

Vertical Distribution of Ark Shell Arcidae Species Larvae along Axial Transects in Sendai Bay, Northeastern Japan

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Abstract

Vertical distribution of planktonic larvae affects their passive horizontal transport. We investigated vertical distributions of ark shell Arcidae species larvae at successive developmental stages monthly from August to October 2009 along axial transects in Sendai Bay, an open embayment along the Pacific coast of northeastern Japan, where the ark shell *Anadara broughtonii* (Schrenck 1867) is the dominant arcid species. Younger larvae (early and mid-umbo stages) were typically distributed in the surface near the shore with salinity <33 psu. Older larvae (late umbo and competent stages) were distributed in the bottom far from the shore with salinity >33 psu. Surface axial distributions of younger larvae were marginally affected by the river discharge volume, tidal height and southerly wind strength. The younger and older larvae were distributed closer inshore and further offshore than the main habitat of the adults, respectively. Therefore, younger larvae were first transported inshore and moved upward to the surface layer, and then transported offshore, increasing their distribution depth. These results indicate that ark shell larvae ontogenetically change their swimming behaviour to increase their distribution depth and their axial distribution patterns may be explained by the different flow patterns among the layers of the water column in Sendai Bay.

Keywords: ark shell, larva, vertical distribution, open embayment

Introduction

The ark shell *Anadara broughtonii* (Schrenck 1867) is an infaunal bivalve distributed in muddy bottom substrates (Kan-no 1966) along the coasts of the Russian Far East, Korea, China and Japan (Lutaenko 1993; Matsukuma and Okutani 2000). This species is commercially important in

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the dredge fishery or aquaculture of these countries. Sendai Bay is an open embayment in northeastern Japan, with a width of 60 km. Recruitment of the ark shell in Sendai Bay tends to severely fail approximately once in 10 years (Sasa 2012). However, the larval transport processes that affect recruitment success are rarely investigated.

Studies of the transport processes of invertebrate larvae in open embayments are rare (Sekiguchi and Odate 1983; Pfeiffer-Herbert et al. 2007; Isogai et al. 2010; Daigle et al. 2014), compared with those in estuaries and enclosed embayments (e.g., Kasuya et al. 2004; Ishii et al. 2005; North et al. 2008; Tamaki et al. 2010; Liu et al. 2015; Biermann et al. 2016). The relative importance of transport mechanisms such as wind stress, tides, and differences in water density and the behaviour of invertebrate larvae would differ between habitats with different degrees of openness, such as estuaries with a large mouth and inlets with a narrow mouth (Biermann et al. 2016). Differences in the transport process and behaviour of invertebrate larvae between open embayments and estuaries or enclosed embayments are not well understood.

Larval behaviour can play a critical role in determining dispersal distance, because the planktonic larval period and dispersal distance are correlated, but there are many exceptions (Shanks 2009). Vertical movement of planktonic larvae can affect their horizontal transport, because the physical flow field may vary among the different layers of the water column (Sponaugle et al. 2002; Largier 2003). An ontogenetic shift in distribution depth could contribute to larval retention in benthic habitats. For example, younger larvae in the surface layer may quickly disperse with strong currents, whereas older larvae in lower layers may be retained with weak currents (Ishii et al. 2005). Vertical swimming behaviour is modified by larval response to environmental cues, such as phototaxis (Bayne 1964; Weidberg et al. 2015), geotaxis (Bayne 1964; Mann et al. 1991), the response to the interfaces of temperature or salinity (Harder 1968; Mann 1988; Gallager et al. 1996; Ma et al. 2006), and turbulence (Fuchs and DiBacco 2011; Weidberg et al. 2015). Published information on the environmental cues that influence swimming behaviour of ark shell larvae is sparse.

The planktonic larval period of the ark shell is 22–28 days in the laboratory at 25 °C (Tanaka 1971). Therefore, larvae would be widely transported within Sendai Bay during the planktonic larval period. However, information on their distribution patterns is scarce across habitats in northeastern Asia and the Russian Far East. Investigation of the *in situ* vertical distribution of ark shell larvae provides basic information concerning passive horizontal transport processes acting on the larvae, which in turn is important for delineating and protecting nursery areas used by ark shell. Previously, Yoo et al. (1977) found that the ark shell larvae were distributed in the bottom layer in water columns shallower than 8 m depth along the southern coast of Korea. Sasaki (1997) found that the larvae at late developmental stage (>200 µm in shell length) were distributed in the bottom layer in the northern part of Sendai Bay.

However, the results of these studies were insufficient to estimate the transport process of the ark shell larvae because the distributions were only investigated at a fixed station or there were too few stations to fully assess a given area, at either the developmental stage or all stages combined.

Passive horizontal transport processes of larvae may affect the success of their retention or return to adult habitats in an open embayment, especially for species that occur in nearshore coastal areas and have a relatively long planktonic larval period, such as the ark shell in Sendai Bay. To investigate the possibility of a developmental shift in the vertical and axial distributions of the ark shell larvae in an open embayment, this study investigated the vertical distribution of ark shell larvae at each developmental stage along axial transects in Sendai Bay.

Materials and Methods

Study site

Larval collection and environmental measurements of the water column were conducted at 5–6 sites along each of two northern transects (N_A and N_B) and a southern transect (S) across the inner shelf (10–30 m depth) in the south-central part of Sendai Bay (Fig. 1). The three transects traverse the primary fishing ground for the ark shell called the northern and southern areas at a depth of 15–30 m (Sasa 2012).

Larval investigations

Because the peak of the ark shell spawning season is around August in Sendai Bay (Fisheries Agency 1977), the surveys were conducted monthly during morning hours from August to October 2009 along transect N_B and S, and once in August 2009 along transect N_A from the offshore to the inshore stations. The surveys along transect S in October were conducted on two successive days; sites S3, S4, and S5 were sampled on 13 October, and then sites S1 and S2 were sampled on 14 October. Plankton samples at 5 m intervals from the surface to 2 m above the bottom were collected by towing two vertically-arranged plankton nets horizontally at each site. The two plankton nets were towed horizontally at different fixed depths because they were arranged vertically by the tension between the buoy at the top and the depressor at the bottom. The series of buoy, nets, and depressor was cast at the starting point of the towing and then towed by a vessel at a speed of 0.5 knots for 3 minutes. Ropes between the buoy and the upper plankton net were ready cut to 10, 20, and 25 m lengths and changed for a given towing depth at each station (i.e., 0 m at first tow, 10 m at second tow). The rope length between the two plankton nets and between the lower plankton net and depressor were 5 and 2 m, respectively. After reaching the end point of each tow, the vessel returned to the starting point and the rope length between the buoy and the upper plankton net was changed before the next tow. The plankton net was cone-shaped with a side length of 1.0 m, and its mouth and mesh openings had a width of 0.3 m and 100 μm , respectively.

The method is less quantitative than the pump-up method because the net could not be closed and filter some water during casting and retrieval. However, the vertical distance covered was far shorter than the horizontally towed distance, and thus had a limited impact on determining the inter-depth tendency of larval density. The filtered water volume was measured with a flow meter attached to the net.

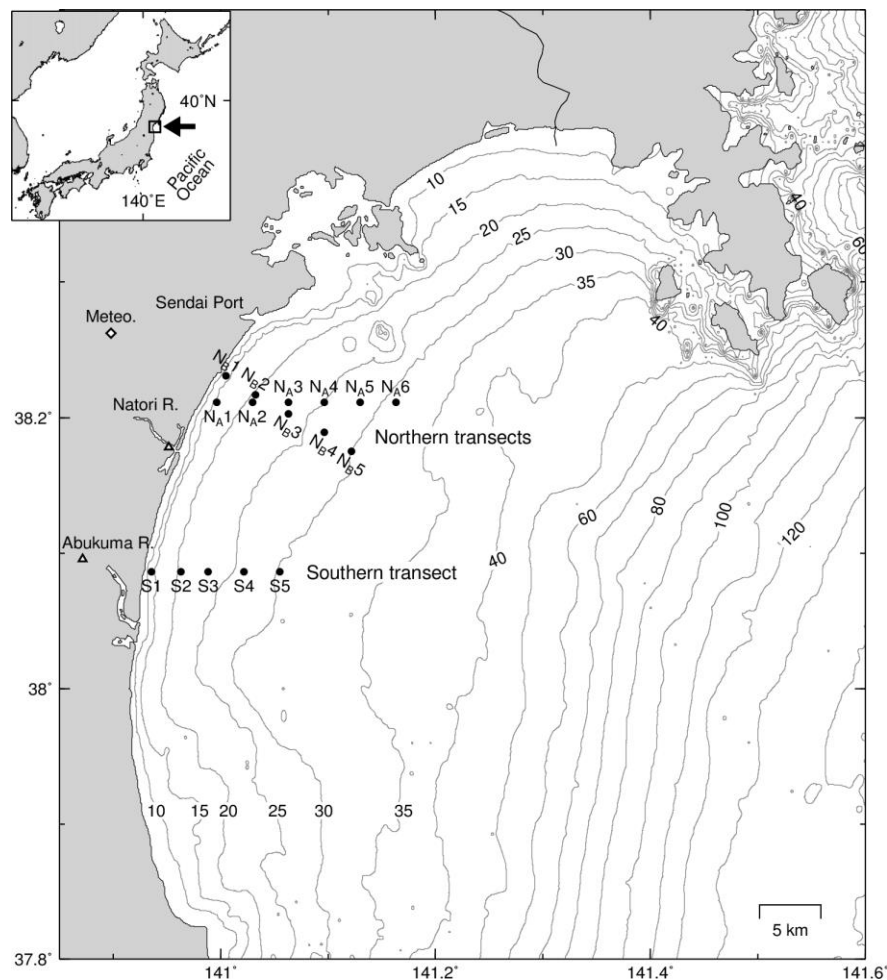


Fig. 1. Sites for larval collection and environmental measurements (solid circles) and bathymetry in Sendai Bay. Meteorological (diamond) and river discharge observatories (triangle) are also shown.

Larval identification

Plankton samples were preserved in 1 % buffered formaldehyde seawater solution prior to microscopic observations. Each plankton sample was concentrated to 100 ml by draining the supernatant with a siphon. Plankton samples were divided into 1–10 aliquots depending on the larval density. Ark shell Arcidae species larvae were identified to the family level using a dissecting microscope, based on shell shape according to the criteria proposed by Tanaka (1979), whereby the shell after the early umbo stage is bilaterally symmetrical, well inflated, anteriorly narrowing, with centred umbo, and brownish, whereas the umbonal and anterior regions are tinged red.

Because the identification of arcid bivalve larvae to the species level is difficult based on shell shape (Tanaka 1979), possible misidentification might occur in our study. A molecular method is required for complete and accurate identification of larvae. Nevertheless, the morphological identification method can approximately estimate the abundance of the ark shell *A. broughtonii* larvae in Sendai Bay because other arcid bivalves such as *Scapharca kagoshimensis* (Tokunaga 1906), *Arca boucardi* (Jousseume 1894) and *Arca avellana* (Lamarck 1819) are rare in the bay; they were not sampled in the coastal area (5–30 m in depth) of the south-central part of the bay in 2012–2013 (Sato and Chiba 2016) or sampled at only 1–2 intertidal sites in the bay in 2003–2015 (Biodiversity Center of Japan 2007; Suzuki T., pers. comm.). Larval developmental stages were defined based on shell length (SL) as follows: early-umbo (140–180 μm SL, 7–12 days post fertilization), mid-umbo (180–220 μm SL), late-umbo (220–260 μm SL), and competent (>260 μm SL, >22 days post fertilisation) stages (Tanaka 1971; modified). The larvae at each developmental stage were counted under a dissecting microscope, with an ocular micrometer. Larval density was calculated by dividing the number of sampled larvae by the filtered water volume.

Environmental observations

Because the northern and southern transects were located near the Natori and Abukuma River mouths (Fig. 1), the daily average discharge of these rivers from August to October 2009 was obtained from the hydrology database of the Japanese Ministry of Land, Infrastructure, Transport, and Tourism (Japanese Ministry of Land, Infrastructure, Transport, and Tourism 2017). The measurement sites were Yuriage 2 for the Natori River and Iwanuma for the Abukuma River.

Daily average wind speed and prevailing wind direction near the sampling site from August to October 2009 were obtained from the Sendai station of the Japanese Meteorological Agency (Japanese Meteorological Agency 2017). The frequency of daily-average wind speeds by prevailing wind direction in each month was plotted on a wind rose diagram. Because south-easterly wind predominates from May to September (Watanabe and Kobayashi 1985) and Ekman upwelling occurs following a continuous southerly wind of $>4 \text{ m}\cdot\text{sec}^{-1}$ in Sendai Bay (Aoki et al. 2015), data on southerly winds that continued for $>24 \text{ h}$ within 48 h before each sampling date were retrieved from hourly averaged database of the Japanese Meteorological Agency (2017).

Vertical profiles of water temperature and salinity were measured at 2.5 m intervals using a multi-parameter water quality meter (DKK-TOA; WQC-24) at the same time as larval investigations. The data were contoured after interpolating with surface commands (tension parameter = 0.25) using the generic mapping tools software. The salinity could not be observed along the transect S on 12 September because of a problem with the multi-parameter water quality meter.

Statistical analyses

Two linear mixed-effect models were used to estimate the effects of environmental and developmental factors on spatial and temporal variation in larval distribution. The first involved overall distribution patterns, while the second involved the surface axial distribution of younger larvae (early and mid-umbo stages). In the analysis of overall distribution patterns, the response variable was the number of larvae of each developmental stage in a sample collected at a given site and depth. The overall distribution pattern was analysed with six target fixed effects (time, measured as calendar month; distance from shore; depth; larval developmental stage; water temperature; and water salinity), with interaction terms between larval developmental stage and each of the other variables. Transect identity was included in the model as a random effect, and the volume of filtered water was included as an offset term to correct for differences in the volume of each sample. In the analysis of the surface axial distribution of younger larvae, the response variable was the average distance from the shore (ADS) of early and mid-umbo larvae sampled in August and September, when larvae were abundant. The ADS of the larvae was calculated using the following equation, modified from that proposed by Shanks and Shearman (2009):

$$ADS = \frac{\sum N_j \times D_j}{\sum N_j}$$

where N_j represents larval density in the surface sampled per site D_j km from the shore, and the sums consist of all the sites sampled per transect. The surface axial distribution of younger larvae was analysed with five target fixed effects (time measured as calendar month; larval developmental stage; river discharge volume of a river closest to each transect (cumulative sum of the daily averaged discharge volumes in the last two days before each sampling date); southerly wind strength (cumulative sum of hourly averaged wind speeds including southerly component within 48 h before each sampling date); and tidal height (estimated value in Shiogama at 9:00 h). Tidal height was obtained from the Hydrographic and Oceanographic Department of the Japanese Coast Guard (2017). Transect identity was included as a random effect, and the distance between the shore and the outermost station along each transect was used as an offset term to correct for differences in the length of each transect. In both analyses, the optimal model was selected based on Akaike information criterion (AIC) values.

Results

For most of the survey period, the volume discharged by the Natori and Abukuma Rivers was approximately $200 \text{ m}^3 \cdot \text{day}^{-1}$; however, discharge increased sharply to volumes greater than $600 \text{ m}^3 \cdot \text{day}^{-1}$ on 11 August and 1 September in the Abukuma River and on 8 October in the Natori River. Such massive river discharge volumes did not occur within 2 days before the larval sampling dates (Fig. 2).

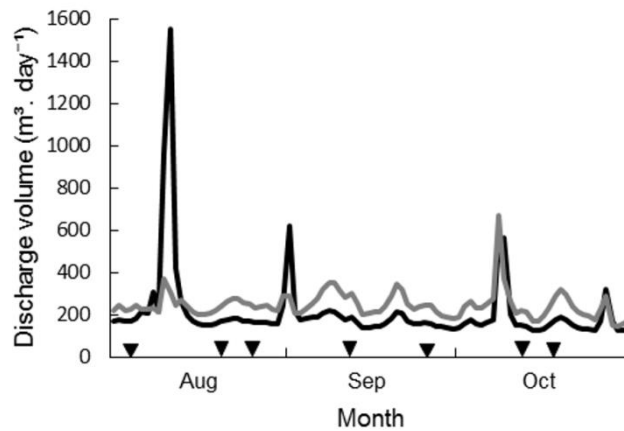


Fig. 2. Daily average discharge volume of the Natori (grey line) and Abukuma (black line) Rivers from August to October 2009. Reversed triangles on the x-axis indicate the survey dates.

A southerly wind dominated in August, followed by a northerly wind from September and October 2009 in Sendai (Fig. 3). A wind speed of $2\text{--}3\text{ m}\cdot\text{sec}^{-1}$ dominated during the southerly winds throughout the study period. A southerly wind with a speed of $3\text{--}4\text{ m}\cdot\text{sec}^{-1}$ blew for 12.9 % (4 days) of the time in August, 0 % (1 day) in September and 3.2 % (1 day) in October. Wind speeds faster than $4\text{ m}\cdot\text{sec}^{-1}$ blew from the north. Among the sampling dates, the prevailing ($>24\text{ h}$) wind blew from the southeast 48 h before 3 and 19 August, with a daily speed ranging from $1.6\text{--}3.5\text{ m}\cdot\text{sec}^{-1}$ (Japanese Meteorological Agency 2017).

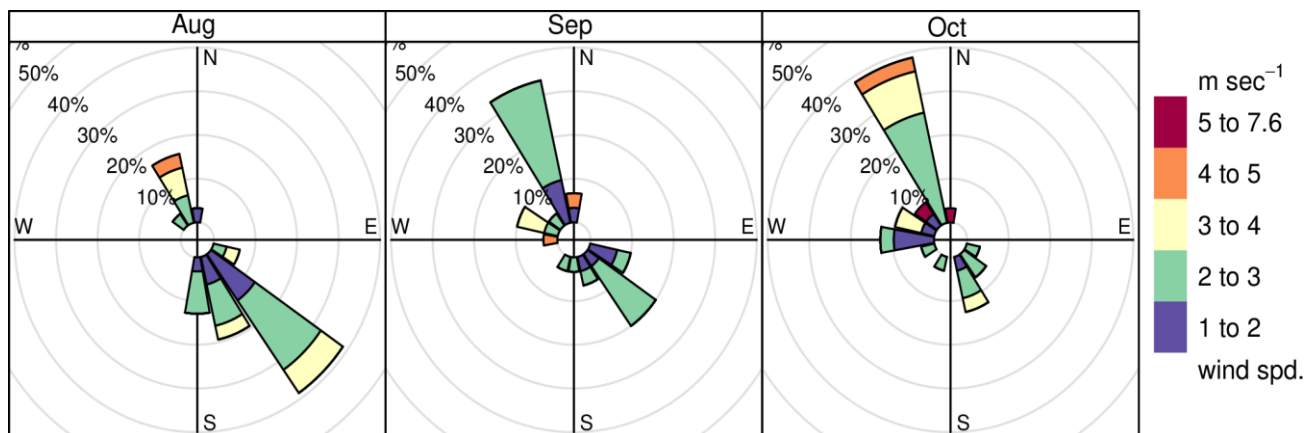


Fig. 3. Wind rose plot showing frequency of daily average wind speeds by prevailing wind direction (%) in Sendai in each month from August–October 2009.

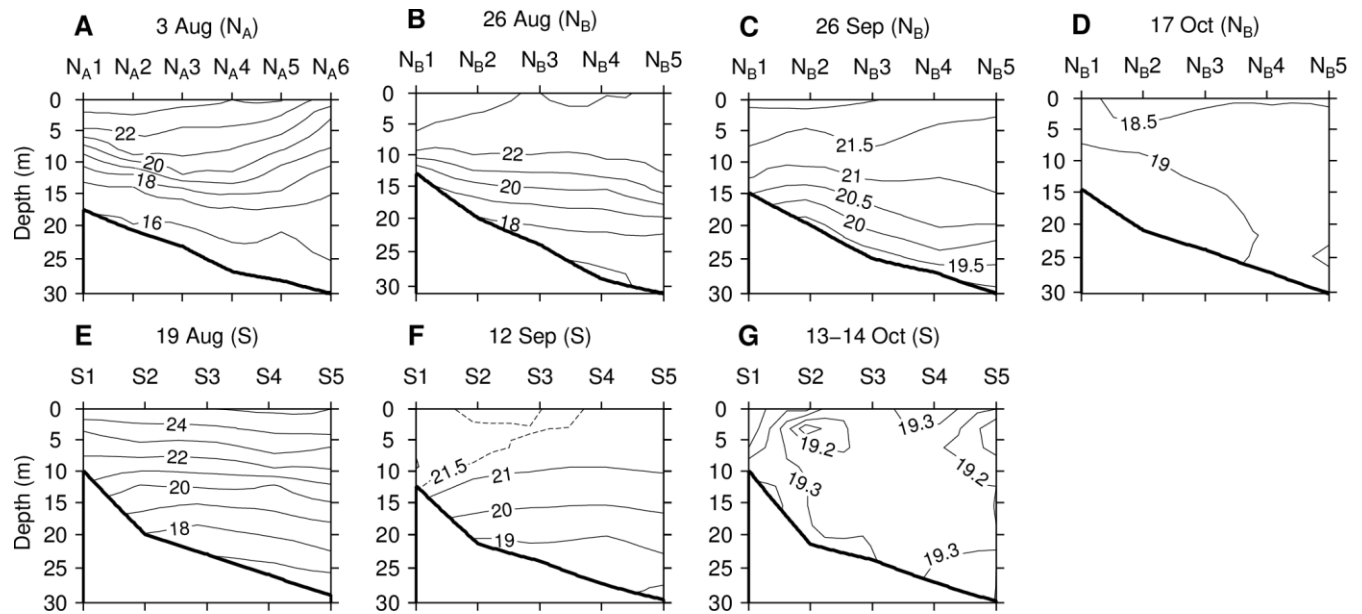


Fig. 4. Isotherms along the (A, B, C, D) northern and (E, F, G) southern transects on each sampling date in 2009. Contour (solid lines) intervals = 1 °C (A, B, E, F), 0.5 °C (C, D) and 0.1 °C (G). Contour (dashed lines) intervals = 0.5 °C (F).

The water column was vertically stratified in August, when isotherms were most crowded (Fig. 4A, B, E). Stratification weakened in September, when the water was warmer throughout the water column (Fig. 4C, F). The stratification almost disappeared in October, when the whole water column was colder (Fig. 4D, G). Low salinity waters (<33psu or practical salinity units which are equivalent to ppt, parts per thousand) were oriented to the surface and the isohalines in the surface generally sloped upwards toward offshore (Figs. 5 and 6). The low salinity waters were sometimes oriented to the nearshore (Fig. 5B, D), but extended further offshore on some days (Figs. 5A, C and 6A, C) along the northern and southern transects. High salinity waters (>33) were distributed in the bottom layer of the offshore water (Figs. 5 and 6).

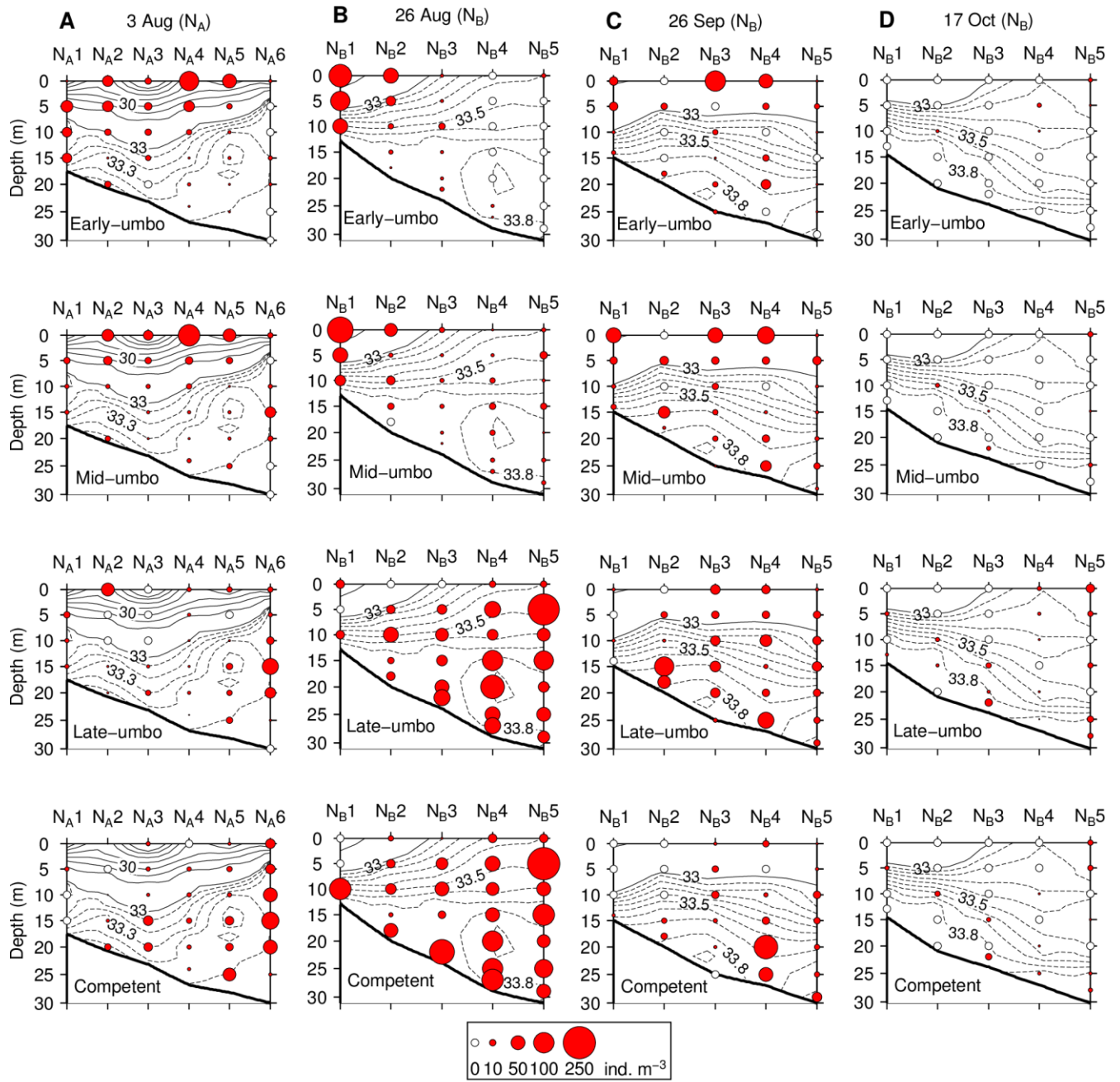


Fig. 5. Vertical distributions of ark shell larvae (circles) and isohalines along the northern transects (N_A and N_B) on (A) 3 August, (B) 26 August, (C) 26 September and (D) 17 October 2009. Isohaline intervals = 1 (solid lines) up to 33 and 0.1 (dashed lines) from 33. Larval density and salinity distributions are shown in the same panel to facilitate observation on the spatial relationship between them.

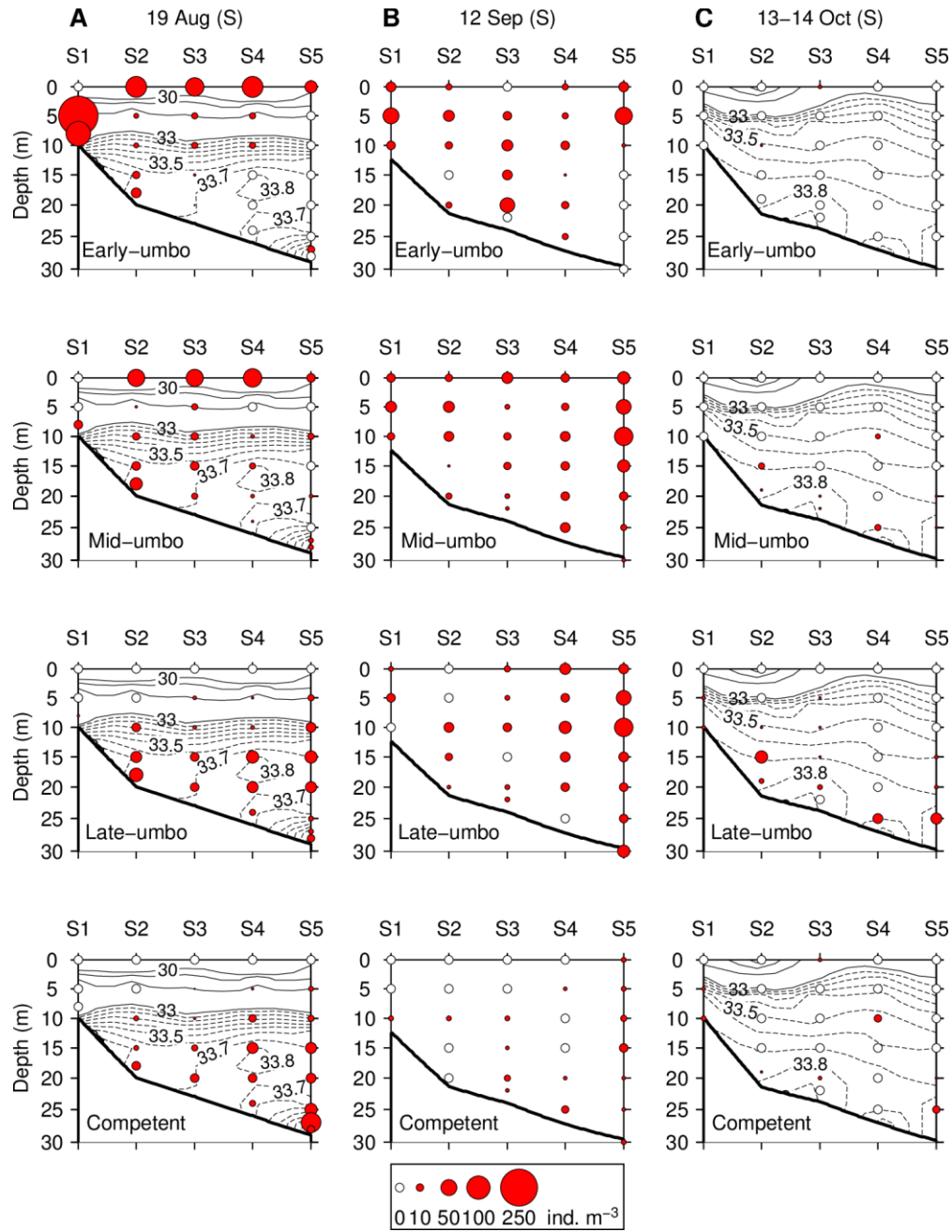


Fig. 6. Vertical distributions of ark shell larvae (circles) and isohalines along the southern transect (S) on (A) 19 August, (B) 12 September and (C) 13–14 October 2009. Isohaline intervals = 1 (solid lines) up to 33 and 0.1 (dashed lines) from 33. Salinity on 12 September: no data. Larval density and salinity distributions were shown in the same panel to facilitate observation of the spatial relationship between them.

Numbers of ark shell larvae decreased with time, developmental stage, depth, and distance from shore; furthermore, depth and distance from shore affected larval development (Table 1). Numbers of ark shell larvae also decreased in higher salinity and colder waters. Table 1 shows that salinity affected larval development.

Ark shell larvae were most abundant in August until September, and then decreased in October along the northern (N_A and N_B) and southern (S) transects (Figs. 5 and 6). Early and mid-umbo larvae accumulated in the surface layer along the northern and southern transects, especially from August to September (Figs. 5 and 6). In contrast, late-umbo and competent larvae were distributed mainly in the bottom layer offshore.

Table 1. Linear mixed-effect models for the number of larvae at each stage in each sample and average distance from the shore (ADS) of early- and mid-umbo larvae in the surface.

Response variable	Effect	Coefficient	Std. error	AIC*
No. of larvae	Intercept	17.96	0.8853	9718
	Time	-1.373	0.02675	
	Distance from the shore	-0.1155	0.009352	
	Depth	-0.05052	0.006262	
	Developmental stage	-5.647	0.3947	
	Water temperature	0.1808	0.01394	
	Water salinity	-0.2234	0.02045	
	Distance from the shore \times Developmental stage	0.05339	0.003218	
	Depth \times Developmental stage	0.02580	0.001788	
	Developmental stage \times Water salinity	0.1548	0.01220	
ADS	Intercept	-11.19	0.3602	20.59
	Time	1.407	0.04296	
	River discharge volume	0.001351	0.0001120	
	Tidal height	-0.01939	0.0007308	
	Southerly wind strength	-0.004604	0.0008257	

*Akaike Information Criterion

The ADS of early and mid-umbo larvae at the surface increased with time and river discharge volume but decreased with tidal height and in the presence of southerly winds; however, time had a greater effect than all other variables, by up to three orders of magnitude (Table 1). High concentrations of early and mid-umbo larvae were limited in the surface of the nearshore half of transect N_B on 26 August (Fig. 5B). They were broadly distributed toward offshore along the northern transects on 3 August and 26 September, and the southern transect on 19 August (Figs. 5A, C and 6A). Early-umbo larvae sometimes accumulated at the innermost stations where the depths were shallower than 20 m (Figs. 5B and 6A). In contrast, competent larvae often accumulated at the offshore stations where the depths were 20–30 m (Fig. 6A, B).

Discussion

The results of this study indicate that the distribution of ark shell larvae shifts, depending on the developmental stage, from the surface near the shore to the bottom far from shore, where salinity levels are higher (Table 1, Figs. 5 and 6). It is inferred that ark shell larvae actively swim upwards at younger stages (early and mid-umbo), and then upward swimming behaviour weakens or becomes intermittent at older stages (late umbo and competent), as demonstrated by Cragg (1980). Although larval preference to low salinity may influence to some extent early upward movement after hatching, once they have reached the surface layer, other cues such as positive phototaxis and negative geotaxis may influence the surface orientation of early and mid-umbo larvae. Ontogenetic change in the sign and intensity of phototaxis or geotaxis (Bayne 1964; Mann et al. 1991) may have contributed to a deeper shift in larval distribution depth at later stages. Younger and older stage larvae did not aggregate near the 33 isohaline, where inter-stage segregation occurred (Figs. 5 and 6). A sharp thermocline was not observed (Fig. 4). Therefore, larval aggregation at the interface of salinity or temperature was not detectable. On the other hand, the weakened thermal stratification in September (Fig. 4C, F) might contribute to the vertically dispersed distribution of ark shell larvae at each developmental stage (Figs. 5C and 6B).

Time played a substantial role in determining temporal variation in the surface axial distributions of early and mid-umbo larvae (Figs. 5 and 6); however, the effect of short-term mechanisms (river discharge volume, tidal height, and southerly wind strength) was comparatively minor (Table 1), suggesting the existence of longer-term or larger-scale mechanisms that could not be observed, such as inflow of oceanic water into the bay (Kudo 1971; Takehi et al. 2012, 2015), or the promotion of estuarine circulation by freshwater input (Takehi et al. 2012). Increasing river discharge volumes had marginal effects on the transportation of younger larvae offshore (Table 1). Such marginal effects may be attributed to the minor variation in river discharge volumes before the sampling dates, which fell within normal levels (Fig. 2). At higher tides, younger larvae were distributed marginally closer to the shore (Table 1). The weak effect of tide in this study coincided with a predominance of subtidal flow over tidal flow off Sendai Port (Watanabe and Kobayashi 1985). Southerly wind strength caused a marginal decrease in the ADS of younger larvae (Table 1), indicating that shoreward wind-driven currents had marginal effects on transporting larvae inshore. The weak effect of wind may be related to the rare occurrences of the prevailing (>24 h) wind before the sampling dates (Japanese Meteorological Agency 2017).

The axial distributions of early-umbo and competent larvae in this study did not coincide with the main distribution area of adult ark shells that have been reported previously. The adult ark shells were most abundant at a depth of 20–25 m in Sendai Bay (Watanabe 2013). The catch quantity of small ark shells (45–60 mm SL) was largest at a depth of 21–22 m, while it was sparse in the nearshore area (<18 m) and offshore area (>25 m) in the dredge-fishing ground of the ark shell (15–30 m) in the bay (Sasa 2012).

The area with a depth of 20–25 m approximately corresponds to the area between sampling sites N_{A2} and N_{A4} , N_{B2} and N_{B3} , and S2 and S4 along transect N_A , N_B , and S, respectively (Fig. 1). Early-umbo larvae sometimes accumulated closer inshore than the 20–25 m depth area (Figs. 5B and 6A). In contrast, competent larvae often accumulated further offshore than the 20–25 m depth area (Figs. 5A, B and 6A). This suggests that bottom inflow is important for larvae to settle around the primary fishing ground of ark shell.

Overall, the axial and vertical transitions in the distributions of the ark shell larvae in Sendai Bay can be summarised in the following manner. (1) Larvae initially move inshore and up to surface in low salinity waters after hatching. (2) Larvae move to the offshore deeper zone of the water column. The transition patterns suggest the existence of different flow patterns between the surface and bottom layer of the water column in the bay. The related species *Anadara* spp. larvae showed a similar transition pattern of cross-shore distribution from the nearshore at umbo stage to offshore at competent stage (Yurimoto et al. 2014). Relatively long-term flow patterns may support the retention of the ark shell larvae in the bay. The residence time of brackish water is 39–44 days in Sendai Bay in summer (Kakehi et al. 2012). This is longer than the larval period of the ark shell of 22–28 days (Tanaka 1971) and thus contributes to the retention of the ark shell larvae in the bay. The inflow of the oceanic water into the bay (Kudo 1971; Kakehi et al. 2012, 2015) may prevent the larvae from being moved offshore. The along-shelf residual current driven by horizontal differences in water density may contribute to larval retention in Sendai Bay in summer (Kakehi 2011). The different distribution patterns of ark shell larvae among the developmental stages in this study may be explained by the layer-specific flow patterns with an along-shelf component as well as an axial one. The dataset of this study can be used in numerical simulations that reveal in detail the processes that regulate larval distribution patterns.

Conclusion

This study demonstrated for the first time that ark shell larvae shift their distribution from the near shore surface to the bottom far away from the shore in Sendai Bay and suggest that the different flow patterns among the layers contribute to their axial distributions and retention in Sendai Bay. Younger larvae (early and mid-umbo stages) drift in the surface layer before dispersing offshore. Older larvae (late umbo and competent stages) migrate to the bottom and begin recruitment in the area of the primary fishing ground, where inflow reaches the bottom layer.

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