

LARVAL ABUNDANCE PATTERNS FOR THREE SPECIES OF *NIHONOTRYPAEA*
(DECAPODA: THALASSINIDEA: CALLIANASSIDAE) ALONG AN ESTUARY-
TO-OPEN-SEA GRADIENT IN WESTERN KYUSHU, JAPAN

Akio Tamaki and Shin Miyabe

Faculty of Fisheries, Nagasaki University, Bunkyo-machi 1–14, Nagasaki 852–8521, Japan
(corresponding author (AT) e-mail: tamaki@net.nagasaki-u.ac.jp)

A B S T R A C T

Based on plankton samples collected from an estuarine system in western Kyushu, Japan, in summer, 1998, larval abundance patterns for three species of *Nihonotrypaea* were examined in relation to the intertidal habitats of adults [*N. japonica*—sandflats within the enclosed estuary (= Ariake Sound); *N. harmandi*—sandflats in the area from the outermost part of Ariake Sound through the waters of an intermediate character (= Tachibana Bay) to the open sea (= the East China Sea); and *N. petalura*—boulder beaches in the same waters as in *N. harmandi*]. Largely, the distribution for adults of the three species reflected abundance patterns of their larvae. Larvae of *N. petalura* comprised only 6% of the sample, reflecting the lower abundance of adults. Zoea 1 of *N. japonica* and Zoea 1 of (*N. harmandi* + *N. petalura*) occurred from Ariake Sound to mostly the northern Tachibana Bay and from Ariake Sound to the entire Tachibana Bay, respectively. It was suggested that 1) with the progression of larval stages for 15–19 days (up to Zoea 5), the three larval species remained in Ariake Sound, while most of them disappeared from the northern Tachibana Bay; and 2) larvae of *N. harmandi* and *N. petalura* were retained throughout development in the southern Tachibana Bay, which corresponded well to the largest local adult populations of each species occurring along the northern coast of an island in the southern Tachibana Bay. Possible mechanisms generating the larval abundance patterns are discussed in relation to the oceanographic conditions of the estuarine system.

Callianassid ghost shrimps are one of the most common macroinvertebrates in marine intertidal and subtidal sediments. Their bioturbating activities have been reported to generate both considerable disturbances to ambient sediments and consequent effects on benthic community structure (e.g., Tamaki, 1994; Ziebis *et al.*, 1996). However, the number of studies on ghost shrimp population dynamics is fewer (e.g., Tamaki *et al.*, 1997). In particular, studies on larval abundance patterns are quite limited (Hailstone and Stephenson, 1961; Sandifer, 1973; Johnson and Gonor, 1982).

The first author (AT) has studied the benthic population dynamics of a callianassid species identified as *Callianassa japonica* Ortmann on an intertidal sandflat in western Kyushu, Japan (e.g., Tamaki *et al.*, 1997) (Fig. 1). Until recently, it was believed that two species of *Callianassa* commonly occurred in intertidal habitats in Japan: *C. japonica* Ortmann and *C. petalura* Stimpson (see Sakai, 1969). However, in their taxonomic revision of the Japanese species, Manning and Tamaki

(1998) revealed that Sakai's "*C. japonica*" was in fact a mixture of *C. japonica* and *C. harmandi* Bouvier. They also proposed a new genus, *Nihonotrypaea*, to include the three Japanese species. Now all the material studied by AT and his colleagues has proven to be *N. harmandi*, exclusively occurring in their main study site [= the Tomioka Bay sandflat (Fig. 1)]. Furthermore, based on their extensive survey on the intertidal distributions and habitats of the three *Nihonotrypaea* species along an estuary-to-open-sea gradient in western Kyushu, including the Tomioka Bay sandflat, Tamaki *et al.* (1999) have shown that in the most part, *N. japonica* and (*N. harmandi* + *N. petalura*) were distributed separately along the gradient (Fig. 2). As regards the larval stages, the descriptions of entire development have been recently completed for all species, with the use of laboratory-reared materials (Konishi *et al.*, 1990; Miyabe *et al.*, 1998; Konishi *et al.*, 1999). This provided several keys to discriminate among larvae of the three species. The purpose of the present paper is to examine the larval abundance pat-

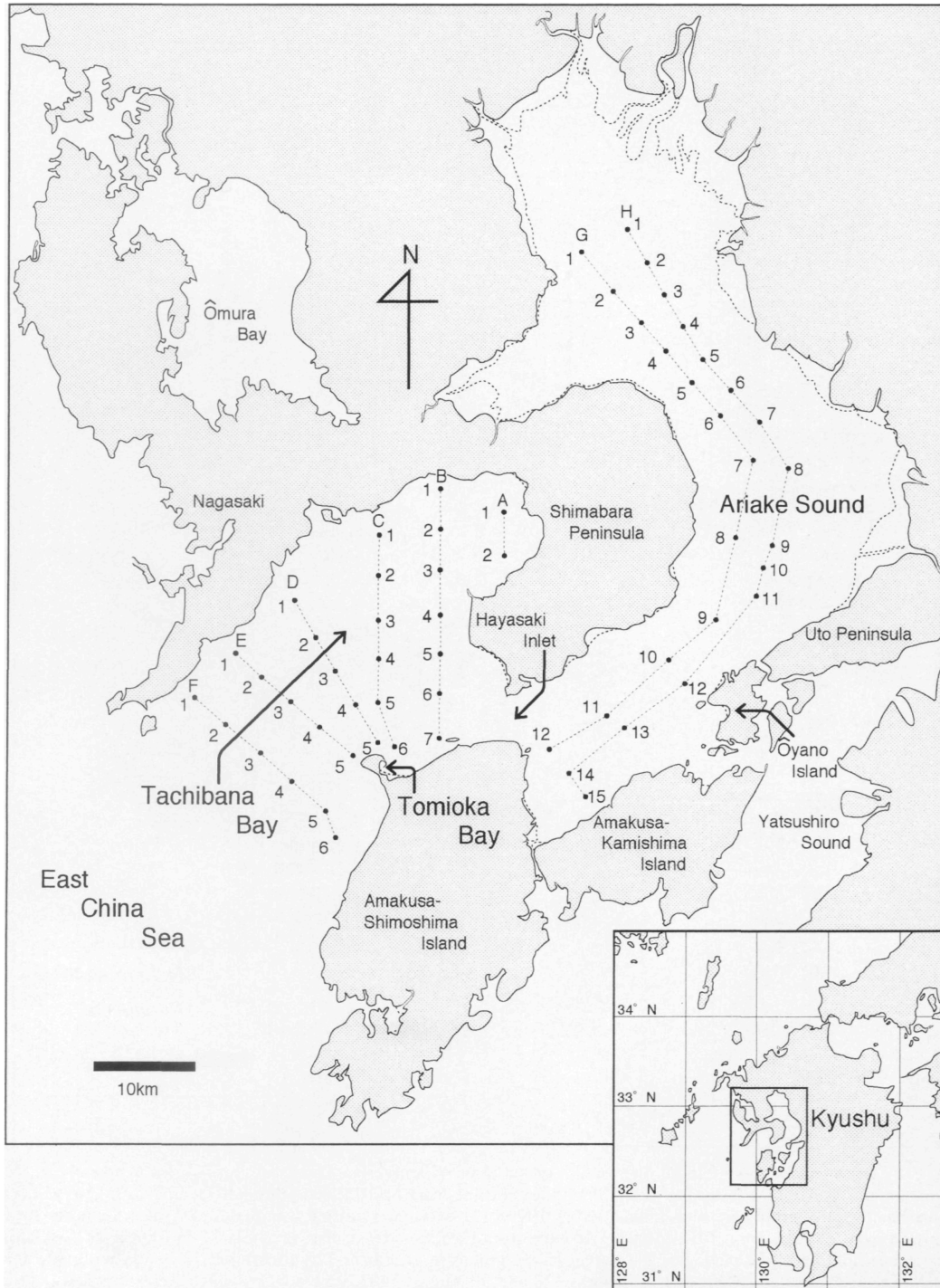


Fig. 1. Location of the study area in western Kyushu, Japan, showing the estuarine system spanning from Ariake Sound (estuary) through Tachibana Bay (intermediate waters) to the East China Sea (open sea). The dotted lines off the coastline indicate the extent of the larger intertidal flats. The numbers on Lines A to H indicate the sampling stations for *Nihonotrypaea* larvae. Tomioka Bay is a part of Tachibana Bay, located on the northwestern corner of Amakusa-Shimoshima Island. The ecological studies on *N. harmandi* (Bouvier) (formerly as *Callianassa japonica* Ortmann) by AT and his colleagues have been done on the Tomioka Bay sandflat.

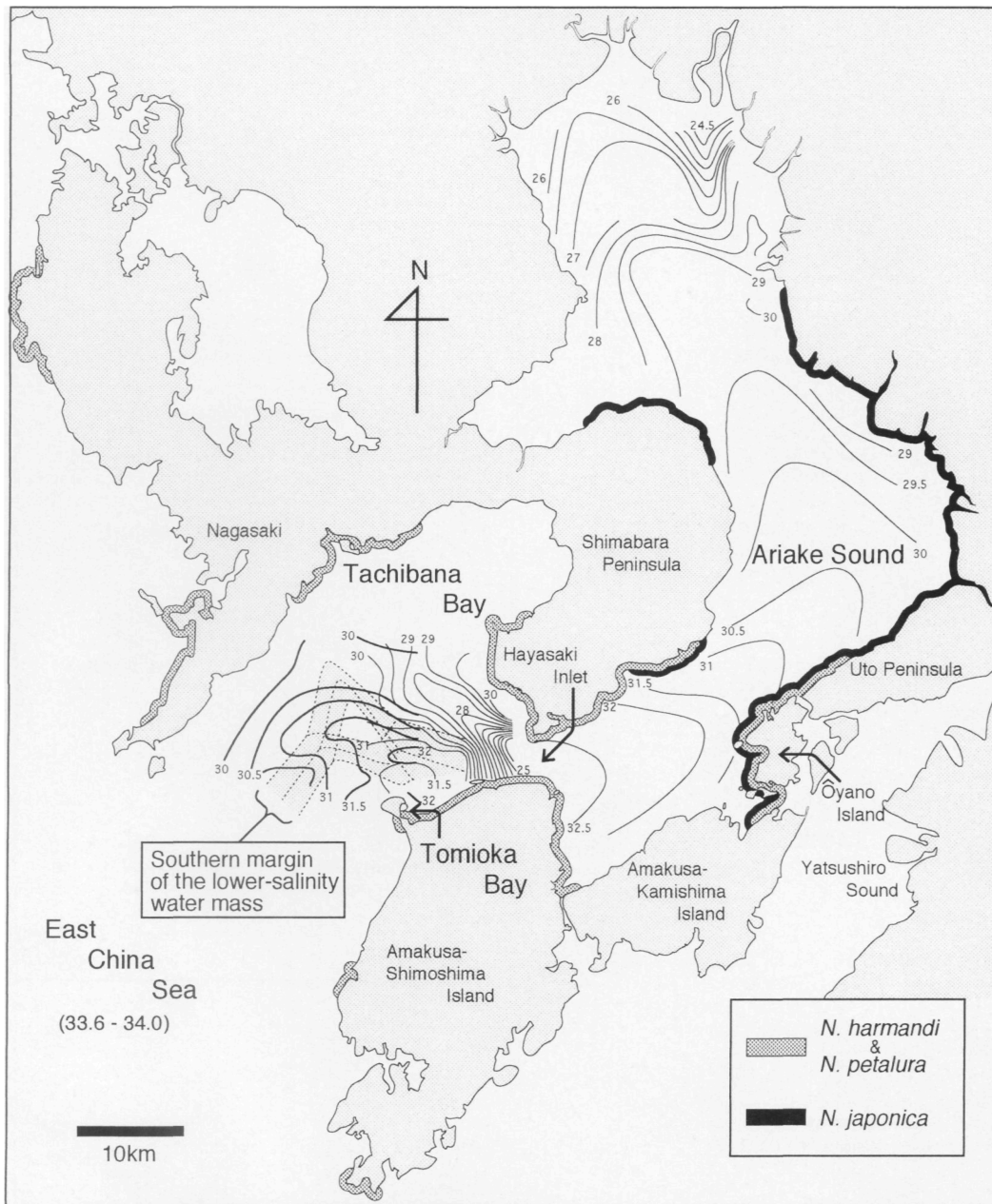


Fig. 2. (1) Ranges of the intertidal distribution of the three *Nihonotrypaea* species (*N. japonica* = black belts; *N. harmandi* and *N. petalura* = stippled belts) along the coastline from Ariake Sound Bay through Tachibana Bay to the East China Sea (adapted from Fig. 8 of Tamaki *et al.*, 1999); (2) isohalines (psu) at 5-m depth of Ariake Sound in July, averaged over 10 years from 1972 to 1981. Adapted from Figs. 6 and 7 of Part II of Ch. 21 in CORC, OSJ (1985), with the permission of the publisher; (3) two isohaline groups in Tachibana Bay [the thinner lines (eastern part) and the thicker ones (western part)] at 1-m depth on 26 and 30 August 1993, respectively, which were recorded after a heavy rainfall amounting to about 40 to 55 mm for 5 days prior to the date of each observation (adapted from Fig. 6 of Matsuno *et al.*, 1999); (4) presumed locations of the southern margin of the lower-salinity water mass distributed in the northern Tachibana Bay during the larval developmental period in the present study (shaded bands; see text); and (5) salinity values written under the "East China Sea" are the July means on the basis of a 24-year data set (CORC, OSJ, 1990).

terns for the three species in relation to the distribution ranges of adults, based on plankton samples collected along the above-mentioned estuary-to-open-sea gradient in summer, 1998.

MATERIALS AND METHODS

Characteristics of the Study Area.—The study area is located in the middle part of western Kyushu, Japan (around 130°E and 32.5°N), where there are two major estuaries, Ariake Sound and Yatsushiro Sound (Fig. 1). The two sounds are separated by both Uto Peninsula projecting from the mainland of Kyushu and three large islands (Ôyano-, Amakusa-Kamishima-, and Amakusa-Shimoshima Islands). Ariake Sound, covering an area of 1,700 km², connects with the outer westward waters, Tachibana Bay, through a 5-km wide inlet (Hayasaki Inlet) located between Shimabara Peninsula and Amakusa-Shimoshima Island. Tachibana Bay, covering an area of 700 km², is open westwardly to the East China Sea (open sea); usually, the western margin of Tachibana Bay is placed around a line connecting the points E5 and F1 in Fig. 1. The waters from Ariake Sound to the East China Sea forms one of the most peculiar estuarine systems in Japan.

Ariake Sound is largely shallow (average, 20 m), though the deepest part (caldron), located 17 km east of Hayasaki Inlet, is about 160 m deep. It is estimated that 99.5% of water exchange between Ariake Sound and the outside seas is made between Tachibana Bay via Hayasaki Inlet, with the remainder being between Yatsushiro Sound, and the tidal current velocities around the inlet reach as high as 3.6 m/s at spring tides [Nagasaki Prefectural Institute of Fisheries (hereafter abbreviated as NPIF), 1956; Coastal Oceanography Research Committee, The Oceanographical Society of Japan (hereafter abbreviated as CORC, OSJ), 1985]. The coast of western Kyushu is under a semi-diurnal tidal regime, with the tidal range varying from 3 m in the East China Sea to 6 m in the innermost Ariake Sound. The largest rivers responsible for the estuarine conditions of Ariake Sound are located on the northern and eastern coasts, where extensive intertidal flats are developed (Fig. 1). Of these intertidal flats the northern ones are mudflats, whereas the eastern ones facing the middle one-third part of the sound are sandflats. The smaller rivers enter the other coast of the sound, correspondingly forming much smaller intertidal flats. Since Japan is under a monsoon climatic regime, salinity of the Ariake Sound waters is lowest during July due to the heaviest seasonal rainfall, when the occurrence of ovigerous females reaches the maxima for the three *Nihonotrypaea* species (Tamaki *et al.*, 1997; Tamaki, unpublished data). The isohalines at 5-m depth of Ariake Sound in July, averaged over 10 years from 1972 to 1981 (CORC, OSJ, 1985), are shown in Fig. 2. From Hayasaki Inlet, salinity (psu) declines from 32.5 to 24.5. The outermost (= toward Hayasaki Inlet) one-third part of Ariake Sound, sandwiched between the 32.5- and 30.5–31.0-isohalines (Fig. 2), has been designated as “the open-sea water (derived from the East China Sea) regime” (NPIF, 1956; CORC, OSJ, 1985). It is less amenable to the weather and climatic conditions than the inner two-thirds of the sound, with higher salinities and lower temperatures in summer and higher salinities and higher temperatures in winter. The year-to-year variation in salinity in the rainy season is much greater in the inner part of the sound.

The deepest part of Tachibana Bay (caldron, about 100 m deep) is located 7 km west of Hayasaki Inlet and the depth of the deepest part of the western limit of the bay is about 80 m (Fig. 1) [see Fig. 1 in Matsuno *et al.* (1999) for the bathymetry]. Along the coastline of Tachibana Bay, there are no rivers as large as those in Ariake Sound. The water characteristics of the bay are influenced by both less saline waters from Ariake Sound and sea waters from the East China Sea [salinity at 5-m depth of the East China Sea just west of Nagasaki in July, averaged over 24 years from 1963 to 1986, ranges from 33.6 to 34.0 (CORC, OSJ, 1990)]. Although, for Tachibana Bay, no long-term data set comparable to those for the other two areas are available, accounts of the distributions of water masses and currents in the bay were recently presented by Matsuno *et al.* (1999), based on a 4-year data set as follows: (1) the lower and higher salinity water masses, most clearly defined along the depths between 10 and 30 m in the water column, are distributed in the northern and southern parts of the bay, respectively, with the latter water mass situated deeper (below 30–40-m depths) northwardly [typical isohalines at 1-m depth observed after a heavy rainfall are shown in Fig. 2 (after Fig. 6 of Matsuno *et al.*, 1999)]; (2) the heavier the rainfall, the closer (a) the southern margin of the lower-salinity water mass moves toward the northern coast of Amakusa-Shimoshima Island (i.e., the shorter distances between the water-mass margin and the coast), and (b) the southern margin of the lower-salinity water mass and the northern margin of the higher salinity water mass approach each other (i.e., the shorter distances between the two water masses; the concordance of the two margins means the formation of a distinct estuarine front). In fact, a significant negative correlation was found between the amount of the 5-day rainfall prior to the dates of observation and the distances mentioned in (a) and (b) above (Figs. 14 and 15 in Matsuno *et al.*, 1999); and (3) as the direction of the low-salinity tongue with densely-packed isohalines just west of Hayasaki Inlet suggests (Fig. 2), an intense discharge of lower-salinity waters from Ariake Sound, of which current was confirmed by a shipboard Acoustic Doppler Current Profiler, is deflected northwestward due to the combined effect of the direction of the inlet axis and Coriolis force. By contrast, just north of Tomioka Bay, the time-averaged eastward current from the East China Sea (about 0.1 m/s) was detected by the current meters moored at 10–15-m depths for 15 days. Although no measurements were made for the northwestern part of Tachibana Bay, the time-averaged current direction there would most probably be westward.

Along the coastline of Tachibana Bay and that facing the East China Sea are scattered relatively small sandy beaches, intertidal sandflats, and mudflats. Of these intertidal flats, the Tomioka Bay sandflat is the largest (Fig. 1). These sandy beaches and intertidal flats are separated by rocky shores, comprising cliffs, boulder-, cobble-, and shingle-beaches.

Intertidal Distributions and Habitats of the Three Species.—A detailed distribution map of adults of the three *Nihonotrypaea* species in the study area is given in Fig. 8 of Tamaki *et al.* (1999), which is summarized below (in Fig. 2, only their distribution ranges along the coastline are shown). *Nihonotrypaea japonica* and (*N. harmandi* + *N. petalura*) mainly occur in the middle one-third part of Ariake Sound and (the coastal waters of the East China Sea + Tachibana Bay + the outermost

one-third part of Ariake Sound), respectively, with a little overlap in their distribution margins. Using the Venice-system terms for the classification of brackish waters, the former species could be designated as a mixo-polyhaline species (hereafter simply called an "estuarine species"), whereas the latter species group could be designated as a euhaline to mixo-euhaline species (hereafter simply called "open-sea species"). From the viewpoint of the substrate conditions and their dimensions, the habitats for the three species were basically characterized as follows: (1) *N. japonica*—both the extensive and less extensive sandflats of medium-fine sands, with boulder beaches, exposed sandy beaches, and mudflats uninhabited; (2) *N. harmandi*—the relatively small sandflats and sandy beaches of medium-fine sands, with boulder beaches, very exposed sandy beaches, and mudflats uninhabited; and (3) *N. petalura*—small sand patches surrounded by boulders in boulder beaches. Of the local populations comprising the metapopulation of *N. harmandi*, that on the Tomioka Bay sandflat is the largest in terms of both the density and the areal proportion occupied (Tamaki *et al.*, 1997, 1999). Likewise, for *N. petalura*, those local populations along the northern coast of Amakusa-Shimoshima Island are the largest, although its total abundance in the study area would be much lower than those of the other two species, reflecting its limited habitat conditions (Tamaki *et al.*, 1999).

Characteristics of Larval Development.—The following descriptions of the larval development are based on the materials reared in the laboratory (*N. japonica*: Miyabe *et al.*, 1998; *N. harmandi*: Konishi *et al.*, 1999; *N. petalura*: Konishi *et al.*, 1990). Only zoeal stages are considered here because no decapodid larvae were collected during the daytime sampling in the present study. All species have five zoeal stages [see the discussion in Miyabe *et al.* (1998) about the number of zoeal stages of *N. petalura* against the originally proposed six stages in Konishi *et al.* (1990)], and their entire durations are in a narrow range: *N. japonica*—in total 16 days = 3d (each of Z1–Z4) + 4d (Z5) at water temperatures of 22.0–24.7°C and salinities of 33.2–33.8; *N. harmandi*—in total 19 days = 5d (Z1) + 3d (Z2) + 4d (Z3) + 2d (Z4) + 5d (Z5) at water temperatures of 24–26°C (no salinity data given) [Y. Fukuda (personal communication) about the material used for Konishi *et al.* (1999)]; and *N. petalura*—in total 15–16 days = 3–4d (Z1) + 2–3d (Z2) + 1–2d (Z3) + 4–6d (Z4) + 3–4d (Z5) at water temperatures of 22–28°C (no salinity data given). The water temperatures measured at 15-m depth throughout the sampling stations in the present study were between 24.9 and 27.1°C, close to the above laboratory values. From morphological characters, zoeal larvae of the three species can be discriminated, as follows: (1) at the Z1 stage, *N. petalura* can be distinguished from the other two species, based on the absence (*N. petalura*) or presence (the other two species) of a coxal seta on maxilliped 2 (Miyabe *et al.*, 1998; Konishi *et al.*, 1999). In the present study, to confirm whether this key can be applied also to the advanced zoeal stages of *N. petalura*, all the larvae used for Konishi *et al.* (1990), deposited under accession numbers ZIHU 872–878 (23 Z2, 36 Z3, 25 Z4, and 5 Z5), were borrowed and examined; (2) at the Z1 stage, *N. harmandi* is significantly smaller than *N. japonica* (see Konishi *et al.*, 1999), which was reexamined in the present study, using a greater number of newly hatched larvae (see the next section); and (3) at the Z3 stage, pereopods

1–5 in *N. japonica* are equipped with exopods with natatory setae [23 specimens were examined from the material used for Miyabe *et al.* (1998)], whereas in *N. harmandi* only pereopods 1 and 2 are fully equipped, with the other three being only buds without setae (see Figs. 11–15 of Konishi *et al.*, 1999). To confirm this point for the greater number of *N. harmandi* larvae used for Konishi *et al.* (1999), 68 specimens deposited at Y. Fukuda were borrowed and examined.

Discrimination of Z1 by Size Between *N. japonica* and *N. harmandi*.—Six ovigerous females of each of *N. japonica* and *N. harmandi*, which seemed to be imminently releasing larvae, were collected on the Okoshiki sandflat [the study site in Miyabe *et al.* (1998)] in the middle of June, 1997, and on the Tomioka Bay sandflat in the middle of June, 1998, respectively. Each female was kept in a 1-l container with filtered sea water until larvae were released. One day later, these Z1 larvae were fixed and preserved in 5% buffered sea-water Formalin. Twenty larvae released from each female were taken, and their total length (TL: from the tip of the rostrum to the medial posterior margin of the telson) was measured. The TL-frequency distribution was made for the combined 120 specimens for each species, and discriminant analysis was conducted to determine the partition point (TL) between the two species.

Collection of Larvae in the Field and Laboratory Treatment.—In summer, 1998, larvae were collected using a 5-ton fisherman's vessel at a total of 58 stations throughout the study area during daytime on 30 July (Lines D–F in the western Tachibana Bay) and 31 July (Stns G7 to G12 and Stns H8 to H15 in the southern Ariake Sound) and on 3 August (Lines A–C in the eastern Tachibana Bay) and 4 August (Stns G1 to G6 and Stns H1 to H7 in the northern Ariake Sound) (Fig. 1). The rough weather that occurred after 31 July precluded consecutive sampling, with the former and latter sampling trips corresponding to the neap tide and 5 or 6 days before the spring tide, respectively. Larval collection was carried out along line by line, with the stations positioned with GPS. At each station, two vertical hauls were conducted using a "Marutoku plankton net" [conical form with a mouth area of 0.16 m² mounted with a TSK flow meter, a lateral length of 1.0 m, and a 0.33-mm mesh opening (NGG54)] from either the sea bottom (in cases of ≤ 40-m depth) or the 40-m depth (in cases of > 40-m depth) to the sea surface. In the latter case, the rope length was adjusted depending on its inclination. The 40-m threshold depth was chosen by a time limitation, with 55% of the Tachibana Bay stations (depth range = 20.7–77.0 m) and 22% of the Ariake Sound stations (depth range = 13.2–63.0 m) exceeding this depth. *Nihonotrypaea* larvae are distributed as deep as about 50 m along the water column, and about 76% of the entire larvae could be collected by the 40-m deep sampling (Tamaki, unpublished data). Each sample was fixed with 5% buffered sea-water Formalin. Later, in the laboratory, all *Nihonotrypaea* zoeal larvae were sorted and identified to the possible species level by each stage, referring to the morphological keys mentioned above. For each station, the mean number of larvae at each stage per m³ water was calculated using the volume value of the filtered sea water, which ranged from 1.7 to 10.8 m³. In Results, the larval distributions are presented by the mean number of larvae in the water column (either to the sea bottom or to the 40-m depth) of a

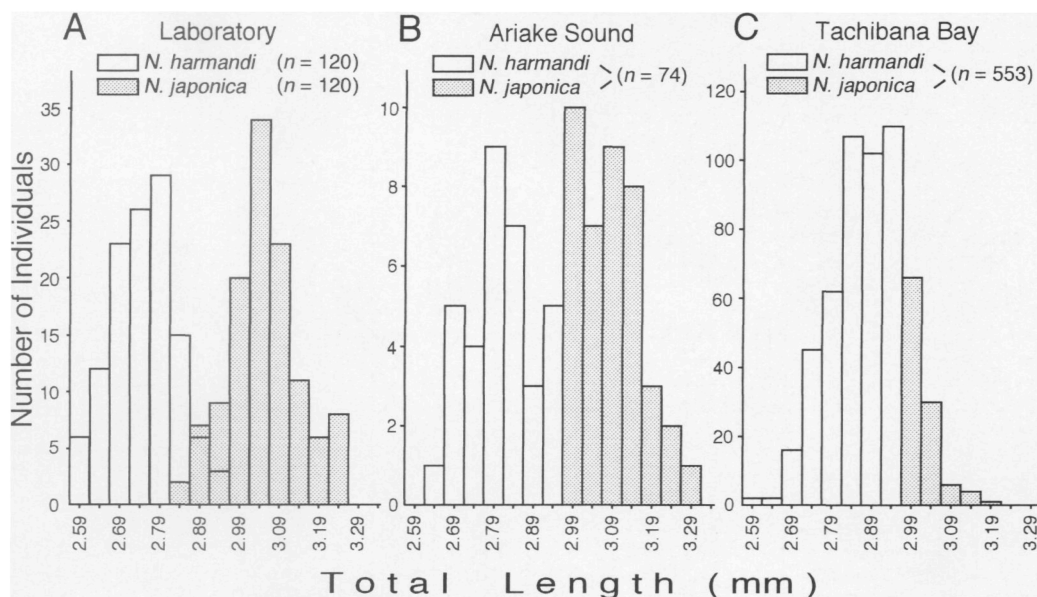


Fig. 3. TL size-frequency distributions of Z1 of *N. harmandi* and *N. japonica* for the newly-hatched larvae in the laboratory (A), the Ariake Sound sample (B), and the Tachibana Bay sample (C). The partition point (TL) of the two species in B and C was determined by discriminant analysis based on the data in A (see text).

cross-sectional area of 1 m² at each station. To save space of the paper, the abundances only for (1) the mixture of (Z1+Z2) of *N. harmandi* and *N. japonica*, (2) the mixture of Z3 of (*N. harmandi* + *N. japonica*) and Z4 of the three species, (3) the mixture of Z5 of the three species, and (4) the mixture of (Z1+Z2+Z3) of *N. petalura* are shown. Furthermore, to examine the proportion of the three species in the Z1 specimens at each station, (1) *N. petalura* was identified according to the morphological key; and (2) TLs of the specimens of the other two species were measured, and the TL-frequency distributions made for the Ariake Sound- and Tachibana Bay-samples, respectively, to which the above-mentioned discriminant analysis was applied to separate *N. japonica* and *N. harmandi*.

Location of the Lower Salinity Water Mass in Tachibana Bay.—With regard to the position of the lower and higher salinity water masses in Tachibana Bay during the larval developmental periods of the three *Nihonotrypaea* species in the present study, (1) the presumed locations of the southern margin of the lower salinity water mass, and (2) the estimated distance between the two water masses were determined by linear regression analyses. Based on the data in Fig. 14 of Matsuno *et al.* (1999), the distance between the southern margin of the lower salinity water mass and the northern coast of Amakusa-Shimoshima Island was linearly regressed against the amount of the 5-day rainfall prior to the dates of observation. The rainfall data for the present study were derived from Japan Meteorological Agency [mean of the data recorded at its six stations surrounding Ariake Sound, just as used in Matsuno *et al.* (1999)]. Tracking back from the plankton-sampling dates (30 July 1998 for Lines D–F and 3 August 1998 for Lines A–C) for consecutive 18 days (the maximum larval developmental period minus one day), the 5-day amount of rainfall prior to each date

was calculated. Their overall means \pm SD were 41.6 ± 13.2 mm ($n = 18$) and 36.3 ± 17.5 mm ($n = 18$), respectively. In Fig. 2, the presumed location of the southern margin of the lower salinity water mass is expressed as a shaded band, with its dotted center- and edge-lines corresponding to the above mean and SD values, respectively; note that (1) the distances to both edges from the center in the band are not equal owing to the definition of the distance between the water-mass margin and the northern coast of Amakusa-Shimoshima Island (see Matsuno *et al.*, 1999); and (2) two possible bands are shown because Matsuno *et al.*'s (1999) data are given for the four subdivided regions from east to west in Tachibana Bay, of which boundaries overlap with several lines of Lines A–F in the present study (Fig. 1). The distance between the lower and higher salinity water masses was estimated in a similar way, based on Fig. 15 of Matsuno *et al.* (1999), and it was in a very narrow range, 0.5–1.8 km.

RESULTS

As regards the larval morphology, it was confirmed that (1) the key to discriminate larvae of *N. petalura* from those of the other two species (i.e., absence or presence of a coxal seta on maxilliped 2) could be used for the Z1 to Z3 stages, but not for the Z4 and Z5 stages; and (2) all the examined Z3 materials of *N. japonica* and *N. harmandi* could be discriminated from each other based on the developmental conditions of the pereopods.

Figure 3A shows the TL size-frequency distributions of Z1 of *N. harmandi* and *N. japonica*

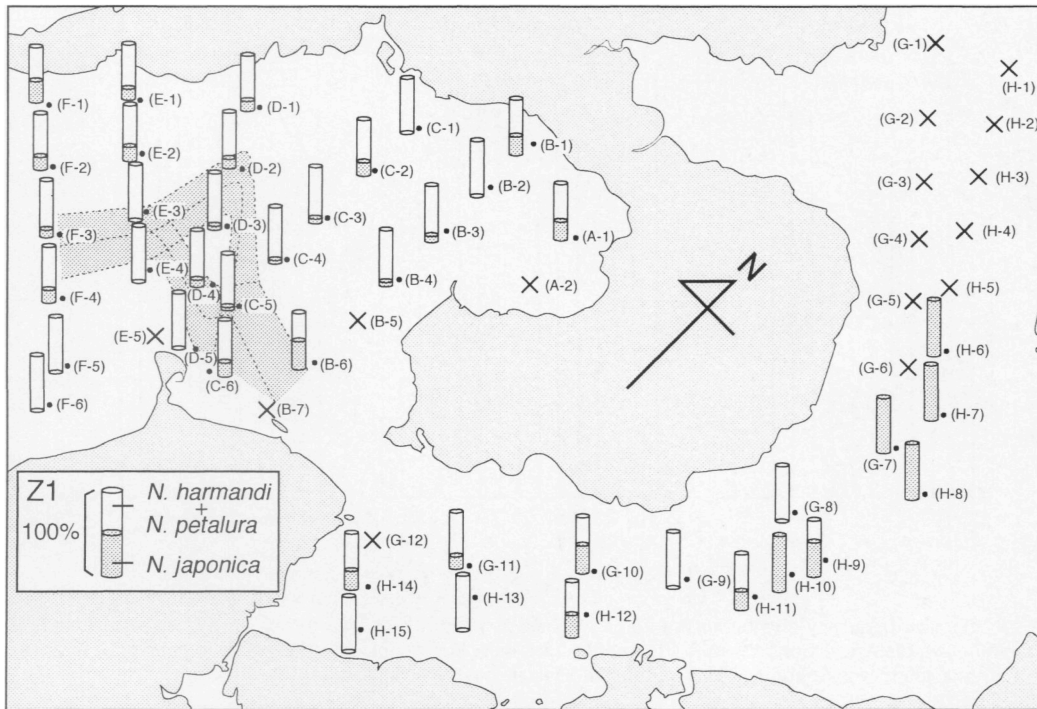


Fig. 4. Percentage proportion of Z1 of *N. japonica* (estuarine species) and (*N. harmandi* + *N. petalura*) (open-sea species) at each station (shown in parenthesis) in the study area. *Nihonotrypaea petalura* was identified according to the morphological key (see text); *N. japonica* and *N. harmandi* were separated by size according to Fig. 3B, C. Cross marks mean that no specimens of the three species were collected. The presumed southern margins of the lower salinity water mass in Tachibana Bay are drawn as shaded bands based on Fig. 2.

ica derived from the newly-hatched larvae in the laboratory. The sizes were significantly smaller in *N. harmandi* (mean \pm SD, TL = 2.75 ± 0.08 mm) than in *N. japonica* (mean \pm SD, TL = 3.05 ± 0.09 mm) ($P < 0.0001$; t -test), with only a little overlap between the two size-distributions. As the sample variances of the two distributions were almost equal, the partition point between the two species in the discriminant analysis was calculated as $(2.75 + 3.05)/2 = 2.90$ -mm TL. The size-frequency distribution of Z1 from the Ariake Sound sample (Fig. 3B) also depicted a bimodal pattern very similar to Fig. 3A, but only a unimodal pattern was observed for that from the Tachibana Bay sample (Fig. 3C). The larvae from the field samples apparently indicate some growth compared with the newly-hatched laboratory sample, and correspondingly, the above partition point was shifted a little to a larger TL value of 2.97 mm in applying to Fig. 3B, C.

Figure 4 illustrates a contrasting distribution pattern of Z1 of the estuarine species (*N.*

japonica) and the open-sea species (*N. harmandi* + *N. petalura*) in the study area. In Ariake Sound, as expected from the distribution ranges of adults (Fig. 2), the stations with the highest proportions of *N. japonica* were located close to the middle portion of the adult distribution range (= around the middle of the sound), with the proportions decreasing toward Hayasaki Inlet, and the distribution limit of Z1 of the open-sea species coincided well with those of the adults, i.e., the inner margin of the open-sea water regime (NPIF, 1956; CORC, OSJ, 1985). In Tachibana Bay, the stations with the higher proportions of *N. japonica* were distributed in the more northern part and the western periphery of the bay (Stns F-1 to F-4), except for Stns C-6 and D-4 surrounded by the stations with either zero or very low abundances in the south of the southern margin of the lower salinity water mass. This suggests that Z1 of *N. japonica* could be flushed out of Ariake Sound and carried away counterclockwise by north-westward to westward currents through the

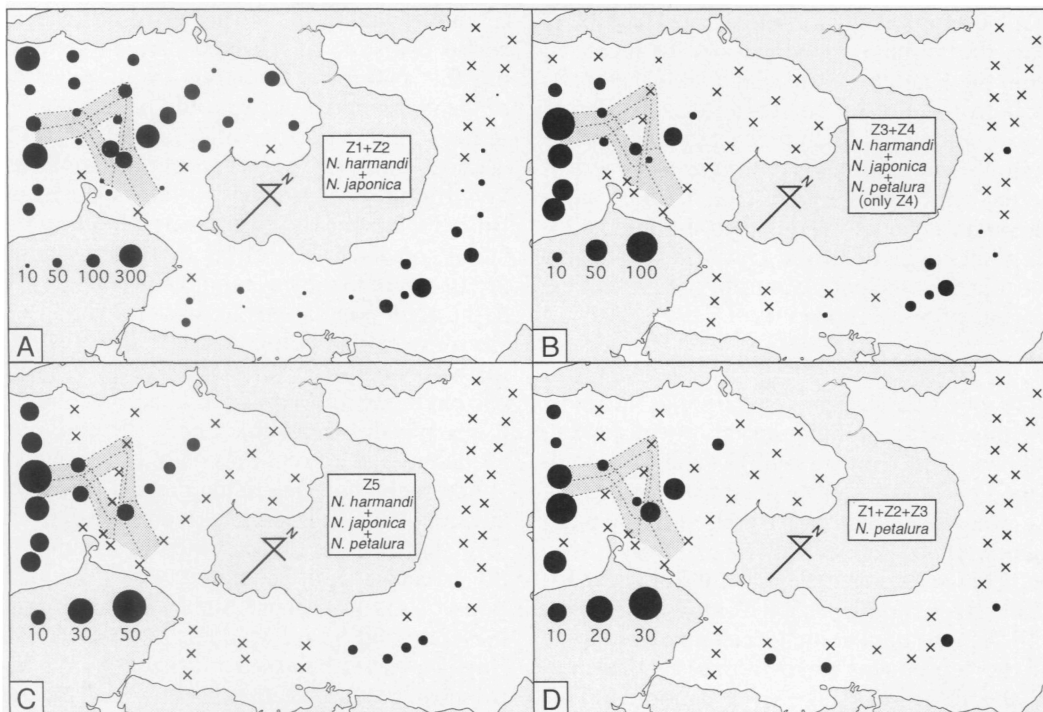


Fig. 5. Number of larvae in the water column of a cross-sectional area of 1 m² to either the sea bottom (in cases of \leq 40-m depth) or the 40-m depth (in cases of $>$ 40-m depth) at each station in the study area for Z1 and Z2 of *N. harmandi* and *N. japonica* combined (A), Z3 of the (*N. harmandi* + *N. japonica*) mixture and Z4 of the three species combined (B), Z5 of the three species combined (C), and Z1, Z2, and Z3 of *N. petalura* combined (D). Cross marks mean that no specimens were collected. Actually, at the Z3 stage, *N. harmandi* and *N. japonica* were distributed separately in Tachibana Bay and Ariake Sound, respectively (see text). The presumed southern margins of the lower salinity water mass in Tachibana Bay are drawn as shaded bands based on Fig. 2.

lower-salinity water mass situated in the northern Tachibana Bay as far down as Stn F-4. Some Z1 larvae of *N. japonica* could have swiftly reached near Tomioka Bay, entrapped by strong ebb currents (Stns C-6 and D-4 as "hot spots").

Figure 5 shows the change in the larval abundance with the progression of zoeal stages for the three species in the study area. The proportion of *N. petalura* among the (Z1+Z2+Z3) larvae of all species was only 6.1% (6.8% for Z1; 5.4% for Z2; 4.9% for Z3), reflecting the lower abundance of the adult population (Tamaki *et al.*, 1997, 1999), and hence its larval abundance pattern would not so much affect the argument on the pattern for the three species inclusive. Hereafter, therefore, comments on Fig. 5A, B, C are described as if only the other two species had been present. In Ariake Sound, the zoeal larvae were retained around the inner margin of the open-sea water regime throughout their

stages (Fig. 5A, B, C). Interestingly, even *N. japonica* larvae do not seem to have protruded very far into the more interior part of the sound. Among a total of 28 Z3 larvae collected from the sound, no *N. harmandi* were found. In Tachibana Bay, it is noteworthy that (1) at first the larvae were distributed widely in the bay (Fig. 5A); (2) but later most of the northern fraction had disappeared (Fig. 5B, C); and (3) among a total of 69 Z3 larvae collected, no *N. japonica* were found. It is suggested that *N. harmandi* larvae were retained throughout development in the higher salinity water mass, which was within about 10 km north to west of Tomioka Bay (see also Fig. 2). Some fraction of the advanced-stage larvae were also distributed in the north of the presumed southern margin of the lower salinity water mass (Fig. 5B, C). The combined data for (Z1+Z2+Z3) of *N. petalura* (Fig. 5D) indicates that (1) in Ariake Sound, the inner distribution limit of larvae accorded well with

that of adults (Fig. 2); and (2) in Tachibana Bay, the highest abundances were recorded from the southern part, which is nearly identical to the presumed retention area for *N. harmandi* larvae. Such highest abundances of both *N. harmandi* and *N. petalura* larvae just north of the northern coast of Amakusa-Shimoshima Island correspond to the largest local adult populations of each species along this coast in the metapopulations of the present estuarine system (Tamaki *et al.*, 1997, 1999).

DISCUSSION

To our knowledge, for callinassid ghost shrimps with pelagic larval development, Johnson and Gonor (1982) is the only published paper that clearly demonstrated the larval abundance pattern in relation to the adult habitat. It was reported that Z1 of *Neotrypaea californiensis* were swept away from a small-scale river mouth (0.5×2 km) in Oregon, U.S.A., into the Pacific Ocean and that larvae of the subsequent stages remained there until the returning stage of decapodids. This scheme of larval dispersal and on-shore transport does not apply to the present case. Apparently, the difference in the larval abundance patterns would be ascribed to that in the configuration and spatial scale of the two estuarine systems.

In Ariake Sound, the reach of larvae of the two open-sea species (*N. harmandi* and *N. petalura*) coincided well with the innermost distribution limit of their adults, which also accorded with the inner margin of the open-sea water regime (= the outermost one-third part of the sound) (Figs. 2, 4, 5). In this respect, studies by Hirota (1974, 1977, 1979) on the distribution of zooplankton in Ariake Sound, especially that of copepods, seem relevant to the findings of the present study. He detected a clear pattern in the distributions of the "oceanic" and "endemic estuarine" zooplankton species, their boundary being around the inner limit of the open-sea water regime. The larval intrusion of *N. harmandi* and *N. petalura* into the inner Ariake Sound might be limited by the excursion range of tidal currents of the open-sea waters (NPIF, 1956; CORC, OSJ, 1985) and/or physiological tolerances of the larvae to the harsher estuarine conditions. Larvae of *N. japonica* were retained throughout development around the inner margin of the open-sea water regime and the area that is extended interiorly a lit-

tle, not invading much further into the inner sound (Figs. 4, 5). The mechanism generating this pattern is unknown. Some fraction of the *N. japonica* larvae could be flushed out of the sound into Tachibana Bay (Fig. 4). It is deduced that these larvae would not have survived long, because the Z3 larvae collected from Tachibana Bay were only *N. harmandi* and *N. petalura*. Therefore, those *N. japonica* larvae swept to the bay would have been a loss to the adult populations in Ariake Sound. Possible mortality factors include the flushing further out by the time-averaged westward current in the northern Tachibana Bay and the lower physiological tolerances of the larvae to the more saline conditions of the open sea.

For Tachibana Bay in the present study, the adjacent sampling stations were too discrete (Fig. 1) to detect the presence or location of the estuarine front accurately. Only the locations of the lower and higher salinity water masses could be inferred by the rainfall data (Fig. 2). Nevertheless, a consistent larval distribution pattern relative to the water masses was observed for the three different species (Figs. 4, 5), in which, with the progression of the stages, (1) larvae in the northern part of the bay with the lower salinity water mass disappeared; and (2) those in the southwestern part of the bay with the higher salinity water mass were retained [the possible nursery ground for larvae of *N. harmandi* and *N. petalura* originated from the largest local adult populations occurring along the northern coast of Amakusa-Shimoshima Island (Tamaki *et al.*, 1997, 1999)]. It is possible that with time, larvae in the northern part of the bay would be lost to the East China Sea by the time-averaged westward current and that those in the southwestern part of the bay would be advected gradually eastward by the time-averaged current, with some larvae eventually retained there and others lost into Ariake Sound. There is also a possibility that the estuarine front would be crossed by larvae from the south in response to its relaxation [i.e., a possible reason for the presence of some advanced-stage larvae in the north of the southern margin of the lower salinity water mass (Fig. 5)]. These possibilities need to be substantiated by future investigation.

ACKNOWLEDGEMENTS

We thank K. Kawamoto, T. Hasegawa, and Y. Watabe for their help with the larval collection. Y. Fukuda and

G. Takaku kindly sent larval specimens of *N. harmandi* and *N. petalura*, respectively, for our reexamination. K. Tamaki assisted with measuring larval dimensions. K. Konishi and T. Matsuno provided valuable information about the larval morphology and the oceanography of Tachibana Bay, respectively. The rainfall data was provided by Japan Meteorological Agency. We wish to express our gratitude to Ray Manning for his continual encouragement. This study was partly supported by the Ministry of Education, Science, Sports and Culture Grant-in-Aid for Scientific Research (C) #09640754.

LITERATURE CITED

- Coastal Oceanography Research Committee, The Oceanographical Society of Japan. 1985. Coastal Oceanography of Japanese Islands. Tokai University Press, Tokyo. xxvi + 1106 pp. [in Japanese.]
- . 1990. Coastal oceanography of Japanese Islands, supplementary volume. Tokai University Press, Tokyo. xxii + 839 pp. [in Japanese.]
- Hailstone, T. S., and W. Stephenson. 1961. The biology of *Callianassa (Trypaea) australiensis* Dana 1852 (Crustacea: Thalassinidea).—University of Queensland Papers, Department of Zoology 1: 259–285.
- Hirota, R. 1974. Occurrence of zooplankton in Ariake-Kai, western Kyushu, I. Regional occurrence of the important zooplankton in the warmer season.—Kumamoto Journal of Science, Biology 12: 1–15.
- . 1977. Occurrence of zooplankton in Ariake-Kai, western Kyushu, II. Occurrence of oceanic copepods in autumn.—Kumamoto Journal of Science, Biology 13: 43–48.
- . 1979. Occurrence of zooplankton in Ariake-Kai, western Kyushu, III. Regional occurrence of the important zooplankton in the colder season.—Kumamoto Journal of Science, Biology 14: 33–41.
- Johnson, G. E., and J. J. Gonor. 1982. The tidal exchange of *Callianassa californiensis* (Crustacea, Decapoda) larvae between the ocean and the Salmon River estuary, Oregon.—Estuarine, Coastal and Shelf Science 14: 501–516.
- Konishi, K., Y. Fukuda, and R. R. Quintana. 1999. The larval development of the mud-burrowing shrimp *Callianassa* sp. under laboratory conditions (Decapoda, Thalassinidea, Callianassidae). Pp. 781–804 in F. R. Schram and J. C. von Vaupel Klein, eds. Crustaceans and the biodiversity crisis. Proceedings of the Fourth International Crustacean Congress, 1998, Vol. 1. Brill, Leiden, The Netherlands.
- , R. R. Quintana, and Y. Fukuda. 1990. A complete description of larval stages of the ghost shrimp *Callianassa petalura* Stimpson (Crustacea: Thalassinidea: Callianassidae) under laboratory conditions.—Bulletin of National Research Institute of Aquaculture, Nansei, Japan 17: 27–49.
- Manning, R. B., and A. Tamaki. 1998. A new genus of ghost shrimp from Japan (Crustacea: Decapoda: Callianassidae).—Proceedings of the Biological Society of Washington 111: 889–892.
- Matsuno, T., M. Shigeoka, A. Tamaki, T. Nagata, and K. Nishimura. 1999. Distributions of water masses and currents in Tachibana Bay, west of Ariake Sound, Kyushu, Japan.—Journal of Oceanography 55: 515–529.
- Miyabe, S., K. Konishi, Y. Fukuda, and A. Tamaki. 1998. The complete larval development of the ghost shrimp, *Callianassa japonica* Ortmann, 1891 (Decapoda: Thalassinidea: Callianassidae), reared in the laboratory.—Crustacean Research 27: 101–121.
- Nagasaki Prefectural Institute of Fisheries. 1956. Investigation of Ariake-Kai No. 6.—Nagasaki Prefectural Institute of Fisheries Data Series 89: 58–117. [in Japanese.]
- Sakai, K. 1969. Revision of Japanese callianassids based on the variations of larger cheliped in *Callianassa petalura* Stimpson and *C. japonica* Ortmann (Decapoda: Anomura).—Publications of the Seto Marine Biological Laboratory 17: 209–252, pls. 9–15.
- Sandifer, P. A. 1973. Mud shrimp (*Callianassa*) larvae (Crustacea, Decapoda, Callianassidae) from Virginia plankton.—Chesapeake Science 14: 149–159.
- Tamaki, A. 1994. Extinction of the trochid gastropod, *Umbonium (Suchium) moniliferum* (Lamarck), and associated species on an intertidal sandflat.—Researches on Population Ecology 36: 225–236.
- , B. Ingole, K. Ikebe, K. Muramatsu, K. Taka, and M. Tanaka. 1997. Life history of the ghost shrimp, *Callianassa japonica* Ortmann (Decapoda: Thalassinidea), on an intertidal sandflat in western Kyushu, Japan.—Journal of Experimental Marine Biology and Ecology 210: 223–250.
- , J. Itoh, and K. Kubo. 1999. Distributions of three species of *Nihonotrypaea* (Decapoda: Thalassinidea: Callianassidae) in intertidal habitats along an estuary to open-sea gradient in western Kyushu, Japan.—Crustacean Research 28: 37–51.
- Ziebis, W., S. Forster, M. Huettel, and B. B. Jørgensen. 1996. Complex burrows of the mud shrimp *Callianassa truncata* and their geochemical impact in the sea bed.—Nature 382: 619–622.

RECEIVED: 21 April 1999.

ACCEPTED: 12 November 1999.