

**Spatial partitioning between species of the phytoplankton-feeding guild on an estuarine
intertidal sand flat and its implication on habitat carrying capacity**

Akio Tamaki^{1,*}, Ayumi Nakaoka¹, Hideki Maekawa¹, Fumihiko Yamada²

1. Faculty of Fisheries, Nagasaki University, Bunkyo-machi 1-14, Nagasaki 852-8521, Japan

*2. Graduate School of Science and Technology, Kumamoto University, Kurokami 2-39-1, Kumamoto
860-8555, Japan*

* Corresponding author.

E-mail address: tamaki@nagasaki-u.ac.jp (A. Tamaki)

Complete postal address: Akio Tamaki, Faculty of Fisheries, Nagasaki University, Bunkyo-machi
1-14, Nagasaki 852-8521, Japan

Telephone number: +81-95-819-2856

Fax number: +81-95-819-2799

Abstract: The fishery yield of Manila clams, *Ruditapes philippinarum*, increased considerably in the 1970s but has decreased rapidly since the middle 1980s on extensive intertidal sandflats in Ariake Sound (Kyushu, Japan). A survey conducted in 2004 on a 3.4-km² sandflat located in the central part of the Sound (Shirakawa sandflat) revealed four dominant species: two thalassinidean shrimps (*Upogebia major* and *Nihonotrypaea japonica*), which are deep-reaching burrow dwellers with strong bioturbating activities, and two bivalves (*Macra veneriformis* and *R. philippinarum*). All four species belong to a phytoplankton (diatom)-feeding guild. In the late 1970s, the Manila clam population prevailed in high densities over the entire sandflat, whereas its distribution was restricted to the lowest quarter of the shore in 2004. In contrast, the population sizes and zones of occurrence of the other phytoplankton feeders have expanded in the absence of *R. philippinarum*, perhaps an indication of competitive release. After establishment, effects of the thalassinidean shrimps on sediment stability appear to have further reduced clam abundances. Across the sandflat in 2004, wet weight population biomass estimates for *N. japonica*, *U. major*, *M. veneriformis*, and *R. philippinarum* (whole body for shrimps and soft tissue for bivalves) were 304, 111, 378, and 234 tonnes, respectively. Based on Manila clam fishery yield records from Shirakawa, the carrying capacity of the Shirakawa sandflat in the late 1970s was estimated to be two times greater than the sum value for the whole phytoplankton-feeding guild in 2004. It is hypothesized that (1) the amount of phytoplankton determines the carrying capacity for the benthic community on the Shirakawa sandflat, with both phytoplankton and benthic biomass at maxima in the late 1970s, and (2) the subsequent increases in competition for space have caused further declines in the Manila clam population biomass to approximately one-eighth of its past value.

Key words: tidal flats, carrying capacity, phytoplankton, suspension-feeding clams, thalassinidean shrimps, bioturbation

Regional index terms: Japan, Kyushu, Ariake Sound

1. Introduction

Filtration of water and the use of suspended particles is a major feeding mode for macrobenthos on intertidal sandflats. Suspension-feeding bivalves among others, such as clams, cockles, mussels, and oysters, can reach exceedingly high densities on sandflats in productive estuarine waters (Herman et al., 1999; Dame et al., 2001; Asmus and Asmus, 2005). They are often targeted by commercial fisheries. The removal of such bivalves during harvest can cause large shifts in species dominance in the sandflat, as other suspension feeders take advantage of the newly available resources including food and habitat space (Reise et al., 1989; Herman et al., 1999; Dame, 2005). Although the supply of suspended food to an estuarine intertidal sandflat may seem unlimited, there is a theoretical carrying capacity in this habitat type, mediated in part by food resources and in part by space availability on the sandflat (Heip et al., 1995; Sarà and Mazzola, 2004). Thus understanding both carrying capacity for the whole suspension-feeding guild and the partitioning of resources by dominant members of the guild is critical for predicting the impacts of fishing and setting limits for maximum allowable catch (Héral, 1993; Dame et al., 2001; Bell et al. 2005).

The Manila or short-necked clam, *Ruditapes philippinarum*, is an important suspension-feeding bivalve to the fishery industry not only in Japan (Sekiguchi and Ishii 2003; Toba et al., 2007) but also in other countries (Toba et al., 1992; Vincenzi et al., 2006; Zhang and Yan, 2006). On the extensive intertidal sandflats along the eastern coast of Ariake Sound, Kyushu, Japan (Fig. 1), the annual fishery yields of *R. philippinarum* increased considerably in the 1970s, reaching a peak of 65 000 tonne in 1977, but has decreased rapidly throughout the 1980s (Fig. 2A). At the peak, clam densities were generally high across entire sandflats from lower to upper shore (Nakahara and Nasu, 2002). For example, on a sandflat located at the mouth of the Shirakawa River in central Ariake Sound (Shirakawa sandflat: Fig. 1), the maximum annual yield of 3 830 tonne was recorded in 1979 [Seikai National Fisheries Research Institute of the Fisheries Research Agency (SNFRI of FRA) and

Fig. 1

Fig. 2

Oshima and Matsuo Fisheries Cooperative Associations (OFCA; MFCA), unpublished data], and the clam occurred across the entire sandflat (OFCA and MFCA, personal communication). The clam distribution is now restricted to the lower shore (Wardiatno et al., 2003), and the annual yield has not exceeded 680 tonne since 1990 (OFCA and MFCA, unpublished data).

On the Shirakawa sandflat, four large-sized infaunal species now dominate the benthic community: *Ruditapes philippinarum*, the mactrid bivalve, *Macra veneriformis*, the thalassinidean mud shrimp, *Upogebia major*, and the thalassinidean ghost shrimp, *Nihonotrypaea japonica* (Wardiatno et al., 2003; Yokoyama et al., 2005b). Of the four species only *R. philippinarum* is substantially harvested by local fishermen. Both *U. major* and *N. japonica* reside in deep burrows: 2 m (Kinoshita, 2002) and 1 m (Tamaki and Ueno, 1998; K. Shimoda, unpublished data), respectively. The two bivalves and *U. major* are suspension feeders (Nakamura, 2001; and Kinoshita, 2002), while *N. japonica* is a deposit feeder (Tamaki and Ueno, 1998; Shimoda et al., 2007). Recent carbon and nitrogen stable isotope studies on the trophic structure of the benthic community on the Shirakawa sandflat have revealed that the above four species all utilize phytoplankton (diatoms) in the estuarine water column as their exclusive food source, with *N. japonica* acting as a subductor of fresh phytodetritus (Yokoyama et al., 2005a,b; Shimoda et al., 2007). The four species, therefore, can be regarded as members of a phytoplankton-feeding guild. During the 1970s to the early 1980s, when populations of *R. philippinarum* were high, the density of seston in the water column (a gross measure of large-sized planktonic diatom abundance) of Ariake Sound was also at a higher level than in the other periods (SNFRI of FRA, 2001; Fig. 2B). In contrast to the *R. philippinarum* population boom, the other three species were present in low abundances and did not dominate benthic communities on the Shirakawa sandflat (OFCA and MFCA, personal communication). However, starting in the 1980s, their population sizes and zones of occurrence began expanding considerably on several sandflats in Ariake Sound [*M. veneriformis*

(see Tokuyama, 2000); *U. major* (see Tokuyama, 2000; M. Sakamoto, unpublished data); *N. japonica* (T. Tanoue, unpublished data; OFCA and MFCA, personal communication)].

The causes of population expansion and decline are difficult to ascertain, even for well-studied species like *Ruditapes philippinarum* (Nakahara and Nasu, 2002; Sekiguchi and Ishii, 2003). On tidal flats in the estuaries of Washington and Oregon, USA, *R. philippinarum* introduced from Japan is negatively affected by the native mud shrimp, *Upogebia pugettensis*, and ghost shrimp, *Neotrypaea californiensis* (Toba et al., 1992; Smith and Langdon 1998). It is supposed that the shrimps compete with clams for space and that shrimps' bioturbating activities contribute to sediment instability, which can ultimately smother small clams. On the Tomioka Bay sandflat located at the northwestern corner of Amakusa-Shimoshima Island, west of Ariake Sound, local extinction of the trochid gastropod, *Umbonium moniliferum*, was ascribed to the population expansion of *Nihonotrypaea harmandi* (Fig. 1; Tamaki, 1994). It is suspected that *R. philippinarum* in Ariake Sound has also been negatively affected by *U. major* and *N. japonica*, resulting in restricted zonation on intertidal sandflats and reduced population biomass. From the viewpoint of a possible change in the ecosystem state of Ariake Sound over the years, it is useful to determine the present levels of space partitioning by the four dominant phytoplankton feeders and the sandflat's overall carrying capacity. By doing this, we will be able to compare and contrast the status of the Shirakawa sandflat at present and around 1979, at the peak of the *R. philippinarum* population boom.

Originally developed as a population parameter, carrying capacity, or *K*, can be defined as the equilibrium population density, which is determined by a range of physical and biological factors such as the availability of food resources and the presence of competitors (Catchpole, 1998). The concept of carrying capacity can also be applied to a collection of similar species exploiting a common resource. In the latter case, the adoption of some common measure, such as biomass or

production, is required to accurately compare among species with varying body dimensions. Here, we used population biomass to examine the partitioning of space on the Shirakawa sandflat by the four large macrofaunal species of the phytoplankton-feeding guild, and we estimated the carrying capacity of the sandflat, following well established protocols for the bivalves and by devising new techniques for the mud shrimp and the ghost shrimp.

2. Materials and methods

2.1. Study site

The tidal flat was bounded by the Shirakawa and Tsuboigawa Rivers, which empty into Ariake Sound [Fig. 1; for detailed tidal flat characteristics, see Yamada and Kobayashi (2004) and Yamada et al. (2008)]. The designed capacity of the Shirakawa River set by the Ministry of Land, Infrastructure and Transport of Japan is ten times that of the Tsuboigawa River ($3\,400$ vs $340\text{ m}^3\text{ s}^{-1}$). The sandflat is wider on the Shirakawa River side, extending to ca. 2.7-km width at the mean low water spring tide (MLWS). Away from the Shirakawa River, both the MLWS and the mean low water neap tide (MLWN) levels incline toward the upper shoreline. Tides in the study area are semidiurnal, with amplitudes averaging 3.9 and 2.0 m at spring and neap tides, respectively. The total area of the flat is about 4.15 km^2 . The flat is divided into a southern sandy part (the area demarcated by the thick line in Fig. 1: 3.39 km^2) and a northern muddy part by a 1 090-m long dike located near the Tsuboigawa River. The four target species in the present study mainly inhabit the southern part, and only this area (= Shirakawa sandflat) was surveyed. A 4-m wide concrete road extends seaward for a distance of 935 m in the central part of the Shirakawa sandflat. This road was constructed in 1984 to increase access to the sandflat (i.e. a pavement for vehicles carrying the Manila clam). The access road has affected the drainage of seawater from the flat; water now accumulates next to the road on the Shirakawa River side at low tide (several cm deep, 5 – 30 m

wide) and flows seaward in a direction parallel to the road.

All sampling described herein was conducted during low spring tides. Five transects running from the upper shoreline to around the MLWS level were established [Transects C, A, K, B, D from north to south, with total lengths of 1 490, 1 496, 1 545, 2 129, and 2 235 m, respectively (Fig. 1)]. Transect K runs along the access road, and the upper two-thirds of this transect is within the above-mentioned drainage flow. On Transects A–D, sampling stations were placed every 80 m (with a few exceptions for logistical reasons). On Transect K, the uppermost station was placed 45 m from the upper edge of the shoreline, and the distance between any two adjacent stations was 75 m. Hereafter Stn i - j means the station which is j m seaward from the 0-m point on Transect i . A total of 20, 20, 21, 28, and 29 stations were established on Transects C, A, K, B, and D, respectively.

2.2. Sampling for bivalves and laboratory treatments

The sampling for *Ruditapes philippinarum* and *Macra veneriformis* was undertaken on Transects A–D in the period from 20 April to 3 July in 2004. At each station, the sediment within a quadrat frame of 25 cm \times 25 cm to a depth of 10 cm (beyond the maximum depth of 7 cm for bivalve inhabitation: A. Tamaki, unpublished data) was passed through a 1-mm mesh sieve and fixed with 10 % neutralized formalin. Four samples were collected separately at each station. In the laboratory, all clams were identified to species and measured for shell length (SL) to the nearest 0.1 mm. The blotted wet weights of 66 – 78 clams over the whole size range for each species population, with shell retained (WW_{shell}) and after shell removal ($WW_{soft\ tissue}$), were measured separately to the nearest 0.1 mg. The regression equations for WW_{shell} or $WW_{soft\ tissue}$ (y) versus SL (x) were established using SPSS (2002), including (1) a linear function ($y = a + b x$) and several nonlinear ones: (2) polynomial quadratic ($y = a + b x + c x^2$), (3) polynomial cubic ($y = a + b x + c x^2 + d x^3$), (4) exponential [$y = a \exp(b x)$], and (5) power ($y = a x^b$). The selection of the best fit

function of the above five was made based on the smallest value for Akaike's (1973) Information Criterion (AIC). All *SL* values at each station were put into this function to estimate *WWshell* or *WWsoft tissue* values, which were further converted into the population biomass values per m².

2.3. Sampling for mud shrimp and ghost shrimp, and laboratory treatments

As *Upogebia major* and *Nihonotrypaea japonica* live deep in the sediment, it was impossible to collect all individuals within fixed plots at each station. Thus population biomass was estimated indirectly, with different procedures applied to the two species.

Given the impracticality of capturing/measuring mud shrimps at all 118 sampling stations, the best method for assessing *Upogebia major* population structure was via an analysis of burrow dimensions (and body-size-frequency distribution). Burrow dimension is known to correlate well with body size (e.g. Dworschak, 1983; Kinoshita, 2002). The burrow of a single individual *U. major* consists of an upper U-shaped part with two (or, more infrequently, up to four) surface openings, and a lower long shaft starting from the center of the bottom of the U (Kinoshita, 2002); the connection of multiple surface openings can be confirmed by checking their concomitant responses to artificially induced water movement in any one burrow. The inner wall of the burrow is lined with mucus plus mud and is quite consolidated; a circular cross section can easily be cut out using a sharp spatula. The burrow opening and the upper portion of each burrow (i.e. 1 – 3 cm beneath the sediment surface) have smaller internal diameters than the deeper part; the value reaches a constant between 5 and 10-cm depth (A. Nakaoka et al., unpublished data). Thus the diameter at approximately 10-cm depth was adopted as a representative measure for each burrow. Adult shrimps defend their space aggressively, which was utilized to catch them. A writing brush slowly put into a burrow opening is grasped by the resident shrimp's chelipeds. For shallower burrows inhabited by the correspondingly smaller shrimps, a longitudinal section of the entire U together

with the substantial part of the lower shaft could be cut out using a spatula, sometimes with a shrimp left inside, which enabled both the measurement of the burrow's diameter and the collection of the shrimp.

As a separate sub-study, we marked and photographed all surface burrow openings of *Upogebia major* in two relatively large plots in high-density parts of the sandflat (a 3-m \times 3-m plot at around Stn A-856 during 1 to 16 June 2004 and a 3.5-m \times 3.5-m plot at around Stn A-776 during 2 July to 16 August 2004). During this period, we were able to identify and calculate the mean number of openings per burrow. After this study, we measured inner diameters of 605 burrows to obtain the size-frequency distribution of shrimp burrows, to which normal distribution curves corresponding to different cohorts were fitted, following Aizawa and Takiguchi (1999).

In the vicinity of the above two plots, after the inner diameters for a number of burrows of *Upogebia major* were recorded, shrimps inside these burrows were collected by hand and fixed with 10 % neutralized formalin. This was to later establish a relationship between individual shrimp biomass and shrimp burrow diameter (*BDmud shrimp*). To add smaller shrimps to the data set, they were caught and kept alive in acrylic aquaria in the laboratory. The substrate in the aquaria was either natural sediment from the Shirakawa sandflat or agar, following the method for the latter devised by K. Kinoshita (unpublished data). The shrimps were maintained for at least 3 days after the completion of their burrows. Some parts of each burrow ran along the transparent aquarium wall, and the inner diameters of two to five parts were measured from outside the wall to give their mean as a representative value for the burrow. The combined data set comprised 84 combinations of biomass and burrow diameter. Furthermore, 152 shrimps derived from the field and aquaria were fixed and measured for their total length (*TLmud shrimp*: along mid-dorsal curvature from tip of rostrum to posterior margin of telson to the nearest 0.1 mm) and wet weight (*WWmud shrimp* to the nearest 0.01 g). The regression equations for (1) *TLmud shrimp* versus *BDmud shrimp* and (2)

WWmud shrimp versus *TLmud shrimp* were determined, following the same procedure as in Section 2.2. These two equations were used to estimate *WWmud shrimp* from *BDmud shrimp*.

At each station where we sampled bivalves (Section 2.2), the number of burrow openings of *Upogebia major* was recorded using $n = 16$ 25-cm \times 25-cm quadrats (i.e. 1-m² area). The total number of surface openings per m² at each station was allocated to burrow-diameter size classes according to the shape of the size-frequency distribution established previously. All frequency values were divided by the mean number of burrow openings per burrow (i.e. per shrimp) to correct for the actual number of shrimps. The median value of each burrow-diameter size class was used as a representative value for that size class. Wet weights for each size class were obtained by multiplication (i.e. wet weights derived from median burrow diameters were multiplied by the actual number of shrimps belonging to each size class). The total population biomass per m² was obtained by summing together wet weights from all individual size classes.

The burrow of *Nihonotrypaea japonica*, inhabited by a single shrimp, has only one surface opening (Tamaki and Ueno, 1998). Although the inner wall of the burrow is lined with mucus plus mud, it is more fragile than that of *Upogebia major*. Thus burrow cross sections are not feasible, and shrimp collections from individual burrows are extremely difficult. As an alternative, 363 shrimps were collected with a 'yabby pump' (similar to that described in Hailstone and Stephenson, 1961) randomly from a densely populated part of the upper shore and fixed with 10 % neutralized formalin on 16 to 19 June in 2004. Normal distribution curves corresponding to different cohorts were fitted to the total-length-frequency distribution. Of these shrimps 301 ones with no loss of appendages were used to establish the relationship between wet weight (*WWghost shrimp* to the nearest 0.01 g) and total length (*TLghost shrimp*: along mid-dorsal curvature from tip of rostrum to posterior margin of telson to the nearest 0.1 mm). The regression equation for *WWghost shrimp* versus *TLghost shrimp* was determined, following the same procedure as in Section 2.2.

At the same time as when *Upogebia major* burrows were counted, burrow openings for *Nihonotrypaea japonica* were tabulated. As with *U. major*, at every sampling station on the Shirakawa sandflat, we had to estimate the body sizes of ghost shrimps in these burrows, and we did so according to the total-length-frequency distributions obtained empirically from the yabby pump samples. The wet weights and estimates of total population biomass (per m²) were also calculated from empirical allometric data.

2.4. Estimation of total population biomass over the sandflat

The total population biomass over the entire sandflat (= the area demarcated by the thick line in Fig. 1) for each of the four species was estimated using a Geographic Information System (GIS), ArcGIS 9.2 Spatial Analyst (ESRI Japan, 2007), based on the distribution of the biomass density at each station on the sandflat. For comparisons between shrimps and bivalves, we used the bivalves' soft-tissue wet weights, as shrimps do not have heavy calcium-carbonate shells. Inverse distance weighted (IDW) interpolation was used to create each population biomass-density distribution map.

3. Results

The shell-length-frequency distribution of the Manila clam, *Ruditapes philippinarum*, based on the values from all sampling stations combined, was bimodal, with clams 20 – 43 mm, or much smaller at 1 – 8 mm (Fig. 3A). The larger grouping is likely the fusion of the 2002 and 2003 cohorts, whereas the smaller clams can be considered 'young-of-the-year' clams that recruited between October 2003 and June 2004 (A. Nakaoka et al., unpublished data). The shell-length-frequency distribution of the bivalve, *Macra veneriformis*, was also bimodal: shell lengths of approximately 18 – 46 mm and 1 – 6 mm, respectively (Fig. 3B). The recruitment pulse of *M. veneriformis* is more temporally restricted (June to August), but the shell-length-frequency

Fig. 3

distribution patterns are similar to those of *R. philippinarum* [i.e. a fused grouping of the 2002 and 2003 cohorts, and a 2004 young-of-the-year recruitment class (J. Nasuda et al., unpublished data)]. The best-fit regression equations for *WWshell* (g) or *WWsoft tissue* versus *SL* were given as power functions in both bivalves (Fig. 4).

Fig. 4

The mean number of surface openings per burrow (or shrimp) for the mud shrimp, *Upogebia major*, was 2.27 (no. of burrows = 125). Four major groups were recognized in the burrow-internal-diameter-frequency distribution of *U. major*, with mean \pm 2SD (i.e. 95 % confidence limits) for normal distribution curves being 6.0 ± 3.7 , 16.5 ± 7.2 , 23.4 ± 2.4 , and 30.1 ± 5.6 mm (Fig. 5). According to Kinoshita et al. (2003), new recruits of *U. major* settle in one pulse per year (May) in Tokyo Bay. The above four groups seem to correspond to the shrimp cohorts that recruited in 2004, 2003, 2002, and prior to 2002, respectively. The best-fit regression equations for total length versus burrow diameter and for wet weight versus total length were given as polynomial quadratic functions (Fig. 6).

Fig. 5

Fig. 6

Four major groups were recognized in the total-length-frequency distribution of the ghost shrimp, *Nihonotrypaea japonica*, with mean \pm 2SD for normal distribution curves being 18.1 ± 5.9 , 27.9 ± 8.2 , 43.6 ± 11.1 , and 56.5 ± 9.3 mm (Fig. 7). According to life-history studies of this species on the Shirakawa sandflat (Kubo et al., 2006; Y. Wardiatno and A. Tamaki, unpublished data), larval recruitment occurs over an extended period in the year (April – December). The above four groups would correspond to the cohorts that recruited in April – July 2003, August – December 2003, April – December 2002, and April – December 2001, respectively. The best-fit regression equation for wet weight versus total length was given as a polynomial cubic function (Fig. 8).

Fig. 7

Fig. 8

Nihonotrypaea japonica was distributed over nearly the entire sandflat (Fig. 9A). The main distribution zone was readily recognizable, as the sediment in this zone was very unstable due to shrimp bioturbation. The zone was situated in the upper part of the sandflat on all transects (except

Fig. 9

for the one or two uppermost stations), with an area of 0.81 km². From Transect D toward Transect C, the inclination of the lower limit line of the main distribution zone was largely in parallel with that of the lowest shoreline. The mean \pm SD individual density in the zone ($n = 36$), as estimated from the burrow-opening count data (no. of ghost shrimps = no. of burrow openings), was 296.7 ± 95.1 shrimps m⁻², which corresponds to the biomass density of 215.9 ± 80.8 g m⁻².

Upogebia major was distributed mainly in the right half of the sandflat (Transects K, A, C: Fig. 9A). The main distribution zone was readily recognizable by the fairly consolidated sediment and characteristic burrows, which was located in the middle to lower part of the sandflat, with an area of 0.87 km². The MLWN-level line traverses the middle part of the main distribution zone. Only very few burrow openings, if any, were present at the three or four lowest stations on each of Transects A–C and K. The main distribution zone of *U. major* was outside of the lower limit of the main distribution zone of *Nihonotrypaea japonica*, except for the relatively high *U. major* densities at the five lowest stations within the main distribution zone of *N. japonica* on Transect K. The mean \pm SD individual density of *U. major* in its main distribution zone ($n = 34$), as estimated from the burrow-opening count data (no. of mud shrimps = no. of burrow openings/2.27), was 8.7 ± 5.2 shrimps m⁻², which corresponds to the biomass density of 104.5 ± 62.1 g m⁻².

For the two bivalves, each species' distribution pattern was different between juvenile and adult clams (Fig. 9B, C). Juveniles of *Ruditapes philippinarum* were widely distributed over the transects except for Transect A, while most adults were outside of the main *Nihonotrypaea japonica* and *Upogebia major* zones, most abundant between the MLWN level and the lowest shore on Transects B and C. In particular, the highest adult densities were recorded at the three lowest stations on Transect C (2 796, 1 100, and 76 clams m⁻² from Stn C-1 330 toward Stn C-1 490). Both juveniles and adults of *Macra veneriformis* were distributed widely from lower to upper shore. The main distribution zone of juveniles was situated between the main distribution zone of *N.*

japonica and the MLWN level, most abundant on Transects B and D. The main distribution zone of adults was from around the MLWN level to the lowest shore, also most abundant on the above two transects [mean \pm SD individual density = 626.5 ± 206.7 clams m^{-2} at the 11 lowest stations on Transect D and 305.0 ± 156.6 clams m^{-2} at the five lowest stations on Transect B (excluding Stn B-1 969)]. On Transect B there was the other peak in density at the three middle contiguous stations (166.7 ± 20.1 clams m^{-2}). For both bivalve species, the population-biomass distribution pattern over the sandflat was mainly determined by that of adults; (1) *R. philippinarum* – although the total number of juveniles was 12.4 times greater than that of adults, the biomass was 130 times higher in the latter and (2) *M. veneriformis* – the number of adults was 6.6 times greater than that of juveniles, and their biomass difference was 2 980 times. Overall, the population biomass of *R. philippinarum* was concentrated around the lowest shore on Transect C (2 466.7, 1 317.6, and 137.4 g m^{-2}) and from middle to lower shore on Transect B [52.2 ± 33.4 g m^{-2} (mean \pm SD, $n = 7$)]. The highest biomass densities of *M. veneriformis* on each transect ranged from 708.9 ± 202.3 g m^{-2} (Transect D, $n = 11$ lowest stations) to 56.1 ± 30.1 g m^{-2} (Transect C, $n = 8$ middle stations).

The wet biomass of the populations of *Nihonotrypaea japonica*, *Upogebia major*, *Ruditapes philippinarum*, and *Macraa veneriformis*, as interpolated by means of the GIS software, was estimated at 304.1, 110.5, 233.8, and 377.6 tonnes, respectively (Fig. 10). In particular, the area with the high biomass (≥ 26 g m^{-2}) zone of *R. philippinarum* was estimated at 0.85 km^2 , which was situated on the lowest shore and accounted for 25 % of the entire area of the Shirakawa sandflat.

Fig. 10

4. Discussion

4.1. Spatial partitioning in the phytoplankton-feeding guild on the Shirakawa sandflat

In 2004, the high biomass-density areas of the four large-sized dominant species of the phytoplankton-feeding guild (two suspension-feeding bivalves, *Ruditapes philippinarum* and *Macraa*

veneriformis, suspension-feeding mud shrimp, *Upogebia major*, and deposit-feeding ghost shrimp, *Nihonotrypaea japonica*) were distributed in a checkerboard pattern (i.e. non-overlapping, sensu Diamond, 1973), each occupying about one-fourth area of the Shirakawa sandflat (Fig. 10). The main distribution zones of adults of the three suspension feeders were situated around the MLWN level and/or further seaward, with *R. philippinarum* restricted to the lowest shore (Fig. 9). This distribution pattern is understandable due to the probable positive effect of submergence time on suspension feeders. Given this physiological constraint, however, *R. philippinarum* abounded on the entire sandflat during the peak of its population boom in Ariake Sound in the late 1970s (OFCA and MFCA, personal communication). In fact, in 2004, juveniles were more widely distributed than adults (Fig. 9B), which suggests the existence of spatially different survival processes. The contraction of the *R. philippinarum* population throughout the 1980s (Fig. 2A) coincided with the expansion of population sizes and zones of occurrence of the other three species on several different sandflats in Ariake Sound (Tokuyama, 2000; M. Sakamoto, unpublished data) as well as on the Shirakawa sandflat (H. Tanoue, unpublished data; OFCA and MFCA, personal communication). More recent observations on the Shirakawa sandflat also indicate interspecific effects among the species, including increases in *R. philippinarum* and *M. veneriformis* recruitment following reductions in *N. japonica* and *U. major* populations (due to predation and a typhoon strike, respectively; A. Tamaki et al., unpublished data). These sequences of events suggest the existence of interference competition for space between *R. philippinarum* and the other three species.

Ghost shrimps discard a large amount of sediment when feeding and constructing burrows (Flach and Tamaki, 2001). Correlative field observations, manipulative experiments, and laboratory studies in various parts of the world have demonstrated negative influences of bioturbation by ghost shrimps on suspension-feeding mollusks (Tamaki, 1994, southern Japan; Dittmann, 1996, northeastern Australia; Berkenbusch et al., 2000, southeastern New Zealand; Peterson, 1977, Murphy,

1985, Feldman et al., 2000, and Dumbauld et al., 2006, the Pacific coast of North America; Pillay et al., 2007, eastern South Africa). Possible mechanisms for the negative effects include smothering/burial of newly-recruited juveniles (Peterson, 1977; Toba et al., 1992; Tamaki, 1994; Dittmann, 1996; Feldman et al., 2000; Dumbauld et al., 2006) and interference with feeding processes (Murphy, 1985; Pillay et al., 2007). In Puget Sound, Washington, USA, the ghost shrimp, *Neotrypaea californiensis*, and the mud shrimp, *Upogebia pugettensis*, are regarded as pests for the aquaculture of *Ruditapes philippinarum*, particularly affecting the survival of small clams (Toba et al., 1992). On the Shirakawa sandflat in 2004, some of the *Mactra veneriformis* individuals in the main *Nihonotrypaea japonica* zone had probably arrived there as they grew (Fig. 9C), as this species is known to gulp air and float buoyantly from place to place during adulthood (J. Nasuda et al., unpublished data). *M. veneriformis* has a heavier and tougher shell than *R. philippinarum*, as suggested by the greater value in the ratio of the WWshell to WWsoft tissue for the former species (Fig. 4). *M. veneriformis* also burrows much more quickly than *R. philippinarum* (A. Tamaki et al., personal observation). These two traits probably enable *M. veneriformis* to cope with unstable sediment conditions set by *N. japonica*. Compared with ghost shrimps, effects of mud shrimp bioturbation on macrobenthos are not well understood (Swinbanks and Luternauer, 1987; Posey et al., 1991; Wynberg and Branch, 1994; Smith and Langdon, 1998; Feldman et al., 2000; Como et al., 2004). The influences of mud shrimps on suspension-feeding bivalves have been described variously as neutral (Posey et al., 1991), positive (Wynberg and Branch, 1994), and negative (Smith and Langdon, 1998). Smothering of *R. philippinarum* due to sedimentation as a result of the activity of *U. pugettensis* in Yaquina Bay, Oregon, USA (Smith and Langdon, 1998) might be ascribed to the inherent nature of the unconsolidated muddy substrate associated with the local mud shrimp habitat. On other tidal flats inhabited by the mud shrimp, including the Shirakawa sandflat, stabilization or consolidation of the substrate by their mucus-lined, semi-permanent burrows appears

to be the rule (Dworschak, 1987; Swinbanks and Luternauer, 1987; Posey et al., 1991; Wynberg and Branch, 1994; Feldman et al., 2000; Kinoshita, 2002; DeWitt et al., 2004; Siebert and Branch, 2006), which would hinder the burrowing of bivalves into the sediment. Although *M. veneriformis* is regarded as a potential competitor with *R. philippinarum* for food (Hiwatari et al., 2002), no studies are yet available on the interference competition between these two species.

As observed for the separate distribution pattern of the main zones of *Nihonotrypaea japonica* (upper shore) and *Upogebia major* (middle to lower shore) on the Shirakawa sandflat (Fig. 9A), the ghost shrimp and the mud shrimp often inhabit the distinct zones along intertidal gradient on other estuarine tidal flats (Swinbanks and Luternauer, 1987; DeWitt et al., 2004; Dworschak, 2004; Dumbauld et al., 2006; Siebert and Branch, 2006). The antagonistic stabilization and destabilization effects on sediment by the mud shrimp and the ghost shrimp are postulated to explain their mutually exclusive distribution patterns in addition to physiological limiting factors (Swinbanks and Luternauer, 1987; Siebert and Branch, 2006). Along Transect K on the Shirakawa sandflat, where a shallow drainage runs beside the access road (Fig. 1), the high-density zone of *U. major* penetrated into the upper shore (Fig. 9A). A similar phenomenon was found for the *U. pusilla* population in the northern Adriatic Sea (Dworschak, 1987). Along the north to south gradient between the two rivers on the Shirakawa sandflat, *U. major* was distributed away from the larger Shirakawa River, which suggests its low tolerance to freshwater runoff, especially in the rainy season. The uppermost constriction in the mud shrimp burrow may prevent the intrusion of overlying water with different salinity characteristics (Dworschak, 1983).

4.2. Carrying capacity of the Shirakawa sandflat in the present and past

In 1979 and 2004, the annual fishery yields of *Ruditapes philippinarum* (with shells) on the Shirakawa sandflat were 3 830 tonne and 538.3 tonne, respectively (Fig. 2A; SNFRI of FRA, OFCA,

and MFCA, unpublished data). The yield value in 2004 is equivalent to a soft-tissue value of 126.1 tonne, using the mean ratio of the WWshell to WWsoft tissue for clams of four representative market-sizes (Fig. 4): 30, 35, 40, and 45-mm shell length ($= 4.27$). From this, the ratio of population biomass to fishery yield is estimated at 1.85. If this ratio is applied to the situation in 1979, when the fishery yield on the soft-tissue basis was 897 tonne ($= 3\,830/4.27$), the population biomass would have been 1\,659 tonne. Thus the carrying capacity of the sandflat in 1979 is estimated to have been at least 1.6 times higher than in 2004. This may be a conservative estimate, given that *Macra veneriformis*, *Nihonotrypaea japonica*, and *Upogebia major* do not factor into the 1979 figures. Assuming that (1) the carrying capacity of the sandflat in 1979 for the whole phytoplankton-feeding guild was two times greater than the 2004 carrying capacity, and (2) the present area occupied by *R. philippinarum* is one-fourth of the entire sandflat (Fig. 10), then the expected fishery yield in 2004 should be one-eighth of that in 1979. This fairly approximates to the actual shrinkage rate given at the top of this paragraph.

As the dominant macrobenthos on the Shirakawa sandflat belong to the phytoplankton-feeding guild (Yokoyama et al., 2005b), decadal changes in the carrying capacity of the sandflat for the guild might have been preceded by changes in phytoplankton abundance in Ariake Sound. In general, mild eutrophication in the coastal waters is expected to result in increased abundance of phytoplankton and benthic microalgae, further leading to increased stocks of their consumers such as zoobenthos and zooplankton with some time-lag (Pearson and Rosenberg, 1978; Gray, 1992; Herman et al., 1999). Such events happened from the late 1970s to the early 1980s with a time-lag of 1 to 2 years between the phytoplankton and zoobenthos abundances in the Skagerrak-Kattegat area of the eastern North Sea (Josefson et al., 1993) and in the western Dutch Wadden Sea (Beukema and Cadée, 1997). Matsuoka (2004) has demonstrated a long-term change in the composition of the dinoflagellate cyst assemblage in the subtidal bottom of the inner part of Ariake Sound, using

sediment core samples dating back to ca. 1850. The proportion of the autotrophic group in the assemblage was stable at about 60 % until the late 1960s, after which the heterotrophic group has abruptly increased to account for about 60 to 70 % by the early 1980s. This suggests that the first progress of eutrophication in the Sound occurred during the 1970s. Unfortunately, no long-term data on chlorophyll *a* concentrations of the water column are available for Ariake Sound. However, a long-term record in seston density (a gross measure of large-sized planktonic diatom abundance) that has been monitored in the inner part of the Sound since 1965 indicates an abrupt increase from 1970, with high values lasting until 1982 and the subsequent values generally remained at a lower range (SNFRI of FRA, 2001; Fig. 2B). Coincidentally, aquacultural production of the red macroalga, *Porphyra yezoensis* (which is now the most important cultured species in Ariake Sound; see Weinstein, 2007, fig. 3), increased remarkably in the 1970s and did not plateau until the late 1980s to the early 1990s (Sasaki, 2005). As *P. yezoensis* is a strong competitor with phytoplankton for nutrients in the water column (Watanabe et al., 2004), the enhancement of red macroalgal production might have caused a reduction in planktonic diatom abundance. To summarize, the population boom of *Ruditapes philippinarum* accompanied by those of the other three species of the phytoplankton-feeding guild during the 1970s to the early 1980s and the subsequent decline of the carrying capacity of the Shirakawa sandflat for the guild may have been caused primarily by the decadal change in planktonic diatom abundance in Ariake Sound.

4.3. Implication for the management of suspension-feeding bivalve resources on estuarine tidal flats

The success in estimating the carrying capacity of the Shirakawa sandflat for *Ruditapes philippinarum* primarily comes from the inclusion of phytoplankton feeders not targeted by the fishery, in particular *Upogebia major* and *Nihonotrypaea japonica*, which are cryptic in their deep-reaching burrows. Species of *Upogebia* may be capable of filtering the entire volume of

water overlying the burrows more than once per day (Dworschak, 1981; Griffen et al., 2004). Despite the potential importance of both the mud shrimp and the ghost shrimp as members of a phytoplankton-feeding guild, very few studies have assessed the population biomasses of these shrimps most probably due to difficulty in dealing with such deep-reaching burrow dwellers. There is one example from the Swartkops estuary, South Africa, where *U. africana* and *Callinassa kraussi* were estimated to make up 82 % and 10 % of the total biomass of the benthic community, respectively (Hanekom et al., 1988). The incorporation of such non-targeted species was also deemed to be valid when estimating the whole-ecosystem productivity of estuarine tidal flats dominated by several introduced species (Ruesink et al., 2006). To properly assess the carrying capacity of habitat for targeted suspension-feeding bivalves, it must be recognized that deposit feeders, consuming fresh phytodetritus (Widbom and Frithsen, 1995; Webb, 1996; Josefson et al., 2002; Moodley et al., 2005), can compete with phytoplankton-feeding guild members, especially when the deposit feeders rapidly subduct phytodetritus into subsurface layers. Examples of rapid subductors include *N. japonica* in the present study (Yokoyama et al., 2005b; Shimoda et al., 2007), malidanid polychaetes (Levin et al., 1997), and spatangoid urchins (Lohrer et al., 2005). In conclusion, the approach as adopted in the present study will provide a more holistic view of ecological dynamics of the benthic community on estuarine intertidal sandflats, more consistent with ecosystem-based management than with the current single-species management approach, for the enhancement of suspension-feeding bivalves.

Acknowledgements

K. Koyama, Y. Aramaki, J. Nasuda, H. Hayase, and M. Matsuo assisted in the field work. K. Kimoto (Seikai National Fisheries Research Institute of the Fisheries Research Agency) provided an unpublished aerial photograph of the Shirakawa sandflat. Seikai National Fisheries Research

Institute of the Fisheries Research Agency, and Oshima and Matsuo Fisheries Cooperative Associations provided unpublished Manila clam fishery yield records and information on the macrobenthos abundance and distribution on the Shirakawa sandflat. K. Kinoshita and M. Sakamoto, H. Tanoue and K. Shimoda, and J. Nasuda provided unpublished information on the biology and ecology of *Upogebia major*, *Nihonotrypaea japonica*, and *Macraa veneriformis*, respectively. K. Shimoda and Y. Agata assisted in data analysis and figure preparation. Constructive comments from A.M. Lohrer and three anonymous reviewers helped improve the manuscript. This study was partly supported by the Japan Society for the Promotion of Science (JSPS) Grant-in-Aid for Scientific Research 13854006, 15570018, 19310148, and Nihon-Seimei Foundation Grant in 2004.

References

- Aizawa, Y., Takiguchi, N., 1999. Consideration of the methods for estimating the age-composition from the length frequency data with MS-Excel. Bulletin of the Japanese Society of Fisheries Oceanography 63, 205–214. (in Japanese)
- Akaike, H., 1973. Information theory and an extension of the maximum likelihood principle. In: Petrov, B.N., Csáki, F. (Eds.), Second International Symposium on Information Theory. Akadémiai Kiadó, Budapest, pp. 267–281.
- Asmus, H., Asmus, R.M., 2005. Significance of suspension-feeder systems on different spatial scales. In: Dame, R.F., Olenin, S. (Eds.), The Comparative Roles of Suspension-Feeders in Ecosystems. Springer, Dordrecht, pp. 199–219.
- Bell, J.D., Rothlisberg, P.C., Munro, J.L., Loneragan, N.R., Nash, W.J., Ward, R.D., Andrew, N.L., 2005. Restocking and Stock Enhancement of Marine Invertebrate Fisheries: Advances in Marine Biology 49. Elsevier Academic Press, San Diego, 374 pp.

- Berkenbusch, K., Rowden, A.A., Probert, P.K., 2000. Temporal and spatial variation in macrofauna community composition imposed by the ghost shrimp *Callinassa filholi* bioturbation. Marine Ecology Progress Series 192, 249–257.
- Beukema, J.J., Cadée, G.C., 1997. Local differences in macrozoobenthic response to enhanced food supply caused by mild eutrophication in a Wadden Sea area: Food is only locally a limiting factor. Limnology and Oceanography 42, 1424–1435.
- Catchpole, R., 1998. Carrying capacity (*K*). In: Calow, P. (Ed.), The Encyclopedia of Ecology & Environmental Management. Blackwell Science, Oxford, p. 118.
- Como, S., Rossi, F., Lardicci, C., 2004. Response of deposit-feeders to exclusion of epibenthic predators in a Mediterranean intertidal flat. Journal of Experimental Marine Biology and Ecology 303, 157–171.
- Dame, R., 2005. Oyster reefs as complex ecological systems. In: Dame, R.F., Olenin, S. (Eds.), The Comparative Roles of Suspension-Feeders in Ecosystems. Springer, Dordrecht, pp. 331–343.
- Dame, R., Bushek, D., Prins, T., 2001. Benthic suspension feeders as determinants of ecosystem structure and function in shallow coastal waters. In: Reise, K. (Ed.), Ecological Comparisons of Sedimentary Shores: Ecological Studies 151. Springer, Berlin, pp. 11–37.
- DeWitt, T., D’Andrea, A.F., Brown, A.A., Griffen, B.D., Eldridge, P.M., 2004. Impact of burrowing shrimp populations on nitrogen cycling and water quality in western North American temperate estuaries. In: Tamaki, A. (Ed.), Proceedings of the Symposium on “Ecology of Large Bioturbators in Tidal Flats and Shallow Sublittoral Sediments – from Individual Behavior to their Role as Ecosystem Engineers”. Nagasaki University, Nagasaki, pp. 101–118.
- Diamond, J.M., 1973. Distributional ecology of New Guinea birds. Science 179, 759–769.
- Dittmann, S., 1996. Effects of macrobenthic burrows on infaunal communities in tropical tidal flats. Marine Ecology Progress Series 134, 119–130.

- Dumbauld, B.R., Booth, S., Cheney, D., Suhrbier, A., Beltran, H., 2006. An integrated pest management program for burrowing shrimp control in oyster aquaculture. *Aquaculture* 261, 976–992.
- Dworschak, P.C., 1981. The pumping rates of the burrowing shrimp *Upogebia pusilla* (Petagna) (Decapoda: Thalassinidea). *Journal of Experimental Marine Biology and Ecology* 52, 25–35.
- Dworschak, P.C., 1983. The biology of *Upogebia pusilla* (Petagna) (Decapoda, Thalassinidea) I. The burrows. *P.S.Z.N.I: Marine Ecology* 4, 19–43.
- Dworschak, P.C., 1987. The biology of *Upogebia pusilla* (Petagna) (Decapoda, Thalassinidea) II. Environments and zonation. *P.S.Z.N.I: Marine Ecology* 8, 337–358.
- Dworschak, P.C., 2004. Biology of Mediterranean and Caribbean Thalassinidea (Decapoda). In: Tamaki, A. (Ed.), *Proceedings of the Symposium on “Ecology of Large Bioturbators in Tidal Flats and Shallow Sublittoral Sediments – from Individual Behavior to their Role as Ecosystem Engineers”*. Nagasaki University, Nagasaki, pp. 15–22.
- ESRI Japan, 2007. *ArcGIS 3D Analyst User’s Guide*. ESRI, Japan, Inc., Tokyo, 379 pp. (in Japanese)
- Feldman, K.L., Dumbauld, B.R., DeWitt, T.H., Doty, D.C., 2000. Oysters, crabs, and burrowing shrimp: review of an environmental conflict over aquatic resources and pesticide use in Washington State’s (USA) coastal estuaries. *Estuaries* 23, 141–176.
- Flach, E., Tamaki, A., 2001. Competitive bioturbators on intertidal sand flats in the European Wadden Sea and Ariake Sound in Japan. In: Reise, K. (Ed.), *Ecological Comparisons of Sedimentary Shores: Ecological Studies* 151. Springer, Berlin, pp. 149–171.
- Gray, J.S., 1992. Eutrophication in the sea. In: Colombo, G., Ferrari, I., Ceccherelli, V.U., Rossi, R. (Eds.), *Marine Eutrophication and Population Dynamics*, Olsen & Olsen, Fredensborg, pp. 3–15.
- Griffen, B.D., DeWitt, T.H., Langdon, C., 2004. Particle removal rates by the mud shrimp *Upogebia pugettensis*, its burrow, and a commensal clam: effects on estuarine phytoplankton abundance.

- Marine Ecology Progress Series 269, 223–236.
- Hailstone, T.S., Stephenson, W., 1961. The biology of *Callinassa (Trypaea) australiensis* Dana 1852 (Crustacea, Thalassinidea). University of Queensland Papers, Department of Zoology 1, 259–285.
- Hanekom, N., Baird, D., Erasmus, T., 1988. A quantitative study to assess standing biomasses of macrobenthos in soft substrata of the Swartkops estuary, South Africa. South African Journal of Marine Science 6, 163–174.
- Heip, C.H.R., Goosen, N.K., Herman, P.M.J., Kromkamp, J., Middelburg, J.J., Soetaert, K., 1995. Production and consumption of biological particles in temperate tidal estuaries. Oceanography and Marine Biology: an Annual Review 33, 1–150.
- Héral, M., 1993. Why carrying capacity models are useful tools for management of bivalve culture. In: Dame, R.F. (Ed.), Bivalve Filter Feeders in Estuarine and Coastal Ecosystem Processes: NATO Advanced Science Institute Series G: Ecological Sciences 33. Springer, Berlin, pp. 455–477.
- Herman, P.M.J., Middelburg, J.J., van de Koppel, J., Heip, C.H.R., 1999. Ecology of estuarine macrobenthos. In: Nedwell, D.B., Raffaelli, D.G. (Eds.), Estuaries: Advances in Ecological Research 29. Academic Press, London, pp. 195–240.
- Hiwatari, T., Kohata, K., Iijima, A., 2002. Nitrogen budget of the bivalve *Macra veneriformis*, and its significance in benthic–pelagic systems in the Sanbanse Area of Tokyo Bay. Estuarine, Coastal and Shelf Science 55, 299–308.
- Josefson, A.B., Jensen, J.N., Ærtebjerg, G., 1993. The benthos community structure anomaly in the late 1970s and early 1980s – a result of a major food pulse? Journal of Experimental Marine Biology and Ecology 172, 31–45.
- Josefson, A.B., Forbes, T.L., Rosenberg, R., 2002. Fate of phytodetritus in marine sediments:

- functional importance of macrofaunal community. Marine Ecology Progress Series 230, 71–85.
- Kikuchi, T., 2000. Significance of conservation of tidal flats and their adjacent waters. In: Sato, M. (Ed.), Life in Ariake Sea: biodiversity in tidal flats and estuaries. Kaiyu-Sha, Tokyo, pp. 306–317. (in Japanese)
- Kinoshita, K., 2002. Burrow structure of the mud shrimp *Upogebia major* (Decapoda: Thalassinidea: Upogebiidae). Journal of Crustacean Biology 22, 474–480.
- Kinoshita, K., Nakayama, S., Furota, T., 2003. Life cycle characteristics of the deep-burrowing mud shrimp *Upogebia major* (Thalassinidea: Upogebiidae) on a tidal flat along the northern coast of Tokyo Bay. Journal of Crustacean Biology 23, 318–327.
- Kubo, K., Shimoda, K., Tamaki, A., 2006. Egg size and clutch size in three species of *Nihonotrypaea* (Decapoda: Thalassinidea: Callinassidae) from western Kyushu, Japan. Journal of the Marine Biological Association of the United Kingdom 86, 103–111.
- Levin, L., Blair, N., DeMaster, D., Plaia, G., Fornes, W., Martin, C., Thomas, C., 1997. Rapid subduction of organic matter by maldanid polychaetes on the North Carolina slope. Journal of Marine Research 55, 595–611.
- Lohrer, A.M., Thrush, S.F., Hunt, L., Hancock, N., Lundquist, C., 2005. Rapid reworking of subtidal sediments by burrowing spatangoid urchins. Journal of Experimental Marine Biology and Ecology 321, 155–169.
- Matsuoka, K., 2004. Changes in the aquatic environment of Isahaya Bay, Ariake Sound, west Japan: from the view point of dinoflagellate cyst assemblage. Bulletin on Coastal Oceanography 42, 55–59. (in Japanese, with English abstract)
- Moodley, L., Middelburg, J.J., Soetaert, K., Boschker, H.T.S., Herman, P.M.J., Heip, C.H.R., 2005. Similar rapid response to phytodetritus deposition in shallow and deep-sea sediments. Journal of Marine Research 63, 457–469.

- Murphy, R.C., 1985. Factors affecting the distribution of the introduced bivalve, *Mercenaria mercenaria*, in a California lagoon – The importance of bioturbation. *Journal of Marine Research* 43, 673–692.
- Nakahara, Y., Nasu, H., 2002. Report from the coastal areas of Ariake Sound, Kumamoto Prefecture; the main fisheries ground for the clam *Ruditapes philippinarum* populations in Japan. *Japanese Journal of Benthology* 57, 139–144. (in Japanese, with English abstract)
- Nakamura, Y., 2001. Filtration rates of the Manila clam, *Ruditapes philippinarum*: dependence on prey items including bacteria and picocyanobacteria. *Journal of Experimental Marine Biology and Ecology* 266, 181–192.
- Omori, M., Ikeda, T., 1992. *Methods in Marine Zooplankton Ecology*. Krieger Publishing Co., Malabar, Florida, 332 pp.
- Pearson, T.H., Rosenberg, R., 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanography and Marine Biology: an Annual Review* 16, 229–311.
- Peterson, C.H., 1977. Competitive organization of the soft-bottom macrobenthic communities of southern California lagoons. *Marine Biology* 43, 343–359.
- Pillay, D., Branch, G.M., Forbes, A.T., 2007. The influence of bioturbation by the sandprawn *Callinassa kraussi* on feeding and survival of the bivalve *Eumarcia paupercula* and the gastropod *Nassarius kraussianus*. *Journal of Experimental Marine Biology and Ecology* 344, 1–9.
- Posey, M.H., Dumbauld, B.R., Armstrong, D.A., 1991. Effects of a burrowing mud shrimp, *Upogebia pugettensis* (Dana), on abundances of macro-infauna. *Journal of Experimental Marine Biology and Ecology* 148, 283–294.
- Reise, K., Herre, E., Sturm, M., 1989. Historical changes in the benthos of the Wadden Sea around

- the island of Sylt in the North Sea. *Helgoländer Meeresuntersuchungen* 43, 417–433.
- Ruesink, J.L., Feist, B.E., Harvey, C.J., Hong, J.S., Trimble, A.C., Wischert, L.M., 2006. Changes in productivity associated with four introduced species: ecosystem transformation of a ‘pristine’ estuary. *Marine Ecology Progress Series* 311, 203–215.
- Sarà, G., Mazzola, A., 2004. The carrying capacity for Mediterranean bivalve suspension feeders: evidence from analysis of food availability and hydrodynamics and their integration into a local model. *Ecological Modelling* 179, 281–296.
- Sasaki, K., 2005. Material circulation and production in estuary and tidal flat, no. 37: the problems of fisheries in Ariake Sea 4 – laver culture. *Aquabiology* 27, 63–70. (in Japanese, with English abstract)
- Seikai National Fisheries Research Institute of the Fisheries Research Agency, 2001. Elucidation of the impact of the change in environmental conditions on biological productions in Ariake Sound. In: Shimizu, M. (Ed.), Interim Report on the Measures against the Poor Harvest of the Red Macroalga, *Porphyra yezoensis*, in Ariake Sound. The Ministry of Agriculture, Forestry and Fisheries of Japan, Tokyo, pp. 84–106. (in Japanese)
- Sekiguchi, H., Ishii, R., 2003. Drastic decreasing of annual catch yields of the Manila clam *Ruditapes philippinarum* in Ariake Sound, southern Japan. *Oceanography in Japan* 12, 21–36. (in Japanese, with English abstract)
- Shimoda, K., Aramaki, Y., Nasuda, J., Yokoyama, H., Ishihi, Y., Tamaki, A., 2007. Food sources for three species of *Nihonotrypaea* (Decapoda: Thalassinidea: Callianassidae) from western Kyushu, Japan, as determined by carbon and nitrogen stable isotope analysis. *Journal of Experimental Marine Biology and Ecology* 342, 292–312.
- Siebert, T., Branch, G.M., 2006. Ecosystem engineers: Interactions between eelgrass *Zostera capensis* and the sandprawn *Callinassa kraussi* and their indirect effects on the mudprawn

- Upogebia africana*. Journal of Experimental Marine Biology and Ecology 338, 253–270.
- Smith, M.D., Langdon, C.J., 1998. Manila clam aquaculture on shrimp-infested mudflats. Journal of Shellfish Research 17, 223–229.
- SPSS, 2002. SPSS Base 11.5J. SPSS Japan Inc., Tokyo, 566 pp. (in Japanese)
- Swinbanks, D.D., Luternauer, J.L., 1987. Burrow distribution of thalassinidean shrimp on a Fraser Delta tidal flat, British Columbia. Journal of Paleontology 61, 315–332.
- 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.
- Tamaki, A., Ueno, H., 1998. Burrow morphology of two callianassid shrimps, *Callianassa japonica* Ortmann, 1891 and *Callianassa* sp. (= *C. japonica*: de Man, 1928) (Decapoda: Thalassinidea). Crustacean Research 27, 28–39.
- Toba, D.R., Thompson, D.S., Chew, K.K., Anderson, G.J., Miller, M.B., 1992. Guide to Manila Clam Culture in Washington. Washington Sea Grant Program, University of Washington, Seattle, Washington, 80 pp.
- Toba, M., Yamakawa, H., Kobayashi, Y., Sugiura, Y., Honma, K., Yamada, H., 2007. Observations on the maintenance mechanisms of metapopulations, with special reference to the early reproductive process of the Manila clam *Ruditapes philippinarum* (Adams & Reeve) in Tokyo Bay. Journal of Shellfish Research 26, 121–130.
- Tokuyama, S., 2000. Life in Ariake Sound. In: Arao City Administration (Ed.), History of Arao City: Environmental and Ethnological Aspects. Arao, Kumamoto, pp. 274–335. (in Japanese)
- Vincenzi, S., Caramori, G., Rossi, R., Leo, G.A.D., 2006. A GIS-based habitat suitability model for commercial yield estimation of *Tapes philippinarum* in a Mediterranean coastal lagoon (Sacca di Goro, Italy). Ecological Modelling 193, 90–104.

- Wardiatno, Y., Shimoda, K., Koyama, K., Tamaki, A., 2003. Zonation of congeneric callinassid shrimps, *Nihonotrypaea harmandi* (Bouvier, 1901) and *N. japonica* (Ortmann, 1891) (Decapoda: Thalassinidea), on intertidal sandflats in the Ariake-Sound estuarine system, Kyushu, Japan. *Benthos Research* 58, 51–73.
- Watanabe, Y., Kawamura, Y., Handa, T., 2004. *Porphyra* (or nori) aquaculture and nutrient condition in the Ariake Bay, Japan. *Bulletin on Coastal Oceanography* 42, 47–54. (in Japanese, with English abstract)
- Webb, D.G., 1996. Response of macro- and meiobenthos from a carbon-poor sand to phytodetrital sedimentation. *Journal of Experimental Marine Biology and Ecology* 203, 259–271.
- Weinstein, M.P., 2007. Linking restoration ecology and ecological restoration in estuarine landscapes. *Estuaries and Coasts* 30, 365–370.
- Widbom, B., Frithsen, J.B., 1995. Structuring factors in a marine soft bottom community during eutrophication – an experiment with radio-labelled phytodetritus. *Oecologia* 101, 156–168.
- Wynberg, R.P., Branch, G.M., 1994. Disturbance associated with bait-collection for sandprawns (*Callinassa kraussi*) and mudprawns (*Upogebia africana*): Long-term effects on the biota of intertidal sandflats. *Journal of Marine Research* 52, 523–558.
- Yamada, F., Kobayashi, N., 2004. Annual variations of tidal level and mudflat profile. *Journal of Waterway, Port, Coastal and Ocean Engineering*, American Society of Civil Engineering 130, 119–126.
- Yamada, F., Kobayashi, N., Sakanishi, Y., Tamaki, A., 2008. Phase averaged suspended sediment fluxes on intertidal mudflat adjacent to river mouth. *Journal of Coastal Research*. (in press)
- Yokoyama, H., Tamaki, A., Harada, K., Shimoda, K., Koyama, K., Ishihi, Y., 2005a. Variability of diet-tissue isotopic fractionation in estuarine macrobenthos. *Marine Ecology Progress Series* 296, 115–128.

- Yokoyama, H., Tamaki, A., Koyama, K., Ishihi, Y., Shimoda, K., Harada, K., 2005b. Isotopic evidence for phytoplankton as a major food source for macrobenthos on an intertidal sandflat in Ariake Sound, Japan. *Marine Ecology Progress Series* 304, 101–116.
- Zhang, G., Yan, X., 2006. A new three-phase culture method for Manila clam, *Ruditapes philippinarum*, farming in northern China. *Aquaculture* 258, 452–461.

Figure captions

Fig. 1. Study area in and around Ariake Sound, western Kyushu, southern Japan. The broken line seaward of the coastline in the lower left panel indicates the extent of the relatively large tidal flats. The black-colored part of the tidal flats indicates the Kumamoto Prefecture administrative division, for which a long-term fishery yield record of the Manila clam, *Ruditapes philippinarum*, is available (Fig. 2A). The gray area in the upper panel showing the Shirakawa sandflat indicates the intertidal area to its mean low water spring tide level, based on aerial photography (K. Kimoto, unpublished data). The area encircled by the thick line was surveyed for estimating the carrying capacity of the sandflat. The access road is used for carrying the Manila clam by local fishermen. Lines A–D and K indicate macrobenthos survey transects. MLWN, marked with a broken line, signifies the mean low water neap tide level.

Fig. 2. Long-term annual fishery yield records of the Manila clam (with shells), *Ruditapes philippinarum*, on all extensive sandflats of the Kumamoto Prefecture administrative division along the eastern coast of Ariake Sound [A, filled circles; adapted from Kikuchi (2000, p. 316, fig. 12-3) and Seikai National Fisheries Research Institute of the Fisheries Research Agency (unpublished data); see Fig.1 for the location of the sandflats] and on the Shirakawa sandflat [A, open circles; adapted from Oshima and Matsuo Fisheries Cooperative Associations (unpublished data)], and a long-term change in the density of seston in the water column (volume per cubic meter of water) recorded off the northern Kumamoto Prefecture administrative division [B; adapted from Seikai National Fisheries Research Institute of the Fisheries Research Agency (2001, p. 100, fig. 6)]. In (A), the record for the Shirakawa sandflat prior to 1979 was unavailable. In (B), plankton samples were collected with a Kitahara net (mesh opening of 95 μm , see Omori and Ikeda, 1992, p. 43) regularly at spring tides. On each sampling occasion, the whole plankton sample fixed with 5 %

neutralized formalin was allowed to settle for 24 h within a graduated 30 – 50-ml test tube with a conical tip and the volume that precipitated at the bottom recorded.

Fig. 3. Shell-length-frequency distributions of the two bivalves, *Ruditapes philippinarum* (A) and *Macra veneriformis* (B), collected from the Shirakawa sandflat in 2004.

Fig. 4. Scatter plots of wet weight with shell or wet weight with soft tissue versus shell length in the two bivalves, *Ruditapes philippinarum* (A) and *Macra veneriformis* (B), collected from the Shirakawa sandflat in 2004. The superimposed curves indicating the best-fit regression equations and regression statistics for *R. philippinarum* are: $WW_{shell} = 1.460 \times 10^{-4} SL^{3.070}$ ($n = 68$, $R^2 = 0.998$, $P < 0.001$); $WW_{soft\ tissue} = 2.972 \times 10^{-5} SL^{3.109}$ ($n = 66$, $R^2 = 0.994$, $P < 0.001$). Those for *M. veneriformis* are: $WW_{shell} = 1.450 \times 10^{-4} SL^{3.162}$ ($n = 78$, $R^2 = 0.993$, $P < 0.001$); $WW_{soft\ tissue} = 1.910 \times 10^{-5} SL^{3.202}$ ($n = 78$, $R^2 = 0.989$, $P < 0.001$).

Fig. 5. Burrow-internal-diameter-frequency distribution of the mud shrimp, *Upogebia major*, measured at two stations along Transect A on the Shirakawa sandflat in 2004, with normal distribution curves corresponding to different cohorts.

Fig. 6. Scatter plots of total length versus burrow diameter (A) and wet weight versus total length (B) in the mud shrimp, *Upogebia major*, collected from the two same stations as in Fig. 5 on the Shirakawa sandflat in 2004. The superimposed curves indicating the best-fit regression equations and regression statistics are: $TL = 0.0761 BD^2 + 1.5751BD + 13.2681$ ($n = 84$, $R^2 = 0.958$, $P < 0.001$); $WW = 0.00228TL^2 - 0.10366TL + 1.28351$ [$n = 152$ (79 males, 40 females, and 33 sex-unidentified juveniles), $R^2 = 0.957$, $P < 0.001$].

Fig. 7. Total-length-frequency distribution of ghost shrimps, *Nihonotrypaea japonica*, collected from the Shirakawa sandflat in 2004, with normal distribution curves corresponding to different cohorts.

Fig. 8. Scatter plots of wet weight versus total length in the ghost shrimp, *Nihonotrypaea japonica*, collected from the Shirakawa sandflat in 2004. The superimposed curves indicating the best-fit regression equations and regression statistics (valid for shrimps ≥ 11.1 -mm TL: Fig. 7) are: $WW = -1.18394 \times 10^{-5}TL^3 + 0.00238TL^2 - 0.07558TL + 0.70545$ [$n = 301$ (145 males and 156 females), $R^2 = 0.917$, $P < 0.001$].

Fig. 9. Individual-density distributions of the ghost shrimp, *Nihonotrypaea japonica*, and the mud shrimp, *Upogebia major* (A), and juveniles and adults of two bivalves, *Ruditapes philippinarum* (B) and *Macraa veneriformis* (C), at transect (A–D, K) stations on the Shirakawa sandflat in 2004. For both shrimps, the values are based on the burrow-opening densities and conversion factor of burrow opening to shrimp numbers. For *R. philippinarum*, juveniles are defined as ≤ 8 -mm shell length, most adults being larger than 20 mm (Fig. 3A). For *M. veneriformis*, juveniles and adults are differentiated at a shell length of 18 mm (Fig. 3B). The lower limit of the main distribution zone of *N. japonica*, as readily recognizable due to the limit of the unstable sediment, is indicated by a dotted line. MLWN: mean low water neap tide level (broken line). The intertidal area of the Shirakawa sandflat is based on aerial photography (K. Kimoto, unpublished data).

Fig. 10. Population-biomass distributions over the entire Shirakawa sandflat in 2004 for the ghost shrimp, *Nihonotrypaea japonica* (A), the mud shrimp, *Upogebia major* (B), the Manila clam, *Ruditapes philippinarum* (C), and the bivalve, *Macraa veneriformis* (D), as interpolated by means of

ArcGIS 9.2 Spatial Analyst (ESRI Japan, 2007). The whole body and soft-tissue measurements were used for shrimp and bivalve biomasses, respectively. The intertidal area of the Shirakawa sandflat is based on aerial photography (K. Kimoto, unpublished data).

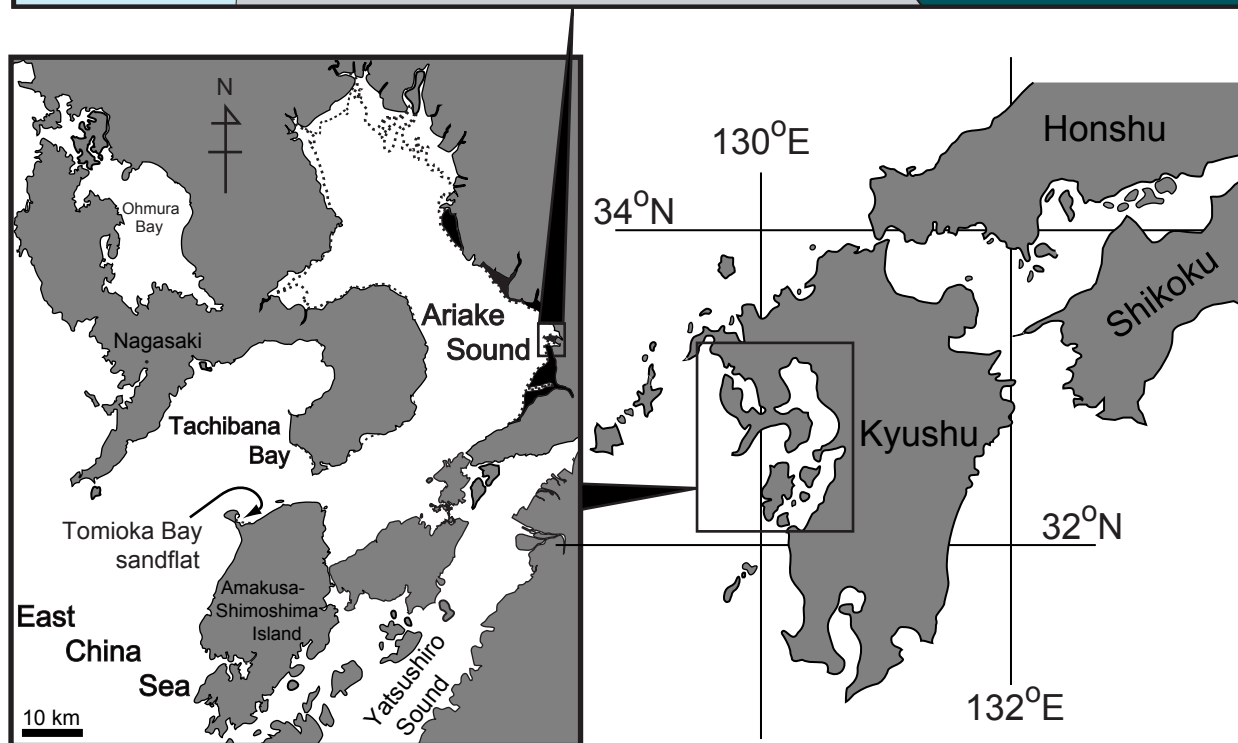
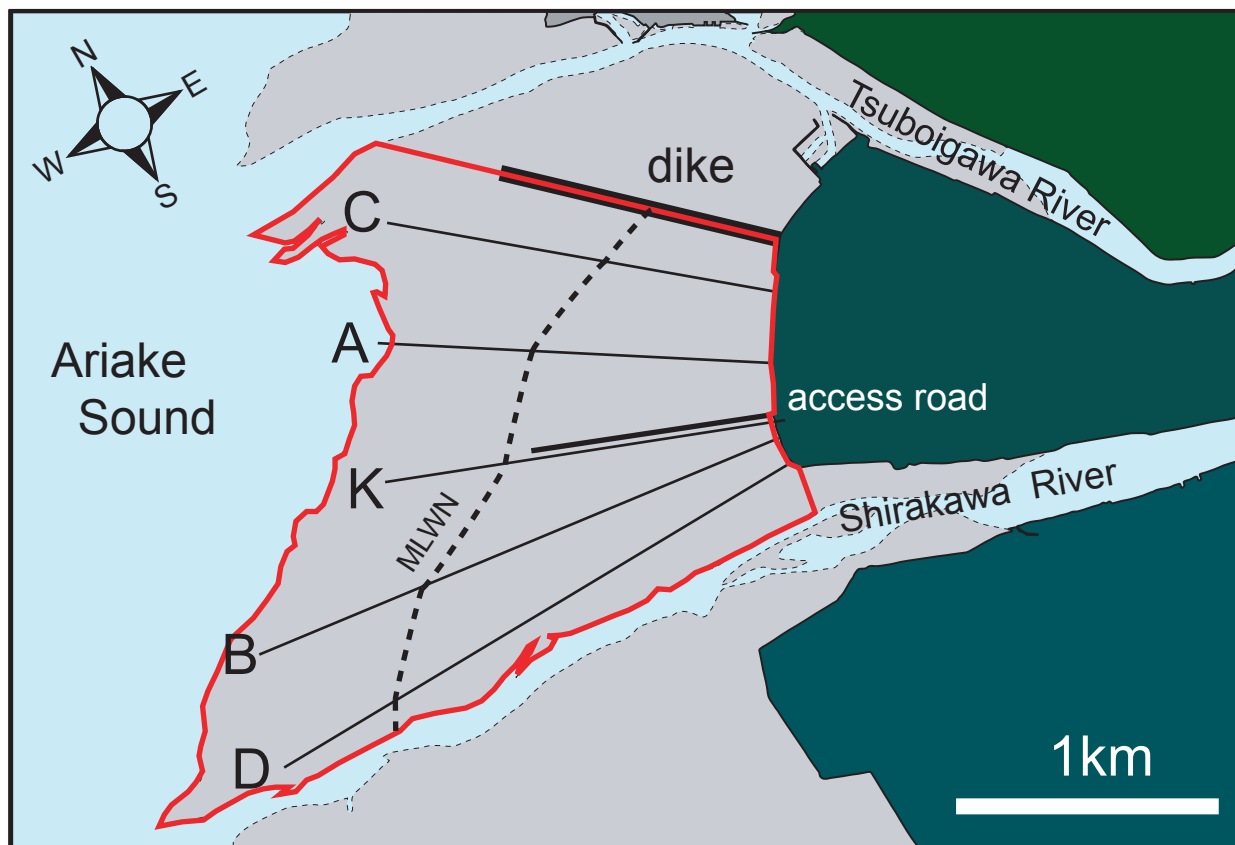


Fig. 1 (revised, Tamaki et al.)

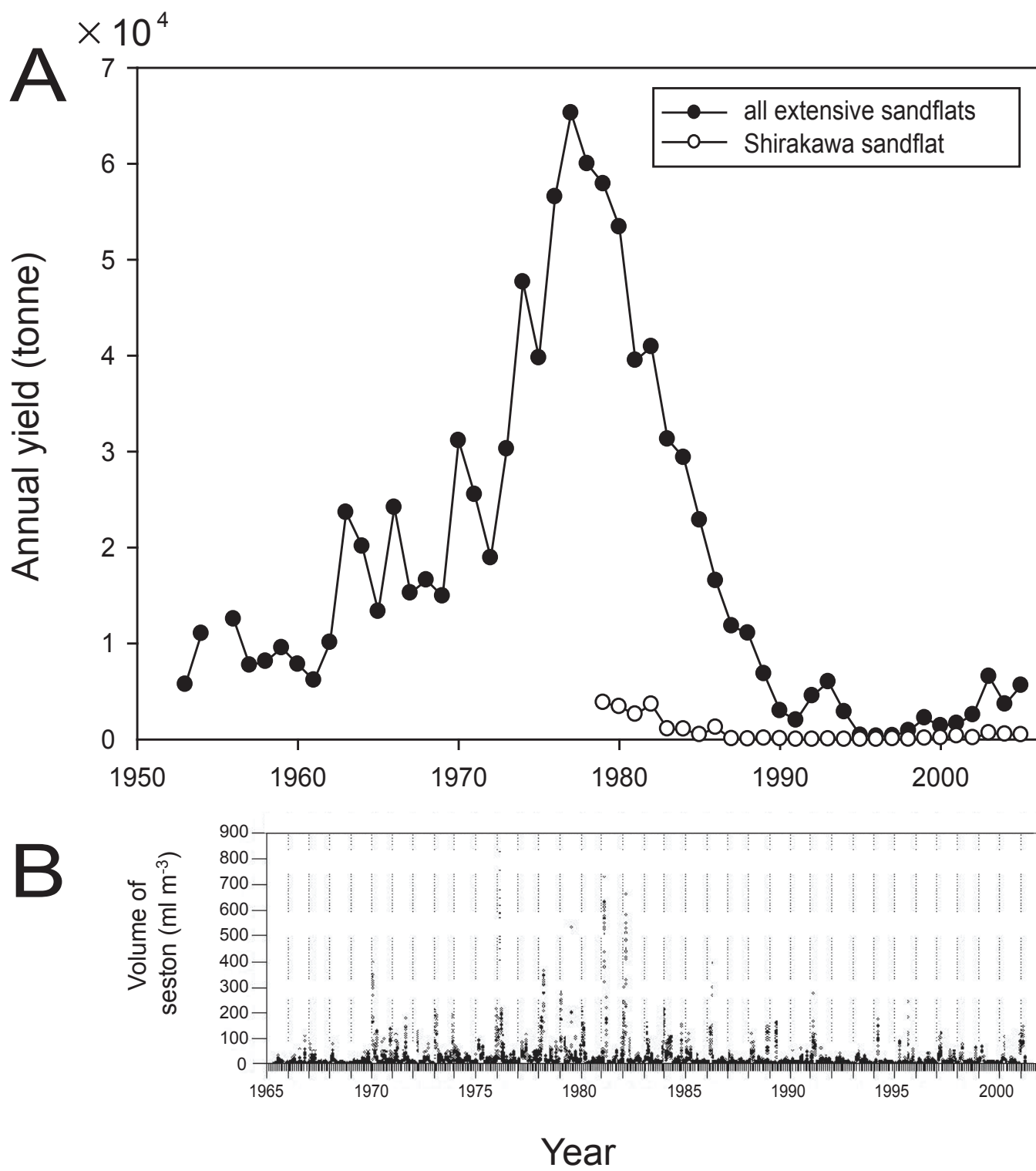


Fig. 2 (revised, Tamaki et al.)

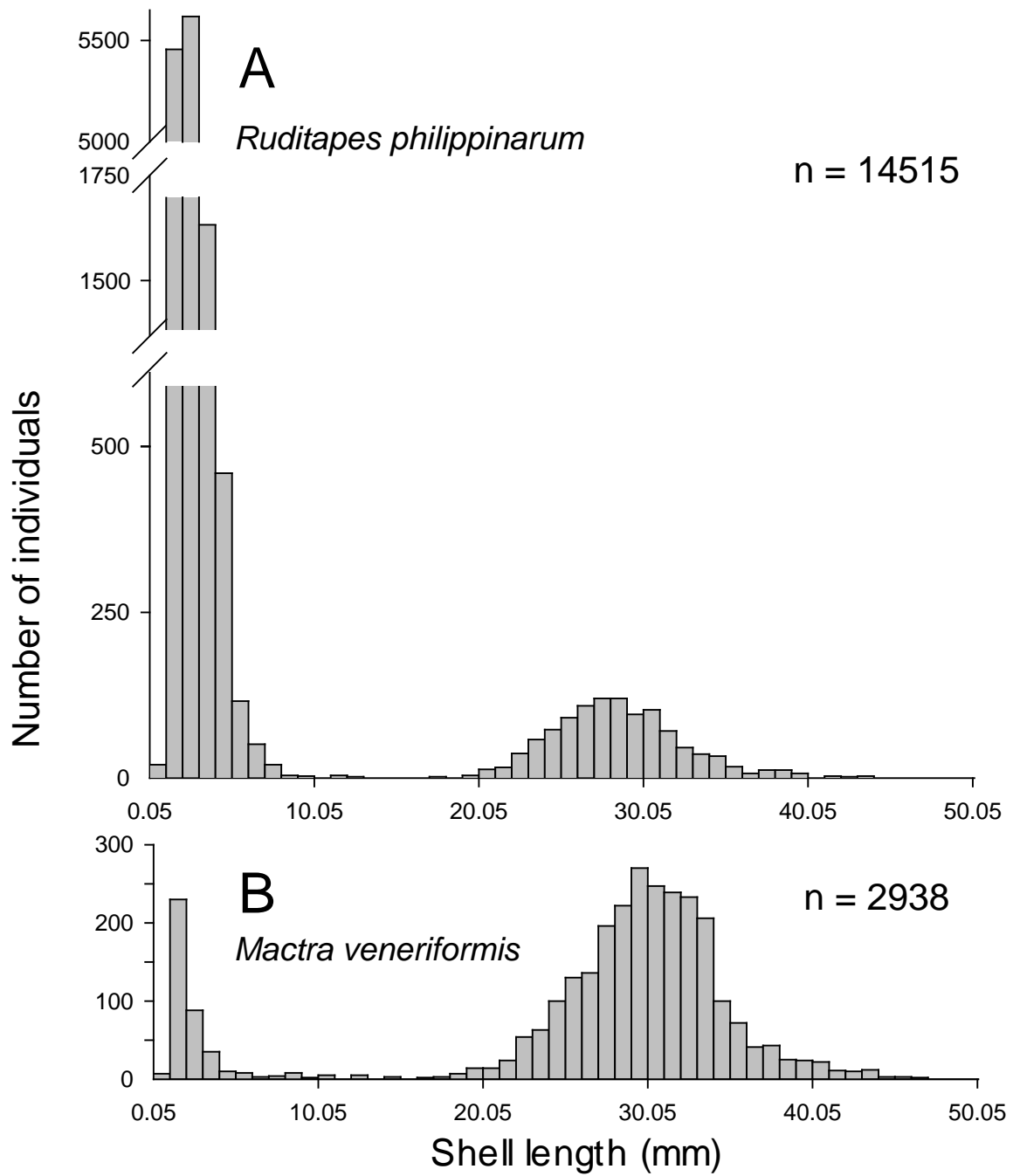


Fig. 3 (revised, Tamaki et al.)

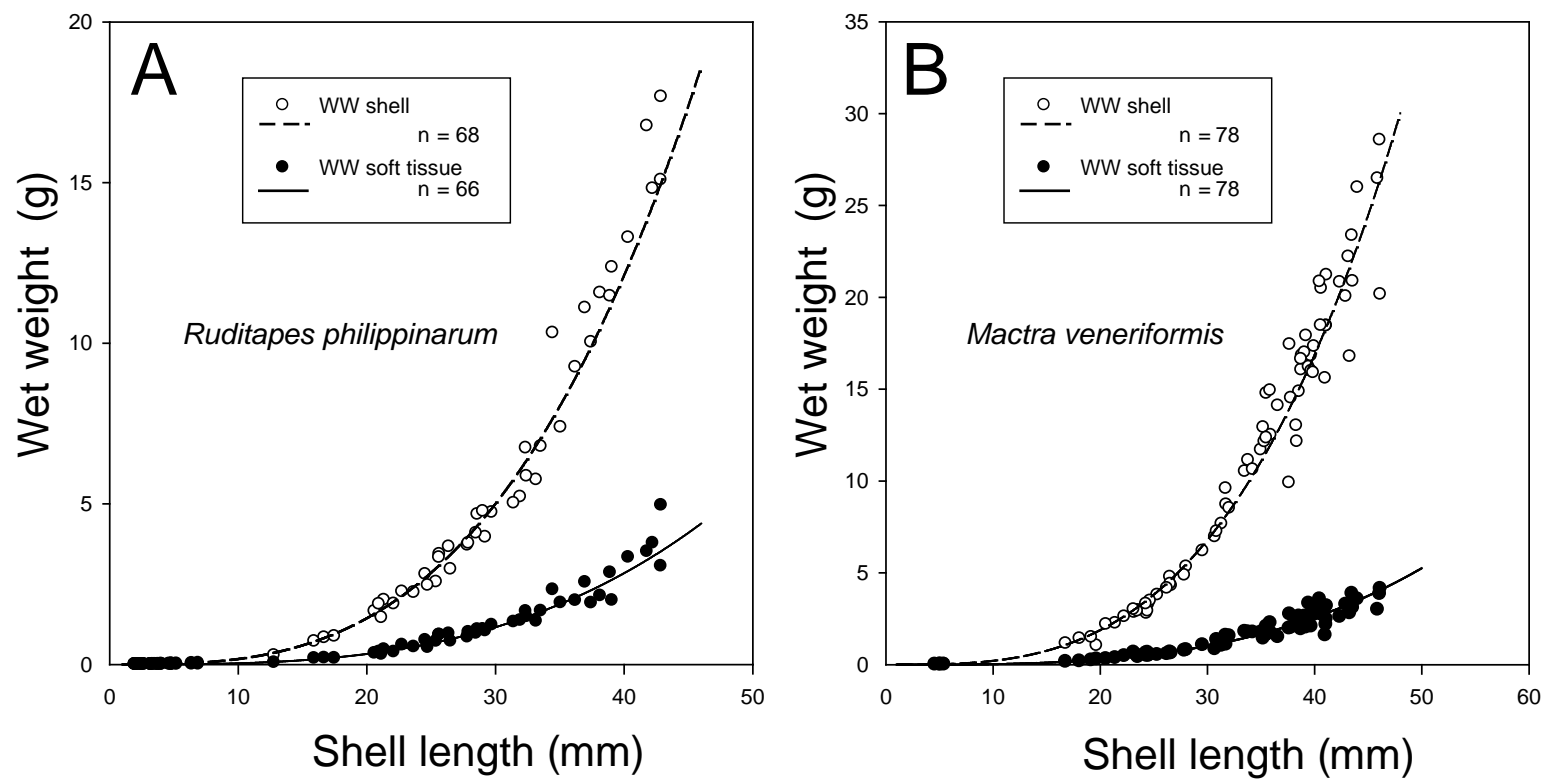


Fig. 4 (revised, Tamaki et al.)

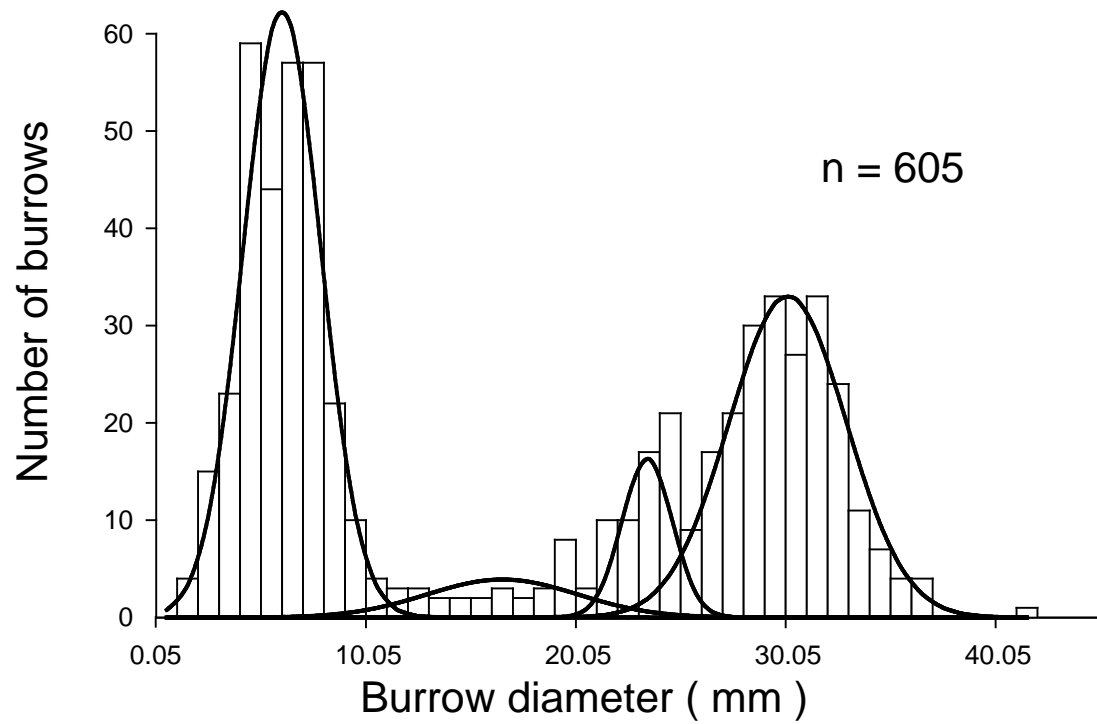


Fig. 5 (revised, Tamaki et al.)

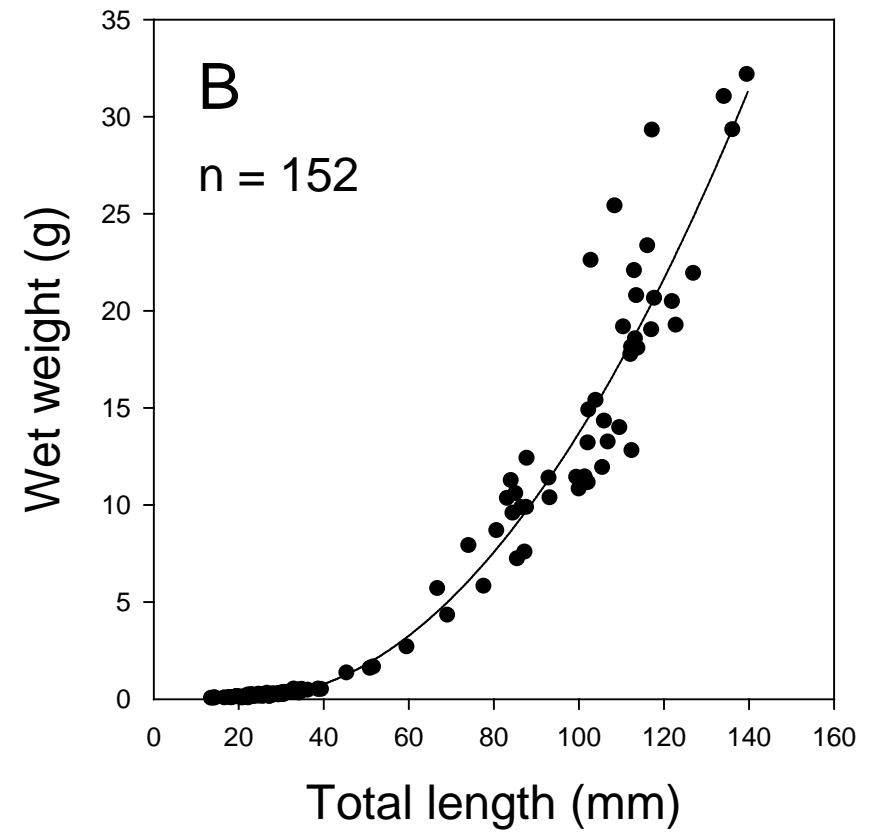
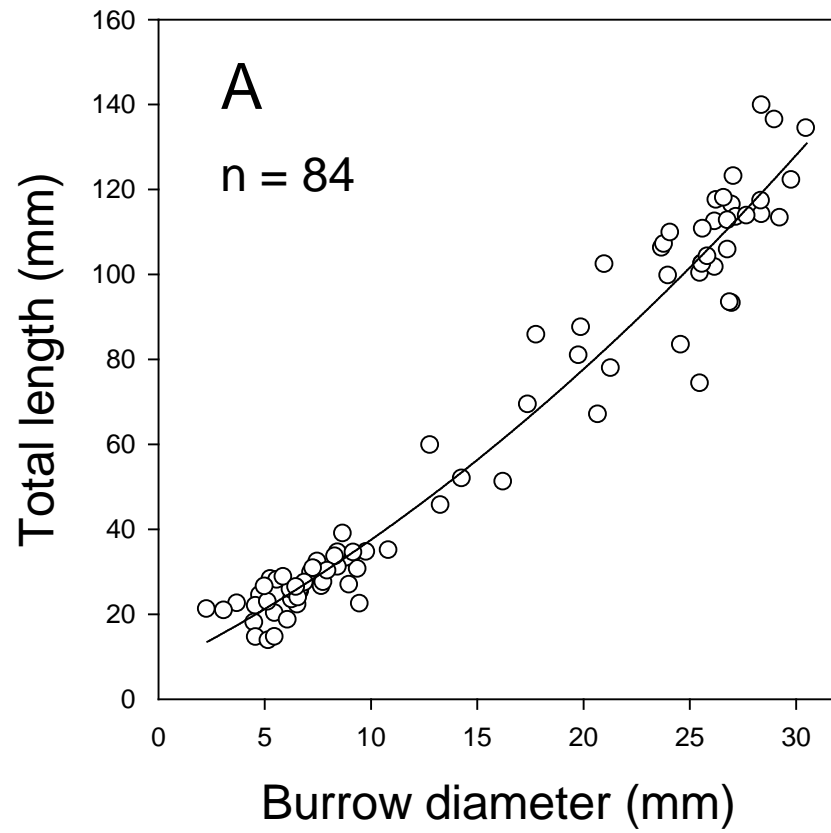


Fig. 6 (revised, Tamaki et al.)

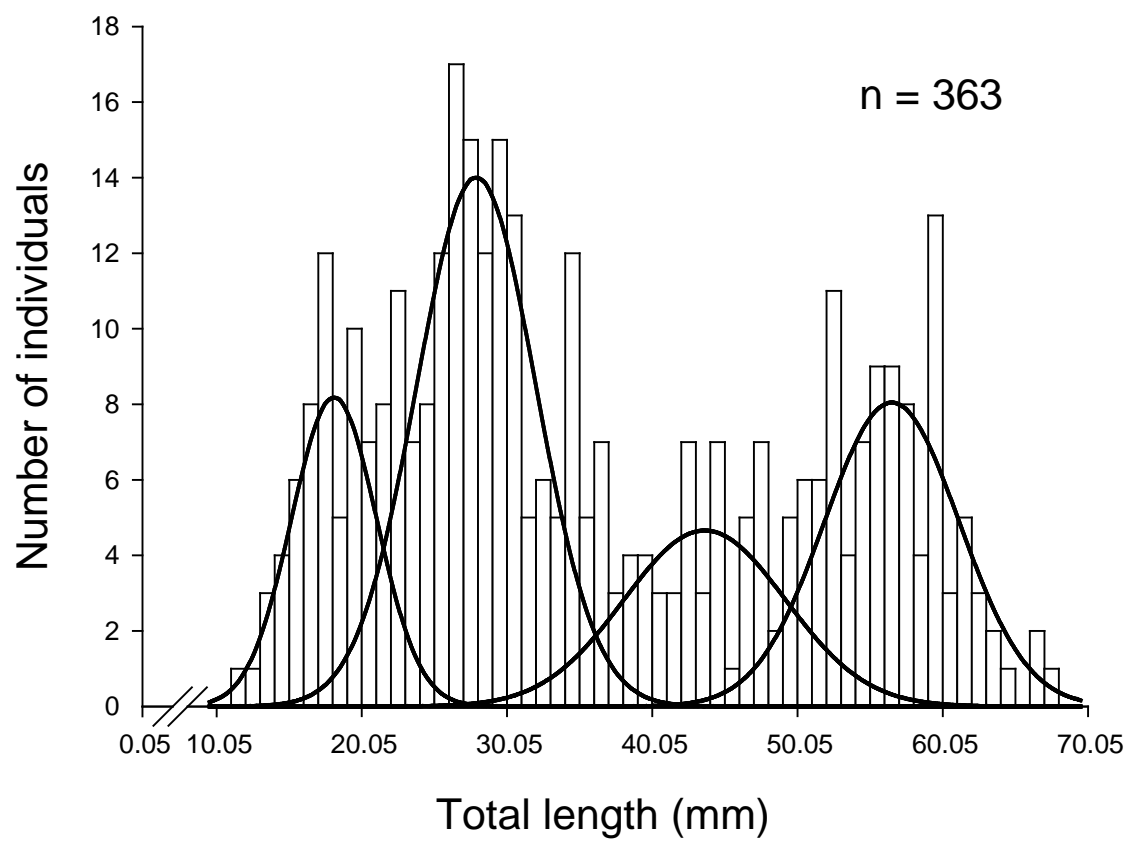


Fig. 7 (revised, Tamaki et al.)

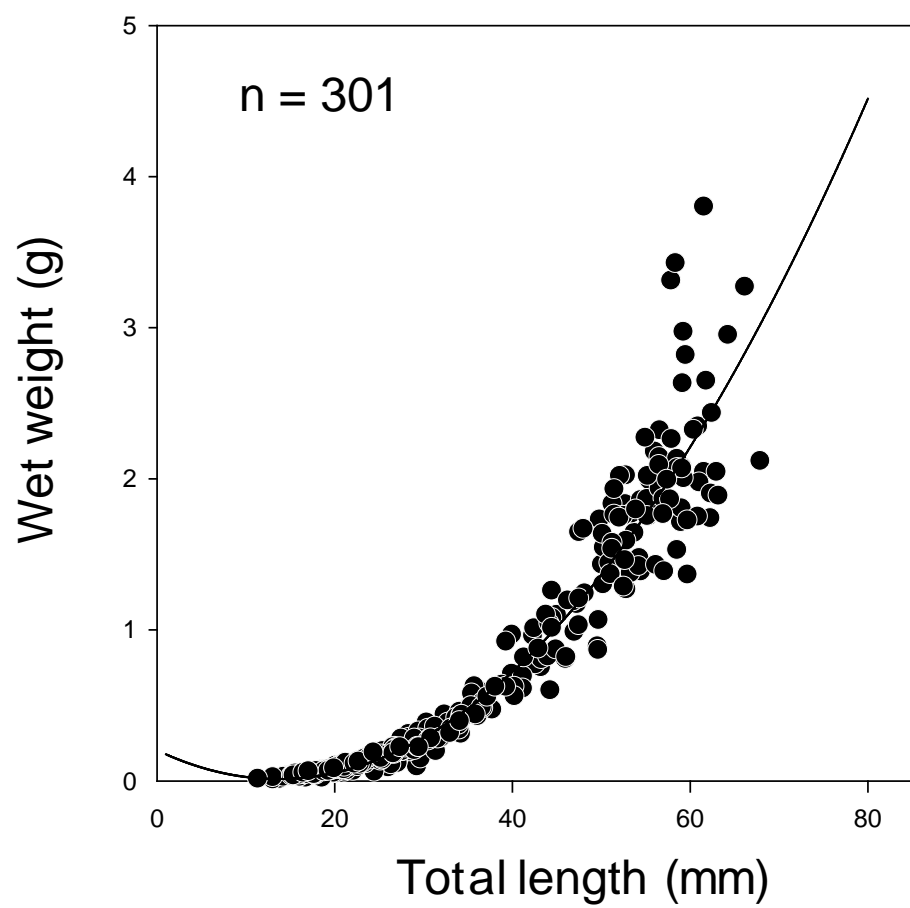


Fig. 8 (revised, Tamaki et al.)

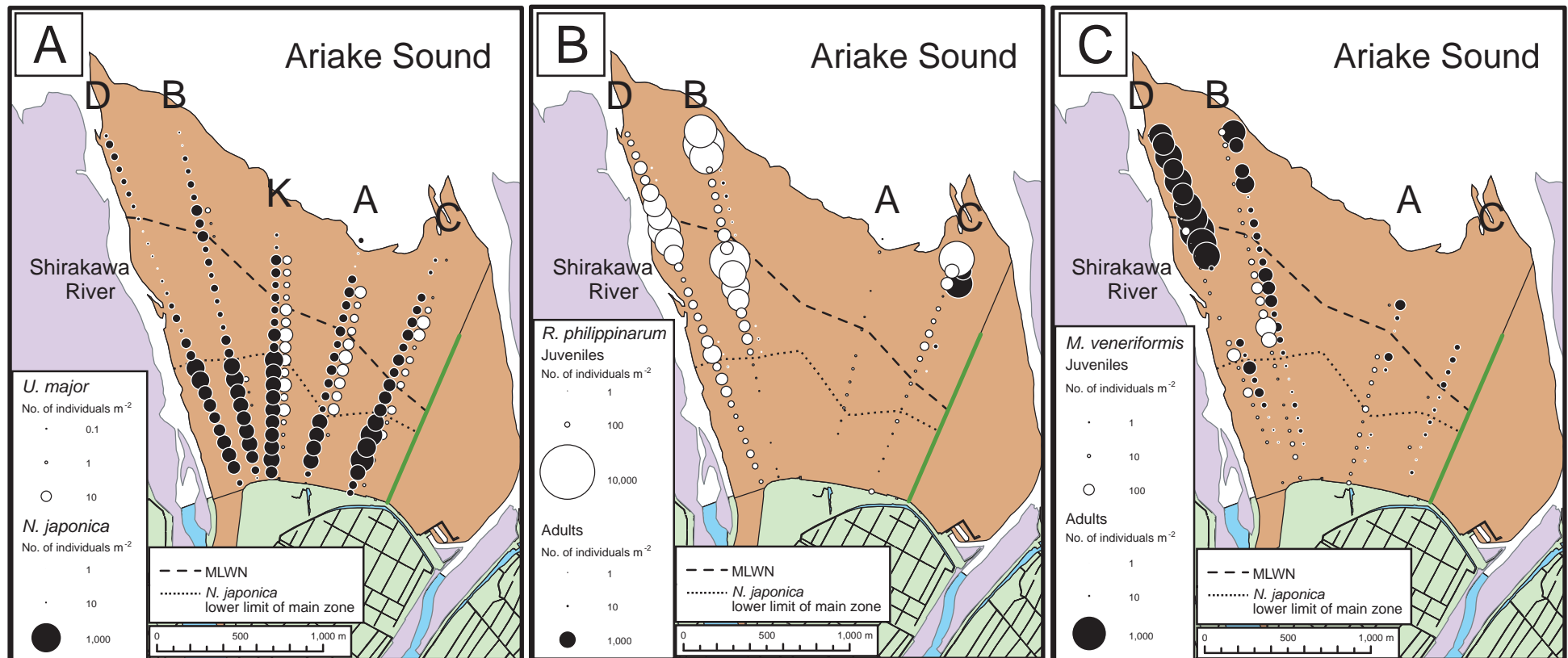


Fig. 9 (revised, Tamaki et al.)

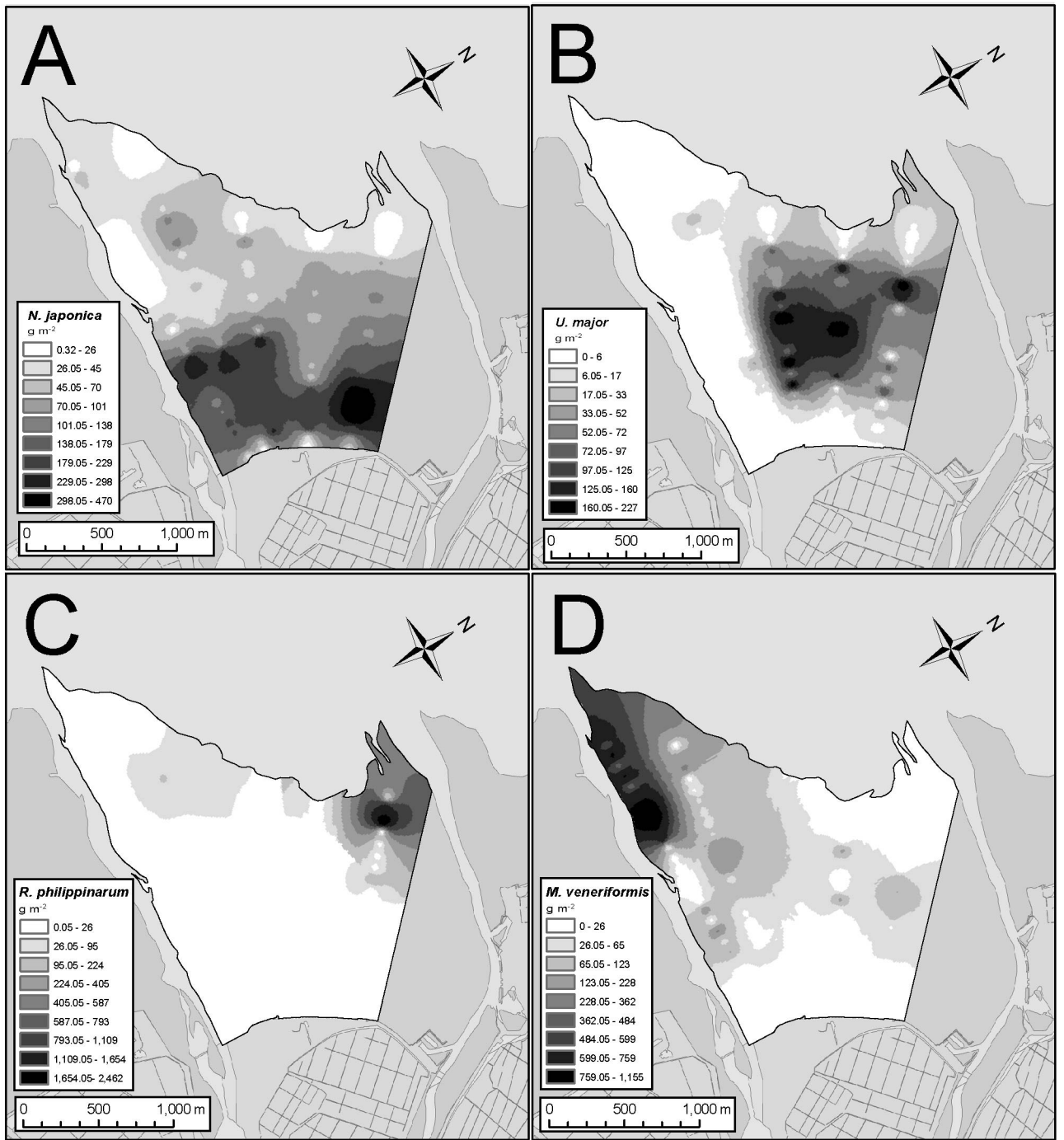


Fig. 10 (revised, Tamaki et al.)