Selectivity on Salinity of Asiatic Brackish Clam Larvae, *Corbicula japonica* Prime, 1864

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Abstract: Selective behaviors in salinity variations of *Corbicula japonica* larvae were experimentally studied with vertical salinity gradients in glass cylinders. Experiments were conducted in dark and illuminated conditions at 7 stages (16, 25, 47, 68, 141, 213 and 309 hours after fertilization). Larvae were active in selecting specific ranges of salinity that changed along developmental stages. Early straight-hinge larvae (25 and 47 hours after fertilization) selected high salinities (15.21–19.21 psu on average) while late straight-hinge larvae (68 hours after fertilization) selected moderate salinities (13.45–14.29 psu). Postlarvae (141 and 213 hours after fertilization) selected low salinities (6.44–11.38 psu). When downward illuminations were given from the water surface, larval aggregations were formed in higher layers than in dark conditions. At 309 hours after fertilization, postlarvae did not form clear aggregation, and some individuals were found settling on the bottom.

Key words: clam, *Corbicula japonica*, larvae, locomotion, salinity

INTRODUCTION

Some varieties of marine benthos have pelagic larval stages in their early life histories. When the community on the substrate is not saturated with new settlers, settlement rate of larvae can be a key factor in the population demography and the community process (Roughgarden et al. 1985; Lewin 1986; Underwood & Keough 2001). For marine sessile organisms, larval dispersal is an important strategy in the population maintenance. Distributional and recovery potentials of populations with pelagic phases have been stressed in the classic literature (e.g. Thorson 1950; Mileikovsky 1971). On the other hand, the offshore transport of larvae increases spatio-temporal uncertainty in larval recruitments. Coe (1956) noted that the larvae of a bivalve, *Donax gouldi*, from Californian beaches have little chance to settle comparatively near their birthplaces. Uncertainties in recruitments of marine resource organisms lead to socioeconomic difficulties in coastal management policies. Some environmental economists are discussing the bioeconomic roles of the source-sink structure, metapopulations (e.g. Die & Watson 1992; Sanchirico & Wilen 2001; Hannesson 2002; Smith & Wilen 2003; Janmaat 2004; Sanchirico 2005).

Larval transports from the source to the sink population are crucial information when spatial arrangements and feasibilities of marine reserves are to be examined. Likewise, when the source and the sink population have considerable overlap, the larval recurrence to birthplaces is significant in reproductive processes. Although pelagic larvae seem to be transported passively in the current, some pelagic larvae have behavioral and mechanical properties in adaptive manners. Coastal polychaetes, *Owenia fusiformis* and *Pectinaria koreni*, control larval vertical distribution patterns in the stratified water helping their recurrence to the birthplaces in the estuary (Thiebaut et al. 1992, 1996). The estuarine crab larvae, *Rhithropanopeus harrisii*, vertically migrate to the depth where no net flow exists (Cronin 1982). Some estuarine bivalve larvae exhibit behavioral selectivity on salinity that facilitates the upward transport of larvae in flood tides (Haskin 1964; Wood & Hargis 1971; Young 1995). Thus, vertical locomotion triggered by environmental cues has determinative effects on the fate of pelagic larvae.
larvae.

An Asiatic brackish clam *Corbicula japonica* Prime, 1864 is one of the three Japanese endemic species in this genus. While other 2 freshwater species, *C. leana* Prime and *C. sandai* Reinhardt, have viviparous and direct reproductive modes, respectively (Ikematsu & Yamane 1977; Shiga Pref. Fish. Exp. Stn. 1996), this species uniquely lives in brackish waters and has pelagic larval phases. Because *C. japonica* is a major resource for clam fisheries in Japan, research on the early life history of the clam is a crucial research task. Tanaka (1984) reported that spawning of this clam occurs in summer, and larvae spend 6 to 10 days as plankton when reared in 26–30°C.

In the present study, we aimed at describing the ontogenetic changes in the selectivity on salinity in *C. japonica* larvae to discuss the behavioral adaptation to hydrodynamic conditions in estuaries because vertical locomotion in stratified water has significant effects on horizontal transport of larvae. *C. japonica* predominates in upstream areas of estuaries. Mizuno et al. (2005) reported that this clam occurred abundantly at 12 km upstream of the Kiso River. In such upstream localities, salinity and tidal forces are relatively low compared to downstream areas in estuaries. It is likely that *C. japonica* larvae have sensitive modes responding to salinity variations, and this species could be a good material for studies on salinity selectivity in bivalve larvae. Our experiments were conducted in both dark and illuminated conditions to assess the effect of light on larval behaviors.

**MATERIALS AND METHODS**

**Description of the habitat site**

Lake Hinuma is a small, 20 km², brackish lagoon along the Pacific coast of Japan, N 36°16’, E 140°30’ (Fig. 1). This lagoon is located in the downstream of the Hinuma River that discharges its water into the mouth of the Naka River through an 8 km narrow channel. The catchment area of the Hinuma River is 209.4 km². The Naka River opens to the Pacific Ocean directly, and there is no embayment that effectively traps planktonic organisms. The lagoon is highly eutrophicated due to agricultural and domestic wastes from the watershed. Local fisheries in the lagoon and the channel produce 1,000–2,000 tons/year of the clam, *Corbicula japonica*. It is empirically known that massive spatls rarely occur in the lagoon while spat recruitment in the channel is annually constant. It is considered that the basis of this spatial difference in the recruitment is the salinity gradient along the Hinuma River. The salinity in the lagoon depletes in summer to the lower range than the physiological limit of the larval survival, approximately 3 PSU (Asahina, 1941).

**Salinity monitoring in the habitat**

We recorded bottom water salinity and temperature using an automatic salinometer (Alec, COMPACT-CT) in order to know salinity variations in the Hinuma River. The

![Fig. 1. The Hinuma River estuary, Ibaraki, Japan. The open circle is the area where parent clams for the experiment were collected and salinities were automatically monitored.](image-url)
monitoring was conducted at the midst of the river (about 3.5 m deep) (Fig. 1). Salinity and water temperature at 0.5 m above the bottom were recorded at 1-minute intervals from 1 July to 30 September 2002 and from 8 July to 30 September 2003.

**Rearing of larvae**

Mature clams were collected in the downstream of the lagoon in 22 July and 5 August 2002. Clams were cooled in a refrigerator overnight. To induce spawning, cooled clams were immediately moved into warm brackish water, 28°C and 5 psu. Spawning was induced within a few hours after this heat shock treatment. Fertilized eggs were collected with a siphon and rinsed with clean brackish water on a 30 μm mesh screen, then they were incubated in gently aerated water at 23°C. Larvae were fed with cultured phytoplankton mixture produced from filtered natural brackish water. Four batches of larvae were obtained in 23 July, 24 July, 6 August and 7 August 2002. The batch produced in 24 July was the most successful in hatching and survival, and enough larvae for the experiment were obtained, then most experiments were performed using this batch. An additional experiment was conducted with the batch produced in 7 August to examine the selectivity on salinity in the early developmental phase, 16 hours after fertilization. At 16, 25, 47, 68, 141, 213 and 309 hours after fertilization, sample specimens of larvae and embryos were obtained, and the stage composition was enumerated. Developmental stages were identified for 200 individuals for 16 hours after fertilization and for 100 individuals in other cases. Larval shell lengths, the maximum dimension of the shell, were measured for 28 to 78 replicates.

**Cylinder experiment**

In a long glass cylinder, a salinity gradient was produced with the mixing method (Coombs 1989; Tanaka 1991) (Fig. 2). The size of the cylinder was 800 mm in height and 50 mm in diameter. A bottle filled with freshwater (Bottle-A) was connected to another bottle filled with condensed seawater (Bottle-B) through a silicon tube. Water from bottle-A was slowly pumped into the bottom of the cylinder through a narrow silicon tube. As water in bottle-A was removed, condensed seawater was supplied gradually from bottle-B. Water in bottle-A was agitated with a magnetic stirrer. Salinity in bottle-A increased gradually, and a salinity gradient was finally produced in the cylinder. Salinities in the cylinder ranged from 0 psu at the surface to approximately 34 psu at the bottom. During the experiment, the cylinder was submerged in 28°C water. A small of volume water in the upper layer of the column was collected with a pipette, and the salinity was measured with an optical salinometer (ATAGO, IS/Mill-E) to detect the layer in which salinity is equivalent to

![Fig. 2. The apparatus used in the experiment. Freshwater in the bottle A was gradually mixed with hyperhaline water from the bottle B while water in the bottle A was moved slowly into the bottom of the cylinder by an electric pump. Thus a salinity gradient was formed. Vertical distributions of larvae were determined with a series of syringe subsections sampled from the bottom.](image-url)
Larvae for the experiment were gathered with 50 μm mesh screen and calmly moved into the 5 psu layer. After the vertical distribution pattern of larvae became stable, water in the bottom of the cylinder was suctioned with a 20 ml syringe through a silicon tube connected. With this procedure, water was suctioned repeatedly to divide the water column into small subsections along the salinity gradient. After the syringe sampling, the cylinder was rinsed with seawater, and settled spatss were retrieved with a 50 μm mesh screen. Salinities of each subsection were measured before all samples were fixed with 3% formaldehyde solution. Larvae in each subsection were enumerated under a binocular. Eighty, as maximum, subsections were obtained from single cylinder experiment. Experiments were performed in the dark and in illuminated conditions at 16, 25, 47, 68, 141, 213 and 309 hours after fertilization. The illuminated conditions were produced with a 60W lamp on the top. The experiment conducted in the dark conditions for 25 hours after fertilization was aborted because of a mishandling.

**Results**

**Salinity variations in the habitat**

Tidal fluctuations in salinity were considerable, often more than ±10 psu (Fig. 3). The range of salinity was from 0 to 24 psu. Water temperature in the channel fluctuated inversely to salinity implying that still water in the lagoon was warmer than seawater from Kashima-Nada Strait. Because the downward discharge from the lagoon predominates at ebb tides, the daily lowest salinity in the river represents salinity in the lagoon. From the annual difference in the daily lowest salinity, it was clear that salinities in the lagoon were greater in 2002 than in 2003. Sometimes salinity in the channel did not increase for a few days as showed on 10 through 20 July 2002 and on 15 through 22 August 2003. In these cases, the Naka River discharged hyposaline water into the Hinuma River because of the heavy rain and the force of flood tide.

**Larval development**

Generally, planktonic bivalve larvae experience trophophore, straight hinge (D-shaped) and umbalon stages. However, in *Corbicula japonica*, late straight hinge larvae functionally resemble pediveliger larvae of other bivalves as they have a ciliated foot and are competent to settle (Kimura et al. 2004). Looking at microscopic photographs of reared larvae, it was found that the massive occurrence of larvae with slightly rounded hinge at 141 hours after fertilization corresponded to the foot formation (Fig. 4). In the present study, late straight hinge larvae with slightly rounded hinge and umbalon shaped larvae were distinguished as post larvae. From 9 days after fertilization, radial ribs were found on the ventral margin.

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**Fig. 3.** Temporal variations in bottom water salinity (black line) and temperature (gray line) at 0.5 m above the floor in the main fishing ground of *Corbicula japonica*, Hinuma River.
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Fig. 4. Corbicula japonica. Left: right side lateral view of a late straight-hinge larva with a slightly rounded hinge and a foot (6 days after fertilization). Right: left side lateral view of an umbonal shaped larva with radial ribs on the ventral margin of the shell (9 days after fertilization). The former picture was taken in 29 July 2002, and the latter was in 6 August 2002 at ×100 magnification.

Fig. 5. Corbicula japonica. Temporal change in stage compositions of larvae. Larvae were reared in 5 psu water at 23°C and fed with natural phytoplankton mixture.

Fig. 6. Corbicula japonica. Growth of larvae in shell length. Error bars indicate standard deviations.

of the shell.

At 16 hours after fertilization, most embryos had developed into blastulas, and 14% were unidentified (Fig. 5). At 25 hours after fertilization, 89% of individuals had developed into the straight hinge larvae, and the other 11% were gastrulas and trophophores. Growth in the larval shell length along incubated time is shown in Fig. 6. The mean shell length of straight hinge larvae was 135.0±7.1 (Mean±SD) μm at that time. At 47 hours, straight hinge larvae commanded an absolute majority (98%), and only 2% of individuals were gastrulas. Post-larvae were first observed at 68 hours after fertilization although they accounted only for 7% of total larvae. Mean shell lengths of all larvae sampled, representative of 28 to 78 specimens, were 136.6±8.0 and 148.0±11.2 μm at 47 and 68 hours, respectively. At 141 hours after fertilization, the major component of larvae was post-larvae (91%), and the remainder was straight hinge larvae. The mean shell length was 172.5±10.4 μm at that time. At 213 hours after fertilization, most larvae were post-larvae, accounting for 98%, and the mean shell length of all larvae sampled was 179.2±13.8 μm. Settled individuals were observed at 309 hours, and the mean shell length was 186.2±17.9 μm. Straight hinge larvae still accounted for 6% at that time. It took 13 days before larvae grew to settled spats in this study. It was considerably longer than the incubation period in the natural temperature regime in which most larvae settled in 7 through 10 days after fertilization (Tanaka 1984). Low temperature at the incubation, 23°C, would be the main reason why the larva grew slower.

Selectivity on salinity

In the dark experiment, distribution patterns of larvae along the salinity gradient exhibited clear ontogenic changes (Fig. 7). At 16 hours after fertilization, blastulas released in 5 psu layer at the upper part of the cylinder did not move clearly from the initial point. Salinity in the
layer where larvae were collected was 8.61±5.12 psu (Mean±SD). It was difficult to know whether blastulas swam actively towards the specific salinities or they were passively suspending. At 47 hours after fertilization, straight-hinge larvae showed strong selectivity on salinity. The larvae released in the 5 psu layer moved downward through the salinity gradient, and salinity in the layer where larvae were collected was 19.21±4.65 psu. The mean downward distance from the initial point was 165 mm. At 68 hours after fertilization, larvae released in the initial point moved downward, and salinity in the layer where larvae were collected was 14.29±5.19 psu. The mean downward distance from the initial point was 110 mm. At 141 hours after fertilization, larvae did not move clearly, and they aggregated around the initial point. Salinity in the layer where larvae were collected was 7.98±5.38 psu. At 25 hours after fertilization, straight-hinge larvae showed strong selectivity and moved downward. Salinity in the layer where larvae were collected was 15.47±6.47 psu. The mean downward distance from the initial point was 115 mm. At 47 hours after fertilization, salinity in the layer where larvae were collected was 15.21±6.30 psu. The mean downward distance from the initial point was 125 mm. At 68 hours after fertilization, salinity in the layer where larvae were collected was 13.45±7.32 psu, and the mean downward distance from the initial point was 110 mm. At 141 hours after fertilization, larvae did not move clearly, and they aggregated around the initial point. The salinity in the layer where larvae were collected was 6.44±4.49 psu. At 213 hours after fertilization, the distribution pattern of larvae was similar to the previous case. Salinity in the layer where larvae were collected was 7.98±5.38 psu. At 309 hours, no peak was observed, and some individuals were found settling on the bottom.

From 47 to 141 hours after fertilization, larvae in the illuminated experiments aggregated in slightly higher layers, with lower salinities, than the corresponding occasion in the dark experiments. At 213 hours after fertilization, distribution patterns of larvae were very similar between the dark and the illuminated condition. At 309 hours after fertilization, swimming larvae distributed rather evenly through the salinity gradient. In this case, it may be possible that larvae in the illuminated condition aggregated in upper layers compared to the case of the dark condition. Wilcoxon-Mann-Whitney test showed
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Table 1. Corbicula japonica. Wilcoxon-Mann-Whitney tests on the difference in vertical distribution patterns of larvae related to salinities between dark and illuminated conditions.

| Hour condition | 16 Dark | 16 Illuminated | 47 Dark | 47 Illuminated | 68 Dark | 68 Illuminated | 141 Dark | 141 Illuminated | 213 Dark | 213 Illuminated | 309 Dark | 309 Illuminated |
|----------------|---------|----------------|---------|----------------|---------|----------------|---------|----------------|---------|----------------|---------|----------------|
| Mean           | 8.6     | 7.0            | 19.2    | 15.2           | 14.3    | 13.5           | 11.4    | 6.4            | 8.0     | 8.1            | 12.7    | 13.3           |
| n              | 53      | 25             | 52      | 106            | 229     | 264            | 144     | 157            | 234     | 222            | 72      | 104            |
| Sum of ranks   | 2160    | 921            | 5325.5  | 7235.5         | 60510   | 61261          | 28635   | 16816          | 52089.5 | 52106.5        | 6526.5  | 9049.5         |
| Correction for tied ranks | 65 | 135 | 2287.5 | 1414.5 | 5564 | 158.5 |
| U              | 729     | 1564.5         | 26281   | 4413           | 24594.5 | 3589.5         |
| U'             | 596     | 3947.5         | 34175   | 18195          | 27353.5 | 3898.5         |
| z              | −0.707  | 11.481         | 2.979   | −6.535         | 0.981   | 8.059          |
| p              | 0.24 ns | <0.01          | **      | <0.01          | **      | 0.16 ns         | <0.01 ** |<0.01          |

that differences in larval distribution patterns between the dark and the illuminated experiment were strongly significant at 47, 68, 141 and 309 hours after fertilization (p<0.01), and not significant in the cases at 16 and 213 hours after fertilization (Table 1). It is likely that C. japonica larvae in most developmental stages have responses to light interacting with selectivity on salinity.

**DISCUSSION**

In brackish water systems, benthic organisms tolerant to salinity fluctuations can exploit abundant algal resources due to high primary production in estuaries. Pelagic larvae of such organisms should adapt to estuarine flow regimes and evolve abilities to stay in and/or return to birthplaces for adult stages. Pelagic larvae respond to a variety of environmental cues, and exhibit different locomotion patterns. Young (1995) summarized general categories of behavioral responses of larvae associated with 5 scalar and 4 vector cues. Scalar cues trigger kinetic responses in which larval behaviors are determined by the strength of ambient stimuli, barokinesis (to pressure), halokinesis (to salinity), thermokinesis (to temperature), photokinesis (to light intensity) and thingmokinesis (to solid objects). Vector cues trigger tactic responses in which larval behaviors are determined by the direction of stimuli, geotaxis (to gravity), phototaxis (to light), rheotaxis (to current) and polarotaxis (to light polarity). In the present study, we obtained some snapshots of larval responses of Corbicula japonica to 2 environmental cues, salinity and light.

First, the strong selectivity of larvae towards high salinity, 15–20 psu, in early stages from 25 to 68 hours after fertilization, suggests effective retention under stratified waters in estuaries. From a similarity in the results between 25 and 68 hours after fertilization in the illuminated condition, it can be inferred that the blank data, at 25 hours after fertilization in the dark condition, would show the similar pattern with the case at 68 hours after fertilization. The gradual decrease of salinity optima in late stages may have some relation with upriver migrations of larvae. From the evidence that C. japonica adults live also in very hyposaline habitat, it is thought that they have some mechanisms to move upriver in early life stages. From the field data in the Hunuma River, salinities at ebb tides were 0–10 psu. Early stage larvae that prefer high salinity, 15–20 psu, are likely to swim downward in low salinities and stay in the boundary layer. On the other hand, salinity rose sharply towards the spring tide. Post larvae that prefer low salinities may swim upward and effectively migrate upriver where adult patches are established.

Second, under the artificial illumination from the top of the cylinder, larvae showed different vertical distribution patterns from those in dark conditions. In most occasions in this study, larvae in illuminated conditions aggregated in higher layers than those in dark conditions. Unfortunately, for two reasons, it was impossible to determine whether these larval responses were triggered by the light direction (phototaxis) or the light intensity (photokinesis). One reason is that light directions in water are multidirectional caused by scattering. The other reason is that larvae may move upward in no relation with light direction if the ciliary propulsion changes responding to ambient light intensities. It was noted that most positive phototaxis reported in the literature are laboratory artifacts and cannot be used to infer field movements (Foward 1988). However, from the evidence that larval locomotion patterns changed in different light conditions, our
experiments verified that *C. japonica* larvae actively selected their vertical positions responding to multiple environmental cues.

Third, we did not consider the effect of water pressure or depth (barokinesis) in the experimental cylinder. If, however, the wild larvae have some functional properties that enable them to aggregate within such shallow ranges equivalent to the height of the cylinder, 800 mm, controlled by water pressure (or depth), they would be easily discharged with surface water into the sea. In such cases, their recurrence in estuarine birthplaces would be very hard. It may be necessary in future to elucidate the effect of water pressures on the locomotion of *C. japonica* larvae. Water temperature in the cylinder is controlled homogenous, so thermokinesis would not work in this experiment.

Furthermore, some methodological aspects of the cylinder experiment require discussion. Mann et al. (1991) examined selectivity on salinity of 3 mactrid bivalve larvae, *Sapisula solidissima*, *Mulinia lateralis* and *Rangia cuneata*, using many combinations of salinity bi-layers. In his work, 3 brackish bivalve larvae exhibited clear responses to salinity, and larvae aggregated in the boundary zone when salinities of both layers were extreme for their preference. Because salinity in each layer was homogeneous, it is clear that larvae swim upward when the ambient salinity is higher than optima and swim downward when the ambient salinity is lower. The nature of larval kinetic responses to ambient salinities, swimming upward or downward, is explicit in their method. However, many combinations of salinity are necessary to complete the whole experiment.

On the other hand, in our method using single salinity gradient, the salinity optima for larvae can be estimated more easily. The initial position where larvae were released was hypo-saline layer (5 psu). Larvae moved downward or stayed around the initial position. Therefore the descending of larvae in low salinities can be clearly detected as in the previous method mentioned above, but the evidence of upward swimming in high salinities has a logical ambiguity. This ambiguity is the difference between “the salinity below which larvae swim upward” and “the salinity below which larvae stop descending”. The latter criterion could be determined through our method, but the former could not be proven directly. But this ambiguity may not be so serious if the mechanism of locomotion of bivalve larvae is considered.

Generally, locomotion of bivalve larvae is the result of the interaction of ciliary propulsion of the velum and specific gravity of the body. In the case of an estuarine Asiatic clam, *Sinonovacula constricta*, larval swimming alternates between a spiral upward/downward movement and then a sinking during which the velum is either retracted or protruded outside the shell valves (but with weakened ciliary beating) (Wang & Xu 1997). Jonsson et al. (1991) observed swimming behaviors of *Cerastoderma edule* (Linnaeus 1758). In still water, larvae of *C. edule* basically swim upward in a right-hand helix with the velum up and the shell umbo pointing down. The larval body has a stable orientation based on the density distribution asymmetry that creates a gravitational torque due to the separation of the center of gravity and the center of buoyancy. Occasionally the velum is retracted and the larva rapidly sinks, and a slower descent is possible by applying some upward propulsion which reduces gravitational sinking. Larvae of an Asiatic surf clam, *Meretrix lamarckii*, respond to ambient salinity changing the upward pitch of helical orbits (Higano & Yasunaga, 1990). Mann & Wolf (1983) reported responses to pressure of ocean quahog larvae, *Arctica islandica*. On increasing pressure, the diameter of the helix and the gain in height per rotation increases. Thus, if these swimming mechanisms are applicable for *C. japonica* larvae, there is no fundamental difference between the salinity in which larvae start swimming upwards and that in which they stop descending; both are the same cues activating ciliary propulsions.

Additionally, *C. japonica* may have several local populations because of distributional patterns restricted to tidal rivers and brackish lakes. Manuel et al. (1996a, b) demonstrated that scallop larvae, *Placopecten megalamicus*, spawned from different populations exhibited different vertical distribution and migration patterns. If *C. japonica* is separated into several populations and each has a different mode of larval halokinesis, information in the present study should be carefully applied when estimating the larval transport in other geographical regions.

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