of the mussel bed coverage. The transects were composed of 1 m² quadrats consecutively laid from the left side of the river to the right. In this method, we defined the six categories of mussel bed coverage based on percentage cover (Table 1), by reference to the Braun-Blanquet cover-abundance scale method. The mussel bed coverage was recorded for each 1 m² quadrat for every observation. Spatial distribution data were obtained along the transect lines. Vertical distribution data were obtained from mean cover area per square meter at one-meter water depth intervals (Fig. 2). The water depth was also measured in every quadrat using a scuba depth gauge. The species name and number of predators observed alongside a mussel bed, such as the red stingray (Hemitrygon akajei), were recorded. Field observations were carried out at approximately one-or two-week intervals from May to December in 2012, 2013, and 2014.

Water environment data

Data of the water environments (salinity, water temperature, and dissolved oxygen) were obtained from two stations near the two cross sections, i.e., stations in the upstream and middle sections located 6.8 km and 3.8 km, respectively, from the river mouth (Fig. 1). The data were obtained at depths (Depth are represented relative to TP. TP is the mean sea level in Tokyo Bay Japan) of 0, 0.5, 1.0, 1.5, 2.0, 2.5, 3.0, and 3.5 m at the upstream station, and at depths of 0.5, 3.5, and 4.8 m at the middle-section station. The 14-day moving average of the daily mean of the water environments was used for data analysis. If any data were missing or the data acquisition rate was <50% over a 14-day period, the corresponding data were excluded from the analysis.

Data analysis

The median value of each category was used for statistical analysis as actual number of the mussel bed coverage (Table 1). The mean cover area per square meter at each 0.5-m depth interval was calculated to analyze the relationship between the coverage and the corresponding water environments (Fig. 2). Pearson’s correlation analysis was used to determine the correlation between the mussel bed coverage and salinity, dissolved oxygen, water temperature, and water depth. To identify the environmental conditions under which there is a high coverage of the mussel bed, the median values of the environmental pa-

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**Table 1.** The category of the mussel bed covering and median value of cover area per one quadrat.

| Categories | The mussel bed covering percentage | Median value of coverage per one quadrat (m²) |
|------------|-----------------------------------|-------------------------------------------|
| 1          | ≥75                               | 0.875                                     |
| 2          | 50–<75                            | 0.625                                     |
| 3          | 25–<50                            | 0.375                                     |
| 4          | 1–<25                             | 0.130                                     |
| 5          | <1                                | 0.005                                     |
| 6          | Absent                            | 0                                         |

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**Fig. 2.** Data acquisition along the transect line. The transects were composed of 1 m² quadrats consecutively laid from the left side of the river to the right. Spatial distribution data were obtained along the transect lines. Vertical distribution data were obtained from mean coverage per square meter at one-meter water depth intervals.
rameters were compared for the six categories using the Steel–Dwass test for multiple comparisons. All the data were analyzed using R ver. 2.81 (R Development Core Team, 2008).

Results

Relationship between the coverage of *A. senhousia* and environmental parameters

The relationship between the mussel bed coverage and environmental parameters (salinity, dissolved oxygen, water temperature, and water depth) were obtained via the Pearson's correlation coefficient test ($P<0.05$, $N=339$). The mussel bed coverage was found to be moderately related to the depth ($r=0.49$) and salinity ($r=0.36$) (Table 2). The relationship between mussel bed coverage and dissolved oxygen was weak ($r=-0.27$) and between mussel bed cov-

| Coverage | Salinity  | Dissolved oxygen | Water temperature | Water depth |
|----------|----------|------------------|-------------------|------------|
| 0.36     | -0.27    | 0.18             | 0.49              |            |

Table 2. The relationship between the mussel bed coverage and environmental parameters (salinity, dissolved oxygen, water temperature, and water depth) which obtained from coefficient of Pearson's correlation test ($P<0.05$, $N=339$).

Fig. 3. Environmental variables measured on the river bottom from January 2012 to December 2014: A) salinity, B) water temperature, and C) dissolved oxygen. Thick gray line: the moving 14-day average at the upstream station; Thin black line: the moving 14-day average at the middle-section station; Cross mark: the daily mean value at the upstream station; Open circle: the daily mean value at the middle-section station.
Major habitats in *Arcuatula senhousia*

Daily and seasonal fluctuations of water environments are shown in Figure 3. The seasonal fluctuations in the salinity were unclear, but they tended to be higher in summer and lower in spring. The maximum and minimum salinity along Line A (in the upstream part of the river) were 27.1 and 1.3, respectively, and those along Line B (in the middle part of the river) were 27.1 and 1.4, respectively (Fig. 3A). These ranges of the salinity values were of the same degree; however, the moving 14-day average of salinity at the middle-section station was generally higher than that at the upstream station (Fig. 3A). As expected, there was a clear fluctuation in water temperature over the year, with water temperatures peaking in summer (August) reaching a minimum in winter (January–March). The maximum and minimum water temperatures at the upstream station were 32.3°C and 2.6°C, respectively, and those at the middle-section station were 32.6°C and 3.4°C, respectively (Fig. 3B). There were also temporal fluctuations in the amount of dissolved oxygen, i.e., it was higher in winter and lower in summer. The maximum and minimum values of the amount of dissolved oxygen at the upstream station were 13.9 mg L\(^{-1}\) and 0.5 mg L\(^{-1}\), respectively, and those at the middle-section station were 13.4 mg L\(^{-1}\) and 0.3 mg L\(^{-1}\), respectively (Fig. 3C). The hypoxic conditions (dissolved oxygen concentration \(\leq 2\) mg L\(^{-1}\)) were often observed in warmer seasons; especially in July-August 2013.

**Spatial and temporal distribution of *A. senhousia***

The cross-sectional terrains were obtained based on the average water depth in each quadrat and distance from the left side of the river (Fig. 4). The river width for Line A and Line B was 155 m and 100 m, respectively. The maximum depth of Line A was 4.5 m and of Line B was 5.0 m. The right end of Line A was a constructed river wall (Fig. 4A).

Spatial distribution of *A. senhousia* over times is illustrated in Fig. 5. The mussel beds were formed only in 2013 (not in 2012 or 2014) for Line A (Fig. 5A, C, E), whereas for Line B, they formed in 2012, 2013, and 2014 (Fig. 5B, D, F). In the case of Line A, the mussel beds expanded from May to September and retreated from late September to December. The maximum width of the bed with high coverage (\(\geq 75\%\) cover) for Line A was 65 m in July 2013 (Fig. 5C). Beds with a higher coverage (50–<75% or \(\geq 75\%\)) were concentrated in the deeper parts of the river (Fig. 4A, 5C). In the case of Line B, the mussel beds expanded from late October 2012 to July 2013 and retreated from September to December 2013 (Fig. 5B, D). Then, the mussel beds expanded from May to July 2014 and retreated in December 2014 (Fig. 5F). The maximum width of the bed with high coverage for Line B was 65 m in December 2012, 82 m in July 2013, and 60 m in July 2014 (Fig. 5B, D, F).

The river bottom along Line A was composed of sand or muddy sand, and along Line B the river bottom was composed of muddy sand. In places where there were mussel beds, the sediment under the bed changed to muddy. However, following the retreat of the mussel beds, the mud was washed away, and sediment returned to normal. Predatory species were observed only once; one *H. akajei* was observed along Line A in September 2013.

**Vertical distribution of *A. senhousia***

The mussel bed cover area increased at all water depths (0–5 m) in 2013 along Line A and Line B, whereas the cover area only increased at greater depths (3–5 m) in 2012 and 2014 along Line B (Fig. 6). The increase and decrease in the bed cover area at the greatest depths (4–5 m) began earlier than those in the shallower areas in 2013 along Line A and Line B (Fig. 6A, C). Along Line A, the mussel bed cover area increased from spring to summer in 2013, peaking in July at the greatest depth (4–5 m), decreasing in autumn, and disappearing in late autumn (Fig. 6A). However, along Line B, the mussel bed cover area increased from autumn 2012 to summer 2013 (Fig. 6B, C) or spring to summer 2014 (Fig. 6D), peaking in June-August 2013 and in July 2014 at the greatest depth (4–5 m), decreasing in September 2013 and December 2014, and disappearing in winter (Fig. 6B–D). The mussel bed cover area along Line B increased significantly from autumn to winter in 2012. During this period, highly saline and non-hypoxic water

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**Fig. 4.** River cross section along Line A and Line B. A) the river along Line A was 155 m wide and 4.5 m deep at its deepest point; B) the river along Line B was 100 m wide and 5.0 m deep at its deepest point. The right end of Line A was a constructed river wall.
Fig. 5. Spatial and temporal changes in the distribution of *A. senhousia* along Line A and Line B: A), B), and C) Line A in 2012, 2013, and 2014, respectively. D), E), and F) Line B in 2012, 2013 and 2014, respectively. The gray-scale indicates the mussel bed coverage (percentage cover).
was observed in the bottom layer of the middle-section station (Fig. 3A, C).

**Ranges of environmental parameters for high coverage of *A. senhousia***

The results of multiple comparison tests are shown with the box plots of the environmental parameters (salinity, water depth, dissolved oxygen, and water temperature) among six categories of mussel bed coverage (Fig. 7). The median value of salinity was significantly higher for the high coverage categories (category 1 and category 2) than for categories 3–6. The median value of the salinity was 15.6 with an interquartile range of 12.8–17.3 for category 1, and 10.9 with an interquartile range of 9.2–14.5 for category 2 (Fig. 7A). There was a significant difference in the median value of the water depth between category 1 and all the other categories; the median value was 5.0 with an interquartile range of 3.5–5.0 m for category 1 (Fig. 7B). There were no significant differences in the median values of the amount of dissolved oxygen (Fig. 7C) and water temperature (Fig. 7D) among the six categories.

**Discussion**

There were two patterns observed in the temporal changes in the mussel bed distribution: one pattern was expansion from spring to summer and retreat during autumn (e.g., in 2013 along Line A and in 2014 along Line B) and the other was expansion from late autumn to the following summer and then retreat during autumn (e.g., from 2012 to 2013 along Line B) (Figs. 5 & 6). In general, the expansion of bivalve populations is discussed based on its recruitment, growth, and water temperature. In previous studies of *A. senhousia*, the expansion of the mussel bed have been explained based on the growth of individuals during the warm season in the Ohashi River (Hosozawa et al. 2015) and the population dynamic was explained based on recruitment throughout the year in Lake Nakaumi (Yamamuro et al. 2003). It is important to note that larvae of the mussels cannot settle at temperatures below 15°C, and this prevents expansion of the colony, although the population is maintained during the winter (Kimura & Sekiguchi 1996, 2012). In addition, Lee et al. (1983) reported that adult individuals could survive at temperatures as low as 0.6°C. These results suggest that water temperature is a good indicator of settlement. At our study sites, the water temperature was less than 15°C from November to May (Fig. 3). Thus, it was considered that *A. senhousia* could recruit from May to November at these sites. Although the water temperature was suitable for mussel recruitment, mussel beds were not observed in 2012 and 2014 along Line A and from May to October 2012 along Line B. These results indicate that environmental parameters other than temperature affect mussel recruitment.

The spatial changes in the mussel bed distribution showed a similar pattern, i.e., the mussel bed spread widely from the deeper part of the river toward the shallow edges of the river (Fig. 5). The mussel bed cover was higher in deeper parts of the river, and the mussel beds in deeper parts developed earlier than those in shallower parts in 2013 (Fig. 6). At our study site, highly saline water advances toward the Ohashi River from Lake Nakaumi (e.g., Fujii et al. 2006, Izumo River Office 2009). Hence, the salinity in the middle-section of the river was slightly higher
than that upstream (Fig. 3A). Along Line B, the occurrence of mussel beds in autumn was observed only in 2012, and during this period, the salinity in the middle-section of the river was higher than that in 2013 and 2014 (Fig. 3A). These results indicate that the mussel beds spread from areas of high salinity in deeper parts of the river.

However, a decrease in the mussel bed coverage was observed from the deepest part to shallower parts in 2013 (Fig. 6A, C). In previous studies, declining mussel populations have been attributed to decreases in salinity caused by floods in warm seasons, hypoxic water in summer, physical destruction caused by floods in warm seasons, high temperatures in summer, and predation by winter ducks (e.g., Yamamuro et al. 2003, Hosozawa et al. 2015). In this study, it is considered that the mussel beds decreased as a result of hypoxic water in the summer of 2013, as the decrease started from deeper parts, and the low salinity during autumn in 2013 and 2014, as shown in Fig. 3A. It is considered that the amount of dissolved oxygen was related not only to the mussel bed distribution, but also to the water depth and salinity. As shown in Table 2, the correlation between depth and salinity was moderate. The amount of dissolved oxygen was weakly related to the depth and salinity, but strongly negatively related to temperature. These results indicate that the decrease in the amount of dissolved oxygen occurs in warmer seasons in deeper and more saline parts of the river.

The warmer season is beneficial for mussel growth, but hypoxic conditions are detrimental to mussel survival (Hosozawa et al. 2015). Nakamura et al. (1997) revealed the weak tolerance of *A. senhousia* to hypoxic water (dissolved oxygen concentration ≤2 mg L⁻¹), as the species died within three days in anoxic water. In addition, *A. senhousia* population density was reduced as a consequence of continuous hypoxia in the deepest waters during the summer in the Honjo Area of Lake Nakaumi (Yamaguchi,...

Fig. 7. The results of multiple comparison tests of the environmental parameters among six categories of mussel bed coverage: A) salinity, B) water depth, C) dissolved oxygen, and D) water temperature in each mussel bed coverage category. ***: a significant difference; NS: non-significant difference between categories using the Steel–Dwass test (*P*<0.05).
et al. 2013). It is also reported that seasonal hypoxia negatively affected the benthic community, e.g., community defaunation and alteration, loss of biodiversity, etc., in subtidal and intertidal habitats (Kodama et al. 2010, 2012, Kanaya et al. 2015). At our study sites, some hypoxia conditions (e.g., dissolved oxygen concentration ≤2 mg L⁻¹) occurred frequently in summer, which corresponded to a decrease in mussel bed coverage (Figs. 3C, 5C, 5D, 6A, 6C). Despite this decline, the mussel beds did not disappear entirely in the summer. This indicates that the mussels were able to survive under hypoxic or anoxic conditions to some extent. The weak correlation between the amount of dissolved oxygen and mussel bed coverage in our study may be caused by the tolerance of the mussels to hypoxia. Therefore, it is considered that salinity and water depth are significant parameters that determine the major habitat of mussels in this study.

The mussel beds tend to be more abundant in deeper parts of the river (Fig. 5). The median salinity values for category 1–2 were significantly higher than those for categories 3–6. The median value of the salinity was 15.6 with an interquartile range of 12.8–17.3 for category 1, and 10.9 with an interquartile range of 9.2–14.5 for category 2 (Fig. 7A). The water depth for category 1 was significantly greater than that for other categories, and the interquartile range was 3.5–5.0 (Fig. 7B). These results indicate that the salinity conditions in deeper parts of the Ohashi River were more suitable for the mussels. Therefore, major habitats of mussels can be assumed to be found in areas with a salinity range of 9.2–17.3. This assumption is supported by a previous study that reported a salinity range of 10.46–16.87 based on a short-term field survey that examined mussel growth and survival (Chiba 1977). However, the limits of salinity tolerance were reported to range from 7 to 40 (Chiba 1977, Guan et al. 1989, Nakamura et al. 1997, Liang et al. 2009). Despite their high salinity tolerance, the major habitats of mussels can be presumed to be found in areas with a salinity range of 9.2–17.3. This assumption is supported by a previous study that reported a salinity range of 10.46–16.87 based on a short-term field survey that examined mussel growth and survival (Chiba 1977). However, the limits of salinity tolerance were reported to range from 7 to 40 (Chiba 1977, Guan et al. 1989, Nakamura et al. 1997, Liang et al. 2009). Despite their high salinity tolerance, the major habitats of mussels in the present study appear to be in areas with a salinity at the lower end of the range.

Several previous studies have suggested that predators contribute to A. senhousia invasion prevention on the local scale (e.g., Reusch 1998, Crooks 2002, Kusner & Hovel 2006). Some species of carnivorous gastropods, crustaceans, echinoderms, fish, and diving ducks are known to feed on A. senhousia (Matsui et al. 1986, Yamamura et al. 1998, Crooks 2002, Kobayashi 2013). Many of these predators inhabit sea or polyhaline water areas. The upper layer of Lake Nakaumi and lower layer of Ohashi River are usually mesohaline and the lower layers become hypoxic in summer; hence, most of these species of carnivorous gastropods and crustaceans are largely absent in the Ohashi River, and they probably have an insignificant role in influencing mussel population density. Among them, two predators, a Leucosid crab, Philyra pisum, and the red stingray (H. akajei), are distributed in areas with brackish water, i.e., Lake Nakaumi, Ohashi River, and Lake Shinji (Izumo River Office 2009); however, except for one sight-

ing of H. akajei, we did not observe any predators. We do not have detailed data to discuss this further, but it is suggested that the predators had a smaller effect in low-salinity areas than in high-salinity areas. Thus, the major mussel habitats were presumed to be found in the salinity range of 9.2–17.3 as the result of this study.

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