Zonation of Congeneric Callianassid Shrimps, *Nihonotrypaea harmandi* (Bouvier, 1901) and *N. japonica* (Ortmann, 1891) (Decapoda: Thalassinidea), on Intertidal Sandflats in the Ariake-Sound Estuarine System, Kyushu, Japan

Yusli Wardiatno†, Katsumasa Shimoda, Kazuki Koyama and Akio Tamaki

Abstract: In the Ariake-Sound estuarine system, western Kyushu, Japan, two congeneric callianassid shrimps, *Nihonotrypaea harmandi* and *N. japonica*, which inhabit deep-reaching burrows on intertidal sandflats, generally occur separately along salinity gradient. The former and latter species appear mainly in (mixo-)euhaline and mixo-polyhaline waters, respectively. The two species co-occur in a restricted water range of intermediate salinity. The present study examined the spatial variation in density of the two species along the intertidal gradient on four sandflats selected from that water range, in relation to various environmental parameters including elevation, duration of exposure, sediment grain-size composition, sediment thickness and firmness, and subsurface-water salinity, temperature, oxygen concentration, and redox potential. On the respective sandflats in the exclusive occurrence ranges, each species inhabited the entire sandflat. In their co-occurrence range, *N. japonica* and *N. harmandi* separately inhabited the upper and lower shores, as a rule. Neither subsurface-water salinity nor temperature variations along the intertidal gradient could explain this zonation pattern. In contrast, the other environmental parameters varied in a shore-level-specific way, and corresponded closely to the zonation. In general, *N. japonica* occupied a broader fundamental niche, which would be associated with the harsher conditions of its primary habitat, i.e., extensive tidal flats in the middle estuary. In particular, a greater tolerance of this species for hypoxic conditions during a longer exposure period was strongly suggested. The abundance pattern of the two species also suggested the competitive dominance of *N. harmandi*, which might result in the exclusion of *N. japonica* from the lower shore.

Key words: Ariake Sound, callianassid shrimps, congeneric species, estuary, intertidal gradient, *Nihonotrypaea*, sandflat, zonation

INTRODUCTION

The analysis of the abundance patterns of congeneric or closely related species is a major focus of the investigation on their adaptive radiation and coexistence (Tokeshi 1998; Schluter 2000). Studies on the distribution patterns of congeneric species along salinity gradients between seawater and freshwater are one of the major subjects of study in estuarine ecology (Perkins 1974; McLusky 1989). However, identifying such patterns is not easy, especially in intertidal benthos. This is because the shore environment is positioned at an intersecting point of the salinity gradient and the other, at least three major environmental gradients, i.e., the intertidal gradient from sea to land, the horizontal gradient of exposure to wave action, and the particle size gradient (Raffaelli & Hawkins 1996; Reise 2001). There are few detailed descriptions of any species distribution pattern incor-
porating all four gradients. Of the decapod crustaceans inhabiting sedimentary shores, brachyuran crabs have been a target group of the most intensive studies for the distribution pattern of closely related species along salinity gradients at various spatial scales (Ono 1959; Macintosh 1988). However, only in a few studies were the distribution pattern of congeneric species along both the salinity and the intertidal gradients recorded (e.g., for ocypodid crabs: Wada 1978; Mouton & Felder 1996; and for grapsid crabs: Frusher et al. 1994; Omori et al. 1998). On a shore where such congeneric species coexist in waters of intermediate salinity, species derived mainly from more saline waters (i.e., closer to the open sea or downstream) and those from less saline waters (i.e., closer to the upper estuary or upstream) tend to occupy the lower and upper parts of the shore, respectively. It is generally expected that species from more saline waters are restricted to the lower shore because of their more stenohaline nature. In contrast, species from less saline waters are often more euryhaline, and it may not be necessary for them to be confined to the upper shore. Actually, the situation is more complicated because (1) the salinity of surface or interstitial waters is not the only factor governing the intertidal distribution (e.g., physiological tolerances for temperature fluctuation, desiccation, siltation on the substratum associated with a heavy freshwater runoff, etc.) and (2) the lower distribution of the upper-shore species could be constrained by predation and/or competitive exclusion by lower-shore species (Willason 1981; Frusher et al. 1994; Omori et al. 1998).

Decapod thalassinidean shrimps of the family Callianassidae are mostly deep-reaching burrow-dwellers, occurring from estuarine intertidal to marine subtidal soft sediments. To our knowledge, no studies have described the distribution patterns of companion species within a family, including congeneric species, along all four environmental gradients listed in the preceding section. In general, for burrow-dwelling thalassinideans like callianassid and upogebiid shrimps inhabiting tidal flats, environmental stresses such as hypoxic or anoxic conditions, hypercapnic conditions, and sulfide toxicity in subsurface waters encountered during low tide add to temperature and salinity fluctuations occurring near the substratum surface (Atkinson & Taylor 1988; Bourgeois & Felder 2001). Thus, ideally, investigation of the intertidal distribution pattern for these shrimps should be accompanied by the measurement of parameters for such gasses and toxic substances as well.

Along an estuary-to-open-sea gradient in the middle part of western Kyushu, Japan (Fig. 1), i.e., the Ariake-Sound estuarine system spanning from Ariake Sound, via Tachibana Bay (waters of intermediate salinity: Matsumoto et al. 1999), to the coastal waters of the East China Sea, Tamaki et al. (1999) surveyed the intertidal distributions and habitats of the congeneric callianassid shrimps Nihonotrypaea harmandi (Bouvier) and N. japonica (Ortmann) at 103 locations [compiled in Fig. 8 in Tamaki et al. (1999) and Fig. 7.5 in Flach & Tamaki (2001)]. Based on 10-year-averaged salinity values for July (= the heaviest rainy season in southern Japan) in the surface waters (i.e., 5-m depth) of the Ariake-Sound estuarine system (data from Coastal Oceanography Research Committee, The Oceanographical Society of Japan 1985), N. harmandi was determined to occur in the salinity range of 30.0–30.5; the isohalines in the estuarine system are given in Fig. 2 of Tamaki & Miyabe (2000). This salinity range spans from the west coastlines of Nishisonogi Peninsula and Amakusa-Shimoshima Island, via the coastline of Tachibana Bay, to the coastline of the outermost one-third of Ariake Sound. Nihonotrypaea japonica mostly occurred in the salinity range of 30.5–28.5, which corresponds to the coastline of the middle one-third of Ariake Sound. The salinity values in the innermost one-third of Ariake Sound range from 28.5 to 24.5, where extensive mudflats are developed along the coastline and neither species occurred. Thus, using the Venice-system terms for the classification of saline waters, N. harmandi could be designated as a euhaline to mixo-euhaline species, while N. japonica could be designated as a mixo-polyhaline species. From the features of the intertidal areas and their substratum grain sizes, the habitats for the two species were basically characterized as follows: N. harmandi, relatively small- to medium-sized sandflats and sandy beaches of medium-fine sands, with uninhabited boulder beaches, very exposed sandy beaches, and mudflats; and N. japonica, extensive sandflats of medium-fine sands, with uninhabited boulder beaches, exposed sandy beaches, and mudflats. Tamaki et al. (1999) also showed that the two species co-occurred on a few small- to medium-sized sandflats distributed in the outermost one-third of Ariake Sound, where the above-mentioned time-averaged salinity values range from 32.5 to 30.5. However, the distribution patterns of the two species along the intertidal gradient on these sandflats have not been examined in detail. The aim of the present study is to establish such distribution patterns on four selected sandflats in relation to several environmental parameters, including subsurface-water ones. The temporal and spatial variations in the environmental parameters on a
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Nishisonogi Peninsula
Ohmura Bay

Tachibana Bay

Fig. 1. Distribution ranges of Nihonotrypaea japonica and N. harmandi on intertidal sandflats in the Ariake-Sound estuarine system spanning from Ariake Sound, via Tachibana Bay (intermediate waters), to the coastal waters of the East China Sea in western Kyushu, Japan (adapted from Fig. 8 in Tamaki et al. 1999). The broken lines seaward of the coastline indicate the extent of the relatively large tidal flats. Six sandflats were selected for investigating the zonation pattern of the two species: as a site with only N. harmandi, from Tomioka Bay located in southern Tachibana Bay (H site); as a site with only N. japonica, from Shirakawa located in the middle one-third of Ariake Sound (J site); and as four sites with the two species, from Mogine (HJ-1 site), Hondo (HJ-2 site), Ohyano (HJ-3 site), and Okoshiki (HJ-4 site) located in the outermost one-third of Ariake Sound.

major sandflat from each species' exclusive occurrence range are also presented as reference patterns.

MATERIALS AND METHODS

Study sites

Ariake Sound and Tachibana Bay are connected by the 5-km-wide Hayasaki Inlet (Fig. 1). The coast of western Kyushu is under a semi-diurnal tidal regime. The average tidal range at spring tides along the coastline from the East China Sea through Tachibana Bay to Hayasaki Inlet is about 3 m and increases to about 6 m in the innermost Ariake Sound. South of Ariake Sound lies Yatsushiro Sound. The two sounds are separated by Uto Peninsula projecting from the mainland of Kyushu and a series of three large islands (Ohyano, Amakusa-Kamishima, and Amakusa-Shimoshima Islands). It is estimated that 99.5% of the water exchange between Ariake Sound and the outside waters occurs through Hayasaki Inlet (Coastal Oceanography Research Committee, The Oceanographical Society of Japan 1985). As a reference site for the exclusive occurrence of Nihonotrypaea harmandi, one sandflat facing Tomioka
Bay, which is located on the northwestern corner of Amakusa-Shimoshima Island, was selected from Tachibana Bay [Tomioka: abbreviated as H (= harmandi) site]. Various aspects of the population ecology of *N. harmandi* on the sandflat have been studied by the last author (A. T.) and his colleagues (e.g., see a review in Flach & Tamaki 2001). Note that in their papers published before 1998, the species name *Callianassa japonica* Ortmann was wrongly used for *N. harmandi* (see Manning & Tamaki 1998; Wardiatno & Tamaki 2001; Tamaki 2003). As a reference site for the exclusive occurrence of *N. japonica*, one sandflat in the middle one-third of Ariake Sound was selected [Shirakawa: J (= japonica) site]. As sites for the co-occurrence of the two species, four sandflats in the outermost one-third of Ariake Sound at Mogine (HJ-1 site), Hondo (HJ-2 site), Ohyano (HJ-3 site), and Okoshiki (HJ-4 site) were selected. Enlarged maps of these six sites are shown in Fig. 2. Of these sites, the sandflats at J site and HJ-2 site are located at the mouths of the largest two
rivers (Shirakawa R. and Tsuboigawa R.) and the second largest two rivers (Hirosegawa R. and Machiyamaguchigawa R.), respectively. The other sites receive much smaller amounts of freshwater inflow. On each sandflat, one or two representative transects were established from the shoreline to the lowest tide line (two for only HJ-3 site, labeled as A, B). The lengths of these transects were approximately 300 m (H site), 350 m (HJ-1 site), 650 m (HJ-2 site), 200 m (HJ-3 site), 400 m (HJ-4 site), and 2,470 m (J site). The elevation profile along each transect was measured using a transit theodolite and a pole with the graduated ruler; only the profile for H site was reproduced from Fig. 8 in Tamaki & Kikuchi (1983). Consulting the tide table for the reference locality nearest to each site, the elevation above the chart datum level was determined for the points placed on each transect. Similarly, the levels of mean high water neap tide (MHWN), mean low water neap tide (MLWN), and mean low water spring tide (MLWS) were determined. The maximum duration of exposure per low tide through the year for each point was estimated by placing a horizontal line for the elevation of that point on a sine curve fitted to the predicted tidal heights over the course of the year.

Temporal change in subsurface environmental parameters at H and J sites

At H site, the yearly changes in temperature and salinity of subsurface waters were monitored from May, 1992 to June, 1993. During low tide at every spring tide, a maximum and minimum thermometer was placed 30 cm below the substratum surface at a point 30 m distant from the shoreline, around the MLWN level (Fig. 5). At about 2-wk intervals, the maximum and minimum temperatures occurring during each preceding period were recorded about 3 h after the sandflat became exposed. At the same time, a 40-cm long acrylic corer with a cross-sectional area of 100 cm² was inserted into the substratum to a maximum depth of 30 cm, and the sediment inside was removed; the method used to determine sediment thickness is described in the next section. The water that subsequently seeped at the bottom of the corer was collected in a bottle and its salinity was measured with a salinity refractometer (S-100, Atago Inc., Japan). At J site, the environmental parameters were regularly monitored from April, 1999 to April, 2000 at a point 244 m distant from the shoreline, a little above the MLWN level (Fig. 6). Although the measurement protocol was similar to that for H site, a YSI Model 85 handheld system (YSI Inc., USA) was used for measuring salinity and dissolved oxygen concentrations, with its sensor placed in the water at the bottom of the corer. The minimum readings for these two variables during the first 20−30 s of measurement were recorded.

Shrimp distribution and environmental parameters along the intertidal gradient

The burrow-opening count and collection of shrimps with the concomitant measurement of the surrounding environmental parameters were conducted at 13 to 28 stations spaced equidistant apart as a rule along each transect (Figs. 2 and 5−11) during daytime low tide at spring tides on 25 June 1998 (H site), 7 September 1998 (HJ-1 site), 11 July 1998 (HJ-2 site), 25 and 26 May 1998 (HJ-3 site), 24 June 1998 (HJ-4 site), 27−30 May 2002 (J site; burrow-opening count), and 13−14 July 2002 (J site; environmental parameters). There was no rainfall during these sampling dates. Under the southern Japanese climate regime, these sampling dates can be grouped into the summer season.

According to Tamaki & Ueno (1998), the burrow of one Nihonotrypaea harmandi has a symmetrical Y-shape with two surface openings, while that of one N. japonica has a single opening. However, the burrow openings of the two species cannot be discriminated by their shapes in the field. In contrast, the burrow openings of Upogebia major, which inhabits the lower shore at J site, could easily be identified by their more round shape and more distinct inner mud-lining than in callianassid shrimps (cf., Swinbanks & Luternauer 1987). To estimate the density of the two Nihonotrypaea species inclusive at each station, the number of burrow openings was counted for a set of 4 × 4 contiguous plots each with a 25 cm × 25 cm unit area. Furthermore, to estimate the actual proportions of the two species in the mixed population at each station, shrimps were collected from a nearby 4 m × 4 m plot using a ‘yabby pump’ similar to that described by Hailstone & Stephenson (1961) and fixed with 10% neutralized formalin-seawater. The mean (± SD) number of shrimps collected per station at the four HJ sites was 34.8 (± 19.9), while the cumulative total number of shrimps collected at H and J sites, including those for the other studies, was over 10,000 at each site (Tamaki et al. 1997; Y. Wardiatno & A. Tamaki, unpublished data). Following the morphological keys given in Wardiatno & Tamaki (2001), the collected shrimps were identified to species and their numbers were counted. Based on the inclusive burrow-opening counts (‘IC’) and the observed ratio of the number of shrimps of the two species in the mixed
population (‘OR’), the actual shrimp densities [mean (± SD) number of shrimps per 625 cm², n = 16] at each station were estimated by solving the simultaneous linear equations for the densities as variables (‘X’: N. harmandi, ‘Y’: N. japonica) as follows: 2X + Y = IC and X/Y = OR. Each density was expressed as number per m².

For granulometric analysis of sediments, a sample to a depth of 3 cm from the substratum surface was collected at each station, and then the median phi, sorting coefficient [quartile deviation, QDs = (Φ75 – Φ25)/2], and silt-clay content (percentage weight fraction smaller than 63 μm) were determined in the laboratory following Buchanan (1984). The sediment samples at H site were collected on 3 August 1997.

The thickness and firmness (or softness) of the sediment column were measured with a Cone-Penetrometer S44R (Maruto Inc., Japan). By vertically pushing the cone tip into the substratum and recording the reading of the dial gauge at 3- to 5-cm depth intervals to a maximum of 88.1 cm, the pressure necessary for maintaining the penetrometer at each depth can be measured. An example graph is shown in Fig. 3. Along every curve connecting the plots was a single distinct inflection point (indicated by the arrow in the figure) from which pressure abruptly increased with depth. The depth of this point was defined as the ‘thickness’ of the sediment column, because this point demarcates the upper column of sand inhabited by shrimps and the lower one dominated by large shell remains and/or coarser sediment grains such as pebble, cobble, and small boulder, and thus unsuitable for shrimp inhabitation (see Fig. 7.6 in Flach & Tamaki 2001). Miller & Curran (2001) demonstrated that the callianassid shrimp Neotrypaea californiensis can penetrate layers of glass plates implanted within the sand column but not densely packed, well-sorted shell beds. To check the possibility of such penetration by the present two species, shrimps were put on the sand column overlaid on the shell bed within a number of aquaria. The shrimps maintained their burrows only in the sand part even after 1 mo (K. Shimoda & A. Tamaki, unpublished data). The firmness of the upper sediment column was defined as the absolute slope value of the linear regression line of pressure on depth, with the greater values indicating the firmer sediments. At J site, only sediment thickness was measured using a long stiff rod.

For subsurface-water parameters at each station, the water that seeped at the depth of 30 cm (or at the lowest depth in cases of sediment thickness < 30 cm) within the corer was targeted. The subsurface waters comprised those that were derived from both the waters of destroyed (through our excavation of sediments) shrimp burrows and the interstitial pore waters that originated from the underground water table. Temperature, salinity, and dissolved oxygen concentration were measured with the YSI Model 85 handheld system, and sediment redox potential (Eh) was measured with an ORP Meter HM-11P (DKK-TOA Corp., Japan). The latter readings were compensated for temperatures. Along the transect on each measurement date, the recording started from the uppermost station 20 min after it became exposed, gradually proceeding seaward as the water edge receded. The measurement at each station was accomplished within 60 min after the water edge had passed. After finally reaching the station closest to the lowest water edge on each date, an additional measurement was made at the bottom of a 20-cm deep seawater column just seaward of the water edge to determine the parameter values from the ‘overlying’ seawater. During the survey of the four HJ sites in 1998, the ORP meter was broken at HJ-1 site, and its Eh values were measured on 13 June 1999.
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RESULTS

Temporal change in the subsurface parameters at H and J sites

The yearly changes in the subsurface-water temperature and salinity at 30-cm depth from the substratum surface at H and J sites are shown in Fig. 4. At H site, the maximum and minimum temperatures varied from 12.3°C (24 Feb. 1992) to 27.2°C (11 Sep. 1992) and from 11.4°C (10 Feb. and 24 Mar. 1993) to 24.2°C (11 Sep. 1992), respectively. At J site, the maximum and minimum temperatures varied from 12.3°C (2 Mar. 1999) to 31.1°C (26 Sep. 1999) and from 7.9°C (23 Feb. 2000) to 26.4°C (26 Aug. 1999), respectively. Thus the amplitudes in the temperatures over the course of the year were greater at J site; the difference between the two sites was 3.9°C for the maximum temperature and 5.7°C for the minimum temperature. The difference between the maximum and minimum temperatures on each measurement date was also greater at J site (0.5–8.1°C vs. 0–4.8°C). Salinities throughout the year were higher and more stable at H site, varying from 33.0 (26 Sep. 1992) to 36.0 (24 Feb. 1993) at H site and from 18.0 (1 July 1999) to 30.0 (16 May 1999) at J site. Through the year at J site, the lower salinities were recorded during periods of heavy rain in southern Japan, i.e., April, late June to mid-July (heaviest of all), and September. Through the year at J site, oxygen concentrations were generally high during the end of December to March (0.97–2.40 mg l⁻¹) than during other months (0.04–1.30 mg l⁻¹), especially during June to November when the maximum subsurface-water temperatures exceeded 20°C. Oxygen concentrations at the stations along the transect at H site at the end of June, 1998 varied from 0.86 to 4.65 mg l⁻¹ (Fig. 5E), which were much higher than those values at J site recorded on the two measurement dates in June, 1999 (Fig. 4).

Shrimp distribution and environmental parameters at all sites

At every site, either Nihonotrypaea harmandi or N. japonica was distributed over the entire transect except for the lowermost station at J site. The variations in the density of the two species and in the environmental parameters along the transect at each site are compiled in Figs. 5–11. The characteristics of each site are summarized below. ‘Stn X’ denotes a station that is X m distant from the shoreline along each transect.

(1) H site. The ground elevation was highest at around the MLWN level situated at Stn 0 to the halfway point, from which it lowered uniformly with a 1/230 inclination (Fig. 5A). The maximum duration of exposure ranged from 3.4 to 6.0 h. Except for Stn 0, the densities of Nihonotrypaea harmandi were in a narrow range over the transect, with mean values of 103.2–200.0 m⁻² (Fig. 5B). The sediments were moderately well- to very well-sorted fine to very fine sands, with a 0.3–1.7% silt-clay content (Fig. 5C). From upper to lower shores, sediments became coarser and better sorted, which is a
Fig. 5. Variations in the density of *Nihonotrypaea harmandi* and in the environmental parameters at the stations along the transect at H site (Fig. 2). Graph A: elevation profile [adapted from Fig. 8 in Tamaki & Kikuchi (1983)] and maximum duration of exposure per low tide through the year. MLWN: mean low water neap tide, MLWS: mean low water spring tide. Graph B: mean (± SD, n = 16) shrimp density. Graph C: median diameter, sorting (quartile deviation), and silt-clay content of the surface 3-cm sediment. Graph D: thickness and firmness of the sediment column as defined in Fig. 3. Graphs E and F: dissolved oxygen concentration, redox potential (Eh), salinity, and temperature of the subsurface water at 30-cm (or a shallower) depth from the substratum surface and of the ‘overlying’ seawater just seaward of the lowest water edge (asterisks).

typical feature of tidal sandflats not located near large rivers (Reise 1985). This was generally true of the *HJ* sites except for the median phi at *HJ*-1 site and for the sorting coefficient on Transect-A of *HJ*-3 site (see Graph Cs in Figs. 7–11). The sediment thickness was mostly 25–30 cm, except for Stn 0 (20 cm) and the lowermost two stations (50 cm) (Fig. 5D). The sediment firmness varied little except for the higher values at Stns 0 and 270. The subsurface-water oxygen concentrations were high for subsurface waters of tidal sandflats, being 16% (at Stn 0) and 30–88% (at the other stations) of the overlying seawater concentration (Fig. 5E). The subsurface-water Eh values were high at all stations, exceeding 420 mV. Except for the lower subsurface-water salinities at the uppermost four stations, the values at the other stations were close to the overlying seawater.
Fig. 6. Variations in the density of *Nihonotrypaea japonica* and in the environmental parameters at the stations along the transect at J site (Fig. 2). The captions for Graphs A to F basically follow those given in Fig. 5. MHWN: mean high water neap tide.

salinity (Fig. 5F). The subsurface-water temperatures were in a narrow range, about 3°C lower than the overlying seawater temperature.

2) J site. The ground level uniformly lowered seaward from Stn 0 situated halfway between the MHWN and MLWN levels, with a 1/1,044 inclination (Fig. 6A). The maximum duration of exposure ranged from 3.1 to 8.7 h. The mean densities of *Nihonotrypaea japonica* increased in a stepwise manner from 27.0 m⁻² at Stn 0 to maxima of 343.0–275.0 m⁻² between Stn 689 and Stn 1,009, from which seaward the values decreased abruptly to 34.1–0 m⁻² (Fig. 6B). The sediments belonged to moderately- to well-sorted fine sands except for the moderately- or well-sorted medium sands at the uppermost and lowermost stations, with a 0.5 to 22.6% silt-clay content (Fig. 6C). The general tendency for a steadily coarsening and better sorting of sediments from the upper to lower shores on tidal sandflats was not observed here. The finer sediments with poorer sorting in the lower shore and the coarsest sediment with better sorting at the lowermost edge could have been due to (1) the localized deposition of fine particles in the lower shore associated with floods of the Shirakawa River after occasional heavy rains (Fig. 2; A. Tamaki, personal
Fig. 7. Variations in the density of *Nihonotrypaea japonica*/*N. harmandi* and in the environmental parameters at the stations along the transect at *HJ*-1 site (Fig. 2). The captions for Graphs A to F basically follow those given in Fig. 5. Graph B: at Stn 120, only the burrow density of the two species inclusive is shown as the gray column because no shrimps could be collected there by the yabby pump to give the proportions of the two species in the mixed population (see text).

observation) and (2) the dumping of allochthonous sand with coarser grains around the lowermost shore conducted by Oshima Fisheries Co-Operative Association in Kumamoto City in 2001 and before for enhancing the settlement of spats of the commercial clam *Ruditapes philippinarum* (O. F. Co-O. A., personal communication). The sediment columns were thick throughout the transect, ranging from 45 to 195 cm (Fig. 6D). In accordance with the high-density zone of *N. japonica* in the upper shore, the subsurface-water oxygen concentrations and *Eh* values were markedly higher there than the quite low values in the lower shore (Fig. 6E). A similar tendency was observed for the subsurface-water temperature along the transect except for Stns 1889 and 1969 (Fig. 6F). The higher values of the above three parameters associated with the higher densities of *N. japonica* could have been due to its burrow-water effects. In contrast, the subsurface-water salinities were generally at a constant level close to the overlying seawater salinity.

(3) *HJ*-1 site. Stn 0 was situated at the MLWN level, and the inclination of the ground elevation to the lowermost station was 1/256 (Fig. 7A). The maximum
Fig. 8. Variations in the density of *Nihonotrypaea japonica*/*N. harmandi* and in the environmental parameters at the stations along the transect at *HJ-2* site (Fig. 2). The captions for Graphs A to F basically follow those given in Fig. 5. Graph C: as the sediment silt-clay contents at Stns 120, 180, and 240 exceeded 25%, the $\phi$ 75 values needed for the calculation of $QD$ $\phi$ were estimated from the extrapolated line connecting the plots for $3\phi$ and $4\phi$ in the cumulative weight curves against $\phi$.

Duration of exposure ranged from 0.8 to 5.9 h. *Nihonotrypaea japonica* was distributed in the upper two-thirds of the transect, with quite low mean densities of 1.6–4.8 m$^{-2}$. In contrast, *N. harmandi* was distributed in the lower two-thirds of the transect, with mean densities generally increasing from Stn 150 seaward (9.6–72.8 m$^{-2}$) (Fig. 7B). Most of the sediments from Stn 0 to Stn 150 was poorly-sorted coarse sand, with a 0.5–3.8% silt-clay content. Further seaward the sediment grain-size characters changed drastically, varying from moderately well-sorted medium sand to well-sorted fine sand, with a 0.3–1.0% silt-clay content (Fig. 7C). The increase in the median phi values seaward is not a normal pattern for tidal sandflats without substantial rivers. This could have been ascribed to the allochthonous whitish sand of coarser grains dumped in the zone between the uppermost edge of the sandflat and the land (the blank part between the gray and black ones at *HJ-1* site in Fig. 2). This dumping was performed in 1993 by the local city administration to provide an artificial beach for tourists (H. Matsumoto, personal communication). It is supposed that some of these coarser grains had settled on
the sandflat and mixed with the natural surface sediment. The sediment thickness also showed a contrasting pattern between the upper and lower shores (10.1–20.1 cm at Stns 0–150 vs. 30.1–73.1 cm at the seaward stations), while a reverse tendency was observed for the sediment firmness (Fig. 7D). Similarly, the subsurface-water oxygen concentrations were contrastingly lower at Stn 0–Stn 150 (2.8–9.5% of the overlying seawater concentration) and much higher at the seaward stations (20.5–67.3%); a similar pattern was seen in Eh values (–69––8 mV vs. 279–315 mV) (Fig. 7E). Subsurface-water salinities varied only slightly over the transect and were close to the overlying seawater salinity (Fig. 7F). The subsurface-water temperatures were lower than the overlying seawater temperature and were almost constant except for the uppermost three stations.

(4) HJ-2 site. Stn 0 was situated close to the MLWN level, and the inclination of the ground elevation to the lowermost station was 1/540 (Fig. 8A). The maximum duration of exposure ranged from 1.5 to 5.7 h. Of all HJ sites, this was the only site where substantial numbers of Nihonotrypaea japonica were distributed in both
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Fig. 10. Variations in the density of *Nihonotrypaea japonica*/*N. harmandi* and in the environmental parameters at the stations along Transect-B at HJ-3 site (Fig. 2). The captions for Graphs A to F basically follow those given in Fig. 5.

The density at each station varied from 22.4 to 120.0 m⁻², with two peaks at Stns 240 and 648 (= the lowermost station). *Nihonotrypaea harmandi* was distributed only in the lower shore (= from Stn 300 seaward), with mean densities of 14.4–51.2 m⁻². The sediments from the lowermost station landward to Stn 300 were moderately well- to well-sorted fine sand, with a 1.4–7.2% silt-clay content (Fig. 8C). Those at the intermediate four stations (from Stn 240 to Stn 90) were moderately- to poorly-sorted very fine sand, with a 23.8–44.8% silt-clay content, taking the extreme values for each of the three parameters along the entire transect. This could have been due to the localized deposition of fine particles there associated with floods of the nearby rivers after occasional heavy rains [A. Tamaki, personal observation; in particular, note the direction of the mouth of the Hirosegawa River toward the site (Fig. 2)]. The sediments at the uppermost three stations were moderately well-sorted fine to medium sand, with a 9.5–13.1% silt-clay content. The sediment thickness was in a relatively small range over the entire transect, 40.1–58.1 cm (Fig. 8D). Except for Stns 180 and 480, the sediment firmness varied little. The subsurface-water oxygen concentrations
Fig. 11. Variations in the density of *Nihonotrypaea japonica*/*N. harmandi* and in the environmental parameters at the stations along the transect at HJ-4 site (Fig. 2). The captions for Graphs A to F basically follow those given in Fig. 5.

were low over the entire transect, 2.9 – 10.4% of the overlying seawater concentration, except for 18.8% at Stn 600 (Fig. 8E). The subsurface-water Eh values had two peaks along the transect; the lower one (188 mV) at Stn 180 and the higher one (331 mV) at Stn 648. The pattern of variation around the lower peak was similar to those for the density of *N. japonica* (Fig. 8B) and for the three sediment-grain-size parameters (Fig. 8C). The increasing Eh values toward the lowest shore appears to be parallel with the general increase in the density of *N. harmandi* (Fig. 8B). The subsurface-water salinities were close to the overlying seawater salinity, with little variation (Fig. 8F). The subsurface-water temperatures were in a narrow range and about 4°C lower than the overlying seawater temperature.

(5) HJ-3 site. Stn 0 was situated well below the MLWN level, and the inclination of the ground elevation to the lowermost station was 1/194 (Transect A) or 1/253 (Transect B) (Figs. 9A and 10A). The maximum duration of exposure ranged from 1.4 to 4.4 h (Transect A) and from 1.7 to 4.1 h (Transect B). *Nihonotrypaea japonica* was distributed in the upper shore from Stn 0 as far as Stn 90, with low densities of 3.2 – 22.4 m² (Figs. 9B and 10B). In contrast, *N. harmandi* was distributed
over the entire transects except for the uppermost few stations. The mean densities were especially high in the lower half of the transects, 89.6–465.6 m⁻², except for the lower density at the lowermost station of Transect B. The sediments along Transect A were moderately well-to well-sorted fine to very fine sands, with a 2.6–20.0% silt-clay content (Fig. 9C). The sediments along Transect B were moderately- to very well-sorted fine to very fine (medium only at Stn 0) sands, with a 0.8–6.8% silt-clay content (Fig. 10C). From the lower shore landward, the abrupt increases in the median phi and silt-clay content values were observed at Stn 90 of Transect A and at Stn 45 of Transect B. Such a contrasting pattern between the upper and lower shores demarcated at these stations appears to be paralleled not only by the patterns for densities of N. japonica and N. harmandi (Figs. 9B and 10B) but also by those for sediment thickness, sediment firmness (Figs. 9D and 10D), subsurface-water oxygen concentrations, and Eh values (Figs. 9E and 10E), i.e., (a) the thinner and thicker sediments (6.9–40.1 cm vs. 35.1–68.1 cm); (b) the firmer and softer sediments; (c) the lower and higher oxygen concentrations (0.3–2.6% vs. 13.0–46.0% of the overlying seawater concentration); and (d) the lower and higher Eh values (10–166 mV vs. 392–490 mV). Except for a few stations, the subsurface-water salinities along both transects were in a narrow range at about half the overlying seawater salinity (Figs. 9F and 10F). The subsurface-water temperatures were also 2.5–5°C lower than the overlying seawater temperature, with two peaks along Transect A and with only a little variation along Transect B.

(6) HJ-4 site. This site is located at the westernmost edge of the extensive sandflats including J site. The site is also situated at the innermost edge of the Nihonotrypaea harmandi distribution range in Ariake Sound for both adults (Tamaki et al. 1999) and planktonic larvae (Tamaki & Miyabe 2000). Stn 0 was situated well below the MLWN level, and the inclination of the ground elevation to the lowermost station was 1/607 (Fig. 11A). The maximum duration of exposure ranged from 2.1 to 3.9 h. Although N. japonica was distributed over the entire transect, its highest mean densities were observed in the upper shore, reaching as far as a little beyond the halfway point, with a decrease from 203.0 m⁻² (at Stn 30) to 136.0 m⁻² (at Stn 213). In contrast, N. harmandi was distributed in the lower shore, reaching up to a little beyond the halfway point, with a decrease in the mean densities from 217.6 m⁻² (at Stn 330) to 16.0 m⁻² (at Stn 155). From the lowermost station landward, the sediments shifted from very well-sorted fine sand, via well-sorted fine sand, to moderately well-sorted very fine sand, with a 0.55–8.95% silt-clay content (Fig. 11C). In particular, the sediments at the uppermost three stations were much finer. The sediment thickness was thinner in the upper shore dominated by N. japonica (15.1–30.1 cm) than in the lower shore dominated by N. harmandi (35.1–53.1 cm) (Fig. 11D). The sediment firmness generally decreased from Stn 0 seaward. The subsurface-water oxygen concentrations were at a low level between 1.1 and 10.7% of the overlying seawater concentration, with those at the uppermost four stations generally lower than those values at the seaward stations (Fig. 11E). Except for Stn 0, the subsurface-water Eh values increased gradually from 185 mV at Stn 30 seaward, reaching a plateau around 485 mV at Stn 252, at which the sediment thickness abruptly increased. The subsurface-water salinities fluctuated over a wide range between 7.5 and 29.4, the latter value closer to the overlying seawater salinity (Fig. 11F). Except for Stn 0, the subsurface-water temperatures varied little, about 5°C lower than the overlying seawater temperature.

(7) Summary of patterns at HJ sites. Except for Nihonotrypaea japonica at HJ-2 site, a clear contrasting distribution pattern was depicted at the HJ sites, with N. japonica dominant in the upper half of the shore and N. harmandi dominant in the lower half of the shore. Except for HJ-1 site, the sediments became generally finer and poorer sorted from the lowermost station landward. The thicker and softer sediments in the lower half of the shore were replaced by those of the opposite properties in the upper half of the shore. The patterns for both subsurface-water oxygen concentration and Eh also differed spatially, with higher values in the lower-half shore. Along each transect, however, there were no significant correlations between the 'relative position values' of the stations and their subsurface-water salinity or temperature values (r = 0.02–0.53; all P > 0.05); the relative position value of each station was defined as that standardized for the total length of the transect. The range and the median value of each of the environmental parameters other than subsurface-water temperature and salinity for N. harmandi and N. japonica are summarized for H-, J-, and the combined HJ-sites (Table 1). At the HJ sites, except for the sediment median phi, every parameter value differed significantly between the two species (SPSS 1999; two-tailed Mann-Whitney U-test, P < 0.01 or 0.05). Compiling data from all sites, it is apparent that N. japonica occupied a generally broader fundamental niche than N. harmandi.
Table 1. Summary of environmental parameters for *N. harmandi* and *N. japonica* at *H, HJ (all combined), and J* sites. ‘n’ in parentheses, the number of stations where either species occurred.

<table>
<thead>
<tr>
<th></th>
<th><em>N. harmandi</em> (<em>H</em> site)</th>
<th><em>N. harmandi</em> (<em>HJ</em> sites)</th>
<th><em>N. japonica</em> (<em>HJ</em> sites)</th>
<th><em>N. japonica</em> (<em>J</em> site)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Exposure (h)</strong></td>
<td>(3.4–6.0; 5.6; 16)</td>
<td>(0.8 – 3.7; 2.9; 41)</td>
<td><strong>(1.5 – 5.9; 3.6; 39)</strong></td>
<td>(4.2 – 8.7; 6.3; 27)</td>
</tr>
<tr>
<td><strong>Median diameter (φ)</strong></td>
<td>(2.35 – 3.13; 2.57; 16)</td>
<td>(0.94 – 3.39; 2.53; 41)</td>
<td><strong>(-0.49 – 3.55; 2.39; 39)</strong></td>
<td>(1.10 – 3.05; 2.36; 27)</td>
</tr>
<tr>
<td><strong>Sorting (φ)</strong></td>
<td>(0.32 – 0.58; 0.38; 16)</td>
<td>(0.31 – 1.28; 0.49; 41)</td>
<td><strong>(-0.31 – 1.82; 0.59; 39)</strong></td>
<td>(0.39 – 0.96; 0.59; 27)</td>
</tr>
<tr>
<td><strong>Silt-Clay (%)</strong></td>
<td>(0.32 – 1.69; 0.67; 16)</td>
<td>(0.34 – 14.25; 2.02; 41)</td>
<td><strong>(-0.47 – 44.78; 3.67; 39)</strong></td>
<td>(0.94 – 22.61; 5.71; 27)</td>
</tr>
<tr>
<td><strong>Thickness (cm)</strong></td>
<td>(20.1 – 49.9; 30.1; 16)</td>
<td>(15.1 – 73.1; 53.1; 41)</td>
<td><strong>(-15.1 – 63.1; 40.1; 39)</strong></td>
<td>(51.5 – 195.0; 155.0; 27)</td>
</tr>
<tr>
<td><strong>Firmness (Pa cm⁻²)</strong></td>
<td>(320.2 – 9506.5; 5053.4; 16)</td>
<td>(308.4 – 44730.3; 4504.5; 41)</td>
<td><strong>(433.6 – 57539.0; 8305.6; 39)</strong></td>
<td>no data</td>
</tr>
<tr>
<td><strong>Oxygen (mg l⁻¹)</strong></td>
<td>(0.86 – 4.65; 3.54; 16)</td>
<td>(0.03 – 4.26; 0.93; 40)</td>
<td><strong>(0.03 – 2.76; 0.43; 39)</strong></td>
<td>(0.03 – 2.58; 0.05; 27)</td>
</tr>
<tr>
<td><strong>Eh (mV)</strong></td>
<td>(429 – 489; 479; 16)</td>
<td>(-61 – 490; 398.5; 40)</td>
<td><strong>(-69 – 490; 116.5; 39)</strong></td>
<td>(28 – 483; 106; 27)</td>
</tr>
</tbody>
</table>

*P < 0.05 or **P < 0.01, two-tailed Mann-Whitney U-test for significant differences between *N. harmandi* and *N. japonica* at HJ sites.

**DISCUSSION**

The segregated intertidal zonation pattern between *Nihonotrypaea japonica* and *N. harmandi* within the same tidal flat was confirmed at all *HJ*-sites except *HJ*-2. Worldwide, such intertidal zonation of congeneric callianassid species, including their extensions into shallow subtidal zones, has been recorded for only a few cases: (1) *Biffarius* (originally as *Callianassa*) *arenosus* in sandy and muddy substrata of the intertidal and shallow (< 10 m) subtidal zone and *B.* (originally as *C.*) *limosa* in sandy and muddy substrata from the intertidal to deeper (> 10 m) subtidal zone in southern Australia (Coleman & Poore 1980); (2) *Callianassa candida* in the higher muddy zone and *C. tyrrhena* in the lower sandy zone on a tidal flat in the northern Adriatic Sea (Dworschak 1987, 1998, 2001); the author also noted that in terms of their geographical distributions, *C. candida* and *C. tyrrhena* occur in less and more saline waters, respectively, and that the former species is common in coarse sand and in shallow subtidal substrata as well; (3) *Neotrypaea* (originally as *Callianassa*) *californiensis* in the higher sandy zone with a lower subsurface water table and *N.* (originally as *C.*) *gigas* in the lower muddy zone with a higher subsurface water table on tidal flats in Baja California, Mexico (Griffis & Chavez 1988); and (4) *Callichirus islagrande* in the upper intertidal zone and *C. major* in the extremely lower intertidal and the shallow subtidal zones of sandy beaches in the northern Gulf of Mexico (Felder & Griffis 1994). Even extending the target membership into the family level, the records of zonation patterns for a set of companion species are still limited: (1) *Trypaea* (originally as *Callianassa*) *australiensis*, *B. arenosus*, and *B. limosa* in the same area as above in southern Australia (Coleman & Poore 1980); (2) *Callichirus major* and *Sergio* (originally as *C.*) *mirim* in southern Brazil (Rodrigues & Hödl 1990); and (3) *Corallianassa longiventris*, *Neocallichirus grandimana*, and *Glypturus acanthochirus* in Belize (Dworschak & Ott 1993). However, further extending the target membership to include not only Callianassidae but also Upogebiidae, a variety of species from the two families have often been recorded to constitute companion members in the same tidal flat, sometimes occupying different tidal zones (e.g., for a review, see Dworschak 1987, pp. 352-354).

On a number of estuarine tidal flats in Japan, *N. japonica* and *Upogebia major* sometimes co-occur, with the former and the latter dominant in the upper and lower shores, respectively (e.g., Mukai & Koike 1984; at *J* site in the present study, A. Tamaki, personal observation).

One obstacle to identifying the causes for the zonation pattern of *Nihonotrypaea harmandi* and *N. japonica* based on the parameters measured in the present study arises from that most of them varied in a common, shore-level-specific way along the intertidal gradient at the *HJ* sites (Figs. 7 – 11). Such a co-varying pattern would make it difficult to determine the prime causative factor responsible for the shrimp zonation. In reality, the interactions between parameters would also be crucial.

It may generally be expected for tidal flats that the temperature and salinity of subsurface waters in the upper shore and in the lower shore are more affected by the lateral penetration of the underground table of freshwater from land and that from the offshore seawater, respectively. In the present study, the higher stability in the subsurface-water temperature and both the higher absolute values and the higher stability in the subsurface-water salinity experienced by *Nihonotrypaea harmandi* at *H* site than by *N. japonica* at *J* site over the course of the year (Fig. 4) imply that these factors, on a long-term
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basis, could in some way determine the zonation pattern of the two species at the HJ sites (Figs. 7B, 9B, 10B, and 11B). Most probably, N. japonica would be more euryhaline and eurythermal. Of the four HJ sites, HJ-2 is the only sandflat where the flows from the local large rivers cover the entire area (Fig. 2). The densities of N. harmandi in the lower shore at HJ-2 site were lower than those at the other three HJ sites, and only at this site was the distribution of N. japonica extended to the lowermost station, with densities in the lower shore comparable to those in the upper shore (Fig. 8B). These data suggest some influence of salinity fluctuation in the long run on the zonation pattern of the two Nihonotrypaea species, in support of the framework given in the first paragraph of the Introduction. However, with only a snapshot data set collected in the present study, no significant relationships between the abundance of each species and subsurface-water temperature or salinity were detected along the transect at each HJ site.

The markedly lower subsurface-water oxygen concentrations in the habitats of Nihonotrypaea japonica than those of N. harmandi over all six sites (Table 1; Fig. 12) suggest that the former species is more tolerant of hypoxic conditions lasting for longer durations of exposure. The consistently low oxygen levels in the subsurface waters at J site over the course of the year, especially during the warmer seasons (Fig. 4), also suggest the higher tolerability of N. japonica. During recent several years, a mass invasion and persistence of N. japonica populations in several penaeid shrimp aquaculture ponds occurred on the coast of Oita Prefecture, eastern Kyushu, causing a marked reduction in the commercial yield (Y. Fukuda, in preparation; A. Tamaki, personal observation). Similar invasions have been recorded from Central and South Americas (Nates & Felder 1998). The N. japonica populations in the ponds survive for as long as 6 mo during the period of drainage, which also suggests the high tolerance of N. japonica to hypoxic as well as harsh salinity and temperature conditions. In their comparative physiological study of N. (originally as Callianassa) japonica and Upogebia major, Mukai & Koike (1984) demonstrated that (1) N. japonica was better adapted to hypoxic conditions in its burrow water than U. major, (2) placed under anoxic conditions, N. japonica began to die after 19 h and had a LD$_{50}$ value of 40 h, while U. major began to die after 5 h and had a LD$_{50}$ value of 9 h, respectively, and (3) these differences in physiological tolerance could explain the higher- and lower-shore segregation of the two species on a tidal flat in northern Japan. Thus even the lowest level of subsurface-water oxygen concentrations during the maximum exposure duration encountered at the present study sites (0.07 mg l$^{-1}$ for 8.7 h at J site: Fig. 6) is considered to be well within the tolerance limit for N. japonica. The difference in respiratory physiological characteristics between N. japonica and U. major may be reflected by their burrow architectures. The burrow of N. japonica has a single surface opening, with more branches along its shafts (Tamaki & Ueno 1998), while that of U. major has a simpler, symmetrical Y-shape, with two surface openings (Mukai & Koike 1984; Hamano 1990; Kinoshita 2002). Thus it is expected that the stagnation of water flow would more easily occur in the burrow of N. japonica during submerged periods. Likewise, based on the difference in tolerances for hypoxic and anoxic conditions between Neotrypaea (originally as Callianassa) californiensis and U. pugettensis (e.g., Thompson & Pritchard 1969), Swinbanks & Murray (1981) and Swinbanks & Luternauer (1987) interpreted the segregated zonation of these two species in the upper and lower shores on two tidal flats in a British Columbia (Canada) estuary. Except for the above two sets of callianassid and upogebiid species among those companion shrimps cited in the first paragraph of the Discussion, no respiratory physiology-based explanations have been given as the causal factors that could determine their intertidal zonation patterns, though results of physiological experiments do exist for several species (e.g.,

Fig. 12. Scatter plots for maximum duration of exposure at spring tides through the year and subsurface-water oxygen concentration at all sites (compiled from the data in Figs. 5–11). The occurrence of (1) Nihonotrypaea harmandi at H site, (2) only N. harmandi, both N. harmandi and N. japonica, and only N. japonica at the combined HJ sites, and (3) N. japonica at J site are indicated separately.
However, it must be noted that some downward limitation along sediment depth could also exist for this species because the deeper part of the burrow would be hardly irrigated (cf., Forster & Graf 1992, 1995). In contrast, specimens of adult *N. japonica* were collected from a wider range of sediment thickness, from 15 cm (HJ-1 and -4 sites) to 195 cm (J site) (Table 1; Figs. 6, 7, and 11) and as thin as 5–10 cm in other localities (Tamaki et al. 1999; A. Tamaki, unpublished data); but note the maximum depth of resin casts of *N. japonica* burrows so far retrieved was 64.5 cm (Tamaki & Ueno 1998). As regards the sediment sorting coefficient, silt-clay content, firmness, and the subsurface-water Eh value over the HJ sites, the occurrences of *N. harmandi* and *N. japonica* in relation to these parameters were significantly separated (Table 1; Graphs C, D, E in Figs. 7–11). The range of the species occurrence for each of the above parameters, together with that for sediment median phi, was generally wider for *N. japonica* than for *N. harmandi* (Table 1). These physical and physicochemical differences in environmental conditions of the two species’ occurrence ranges would reflect their primary habitat conditions along the gradients of salinity, exposure to wave action, and particle size (and their interactions) (e.g., Raffaelli & Hawkins 1996; Reise 2001). In general, poorly sorted sediment with a high silt-clay content is characteristic of relatively large tidal sandflats formed around the mouth of large rivers. Filling of interstitial space of such poorly sorted sediment by finer particles with a higher organic content would concurrently result in the increased firmness, hindrance of deeper oxygen penetration, and more intensified reduced conditions. In contrast, pocket beaches and small sandflats formed between rocky headlands (e.g., HJ-1 and -3 sites) or at the base of a tombolo (e.g., H site), which are subjected to increasing exposure to wave action and limited freshwater inflows, have the opposite sedimentary traits. These basic characteristics could be modified by the presence of relatively large rivers such as seen at HJ-2 site, which would explain the fairly high densities of *N. japonica* and low densities of *N. harmandi* in the lower shore (Fig. 8).

What makes the situation complex when trying to identify causal relationships linking the environmental parameters to the abundance of the two *Nihonotrypaea* species is the possibility that shrimp activity would affect these parameters. Well-documented effects caused by the presence of callianassid shrimp burrows or by their bioturbation in high densities over the sediment column include: (1) softer (less compact) sediments due to void burrow space and rapid overturn of sediments (Miller 1984; Nates & Felder 1998); (2) retention of burrow...
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water during exposed periods, resulting in an elevated water table that contains higher concentrations of oxygen derived from fresh seawater (Miller 1984; Swinbanks & Luternauer 1987; Nates & Felder 1998); (3) increased rates of fine-sediment resuspension and/or lateral bedload transport, resulting in a reduced silt-clay content and increased erodibility of the substratum surface (Ott et al. 1976; Shinn 1968; Roberts et al. 1982; Suchanek 1983; Vaugelas et al. 1986); (4) vertical sediment sorting, resulting in the maintenance of a better-sorted upper layer and the downward accumulation of coarser grains such as gravel, shell remains, and coral fragments (Suchanek 1983; Tudhope & Scoffin 1984; Dworschak & Ott 1993; Nates & Felder 1998); and (5) increased porosity and permeability of sediments, causing the oxygenated and oxidized surface to descend to considerable depths (Ott et al. 1976; Miller 1984; Forster & Graf 1992, 1995; Ziebis et al. 1996; Nates & Felder 1998).

Most of these studies demonstrated only local effects surrounding shrimp patches; only a few have extended their scope into landscape-level effects (e.g., Roberts et al. 1982). At H site in the present study, following the population expansion of *N. harmandi* from the upper one-third of the shore to the lowermost edge, which rapidly occurred during 1979 to 1983, the modifications in all sediment parameters as listed above were observed over the lower two-thirds of the shore (Tamaki & Kikuchi 1983; Tamaki 1984; Tamaki 1988; Tamaki & Suzukawa 1991; Tamaki & Ingole 1993; Tamaki 1994; Flach & Tamaki 2001). As the lowest mean shrimp density established in the newly-colonized zone at H site at that time was 400 m⁻², the densities of *N. harmandi* observed in some part of the lower shore at HJ-3 site (Figs. 9B and 10B) are the figures that could well have altered the ambient sedimentary conditions. It would be interesting to investigate whether and to what extent the lower shrimp densities recorded at the other HJ sites could affect sediment parameters at the landscape level. For example, the linear regression lines with the significantly positive slopes of subsurface-water oxygen concentration on shrimp density (combined from all stations at the HJ sites) would suggest the existence of a density-dependent positive effect due to shrimp burrow waters (Fig. 13). Although no investigation has been made for the burrow/bioturbation effects of *N. japonica* to date, there is strong suggestion that they could also alter sediment parameters. For example, at J site, apparently positive relationships were observed between shrimp abundance and subsurface-water oxygen concentration or Eh value (Figs. 6B, E). Such habitat amelioration in terms of oxygen concentration by *N. japonica* through a kind of positive feedback process under its higher densities would enable shrimps to allocate more energy to growth and reproduction even in the originally unfavorable sedimentary environment of the upper shore on an extensive
tidal flat like J site (cf., Bruno & Bertness 2001). Likewise, in the upper shore at H site, the elevated subsurface-water oxygen concentrations would have benefited *N. harmandi* to survive the maximum of 6-h exposure as discussed earlier (Figs. 5A, B, and 12; see also Tamaki & Ingole 1993).

The absence or quite low densities, if any, of *Nihonotrypaea japonica* in the lower shore at HJ-1, -3, and -4 sites, where *N. harmandi* were abundant (Figs. 7B, 9B, 10B, and 11B), suggests that some negative effects could have been exerted by the latter species on the former species. The presence of *N. japonica* over the entire shore at J site, with the absence of *N. harmandi*, may also point to this idea. When the mean densities of *N. japonica* are plotted against those of *N. harmandi* using all HJ-site data (Fig. 14), it could be postulated that the lowest density of *N. harmandi* potentially excluding *N. japonica* is about 80 m⁻². At HJ-2 site, the densities of *N. harmandi* in the lower shore (maximum = 51.2 m⁻²) were below this assumed critical value, accompanied by the relatively high densities of *N. japonica* (Fig. 8B). Future investigation is needed to determine whether *N. harmandi* is competitively superior to *N. japonica*. Asymmetrical interference competition through bioturbation was assumed to explain the segregated zonation patterns for (1) *Neotrypaea californiensis* (the superior competitor) and *Upogebia pugettensis* (Swinbanks & Luternauer 1987) and (2) *Glypturus acanthochirus* (the superior competitor) and *Neocallichirus grandiman*a (Dworschak & Ott 1993).

**CONCLUSIONS**

The data for the environmental parameters measured in the present study have revealed that *Nihonotrypaea japonica* occupies a generally broader fundamental niche than *N. harmandi*. This could be most reasonably understood in light of the harsher environmental conditions primarily associated with extensive tidal flats in a middle estuary inhabited by the former species except for the less exposure to wave action. Furthermore, if any kind of asymmetrical competition between the two species is proved to exist, their distribution patterns observed over the four HJ sites will add another example to one typical marine ecological system comprising two closely related species in competition; there, the inferior species can coexist in the same intertidal shore by virtue of its greater physiological tolerance of the harsher environmental conditions in the upper zone (e.g., for an extensive review, see Branch 1984).

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**REFERENCES**


Coleman, N. and G. C. B. Poore 1980. The distribution of
Zonation of congeneric callianassid shrimps


Nickell, L. A. and R. J. A. Atkinson 1995. Functional morphology of burrows and trophic modes of three thalassinidean shrimp species, and a new approach to the classification of...


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