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Alongshore configuration and size of local populations of the callianassid shrimp *Nihonotrypaea harmandi* (Bouvier, 1901) (Decapoda: Thalassinidea) in the Ariake-Sound estuarine system, Kyushu, Japan

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Abstract.— In the Ariake-Sound estuarine system, intertidal sandflats or sandy beaches inhabited by *Nihonotrypaea harmandi* are distributed along the western half of the coastline. In these habitats, the ghost shrimp occupies zones or patches mostly composed of moderately (well) sorted fine sand. A previous study has identified 38 local shrimp populations along the coastline. Of these, 26 main populations were surveyed to estimate their sizes prior to the breeding season in 1998. For each location, the shrimp-inhabited zones/patches were mapped, and density was assessed by counting the number of burrow openings at a number of stations. The total number of shrimps at each zone/patch was estimated by multiplying the mean shrimp density by its area. The entire population size was given as the sum total of those from all zones/patches. Of all local populations, the population size on one sandflat situated at the south-western periphery of the target waters was by far the largest due to both the highest density and the largest area, accounting for 70% of the total number of shrimps in the estuarine system. This sandflat is closest to the largest larval retention ground in the waters lying 10 to 20 km offshore.

Introduction

Decapod thalassinidean shrimps of the family Callianassidae are among the commonest macro-invertebrates, occurring from estuarine intertidal to marine subtidal soft sediments. The shrimp resides in a burrow for shelter, reproduction, and feeding. In Japanese waters, three species of the genus *Nihonotrypaea* are commonly found in intertidal habitats (Manning & Tamaki, 1998; Tamaki, 2003). Of these species, both *N. harmandi* (Bouvier, 1901) and *N. japonica* (Ortmann, 1891) are distributed on bare sandflats, whereas *N. petalura* (Stimpson, 1860) is on boulder beaches (Tamaki *et al.*, 1999; Shimoda & Tamaki, 2004; Shimoda *et al.*, 2005). Note that in papers by A. Tamaki and his colleagues published before 1998, the species name, *Callianassa japonica*, was incorrectly applied to *N. harmandi* (see Tamaki, 2003). Since 1979, A. Tamaki and his colleagues have studied the population dynamics of *N. harmandi* on an intertidal sandflat facing Tomioka Bay (Tomioka Bay sandflat). The bay is situated at the south-western periphery of the Ariake-Sound estuarine system, western Kyushu (the system ranges from Ariake Sound, via Tachibana Bay, to the coastal waters of the East China Sea; Fig. 1). The waters of Tachibana Bay are of an intermediate character (Matsuno *et al.*, 1999). It is estimated that 99.5% of water exchange between Ariake Sound and the outside waters is made through Hayasaki Inlet situated between Ariake Sound and Tachibana Bay (Coastal Oceanography Research Committee, the Oceanographical Society of Japan, 1985). In the Ariake-Sound estuarine system, the distribution range of *N. harmandi* is limited to the outermost one-third of Ariake Sound and Tachibana Bay

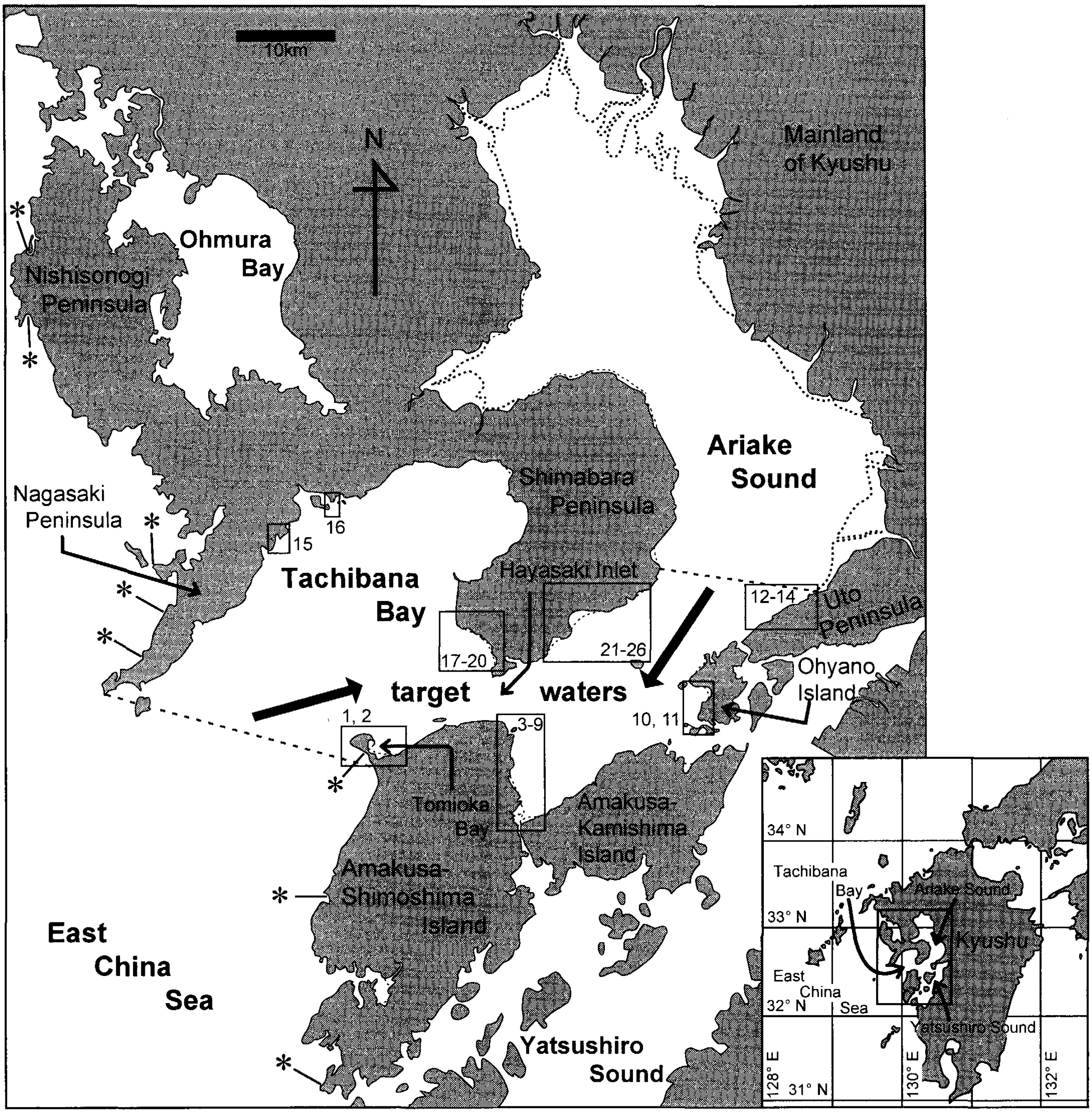

Fig. 1. Target waters for the survey of local populations of *Nihonotrypaea harmandi* on intertidal sandflats/sandy beaches in the Ariake-Sound estuarine system extending from Ariake Sound, via Tachibana Bay, to the coastal waters of the East China Sea, western Kyushu, Japan. The broken lines seaward of the coastline indicate the extent of the relatively large tidal flats. The target local populations (Locations 1 – 26) are grouped into eight blocks, whose detailed maps are shown in Figs. 3 – 9. The asterisks along the coastline facing the East China Sea denote the locations with *N. harmandi* which were not examined in the present survey except for Location 2.

(Tamaki *et al.*, 1999).

On the Tomioka Bay sandflat, the shrimp population expanded considerably in the early 1980's, which was followed by a steady state for the subsequent 10 years (Tamaki & Ingole, 1993; Tamaki, 1994; Tamaki *et al.*, 1997; Flach & Tamaki, 2001). Where shrimps exist in high densities, their numerous burrow openings on the sediment surface are evident, together with a very softened sediment column due to bioturbation. A similar explosive increase in the local population size has occurred also on other sandflats in the Ariake-Sound estuarine system

(Flach & Tamaki, 2001). When looking for explanations of such widespread population explosions, it is necessary to have a metapopulation perspective. Although growing attention has been paid to metapopulation concepts for marine benthos recently (Grimm *et al.*, 2003), little substantial data are available on the spatial configuration and size of the local populations comprising a supposed regional metapopulation (Reise, 2003; Armonies & Reise, 2003). The acquisition of such data sets is a prerequisite for promoting the study of marine benthic populations. The aim of the present paper is to describe the size of the main local populations of *N. harmandi* along the coastline in the outermost one-third of Ariake Sound and Tachibana Bay (hereafter collectively called the target waters: Fig. 1). The distribution pattern of these local populations will be discussed in relation to ghost shrimp larval abundance pattern in the target waters given in Tamaki & Miyabe (2000).

Materials and Methods

Detailed habitat characteristics of two tidal-flat species of Nihonotrypaea

Tamaki *et al.* (1999: Fig. 8) presented a distribution map of intertidal sandflats inhabited by *Nihonotrypaea harmandi* and *N. japonica* in the Ariake-Sound estuarine system. Generally the two species occur separately along the salinity gradient [also compiled in Fig. 7.5 of Flach & Tamaki (2001) and Fig. 1 of Wardiatno *et al.* (2003)]. These different distribution patterns correspond well to a set of 10-year-averaged salinity values for July (= heaviest rainy season in southern Japan) in the surface (at 5-m depth) waters of the estuarine system. *Nihonotrypaea harmandi* occurred in the salinity range of 30.5 - 34.0; salinity data are cited from Coastal Oceanography Research Committee, the Oceanographical Society of Japan (1985), and the isohalines are given in Fig. 2 of Tamaki & Miyabe (2000). This salinity range extends from the coastline of the outermost one-third of Ariake Sound, via Tachibana Bay, to the northern coastline of Nagasaki Peninsula, the western coastline of Nishisonogi Peninsula, and the western coastline of Amakusa-Shimoshima Island (Fig. 1). *Nihonotrypaea japonica* mainly occurred in the salinity range of 28.5 - 30.5, which corresponds to the coastline of the middle one-third of Ariake Sound. The two species' distributions overlapped in the outermost one-third of Ariake Sound. According to Wardiatno *et al.* (2003), the shrimp appeared on the entire shore in allopatric areas, whereas in their co-occurrence range, *N. japonica* and *N. harmandi* separately occupied the upper and lower shores as a rule. The averaged salinity values in the innermost one-third of Ariake Sound range from 24.5 to 28.5, 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* and *N. japonica* are designated as a euhaline or mixo-euhaline species and a mixo-polyhaline species, respectively.

Tamaki *et al.* (1999) also summarized the general characteristics of the habitats for *N. harmandi* and *N. japonica* in terms of the features of the intertidal areas and their substratum grain sizes. First, neither species was distributed on boulder shores, open sandy beaches, or mudflats. The burrow construction by shrimps appears to be prevented by wave surges or too sticky substrates. Second, *N. harmandi* was distributed on relatively small- to medium-sized sandflats and protected sandy beaches, while *N. japonica* was on extensive sandflats as well as some smaller ones. The size of these sandflats/sandy beaches inhabited by each species generally reflects their spatial arrangement along the salinity gradient in the Ariake-Sound estuarine system. Finally, on each sandflat/sandy beach, both species inhabit a part mostly composed of fine to medium sands. Based on their analysis of sediment samples from 60 stations placed at five locations in the target waters, Wardiatno *et al.* (2003) gave more detailed granulomet-

Fig. 2. Proportions of the sand types (*sensu* Folk, 1974) inhabited by *Nihonotrypaea harmandi* among 60 stations placed on five intertidal sandflats in the target waters (after Wardiatno *et al.*, 2003).

ric characteristics of sediments associated with *N. harmandi*. First, the sediments were mainly composed of sand and mud, with a negligibly low gravel fraction. In such gravel fraction, only granules (2 to 4 mm in diameter) were present. Second, the mud (= silt-clay) content of the sediments was mostly low, with 0.3 to 1.8% at 39 stations, 2.0 to 4.9% at 15 stations, 5.2 to 8.0% at four stations, and 11.4 to 14.3% at two stations. Thus, according to Folk's (1974: Table 1) definition for the sediment type, it can be concluded that *N. harmandi* occurred almost exclusively in sand. The uninhabited sediment types are gravel, sandy gravel, muddy sandy gravel, muddy gravel, gravelly sand, gravelly muddy sand, gravelly mud, sandy mud, and mud. Finally, moderately sorted or moderately well sorted fine sand dominated all kinds of the sand substrata inhabited by *N. harmandi* (*i.e.*, at 83% of the stations), with the sand at the other 17% stations composed of very fine to coarse sand with various degrees of sorting (Fig. 2).

Within the target waters, a total of 31 locations had been identified as the habitat for *N. harmandi* and *N. japonica* (Fig. 8 in Tamaki *et al.*, 1999). Of these locations, 26 were selected for the present survey and census (Locations 1 - 26 in Fig. 1). At the other five locations, either only a few shrimp burrow openings were sporadically distributed in small areas or individuals of only *N. japonica* were present. Outside the target waters, *N. harmandi* was distributed at two, three, and three locations along the open coastline of western Nishisonogi Peninsula, northern Nagasaki Peninsula, and western Amakusa-Shimoshima Island, respectively (locations with asterisks in Fig. 1). The area occupied by the shrimp population at each of these eight locations was situated under protected conditions, being at the lee of headlands or jetties, of close-lying offshore islands or breakwaters, etc. As the sizes of these local populations were apparently much smaller than those along the coastline of the target waters, they were not included in the present survey, except for the population at Location 2 (Figs. 1 and 3), which is close to the Tomioka Bay sandflat (Location 1). Most of the 26 target locations were inhabited by *N. harmandi* alone, with the cohabitation of *N. japonica* at Locations 7, 8, 10, 14, and 22 (Fig. 1). The shapes of burrow openings of the two species are similar, so at these locations, the species identity for respective burrows cannot be determined from the sediment surface.

The coast of Tachibana Bay and Ariake Sound are under (semi-)sheltered conditions owing to the relatively short fetch of the prevailing waves, and thus, in terms of shore types, the locations with shrimp occurrence belong to either sandflats or protected sandy beaches; of these, only Locations 15 - 20 are influenced by the relatively strong wave action and hence designated as protected sandy beaches. All sandflats/sandy beaches are contained within the bounding headlands or artificial projections from land, except for Location 14 situated at the western edge of an extensive sandflat, where *N. japonica* dominates (Wardiatno *et al.*, 2003). Each headland has a seaward extended area of various kinds and dimensions, including a sea cliff or nip with its shore platform of rocks and boulders together with other components of gravel. The artificial projections from land involve jetties, breakwaters, walls of penaeid shrimp aquaculture ponds, etc. The rivers flowing into the coast of the target waters are much smaller than those entering the inner Ariake-Sound coast at which extensive tidal flats are formed, associated with the development of large deltas. In the target waters, the much smaller deltas are formed at the mouths of several substantial rivers (Locations 1, 3, 5, 8, 9, and 22 – 25). The substrate types of these deltas are gravel, sand, mud, or a mixture.

The coast of western Kyushu is under a semi-diurnal tidal regime. The maximum tidal range in the target waters at spring tides through the year is 3.3 m (Tachibana Bay) to 4.3 m (outermost one-third of Ariake Sound). *Nihonotrypaea harmandi* occurs in the lower intertidal, from the level of mean low water neap tide seaward, in which the sediment surface is more or less wet or waterlogged during the exposed period. The maximum duration of exposure per low tide through the year for the occurrence zone of *N. harmandi* ranged from 0.8 to 6 h (Wardiatno *et al.*, 2003).

The burrow of *N. harmandi* is Y-shaped, inhabited by a single adult shrimp (Tamaki & Ueno, 1998; Shimoda *et al.*, 2005); the number of completely retrieved burrow casts was rather limited, but including a total of 59 incomplete ones (*i.e.*, lacking in their lower part) so far obtained, the upper part had only two surface openings without exceptions (A. Tamaki, unpublished data). Thus, two burrow openings on the sediment surface correspond to one shrimp. By contrast, the burrow of *N. japonica* has a single surface opening only (Tamaki & Ueno, 1998). The node of the burrow for an adult *N. harmandi* is positioned at a mean depth of 9.6 cm below the sediment surface (Tamaki & Ueno, 1998). The sand-layer thickness of about 10 cm appeared to be the minimum requirement for shrimp burrow construction (Wardiatno *et al.*, 2003). At several locations, only relatively thin sand layers overlie a bedrock or a bed of shell remains.

The physically determined sediment characteristics for *N. harmandi*'s habitats so far described can be modified by the presence of burrows or by bioturbating activities of the shrimp, especially where it exists in high densities (Wardiatno *et al.*, 2003). These modified substrate conditions can be easily discriminated from those of the uninhabited surroundings. They include (1) bumpy surface with sediment mounds ejected from shrimp burrows, which remain only under very weak wave conditions, (2) softer (less compact) substrates due to void burrow space and rapid turnover of sediments, (3) retained burrow water during exposed periods, resulting in an elevated water table, (4) maintained better-sorted upper layer and downwardly accumulated coarser grains such as gravel and shell remains along the sediment column due to vertical material sorting, and (5) depressed oxidized surface, usually brown in color, to considerable depths (*e.g.*, tens of cm) in the sediment column due to increased porosity and permeability.

Estimation of local population sizes of Nihonotrypaea harmandi

The distribution and density of *Nihonotrypaea harmandi* at the 26 target locations was surveyed during low tide at spring tides from the end of February to the end of April, 1998, except for Location 14 in June, 1998 (Fig. 1). Generally in southern Japan, this period of the year provides a most suitable occasion for daytime access to the entire intertidal range. The larval settlement of *N. harmandi* occurs from early July to early October, and the life span of the species is about two years (Tamaki *et al.*, 1997). Thus, the shrimp population during the survey period consisted of 0+- and 1+-year-old cohorts. Generally, wherever suitable fine sand was available, *N. harmandi* was found to occur. However, callianassid shrimps are excluded by a dense stand of eelgrass such as *Zostera japonica* growing on such fine sand (*e.g.*, Dumbauld & Wyllie-Echeverria, 2003). In the present estuarine system, this eelgrass species was found at Locations 3, 9, 10, 21, 22, and 25 (Fig. 1). At each of the 26 target locations, the population either occupied a zone parallel to the high- and/or low-tide shorelines or was patchy. In the present study, the low-tide shoreline was defined as that of the mean low water spring tide level. These shrimp zones/patches were identified by walking over the entire intertidal area to find burrow openings on the sediment surface, with several associated keys in substrate conditions as listed in Section 1, and by actually extracting animals using a 'yabby pump' similar to that described in Hailstone & Stephenson (1961). At some locations, the entire intertidal area was densely inhabited, sometimes with an extension into the subtidal area. Thus, the total population size at several of these locations was underestimated. At the other locations, the shrimp distribution was limited to a part of the intertidal area. The shrimp zones/patches were marked on the corresponding aerial photographs (scales = 1:12,500, 1:25,000, 1:30,000, and 1:40,000) or maps (1:25,000 scale topographic maps or 1:25,000 scale topographic maps of coastal areas) published by the Geographical Survey Institute, the Ministry of Land, Infrastructure and Transport. The aerial photographs, which include the target shores in their tidal exposure conditions taken on the dates closest to the present survey period, were used wherever available (KU-94-2X or KU-92-5X series). In the case in which clear pictures for exposed conditions were unavailable prior to the present survey, the shrimp zones/patches were drawn on the photographs published thereafter (KU-97-3X or KU-99-2X series for Locations 12 – 14, 17 – 20, 25, and 26). All photographs were enlarged by photocopying to an approximately 1:12,000 to 1:18,000 scale before use. For Locations 11, 15, and 16, no aerial photographs were available, and only maps were used.

When drawing the boundary of a shrimp zone/patch on the aerial photograph or map of each location, the positions of several marking points relative to the selected conspicuous topographic points along the coastline were determined in terms of direction and distance. In all cases of a patchy distribution and some cases of a zoned distribution, the shrimp-inhabited area was measured after division into constituent trapezoids, rectangles, and triangles of approximate shape. In the other cases of zoned distribution, the entire area with more or less irregular shape was measured using a computer coordinating area-curvimeter, X-PLAN 360d (Ushikata Mfg. Co., Ltd., Tokyo).

Shrimp density was estimated by counting burrow openings per unit area. For the case of the zoned distribution parallel to the either high- or low-tide shoreline, at least one transect (approximately) perpendicular to the shoreline was established, each with a number of stations on it. At Locations 9 and 26 (Fig. 1), transects (approximately) parallel to the shoreline were established. Both the transects and the stations on each transect were properly spaced out so that the entire inhabited area was well represented. At each station, four to 10 quadrat plots of a

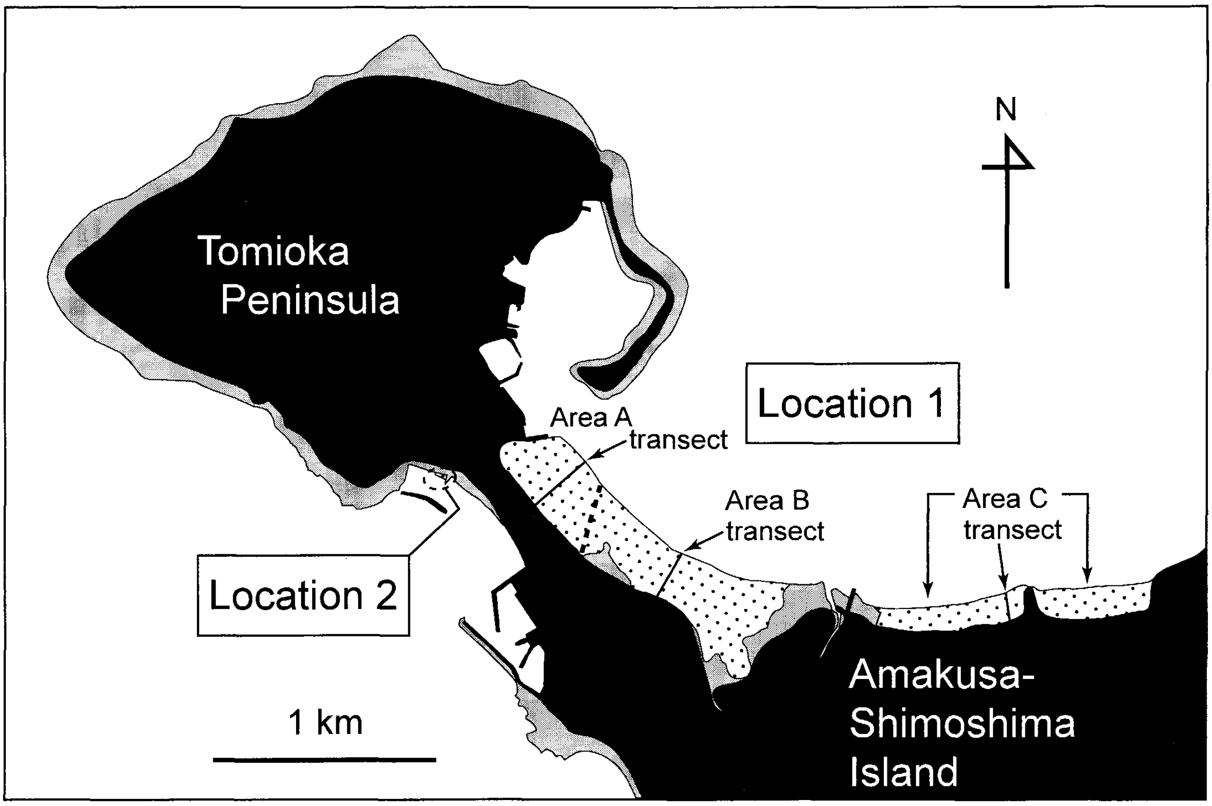

Fig. 3. Locations 1, 2. The dotted parts stand for the area inhabited by *Nihonotrypaea harmandi* and the shaded ones for the uninhabited area on the shore. Location 1 was divided into three areas according to the large-scale topographic feature, each with one representative transect for shrimp density census. The black bar off Location 2 indicates a breakwater.

unit area of 25 cm × 25 cm were incised on the sediment surface. The number of quadrat plots per station was the same for each location except for Location 21. In the case of a patchy distribution of the shrimp, a number of such stations were scattered as uniformly as possible within each patch. The total number of shrimp at each zone/patch was estimated by multiplying the mean shrimp density by the area of the zone/patch. For the locations in which *N. harmandi* and *N. japonica* co-occurred (third paragraph in Section 1), correction was made for the total number of *N. harmandi* according to the numerical ratio of the two species' populations at each location. For Locations 7, 8, 10, and 14, such ratio data could be cited from Wardiatno *et al.* (2003), in which direct shrimp collection was made; for Location 22, no quantitative data had been obtained (see Tamaki *et al.*, 1999). Based on the inclusive burrow-opening counts ('*IC*') and the already established ratio of the number of *N. harmandi* in the two species' mixed population ('*ER*'), the actual mean densities of *N. harmandi* ('*X*') and *N. japonica* ('*Y*') were estimated by solving the simultaneous linear equations, as follows: $2X + Y = IC$ and $X / (X + Y) = ER$. Thus, $X = (IC \cdot ER) / (1 + ER)$.

For *N. harmandi*, the shrimp population size at the entire location was given as the sum total of the total numbers of ghost shrimps from all zones/patches. The mean shrimp density at the entire location was given as the shrimp population size divided by the sum total of the shrimp-inhabited areas from all zones/patches.

Results

The detailed maps for the locations with

Nihonotrypaea harmandi zones/patches are shown in Figs. 3 – 9. The transects for the shrimp density census were also depicted for several locations in which the shrimp occupied relatively large areas (Locations 1, 3 - 10, and 14). The remarks for respective locations are made below. The local site name is indicated in parenthesis following each location number. Although the mean shrimp burrow density at each zone/patch is given to one decimal place below, the value to two decimal places was used when calculating the total shrimp number.

Location 1 (Tomioka Bay sandflat). The location is situated on the northwestern corner of Amakusa-Shimoshima Island in Tachibana Bay (Fig. 3). The sandflat is developed along the tombolo connecting the mainland of Amakusa-Shimoshima Island and Tomioka Peninsula. The shrimp was distributed over the entire sandflat with an area of 558,519 m^2. This area was the largest of all shrimp-inhabited areas at the 26 target locations (Fig. 10). The Tomioka Bay sandflat could be divided into three areas in light of the large-scale topographic feature, which is evident in the aerial photograph (*e.g.*, KU-94-2X, C9-2). Such topographic division apparently reflects the spatial difference in the prevailing current and wave regime. Area A, with an area of 138,140 m^2, is dominated by weakly formed sand waves with wave lengths of 15 - 40 m that are arranged (approximately) vertically to the shoreline. By contrast, Area B, with an area of 271,410 m^2, is dominated by distinct sand waves with wave lengths of 30 - 50 m that are arranged parallel to the shoreline. The surface of Area C, with an area of 148,969 m^2, is flat and has no sand waves. Going away from Area A to Area C with diminishing protective effects of Tomioka Peninsula and its sand spit, a gradient exists in the degree of exposure to wave action. In the present survey, each area was represented by one transect with 15 stations (Area A), 11 stations (Area B), and 13 stations (Area C) placed every 10 to 20 m. The number of quadrat plots per station was eight. The mean (± SD) burrow densities 625 cm^{-2} were 27.8 ± 10.5 in Area A, 38.1 ± 11.6 in Area B, and 30.5 ± 16.9 in Area C. The shrimp population size and the mean shrimp density at the entire location are estimated at 149,830,100 and 268.3 m^{-2}, respectively.

Location 2 (Tomioka, west). The location is situated on the open shore that is opposite to Location 1 across the tombolo (Fig. 3). The environmental setting around Location 2 is generally unsuitable for the shrimp to inhabit, consisting of either rocky shores or open sandy beaches. However, a small area of 1,576 m^2 protected by the close-lying offshore breakwater was inhabited by the shrimp. The location was represented by one transect with three stations placed every 20 m. The number of quadrat plots per station was 10. The mean (± SD) burrow density 625 cm^{-2} was 6.3 ± 5.2. The shrimp population size and the mean shrimp density at the entire location are estimated at 79,783 and 50.6 m^{-2}, respectively.

Location 3 (Oniike). Locations 3 to 9 are situated along the eastern coastline of Amakusa-Shimoshima Island in the outermost one-third of Ariake Sound (Fig. 4). Location 3, with an area of 41,765 m^2, was represented by two transects, each with eight or 10 stations placed every 10 m. The number of quadrat plots per station was six. Overall, the mean (± SD) burrow density 625 cm^{-2} was 25.4 ± 13.5. The shrimp population size and the mean shrimp density at the entire location are estimated at 8,479,223 and 203.0 m^{-2}, respectively.

Location 4 (Goryo, north). The location, with an area of 83,075 m^2, was represented by two transects, each with nine stations placed every 20 m (Fig. 4). The number of quadrat plots per station was six. Overall, the mean (± SD) burrow density 625 cm^{-2} was 2.9 ± 3.5. The shrimp population size and the mean shrimp density at the entire location are estimated at 1,897,802 and 22.8 m^{-2}, respectively.

Location 5 (Goryo, south). The location, with an area of 100,975 m^2, was represented by two transects with 11 stations placed

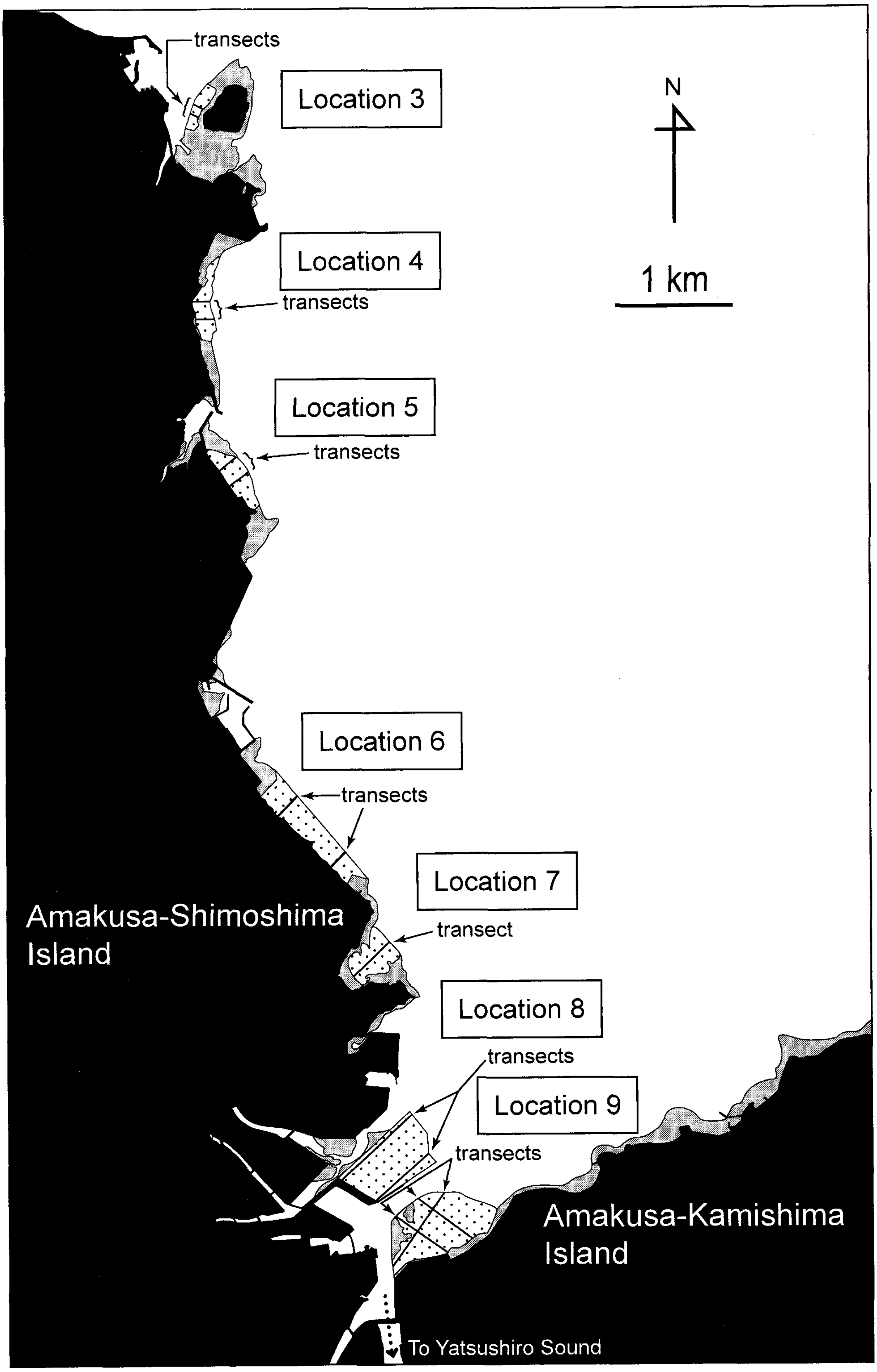

Fig. 4. Locations 3 – 9. The dotted parts stand for the area inhabited by *Nihonotrypaea harmandi* and the shaded ones for the uninhabited area on the shore. Each location was represented by one to three transects.

every 10 to 20 m on one and 12 stations placed every 20 m on the other (Fig. 4). The number of quadrat plots per station was six. Overall, the mean (± SD) burrow density 625 cm^{-2} was 5.3 ± 6.3. The shrimp population size and the mean shrimp density at the entire location are estimated at 4,291,876 and 42.5 m^{-2}, respectively.

Location 6 (Saitsu). The location, with an area of 219,658 m^2, was represented by two transects with 10 stations placed every 20 m on one and 13 stations placed every 10 to 20 m on the other (Fig. 4). The number of quadrat plots per station was six. Overall, the mean (± SD) burrow density 625 cm^{-2} was 4.5 ± 4.8. The shrimp population size and the mean shrimp density at the entire location are estimated at 7,968,810 and 36.3 m^{-2}, respectively.

Location 7 (Mogine). The location, with an area of 100,558 m^2, is identical to *HJ*-1 site in Wardiatno *et al.* (2003) and was represented by one transect with 21 stations placed every 20 m (Fig. 4). The number of quadrat plots per station was six. It can be assumed from Wardiatno *et al.* (2003) that *N. harmandi* appeared at the station 120 m distant from the high-tide shoreline and seaward (in total, 15 stations), accounting for 98.4% of the total number of shrimps of *N. harmandi* and *N. japonica*. At these stations contained in the area of 74,547 m^2, the mean (± SD) inclusive burrow density 625 cm^{-2} was 4.8 ± 3.3. The shrimp (*N. harmandi*) population size and the mean shrimp density at the entire location are estimated at 2,828,001 and 37.9 m^{-2}, respectively.

Location 8 (Hondo, north). The location, with an area of 275,655 m^2, is identical to *HJ*-2 site in Wardiatno *et al.* (2003) and was represented by two transects with 39 stations placed every 20 m on the longer one and 29 stations placed every 10 to 30 m on the shorter one (Fig. 4). The number of quadrat plots per station was six. It can be assumed from Wardiatno *et al.* (2003) that *N. harmandi* appeared at the station 340 m (on the longer transect) or at the station 260 m (on the shorter transect) from the high-tide shoreline and seaward (in total, 22 and 16 stations, respectively), accounting for 38.5% of the total number of shrimps of *N. harmandi* and *N. japonica*. At these stations contained in the area of 163,137 m^2, the mean (± SD) inclusive burrow density 625 cm^{-2} was 4.6 ± 2.7. The shrimp (*N. harmandi*) population size and the mean shrimp density at the entire location are estimated at 3,309,732 and 20.3 m^{-2}, respectively. More conservatively, on the basis of the whole transect data at this location, *N. harmandi* accounted for 20.1% of the total number of shrimps of the two species (Wardiatno *et al.*, 2003). The mean (± SD) inclusive burrow density 625 cm^{-2} was 3.7 ± 2.8 at the total of 68 stations in the present survey. Under these conditions, the shrimp (*N. harmandi*) population size and the mean shrimp density at the entire location are estimated at 1,603,218 and 9.8 m^{-2}, respectively.

Location 9 (Hondo, south). The location, with an area of 326,613 m^2, was represented by three transects, with 16 stations placed every 10 to 80 m on the western transect running from the high-tide shoreline, 25 stations placed every 20 to 75 m on the eastern transect as above, and 33 stations placed every 15 to 65 m on the other transect crossing the former two (Fig. 4). The number of quadrat plots per station was six. The mean (± SD) inclusive burrow density 625 cm^{-2} was 3.5 ± 2.7. No survey had been conducted previously for this location. Due to its position in close proximity to Location 8, the similar conditions could be assumed regarding the co-occurrence of *N. harmandi* and *N. japonica*, with the 20.1-% proportional occupancy of the former species in the mixed population over the 59.2% of the entire area. Under these assumptions, the shrimp (*N. harmandi*) population size and the mean shrimp density at the entire location are estimated at 1,827,123 and 9.4 m^{-2}, respectively.

Location 10 (Ohyano). The location, with an area of 132,373 m^2, is identical to *HJ*-3 site in Wardiatno *et al.* (2003) and was represented by one transect with 12 stations placed every 20 m (Fig. 5). The transect was close

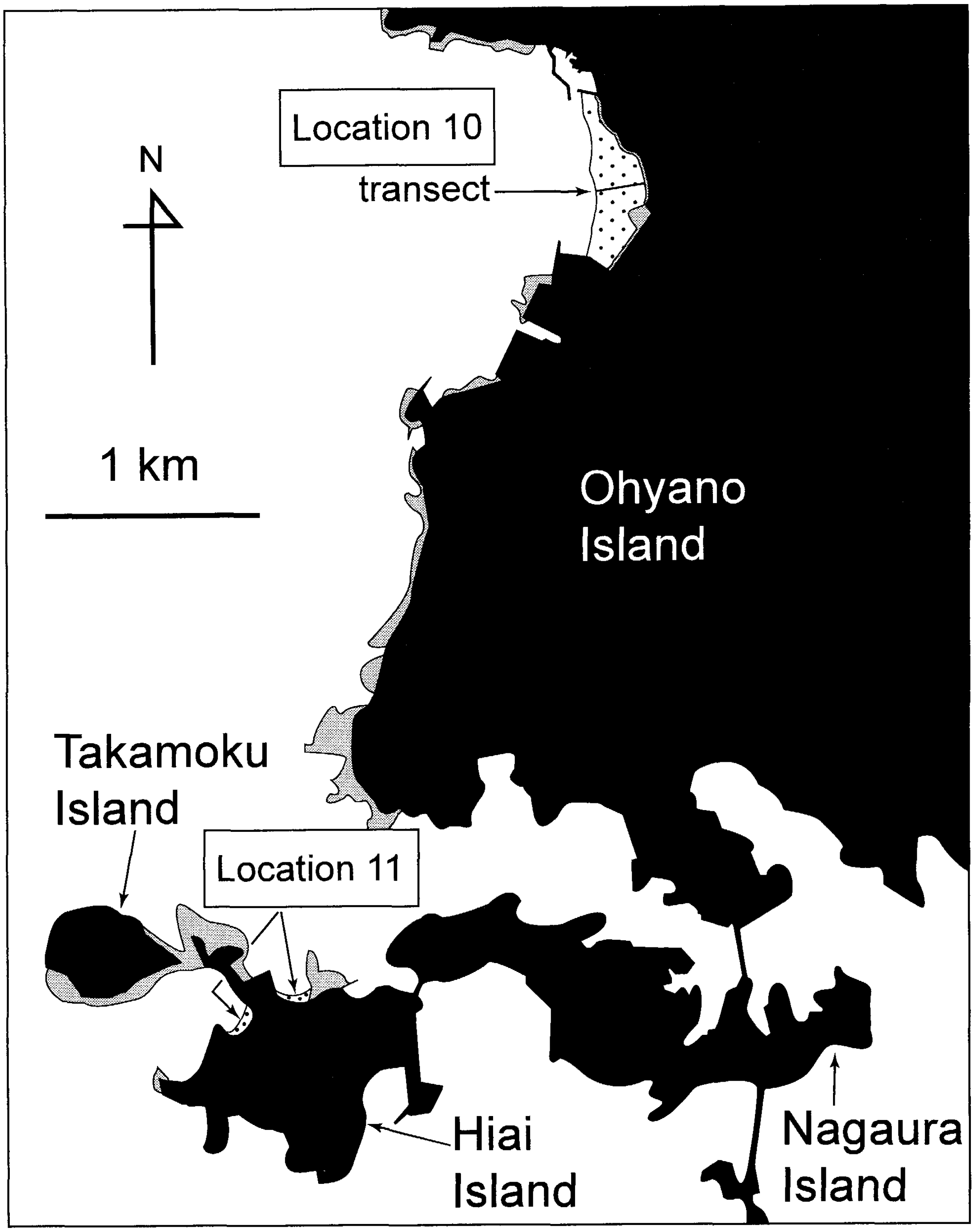

Fig. 5. Locations 10, 11. The dotted parts stand for the area inhabited by *Nihonotrypaea harmandi* and the shaded ones for the uninhabited area on the shore. The transects are not shown for Location 11.

to Transect B at *HJ*-3 site. The number of quadrat plots per station was six. It can be assumed from Wardiatno *et al.* (2003) that *N. harmandi* appeared at the station 40 m distant from the high-tide shoreline and seaward (in total, 10 stations), accounting for 90.3% of the total number of shrimps of *N. harmandi* and *N. japonica*. At these stations contained in the area of 116,268 m^2, the mean (± SD) inclusive burrow density 625 cm^{-2} was 21.6 ± 12.7. The shrimp (*N. harmandi*) population size and the mean shrimp density at the entire location are estimated at 19,066,974 and 164.0 m^{-2}, respectively.

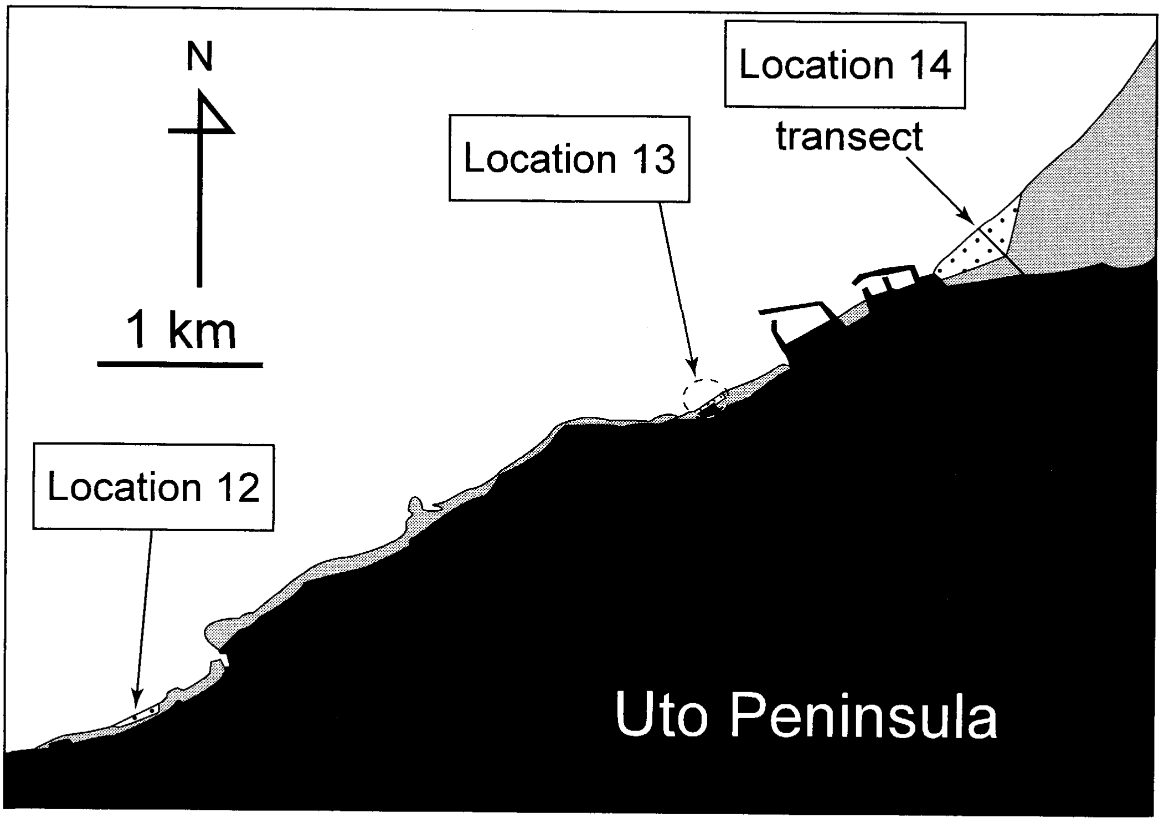

Fig. 6. Locations 12 – 14. The dotted parts stand for the area inhabited by *Nihonotrypaea harmandi* and the shaded ones for the uninhabited area on the shore. The transects are not shown for Locations 12 and 13.

Location 11 (Hiai). The location comprised two sandflats, the western one with an area of 4,502 m^2 and the eastern one with an area of 2,382 m^2 (Fig. 5). The western sandflat was divided into three areas according to the down-shore length. Each area was represented by one transect with eight stations on one area and five stations on the other two. The stations were placed every 5 m, with the number of quadrat plots per station being eight. Overall, the mean (± SD) burrow density 625 cm^{-2} was 3.7 ± 5.1. The total number of shrimps is estimated at 131,447. Similarly, the eastern sandflat was divided into two areas, which were represented by one transect with three stations on one and by one transect with six stations on the other. The stations were placed every 5 m, with the number of quadrat plots per station being eight. Overall, the mean (± SD) burrow density 625 cm^{-2} was 4.5 ± 6.9. The total number of shrimps is estimated at 85,576. The shrimp population size and the mean shrimp density at the entire location are estimated at 217,023 and 31.5 m^{-2}, respectively.

Location 12 (Ohtao). Locations 12 to 14 are situated along the northern coastline of Uto Peninsula in the outermost one-third of Ariake Sound (Fig. 6). Location 12 was divided into three areas according to the down-shore length. Each area was represented by one transect with four, five, and seven stations. The stations were placed every 5 m, with the number of quadrat plots per station being eight. Overall, the mean (± SD) burrow densities 625 cm^{-2} was 3.8 ± 4.9 in the combined area of 6,051 m^2. The shrimp population size and the mean shrimp density at the entire location are estimated at 185,893 and 30.7 m^{-2}, respectively.

Location 13 (Akasé). The location was

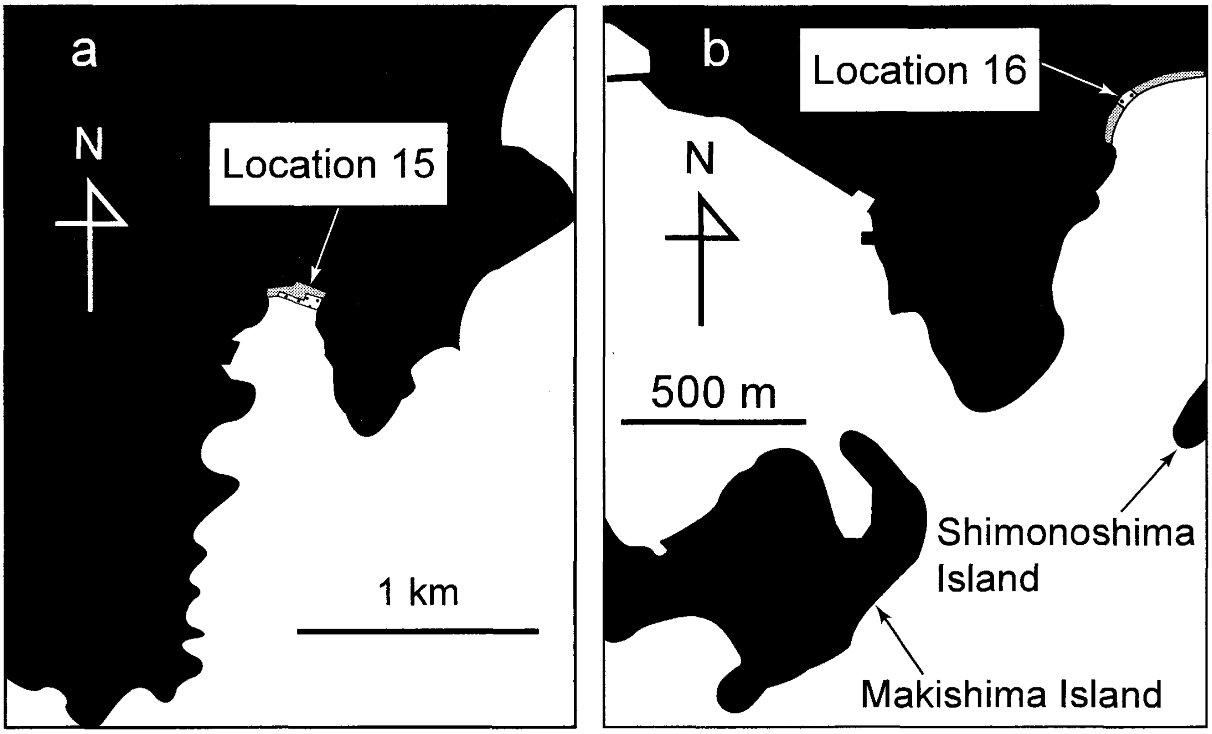

Fig. 7. Locations 15, 16. The dotted parts stand for the area inhabited by *Nihonotrypaea harmandi* and the shaded ones for the uninhabited area on the shore. The transects are not shown.

divided into three areas according to the down-shore length (Fig. 6). Each area was represented by one transect, with eight, five, and five stations, respectively. The stations were placed every 5 m, with the number of quadrat plots per station being eight. Overall, the mean (± SD) burrow densities 625 cm^{-2} was 9.0 ± 5.3 in the combined area of 5,466 m^2. The shrimp population size and the mean shrimp density at the entire location are estimated at 392,262 and 71.8 m^{-2}, respectively.

Location 14 (Okoshiki). The location is identical to *HJ*-4 site in Wardiatno *et al.* (2003), and the estimation of both shrimp density and its total number in the present study is based on the data given therein. *Nihonotrypaea harmandi* and *N. japonica* separately occupied the lower and upper parts of the transect illustrated in Fig. 6 (see also Fig. 11 in Wardiatno *et al.*, 2003). On the 360-m long transect, the density of *N. harmandi* was especially high around the low-tide shoreline. The mean value from the two stations, situated at 330 m and 360 m from the high-tide shoreline, was 175.2 m^{-2} (the 'high-density' zone). The densities at the other, upper three stations, situated at the 155-m, 213-m, and 286-m points, were lower, giving a mean value of 50.1 m^{-2} (the 'low-density' zone). The eastern limit of the area inhabited by *N. harmandi* was determined based on the data that had been obtained in the previous year (Miyabe *et al.*, 1998; Tamaki & Ueno, 1998). For the westernmost limit, it was assumed that *N. harmandi* inhabited the lower shore, with the 'high- and low-density' zones proportionally occupying as above. Thus, the areas of the 'high- and low-density' zones at the entire location were 33,281 m^2 and 61,701 m^2, respectively. The shrimp (*N. harmandi*) population size and the mean shrimp density at the entire location are estimated at 8,923,986 and 94.0 m^{-2}, respectively.

Location 15 (Ikano-Ura). Locations 15 to 20 are situated in the northern to eastern part of Tachibana Bay (Figs. 7a, b, 8).

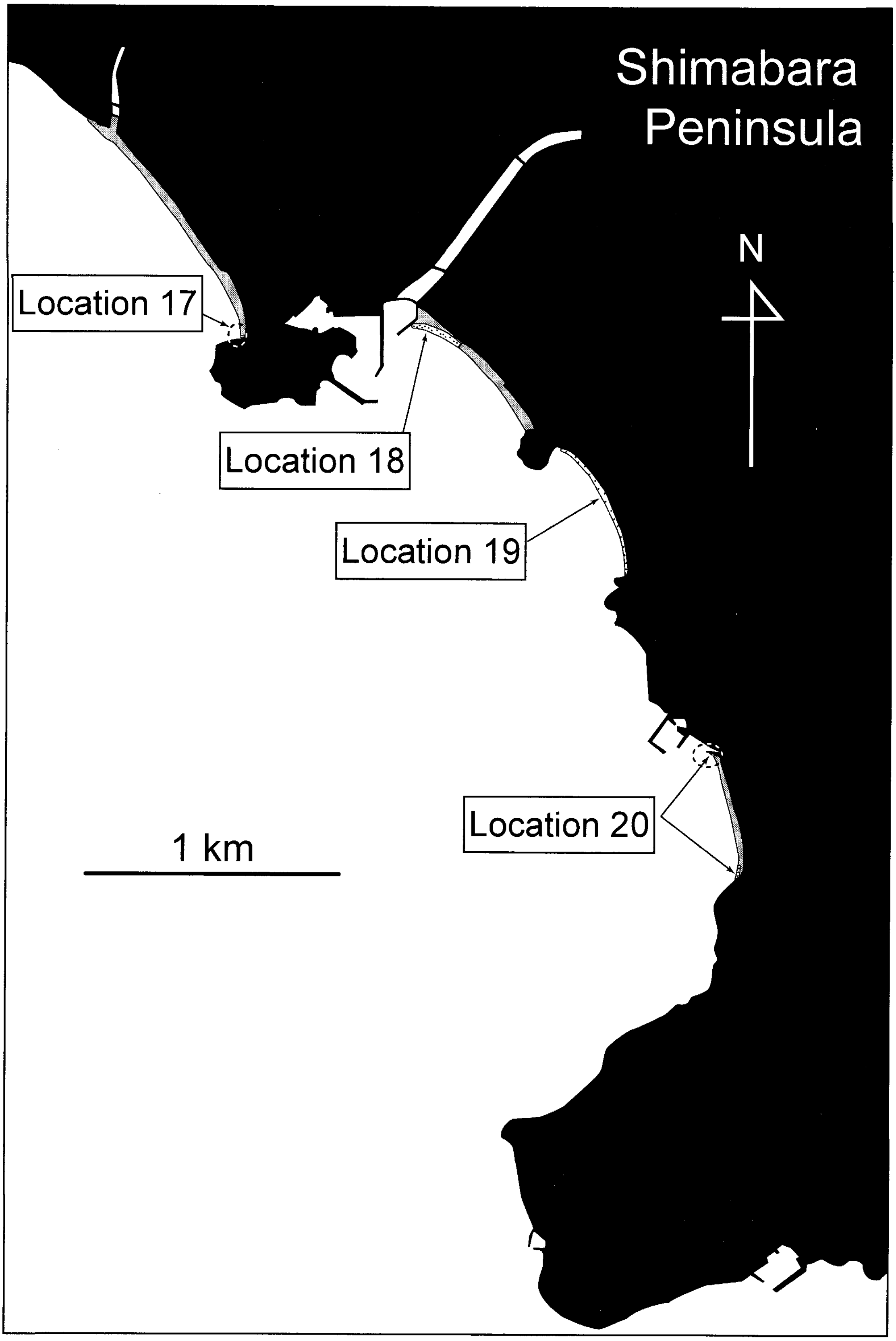

Fig. 8. Locations 17 – 20. The dotted parts stand for the area inhabited by *Nihonotrypaea harmandi* and the shaded ones for the uninhabited area on the shore. The transects are not shown.

Location 15 was divided into two areas according to the down-shore length (Fig. 7a). The eastern area was represented by two transects, each with 10 stations, and the western area by one transect with four stations. The stations were placed every 5 m, with the number of quadrat plots per station being eight. Overall, the mean (± SD) burrow density 625 cm^{-2} was 4.0 ± 3.2 in the combined area of 5,360 m^2. The shrimp population size and the mean shrimp density at the entire location are estimated at 169,376 and 31.6 m^{-2}, respectively.

Location 16 (Tayui). The location, with an approximately rectangular area of 1,500 m^2, was represented by two transects, each with six stations placed every 5 m (Fig. 7b). The number of quadrat plots per station was eight. Overall, the mean (± SD) burrow density 625 cm^{-2} was 7.5 ± 10.1. The shrimp population size and the mean shrimp density at the entire location are estimated at 90,120 and 60.1 m^{-2}, respectively.

Location 17 (Nodahama Beach). Locations 17 to 20 are situated along the southern coastline of Shimabara Peninsula in Tachibana Bay (Fig. 8). Of all locations in the target waters except for Location 2, these locations are influenced by the strongest wave action due to the longest fetch of southwesterly winds blowing especially during summer (Fig. 1). Therefore, the habitat type of these locations can be designated as protected sandy beaches, as mentioned earlier. Within each sandy beach, the occurrence of *N. harmandi* was restricted to more or less sheltered parts except for Location 19. At Location 17, the shrimp was confined to a small patch with an area of 280 m^2 situated at the southernmost part of the beach. The number of stations was six, each with eight quadrat plots. Overall, the mean (± SD) burrow density 625 cm^{-2} was 1.5 ± 2.8. The shrimp population size and the mean shrimp density at the entire location are estimated at 3,356 and 12.0 m^{-2}, respectively.

Location 18 (Maehama Beach, north). The shrimp was distributed in a zone situated at the northernmost part of the beach (Fig. 8). The zone, with an area of 5,991 m^2, was divided into five areas according to the down-shore length. Each area was represented by one transect with six to eight stations placed every 5 m. The number of quadrat plots per station was eight. Overall, the mean (± SD) burrow density 625 cm^{-2} was 2.9 ± 3.3. The shrimp population size and the mean shrimp density at the entire location are estimated at 139,470 and 23.3 m^{-2}, respectively.

Location 19 (Maehama Beach, south). The shrimp was distributed in most of the alongshore stretch of the beach, forming a zone with an area of 13,320 m^2 (Fig. 8). The densities were especially high in a waterlogged runnel situated in the upper shore, with those at the southernmost part of the beach highest. The zone was represented by five transects, each with seven to nine stations placed every 5 m. The number of quadrat plots per station was eight. Overall, the mean (± SD) burrow density 625 cm^{-2} was 3.7 ± 3.7. The shrimp population size and the mean shrimp density at the entire location are estimated at 392,141 and 29.4 m^{-2}, respectively.

Location 20 (Shirahama Beach). The shrimp was distributed in patches at both edges of the beach, two in the north and one in the south (Fig. 8). Each northern patch, with an area of 92 m^2 and 90 m^2, respectively, were represented by six stations, each with eight quadrat plots. Overall, the mean (± SD) burrow density 625 cm^{-2} was 13.4 ± 7.7 and 2.7 ± 2.0, respectively. The total numbers of shrimps are estimated at 9,894 and 1,914. The southern patch, with an area of 449 m^2, formed a small zone and represented by three transects, each with three stations placed every 5 m. The number of quadrat plots per station was eight. Overall, the mean (± SD) burrow density 625 cm^{-2} was 2.6 ± 5.6. The total number of shrimps is estimated at 9,237. The shrimp population size and the mean shrimp density at the entire location are estimated at 21,045 and 14.6 m^{-2}, respectively.

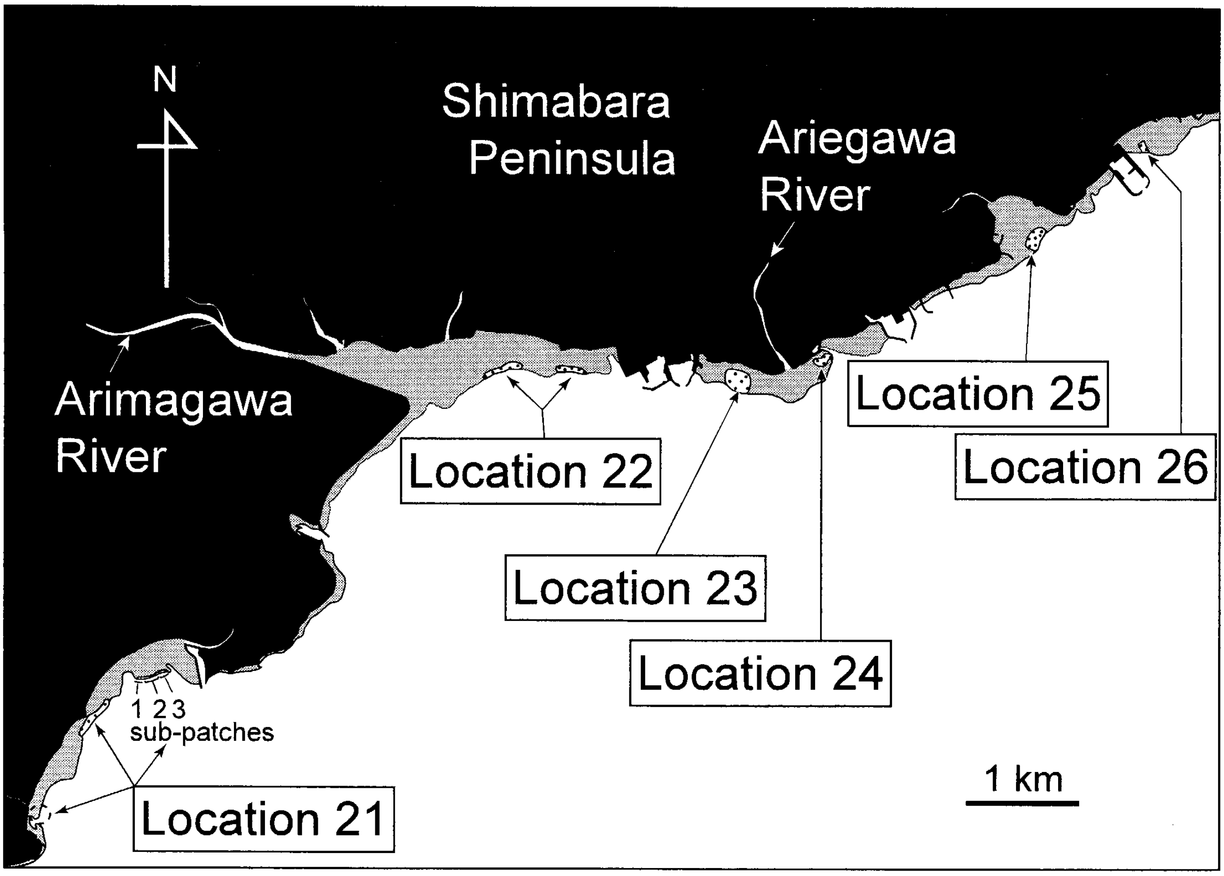

Fig. 9. Locations 21 – 26. The dotted parts stand for the area inhabited by *Nihonotrypaea harmandi* and the shaded ones for the uninhabited area on the shore. The transects are not shown.

Location 21 (Ohé). Locations 21 to 26 are situated along the southern coastline of Shimabara Peninsula in the outermost one-third of Ariake Sound (Fig. 9). At all these locations, the *N. harmandi* zones/patches were situated in the lower shore. Tamaki *et al.* (1999) recorded the occurrence of *N. japonica* at Location 22, and it was from the gravelly muddy sand in the upper shore at the mouth of the largest river at this location, Arimagawa River. No individuals of *N. japonica* were collected from the *N. harmandi* zones/patches at the above six locations. At Location 21, three zones/patches existed. One patch, with an area of 528 m^2, was situated in the western part of the sandflat. The patch was represented by five stations, each with four quadrat plots. Overall, the mean (± SD) burrow density 625 cm^{-2} was 5.4 ± 4.7. The total number of shrimps is estimated at 22,598. Another patch (actually a zone), with an area of 21,265 m^2, was situated in the middle part of the sandflat. The zone was represented by three transects, each with seven to 12 stations placed every 5 m (on two transects) or 10 to 20 m (on the other one transect). The number of quadrat plots per station was six. Overall, the mean (± SD) burrow density 625 cm^{-2} was 3.8 ± 4.3 (n = 168). The total number of shrimps is estimated at 653,261. The other patch was situated in the eastern part of the sandflat. The patch was subdivided into three patches (sub-patches 1 to 3 from west to east). The sub-patch 1, with an area of 190 m^2, was represented by four stations, each with four quadrat plots. Overall, the mean (± SD) burrow density 625 cm^{-2} was 19.8 ± 5.9. The total number of shrimps is estimated at 30,124. The sub-patch 2, with an area of

1,165 m^2, was represented by five stations, each with four quadrat plots. Overall, the mean (± SD) burrow density 625 cm^{-2} was 4.2 ± 3.9. The total number of shrimps is estimated at 38,671. The sub-patch 3, with an area of 631 m^2, was represented by five stations, each with four quadrat plots. Overall, the mean (± SD) burrow density 625 cm^{-2} was 4.5 ± 4.7. The total number of shrimps is estimated at 22,919. The shrimp population size and the mean shrimp density at the entire location are estimated at 767,573 and 32.3 m^{-2}, respectively.

Location 22 (Tatsuishi). Two shrimp zones existed at the location (Fig. 9). The western zone, with an area of 40,329 m^2, was represented by three transects, each with 10 to 14 stations placed every 10 m. The number of quadrat plots per station was six. Overall, the mean (± SD) burrow density 625 cm^{-2} was 2.3 ± 3.3. The total number of shrimp is estimated at 754,961. The eastern zone, with an area of 20,939 m^2, was represented by three transects, each with six to seven stations placed every 10 to 20 m. The number of quadrat plots per station was six. Overall, the mean (± SD) burrow density 625 cm^{-2} was 4.3 ± 4.8 (n = 120). The total number of shrimps is estimated at 716,952. The shrimp population size and the mean shrimp density at the entire location are estimated at 1,471,913 and 24.0 m^{-2}, respectively.

Location 23 (Sugawa). This location and Location 24 together make up a continuous shore, but its sandflat parts inhabitable by the shrimp are separated by the boulder delta formed at the mouth of Ariegawa River (Fig. 9). At Location 23, a single shrimp zone occupied a substantial part of the entire sandflat, with an area of 37,870 m^2. The zone was represented by three transects, each with five to eight stations placed every 10 m. The number of quadrat plots per station was eight. Overall, the mean (± SD) burrow density 625 cm^{-2} was 4.8 ± 3.3. The shrimp population size and the mean shrimp density at the entire location are estimated at 1,442,124 and 38.1 m^{-2}, respectively.

Location 24 (Nakasugawa). A single shrimp zone, with an area of 12,065 m^2, existed at the location (Fig. 9). The zone was represented by two transects, each with six to 10 stations placed every 20 m. The number of quadrat plots per station was eight. Overall, the mean (± SD) burrow density 625 cm^{-2} was 0.5 ± 0.8. The shrimp population size and the mean shrimp density at the entire location are estimated at 46,042 and 3.8 m^{-2}, respectively.

Location 25 (Kamaga). A single shrimp zone, with an approximately trapezoid area of 24,453 m^2, existed at the location (Fig. 9). The zone was represented by three transects, each with seven stations placed every 10 m. The number of quadrat plots per station was eight. Overall, the mean (± SD) burrow density 625 cm^{-2} was 6.7 ± 4.2. The shrimp population size and the mean shrimp density at the entire location are estimated at 1,312,637 and 53.7 m^{-2}, respectively.

Location 26 (Dohzaki). A single shrimp patch, with an area of 3,291 m^2, existed at the location (Fig. 9). The patch was represented by two transects parallel to the shoreline, each with eight stations placed every 5 m. The number of quadrat plots per station was eight. Overall, the mean (± SD) burrow density 625 cm^{-2} was 3.3 ± 2.9. The shrimp population size and the mean shrimp density at the entire location are estimated at 87,678 and 26.6 m^{-2}, respectively.

Discussion

The shrimp (*Nihonotrypaea harmandi*)-inhabited area (sum total of all zones/patches), the mean shrimp density, and the shrimp population size at the 26 target locations are ordered by dimensions in Fig. 10. The latter two values at these locations in the target waters are illustrated in Fig. 11.

Of all local populations of *N. harmandi*, the shrimp population size on the Tomioka Bay sandflat (Location 1) was by far the largest, constituting 70% of the total number of shrimps in the target waters. Tamaki *et al.* (1997) recorded the temporal change in the shrimp density on this sandflat during

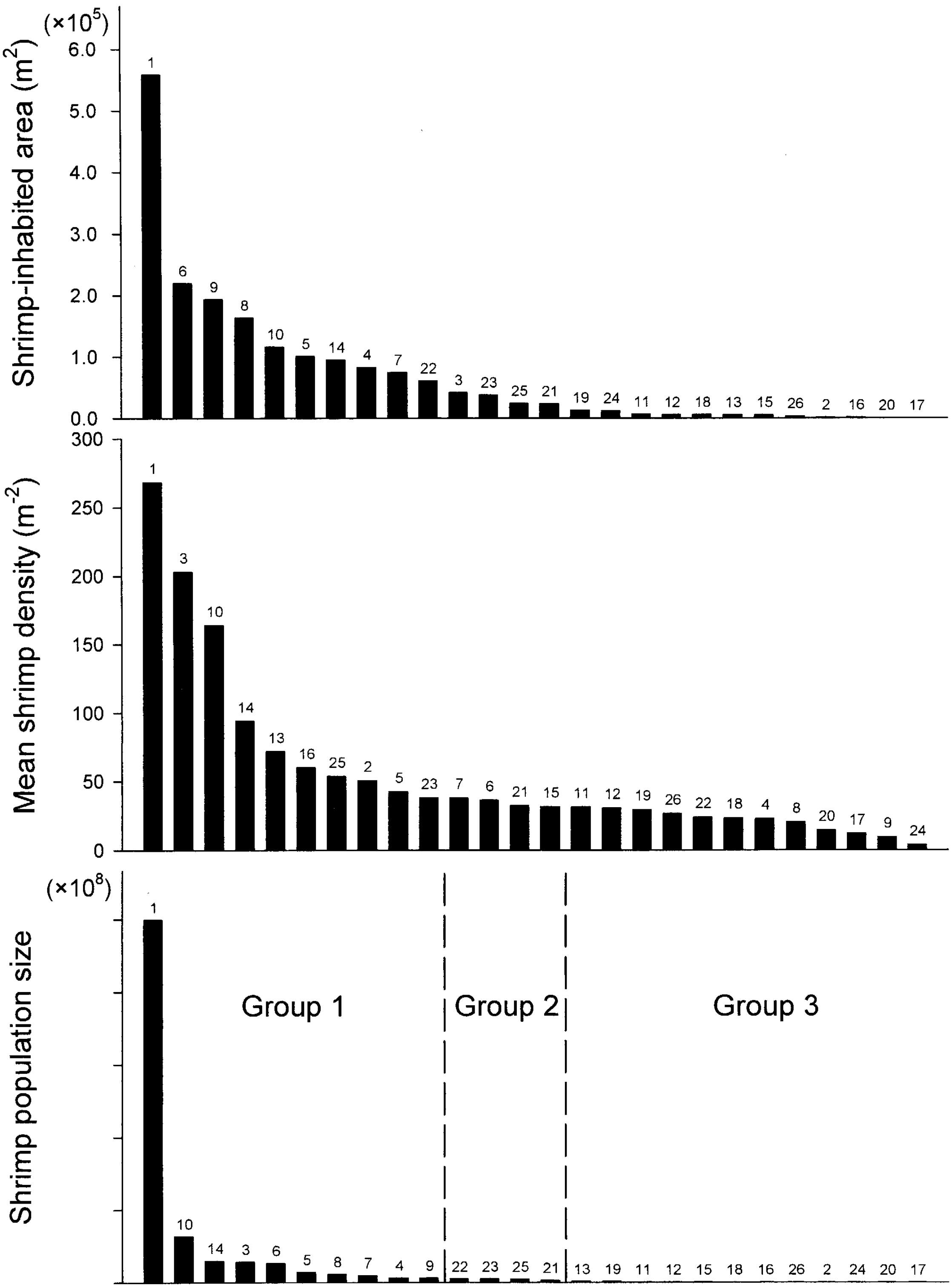

Fig. 10. *Nihonotrypaea harmandi*-inhabited area (top), mean shrimp density (middle), and shrimp population size (bottom) at the 26 target locations, ordered by dimensions. The number above each column denotes the location number. The mean shrimp density and the shrimp population size at Location 8 come from the larger of the two estimates for each category (see text). The 26 local shrimp populations could be divided into three groups according to both size and position along the coastline of the target waters (bottom).

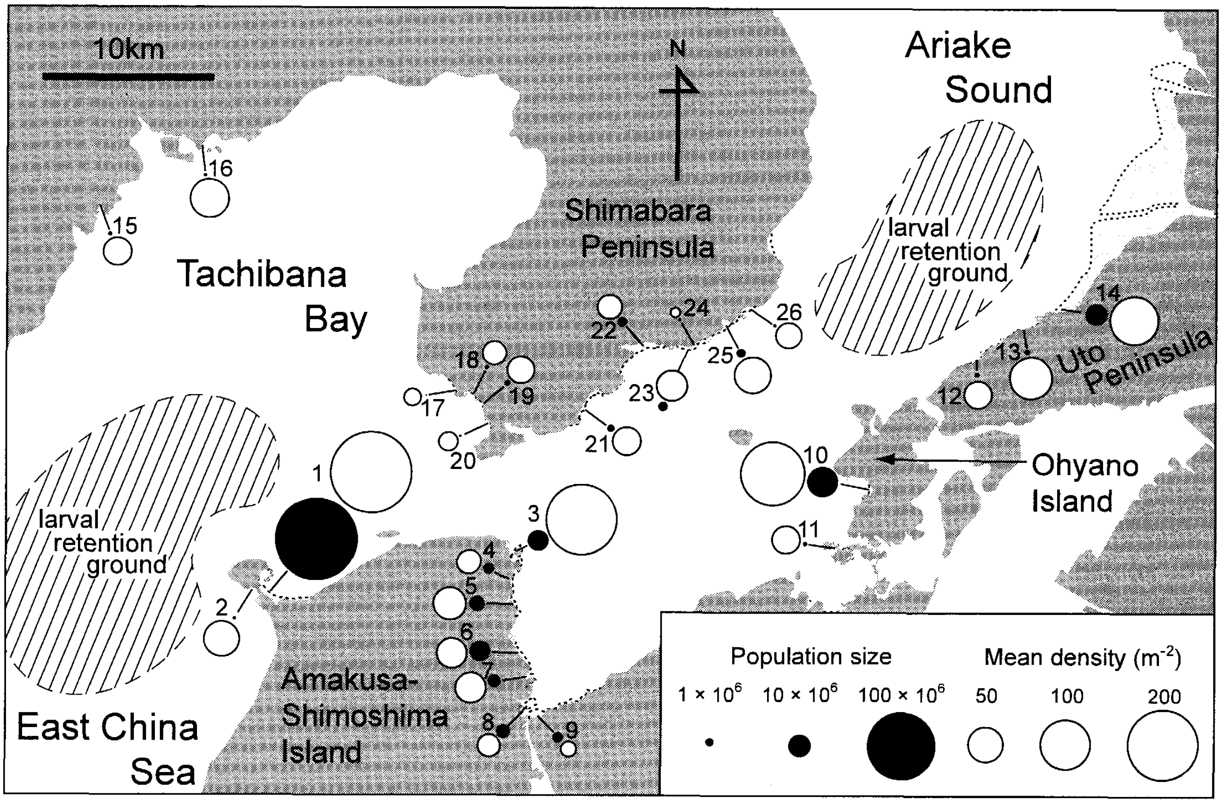

Fig. 11. Distribution of the 26 main locations inhabited by *Nihonotrypaea harmandi* along the coastline in the target waters, with the shrimp population size and the mean shrimp density indicated by solid and open circles, respectively. The mean shrimp density and the shrimp population size at Location 8 come from the larger of the two estimates for each category (see text). The broken lines seaward of the coastline indicate the extent of the relatively large tidal flats. The position of the two retention grounds for larvae of the three species of *Nihonotrypaea* is based originally on Tamaki & Miyabe (2000: Fig. 5) and, in a modified form, on Flach & Tamaki (2001: Fig. 7.5).

May, 1989 to April, 1991. On the first sampling occasion in each of these three years, the population densities were 912, 1011, and 887 m^{-2}, respectively, giving a mean value of 937 m^{-2}. This is 3.5 times greater than the mean shrimp density recorded in the present study (268 m^{-2}). Thus, the former shrimp population size on the sandflat can be estimated at about five hundred millions. It is suspected that the recent decline in the shrimp population size could be due to increased predation pressure exerted by the stingray, *Dasyatis akajei*, from 1995 (Flach & Tamaki, 2001).

The local shrimp populations in the target waters can be divided into three groups according to both shrimp population size and position along the coastline: (1) Locations 1, 10, 14, ----, 4, and 9 (see Fig. 10, bottom) situated in the southern part of both Tachibana Bay and the outermost one-third of Ariake Sound (see Fig. 11); (2) Locations 22, 23, 25, and 21 in the northern part of the outermost one-third of Ariake Sound; and (3) Locations 13, 19, 11, ----, 20, and 17 in the northern to eastern part of Tachibana Bay. In Group (1), the top three locations had both the higher mean shrimp densities and the larger shrimp-inhabited areas. In fact, the largest shrimp population size at Location 1 was due to both the highest mean shrimp density and the largest area. The large shrimp population size at the fourth location (Location 3) was derived from the second highest mean shrimp density rather than from the size of its area. The large shrimp population sizes at the other six locations were mainly due to their large areas rather than to their densities. The shrimp population sizes at the four locations comprising Group (2) largely reflected their intermediate areas of similar dimensions. The mean shrimp densities at these locations ranged from relatively high (Location 25) to relatively low (Location 22), but their differences were rather small. The shrimp population sizes at the 12 locations comprising Group (3) resulted from both their small areas and the low mean shrimp densities except for Locations 13, 16, and 2.

The alongshore configuration and size of the local populations of *N. harmandi* in the target waters appear to correspond to the larval abundance pattern for the three species of *Nihonotrypaea* included in the Ariake-Sound estuarine system. The larval distribution was surveyed in late July - early August, 1998 [compiled in Fig. 5 in Tamaki & Miyabe (2000) and Fig. 7.5 in Flach & Tamaki (2001)]. The larval development of the three species consisted of five zoeal stages, which lasted 16 - 19 d in June - August, and one decapodid stage (Konishi *et al.*, 1990; Tamaki *et al.*, 1996; Miyabe *et al.*, 1998; Konishi *et al.*, 1999). Note that the estimated population size of *N. petalura* is much smaller than those of the two tidal-flat species, accounting for only 6% of the total number of shrimps of *Nihonotrypaea* in the Ariake-Sound estuarine system (Tamaki & Miyabe, 2000). In the target waters, there are two larval retention grounds through all zoeal stages, one situated 10 to 20 km north - northwest of the Tomioka Bay sandflat (Location 1) in Tachibana Bay and the other situated off Uto Peninsula in Ariake Sound (off Locations 12, 13, and 14, with an extended area into the middle one-third of the sound) (Fig. 11). The larval pool in the former ground, which is supposed to be composed of *N. harmandi* larvae almost exclusively, is much greater in size than that in the latter ground containing more *N. japonica* larvae (Tamaki & Miyabe, 2000). Matsuno *et al.* (1999) revealed that the water mass in southern Tachibana Bay, including the former larval retention ground, is characterized by the open-sea waters derived from the East China Sea in contrast to that in the northern bay influenced by the waters derived from Ariake Sound. The higher mean shrimp densities at Locations 1, 3, 10, and 2 in the target waters could be explained by their close proximity to the larval retention ground in Tachibana Bay and/or in line with the major axes of M_2 tidal current ellipses lying between the larval retention ground and Location 10; the highest M_2 flood tidal current speed reaches 250 cm s^{-1} at Hayasaki Inlet situated between Ariake Sound and Tachibana Bay (Tsukamoto & Yanagi, 2002). It is especially noteworthy that the larval retention ground in Tachibana Bay is closest to the largest local population of *N. harmandi* on the Tomioka Bay sandflat situated at the southwestern edge of the target waters. All these conditions should render the population of this sandflat fair isolation from the other local populations, affording it some self-sustaining recruitment mechanism. Similarly, the higher mean shrimp densities at Locations 14 and 13 may be related to their close proximity to the larval retention ground in Ariake Sound.

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