Mesocosm experiment on the succession of microbial community in response to oil contamination to coastal seawater.

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Abstract: The influence of oil contamination on marine bacterial communities was examined with a pair of meso-scale tanks filled with 5 tons of surface seawater from a semi-enclosed bay, Hamana-ko, Japan. One of the tanks was contaminated with the water-soluble fraction of Rank-A residual oil, while the other was kept uncontaminated for comparison. Surface seawater in the two tanks was periodically taken to monitor microbial abundance and community structure. Bacteria in the oil tank proliferated within a day, which was followed by an increase in viral abundance. Then, the number of bacterial cells and viral particles returned to the initial levels within three days. Denaturing gradient gel electrophoresis of bacterial 16S-rDNA amplicon showed distinctive differences in band patterns between the oil and control tanks. The following conclusions can be made from the experiments. The succession of oil-exposed microbial community was made up of three steps, as follows: (i) Bacteria increased in number within a day with a slight increase of 16S rDNA sequence types. (ii) After three days, bacterial cell numbers returned to the initial levels, but sequence types increased to the maximum. (iii) Finally, bacterial numbers stayed put with the decline in sequence types.

Keywords: oil pollution, marine bacteria, mesocosm and DGGE

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1. Introduction:

Oil pollution in the ocean, which ruins the spot area and inflicts a loss of marine resources on the neighboring environments, is one of the most devastating disasters caused by human activities. In aquatic environments, some oil compounds are well known as toxic to plants and animals (Albers, 1995). In addition, it has been evident that polycyclic aromatic hydrocarbons (PAHs) exhibited the effect of growth inhibition upon marine and freshwater microalgae (Okumura *et al.*, 2003; Djomo *et al.*, 2004).

Part of these aromatics are finally doomed to be broken down and transformed into non-toxic forms through the processes of microbial degradation. As hydrocarbon degradation hinges on enzyme activities of indigenous oil-degraders and on environmental imbalances, such as, oxygen, nitrogen, phosphate, temperature, salinity levels (Leahy and Colwell, 1990;

ATLAS and BARTHA, 1992), it is important to understand relationship between microbial populations and hydrocarbon degradation activities under natural environmental conditions upon oil degradation in the ocean. Mesocosm has been considered suitable for monitoring the impacts of oil-contamination upon aquatic microbes because it impounds fairly large amounts of water, which include all sorts of microbial assemblage playing the leading part of primary production and catabolism of organic substances (LACAZE, 1974; BAK and NIEUWLAND, 1987; DELILLE and SIRON, 1993; MAKI *et al.*, 1999). By using 5-ton-capacity mesocosm tanks, we examined the fate of soluble fractions of discharged rank-A heavy oil, the chemical fate of toxic constituents, and their effects upon marine coastal organisms (OHWADA *et al.*, 2003; YAMADA *et al.*, 2003). It has been shown in the previous report that bacterial growth rates quickly accelerated in response to the oil contamination, and their abundance and growth rates appeared to vary with the growth of other trophic levels (TOYODA *et al.*, 2005). Although biomass fluctuation of microbes was disclosed in previous studies, little was known about the effect of oil contamination in seawater on the structure of microbial community. In our most recent survey on microbial community change, a Denaturing Gradient Gel Electrophoresis (DGGE: MUYZER *et al.*, 1993) and multidimensional scaling analysis has been undertaken (YOSHIDA *et al.*, 2006).

In this experiment, the microbial community change was simply deduced from the band numbers of 16S rDNA sequence types. The impact strength of oil pollution and other biological factors controlling microbial community structure were discussed.

2. Materials and Methods:
2.1 Mesocosm experiment:

Meso-scale experimental tanks were built on the seaside of Hamana-ko, a semi-enclosed bay located on the Pacific coast of central Japan. Details of the mesocosm facilities have previously been shown (OHWADA *et al.*, 2003). First, seawater was pumped from the surface water of Hamana-ko into the two reservoirs.

Secondly, the reserved seawater was equally distributed to two experimental tanks. Tank tops were covered with transparent acrylic plates to let the sunlight in. Before conducting a series of experiments, it was confirmed that general environmental conditions among four experimental tanks did not show any remarkable differences. The present experiment was conducted from Oct. 26 to Nov. 6 in 2000. For the microbial experiments shown herein, water samples were collected periodically from days (0, 1, 2, 3, 4, 5, and 6). Water samples for genetic analysis were collected on Day 1, Day 3 and Day 6. The reservoir water of Day 0 was also taken for comparison. The experiment was further carried out for chemical analyses (data not shown).

2.2 Preparation of water-soluble fractions of heavy oil and operation of experimental tanks:

Rank-A heavy residual oil was obtained through the courtesy of Showa-Shell Co. Water-soluble fractions were prepared by mixing the oil vigorously at 800 rpm with a twenty-fold volume of seawater for two hours. The water-oil mixture was held stationary for an hour. Then thirty liters of water soluble fraction were poured into one of the experimental tanks, and then the tank water was stirred with the blades until the added oil became well mixed. We envisioned the mesocosm designed to simulate a slight oil pollution, which can be seen in a port facility and littoral industrial zone. Further information on the oil pollution level is contained in the previous report (OHWADA *et al.*, 2003). The other tank stayed uncontaminated to work as a negative control. This experiment was conducted, in the first place, with the aim of examining antiproliferative effect of oil components. The experimental tanks were amended with KNO_3 and K_3PO_4 at $720mg/m^3$ and $44mg/m^3$ respectively so that nutrient deficiency could not be a growth limiting factor in surface water enclosed.

2.3 Determination of salinity, temperature, dissolved oxygen and chlorophyll *a*:

A portable STD system (YSI Model 610-DM) was used to obtain vertical profiles of salinity, temperature, and dissolved oxygen. Water was

sampled at a 50-cm depth and pumped into bottles with a handmade sampler assembled by stainless pipe and Tefron tubing. Fifty-milliliters of water were filtered through a glass fiber membrane (GF/F). Then the pigments were extracted in N, N-dimethylformamide (SUZUKI and ISHIMARU, 1990), and chlorophyll a concentrations were measured using a Turner-designed fluorometer.

2.4 Bacterial and viral counts:

Microscopic examination revealed bacterial and viral abundance in the water sampled at a 50-cm depth. Ten-milliliter samples were fixed with formalin at the final concentration of 2 % (vol/vol). Bacteria were stained with DAPI according to the method by PORTER and FEIG (1980). Then, they were concentrated on a 0.2 μm-pore black filter, and enumerated on epifluorescence microscopy (Nikon Eclipse E-800). Dividing cells were differentiated and enumerated in the same field of vision, thereby estimating frequency of dividing cells (FDC). Another ten milliliters were fixed with 2% of formalin for viral particle count. Viral particles were stained with SYBR Green-I, concentrated on a 0.02 μm-pore filter and enumerated under the Nikon microscope (NOBLE and FUHRMAN, 1998).

2.5 PAH analysis:

Water sampled at a 50-cm depth was filtered with a pre-baked glass fiber filter (GF/F, Whattman). Solid-phase extraction of oil components were performed by using a disposable column (SEP-PAK C18 plus environmental cartridge, Waters). Extracts were further purified and fractionated through an activated silica gel column and oil components were finally obtained. All the oil components were analyzed by means of gas chromatography and mass spectrometry (GC-MS) as has been previously reported (YAMADA et al., 2003).

2.6 DNA extraction and Denaturing Gradient Gel Electrophoresis (DGGE):

One liter of water sampled at a 50-cm depth was pre-filtered with a 5.0 μm-pore polycarbonate filter and introduced into a cylindrical filter unit (Sterivex-GS : Millipore Corp.). Bacterial concentration and subsequent DNA extraction were performed by the method

of SOMERVILLE et al. (1989) with modification of STEWARD and AZAM (1999). Two primers, GC341F and 907R were used for DGGE analysis (MUYZER et al., 1995). Gene segments of bacterial 16SrDNA were amplified by using HS-taq polymerase (TAKARA Inc.) according to the supplier's instruction. A hot-start and touch-down PCR was performed as follows. In the first 19 cycles, the annealing temperature was initially set at 65℃ and decreased 0.5℃ every cycle. Then it was set at 55℃ for a further 9 cycles. Cycling was followed by 10 min of incubation at 72℃. PCR product concentrations were determined by means of fluorodensitometry, and 250ng of the product was loaded onto an each lane of the DGGE gel. The DGGE fingerprinting was carried out on the Dcode system (BIO-RAD Inc.) according to the manufacturer's instruction and previous reports (MUYZER et al. 1993; SCHAFER et al. 2000). Gel images were captured with a FLA 2000 and analyzed by using a Science lab 2001 (FUJIFILM Inc.).

3. Results and Discussion:
3.1 Environmental and microbial parameters

The temperature dropped from 21℃ to 19℃ due to a cooling of cold north winds during the 7-day experiment. Salinity was rather constant (ca. 30.5). Figure 1 summarizes changes of dissolved oxygen, chlorophyll a, PAHs, FDC, bacterial cells and viral particles. Dissolved oxygen in the oil tank gradually decreased up to 4mg/liter, whereas that of the control tank remained constant (Fig.1-A).

Oil components decreased quickly during the first two days. Changes of two major low molecular oil components, naphthalene and phenanthlene, are shown in Fig.1-B. Alkans decreased in the same way as naphthalene and phenanthrene. Hopane, a representative indecomposable component, decreased to 70% of the initial amount in the first day, and to 40% after five days (data not shown). The concentration of chlorophyll a in the oil tank rose dramatically and dropped after Day 3, while in the control tank showed a bimodal increase and reached a peak value of 5.7mg m^{-3} on Day 6 (Fig.1-C). Nutrient assays revealed that dissolved inorganic nitrogen, phosphate and
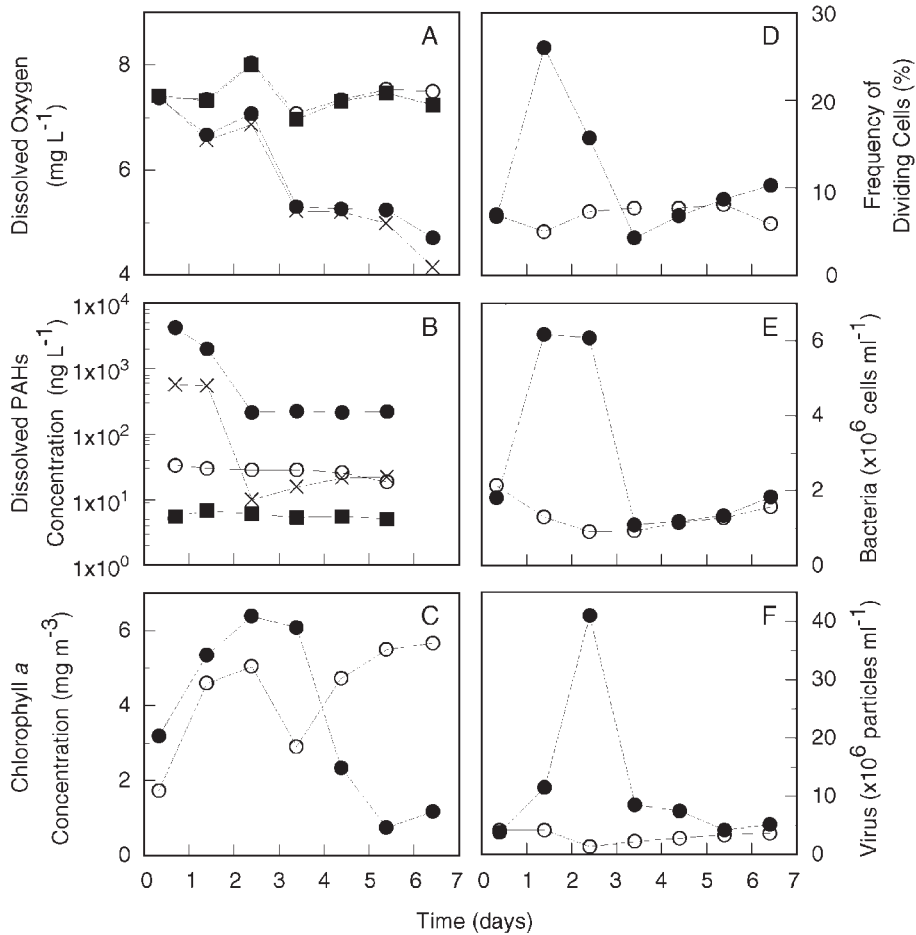
Fig.1 Time courses of environmental and microbial parameters in oil and control tanks

Panel-A: Dissolved oxygen measured at the surface and near the bottom of tanks

   (○) control tank_ 0.5m deep, (●) oil tank_0.5m deep, (■) control tank_2.5m deep, (×) oil tank_2.5m deep.

Panel-B: Dissolved PAHs concentration in water samples collected at 0.5m

   (○) control tank_ naphthalene, (■) control tank_phenanthrene, (●) oil tank_naphthalene,

   (×) oil tank_phenanthrene.

Panel-C: Chlorophyll *a* concentration in water samples collected at 0.5m

   (○) control tank_0.5m, (●) oil tank_0.5m.

Panel-D: FDC in water samples collected at 0.5m

   (○) control tank_0.5m, (●) oil tank_0.5m.

Panel-E: Bacterial cells in water samples collected at 0.5m

   (○) control tank_0.5m, (●) oil tank_0.5m.

Panel-F: Viral particles in water samples collected at 0.5m

   (○) control tank_0.5m, (●) oil   tank_0.5m.

Dotted lines represent the time of oil addition

silicate stayed high, over the lapse of the ex-
periment (data not shown).　This result im-
plies that the algal fall had nothing to do with
nutrient depletion. In the oil tank, there was a
considerable increase in the number of bacterial

cells and viral particles and the FDC percent-
age, while no remarkable changes were found
in the control tank. Then, the number of bacte-
rial cells and viral particles and the FDC per-
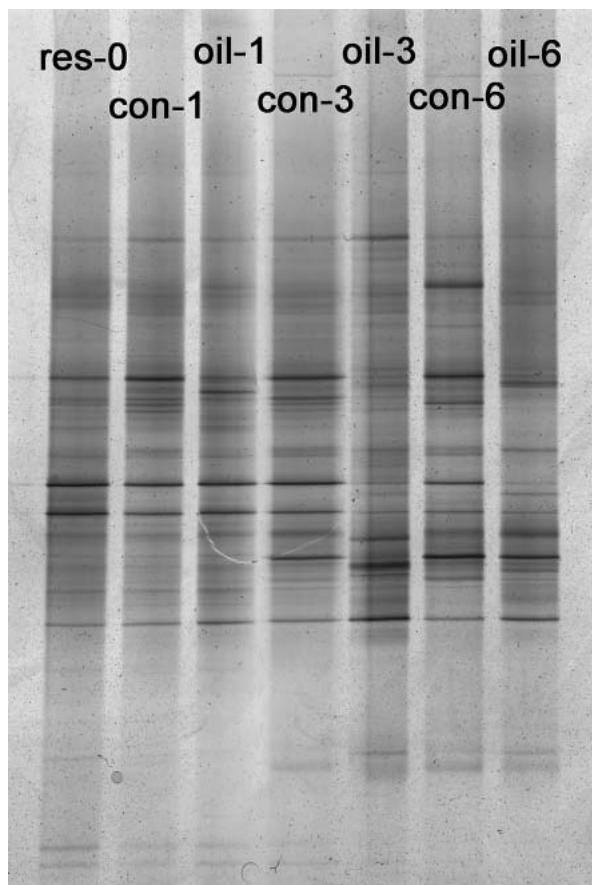centage returned to the initial levels within

Fig.2 Gel image of DGGE analysis of 16S rDNA fragments amplified from water samples collected from oil and control tanks
res-0; reservoir of Day 0.
con-1; control of Day 1. oil-1; oil-contaminated of Day 1.
con-3; control of Day 3. oil-3; oil-contaminated of Day 3.
con-6; control of Day 6. oil-6; oil-contaminated of Day 6.

three days, respectively (Figs. 1-D, 1-E, 1-F). If we consider a rapid decrease in dissolved oxygen in the oil tank was caused by microbial activity during the decomposition of major oil components, a big difference of dissolved oxygen between the two tanks (Figs. 1-A, 1-D, 1-E) is reasonable. We also infer from the figures 1-B and 1-D that the oil components would have been utilized, as a carbon source for the bacterial growth. Viral particles proliferated one day later than bacterial growth in the oil tank (Fig.1-E, 1-F). It is difficult at the present time to determine whether those viruses were algae-infectors or bacteriophages, as we did not conduct culture experiments to confirm the host

organisms.

3.2 DGGE analysis of microbial community structure during oil contamination

Figure 2 shows the band patterns of DGGE analysis. The three lanes from the left (res-0, con-1 and oil-1) show little difference in the band patterns. This suggests that the microbial community structure in experimental tanks did not substantially change during the 24 hours after the introduction of oil components. Although a drastic increase of bacterial cells took place up to Day 1 (Fig. 1), a major change of the microbial community appeared after a delay of a few days (Fig. 2; con-3 and
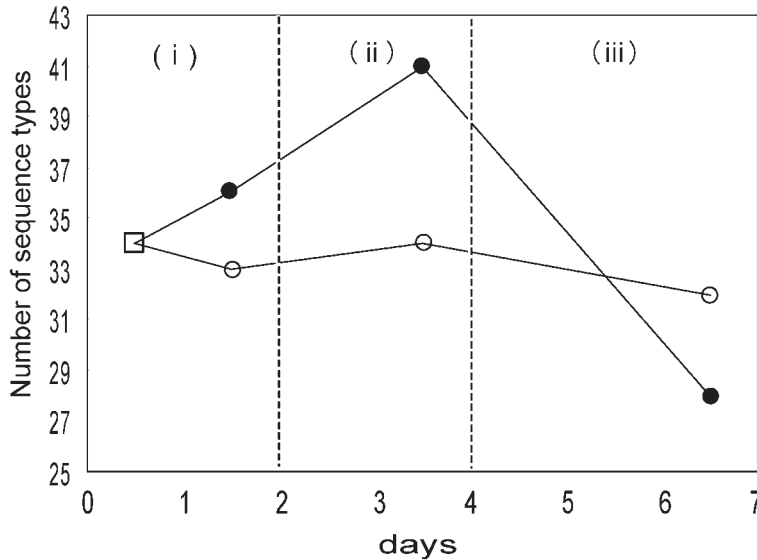
Fig.3 Changes of the number of sequence types on the basis of DGGE analysis shown in Fig.2
(◯) control tank, (●) oil tank. (☐) Day-0 reservoir tank.
Microbial change of each phase(ⅰ,ⅱ,ⅲ) are mentioned in the last paragraph of the text.

oil-3). This phenomenon was observed again in the following experiment conducted in 2001 (YOSHIDA *et al.*, 2006). The fact that the increase of bacterial cell number was not coincident with the change of the DGGE band patterns suggests that the fast-growing oil degraders were composed of a few limited numbers of species.

Figure 3 shows the number of bands visible in each sample lane of the DGGE gel. The band number in the oil tank reached up to 41 on Day 3, and decreased to 28 at the end of the experiment, while in the control tank, it ranged from 34 at the start, and to 32 at the end. This implies that the growth rate of other groups of bacteria in the oil tank was also accelerated during the 2nd and 3rd days, and several species of bacteria present in the tank disappeared after Day 3.

In conclusion, it seems reasonable to consider that the fluctuation of oil-exposed microbial community was made up of three steps as follows: (ⅰ) Bacteria proliferated and increased in number quickly within a day with a slight increase of 16S rDNA sequence types. (ⅱ) After a few days of the experiment, bacterial numbers returned to the initial level, but the sequence types increased to the maximum. (ⅲ) Then bacterial numbers stayed put with the decline of sequence types.

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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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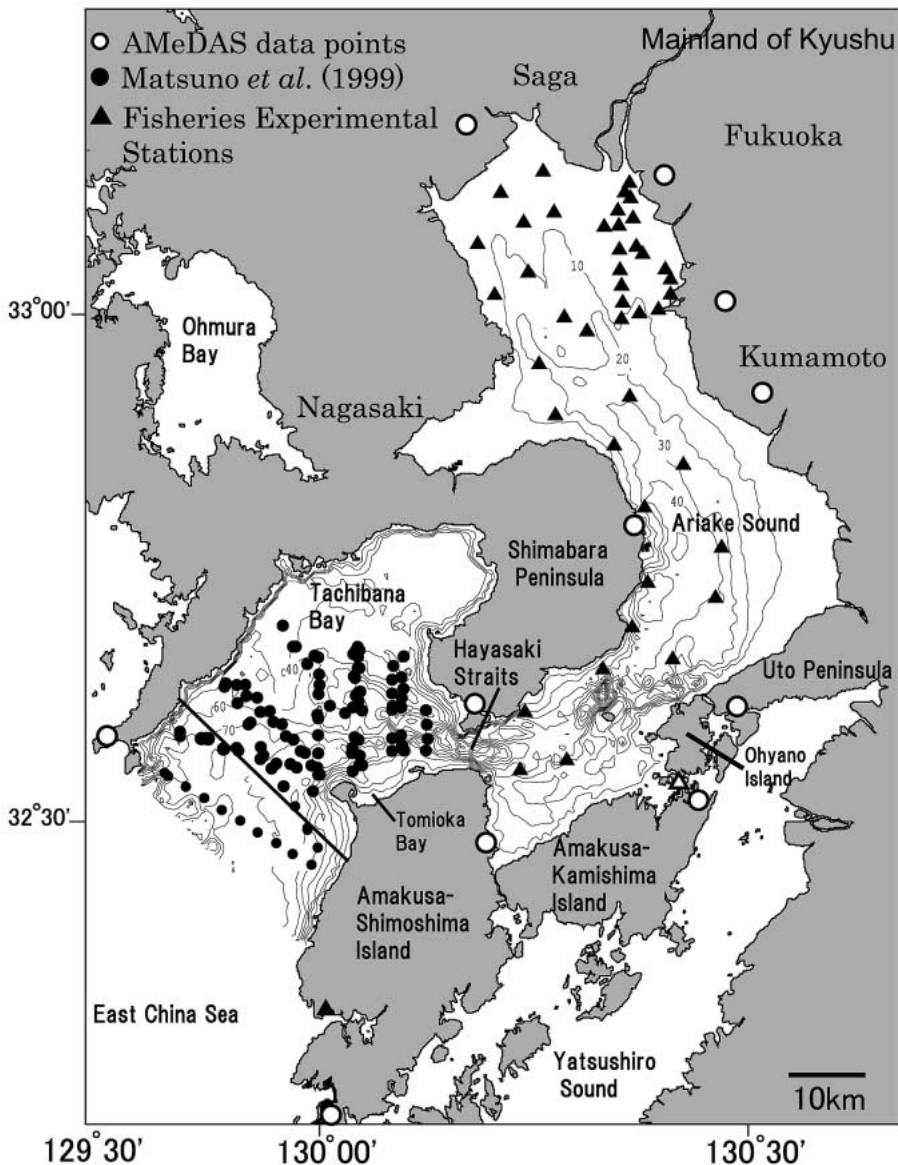
Fig. 1 Model area with bathymetry in the Ariake Sound estuarine system spanning from Ariake Sound, via
        Tachibana Bay, to the coastal waters of the East China Sea. The depth contour interval is 10 m. Black cir-
        cles, white circles and black triangles are the observation points by Matsuno *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
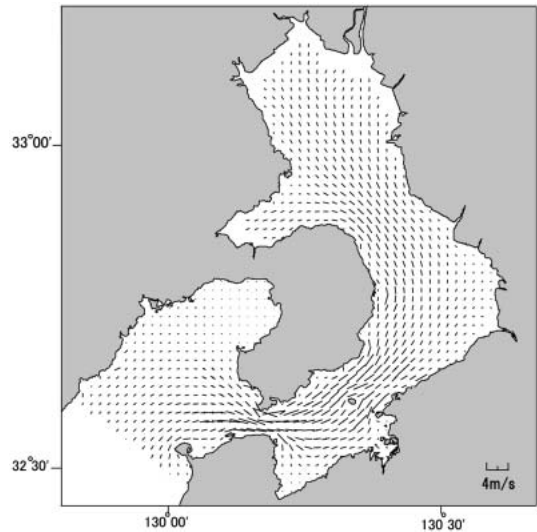
TSUKAMOTO and YANAGI (2002) calculated

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
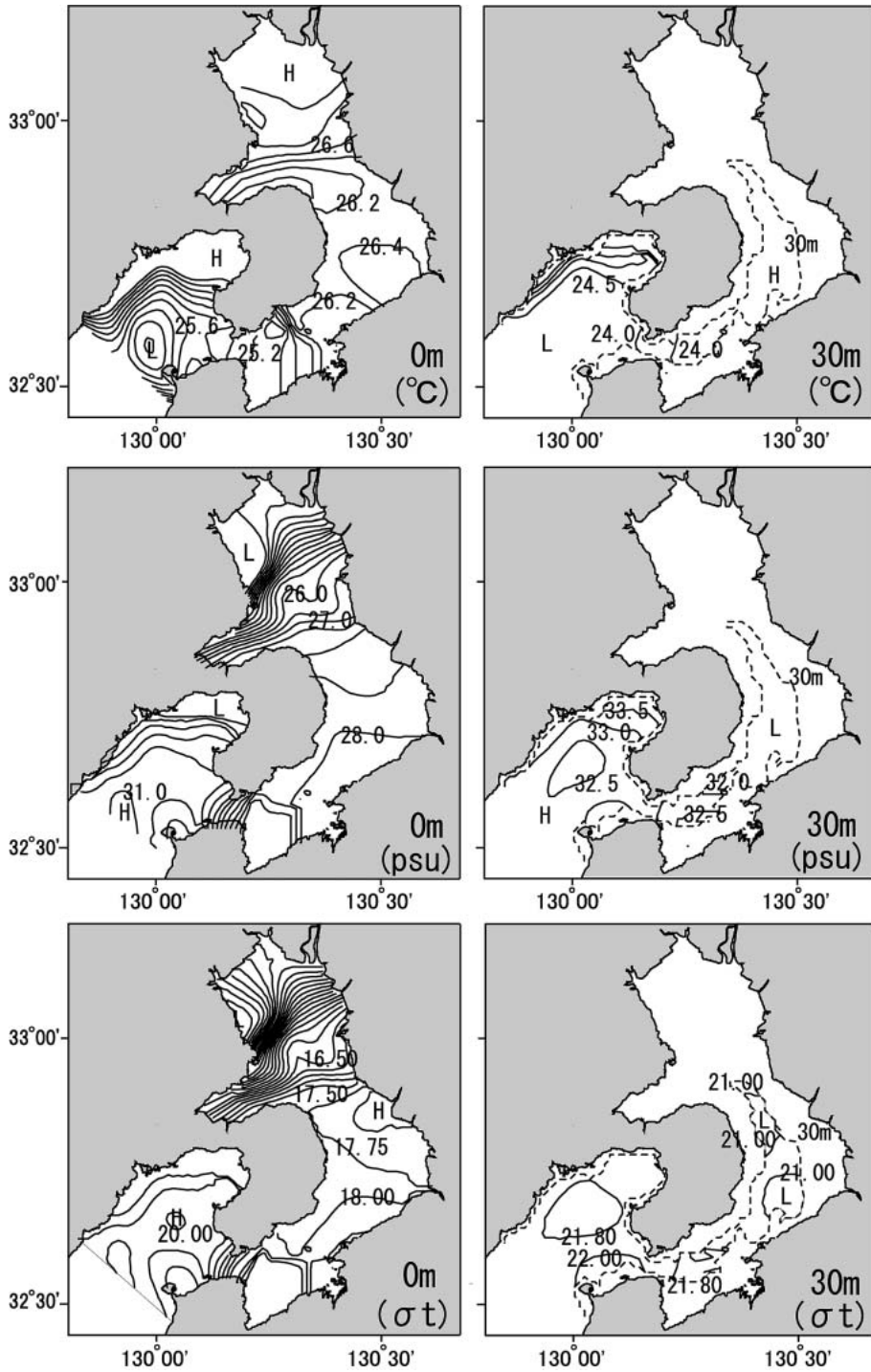
Fig. 3 Horizontal distributions of temperature (upper), salinity (middle), and density (lower) at 0-m and 30-m depths. Broken lines represent the isobath lines of 30-m depth in the study region (after FUJIIE *et al.*, 2004).

(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
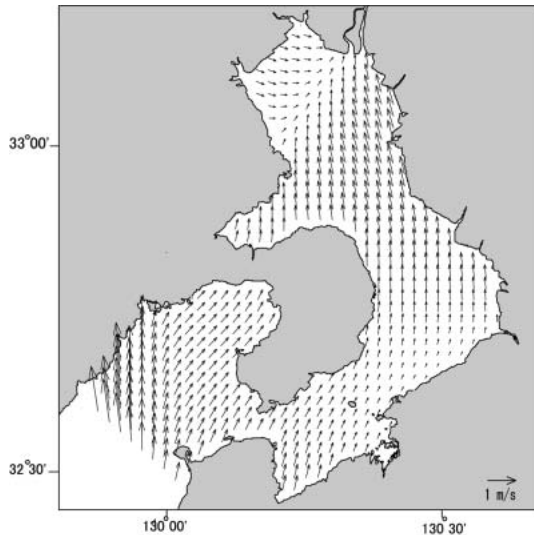

Fig. 4 Horizontal distribution of wind vectors in August 1993 in the study region (after FUJIIE *et al.*, 2004).

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-
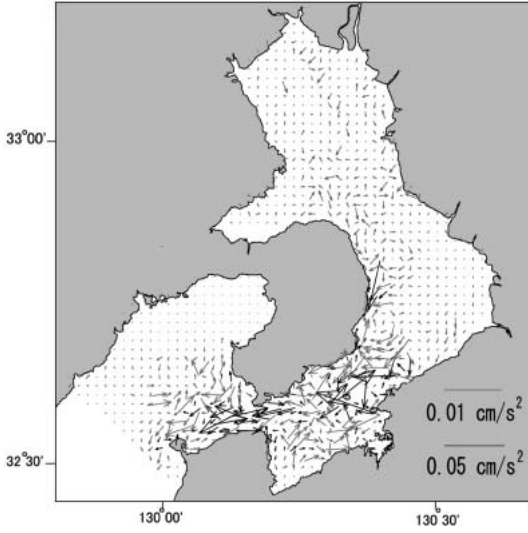
Fig. 5 Horizontal distribution of calculated tidal stress vector in the study region (after Tsukamoto and YANAGI, 2002). Note the two kinds of vectors with different units.

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 southern 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 calculations in FUJIIE et al. (2004) agreed well with the observations in MATSUNO et al. (1999) conducted 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 current 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 vertically depending on their developmental stage (SAITOU, 2002). The diurnal vertical migration of *N. harmandi* strongly influences their horizontal 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 vertical 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 nighttime. 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 calculated 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 eastward, northward and upward velocities, respectively, including the tidal current and residual
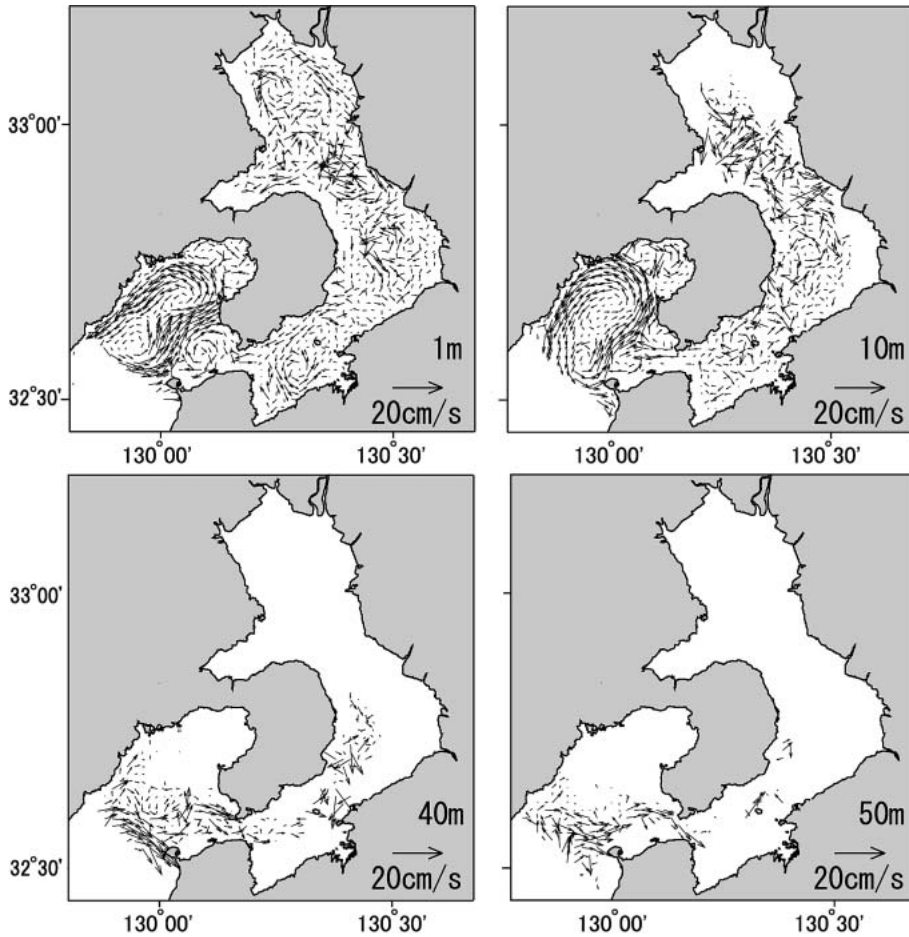
Fig. 6 Distribution of residual flows at 1-, 10-, 40- and 50-m depths in the study region (after FUJIIE *et al.*, 2004).

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
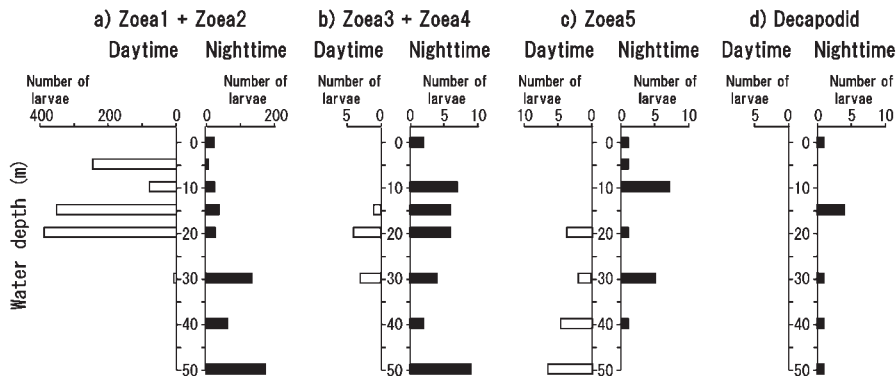
Fig. 7 Number of (a) combined Zoea 1 and Zoea 2 larvae, (b) combined Zoea 3 and Zoea 4 larvae, (c) Zoea 5 larvae, and (d) decapodid larvae of *Nihonotrypaea harmandi* per 5-min horizontal haul with a MTD net from 8 depth-layers (0m, 5m, 10m, 15m, 20m, 30m, 40m and 50m) off Tomioka Bay around daytime 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
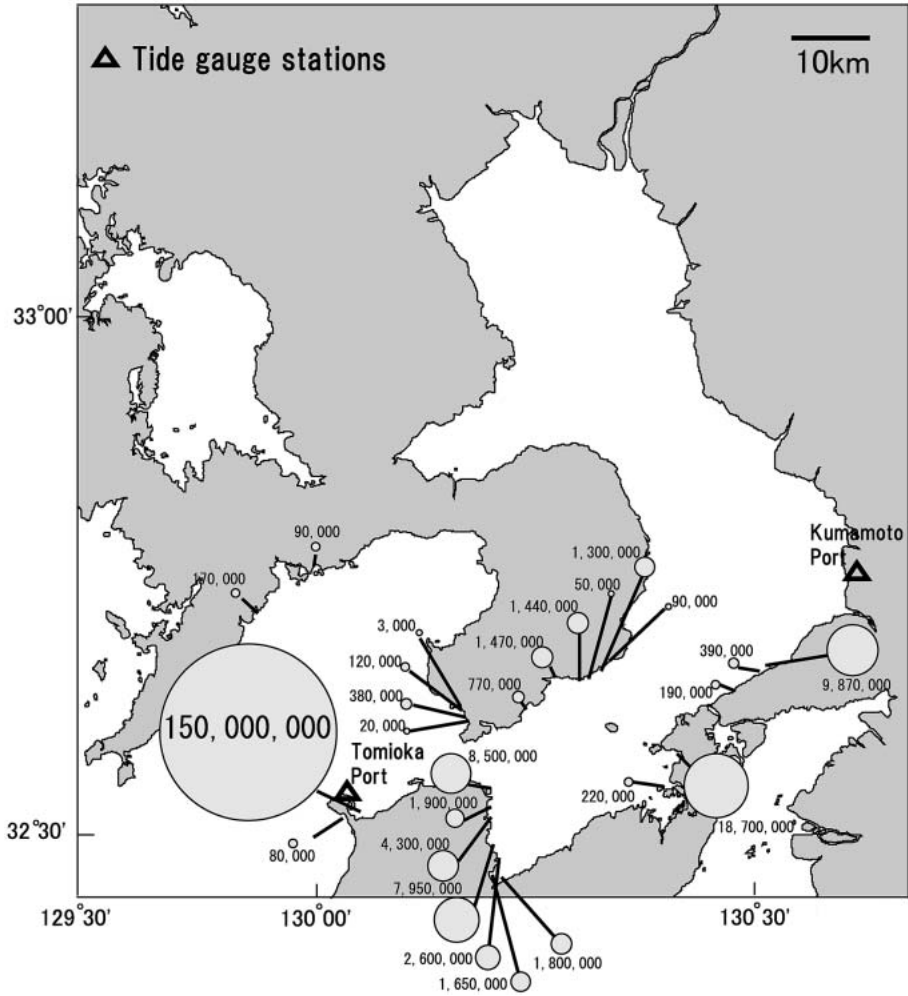
Fig. 8   Local population size of *Nihonotrypaea harmandi* on 26 intertidal sandflats in Tachibana Bay and the outermost one-third of Ariake Sound (after TAMAKI and Harada, 2005). The tide gauge stations at Kumamoto Port and Tomioka Port are shown with triangles.

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 km^2) of the Tomioka tidal flat is much larger than those of the other tidal flats (0.01–0.2 km^2) 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
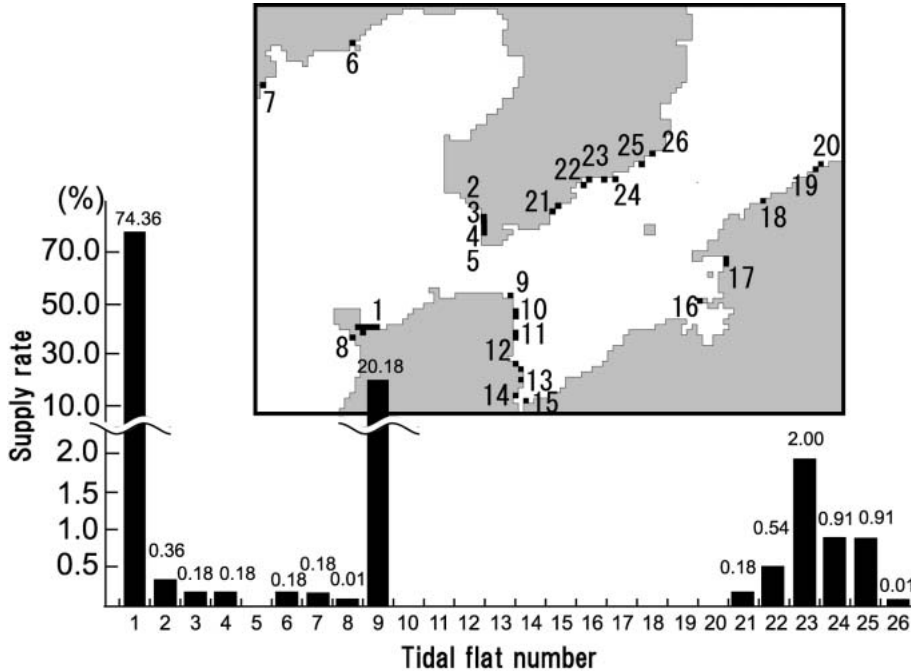

Fig. 9   Supply rate of *Nihonotrypaea harmandi* larvae from the Tomioka tidal flat to each tidal flat in the study region. The black squares with the serial numbers on the inset map stand for the tidal flats with *N. harmandi* indicated in Fig. 8. See text for the definition of supply rate.
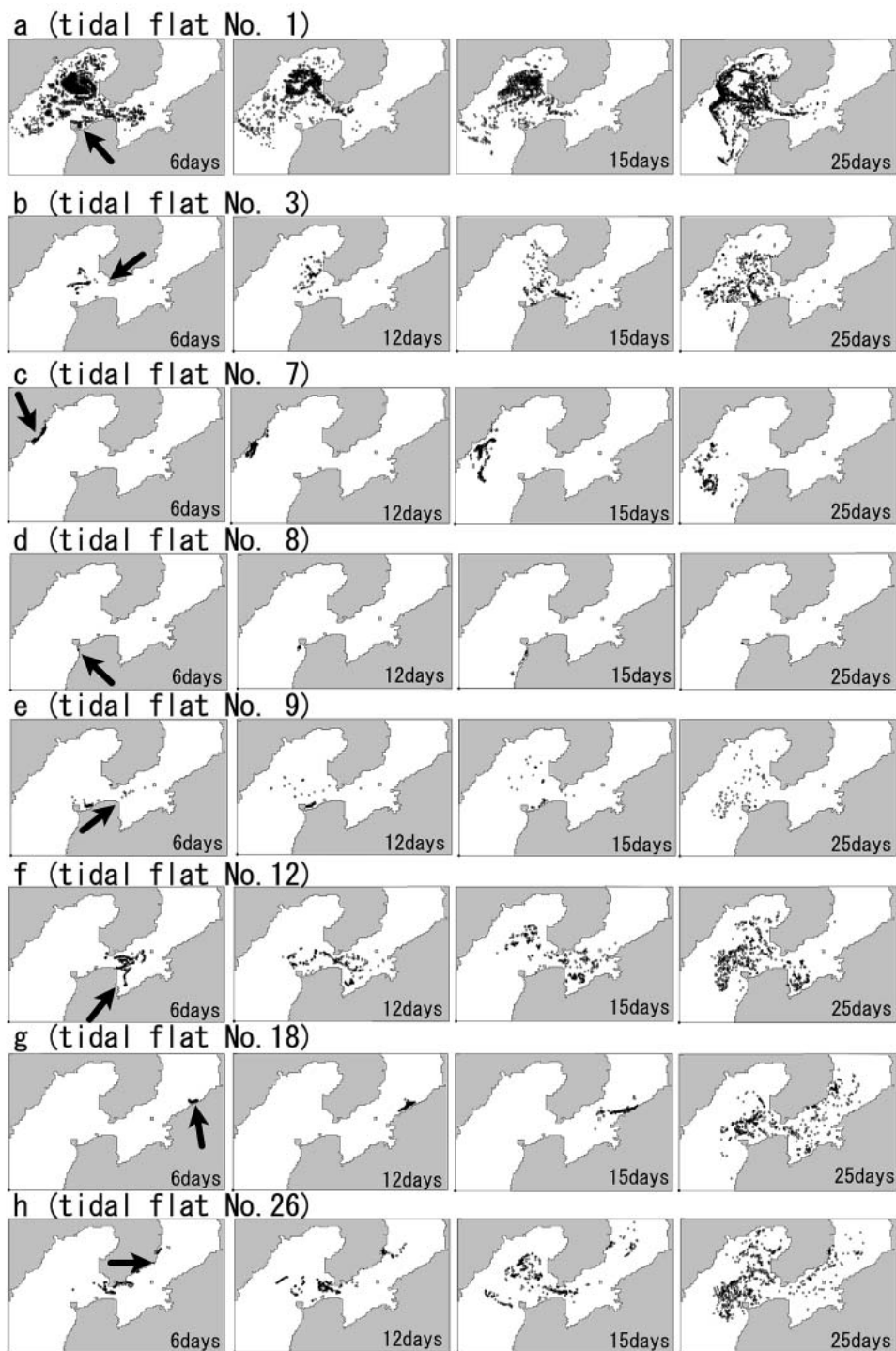
Fig. 10   Time course of calculated horizontal distributions of *Nihonotrypaea harmandi* larvae 6 to 25 days after being released from the populations on eight representative tidal flats (arrows) in the study region. The tidal flat numbers correspond to those given in Figs. 9 and 11.
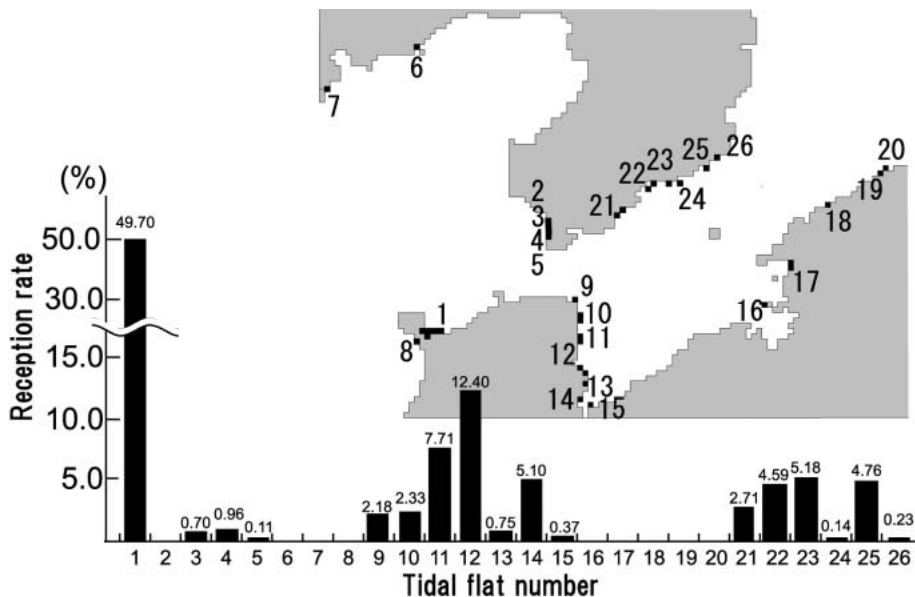
Fig. 11 Reception rate of *Nihonotrypaea harmandi* larvae by the Tomioka tidal flat from each tidal flat in the study region. The black squares with the serial numbers on the inset map stand for the tidal flats with *N. harmandi* indicated in Fig. 8. See text for the definition of reception rate.

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 contrast, in the area enclosed by the eastern coastline of Amakusa-Shimoshima Island and the northern coastline of Amakusa-Kamishima Island, a uniform residual flow which flows from Shimabara Peninsula toward this area did not exist as shown in Fig. 6 (a), (b). This may explain the fact that there was no supply of larvae 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 transmitted 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 being only about 2%. It is expected that larvae released 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 upper 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
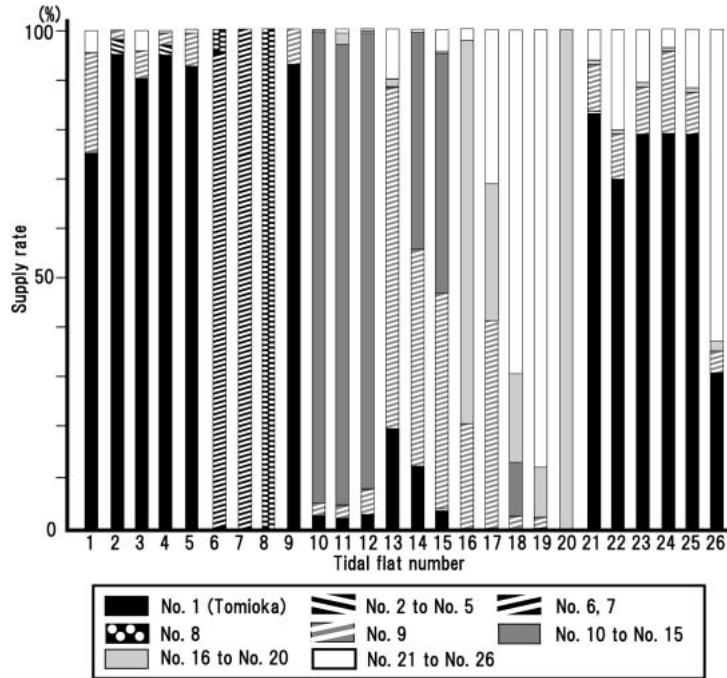
Fig. 12 Proportional supply rates of *Nihonotrypaea harmandi* larvae from each tidal flat to all tidal flats in the study region. The X axis indicates the source of larval supply to each tidal flat. See Figs. 9 and 11 for the location of tidal flats.
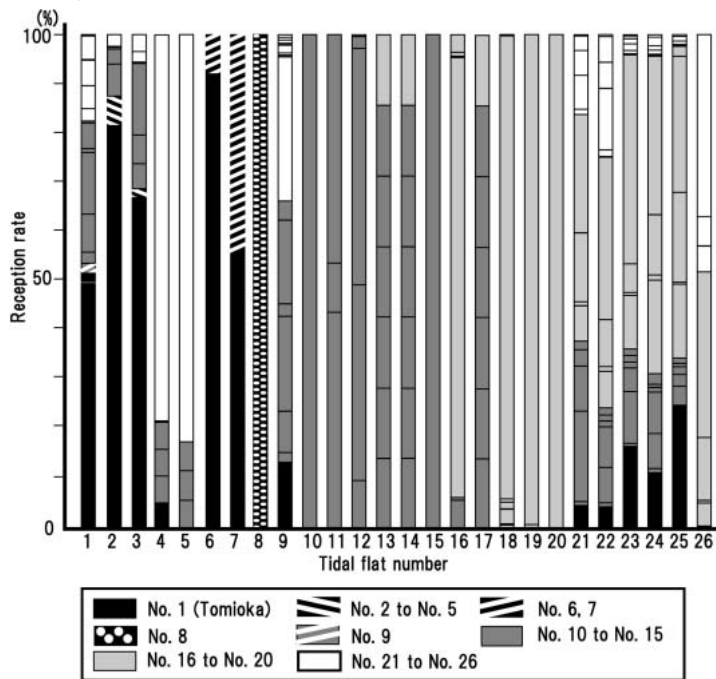

Fig. 13 Proportional reception rates of *Nihonotrypaea harmandi* larvae by each tidal flat from all tidal flats in the study region. The X axis indicates the destination for larvae released from each tidal flat. See Figs. 9 and 11 for the location of tidal flats.

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
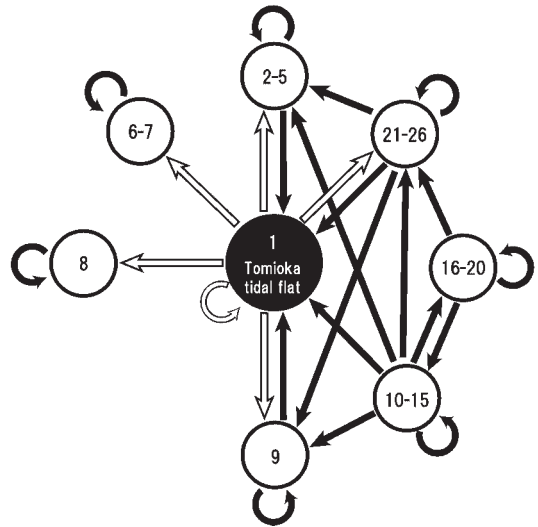

Fig. 14 Larval connection network of *Nihonotrypaea harmandi* among the 26 main tidal flat populations in Tachibana Bay and the outermost one-third of Ariake Sound. Arrows indicate direction of larval supply. See Figs. 9 and 11 for the location of tidal flats.

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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Fishing strategy for target species of small-scale fisheries in Pelabuhanratu Bay, Indonesia

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Abstract: In order to have better understanding of the gear employed in small-scale fisheries of Pelabuhanratu Bay, Indonesia, the fishing strategy for target species in relation with species composition and catch composition similarities of five types of gear were studied on monthly basis in a full year cycle. The result of the analyses showed that the fishing activity of fishermen in employed fishing gears related to seasonal pattern of fish landed. The species composition varied between seasons and fishing gear. During dry season, fishermen employed most fishing gear types, exploiting scattered fishing ground and capturing a greater diversity of fish species. In rainy season, catch were less diversified, and more specialized fishing gear (hand lines) were employed more intensively, harvesting hairtail. Using the information provided by the present study, fisheries management strategy was proposed

Keywords: fishing strategy, small-scale fisheries, species composition, Indonesia

1. Introduction

Small-scale fisheries, which dominate in developing countries, contribute more than 25 percent of the world catch (Food and Agriculture Oganization, 2001). The increasing number, type, size and efficiency of gears in small-scale coastal fisheries of developing countries have greatly increased the fishing pressure on the available fish stocks. In Indonesia, small-scale/artisanal fisheries contributed 94% to the total fishing unit. Since mechanization, modernization and use of other fabricated inputs are taking place, small-scale fisheries are growing steadily in number (Purwanto, 2003). Like in other developing countries, the rapid expansions of small-scale fisheries in Indonesian fisheries have been facing difficulties with problems concerning overcapacity and with excessive effort capacity (Berkes et al., 2001). Several parts in Indonesian waters, especially the western parts of Indonesian waters of highly populated region like northern Java and eastern Sumatra coasts were identified to be affected by overcapacity and are over-exploited (Mous et al., 2005). Fisheries productivity has been decreasing, resulting in increasing levels of impoverishment among small-scale fishers.

Despite the social and economic importance of Indonesian small-scale fishery, there has been no comprehensive analysis of its major features (e.g., species composition in relation to fishing strategy and catch composition similarities between gear types). Most previous studies conducted were academic in nature and peripheral to the management questions at hand (Silvestre and Pauly, 1997). In the case of multispecies-multigear fisheries especially in tropical small-scale fisheries, fisheries management is more complicated and difficult (Food and Agriculture Organization, 1994, Pauly, 1979). This is

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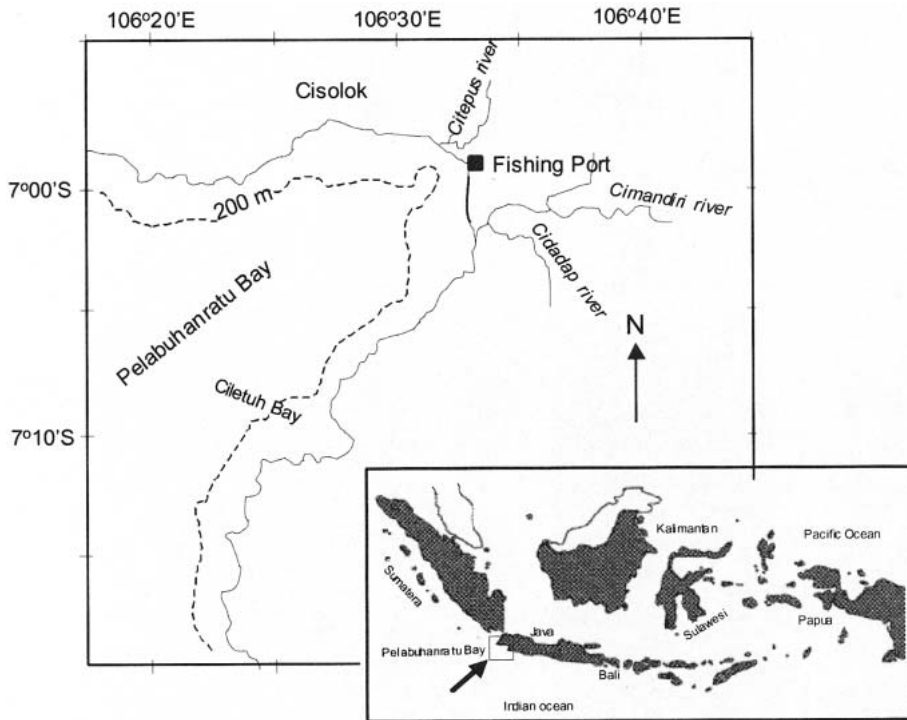Email: eko_ipb@yahoo.com

Fig. 1. The map of study area

because diversity of gears (multi-gear) that be used to capture diverse target species (multi-species) in tropical coastal fisheries has caused ecological and technological interactions (RIJNSDORP *et al.*, 2000 and ULRICH *et al.*, 2001). In this fisheries, two or more competing or prey-predator species constitute the target species of different fisheries would change the magnitude and direction of the ecological interaction and relative abundance of species and trophic level. In addition, the dynamics of fishing effort could change the population structure, dynamics of the target species and associated bycatch, imposing the negative effect to other fishers and affecting the abundance of incidental species (SEIJO, DEFEO and SALAS, 1998). The gear type employed can affect the efficiency of fish capture, the selectivity and composition of fish resources (STERGIOU, PETRAKIS and POLITOU, 1996). Moreover, the high intensity in capturing top predator (e.g. grouper) by small-scale fisheries has lead to fishing down the food web (PAULY, PALOMARES, FROESE, SA-A, VAKILY, PREIKSHOT and WALLACE, 2001). It has been

noted that small-scale fisheries activities have been correlated to reductions in the biomass, abundance, and individual sizes of target fish.

In the present study, fish catch in relation to fishing strategy in the small-scale fisheries of Pelabuhanratu Bay was studied. The study site was chosen because the area shows the common characteristics of Indonesian small-scale and multi-species coastal fisheries. More precisely, the objective of this study is to study the catch compositions, catch abundance and catch composition similarities of gear types. This information would be useful for rational management of the excessive fishing effort in small-scale fisheries.

2. Materials and methods
2.1 Fishery in the study area

Pelabuhanratu Bay is a small bay facing the Indian Ocean on the southern coast of West Java, Indonesia, located at 6° 55′ and 7° 55′ S, and 106° 15′ E and 106° 35′ E (Fig. 1). The fishing activity in the bay is a multispecies-multigears tropical coastal fishery, which represent Indonesian fisheries. Based on the

statistical report of Pelabuhanratu Fishing Port 2002 (WIDODO, *et al.,* 2003), there are 9 main types of gears that are being operated in Pelabuhanratu Bay: hand lines (187 units), seine nets (85 units), inboard gillnets (124 units), lift nets (142 units), long lines (29 units), purse seine (6 units), drift gillnets (44 units), fixed gillnets (19 units) and trammel nets (39 units).

2.2 Source of data and pre-processing

The data used in this paper were based on the Local Fisheries Auction Centre of Pelabuhanratu Bay from 1993 to 2003. The data contained information per fishing boat at a trip level, including catch weights (kg) and values (Rp. Kg^{-1}) by species and gear types. Prior to data analysis, the data were already separated into small-scale coastal fisheries data and others. There is no single definition of what a small-scale fishery is and it varies between countries (PANAYOTOU, 1982). For the purpose of this study, we define small-scale fisheries as fisheries that do not use boats, or use of boat less than 10 gross tonnage (GT). Based on this working definition, this study was limited to five gears: drift gillnets, seine nets, fixed gillnets, lift nets and hand lines and their catch. The daily records of boat activity were extracted to obtain monthly data containing monthly aggregates on the gear level of landed of the species (kg month^{-1}) and monthly aggregates of the number of fishing trips (trips month^{-1}).

2.3 Data analysis

The analysis of catch composition was conducted both totally and separately for each fishing gear types. To express the seasonal dynamics of catch composition between seasons, catch composition are presented as the average weight (kg) of fish catch per gear types per month in a full year cycle.

Catch per unit effort (CPUE) was used to analyse the monthly productivity of gears on target species. This was done separately for each gear based on monthly catch and effort data of gears. Since fishing trips, which determined fishing intensity varied between fishing gears and months, we computed fishing effort by the number of monthly fishing trips of gears. With the assumption that the seasonal pattern of CPUE was not changing between years, the productivity of gear to target species was calculated as the average CPUE per month. A high CPUE indicates that the gears were productive in the capture of the target species, and vice versa.

We used cluster analysis to classify the monthly dynamics of species composition similarity among fishing gear in a full year circle. Since variable data have different range values, Z-score transformation was applied to eliminate invalid distance measurements (SPSS, Chicago, IL, USA). Furthermore the average monthly transformed data (catch per trips (kg.trips^{-1})) by species for each fishing gear) was computed for this purpose. Distinctive catch similarity patterns between months were described by hierarchical cluster analysis based on the centroid and squared euclidean distance interval methods (VAN TONGEREN, 1995). If some fishing gears clustered into one group, it means that the fishing gears have similar composition of target species. On the contrary, if a fishing gear is out of the group it means that the fishing gear is not targeting the same species.

3. Result
3.1 Fishing activity

Five types of fishing gear were employed in small-scale fisheries of Pelabuhanratu Bay. Based on the relative behaviour of the target species and the fishing gear, fishing gear types can be classified into two main categories: passive and active fishing gear. Since capture of fish base on movement of the target species toward the gear, four fishing gears (e.g. hand lines, lift nets, fixed gillnets and drift gillnets) were categorized as passive fishing gear. While, seine nets, which capture target species based on an aim chase of the target species was categorized as active fishing gear.

Drift gillnets and seine nets were being operated within a few miles from the shore by using an outboard engine on small-scale vessels, for one-day fishing operations. The length of seine nets vessels varied from 9 to 12 meters and 4 to 5 meters for drift gillnets. The main target
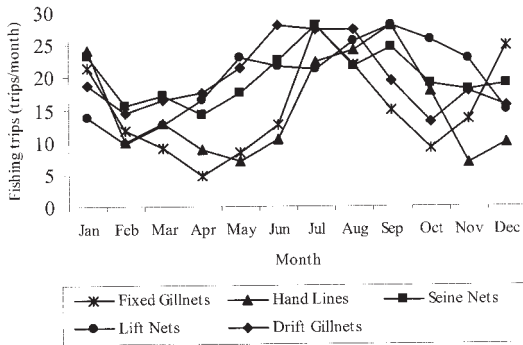
Fig. 2. The monthly average of fishing trips by fishing gear between 1993 and 2003.

species of seine nets is frigate tuna, little tuna, ponyfish and scads. Most similarly with seine nets, the main target species of drift gillnets is little tuna, hairtail, frigate tuna, and shark. Bamboo-platform lift nets (lift nets) were one of the types of gear being traditionally used by fishermen along shallower water of coast of Pelabuhanratu Bay. The average size of platform was 9.8 meters^2, and the box-shaped nets of 8.8 meters$^2 \times$ 3.0 meters, with 0.5 centimeter mesh size. The main target species of lift nets is sardine, hairtail, ponyfish and scad. The fixed gillnets are the type of bottom setting in the very shallow water of the bay, for targeting the sardine which concessionary migrates closely near the coast. Hand lines were the most specific and most simple among the types of gear being operated in Pelabuhanratu Bay. Hand lines were operated for one-day fishing along the coast especially in the rocky and coral areas where hairtail usually inhabits. The vessel length and system engine that were being used to operate handlines and fixed gillnets were similar to drift gillnets vessel, 4 to 5 meters with outboard engines of 5 HP.

The average number of monthly trips of gears varied seasonally. During the peak fishing season, most gears were operated every day (25–28 trips month^{-1}) but during the off fishing season, the number of fishing trips falls to 10 trips month^{-1}. In general, the number of fishing trips increased during the dry season and decreased during the rainy season (Fig. 2).

3.2 Catch composition and CPUE

Although about 50 fish species were landed in Pelabuhanratu Bay, the compositions of catch were dominated by only frigate tuna, *Auxis thazard* (34.0%), hairtail, *Trichiurus* spp. (18.1%), and ponyfish, *Leiognathus* spp. (13.6%). Percentage of the main species differed among season and fishing gear. Frigate tuna made up to 45.2 % of seine nets catch and 18.2% of drift gillnets catch. Hairtail contributed up to 90% of hand lines catch and 24.7% of drift gillnets catch. Ponyfish was the only species that was relatively abundant in most fishing gear but contributed highest percentage to lift nets catch (Fig. 3).

From January to March, during the hairtail peak fishing season, most of the fishing gear captured hairtail and contributed about 40 to 60 % of the main catch. On the contrary, during the months of April to December, most fishing gears targeted frigate tuna and increased the contribution of frigate tuna to the total catch of about 30 to 70%. Seine nets, which targeted frigate tuna, took about 78.72% of the total small-scale fisheries catch. On the other hand, lift nets which targeted sardine took about 11.18% of the total catch. While drift gillnets, hand lines and fixed gillnets contributed 5.34%, 3.01% and 1.75% of the total fish catch, respectively (Fig. 4).

Since both fishing trips and species composition dynamics seasonally, CPUE of most gears also showed varied temporally (Fig. 5). Comparing to the other gears, the total CPUE of seine nets, which ranged from 19.08 kg/-trips (in February) to 99.47 kg/trips (in November) was the highest among gears. The average monthly CPUE of seine nets in capturing frigate tuna, little tuna, ponyfish and scads also were higher than the other gears. On average, seine nets were able to capture frigate tuna 24.21 kg/trips, little tuna 11.45 kg/trips, ponyfish 17.61 kg/trip and scads 4.74 kg/trip. Although fixed gillnets showed the highest CPUE in capturing scads, it showed the lowest total CPUE, ranging from 3.18 kg/trip (in August) to 27.27 kg/trip (in March). Hand lines are the most productive gears for capturing hairtail, which on average, could capture at 12.98 kg/trip with a range of

Fig. 4.   The monthly average of catch composition (%) of seine nets (a), drift gillnets (b) and lift nets (c).
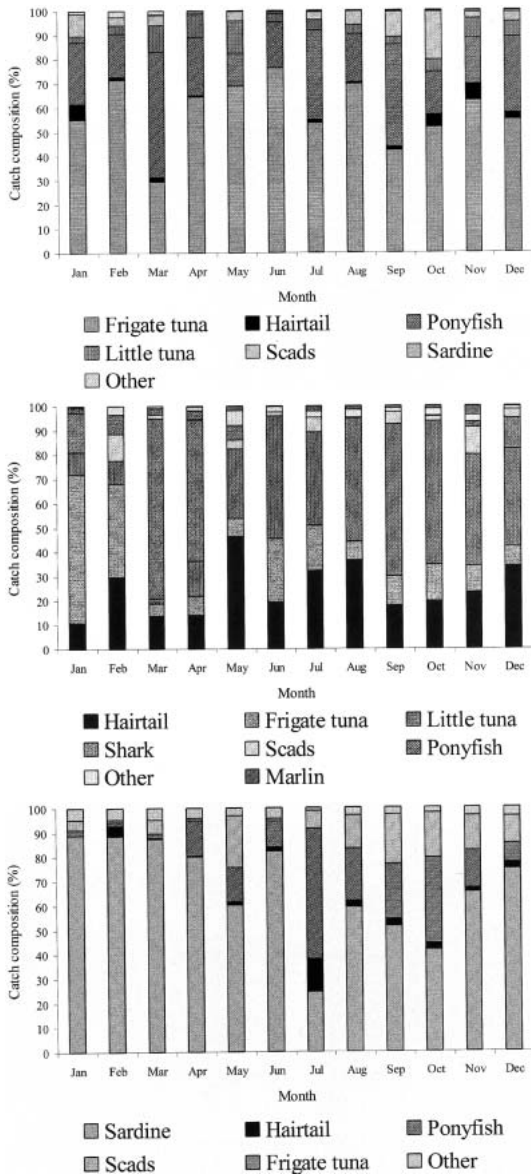
Fig. 3.   The monthly average of total catch proportion (%) by fishing gear between 1993 and 2003.

6.71 kg/trips (in November) to 20.47 kg/trip (in January).

3.3 Catch composition similarity

The results of the cluster analysis showed that the fishing gear cluster pattern is relatively stable throughout the year. In general, the fishing gear can be grouped into 2 clusters;
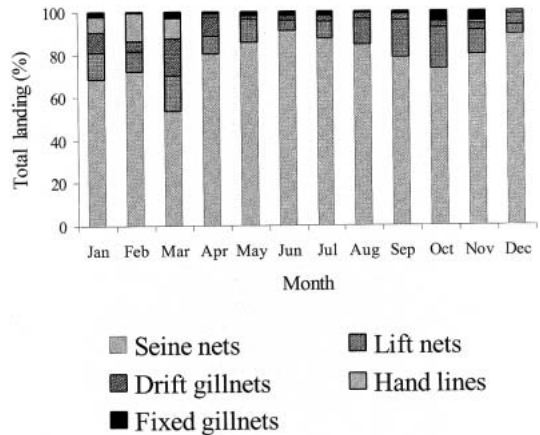
the passive fishing gear (lift nets, fixed gillnets, hand lines, and drift gillnets) cluster and the active fishing gear (seine nets), the other cluster. However, the cluster pattern of passive fishing gear can be further subdivided into three subgroups: (i) lift nets and fixed gillnets, (ii) drift gillnets, and (iii) hand lines (Fig. 6). Limited capacity of passive fishing gear to move in finding new fishing grounds over a long distance, may have forced the passive fishing gear fishermen to fish for limited fish resources and in limited fishing grounds throughout the year. However, the dynamics of main target species of each gear may have caused the cluster pattern of passive gear changing seasonally. From November to July during fishing season of hairtail, hand lines showed a low similarity to lift nets and fixed gillnets, but from August to October when hairtail reached low season, showed a high similarity. Although relatively stable with a low degree of similarity to the other passive gear throughout the year, during rainy season (from December to January) drift gillnets showed the least similarity to other passive gear and tended to have a similarity to seine nets.

On the other hand, seine net fishing activity, which is dependent on the target species, frigate tuna, clustered into different group throughout the year (Fig. 6). The higher capacity of seine nets to move in catching the
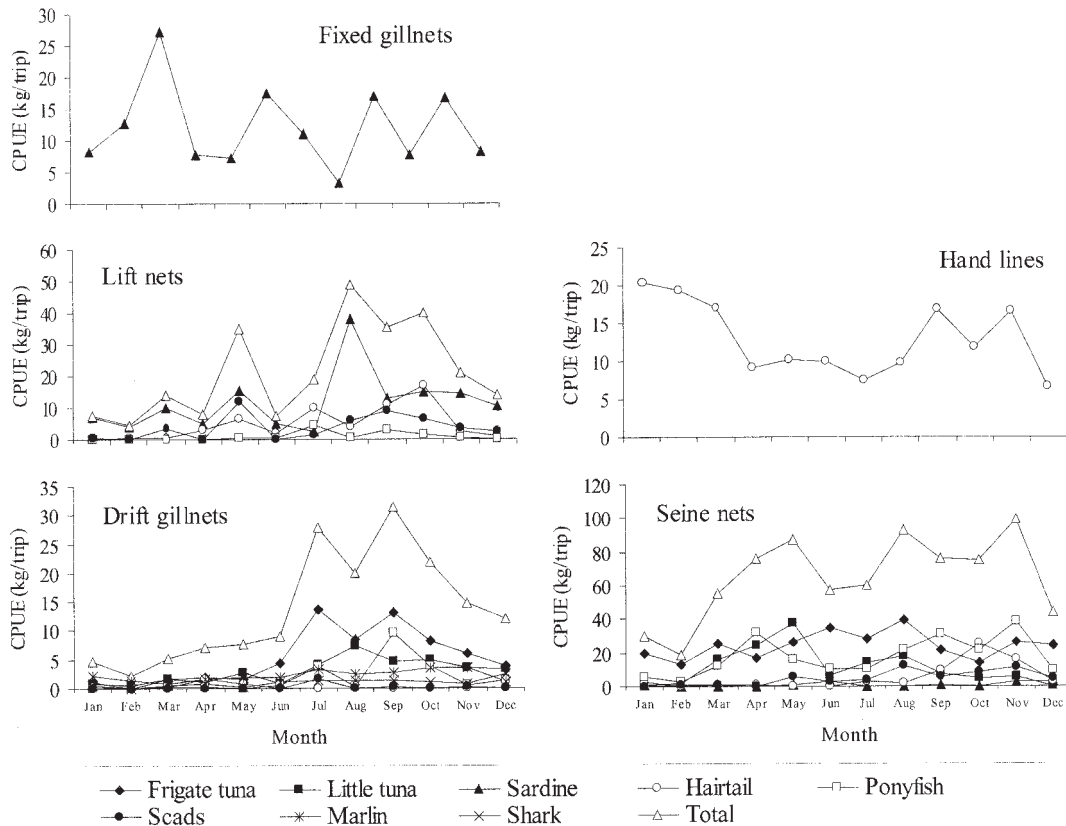
Fig. 5. The monthly average of catch per unit of effort of fishing gear between 1993 and 2003

target species, especially frigate tuna comparing to other gears may have caused the fish catch of seine nets was different from the other fishing gears.

4. Discussion

A number of factors influenced the fish catch of small-scale tropical coastal fisheries seasonally. These factors include the dynamics of fish abundance, oceanography, fishing strategy and possibility of existence of gear interaction. However, study about mechanism dynamics of fish catch between seasons in tropical multispecies-multigear is lack. In the present study, the seasonal dynamics of fish catch (composition and abundance) in relation to fishing strategy is studied.

Catch composition and abundance of fish species in study area showed dynamics seasonally. From the total number of species landed, only eight of which are considered important.

Preference of fishermen to capture target species, which have higher volume of fish catch and longer fishing season may have caused the fish catch only dominated by few target species. Although fish abundance changed seasonally, the fishermen did not change their gears. Fishing vessels always remained using similar gears and captured the available species throughout the year. The difference in CPUE between gears, which tends to change temporally, indicated that productivity of gears to capture target species was different with each other and changed temporally relative to the target species abundance fluctuation. Most fishermen increase their fishing trips (Fig.2) during high abundance of most target species in the dry season (Fig. 5) and decrease their fishing trips during low fishing season of most target species in the rainy season. These mean that seasonal fluctuation of fish catch (in volume and composition) has governed fishing
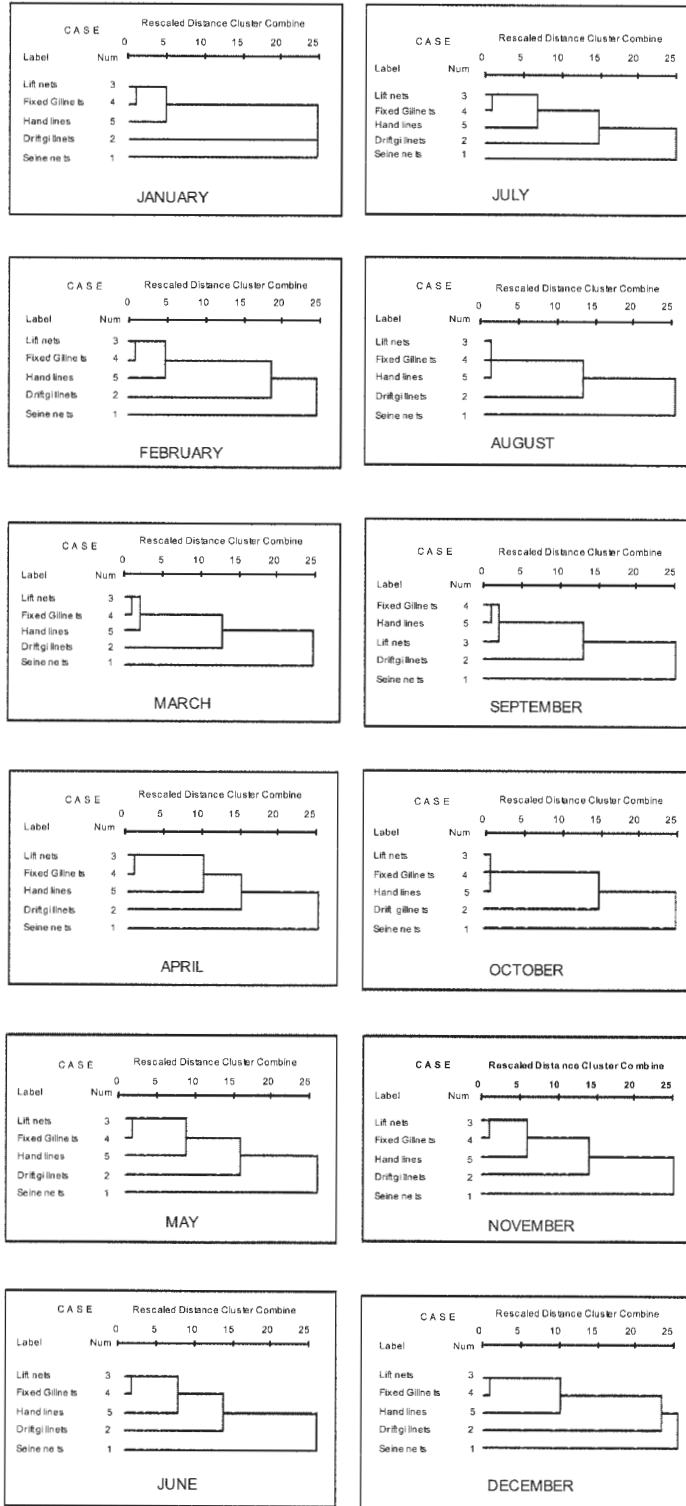
Fig. 6. The Monthly cluster pattern of fishing gear in small scale fiseheries of Pelabuhanratu Bay

strategy of fishermen in capture target species, and vice versa.

Although fishing trips allocation of most small-scale fisheries in study area did not govern by total catch (WIYONO, *et al.*, 2006), the result of present study confirmed that the changes in catch composition have governed fishermen to changed fishing strategy. Using the seasonal dynamics of catch composition similarity pattern, the results indicated that there are some differences in fishing strategies for target species between seasons. We expected that the whole of catch composition similarity patterns dynamics were strictly dictated by seine nets and hand lines fishing activity, which depend on their main target species, frigate tuna and hairtail fishing season (WIYONO *et al*, 2006). In addition, the cluster pattern of fishing gear that differentiated into four main groups; 1) seine nets, 2) hand lines, and 3) drift gillnets, and 4) fixed gillnets and lift nets indicated that despite having different physical characteristics, the last group of three fishing gears have similar strategy in capture target species.

The seasonal dynamic of oceanography factor that influenced both fish abundance and fishermen behavior in allocate their gear seasonally might have governed this processes. As MATSUYAMA *et al.* (1996) reported, the rainfall levels (159 - 403 mm) and variations of physical properties of waters of Pelabuhanratu Bay are lower in the dry season than in the rainy season. During the dry season (July-September) when river discharge is low, sea surface mixed layer near the coast become shallower, and fish species diversity is increased. In this period of safe weather condition, the fishing ground become scattered in several locations and fishing season of several gear which are used to capture diverse target species reach peaks levels. The highest capacity of seine nets to move in catching target species especially frigate tuna during this season, caused seine nets clustered into low degree of catch composition similarity to other gears. Conversely, during the rainy season (December-January), when rainfalls, storms and the river discharge increases, the sea surface mixed layer near the coast become deeper

and causes both species landing and fish species diversity to decrease. Most of the fish species disappear and fishing ground is limited in the northwestern part of bay (Cisolok waters). Only hairtail, which is targeted by hand lines shows increasing landings. Because of the difficulties in fishing activity, during this period of bad weather conditions of rainy season, fishing activity concentrated in limited area and caused drift gillnets and seine nets which are targeted similar target species have high similarity of catch landing.

To purpose of fisheries management, proportionate reduction of excessive gears can be initiated by reducing the number of gears that have the highest catch composition similarities. The decrease of fishing pressure can contribute to decrease the competitions among gears in fishing operation and simplify the monitoring of the dynamics and distribution of gear, which are used in stock assessment. In general, the landings of most of gears in the present case study overlap with those of other gear, and show the similarity among gears. However, lift nets, fixed gillnets and drift gillnets showed a higher catch composition similarities with the seine nets and hand lines. According to the information provided by the present study, to reducing the fishing efforts of lift nets, which are still used in high numbers, will be proposed.

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資　料

第 44 巻第 2 号掲載欧文論文の和文要旨

西村昌彦[1]・吉田明弘[1]・豊田圭太[1*]・山田美穂子[2]・野村英明[1]・和田実[1]・岡本研[3]・柴田晃[4,3]・高田秀重[2]・大和田紘一[5]：低濃度の石油が混入した実験的閉鎖生態系における海洋細菌群集の変動
　海洋現場での石油汚染を模した実験的閉鎖生態系（メソコスム）を作り，系内の生物群集が石油成分によりどのような影響を受けるのかについて調査を行った。浜名湖水 5 トンを注入した実験水槽に，A重油から調製した石油水溶性画分を添加し，これを油濁海水の実験区とした。また，別の水槽一基には浜名湖水のみを注入して，これを海水対照区とした。本実験では，石油汚染環境下での海洋細菌群集の量的・質的変動について着目し，経日的に表面水を採取して，細菌現存量，細菌生産速度，さらにはその細菌群集組成を変性剤密度勾配ゲル電気泳動法(DGGE法)による細菌16S-rDNA解析法により調べた。油濁により汚損した細菌群集の変化は，時間の経過と共に以下の 3 つの段階に分けられた。（ⅰ）油添加直後に細菌現存量は一過性の増加を見せたが，この時の16S-rDNAのバンド数の増加はわずかなものであった。（ⅱ）油添加 3 日後には細菌現存量は初発菌数まで減少したが，このとき16S-rDNAタイプ数は最大となった。（ⅲ）その後，細菌現存量・生産速度共に安定していたが，16S-rDNAタイプ数は大幅に減少し，石油を混入しなかったメソコスムと比べると，細菌群集組成の変化は大きかった。
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藤家　亘[*]，柳　哲雄[**]，玉置　昭夫[***]：西九州，橘湾・有明海におけるハルマンスナモグリ幼生の干潟個体群間受給ネットワークの数値モデルによる解析
　橘湾と有明海の湾口部側1/3の海域にはハルマンスナモグリ（甲殻十脚目スナモグリ科）が生息する砂質干潟が多く存在する。本海域に生息するハルマンスナモグリの約70%は橘湾の南東部に位置する富岡干潟に生息している。有明海や橘湾のような半閉鎖的な海域では干潟間での幼生の相互供給が行われていると考えられる。そこで本研究では，数値モデルを用いて，当該海域における26個の主要なハルマンスナモグリ地域個体群間での幼生受給ネットワークを解明することを目的とした。ハルマンスナモグリ幼生の日周鉛直移動を幼生追跡モデルに取り入れるために，富岡湾沖合いにおいて幼生の深度別分布調査を行った。その結果，幼生には発育段階ごとの日周鉛直移動に顕著な差が見られ，発育段階が進むにつれて，中・底層に存在する時間が多くなることが明らかとなった。幼生追跡モデルの計算結果により，有明海と橘湾でハルマンスナモグリ個体群が生息する干潟は，幼生の受給関係から 4 つのグループに分類できた。第 1 のグループは富岡干潟と相互幼生供給関係を持つ干潟群である。第 2 のグループは富岡干潟から幼生を供給されるにもかかわらず，富岡干潟に対して幼生を供給しない干潟群，第 3 のグループは富岡干潟に対して幼生を供給するが，富岡干潟および第 1 グループから幼生を供給されない干潟群である。第 4 のグループは第1グループおよび第 3 グループに幼生を供給するが，富岡干潟から幼生を供給されない干潟群である。幼生供給量から見れば，当該海域におけるハルマンスナモグリ幼生の干潟個体群間受給ネットワークは富岡干潟個体群を中心に成立していると考えられた。
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Eko Sri Wiyono[*,**]・山田作太郎[*]・田中栄次[*]・北門利英[*]：インドネシアのプラブハンラトゥ湾における小規模漁業の目的種漁獲戦略
　インドネシアのプラブハンラトゥ湾での小規模漁業において，漁具利用のよりよい理解を得るために，5 つの主な漁具について，月単位データに基づいて種組成及び漁獲種組成の類似性から捕獲目的種の漁獲戦略を調べた。解析の

結果によると，漁業者が用いる漁具は捕獲魚の季節的変動に関係していた。乾季では漁業者は大方の利用できる漁具を使用し，分散した漁場を利用し，多様な捕獲魚組成を示した。一方雨季では捕獲の多様性は薄れ，より限定的な漁具（手釣り）が多く使用されタチウオが捕獲された。本研究から得られた情報を用いて漁獲管理戦略が提案された。

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〈お知らせ〉
　当学会の編集委員会の海外委員、H. J. CECCALD博士は2006年4月29日叙勲で「旭日中綬賞」を受賞された。また、同年9月仏国からレジオンドヌール勲章「シュバリエ」（騎士）をも受賞され、須藤英雄会長の名で両賞についてお祝いのメッセージを打電した。なお、フランス（マルセイユ）留学中の副会長八木広樹氏から先生の授賞式へ出席し、その折「日仏海洋学会（日本）に感謝する…」旨の返辞の言葉があったと事務局へ連絡がありました。（庶務幹事）

賛　助　会　員

日仏海洋学会入会申込書

（正会員・学生会員）

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