Numerical simulation for larval connection network of the ghost shrimp *Nihonotrypaea harmandi* population among intertidal sandflats in Tachibana Bay and Ariake Sound, western Kyushu, Japan

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Abstract: In Tachibana Bay and the outermost one-third of Ariake Sound, western Kyushu, Japan, there are a number of intertidal sandflats inhabited by the ghost shrimp *Nihonotrypaea harmandi* (Decapoda: Thalassinidea: Callianassidae). An intertidal sandflat facing Tomioka Bay (Tomioka tidal flat), situated at the southwestern periphery of Tachibana Bay, has a much larger shrimp population than the other tidal flats, accounting for 70% of the total number of shrimps in the region. It is anticipated that exchange of planktonic larvae will occur among local shrimp populations. The purpose of this study was to clarify the larval connection network of *N. harmandi* among the 26 main local populations in the region by using a numerical tracer model. Our numerical model included vertical migrations of *N. harmandi* larvae, based on observations of larval vertical distributions. From the viewpoint of the larval supply and reception relationships, the local populations were subdivided into four groups. The first group exchanges larvae with the Tomioka tidal flat population. The second group receives larvae from the Tomioka tidal flat population but does not supply larvae to the latter. The third group supplies larvae to the Tomioka tidal flat population and the first group but does not receive larvae reciprocally. Although the last group supplies larvae to a part of the first group and the third group, it does not have a reciprocal relationship with the Tomioka tidal flat population. In terms of larval flux, the Tomioka tidal flat population was concluded to be the center of the larval connection network in the region.

Keywords: Callianassid shrimp, Tracer model, Larval connection network, intertidal sandflats, Ariake Sound estuarine system

1. Introduction

Since 1979, A. Tamaki and his colleagues have studied the dynamics of the macrobenthos community dominated by the ghost shrimp *Nihonotrypaea harmandi* (Decapoda: Thalassinidea: Callianassidae) on an intertidal sandflat facing Tomioka Bay (Tomioka tidal

flat) on the northwestern corner of Amakusa-Shimoshima Island, western Kyushu, Japan (Fig. 1). Tomioka Bay constitutes a part of Tachibana Bay, situated at the southwestern periphery of the Ariake Sound estuarine system ranging from Ariake Sound (1700 km² estuary) through Tachibana Bay (700 km²) to the coastal waters of the East China Sea. At spring tides, the Tomioka tidal flat is exposed for 150－700 m seaward over a distance of 4 km along the coastline. The shrimp reside in deep-reaching burrows for shelter, reproduction, and feeding, and their bioturbating activity modifies the ambient sediment properties considerably to cause a remarkable change in the

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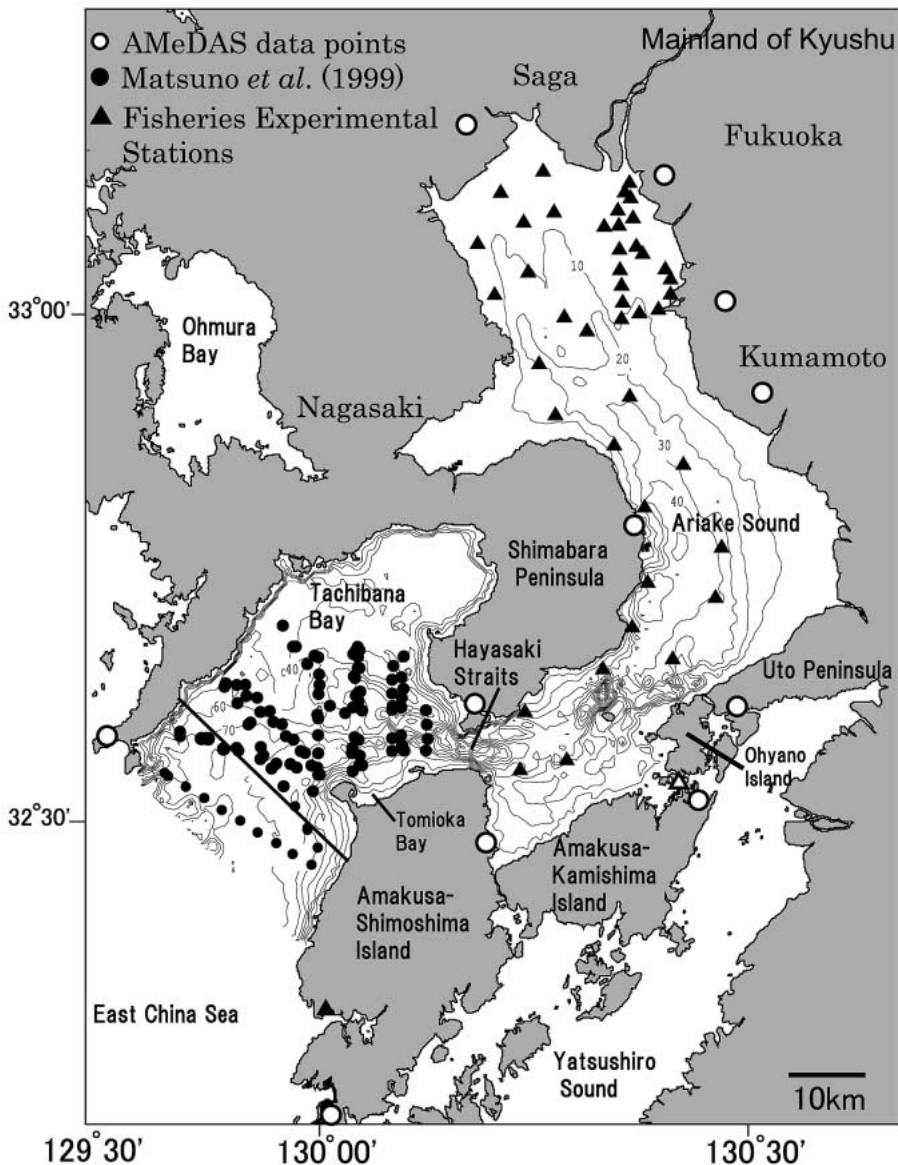
Fig. 1   Model area with bathymetry in the Ariake Sound estuarine system spanning from Ariake Sound, via
Tachibana Bay, to the coastal waters of the East China Sea. The depth contour interval is 10 m. Black cir-
cles, white circles and black triangles are the observation points by Matsuno *et al.* (1999), the AMeDAS
data points and the observation points by the four prefectural (i.e. Saga, Fukuoka, Kumamoto, Na-
gasaki) Fisheries Experimental Stations, respectively. The solid line at the mouth of Tachibana Bay is the
boundary of the present numerical model.

benthic community on the sandflat (FLACH and
TAMAKI, 2001; TAMAKI, 2004). In the Ariake
Sound estuarine system, *N. harmandi* are re-
stricted to the tidal flats at Tachibana Bay and
the outermost one-third of Ariake Sound
(TAMAKI *et al.*, 1999). Of the 26 main local

shrimp populations surveyed, the population
on the Tomioka tidal flat was largest, account-
ing for 70% of the total number of shrimps in
the region (TAMAKI and HARADA, 2005). This
was due to the high shrimp density (mean of
ca. 270 ind. m^{-2}) and the large area of the

Tomioka tidal flat (ca. 560,000 m²).

On the Tomioka tidal flat, the *N. harmandi* population size expanded considerably in the early 1980's, followed by a steady state for the subsequent 10 years (TAMAKI, 1994; TAMAKI *et al.*, 1997; FLACH and TAMAKI, 2001). A similar explosive increase in the local population size of *N. harmandi* has also occurred on some other intertidal sandflats in Tachibana Bay and the outermost one-third of Ariake Sound (FLACH and TAMAKI, 2001). Finding for the mechanism of such widespread population explosion requires a metapopulation perspective. Zoeal larvae of *N. harmandi* grow to the decapodid stage in the same local waters (TAMAKI and MIYABE, 2000). It can be surmised that the Tomioka tidal flat population acts as the main source of larval supply in this region due to its overwhelmingly large population size (TAMAKI and MIYABE, 2000; TAMAKI and HARADA, 2005; KUBO *et al.*, 2006). The processes for dispersal of larvae from the Tomioka tidal flat, retention in the offshore waters, and on-shore transport to the same tidal flat were investigated by field observations and numerical experiments (FUJIIE *et al.*, 2004). However, the larval exchange among all main local populations in Tachibana Bay and the outermost one-third of Ariake Sound has yet to be explored. The purpose of this study is to clarify the larval connection network of the *N. harmandi* population among the main tidal flats in the region using a numerical tracer model.

2. Current field in Tachibana Bay and Ariake Sound

The study area is the Ariake Sound estuarine system (Fig. 1). The horizontal transport of *N. harmandi* larvae is mainly controlled by the current, because the horizontal swimming velocities of larvae are much smaller than the current velocities. The major current components in the coastal area of this region are tidal currents and residual flows (YANAGI, 1999). We need to calculate tidal currents and residual flows in Tachibana Bay and Ariake Sound to simulate the horizontal transport of larvae.

2.1 Tidal current
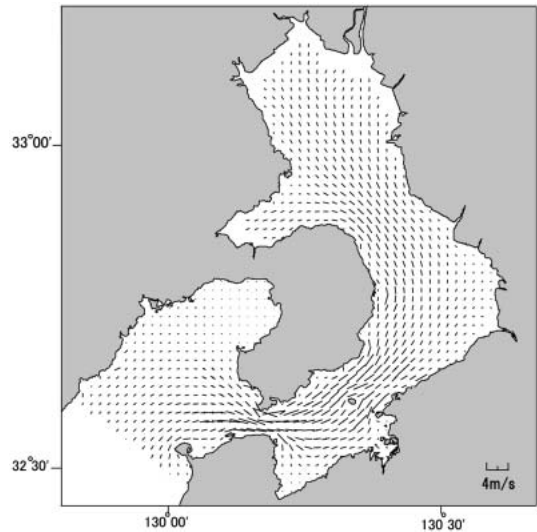
TSUKAMOTO and YANAGI (2002) calculated

Fig. 2   Major and minor axes of M_2 tidal current ellipse in the study region (after Tsukamoto and YANAGI, 2002).

the tidal current in Tachibana Bay and Ariake Sound using a dynamical numerical model. The result for the M_2 tidal current was used in this study, because M_2 is the dominant tide in this region. Their numerical model is a two-dimensional barotropic model. The horizontal unit grid size is 500 m × 500 m. The calculated major and minor axes of M_2 tidal current ellipses are shown in Fig. 2. The maximum M_2 tidal current speeds are about 150 cm s^{-1} at Hayasaki Straits situated between Tachibana Bay and Ariake Sound (Fig. 1) and about 100 cm s^{-1} in Ariake Sound. The M_2 tidal current speed is less than 4 cm s^{-1} at the northeastern part of Tachibana Bay. The M_2 tidal current flows parallel to the coastline in Ariake Sound. The minor axis is much shorter than the major axis in Tachibana Bay and Ariake Sound. M_2 tidal current has horizontal shear through the region, resulting in the dispersion of particles by tidal currents (AWAJI *et al.*, 1980).

2.2 Residual flow

The residual flow plays an important role in the long-term transport of *N. harmandi* larvae in Tachibana Bay and Ariake Sound (FUJIIE *et al.*, 2004). The residual flow in the coastal sea consists of tide-induced residual current, wind-driven current and density-driven current
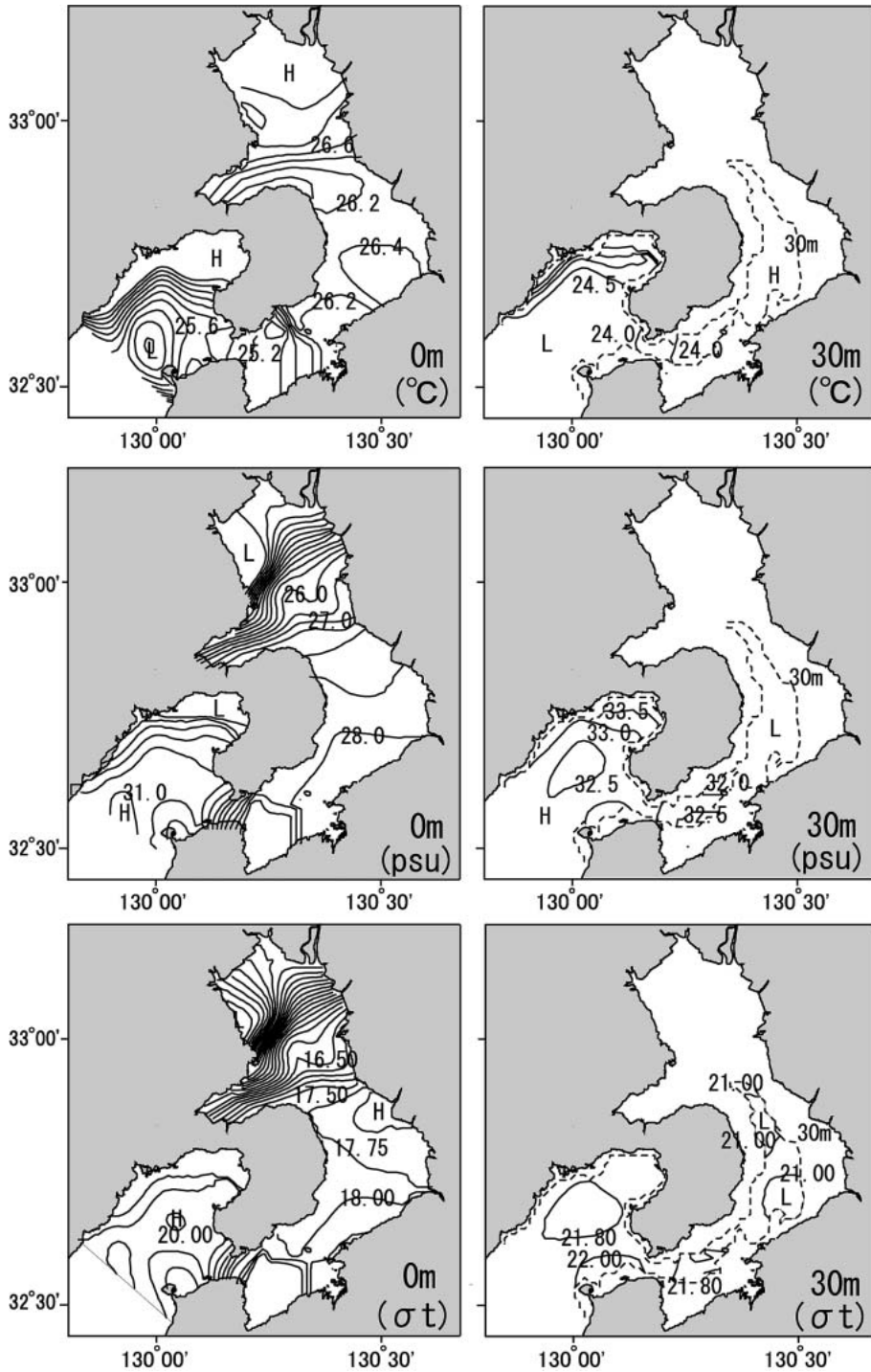
Fig. 3   Horizontal distributions of temperature (upper), salinity (middle), and density (lower) at 0-m and 30-m depths. Broken lines represent the isobath lines of 30-m depth in the study region (after FUJIIE *et al.*, 2004).

(YANAGI, 1999). According to the previous study on the *N. harmandi* population on the Tomioka tidal flat (TAMAKI *et al.*, 1996; TAMAKI *et al.*, 1997), one part of the main breeding season is in August. We therefore tried to reproduce the density-driven current and the wind-driven current in Tachibana Bay and Ariake Sound in August diagnostically using the Princeton Ocean Model (POM) (BLUMBERG and MELLOR, 1987). The horizontal unit grid size is the same as in the tidal model by TSUKAMOTO and YANAGI (2002). The vertical division consists of 20 layers. Bottom topography is based on the JODC dataset with 500 m resolution.

The horizontal and vertical distributions of water temperature and salinity were observed in August 1993 and August 1994 by MATSUNO *et al.* (1999) and Saga, Fukuoka, Kumamoto and Nagasaki Prefectural Fisheries Experimental Stations surrounding Ariake Sound and Tachibana Bay. The observation points in MATSUNO *et al.* (1999) and the four Prefectural Fisheries Experimental Stations are shown with solid circles and triangles in Fig. 1, respectively. Figure 3 shows the horizontal distributions of water temperature, salinity and density at 0-m and 30-m depths in Tachibana Bay and Ariake Sound. The broken line in Fig. 3 represents the isobath line at 30-m depth. Water temperature was high and salinity was low at the northeastern part of Tachibana Bay and the head of Ariake Sound, while water temperature was low and salinity was high at the mouth of Tachibana Bay. Therefore, the surface water at the mouth of Tachibana Bay was heavier than that at the head of Ariake Sound.

The monthly-averaged wind field in August 1993 was obtained by interpolating the observations at 11 Automated Meteorological Data Acquisition System (AMeDAS) points, which are shown with open circles in Fig. 1. YANAGI (1980) has estimated that the wind velocity on the coastal sea is about 1.5 times that on land in Osaka Bay, Japan. The region in this study is a semi-closed area similar to Osaka Bay. As there is no observation data for wind velocity and direction in Tachibana Bay and Ariake Sound, wind velocity on the sea surface was
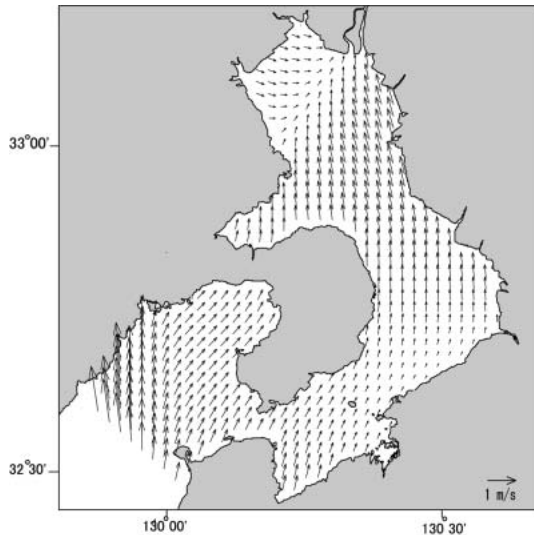

Fig. 4   Horizontal distribution of wind vectors in August 1993 in the study region (after FUJIIE *et al.*, 2004).

assumed to be 1.5 times that on land. Figure 4 shows the horizontal distribution of interpolated wind vectors in the region in August 1993. The wind was blowing from the south except at the head of Ariake Sound, where the wind was blowing from the west. The horizontal shear of wind vector was large in the study area.

In order to include the tide-induced residual current in our model, the tidal stress calculated from the results of TSUKAMOTO and YANAGI (2002) was incorporated into the POM. Tidal stress can be calculated by the following equations,

$$S_x = -\left(\overline{u'\frac{\partial u'}{\partial x} + v'\frac{\partial u'}{\partial y}}\right) \quad (1)$$

$$S_y = -\left(\overline{u'\frac{\partial v'}{\partial x} + v'\frac{\partial v'}{\partial y}}\right) \quad (2)$$

where u' and v' denote the calculated tidal current velocity in east and north directions, respectively. The horizontal distribution of calculated tidal stress is shown in Fig. 5. The maximum M_2 tidal stress was about 0.05 cm s^{-2} at Hayasaki Straits and less than 0.001 cm s^{-2} in Tachibana Bay and Ariake Sound.

Figure 6 shows the horizontal distributions of the calculated residual flow, which is composed of density-driven, wind-driven and tide-
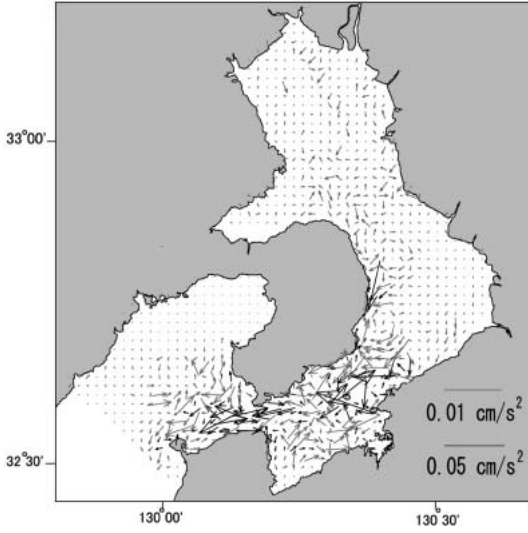
Fig. 5   Horizontal distribution of calculated tidal
        stress vector in the study region (after
        Tsukamoto and YANAGI, 2002) . Note the two
        kinds of vectors with different units.

induced residual currents at depths of 1m, 10m,
40m and 50m. There was a residual flow in the
surface layer along the coastline of the south-
ern part of Shimabara Peninsula in Ariake
Sound. This residual flow connects Tachibana
Bay and Ariake Sound through Hayasaki
Straits. In the center of Tachibana Bay, water
density is high in the surface layer (Fig. 3).
Therefore, at Tachibana Bay, there was a
counter-clockwise circulation of about 5 cm s^{-1}
in the center of the upper layer. In the lower
layer, the residual flow was toward the head of
Ariake Sound.

The horizontal distribution of the calculated
residual flow in Tachibana Bay is the same as
that given in FUJIIE *et al.* (2004). The calcula-
tions in FUJIIE *et al.* (2004) agreed well with
the observations in MATSUNO *et al.* (1999) con-
ducted in Tachibana Bay. It seems reasonable
to assume that the calculated current field in
Tachibana Bay and Ariake Sound given in Fig.
6 are a good representation of the actual cur-
rent field.

3. Diurnal vertical migration of *N. harmandi* larva

Larvae of *N. harmandi* grow to the
decapodid stage through five zoeal stages. It is
well known that zooplankton migrates verti-
cally depending on their developmental stage
(SAITOU, 2002). The diurnal vertical migration
of *N. harmandi* strongly influences their hori-
zontal distribution (FUJIIE *et al.*, 2004). A.
TAMAKI and his colleagues observed the vertical
migration of *N. harmandi* larvae in Tachibana
Bay (TAMAKI *et al.*, unpubl.) in October 1994
during the N. harmadi breeding season (KUBO
et al., 2006).   Horizontal plankton tows were
collected using a MTD net (MOTODA, 1971) off
the coast of Tomioka Bay at eight different
depths (0m, 5m, 10m,15m, 20m, 30m, 40m and
50m) for 5 min per sample in 60m water depth
during daytime and nighttime low tides on 3-4
October. Figure 7 illustrates the observed verti-
cal distribution for the combined of Zoea 1 and
Zoea 2 larvae, the combined of Zoea 3 and Zoea
4 larvae, the Zoea 5 larvae and the decapodid
larvae of *N. harmandi* in daytime and night-
time. Decapodid larvae were collected only in
nighttime, probably because they grasp the
bottom substratum in daytime.

4. Tracer model

Transport of *N. harmandi* larvae was calcu-
lated by the Euler-Lagrange method using the
calculated tidal current and residual flow. The
position of larvae ($x^{t+\Delta t}$, $y^{t+\Delta t}$, $z^{t+\Delta t}$) at time $t+\Delta t$ can be calculated from the position (x^{t}, y^{t},
z^{t}) at time t by the following equations
(YANAGI *et al.*, 1995),

$$x^{t+\Delta t} = x^{t}+u^{t}\cdot\Delta t+\frac{1}{2}\frac{\partial u^{t}}{\partial x}\cdot u^{t}\cdot\Delta t^{2}+\frac{1}{2}\frac{\partial u^{t}}{\partial y}\cdot v^{t}\cdot$$

$$\Delta t^{2}+\frac{1}{2}\frac{\partial u^{t}}{\partial z}\cdot w^{t}\cdot\Delta t^{2} \tag{3}$$

$$y^{t+\Delta t} = y^{t}+v^{t}\cdot\Delta t+\frac{1}{2}\frac{\partial v^{t}}{\partial y}\cdot u^{t}\cdot\Delta t^{2}+\frac{1}{2}\frac{\partial v^{t}}{\partial z}\cdot v^{t}\cdot$$

$$\Delta t^{2}+\frac{1}{2}\frac{\partial v^{t}}{\partial z}\cdot w^{t}\cdot\Delta t^{2} \tag{4}$$

$$z^{t+\Delta t} = z^{t}+w^{t}\cdot\Delta t+\frac{1}{2}\frac{\partial w^{t}}{\partial x}\cdot u^{t}\cdot\Delta t^{2}+\frac{1}{2}\frac{\partial w^{t}}{\partial y}\cdot v^{t}\cdot$$

$$\Delta t^{2}+\frac{1}{2}\frac{\partial w^{t}}{\partial z}\cdot w^{t}\cdot\Delta t^{2} \tag{5}$$

where u, v and w denote the calculated east-
ward, northward and upward velocities, respec-
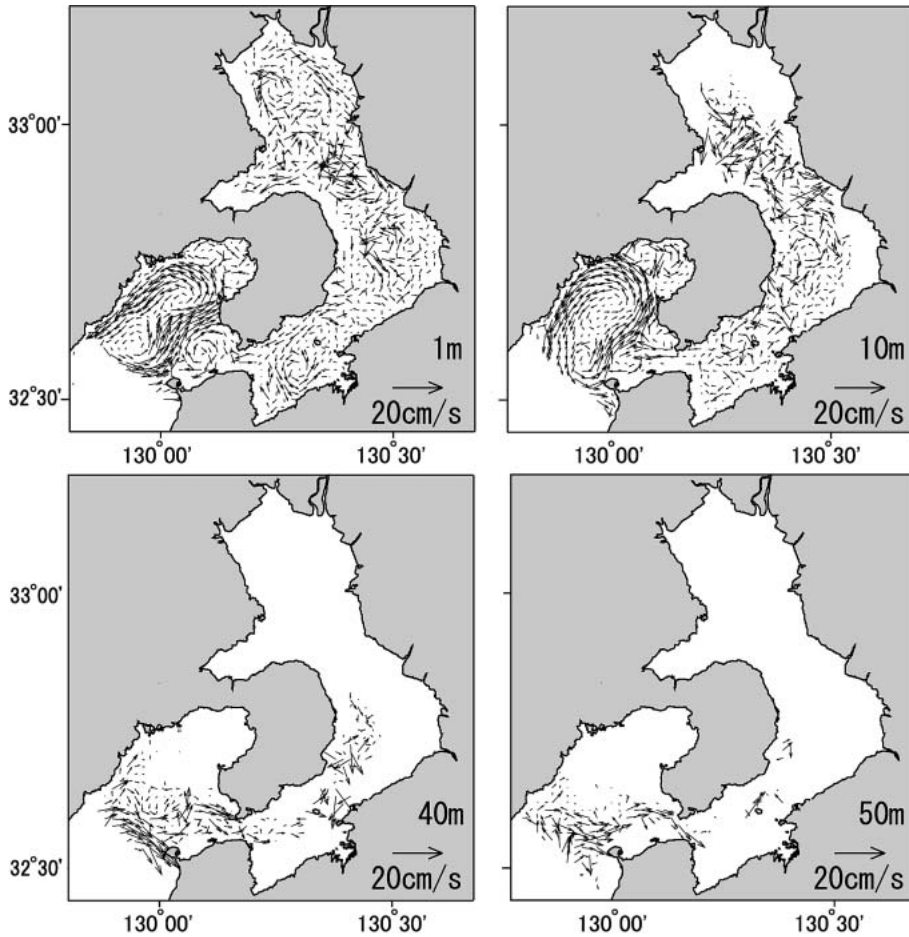tively, including the tidal current and residual

Fig. 6 Distribution of residual flows at 1-, 10-, 40- and 50-m depths in the study region (after FUJIIE *et al.*, 2004).

flow. The third, fourth and fifth terms on the right side of Eqs. (3), (4) and (5) denote the effect of current shear. The weight and size of *N. harmandi* larva were ignored.

Larvae of *N. harmandi* are released at high water in spring tides (TAMAKI *et al.*, 1996), and the study period included both spring and neap tides. The M_2 tidal current amplitude fluctuated in a 15-day period. As the amplitude of S_2 tide is 44% of that of M_2 tide in Tachibana Bay and Ariake Sound (Japan Coast Guard, 1983), the tidal amplitudes in neap and spring tides were determined as 0.56 and 1.44 times that of the M_2 tidal current amplitude, respectively.

Figure 8 shows the distribution of the population size of *N. harmandi* at the 26 main locations along the coastline from Ariake Sound to Tachibana Bay (after TAMAKI and HARADA, 2005). The number of larvae released from each tidal flat was determined in proportion to the observed population size of *N. harmandi* on each tidal flat given in Fig. 8. The release points were arranged at equal intervals within each tidal flat. The larvae were released from 1m above the sea bottom. Bottom topography is the same as in the current model.

Although the northern limit of the distribution of adult *N. harmandi* was located at the middle part of Uto Peninsula (TAMAKI and HARADA, 2005; Fig. 1, 8), Kumamoto Port, ca. 10 km north, was regarded as the northernmost extent of larvae for the present numerical
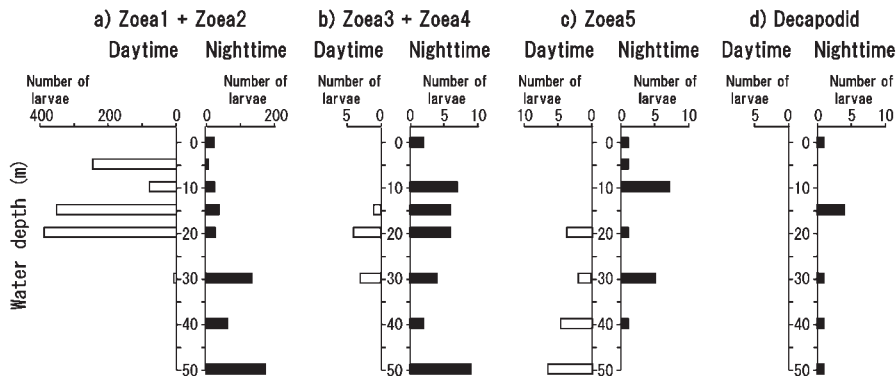
Fig. 7 Number of (a) combined Zoea 1 and Zoea 2 larvae, (b) combined Zoea 3 and Zoea 4 larvae, (c) Zoea 5 larvae, and (d) decapodid larvae of *Nihonotrypaea harmandi* per 5-min horizontal haul with a MTD net from 8 depth-layers (0m, 5m, 10m, 15m, 20m, 30m, 40m and 50m) off Tomioka Bay around daytime lowest slack tide (12:39PM) on 3 October and nighttime lowest slack tide (1:02AM) on 4 October in 1994, respectively.

experiment because the nearest tide gauge station was at Kumamoto Port (Fig. 8). As the southernmost tide gauge station in the study area, the one at Tomioka Port was used. The difference in the time of high water between these tide gauge stations is 50 minutes (Japan Coast Guard, 1983). Such time difference in high water tide is short compared with the total release time of *N. harmandi* larvae which lasts for 3 hours (FUJIIE *et al.*, 2004). Thus, the start of the release time of *N. harmandi* larvae was set the same for every tidal flat. The larvae were released at 20:41 on August 2, 1993 in the tracer model for the comparison to the observational results given in TAMAKI and MIYABE (2000). This time corresponded to the high water in the spring tide on the Tomioka tidal flat.

The time interval for each zoeal stage is 3 days and that for the decapodid stage is 10 days (MIYABE *et al.*, 1998; KONISHI *et al.*, 1999). Thus, the total calculation time of the model was 25 days. The time step of the calculation was 2 seconds. When the larva flowed out to the East China Sea, it was assumed that the larva did not return to the study area.

Based on observed larval distributions shown in Fig. 7, vertical migration patterns of *N. harmandi* larvae were incorporated in the model as follows. Time in the tracer model was partitioned into the daytime (12h) and nighttime (12h). Based on the field observation, the following behavioral characteristics were established for each developmental stage in the tracer model. The Zoea 1 and Zoea 2 larvae occur between 5m and 20m in daytime and between 30m and the bottom in nighttime. The Zoea 3 and Zoea 4 larvae occur between 15m and 30m in daytime and between 0m and the bottom in nighttime. The Zoea 5 larvae occur between 20m and the bottom in daytime and between 0m and 40m in nighttime. The decapodid larvae are not present in the water column and remain stationary on the sea bed in daytime, but they occur between 0m and the bottom in nighttime. The larvae are normally transported vertically by the flow according to depth within the range. When the position of the larva lies outside the range due to alternation of daytime and nighttime or the flow according to depth, the larva is moved deterministically over the course of an hour to the inside of the range. For example, if the Zoea 1 larvae which were distributed at 1m depth in daytime, they were moved to 5m depth over the course of an hour. Horizontal transportation of the larvae is due to horizontal flow at that depth, while vertical transportation is by their additional vertical shift to the inside of the range. The passively sinking velocity of larvae was assumed to be zero.

FUJIIE *et al.* (2004) calculated the horizontal distribution of *N. harmandi* larvae for each developmental stage using the same method as in this study. A good correspondence could be seen between the calculated results and the
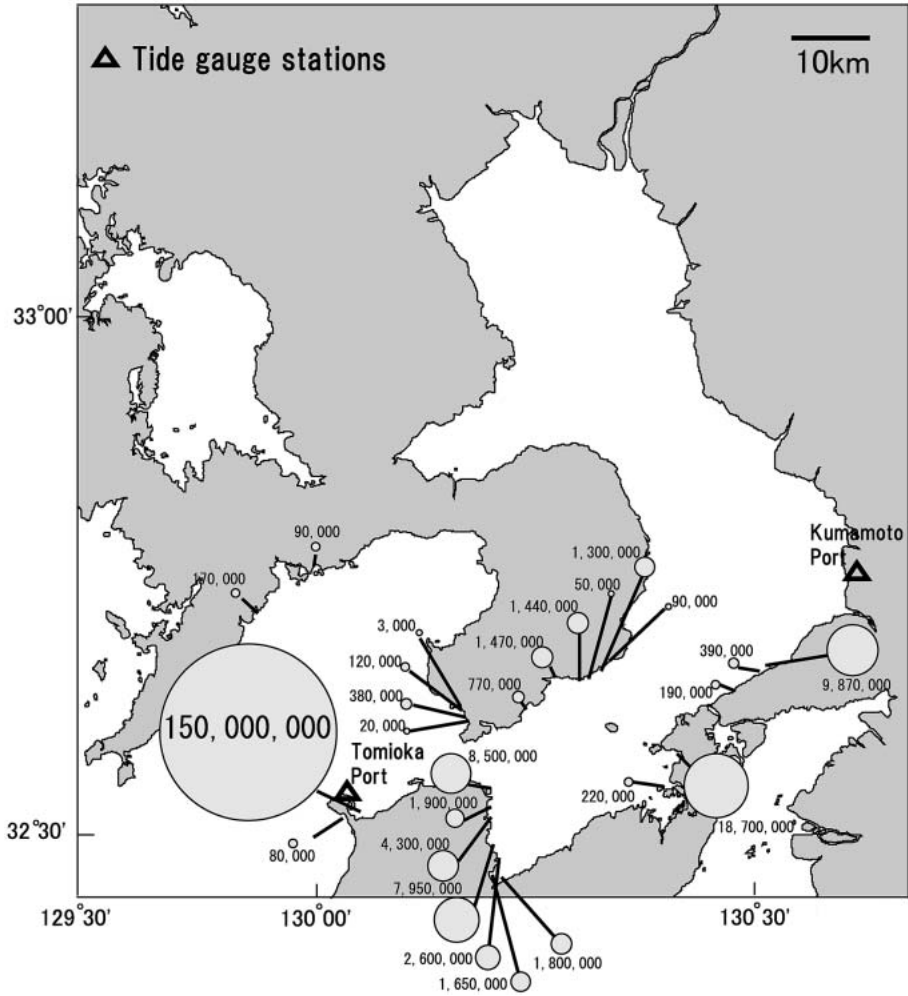
Fig. 8 Local population size of *Nihonotrypaea harmandi* on 26 intertidal sandflats in Tachibana Bay and the outermost one-third of Ariake Sound (after TAMAKI and Harada, 2005). The tide gauge stations at Kumamoto Port and Tomioka Port are shown with triangles.

observed results (FUJIIE *et al.*, 2004). Therefore, it can be assumed that the movement of the larvae will be reproduced also in this study.

5. Results and Discussion

Two parameters are defined to clarify the *N. harmandi* larval connection network in Tachibana Bay and Ariake Sound. The supply rate of larvae from each tidal flat and the reception rate of larvae by each tidal flat are defined by the following equations,

$$Su_{AB} = \frac{ARR_{AB}}{TOS_A} \times 100, \tag{6}$$

$$Rc_{AB} = \frac{ARR_{BA}}{TOA_A} \times 100, \tag{7}$$

where Su_{AB}, ARR_{AB}, TOS_A, RC_{AB} and TOA_A denote the supply rate (%) from a tidal flat A to another tidal flat B, the number of larvae that arrived from A to B, the total number of larvae that arrived from A to all tidal flats, the reception rate (%) by A from B, and the total number of individuals that arrived from all tidal flats to A, respectively. The supply rate and the reception rate of larvae were calculated based on the calculation results of the tracer model.

5.1 Role of the Tomioka tidal flat population in the larval connection network

First we examine the role of the Tomioka tidal flat population in the larval connection network of *N. harmandi* in Tachibana Bay and Ariake Sound. Figure 9 shows the supply rate from the Tomioka tidal flat population to each of the 26 tidal flat populations in the region. The serial numbers are given to the tidal flats in the location map and the supply rate values less than 0.01% are omitted in the figure. About 75% of larvae supplied from the Tomioka tidal flat arrived at the tidal flats in Tachibana Bay (No. 1 to No. 8). Such high supply rate is due to the effect of the residual circulation occurring off Tomioka Bay as shown in Fig. 6 (a), (b) (FUJIIE *et al.*, 2004). Figure 10 shows the temporal change in the horizontal distribution of *N. harmandi* larvae, which were originally released from eight representative tidal flats in Tachibana Bay and Ariake Sound. The arrows indicate the tidal flats with larval release. The residual circulation retained larvae released from the Tomioka tidal flat in the center of

Tachibana Bay until the larvae became the Zoea 5 stage (Fig. 10a). After the Zoea 5 stage, larvae were transported by the tidal current and the residual flow in the lower layer to the tidal flats along the coastline of Tachibana Bay. About 74% of the larvae were supplied to the Tomioka tidal flat itself. The main reason for this high return rate may be that the area (0.56 km²) of the Tomioka tidal flat is much larger than those of the other tidal flats (0.01–0.2 km²) in Tachibana Bay.

The second largest part of the *N. harmandi* larval population that were released from the Tomioka tidal flat was transported to Hayasaki Straits by the dispersion effect of tidal current shear and the residual flow in the lower layer of Tachibana Bay (Fig. 9). The supply rate from the Tomioka tidal flat to the tidal flat on the northeastern corner of Amakusa-Shimoshima Island (No. 9) was about 20%. The supply rate to the tidal flats along the southern coastline of Shimabara Peninsula in Ariake Sound (No. 21 to No. 26) was about 5%. In the simulation, larvae flowing into
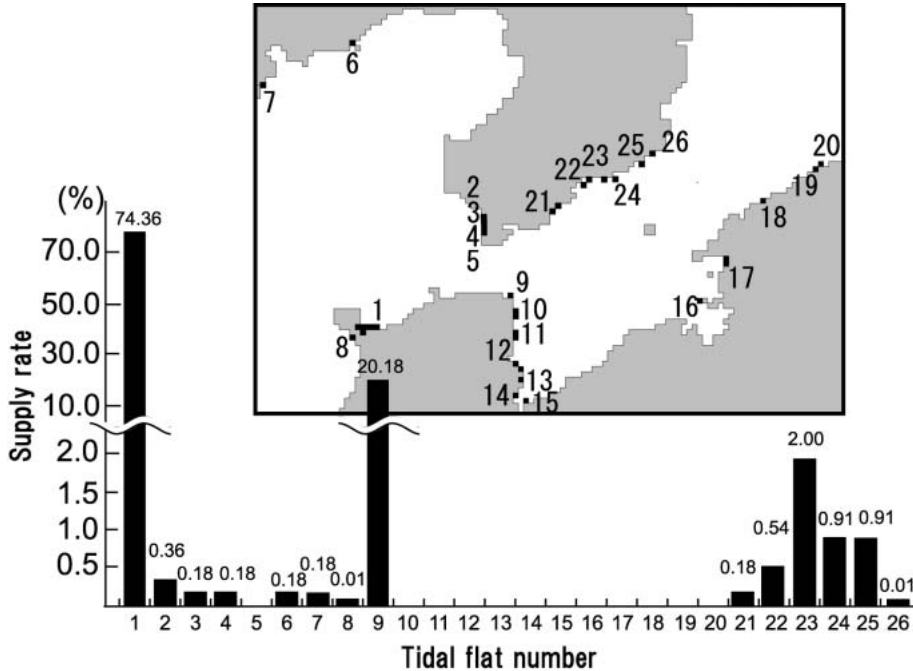

Fig. 9   Supply rate of *Nihonotrypaea harmandi* larvae from the Tomioka tidal flat to each tidal flat in the study region. The black squares with the serial numbers on the inset map stand for the tidal flats with *N. harmandi* indicated in Fig. 8. See text for the definition of supply rate.
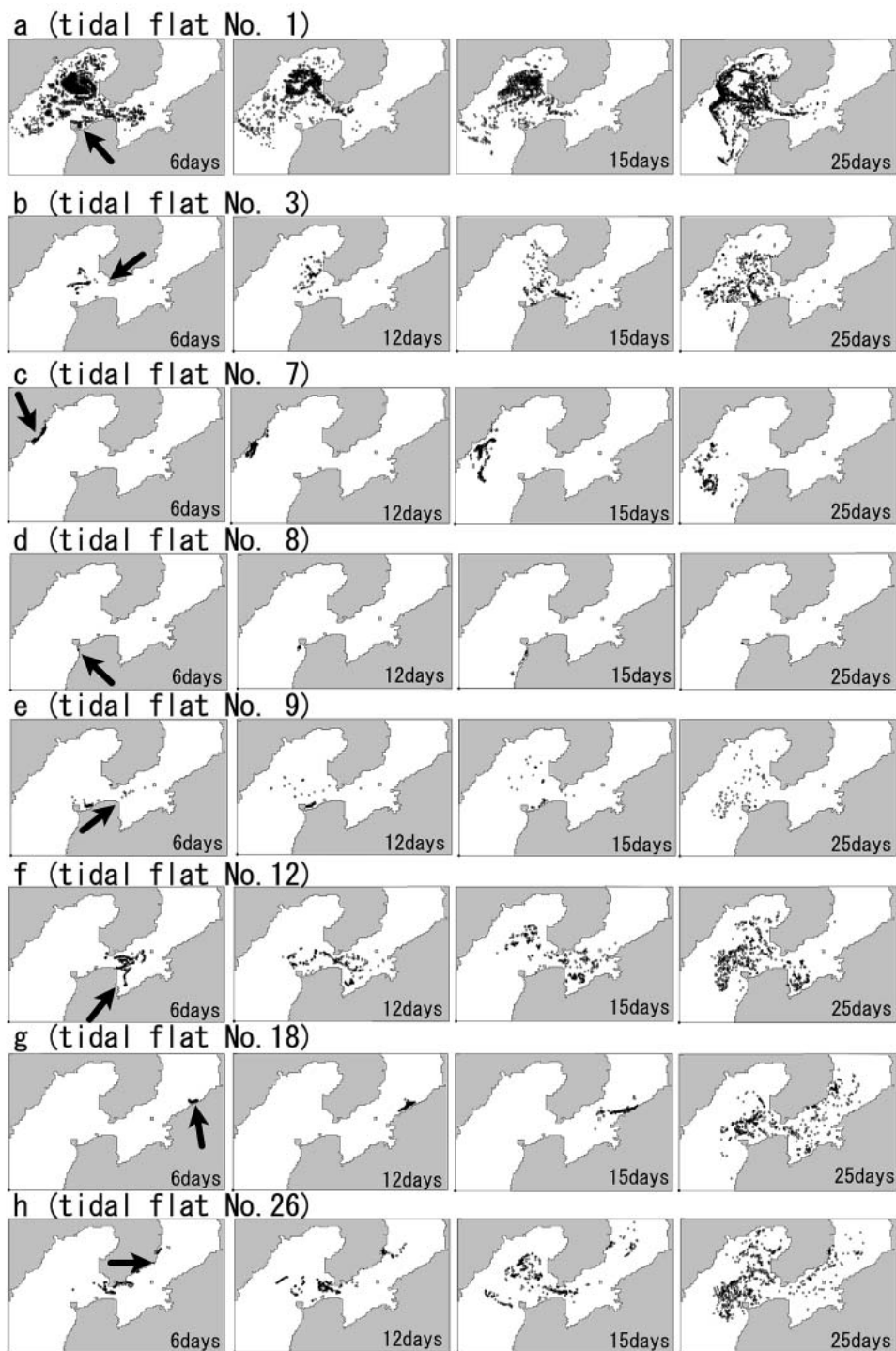
Fig. 10 Time course of calculated horizontal distributions of *Nihonotrypaea harmandi* larvae 6 to 25 days after being released from the populations on eight representative tidal flats (arrows) in the study region. The tidal flat numbers correspond to those given in Figs. 9 and 11.
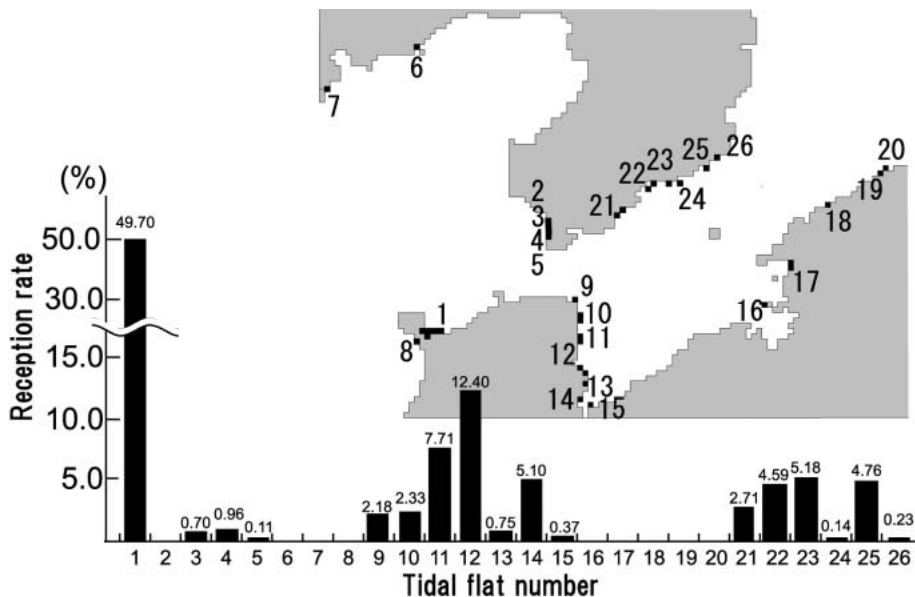
Fig. 11 Reception rate of *Nihonotrypaea harmandi* larvae by the Tomioka tidal flat from each tidal flat in the
study region. The black squares with the serial numbers on the inset map stand for the tidal flats with *N.
harmandi* indicated in Fig. 8. See text for the definition of reception rate.

Ariake Sound from the Tomioka tidal flat were
not transported to the eastern coastline of
Amakusa-Shimoshima Island and the northern
coastline of Uto Peninsula (No. 10 to No. 20).
The residual flow in the lower layer at
Hayasaki Straits flowed toward the head of
Ariake Sound along the southern coastline of
Shimabara Peninsula (Fig. 6 (c), (d)). By con-
trast, in the area enclosed by the eastern coast-
line of Amakusa-Shimoshima Island and the
northern coastline of Amakusa-Kamishima Is-
land, a uniform residual flow which flows from
Shimabara Peninsula toward this area did not
exist as shown in Fig. 6 (a), (b). This may ex-
plain the fact that there was no supply of lar-
vae to the tidal flats No. 10 to No. 20 (Fig. 10a).
As larvae of *N. harmandi* released from the
Tomioka tidal flat were supplied to the half of
the tidal flats in Tachibana Bay and Ariake
Sound (Fig. 9), the population fluctuation on
the Tomioka tidal flat would directly be trans-
mitted to the populations on these tidal flats.

Next we examine the reception rate by the
Tomioka tidal flat population. Figure 11 shows
the reception rate of *N. harmandi* larvae by
the Tomioka tidal flat from the other tidal
flats in Tachibana Bay and Ariake Sound. The

self-reception rate by the Tomioka tidal flat
was about 50%. The other 50% larvae mainly
came from the tidal flats along the eastern
coastline of Amakusa-Shimoshima Island and
the southern coastline of Shimabara Peninsula
in Ariake Sound. Larvae released from the tidal
flats along the southern coastline of Shimabara
Peninsula in Tachibana Bay (No. 3 to No. 5)
were supplied to the Tomioka tidal flat, with
the reception rate by the Tomioka tidal flat be-
ing only about 2%. It is expected that larvae re-
leased from the tidal flats in Tachibana Bay are
retained in the center of the bay by the
counter-clockwise residual circulation and are
thus transported to each tidal flat in the bay
(FUJIIE *et al.*, 2004) (Fig. 10b). The reception
rates of larvae released from the tidal flats
along the northern coastline of Tachibana Bay
(No. 6, 7) and the western coastline of Tomioka
Peninsula (No. 8) by the Tomioka tidal flat
were much lower (less than 0.1%). This would
be due to the residual current flows in the up-
per layer directed toward the East China Sea
around these areas as shown in Fig. 6 (a).
Most larvae released from these areas flowed
out to the East China Sea by these residual
flows (Fig. 10c,d). There was a mutual larval

exchange relationship between the tidal flats No. 3 to No. 5 and the Tomioka tidal flat. The tidal flats No. 6 to No. 8 received larvae from the Tomioka tidal flat but did not reciprocally supply larvae.

The larvae of *N. harmandi* released from the tidal flats along the eastern coastline of Amakusa-Shimoshima Island (No. 9 to No. 15) accounted for about 32% of the larvae supplied from all tidal flats in Tachibana Bay and Ariake Sound to the Tomioka tidal flat (Fig. 11). By contrast, these tidal flats did not receive larvae from the Tomioka tidal flat except for the one on the northeastern corner of Amakusa-Shimoshima Island (No. 9). Only the tidal flat No. 9 mutually exchanged larvae with the Tomioka tidal flat.

The sum total reception rates by the Tomioka tidal flat from the tidal flats along the southern coastline of Shimabara Peninsula in Ariake Sound (No. 21 to No. 26) was about 18% (Fig. 11), indicating the mutual larval exchange relationship between these tidal flats and the Tomioka tidal flat. The tidal flats in Uto Peninsula (No. 16 to No. 20), which face Shimabara Peninsula, did not supply larvae to the Tomioka tidal flat.

With the above results as the background information, we now examine the observed self-return rate of *N. harmandi* larvae to the Tomioka tidal flat. It can be estimated from TAMAKI *et al.*'s (1997) data that the self-return rate of larvae on the Tomioka tidal flat was about 0.1%. This figure was based on the difference between the number of larvae released from the Tomioka tidal flat (actually as the number of eggs prior to the larval release per square meter) and the corresponding number of newly settled juveniles per square meter there. Based on the physical transport process only, FUJIIE *et al.* (2004) also gave the self-return rate of about 0.1%. However, it must be noted that the actual larval return process involves not only purely physical transport but also other mortality-causing factors such as starvation and predation. Considering the self-reception rate of larvae by the Tomioka tidal flat through the physical transport process only was about 50% (Fig. 11), the true self-return rate of the larvae released from the

Tomioka tidal flat through all possible processes is estimated at 0.05%.

5.2 Role of the other tidal flat populations in the larval connection network

It is true that the Tomioka tidal flat population is the center of the supply and reception network of *N. harmandi* larvae in Tachibana Bay and Ariake Sound, but the contribution from the other tidal flat populations cannot be ignored. The latter can be examined from the calculated supply and reception rates for all tidal flats.

Figure 12 shows the supply rate from each tidal flat to the other ones in Tachibana Bay and Ariake Sound. The mutual exchange of larvae occurs between the Tomioka tidal flat and: (1) a part of the tidal flats in Tachibana Bay (No. 1 to No. 5); (2) the tidal flat on the northeastern corner of Amakusa-Shimoshima Island (No. 9); and (3) the tidal flats along the southern coastline of Shimabara Peninsula in Ariake Sound (No. 21 to No. 26). The larval transport path connecting Ariake Sound and Tachibana Bay is the residual flow offshore of Shimabara Peninsula flowing toward Tachibana Bay in the upper layer and toward the opposite direction in the lower layer through Hayasaki Straits. Larvae of the early developmental stages are transported toward Tachibana Bay through the upper layer of this path. In the later stages, larvae are transported toward Shimabara Peninsula through the lower layer of the path. Therefore, the mutual supply and reception relationship between each tidal flat lying near Hayasaki Straits and Shimabara Peninsula is also expected to occur. The mutual supply and reception relationships among the three tidal flat groups (No. 1 to No. 5, No. 9, and No. 21 to 26) as pointed out above can be understood visually from Fig. 10a, b, e and h.

The populations of the tidal flats along the northern coastline of Tachibana Bay (No. 6, 7) and the western coastline of Tomioka Peninsula (No. 8) did not supply *N. harmandi* larvae to the other tidal flats in Tachibana Bay and Ariake Sound (Fig. 12). Larvae released from the tidal flats No. 6, 7 were transported toward the southwest by the residual circulation. A part of these larvae went back to
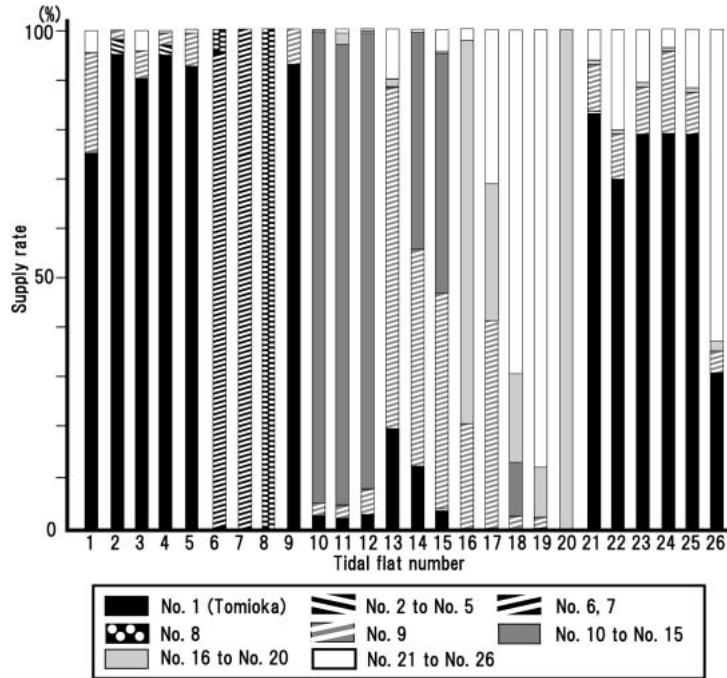
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Fig. 12 Proportional supply rates of *Nihonotrypaea harmandi* larvae from each tidal flat to all tidal flats in the study region. The X axis indicates the source of larval supply to each tidal flat. See Figs. 9 and 11 for the location of tidal flats.
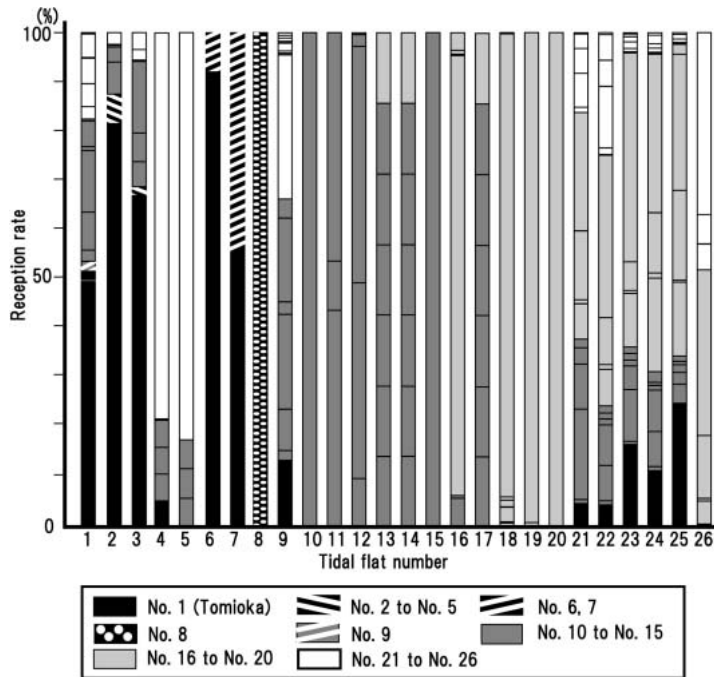

Fig. 13 Proportional reception rates of *Nihonotrypaea harmandi* larvae by each tidal flat from all tidal flats in the study region. The X axis indicates the destination for larvae released from each tidal flat. See Figs. 9 and 11 for the location of tidal flats.

Tachibana Bay by this residual circulation but most of them flowed out to the East China Sea (Fig. 10c). Similarly, larvae released from the tidal flat No. 8 flowed out to the East China Sea by the residual flow (Fig. 10d). These larval transport patterns would help explain the quite low or zero supply rates from these tidal flats to the other tidal flats.

The supply rates from the tidal flat populations along the eastern coastline of Amakusa-Shimoshima Island (No. 10 to No. 15) to the tidal flats in Tachibana Bay and the other tidal flats in Ariake Sound were lower than the self-supply rates (Fig. 12). Larvae released from the eastern coastline of Amakusa-Shimoshima Island were transported by the diffusive effect of tidal current shear, because the current speed around this area is small. Therefore a substantial part of the larvae was retained through time around the sea area off the eastern coastline of Amakusa-Shimoshima Island (Fig. 10f). A small part of those larvae was carried to the offshore area of Shimabara Peninsula and was transported to Tachibana Bay by the above-mentioned larval transport path. Fifteen days after the larval release, the larvae that had been transported to Tachibana Bay and distributed in its center were transported to the tidal flats in the bay by the diffusive effect of tidal current shear.

The residual flow around the northern coastline of Uto Peninsula was not uniform in direction. Therefore, *N. harmandi* larvae released from the tidal flats No. 16 to No. 20 were supplied to the tidal flats in Ariake Sound by the horizontal diffusion. A part of the larvae could ride the above-mentioned main larval transport path connecting Ariake Sound and Tachibana Bay after 15 days (Fig. 10g). Because the larvae transported from Uto Peninsula to Tachibana Bay already reached the decapodid stage when they arrived at the bay, the supply rates from the tidal flats No. 16 to No. 20 to the tidal flats in Tachibana Bay were very small.

Figure 13 shows the larval reception rate by each tidal flat in Tachibana Bay and Ariake Sound. The *N. harmandi* local populations in Tachibana Bay mainly depend on the larval supply from the Tomioka tidal flat. The self-supply rate of tidal flats along the southern

coastline of Shimabara Peninsula in Tachibana Bay (No. 2 to No. 5) is less than about 6%. The populations on the northern tidal flats along the southern coastline of Shimabara Peninsula in Tachibana Bay (No. 2, 3) depend on the larval supply from the Tomioka tidal flat. By contrast, those on the southern tidal flats (No. 4, 5) depend on the larval supply from the southern coastline of Shimabara Peninsula in Ariake Sound (No. 21 to No. 25). The populations on the tidal flats along the northern coastline of Tachibana Bay (No. 6, 7) and the western coastline of Tomioka Peninsula (No. 8) are maintained by both the self-return and the supply of larvae from the Tomioka tidal flat.

The population of the tidal flat on the northeastern corner of Amakusa-Shimoshima Island (No. 9) depends on the larval supply from other tidal flats in Tachibana Bay and Ariake Sound. This is because that the northeastern corner of Amakusa-Shimoshima Island lies near Hayasaki Straits. Therefore, the self-supply rate here is less than about 0.1%.

The *N. harmandi* larvae supplied to the tidal flats along the southern coastline of Shimabara Peninsula in Ariake Sound (No. 21 to No. 26) come from those on the eastern coastline of Amakusa-Shimoshima Island, the northern coastline of Uto Peninsula, the Tomioka tidal flat, as well as through self-return. Larvae are transported from Uto Peninsula to the southern part of Shimabara Peninsula in Ariake Sound after 15 days, during which time they are transported slowly by the diffusivity (Fig. 10g). After 15 days, the larvae are positioned mainly in the lower layer, as they have reached the decapodid stage. Therefore, these larvae are unlikely to be transported toward Tachibana Bay.

The mutual supply and reception relationship of *N. harmandi* larvae exists between the tidal flats along the eastern coastline of Amakusa-Shimoshima Island (No. 10 to No. 15) and those along Uto Peninsula (No. 16 to No. 20). However, the degree of mutual dependence is not so high, as (1) larvae are exchanged by the diffusivity of tidal current shear between these tidal flat groups and (2) each local population group is mainly self-maintained. The self-supply rate of these tidal flat groups

becomes high, because currents around these area are small, and a substantial part of the larvae was retained through 15 days around the area.

Figure 14 shows the larval connection network of *N. harmandi* among the 26 main local populations on their tidal flats in Tachibana Bay and Ariake Sound. The white arrows represent larval supply from the Tomioka tidal flat to other tidal flats in Tachibana Bay and Ariake Sound. The Tomioka tidal flat population is the main source of larval supply. Its population fluctuation would be transmitted to the populations on the tidal flats along the southern coastline of Shimabara Peninsula in Tachibana Bay (No, 2 to No. 5), the northern coastline of Tachibana Bay (No. 6, 7), the western coastline of Tomioka Peninsula (No. 8), the northeastern corner of Amakusa-Shimoshima Island (No. 9), and the southern coastline of Shimabara Peninsula in Ariake Sound (No. 21 to No. 26). Although the tidal flats along the eastern coastline of Amakusa-Shimoshima Island (No. 10 to No. 15) supply larvae to the Tomioka tidal flat, they do not receive larvae reciprocally. The tidal flats along the northern coastline of Uto Peninsula (No. 16 to No. 20) do not mutually exchange larvae with the Tomioka tidal flat. They supply larvae to the tidal flats along the southern coastline of Shimabara Peninsula in Ariake Sound (No. 21 to No. 26) which have the mutual relationship with the population on the Tomioka tidal flat. The population fluctuation on the Tomioka tidal flat would not be transmitted to the tidal flat populations along Uto Peninsula. The latter could supply larvae to the Tomioka tidal flat indirectly through the tidal flats along the southern coastline of Shimabara Peninsula in Ariake Sound.

6. Summary and perspective

It was revealed that the connection network of *N. harmandi* larvae among the 26 main local populations in Tachibana Bay and Ariake Sound was centered on the Tomioka tidal flat population. The tidal flat populations in the region were subdivided into four groups. The first group (Nos. 2 to 5, 9, 21 to 26) has a strong larval supply and reception relationship
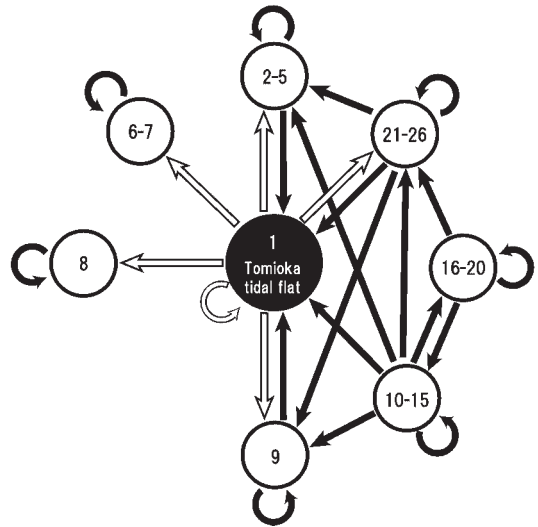

Fig. 14 Larval connection network of *Nihonotrypaea harmandi* among the 26 main tidal flat populations in Tachibana Bay and the outermost one-third of Ariake Sound. Arrows indicate direction of larval supply. See Figs. 9 and 11 for the location of tidal flats.

with the Tomioka tidal flat population through the larval transport path connecting Ariake Sound and Tachibana Bay, in which the residual flow offshore of Shimabara Peninsula flows toward Tachibana Bay in the upper layer and toward opposite direction in the lower layer through Hayasaki Straits. The second group (No. 6 to 8) receives larvae only from the Tomioka tidal flat. The third group (No. 10 to 15) acts as a source of larvae to the first group. The fourth group (No. 16 to 20) is related to the Tomioka tidal flat population only indirectly.

GRIMM *et al.* (2003) classified the configuration of the local populations comprising a metapopulation of marine benthos into five types. The larval supply and reception network of *N. harmandi* in the present study seems to most approximate their "mainland-island" configuration, with the Tomioka tidal flat population acting as the mainland. However, the population fluctuation on the Tomioka tidal flat is unlikely to be transmitted to the populations on 42% of the main tidal flats in Tachibana Bay and Ariake Sound (No. 10 to No. 20). When the Tomioka tidal flat

population declines, it could be recovered by an effective larval supply from these tidal flats. The populations on these tidal flats would be maintained by self-supply. These processes could contribute to the long-term stability of the *N. harmandi* population in Tachibana Bay and Ariake Sound. In the future, the larval connection network depicted in this study could be examined by analyzing genetic markers of the local populations. From this point we might go on to an even more detailed examination of the relation between Tomioka tidal flat and the third and fourth groups.

Acknowledgements

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