Complex vertical migration of larvae of the ghost shrimp, *Nihonotrypaea harmandi*, in inner shelf waters of western Kyushu, Japan

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ABSTRACT

The position of meroplanktonic larvae in the water column with depth-dependent current velocities determines horizontal transport trajectories. For those larvae occurring in inner shelf waters, little is known about how combined diel and tidally-synchronized vertical migration patterns shift ontogenetically. The vertical migration of larvae of *Nihonotrypaea harmandi* (Decapoda: Thalassinidea: Callianassidae) was investigated in mesotidal, inner shelf waters of western Kyushu, Japan in July-August 2006. The larval sampling at seven depth layers down to 60 m was conducted every 3 h for 36 h in a 68.5-m deep area 10 km off a major coastal adult habitat. Within a 61-65-m deep area 5-7.5 km off the adult habitat, water temperature, salinity, chlorophyll *a* concentration, and photon flux density were measured, and water currents there were characterized from harmonic analysis of current meter data collected in 2008. The water column was stratified, with pycnocline, chlorophyll *a* concentration maximum, and 2 % of photon flux density at 2 m recorded at around 22-24 m. The stratified residual currents were detected in their north component, directed offshore and onshore in the upper and lower mixed layers, respectively. More than 87 % of larvae occurred between 20 m and 60 m, producing a net onshore transport of approximately 1.3 km d^{-1}. At the sunset flooding tide, all zoeal-stage larvae ascended, which could further promote retention (1.4-km potential onshore transport in 3 h). The actual onshore transport of larvae was detected by observing their occurrence pattern in a shallow embayment area with the adult habitat for 24 h in October 1994. However, ontogenetic differences in the vertical migration pattern in inner shelf waters were also apparent, with the maximum mean positions of zoeae deepening with increasing stages. Zoeae I and II performed a reverse diel migration, with their minimum and maximum depths being reached around noon and midnight, respectively. Zoeae IV and V descended continuously. Zoeae III had behaviors that were intermediate to those of the earlier- and later-stage zoeae. Postlarvae underwent a

normal diel migration (nocturnal ascent) regardless of tides, with the deepest position (below 60 m and/or on the bottom) during the day. These findings give a new perspective towards how complex vertical migration patterns in meroplanktonic larvae enable their retention in inner shelf waters before the final entry of postlarvae into their natal populations.

1. Introduction

Dispersal of the meroplanktonic larvae of marine benthic invertebrates is a crucial process affecting the connectivity of local populations (Sponaugle et al., 2002; Kinlan et al., 2005). The position of larvae in the water column with depth-dependent current velocities determines horizontal transport trajectories. Larvae can control their vertical positions in the water column with active upward or downward swimming and passive sinking in phase with diel and tidal cycles. Three patterns of diel vertical migration (DVM) have been described for meroplanktonic larvae and holoplankton (Forward, 1988; Pearre, 2003). The most common pattern is an ascent to a minimum depth at night and a descent to a maximum depth during the day, termed nocturnal or “normal” DVM. Usually, the ascent and descent begin near sunset and sunrise, respectively. The second pattern is “reverse” DVM, with the ascent to a minimum depth during the day and the descent to a maximum depth at night. The third pattern is twilight DVM: an ascent to the surface at sunset, a descent to deeper water around midnight, a second ascent to the surface in the early morning hours, followed by a final descent to deeper water at sunrise. Records of the latter two patterns for meroplanktonic larvae are much rarer than for holozooplankton (Young and Chia, 1987; Queiroga and Blanton, 2005). For estuarine macrobenthos living in areas dominated by tidal currents, tidal cycles of vertical migration that promote horizontal transport are also known (e.g. selective tidal-stream transport, STST: Forward and Tankersley, 2001; Gibson, 2003). While normal DVM is widely acknowledged for meroplanktonic larvae appearing in estuarine, coastal, shelf,

and oceanic waters, observations of STST have been substantially limited to larvae from shallow estuaries. For larvae occurring in inner shelf waters, almost nothing is known about how combined diel and tidally-synchronized migration patterns shift ontogenetically.

Decapod crustaceans, brachyurans in particular, are the most intensively targeted invertebrate group for research of larval vertical migration and consequent dispersal processes. Five dispersal types along the estuary to ocean gradient have been recognized (Queiroga and Blanton, 2005): (1) retention of the larval series within estuaries; (2) export from estuarine habitats, dispersal over the shelf, and re-invasion of estuaries by the last stage; (3) hatching in shelf waters and immigration to estuaries by late larvae or postlarvae; (4) complete development over the shelf; and (5) hatching in shelf waters, long-range dispersal in the ocean, with a return to shelf waters during the late stages of larval life. There are rich case studies for STST from shallow estuaries (Forward and Tankersley, 2001; Queiroga and Blanton, 2005). Crab zoeae of dispersal type 1 undergoing STST have been shown to migrate vertically across a depth of no net water flow. One subtype of the STST for members of dispersal type 2 is ebb-tide transport of the 1st zoeae hatched in estuaries and exported into shelf waters. The other subtype is flood-tide transport of postlarvae from the estuary mouth upstream. Both subtype migrations often occur at night. By contrast, in decapod larvae collected from shelf and oceanic waters, tidally-synchronized vertical migrations have never been identified, except for a few instances of flood-tide transport of late- or postlarvae of penaeid shrimps from coastal spawning grounds to estuarine nursery habitats (dispersal type 3: e.g., Rothlisberg et al., 1995; Criales et al., 2007). It is generally believed that once exported into shelf waters, larvae of dispersal type 2 either stay in the shallow layers throughout all stages of larval development or perform only DVM, with their mean positions becoming deeper ontogenetically (Epifanio and Garvine, 2001; Queiroga et al., 2006; Yannicelli et al., 2006a). Thus, regarding the return of late-stage larvae from the shelf to an estuary, the distinctly different processes between shelf and estuary have been conceptualized

as a two-step transport model (Miller and Shanks, 2004; Queiroga et al., 2006). However, it is still uncertain whether larvae dispersed over the mid to outer shelf can eventually return home to the estuary, or whether a proportion of the natal population is "lost" or "wasted" or contributes to other local populations of a metapopulation (Sponaugle et al., 2002; Kinlan et al., 2005). Though not identified so far for the dispersal type-2 decapod larvae occurring in the inner shelf, flood-tide transport could be one key process that enables their retention throughout ontogenetic development around the estuary mouth. One promising way to demonstrate this is to deal with species whose adult populations are not enclosed in the estuary but are instead located on the open coast (Zeng and Naylor, 1996).

The purpose of the present paper is to examine if there are (1) a combined diel and tidally-synchronized vertical migration pattern and (2) an ontogenetic shift in the pattern for dispersal type-2 decapod crustacean larvae in inner shelf waters. The material used was a species of the ghost shrimp, *Nihonotrypaea harmandi* (Thalassinidea: Callianassidae). Adults of this functionally important group occupy deep burrows in intertidal or subtidal soft sediment habitats (Flach and Tamaki, 2001; Atkinson and Taylor, 2005). The existence of both diel change and ontogenetic shift in vertical distribution of *N. harmandi* larvae has been suggested, though this was based on the results from only one daytime and one nighttime sampling (Fujiie et al., 2006). Such larval vertical migration patterns have also been suggested for other callianassid species, *Callianassa subterranea* in the Celtic Sea (Lindley, 1986) and *Neotrypaea uncinata* in coastal waters of central Chile (Yannicelli et al., 2006a, b), whose adults inhabit subtidal muddy bottoms. However, these patterns were insufficiently described due to low resolution of sampling in time and space. In the present study, a finer-scale stratified sampling in the water column was conducted over a period covering eight combinations of diel and tidal phases (i.e., day/night × high/ebb/low/flood tides). Furthermore, the larval vertical distribution was examined in relation to water currents and stratification. We hypothesized that vertical migration contributed to larval retention around

and entry into a local natal population. The actual onshore transport of larvae was observed by monitoring their occurrence in a shallow embayment area with the adult habitat for 24 h.

2. Materials and methods

2.1. Study site and ghost shrimp distribution

In an estuarine system ranging from Ariake Sound via Tachibana Bay to the coastal waters of the East China Sea located in southwestern Japan, intertidal sandflats inhabited by *Nihonotrypaea harmandi* are distributed along the outer half of the system (Tamaki and Harada, 2005; Fig. 1). Note that in papers by A. Tamaki and his colleagues published before 1998, the name *Callianassa japonica* was incorrectly applied to *N. harmandi* (see Manning and Tamaki, 1998). Of the 26 main local populations of *N. harmandi*, the population size on one sandflat (Tomioka sandflat) at the outermost periphery of the estuarine system was estimated to account for 70 % of the total number of shrimps in the waters (Tamaki and Harada, 2005). This sandflat is located in an embayment near the inner shelf (inside the 20-m depth contour). The waters are under a mesotidal, semi-diurnal tidal regime, with the average tidal range at spring tides being about 3 m. The M_2 tidal currents are dominant in the current field, with much prevalence of the east over north components, and the maximum current speeds are 150 cm s^{-1} around the strait between Tachibana Bay and Ariake Sound and 50 cm s^{-1} in the embayment area embracing the Tomioka sandflat (Fujiie et al., 2006). A numerical simulation of water currents has demonstrated large-scale, weak counterclockwise residual flows up to 5 cm s^{-1} from the surface to the 40-m depth off the Tomioka sandflat in central Tachibana Bay (Fujiie et al., 2006). The residual flows at the 50-m depth are directed towards Ariake Sound. In late summer, when the larval sampling was conducted, the prevailing southwesterly winds are weak, with a speed of about 4 m s^{-1} (Fujiie et al., 2006),

and the water stratification structure is stable in the southwestern part of Tachibana Bay and its westward shelf area (Matsuno et al., 1999). The breeding season of *N. harmandi* is from June to October (Tamaki et al., 1997). The larval series consists of five zoeal and a decapodid (= postlarval) stages (Konishi et al., 1999). The durations of each zoeal and decapodid stages were estimated at 3-5 d and 5 d, respectively (Tamaki et al., 1996; Konishi et al., 1999). The larvae hatched from the Tomioka sandflat are exported into the inner shelf waters, and larvae of all stages tend to remain within 10 to 20 km north to west of the sandflat, where water depth reaches 70-80 m (Tamaki and Miyabe, 2000; Fig. 1). In Tachibana Bay, the sampling point nearest to the Tomioka sandflat at which zoeae V were collected was located 6.7 km northwest of the sandflat (Tamaki and Miyabe, 2000). The entry of the later-stage larvae including decapodids into the sandflat with flood tide is expected to occur from the area around this sampling point. Furthermore, a recent survey for the horizontal distribution of larvae in phase with ebb and flood tides has indicated the movement of a later-stage zoeal assemblage back and forth between the above area and its westward shelf area, with alternate appearance and disappearance of zoeae in the former area with flood and ebb tides, respectively (A. Tamaki et al., unpublished data). In the present study, therefore, the “onshore” direction for the later-stage larvae to return to the adult habitats can be defined on two different spatial scales, from the coastal waters of the East China Sea towards Tachibana Bay and from the southernmost part of Tachibana Bay towards the Tomioka sandflat. Hereafter, the latter localized definition is mainly used for the onshore direction.

2.2. Vertical distribution of larvae in inner shelf waters

The stratified larval sampling was conducted on board the RV “Kakuyo-Maru” (155 tonne) of Nagasaki University, using a MOCNESS-1/4 (Multiple Opening/Closing Net Environmental Sensing System with a mouth opening area of 0.25 m^2 and a net mesh opening

of 0.33 mm, Biological Environmental Sampling Systems, Inc.). Between 30 July and 1 August 2006, 13 sets of towing (one every 3 h) were performed in an area west of the Tomioka sandflat (Fig. 1; 129°56.5′E and 32°32.7′N at the center of the area; mean depth, 68.5 m), with sampling sets of 1, 2, 3, 8, 9, 10, and 11 occurring during the day and the rest at night. The sampling in this area was expected to stably obtain a sufficient number of larvae irrespective of tidal phases. The weather was fine and the sea was calm over the sampling period. One sampling set (no. 4) had to be discarded, as the ship captain must avoid a collision. The mid-point of each sampling interval coincided with high-, low-, or mid-tides. The tidal height difference between two consecutive high and low tides varied from 1.4 to 1.9 m. The final sampling set was 1 d before the neap tide. During each sampling set, the MOCNESS was towed horizontally at 2 knots through seven depth layers (every 10 m from 60 to 10 m, and 2 m) each for 10 min. After completing the tow of one depth layer, the net system was swiftly lifted to the next layer and the mouth of the previous net closed. The collected samples were fixed with 5 % neutralized filtered-seawater formalin. In the laboratory, larvae of *Nihonotrypaea harmandi* were sorted and identified to stages, following the morphological keys given in Konishi et al. (1999). Although two other species of *Nihonotrypaea* occur in the Ariake Sound estuarine system, contamination by their larvae in the plankton sample for *N. harmandi* collected from the area is negligible due to their much lower abundances (Tamaki and Miyabe, 2000). The concentration of larvae (number per unit volume of water) was calculated according to the volume of water passing through the net as determined by MOCNESS flowmeter data. The volume of filtered water per net ranged from 201.0 to 450.2 m^3 (mean ± SD: 304.1 ± 36.9 m^3, n = 84). Based on the concentration values at respective depth layers for each larval stage, the weighted mean depth (WMD) of larval position was calculated as $\Sigma(C_i d_i) / \Sigma C_i$, where C_i stands for larval concentration at depth d_i (i, depth layer number) (Pearre, 2003). To statistically detect differences in the median depth positions (1) among the eight combinations of diel and tidal

phases for each larval stage and (2) among the larval stages for each combination of the diel and tidal phases, Kruskal-Wallis tests and Steel-Dwass multiple comparison tests were performed based on the percentage larval number nearest to integers for each depth layer (α = 0.05). Before conducting these analyses, a combined water-depth distribution of larvae at each stage was made for each group with the same combination of diel and tidal phases.

2.3. Occurrence pattern of larvae close to the adult habitat

To examine the diel and tidal pattern in the occurrence of *Nihonotrypaea harmandi* larvae in close proximity to the adult habitat, sampling was conducted at a 10-m deep station 0.5 km off the Tomioka sandflat (Fig. 1). Using a small vessel, a net (mouth diameter, 36 cm; lateral length, 135 cm; mesh opening, 0.33 mm) positioned at a depth of 5 m was horizontally towed for 5 min at a speed of 2 knots every 20 min for 24 h from 10:30 on 5 October 1994. The weather was fine and the sea was calm over the sampling period. The 35th sampling set was unsuccessful. The final (72th) sampling set was 1 d before the spring tide. The tidal height difference between two consecutive high and low tides varied from 2.7 to 3.1 m. The collected samples were fixed as in the MOCNESS sampling. The number of zoeae I and II was counted based on split subsamples when abundant, while all larvae were enumerated for the other stages. To make a smoothing for the variation in zoeal abundance over time, three-term moving averages for the number of larvae per haul were given. For the 35th sampling set, the mean value from the 34th and 36th sampling sets was used. The number of decapodids was much fewer and its raw data given.

2.4. Water currents and water stratification

To measure water currents in the inner shelf area, a 600 kHz Workhorse Acoustic Doppler

Current Profiler (Express-ADCP, Teledyne RD Instruments, Co.), with data logging of a 2-m bin size and a 10-min interval, was deployed 5 m above the 61.3-m deep bottom 5 km northwest of the Tomioka sandflat during 25 July to 4 November 2008 (Fig. 1). The measurement station was located around the area where the flood-tide entry of later-stage larvae of *Nihonotrypaea harmandi* into the embayment with the sandflat was expected to occur. It is impossible to place a current meter in the MOCNESS sampling area, which is a local fishermen's trawling ground for penaeid shrimp. With high speeds of the east component of tidal currents around this area (several tens of cm s^{-1}), the time-lag in tidal phases between the ADCP station and the MOCNESS sampling area is negligible.

The ADCP was maintained in an upright position with underwater buoys, with the 1st bin height being 7.6 m above the bottom. The vertical current profiles corresponding to the larval sampling period in 2006 were reproduced from the entire 2008 record by harmonic analysis with a least square method (Pugh, 1987). The data from the uppermost 6 % depth range were discarded to eliminate echo effects from the sea surface. The current velocities at every 1-m depth interval were linearly interpolated. One representative onshore direction for larval transport from the ADCP station towards the Tomioka sandflat was defined as 163.14° clockwise from magnetic north (Fig. 1, along the arrow from the station). The onshore current velocity was calculated as $U\cos(73.14°) + V\cos(-163.14°)$, where U and V are the east and north components in the ADCP velocity, respectively. The averaged vertical profile of the onshore currents along the water column for each larval sampling set was based on the mean velocities from seven measurements near the mid-point of the sampling interval.

To examine water-column stratification structure, the record in the water temperature and salinity sensors attached to the MOCNESS was used. The present MOCNESS was unequipped with chlorophyll (chl) *a* concentration and photon sensors. To compensate for lack of these parameters, a SBE-911plus Conductivity Temperature Depth Profiler (CTD, Sea-Bird Electronics, Inc.) was cast at a 65-m deep station near the MOCNESS sampling area

at 7:00 on 8 August 2006, when the weather was fine (Fig. 1).

3. Results

The record for water temperature and salinity with the MOCNESS sensors indicates each characteristic stratification structure in the water column (Fig. 2). In the water temperature, a significant diel fluctuation was detected only in the uppermost layer (i.e., 2-m depth); the overall means (and ranges) from all sampling sets in the daytime inclusive (n = 7) and those in the nighttime inclusive (n = 5) were 27.0°C (25.1-28.1°C) and 25.8°C (24.7-26.7°C), respectively, with their median values significantly different ($p < 0.05$, Mann-Whitney U-test). In the lower water column, the temperature varied largely linearly along depth, from 24.5°C at 10 m to 19.1°C at 60 m (both overall grand mean values). The water salinity varied from 31.65 at 2 m to 34.2 at 60 m (both overall grand mean values), with one disjunction in depth gradient found at 20 m and the others at 40 m and 50 m. At the CTD station in early August of 2006, a similar water-column stratification structure was observed (Fig. 3a). The thermoclines existed at 14 m and 48 m, and the haloclines at 14 m and 22 m. These were reflected on three disjunctions in the water-density (sigma-t) profile along depth. The depth with a maximum chl a concentration (24 m) was slightly below a pycnocline mainly caused by the corresponding halocline at the 22-m depth. In the upper mixed layer from 2 to 21 m, the water temperature, salinity, and sigma-t changed from 25.9 to 23.5°C, from 31.6 to 32.8, and from 20.5 to 22.1, respectively. In the lower mixed layer from 22 to 60 m, those parameters changed from 22.8 to 19.1°C, from 33.3 to 34.2, from 22.7 to 24.4, respectively. The photon flux density given as PAR (Photosynthetically Available Radiation) attenuated sharply in the surface 10-m layer, becoming less than 10 μmol quanta m^{-2} s^{-1} at 23 m (2 % of the value at 2 m) and less than 1 μmol quanta m^{-2} s^{-1} at 44 m (Fig. 3a). The water currents at the ADCP station were dominated by the east over north components, their maximum speeds

being 75.1 and 15.1 cm s^{-1} for 24.8 h (during 23:00, 30 July to 23:50, 31 July 2006), respectively. The residual currents of the east component in the same period were directed eastwards through the water column, with higher velocities at shallower depths (Fig. 3b). The directions in the north component were separated at a depth of 25 m, northwards (offshore) and southwards (onshore) in the upper and lower water columns, respectively. This depth is close to the pycnocline, suggesting the existence of the density-driven, two-layered water currents flowing in the opposite directions.

In the MOCNESS sampling for *Nihonotrypaea harmandi* larvae, the total number of the collected larvae was greater in the sampling set no. 1 to 8 than in the subsequent sampling sets (Fig. 4), which might be due to spatial variation in the larval horizontal distribution within the sampling area. The larval vertical distribution along water depth indicated the occurrence of all stages throughout the water column, but mostly in the middle to deeper layers especially for zoeae. Across all daytime samples, the proportion of each-stage zoeae present in the two surface layers (2 m and 10 m) ranged from 2.5 % (zoea I) to 4.5 % (zoea IV). At night, it ranged from 6.1 % (zoea I) to 13.2 % (zoea IV). An ontogenetic shift was detected for the WMD of larval position (Fig. 5a). Zoeae I migrated within the narrowest range (22-m vertical distance) between the depths of 22 m and 44 m, whereas the migration range of zoeae II-V was wider (28-33-m vertical distance). The shallowest positions of zoeae II-IV were 23-24 m, while that of zoeae V was 29 m. The deepest positions of zoeae II-V were 53-58 m, with maximum depths slightly deeper with each successive stage. The overall grand mean WMDs over the sampling sets also became greater with increasing stages for zoeae but not for decapodid (zoea I: 36.3 m, zoea II: 40.0 m, zoea III: 40.6 m, zoea IV: 41.7 m, zoea V: 46.2 m, decapodid: 41.1 m).

A clear ontogenetic shift was detected for the diel and tidal pattern in the WMD of larval position of *Nihonotrypaea harmandi* (Fig. 5a). A distinct reverse DVM pattern was observed for zoeae I and II, with their minimum and maximum depths being reached around

noon and midnight, respectively. By contrast, zoeae IV and V continued to descend from the nighttime minimum depth to a daytime maximum depth immediately before sunset the next day. The migration pattern of zoeae III was transitional between the two. The abundance of decapodids was about half that of zoeae V in the nighttime but only 1/30 in the daytime (Fig. 4), suggesting the deepest position of decapodids along the water column during the day (below 60 m and/or on the bottom) and their ascent during the night irrespective of tidal phases (mean WMD of 22 m). The temporal changes in the tidal height and the vertical profile of the onshore current velocities from the ADCP station towards the Tomioka sandflat indicate the coincidence of high tide and slack water, falling mid-tide and ebb current, and rising mid-tide and flood current, but the prevalence of flood currents at low tide, with higher velocities recorded at greater depths (Fig. 5b). A conspicuous pattern common to all zoeal stages was observed during the low to the flood tide around sunset (Fig. 5a, sampling set no. 11 to 12), which appeared to be a tidally-synchronized rapid ascent from the deepest water (38-58 m) to the minimum depths of a narrow range (22-29 m). This ascent was followed by descent by the midnight high tide.

The vertical migration speeds of *Nihonotrypaea harmandi* larvae can be quantified from a summary figure, in which a combined WMD value is given for each group with the same combination of diel and tidal phases plotted at the corresponding averaged time (Fig. 5c). The larval migration speed between any two adjacent diel- and tidal-phase combinations was defined as the vertical displacement divided by the time interval between them. At the daytime high tide immediately before noon, the positions of the zoeal stages are ordered ontogenetically from zoea I to zoea V towards greater depths. Until the low tide immediately before sunset, zoeae of the five stages continue to descend at a speed of 0.04-0.08 cm s^{-1}. Around sunset, zoeae of the five stages ascend with flood tide at 0.18-0.30 cm s^{-1}, which is one order of magnitude higher than their ascending speeds in the other period. Following this flood tide, the descending speeds of zoeae are ordered ontogenetically from

zoea I (0.17 cm s^{-1}) to zoeae IV and V (0.06-0.08 cm s^{-1}), resulting in the deepest position by zoea I, followed by zoeae II = V, zoea III, and zoea IV at the midnight high tide. From then, zoeae I turn to ascend at a speed of 0.03-0.04 cm s^{-1} (except for the initial 0.01 cm s^{-1}) until around the noon high tide. Zoeae II ascend slower at 0.00-0.02 cm s^{-1}. Zoeae IV and V continue to descend at 0.04-0.05 cm s^{-1}, though the speed for the latter stage is less constant. Zoeae III descend at 0.01-0.02 cm s^{-1}. The minimum WMD attained by zoeae I at noon is near the depth with a maximum chl *a* concentration (Fig. 3a). During the daytime to the flood tide after sunset, decapodids migrate in a way similar to zoeae IV and V. Even after this flood tide, decapodids remain throughout the water column until around sunrise, when they descend at 0.29 cm s^{-1}.

The difference in the median depth positions among the eight diel- and tidal-phase combinations over the six larval stages of *Nihonotrypaea harmandi* in the MOCNESS data set was statistically confirmed (Kruskal-Wallis tests; all $p < 0.001$; $n = 99$ to 106 for each larval stage at each phase combination). The Steel-Dwass multiple comparison tests detected an ontogenetic shift in the number of phase combination pairs with no significant differences (Table 1). The numbers were the largest at zoea II (15) and zoea III (11), followed by zoea I (9), zoeae IV and V (both 7), and decapodid (5). The ascent and descent migration pattern for each larval stage in the course of diel- and tidal-phase shifts observed for the WMDs (Fig. 5c) was consistent with the changing pattern for the median depths (Fig. 6), where the adjacent diel- and tidal-phase combination pairs and the every other ones with significant differences are connected by arrows. The difference in the median depth positions among five zoeal stages of *N. harmandi* over the eight diel- and tidal-phase combinations was also statistically confirmed (Kruskal-Wallis tests; $p < 0.001$ or < 0.01 or < 0.05; $n = 99$ to 103 for each zoeal stage at each phase combination). The Steel-Dwass multiple comparison tests showed that (1) in the nighttime, the overlapping distributions of all stages generated by the flood-tide ascent around sunset were once fairly separated at the high tide, but followed by the

second overlap at the ebb tide, (2) after the low tide near sunrise, the separation of positions among stages progressed from flood via high to ebb tides during the daytime, and (3) at the low tide before sunset, the overlaps increased again (Table 2).

A distinct occurrence pattern during the 24-h sampling for *Nihonotrypaea harmandi* larvae from the 5-m depth layer at the 10-m deep station in front of the Tomioka sandflat was that the abundance of all-stage zoeae increased sharply around the sunset flood tide, followed by the highest peak for zoeae I at the nighttime high tide (Fig. 7). There was a reduction in the zoeae II-V abundance at this high tide, after which two lower peaks were observed at the ensuing ebb and flood tides before sunrise. During the daytime, the abundance of zoeae was at a much lower level except for an increase in that of zoeae II at the late afternoon flood tide. Decapodids appeared only during the nighttime, occurring at both flood and ebb tides.

4. Discussion

The adaptive significance for the export of meroplanktonic larvae from estuary to shelf has been interpreted from a viewpoint of avoidance of harsher physical stresses (thermal, osmotic, ultraviolet, etc.) and higher predation pressure associated with shallow estuaries (Young and Chia, 1987; Morgan, 1995). In the callianassid shrimp, the export of zoeae I from estuary to shelf and the return of decapodids was recorded for *Neotrypaea californiensis* (see Johnson and Gonor, 1982). More than 95 % of the *Nihonotrypaea harmandi* larvae in the water column occurred between 20 m and 60 m during the daytime (Fig. 4). Those larvae in the lower mixed layer would experience the more stable conditions with lower temperatures and higher salinities than in the upper mixed layer (Figs. 2, 3a). The positions of pycnocline and chl *a* concentration maximum coincided at around 22-24 m, which is a typical feature of the stratified water column in temperate waters in summer (Falkowski and Raven, 1997; Woodson and McManus, 2007). Light penetration also tends to decrease

sharply beneath the pycnocline (Falkowski and Raven, 1997). Such typical depth profile in photon flux density was confirmed also in the present study (Fig. 3a). The WMDs of all-stage larvae of *N. harmandi* present mostly below 25 m in the daytime could afford them better protection against visual predators like fish and against ultraviolet than in the upper mixed layer (Figs. 3a, 5a). In another inner shelf water area west of Nagasaki, where light penetrates deeper (Fig. 1), the WMDs of all-stage zoeae tended to be at greater depths than in the present study area (A. Tamaki et al., unpublished data). In the Celtic Sea, zoeae of *Callianassa subterranea* (four stages) occurred in the upper mixed layer with water temperature of 11.4-14°C above the thermocline situated at a depth of 35 m in June (Lindley, 1986). The mode in the vertical distribution of zoeae lay at 10-25 m. In inner shelf waters of central Chile, zoeae of *Neotrypaea uncinata* (five stages) occurred mostly below the thermocline situated at a depth of 10-20 m in November, December, and March, where water temperatures were 10-11°C and the zoeal WMDs of all stages inclusive were 29-35 m (Yannicelli et al., 2006a, b).

The adaptive significance for zoeal larvae of *Nihonotrypaea harmandi* to stay mostly in the lower mixed layer can also be considered in light of an increased chance of retention. The WMDs of zoeae could enable them to be retained in an inner shelf area near the Tomioka sandflat, owing to the onshore residual current in the lower mixed layer, where a mean onshore transport distance of 1.3 km d^{-1} is expected (Fig. 3b). At this rate, some portion of the larval assemblage in the lower mixed layer may eventually be carried to the 25-m deep area and further shorewards when encountered by flood currents. However, those larvae entrained in the shallow water of the embayment with the sandflat could be returned to the inner shelf by ebb currents (Fig. 7), where they would descend to the lower mixed layer again. Therefore, the hypothesized larval retention process is horizontal movement by tidal currents back and forth between inner shelf and embayment areas, with the intervening larval vertical migration. On a larger spatial scale, it can be pointed out that zoeae I initially flushed out

westwards by ebb currents from the Tomioka sandflat would be gradually transported back by the eastward residual current in the course of ontogenetic development (Figs. 1, 3b).

The vertical migration speed is a species-specific trait in meroplanktonic larvae of marine invertebrates (Young and Chia, 1987; Morgan, 1995). The maximum ascending speeds of larvae of *Nihonotrypaea harmandi* (0.18-0.30 cm s^{-1}; Fig. 5c) are the smallest yet recorded for decapod crustacean larvae (Queiroga and Blanton, 2005). The maximum descending speeds of *N. harmandi* zoeae (0.04-0.08 cm s^{-1}) are one order of magnitude lower than the passive sinking rates of anesthetized crab zoeae (Sulkin, 1984). When reared in a laboratory aquarium under the shade of a canopy, zoeae of *N. harmandi*, the later-stage ones in particular, normally stay still near the bottom but are triggered to rush upwards immediately in response to food supply (A. Tamaki et al., personal observation). Thus the descent migration process by zoeae would involve both the reduced locomotion that is subject to settling due to gravity and the rising due to intermittent hopping associated with feeding or water turbulence.

The five zoeal-stage larvae of *Nihonotrypaea harmandi* exhibited a clear ontogenetic shift in the vertical migration pattern, with zoea II, and zoea III in particular, being transitional between the earlier and later stages. The degree of overlap among median depths increased from zoea I to zoea II and decreased from zoea III to zoea IV (Tables 1, 2; Fig. 6). The ontogenetic increase in the migration range (Figs. 5a, c, 6) is coincident with the development of appendages used for swimming (see Konishi et al., 1999): pereopods (developed from zoea II), pleopods (buds occasionally present at zoea III), and uropods (becoming biramous at zoea III). Basically zoeae I and II performed a reverse DVM, with the minimum depth being reached around noon and the maximum depth around midnight (Figs. 5a, c). The possibility that this daily pattern is indifferent to tidal height variations is suggested by the results of a multiple opening/closing net sampling with a Motoda net system (MTD net, see Omori and Ikeda, 1992) conducted near the present ADCP station around the noon and midnight low tides at 12:39 and 01:02 on 3-4 October 1994 (Fujiie et al., 2006). At noon low tide, the

WMDs for the combined zoeae I and II, zoeae III and IV, zoea V, and decapodid were 14.4 m, 41.9 m, 38.3 m, and nil (absent in the water column), respectively. Around midnight low tide, those WMD values were 33.9 m, 26.0 m, 17.9 m, and 22.8 m, respectively. Generally, daily maximum photosynthesis occurs around noon (Falkowski and Raven, 1997). The minimum depth layer reached by zoeae I of *N. harmandi* was near the depth of the chl *a* concentration maximum (Figs. 3a, 5a), which might provide them with more phytoplankton- and microzooplankton food specifically required for the early-stage larvae (see Ouellet and Allard, 2006; Woodson and McManus, 2007). In the laboratory, zoeae I of *N. harmandi* consume rotifers and the chlorophyte, *Chlorella* sp., whereas later-stage zoeae consume larger organisms such as brine shrimp nauplii (Konishi et al., 1999). Such ontogenetic shifts in food item and size (towards mesozooplankton) seem to be common in decapod crustacean larvae (Omori and Ikeda, 1992; Anger, 2001; Ouellet and Allard, 2006). The reverse DVM of zoeae I and II might be ascribed to hunger-driven ascent and satiation-driven descent hypothesized for holozooplankton (Pearre, 2003).

A few fragmentary findings available for the diel vertical migration pattern and its ontogenetic shift in the callianassid larvae partly support the patterns observed for *Nihonotrypaea harmandi* larvae. The diel vertical migration pattern for zoeae of *Callianassa subterranea* was not evident, except for a slight tendency for a nighttime ascent at the zoea II (Lindley, 1986). For zoeae of *Neotrypaea uncinata*, the generally shallower positions during the nighttime were recorded, except for a reverse tendency at the zoea I (Yannicelli et al., 2006a, b). Furthermore, zoeae IV and V showed an overall trend to be positioned deeper than the earlier-stage zoeae. The authors suggested that zoeae I to IV would be transported offshore, while zoeae V could be carried back towards the coast. This is different from our view in that all-stage zoeae of *N. harmandi* could potentially be retained in an inner shelf area near their natal habitat.

The rapid ascent at sunset flood tide shared by all-stage zoeae of *Nihonotrypaea harmandi*

(Figs. 4, 5a) suggests the existence of tidally-synchronized ascent migration for decapod crustacean larvae with the type-2 dispersal in inner shelf waters. This migration was a modifier of the diel patterns and may enhance concentration of larvae near their natal habitat, which would be most effective in mesotidal systems (Queiroga et al., 2006). In *Neotrypaea uncinata*, an onshore transport of zoeae V at the nighttime flood tide was suggested, but it is uncertain whether this was derived by the larval ascent in the water column (Yannicelli et al., 2006b). Accompanied with their ascent to the minimum depths of 22-29 m, an onshore transport distance of 1.2-1.4 km in about 2.5-3 h would be gained by larvae of all stages of *N. harmandi* (Fig. 1, along the arrow from the ADCP station). This estimation is based on the linearly interpolated larval WMDs and the current velocities along the water column at every 10 min during the larval sampling set no. 11 to 12 (Figs. 5a, b). Here, it is assumed that the current velocities at the 60-m depth were equal to those at the 1st bin height above the ADCP and that the WMD for uncollected decapodids at the 11th sampling set was 60 m as in the 3rd sampling set (both low tides near sunset). The sharp increase in the abundance of all-stage zoeae in front of the Tomioka sandflat around the sunset flood tide could be explained by their tidally-synchronized ascent migration in the water column that should have occurred close offshore (Fig. 7). The earlier occurrence of zoeae II in the late afternoon hours might be ascribed to that (1) a part of their assemblage in the inner shelf area was distributed closer to the Tomioka sandflat than the later-stage zoeae (A. Tamaki et al., unpublished data) and (2) their ascent migration could be induced by dwindling light prior to sunset. The highest peak in the abundance of zoeae I found at the nighttime high tide was most probably due to a mass releasing of zoeae by the female population on the Tomioka sandflat, which regularly occurs every spring tide during the breeding season (Tamaki et al., 1996, 1997). The lower peak in zoeal abundance at the nighttime ebb tide would be derived from a larval assemblage that had hit on the upper shoreline of the sandflat with flood currents and returned from there with ebb currents. The subsequently recorded, lower peak in the abundance of zoeae at the second

flood tide in the nighttime suggests that their tidally-synchronized ascent migration is not limited to around the sunset hours but could occur at any of the nighttime. To confirm this suggestion, larval sampling in the inner shelf area during the nighttime with a flood tide occurring due after the time of sunset will be required. To maintain themselves within a 20-60-m depth range in the inner shelf waters, zoeae of any stage must regularly ascend for a distance of 20-30 m per day, following the period of a continuous descent (Fig. 5c). To be retained in the vicinity of the natal habitat and to avoid visual predators, it would be most advantageous for those zoeae to conduct a long-range ascent at flood tides occurring between sunset and sunrise. In the rest of the night and during the day, zoeae IV and V continue to descend. Thus their migration assumes a saw-tooth vertical trajectory form over time. This is not regarded as a normal DVM that is indifferent to tidal height variations.

Subsequent to their ascent after sunset, all zoeal-stage larvae of *Nihonotrypaea harmandi* descended by the time of the high slack tide (Fig. 5c), which is another feature characterizing the flood-tide STST for decapod crustacean larvae in shallow estuaries (Forward and Tankersley, 2001; Queiroga and Blanton, 2005). In particular, zoeae I and II of *N. harmandi* descended at faster speeds than the later-stage zoeae to reach the lowest positions around midnight, suggesting the involvement of active movement. One interpretation about adaptive significance for reverse DVM conducted by small-bodied holozooplankton is their avoidance of larger predatory invertebrates that perform normal DVM to escape from visual predators (Ohman et al., 1983; Pearre, 2003). Even conspecific late-stage- or post-larvae of decapod crustaceans can be cannibalistic to early-stage larvae (Anger, 2001).

Decapodids of *Nihonotrypaea harmandi* underwent a normal DVM, with the nighttime ascent without regard to tidal height variations and the daytime position close to and/or on the bottom (Figs. 5a, 6, 7). For those decapodids present in the inner shelf waters, the ascent up to 20-25 m (their WMD) is mandatory to enter the shallow embayment area with the Tomioka sandflat (Fig. 1). Upon entry, decapodids could be trapped in a small-scale clockwise

residual current to reach the sandflat (Fujiie et al., 2006). For decapod crustacean postlarvae that have been transported into estuaries, the nocturnal ascent only at flood tide appears to be the rule (Forward and Tankersley, 2001; Queiroga and Blanton, 2005). In the case of shelf waters, the occurrence of premature decapod postlarvae in the water column at the time of ebb tide is considered adaptive in that they would not be stranded too early (Zeng and Naylor, 1996). Alternatively, the WMD of 20-25 m for *N. harmandi* decapodids may enable them to settle on the embayment bottom in front of the Tomioka sandflat even at ebb tide. These larvae could reach the sandflat in a short time at the following nighttime flood tide. The flood-tide transport may be adaptive for postlarvae that have reached the mouth of a shallow estuary and must go further for a long distance towards the upstream adult habitat against downstream ebb flows. For postlarvae of the species whose adult populations are located on the open coast, a different vertical migration behavior could have evolved to successfully arrive at their adult habitat.

In the field of metapopulation dynamics, biogeography, fishery resource management, and in the designing of marine protected areas for coastal invertebrates and fish, considerable effort has been made on the simulation of horizontal transport processes of meroplanktonic larvae based on their vertical migration patterns. Recently, increased attention has been paid to the mechanisms by which larvae remain near their natal habitats, leading to self-recruitment (Sponaugle et al., 2002; Kinlan et al., 2005). The type-2 larval dispersal of decapod crustaceans in shelf waters comprises two subtypes: (1) wide-range dispersal as far as the mid to outer shelf, owing to larval positions in surface layers through all stages, such as in the blue crab and the mole crab, for which wind-induced currents are often regarded responsible for larval return to the estuary mouth or the adult habitat facing open coastal waters (Epifanio and Garvine, 2001; Yannicelli et al., 2006a, b); and (2) retention of a substantial assemblage of larvae near the adult habitat, such as in the fiddler crab and the ghost shrimp, with their vertical migration range extended for several tens of meters (Petrone

et al., 2005; Yannicelli et al., 2006a, b). For the former subtype, two-step transport models would apply. For the latter subtype, especially where adult habitat faces open coastal waters, one-step transport models may suffice to describe the larval return process. The past view for this subtype has stressed only the role of ontogenetic deepening of the position of larvae on their onshore transport, which is aided by the density-driven onshore current in the lower mixed layer of the stratified water column. Our findings on the vertical migration of *Nihonotrypaea harmandi* larvae give a new perspective on how combined diel and tidal migration patterns in those larvae can shift ontogenetically and enable their retention in inner shelf waters before the final entry of postlarvae into their natal populations.

5. Conclusions

The ontogenetic shift in the combined diel and tidally-synchronized vertical migration pattern for *Nihonotrypaea harmandi* larvae appeared to be closely associated with water-column stratification in an inner shelf water area in summer. In particular, the adaptive significance of the vertical migration performed by larvae within the lower mixed layer was suggested for increasing their survival and retention around a local natal population. Further sampling from the same and different inner shelf areas with other diel- and tidal-phase combinations through the species' breeding season will be needed to examine the general applicability of the pattern observed in the present study.

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Figure captions

Fig. 1. Coastal waters of the Ariake Sound estuarine system, Kyushu, Japan, with every 10-m depth contours. The main intertidal sandflats are indicated in black along the coastline. Tomioka sandflat is the largest habitat for the population of *Nihonotrypaea harmandi* in the estuarine system. For the definition of onshore direction for larval transport, see text (Section 2.1). CTD = Conductivity Temperature Depth Profiler. ADCP = Acoustic Doppler Current Profiler. MOCNESS = Multiple Opening/Closing Net Environmental Sensing System.

Fig. 2. Vertical profile of water temperature and salinity recorded with the MOCNESS sensors between 30 July and 1 August 2006 (Fig. 1). The mean values for the seven daytime and five nighttime sampling sets are given, respectively.

Fig. 3. (a) Vertical water stratification with the distributions of chl *a* concentration and photon flux density (Photosynthetically Available Radiation), based on the CTD record measured at a station near the MOCNESS sampling area (Fig. 1, triangle mark) on 8 August 2006. (b) Vertical profile of the residual current components for 24.8 h during 23:00, 30 July to 23:50, 31 July 2006 at the ADCP station (Fig. 1, filled circle mark).

Fig. 4. Temporal change in the concentration along water depth for each of the six stages of *Nihonotrypaea harmandi* larvae in the course of 13 sets of the MOCNESS sampling conducted for 36 h between 30 July and 1 August 2006. The 4th sampling set had to be abandoned. The time given in each panel indicates the mid-point of each sampling set.

Fig. 5. (a) Temporal change in the weighted mean depth (WMD) for each of the six stages of

Nihonotrypaea harmandi larvae in the course of diel- and tidal-phase shifts. The definition of WMD is given in text (Section 2.2). The WMD values based on data in Fig. 4 are plotted at the mid-point of each of the 13 MOCNESS sampling sets conducted during 30 July to 1 August 2006 (Fig. 1). (b) Vertical profile of the averaged onshore current velocities from the ADCP station (Fig. 1; onshore: arrow direction from the circle), based on seven measurements near the mid-point of each MOCNESS sampling set; the sea surface was presented as fixed at the mean depth for the entire sampling period. (c) Combined larval WMDs for each group with the same combination of diel and tidal phases plotted at the corresponding averaged time, based on data in panel (a).

Fig. 6. Temporal change in median depths of *Nihonotrypaea harmandi* larvae in the course of diel- and tidal-phase shifts. The combined median depths are indicated for each group with the same combination of diel and tidal phases (Fig. 5c). The pairs of adjacent phase combinations and of every other ones with significant statistical differences in the larval median positions are connected by arrows (Table 1). The other pairs with significant differences are not indicated. Although the median depths at the daytime ebb and low tides for zoea V were the same (60 m), the proportion of zoeae present at this depth layer was greater at the low tide (Fig. 4). Note that in each panel, the identical data for the nighttime ebb and low tides are illustrated on both edges, respectively.

Fig. 7. Temporal change in the number of each of the six stages of *Nihonotrypaea harmandi* larvae per 5-min horizontal haul from the 5-m depth layer at a 10-m deep station in front of the Tomioka sandflat in the course of diel- and tidal-phase shifts during 5 to 6 October 1994 (Fig. 1, cross mark). The three-term moving average values are given for all-stage zoeae in the 2nd to 71st sampling sets.