Mesocosm studies on phytoplankton community succession after inputs of the water-soluble fraction of Bunker A oil

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Abstract: We monitored the succession of a phytoplankton community for 10 days in an enclosed meso-scale seawater tank (mesocosm), into which the water-soluble fraction of Bunker A oil was spiked, with or without a chemical dispersant. Diatoms such as Chaetoceros spp. and Skeletonema costatum contributed more than 50% of the total phytoplankton abundance for the first 3 days in all tanks. In the seawater tank that was devoid of the oil contamination, phytoplankton abundance fluctuated greatly, but diatoms predominated until day 8. However, in the oil-spiked tanks, autotrophic flagellates predominated over diatoms by day 5 after the oil addition. Daily monitoring of sediment trap contents revealed that the oil-spiked seawater resulted in a significantly reduced flux of diatom cells compared with the seawater tank. The decline in the diatom contribution to total phytoplankton abundance in both seawater and trap contents was more pronounced in the presence of the dispersant than in its absence. From these results, the mesocosm experiments clearly demonstrated adverse effects of Bunker A oil components on planktonic diatom assemblages under experimental conditions similar to those found in natural coastal environments. A combination of careful observation of the succession within the phytoplankton population in the water column and analysis of sediment trap samples have provided insights into the possible impacts of low levels of oil contamination on grazing food webs in natural marine environments.

Keywords: diatoms, flagellates, phytoplankton, succession, oil, dispersants, mesocosms

Introduction

Accidental oil spillage is one of the severe problems facing marine ecosystems, because the chemical components that diffuse from spilled oil often show acute or chronic eco-toxicity to diverse types of plants and animals (Albers, 1995). Evaluation of the environmental damage caused by such spilled oil has been a substantial challenge because of the lack of baseline information about the species present at a site, and their interactions and physiological states prior to the oil contamination. Although laboratory experiments on the effects of oil contamination on particular species of marine organisms are necessary, it is often difficult to apply the results of these studies directly to predict population- or community-level impacts that would affect the structure and function of the natural ecosystem.

Field experiments in a meso-scale, controlled ecosystem (mesocosm) have been conducted to overcome such difficulties in evaluating the impacts of pollutants on biological processes (Lee and Takahashi, 1977; Oviatt et al., 1982; Parsons et al., 1984; Linden et al., 1987). In
contrast to a glass flask in a laboratory, a mesocosm tank is designed to hold a water mass large enough to allow a diverse array of planktonic organisms at different trophic levels to exist under conditions similar to the natural environment in terms of temperature, sunlight, wind, and rainfall (MENZEL, 1977; PARSONS et al., 1984). An enclosed marine mesocosm near the mouth of Lake Hamana (Hamana–ko), a seawater lake in Shizuoka prefecture, Japan, has been used to study the impacts of contamination from the water–soluble fraction (WSF) of Bunker A oil on the microbial food web in seawater (OHWADA et al., 2003; TOYODA et al., 2005; NISHIMURA et al., 2006; YOSHIDA et al., 2006). One of the conclusions from these studies was that even low levels of oil contamination can disturb species composition and trophic interactions in the microbial food web.

In the present paper, we report on the success of the phytoplankton community in the same mesocosm system, into which the WSF of Bunker A oil was added, with or without a chemical dispersant. We also describe the phytoplankton composition in sediment trap samples retrieved daily from the mesocosm. From these results, we discuss the possible impacts of low concentrations of the oil components on the phytoplankton community and grazing food web in natural marine environments.

Materials and methods

The mesocosm experiments were carried out from 23 May to 2 June 2001 using three experimental tanks. Each cylindrical tank has a 1.5–m diameter, a 3.0–m depth, and a 5000–L capacity (OHWADA et al., 2003). Surface water from Hamana–ko was introduced into the two reservoirs for three tanks by using an electric submersible pump (OYORI and JO, 1989), and then distributed equally into the experimental tanks. On 22 May, nutrients (KNO₃, 100 µg N L⁻¹; KH₂PO₄, 10 µg P L⁻¹; Na₂SiO₃·9H₂O, 10 µg Si L⁻¹) were added to each experimental tank to maintain biological activity during the experiment, and the tanks were stirred for 0.5 h using stainless–steel blades (YOSHIDA et al., 2006).

We prepared a mixture of the WSF of Bunker A oil and autoclaved seawater from Hamana–ko (YAMADA et al., 2003). We also prepared a mixture of the WSF and a chemical dispersant (nonionic surfactant; Taiho Self Mixing S-7, Taiho Industries, Tokyo, Japan). Details of the procedure for the preparation and handling of the WSF and the dispersant were described in YAMADA et al. (2003) and YOSHIDA et al. (2006). After introducing water into the experimental tanks, either the WSF or the mixture of WSF and chemical dispersant was added to the mesocosm tanks, which were designated as the “OIL” tank or the “OD” tank, respectively. The last tank was kept free of contamination from both oil and dispersant as a control and was designated as the “SEA” tank.

Oil concentration just after the addition of the WSF in the OIL tank was estimated to be 224 µg L⁻¹, as measured by fluorometric analysis according to the method of Integrated Global Ocean Services System (IGOSS, 1974; referenced in: the Oceanographic Society of Japan, 1979). This oil concentration is comparable to that found in the inner part of the port of Tokyo Bay and is similar to that of MARL experiments in the early 1980s (OVIATT et al., 1982). Determination of the oil concentration in the OD tank failed due to a poor extraction efficiency caused by the dispersant used (M. YAMADA, personal communication). Concentrations of four representative polyaromatic hydrocarbon (PAH) compounds—napthalene (C₁₀H₈), phenanthrene (C₁₆H₁₂), fluoranthene (C₁₈H₁₄), and chrysene (C₂₀H₁₆)—were determined by gas chromatography/mass spectrometry (YAMADA et al., 2003).

Before pouring the oil–water mixture into the tanks, a sample of tank water was collected and subjected to microscopic observation of phytoplankton. For chemical analysis, another water sample was collected just after the introduction of the oil–water mixture. These are referred to as “day 0” samples. Water samples were siphoned to collect periodically from day 0 through day 10 from a depth of 0.5 m, using teflon tubing attached to the stainless–steel pipe, carefully introduced into glass bottles, and stored at appropriate temperature until analysis. At the same time as water sampling, a portable STD system (model 610–DM; YSI,
Table 1. Changes of water temperature, salinity, and PAHs in the subsurface water during the mesocosm experiments.

<table>
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<th>Time (days)</th>
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<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>10</th>
</tr>
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<td>19.7</td>
<td>20.4</td>
<td>22.6</td>
<td>23.6</td>
<td>22.7</td>
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<td>20.0</td>
<td>20.2</td>
<td>21.4</td>
<td>22.4</td>
<td>22.1</td>
</tr>
<tr>
<td></td>
<td>OD</td>
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<td>20.2</td>
<td>21.4</td>
<td>22.3</td>
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</tr>
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<td>31.54</td>
<td>31.44</td>
<td>31.40</td>
<td>30.92</td>
<td>31.42</td>
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<tr>
<td></td>
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<td>190.8</td>
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<td>159.6</td>
<td>146.1</td>
<td>158.9</td>
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<td>11.1</td>
<td>12.1</td>
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<tr>
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<td>24.0</td>
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<td>10.4</td>
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<tr>
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<td>2.5</td>
<td>2.3</td>
<td>1.5</td>
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<td>5.0</td>
<td>4.8</td>
<td>4.7</td>
<td>6.3</td>
<td>4.9</td>
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</table>

SEA: natural seawater without oil and/or chemical dispersant
OIL: seawater with oil alone
OD: seawater with oil plus chemical dispersant

Yellow Springs, OH, USA) was used to make a depth profile of temperature, salinity, and dissolved oxygen. Water temperature and salinity in all the experimental tanks ranged from 19.6 to 23.1 °C, and from 30.9 to 31.6, respectively, during the 10 days of incubation (Table 1).

Water samples were fixed with formalin (final concentration: 1%, v/v) and observed with an inverted Nomarski-type microscope (model TE300; Nikon, Tokyo, Japan) to taxonomically identify and enumerate phytoplankton cells. A 25% glutaraldehyde solution (final concentration: 2%, v/v) was used to gently fix autotrophic nanoflagellates (ANFs) in water samples. The ANF cells were stained with FITC and DAPI (Sherr and Sherr, 1983), filtered onto a polycarbonate Nuclepore (Whatman, Springfield Mill, UK) membrane (pore size, 0.8 μm), and counted under an epifluorescence microscope (type E800; Nikon) in a dark room. ANFs were distinguished from heterotrophs by the autofluorescence of photosynthetic pigments observed under blue light excitation. To minimize the masking effect of the protein-binding dye FITC to the autofluorescence of photosynthetic pigments (Sherr et al., 1993), we empirically set the staining time (5 minutes) and the final concentration (3 μg ml⁻¹).

To measure the concentration of chlorophyll a (Chl), a 100-ml water sample was filtered through a Whatman GF/F glass-fiber filter (Whatman, Springfield Mill, UK), and the filters were soaked in N,N-dimethylformamide (Suzuki and Ishimaru, 1990). Filters were stored in the dark at approximately −20 °C for fewer than 10 days before Chl content was measured with a fluorometer (type 10R; Turner Designs, Sunnyvale, CA, USA). A calibration curve was obtained using a Chl standard (Sigma, St. Louis, MO, USA). The filtrate collected during Chl sample preparation was used to analyze for nitrogen (NO₃⁻ + NO₂⁻) and phosphate (PO₄³⁻) concentrations using an auto-analyzer (model AAAC3; BRAN+LUEBBE, Norderstedt, Germany).

Every day, four glass vials (120-mm height, 30-mm inner diameter, and 100-ml volume) were suspended in the tanks using a thread at a depth of 2.5 m to collect sinking particles. Vials were gently retrieved after 1 day and used
Fig. 1. Temporal variation of concentration of dissolved oxygen (DO) (A), transparency (B), nitrogen (N: NO₂-N + NO₃-N) (C), phosphate (P: PO₄-P) (D), and NP ratio (E) during the mesocosm run from 23rd of May to 2nd of June in 2001. The arrow denotes the time of oil contamination. SEA: natural seawater in the mesocosm tank, OIL: natural seawater with WSF mixture, OD: natural seawater with WSF-chemical dispersant mixture.

for analysis of phytoplankton abundance and Chl content. The phytoplankton trapped in the vials were fixed immediately by formalin (final concentration: 1%, v/v) and stored in the dark at 4 °C until microscopic analysis. Identification and enumeration were conducted in the same way as described for the water samples.

We measured water transparency by using a white ceramic disc 80 mm in diameter (smaller than a standard Secchi disc, which is 200 or 300 mm in diameter). According to Preisendorfer (1986), transparencies measured with the smaller disc and the standard ones are practically the same. The compensation depth (CD, m) was calculated using transparency depth (Ds, m) with the equation described in Aruga (1986): CD = 2.67Ds.

Results and discussion

Changes in physico-chemical parameters

The highest concentrations of PAHs were found in the tank to which seawater and the WSF of Bunker A oil and a dispersant (OD) were added (Table 1). Relatively lower molecular weight (LMW) PAHs, naphthalene and phenanthrene, dramatically decreased to less than 10% of the initial concentrations in the first 2 days, whereas higher molecular weight (HMW) PAHs, fluoranthene and chrysene, decreased more slowly. The rapid decrease in the LMW-PAHs can be ascribed to microbial degradation, and the slower removal of the HMW–PAHs (and HMW–alkanes and hopanes; data not shown), from the water column presumably results from settling or sedimentation.
(Yamada et al., 2003).

Dissolved oxygen (DO) concentration in all the tanks was initially 9.5 mg L$^{-1}$, decreasing by day 7 to 7.2 mg L$^{-1}$ in the OIL tank and to 3.8 mg L$^{-1}$ in the OD tank (Fig. 1A). DO concentrations in the OIL tank became to initial level by day 10, while those in the OD tank continued to decrease. In the control seawater (SEA) tank, DO fluctuated greatly, but it remained above 7.5 mg L$^{-1}$ during the entire incubation period. It is likely that bacterial respiration during the degradation of hydrocarbons in the WSF, the dispersant, or both, substantially contributed to the decline in DO (Yoshida et al., 2006).

Initial concentrations of inorganic nitrogen ($\text{NO}_2^- + \text{NO}_3^-$) and phosphate (PO$_4^{3-}$) in the tanks ranged from 5 to 9 $\mu$M and from 0.3 to 0.5 $\mu$M, respectively (Fig. 1C, D). Although both nitrogen and phosphate disappeared almost entirely by day 10, the patterns of disappearance varied between the nutrients and between the tanks. Nitrogen decreased more slowly in both the OIL and the OD tanks compared with that in the SEA tank. Phosphate tended to disappear more rapidly than nitrogen, particularly in the OD tank during the first 2 days. These differences in nutrient removal from the tanks were reflected in the molar ratio of nitrogen to phosphorus (N:P ratio) (Fig. 1E). The N:P ratio was about 14:1 in all of the tanks at day 0 and decreased to less than 10 by day 5 in the SEA tank. In contrast, the N:P ratios in the OIL and OD tanks remained above the initial value through through day 7, with larger fluctuations in the OD tank. Because the N:P ratio of the natural phytoplankton community is 16:1 (Redfield et al., 1963), the SEA tank was under N–limited conditions from day 5, whereas the OIL and OD tanks were under P–limited conditions for almost the entire period of the experiment.

Differences in phytoplankton community structure

A total of 62 species of phytoplankton, comprising 47 diatoms, 10 dinoflagellates, and 5 other species, was found in the mesocosm tanks during the experiment (Table 2). While most of them (59 species) were found in the SEA tank, about half were found in the OIL and the OD tanks, suggesting that phytoplankton species richness was higher in the SEA tank.

During the initial phase of the incubation (from day 0 to day 3), planktonic diatoms, including some chain-forming species such as Chaetoceros setigus, C. debilis, C. dydimus, and S. costatum, contributed more than 50% of the total phytoplankton abundance in all of the tanks (Fig. 2). The rest of the phytoplankton population during this period was mainly composed of autotrophic flagellates, such as Proorocentrum minimum, and coccolithophorids.

After day 3, the relative contribution of diatoms to the total phytoplankton population became less pronounced. Although diatoms continued dominating total phytoplankton abundance in the SEA tank until day 8, autotrophic flagellates, namely P. minimum, gradually increased after day 5 and finally became dominant (75% of the total phytoplankton population) by day 10. In addition to flagellates, coccolithophorids contributed about 20% of the total phytoplankton population at day 10 in the SEA tank. A succession from diatoms to flagellates in a phytoplankton population is a typical phenomenon in an enclosure system devoid of water turbulence (Lee and Takahashi, 1977; Ægge and Aksnes, 1992). In contrast, autotrophic flagellates, particularly ANFs, rapidly dominated the phytoplankton populations in the OIL and OD tanks after day 5. In the oil–contaminated tanks (with and without dispersant), coccolithophorids disappeared from the water column by day 6.

Beneficial or adverse effects of petroleum substances on phytoplankton should vary depending on the phytoplankton species. Based on previous studies certain autotrophic flagellates appeared to be petroleum–insensitive (Pulich et al., 1974; Parsons et al., 1976; Lee and Takahashi, 1977; Karydis, 1981; Morales–Loo and Goutx, 1990; Siron et al., 1991; Okumura et al., 2003), although coccolithophorids suffered severely under oil–contaminated conditions. In another set of mesocosm studies using the same tanks, we confirmed by a vital FDA (fluorescein
Table 2. List of phytoplankton species occurred from the water column of mesocosm tanks during experiments. 
Water from the surface layer of the mouth part of Hamana-ko was directly brought into tanks via an under-ground tubing water supply pump on May 22, 2001.

<table>
<thead>
<tr>
<th>Species</th>
<th>SEA</th>
<th>OIL</th>
<th>OD</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Division Dinophyta</strong></td>
<td></td>
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</tr>
<tr>
<td><strong>Class Dinophyceae</strong></td>
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<td></td>
<td></td>
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<tr>
<td>Order Prorocentrales</td>
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<tr>
<td><em>Prorocentrum compressum</em></td>
<td>+</td>
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<tr>
<td><em>P.</em> dentatum</td>
<td>+</td>
<td>+</td>
<td>-</td>
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<tr>
<td><em>P.</em> micans</td>
<td>+</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><em>P.</em> minimum</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td><em>P.</em> triestinum</td>
<td>+</td>
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<tr>
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<td></td>
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<tr>
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<td>-</td>
<td>+</td>
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<td>Order Gymnodiniales</td>
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<td></td>
</tr>
<tr>
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<td>-</td>
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<tr>
<td>Order Gonyaulacales</td>
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<tr>
<td><em>Ceratium kofoidii</em></td>
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<td>+</td>
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<tr>
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<td><em>Peridinium quinquecorn</em></td>
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<td><em>Protothecocystis spp.</em></td>
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<tr>
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<td><em>Ebria tripartita</em></td>
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<td>+</td>
<td>-</td>
</tr>
<tr>
<td><em>Lauderia annulata</em></td>
<td>+</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

+: occurred, -: not occurred
diacetate) staining (Bentley–Mowat, 1982) that most autotrophic flagellates were active even at the same levels of WSF of Bunker A oil used in the present study (data not shown).

**Phytoplankton in sediment trap samples**

Daily monitoring of sediment trap samples from the mesocosm tanks revealed that downward fluxes of Chl in the SEA, OIL, and OD tanks averaged 8.7 (1.0–19.3), 2.8 (0.4–5.6), and 1.7 (0.8–3.7) mg m$^{-2}$ d$^{-1}$, respectively (Fig. 3). The total phytoplankton and diatom fluxes in the SEA tank averaged 2.3$\times$10$^8$ and 2.2$\times$10$^8$ cells m$^{-2}$ d$^{-1}$, respectively, which were one order of magnitude higher than those in the OIL and OD tanks. Although Chaetoceros vegetative cells mainly contributed to the fluxes in the SEA tank during the entire incubation period, their resting spores clearly increased in the latter half of the incubation period, exhibiting a peak of more than 5$\times$10$^7$ cells m$^{-2}$ d$^{-1}$ on day 7. In contrast, the number of the resting spore in the trap samples from the OIL and OD tanks was extremely low, fewer than 1$\times$10$^7$ cells m$^{-2}$ d$^{-1}$ on average, whereas autotrophic flagellates contributed more to the total phytoplankton fluxes in the oil–contaminated tanks than in the SEA tank.

Species of Chaetoceros produce resting spores immediately following blooms (e.g., Odate and Maita, 1990), and nitrogen depletion is one of the essential factors inducing spore formation in centric diatoms (French and Hargraves, 1980; Kuwata and Takahashi, 1990; Oku and Kamatani, 1995, 1997; McQuoid and Hobson, 1996). Our results are consistent with these observations; resting spore formation by Chaetoceros in the SEA tank became intensive after nitrogen was depleted from the seawater. Besides nitrogen, phosphate depletion can be a factor leading to resting spore formation in diatoms (Oku and Kamatani, 1995). However,
this probably did not occur in our mesocosm tanks, because phosphate was depleted faster in the OD tank than in the SEA tank (see Fig. 1D) and yet the OD tank had fewer spores than the SEA tank (Fig. 3). Although the lower numbers of resting spores in the OIL and OD tanks may be partly explained by the relatively slow depletion of nitrogen compared with the SEA tank, it is more likely that chemical components in the WSF of Bunker A oil were responsible for limiting spore formation.

Because the spore formation by planktonic diatoms in the SEA tank is adequately explained by nitrogen limitation alone, it is unlikely that other elements such as silicon (Si) were limiting for diatom growth and spore formation in the present study. In support of this, we did not observe any Si depletion in the
previous mesocosm study with the same experimental conditions. For instance, the Si:N ratio in the seawater tank in the previous experiment (autumn 2000) ranged from 0.9:1 to 1.2:1 (average = 1.1:1) during the initial 9 days of incubation (data not shown). Actively growing diatom cells have a Si:N composition ratio of 1.2:1 (Brzezinski, 1985), so it is likely that diatoms in the SEA tank did not face serious Si depletion either in the present or in the previous experiments.

Morinaga and Arakawa (2000) reported that an oil slick on the sea surface attenuated the photosynthetically available radiation (PAR) below the sea surface. Such changes in the optical environment can be detrimental to autotrophic plankton, although the optimum PAR may vary depending on the species. Parsons et al. (1984) reported depressed primary production in the mesocosm tank resulting from light attenuation after the input of dispersed oil. In the present study, the transparency of the OD tank immediately decreased from 3 to 1.3 m after the addition of the
mixture of the WSF of Bunker A oil and a dispersant. It took 5 days to return to the original level of transparency, whereas transparency remained constant in the SEA tank and the OIL tank (see Fig. 1B). Based on ARUGA’s equation, the compensation depth of the OD tank on day 2 was estimated to be 3.3 m. However, it was more than 7.7 m in the SEA and OIL tanks. Because sunlight attenuates drastically with depth, diatoms that cannot maintain their vertical position at a depth of optimum light conditions are likely to be outcompeted by motile flagellates.

Spilled oil has both inhibitory and stimulatory impacts on phytoplankton, which vary with the type of oil and concentrations of the petroleum components (ALBERS, 1995). Results of the present study suggest that the WSF of Bunker A oil is detrimental to diatoms, whereas it is less inhibitory to the flagellate population. Consequently, flagellates gained better access to the light and nutrients in the water column. Dispersants increase the concentrations of oil components in the water, thereby creating more harsh conditions for the diatom population (PARSONS et al., 1984; YAMANE et al., 1984; SIRON et al., 1996). In the context of grazing food webs, the WSF of Bunker A oil altered not only the community structure but also the functions of the primary producers. The decreased flux of diatom cells from the upper layer implies a reduced transport of organic matter in the water column, which could interrupt the plankton-benthos coupling in natural environments (AMBROSE and RENAUD, 1995).

The physical microturbulence in a water mass is removed or weakened in an enclosed mesocosm (LALLI and PARSONS, 1993), therefore, it might be difficult for planktonic diatoms to remain suspended in the water column in mesocosm tanks such as those used in the present study, which could complicate interpretation of our results. Due to this intrinsic characteristic of these tanks, they may only be suitable for short-term observations of diatom populations in the water column. Nonetheless, the combination of careful observations of the phytoplankton population in the water column and in the sediment trap samples makes it possible to determine with great sensitivity the impacts of low levels of spilled oil on both the phytoplankton community structure and the trophic interactions in the grazing food webs in aquatic environments.

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References
FRENCH, F.W. and P.E. HARGRAVES (1980) : Physiological characteristics of plankton diatom...


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Role of tidal flat in material cycling in the coastal sea

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Abstract: A simple tidal flat model with pelagic and benthic ecosystems was developed in order to analyze the nitrogen cycling in an inter–tidal flat of the Seto Inland Sea, Japan. After the verification of calculation results with the observed results in water quality and benthic biomasses, the role of this tidal flat in nitrogen cycling was evaluated from the viewpoint of water quality purification capability. When there is no suspension feeder in the tidal flat, the water quality purification capability of this tidal flat becomes lower because the outflow of organic nitrogen increases compared to the present case, and the red tides may be generated.

Keywords: tidal flat, ecosystem model, nitrogen cycling, water quality purification capability

1. Introduction

A tidal flat is known as the important place for the biological production in the coastal sea. Moreover a tidal flat is paid to attention because the removing function of bio-elements such as nitrogen and phosphorus from the water column is very high. NAKATA and HATA (1994) claims that the material cycling (mineralization or organization of bio-elements) in the tidal flat determines the water purification function there. SASAKI (2001) qualitatively points out that bivalves in the tidal flat play an important role in the water purifying function in the coastal sea. It is necessary to clarify the material cycling and budget quantitatively in order to understand the ecosystem characteristics and the purification function of the tidal flat. A numerical ecosystem model is a very useful tool to clarify them.

For the ecosystem model of the tidal flat, the Ems–Dollard ecosystem model (BARETTA and RUARDLIJ, 1988) is very famous. Their model is constructed with pelagic, benthic and epibenthic sub–models and simulates the seasonal variation in the tidal flat ecosystem, focusing on the carbon cycling. In Japan, HATA et al. (1995) produced a tidal flat ecosystem model based on the Ems–Dollard ecosystem model. Their model emphasizes the benthic ecosystem, focusing on the nitrogen cycling. SOHMA et al. (2000) produced a new numerical ecosystem model for the tidal flat and simulated the eco–dynamics over a short–time scale (< 24h). However, these models are too complex to interpret well the calculated results.

In this paper, a simple tidal flat ecosystem model with pelagic and benthic ecosystems is developed on the basis of a pelagic ecosystem model of KAWAMIYA et al. (1995). We reproduce the seasonal variation of the observed nitrogen values in a tidal flat of the Seto Inland Sea, Japan from January to December 2000 using the developed simple ecosystem model. From this model results, we clarify the nitrogen cycling and budget in the tidal flat. The relation between a decrease of the biomass of

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bivalve and the red tide occurrence is investigated by using this model. Finally, the role of this tidal flat is evaluated from the viewpoint of water purifying function in the coastal environment.

2. Study area and Observed data

Our study area is a sandy tidal flat located in the central part of the Seto Inland Sea, southwestern Japan (Fig. 1). The tidal flat covers an area of about 148,000 m² and has an average depth of 1 m with the average tidal range of about 2 m. Station B4 is an observation point of benthic biomass in the tidal flat. Stations U and K are the observation points of water characteristics above the tidal flat. Stations KA9 and KA10 are the observation points outside the tidal flat. Station M is an observation point of meteorological parameters by the Takamatsu Meteorological Observatory. There are river discharges into this tidal flat from the Shin, Kasuga and Tsumaeta Rivers (Fig. 1).

Samplings were conducted every month at low tide from January to December 2000. At Stn. B4, water temperature, Dissolved Inorganic Nitrogen (DIN) and Chlorophyll. a (Chl. a) concentrations at the surface (0.0–0.5 cm) and sub–surface (0.5–2.0 cm) layers in the pore water of tidal flat were observed. Nitrogen concentration of microphytobenthos was estimated using C:Chl. a ratio (C:Chl. a=33.7:1; MONTANI et al., 2003) and C:N ratio (C:N=75.7:10.1; MONTANI et al., 2003). The sampling of macrozoobenthos (polychaeta and bivalve) was carried out between 0 and 10 cm depth by a 10 × 10 cm quadrat method at the same time. Nitrogen concentrations of macrozoobenthos were estimated using a linear empirical equation based on the field observations, that is, the nitrogen concentration of polychaeta Np (gN) =0.45 × 0.17 × (0.2 × total wet weight (g)), and that of bivalve Nb (mgN) =96.5 × (0.184 × (0.167 × total wet weight (g) +0.025) +0.0005). We assume that the data at Stn. B4 are representative throughout this tidal flat shown in Fig. 1, that is, the observed data of surface and sub–surface layers in the pore water are assumed to be the data of Box 2 and Box 3 shown in Fig. 2, respectively. While, at Stns. U (water depth was 20 cm in winter and 50 cm in summer) and K (water depth was 20 cm in winter and 50 cm in summer), water temperature, salinity, DIN, Particulated Organic Nitrogen (PON) and Chl. a concentrations in the surface water were observed. Nitrogen concentration of phytoplankton was estimated using C:Chl. a ratio (C:Chl. a=30:1; PARSONS et al., 1984) and Redfield ratio (C:N=106:16; REDFIELD et al., 1963). The observations at Stns. U and K were conducted within one hour before or after the
observation at Stn. B4. We can expect that the water at Stn. U covers this tidal flat during the flood tidal current and that at Stn. K during the ebb tidal current, therefore the average data at Stns. U and K represent the sea–water characteristics above this tidal flat, that is, the average observed data at Stns. U and K are the data of Box 1 shown in Fig. 2.

At the same time, the observations of salinity, DIN and Chl. a concentrations at Stns. KA9 and KA10 in the Bisan–seto were carried out every month from January to December 2000 by the Kagawa Prefectural Fisheries Experimental Station. We assume that the average data of Stns. KA9 and KA10 are the boundary condition offshore, that is, the observed average data at Stns. KA9 and KA10 are the data of Box 4 shown in Fig. 2.

The load of Total Nitrogen (TN) from three rivers is estimated based on the monthly averaged values of river discharges from three rivers and annually averaged values of TN concentrations in three rivers. The annually averaged river discharge from three rivers and annually averaged TN concentration in three rivers in 2000 are 0.63 m$^3$ s$^{-1}$ and 2.4 mg L$^{-1}$, respectively. The monthly averaged river discharge ($R$) was estimated from the monthly averaged water levels in three rivers, which were measured by Kagawa Prefecture. We assumed that TN concentrations in three rivers did not change seasonally in 2000 because there was no data on the seasonal variations of TN concentrations in three rivers.

The monthly averaged data of solar radiation and wind speed in 2000 at the Takamatsu Meteorological Observatory were quoted from the Geophysical Review published by the Japan Meteorological Agency.

3. Box model

Fig. 2 shows the box model of this tidal flat. Box 1 is the pelagic ecosystem with 1 m water depth, and Box 2 is the benthic ecosystem for the benthic algae with 0 to 0.5 cm sediment depth and that for the suspension and deposit feeders with 0 to 10 cm sediment depth. We consider the pelagic ecosystem with 1 m depth above the tidal flat because the average tidal range at this tidal flat is about 2 m (Montani et al., 2003) and we focus the annually averaged ecosystem there. The boundary condition for Box 2 is given at Box 3, and the boundary condition offshore of Box 1 is given at Box 4 in the Bisan–seto.

The horizontal advection velocity ($U_{ti}$) and the horizontal eddy diffusivity ($K_{hi}$) required for the ecosystem model calculation in this study are decided by the physical box model. The equation of water mass conservation is expressed by:

$$R = U_{ti} \times A_{ti}$$

(1)

where $R$ (m$^3$ s$^{-1}$) is the river discharge from three rivers (shown in Fig. 3 d), $U_{ti}$ (m s$^{-1}$) is the horizontal advection velocity between Box 1 and Box 4, $A_{ti}$ (m$^2$) is the cross–sectional area between Box 1 and Box 4 (shown in Table 1).

The equation of salt conservation is expressed by:

$$-U_{ti} \times S_i \times A_{ti} + K_{hi} \times \frac{S_i - S_f}{L_{ti}} \times A_{ti} = 0$$

(2)

where $S_i$ and $S_f$ are salinity of Box 1 and Box 4, respectively (shown in Fig. 3 c). $K_{hi}$ (m$^2$ s$^{-1}$) is the horizontal eddy diffusivity between Box 1 and Box 4, and $L_{ti}$ (m) is the length between Box 1 and Box 4 (shown in Table 1). The temporal variation term in salinity is assumed to be zero because it is much smaller than the spatial variation terms in Eq. (2). The advection and mixing effects by tidal current is expressed by this horizontal eddy diffusivity $K_{hi}$ in this analysis.

$U_{ti}$ and $K_{hi}$ computed from equations (1) and (2) using the observed data are shown in Fig. 3 (g), (h) respectively.
Fig. 3. Seasonal variations in monthly mean input data and boundary conditions for the model calculation. (a) $I_0$: solar radiation, (b) $T$: sea water temperature in Box 1 and $T_2$: pore water temperature in Box 2, (c) $S_1$ and $S_4$: salinity in Box 1 and Box 4, respectively, (d) $R$: river discharge, (e) DIN$_1$: (left axis) and DIN$_4$: (right axis): DIN concentration in Box 3 and Box 4, respectively, (f) PHY$_4$: PHY concentration in Box 4, (g) $U_{14}$: horizontal advection velocity, (h) $Kh_{14}$: horizontal eddy diffusivity, (i) $W_{2d}$ and $W_{2s}$: soft-body dry weight per individual of deposit feeder and $W_{2s}$: soft-body dry weight per individual of suspension feeder, (j) $W$: monthly averaged wind speed.
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<thead>
<tr>
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4. Ecosystem models

In the boxes of Box 1 and Box 2 (Fig. 2), a physical, biological and chemical processes concerning the nitrogen cycling shown in Fig. 4 are considered.

The compartments of Box 1 are Dissolved Inorganic Nitrogen (DIN,), Dissolved Organic Nitrogen (DON,), phytoplankton (PHY,), zooplankton (ZOO,), and detritus (DET,) within 1 m water column. The compartments of Box 2 are Dissolved Inorganic Nitrogen (DIN,), Dissolved Organic Nitrogen (DON,), microphytobenthos (PHY,) and detritus (DET,) within 0.5 cm sediment depth, and deposit feeder “polychaeta” (ZOO,) and suspension feeder “bivalve” (ZOO,) within 10 cm sediment depth. Reproduction of seasonal variations in DIN, PHY, PON, (particulated organic nitrogen in Box 1 = PHY + ZOO + DET,), DIN, PHY, ZOO, and ZOO, concentrations at Box 1 and Box 2 is tried in this numerical experiment.

The temporal variations in 9-compartment concentrations at Box 1 and Box 2 are given by the following equations, based on KAWAMIYA et al. (1995).

\[
\frac{d\text{DIN}_1}{dt} = \text{Load from rivers (DIN_{\text{load}})}
- \text{Photosynthesis (PHY,)}
+ \text{Excretion (ZOO,)}
+ \text{Decomposition (DET,} \to \text{DIN,)}
+ \text{Decomposition (DET,} \to \text{DON,)}
+ \text{Excretion (ZOO,)}
- \text{Vertical Diffusion (DIN,} \to \text{DIN,)}
- \text{Horizontal Diffusion (DIN,} \to \text{DIN,)}
- \text{Horizontal Advection (DIN,)}
\]

(3)
\[
V_1 \frac{d \text{DON}_1}{dt} = \text{Load from rivers (DON}_{\text{LAI}}) \\
+ \text{Extracellular excretion (PHY}_{1}) \\
+ \text{Decomposition (DET}_{1} \rightarrow \text{DON}_1) \\
- \text{Decomposition (DON}_1 \rightarrow \text{DIN}_1) \\
- \text{Vertical Diffusion (DON}_1, \ \text{DON}_2) \\
- \text{Horizontal Diffusion (DON}_1, \ \text{DON}_2) \\
- \text{Horizontal Advection (DON}_1) \\
\tag{4}
\]

\[
V_1 \frac{d \text{PHY}_1}{dt} = \text{Photosynthesis (PHY}_{1}) \\
- \text{Extracellular excretion (PHY}_{1}) \\
- \text{Mortality (PHY}_{1}) \\
- \text{Grazing (PHY}_{1} \rightarrow \text{ZOO}_1) \\
- \text{Grazing (PHY}_{1} \rightarrow \text{ZOO}_2) \\
- \text{Horizontal Diffusion (PHY}_1, \ \text{PHY}_2) \\
- \text{Horizontal Advection (PHY}_1) \\
+ \text{Suspension (PHY}_1) \\
\tag{5}
\]

\[
V_1 \frac{d \text{ZOO}_1}{dt} = \text{Grazing (PHY}_1 \rightarrow \text{ZOO}_1) \\
+ \text{Excretion (ZOO}_1) \\
+ \text{Egestion (ZOO}_1) \\
- \text{Mortality (ZOO}_1) \\
- \text{Horizontal Diffusion (ZOO}_1, \ \text{ZOO}_2) \\
- \text{Horizontal Advection (ZOO}_1) \\
\tag{6}
\]

\[
V_1 \frac{d \text{DET}_1}{dt} = \text{Load from rivers (DET}_{\text{LAI}}) \\
+ \text{Mortality (PHY}_1) \\
+ \text{Egestion (ZOO}_1) \\
+ \text{Mortality (ZOO}_1) \\
- \text{Decomposition (DET}_1 \rightarrow \text{DIN}_1) \\
- \text{Decomposition (DET}_1 \rightarrow \text{DON}_1) \\
- \text{Horizontal Diffusion (DET}_1, \ \text{DET}_2) \\
- \text{Horizontal Advection (DET}_1) \\
- \text{Sinking (DET}_1) \\
+ \text{Suspension (PHY}_1) \\
+ \text{Suspension (DET}_1) \\
+ \text{Egestion (ZOO}_2) \\
\tag{7}
\]

\[
V_1 \frac{d \text{DIN}_2}{dt} = \text{Photosynthesis (PHY}_2) \\
+ \text{Decomposition (DET}_1 \rightarrow \text{DIN}_1) \\
+ \text{Decomposition (DON}_1 \rightarrow \text{DIN}_1) \\
- \text{Vertical Diffusion (DIN}_1, \ \text{DIN}_2) \\
- \text{Nitrification (DIN}_1) \\
\tag{8}
\]

\[
V_2 \frac{d \text{DON}_2}{dt} = \text{Extracellular excretion (PHY}_{2}) \\
+ \text{Decomposition (DET}_2 \rightarrow \text{DON}_2) \\
- \text{Decomposition (DON}_2 \rightarrow \text{DIN}_2) \\
- \text{Vertical Diffusion (DON}_2, \ \text{DON}_1) \\
- \text{Vertical Diffusion (DON}_1, \ \text{DON}_2) \\
\tag{9}
\]

\[
V_2 \frac{d \text{PHY}_2}{dt} = \text{Photosynthesis (PHY}_{2}) \\
- \text{Extracellular excretion (PHY}_{2}) \\
- \text{Mortality (PHY}_{2}) \\
- \text{Suspension (PHY}_{2}) \\
- \text{Grazing (PHY}_2 \rightarrow \text{ZOO}_1) \\
\tag{10}
\]

\[
V_2 \frac{d \text{ZOO}_2}{dt} = \text{Grazing (PHY}_2 \rightarrow \text{ZOO}_2) \\
+ \text{Grazing (DET}_2 \rightarrow \text{ZOO}_2) \\
- \text{Excretion (ZOO}_2) \\
- \text{Egestion (ZOO}_1) \\
- \text{Mortality (ZOO}_2) \\
\tag{11}
\]

\[
V_2 \frac{d \text{ZOO}_3}{dt} = \text{Grazing (PHY}_2 \rightarrow \text{ZOO}_3) \\
+ \text{Grazing (DET}_2 \rightarrow \text{ZOO}_3) \\
- \text{Excretion (ZOO}_3) \\
- \text{Egestion (ZOO}_1) \\
- \text{Mortality (ZOO}_3) \\
\tag{12}
\]

\[
V_1 \frac{d \text{DET}_2}{dt} = \text{Mortality (PHY}_1) \\
- \text{Decomposition (DET}_1 \rightarrow \text{DIN}_1) \\
- \text{Decomposition (DET}_1 \rightarrow \text{DON}_1) \\
- \text{Suspension (DET}_1) \\
- \text{Grazing (DET}_1 \rightarrow \text{ZOO}_2) \\
+ \text{Egestion (ZOO}_2) \\
+ \text{Mortality (ZOO}_1) \\
+ \text{Mortality (ZOO}_2) \\
+ \text{Sinking (DET}_1) \\
- \text{Sediment (DET}_1) \\
\tag{13}
\]
Fig. 5. Seasonal variations in calculated (full line) and observed (dot) values of DIN, PHY, PON, DIN, PHY, ZOO, and ZOO in the tidal flat of the Seto Inland Sea.

The details of each term are described in Appendix.

Parameters used in this numerical experiment are shown in Table 1. Almost all parameters are the values referred from the references. The major differences between our parameters and those of references are 1) the vertical eddy diffusivity between Box 2 and Box 3 (K_v = 6.8 \times 10^{-7} \text{ m}^2 \text{ s}^{-1}), that is, vertical eddy diffusivity for the pore water in our model is larger than that of HATA et al. (1995) (9.8 \times 10^{-8} \text{ m}^2 \text{ s}^{-1}), 2) the sinking speed of detritus and mortality of phytoplankton at 0°C are larger than those from the references. Tuning 1) is necessary for reproducing DIN concentration and 2) for reproducing PON and PHY concentrations. While the mortalities of microphytobenthos (PHY), deposit feeder (ZOO) and suspension feeder (ZOO) are tuned to reproduce their observed concentrations because there is no reference on these parameters.

Figure 3 shows the input data and boundary conditions for the model calculation. We assume that Dissolved Organic Nitrogen in Box 3 (DON_3), that in Box 4 (DON_4), zooplankton in Box 4 (ZOO_4), and detritus in Box 4 (DET_4) concentrations are equal to DIN in Box 3 (DIN_3), that in Box 4 (DIN_4), 0.1 times phytoplankton in Box 4 (PHY_4) and DIN, respectively. The loads of DIN, DON and DET from rivers are given as 45, 22 and 33% of TN load from three rivers, respectively, based on the results of field observation (Dr. K. Ichimi, personal communication).

The initial conditions for model compartments are given by setting the annually
averaged values of observed data in the tidal flat. The integration was carried out with a time step of 100 seconds and quasi-steady seasonal variations were obtained 3 years after the start of the calculation. The seasonal variations in the fourth year were analyzed.

5. Results and Discussion

Verification of calculation

Figure 5 shows the seasonal variations in calculated (full line) and observed (dot) DIN₁, PHY₁, PON₁, DIN₅, PHY₅, ZOO₂d and ZOO₂s concentrations at the tidal flat. The observed DIN₁ concentrations in February and November were missing. The details of seasonal variations are not reproduced enough, but the annually averaged values and phases of seasonal variations are roughly reproduced by our model. Therefore we may consider that this model results reproduce the annually averaged situation of this tidal flat.

Figure 6 (a) shows a correlation between observed and calculated values of nitrogen concentration. Only PHY₁ values are very high because they are concentrated at the surface of bottom mud of tidal flat. The correlation coefficient and the root mean squared error are 0.93 and 15.9 mgNL⁻¹, respectively. Fig. 6 (b) shows the ratio of the annually averaged calculated value to the annually averaged observed value of each compartment. We can understand that the differences between the calculated and observed values of each compartment are less than 6.0 % from Fig. 6 (b). After this, our discussion will be focused on the annually averaged values.
Present case and the case where there is no suspension feeder (bivalve)

Figure 7 shows the annually averaged values of nitrogen standing stocks and their fluxes in the present case with the suspension feeder (bivalve) at the tidal flat. The numbers in the small box show the standing stocks with the unit of KgN. The numbers on the arrow show the fluxes with the unit of KgN d^{-1}. The main pathway of the nitrogen cycling in the tidal flat was nutrients in Box 1 (DIN_{n}) \rightarrow phytoplankton (PHY_{n}) \rightarrow suspension feeder (ZOO_{n}) \rightarrow nutrients in Box 1 (DIN_{n}). The suspension feeder plays an important role in the exchange of nitrogen between the pelagic and benthic ecosystems in the tidal flat.

In recent years, the standing stock of suspension feeder has dramatically decreased while the number of red tide occurrence has increased in Japanese coastal seas with tidal flats though the nutrient load from the river has not increased (e.g. Tsutumi et al., 2003). We pay our attention to the role of suspension feeder, which is known to have the water quality purification capability by filtration of suspended matter, and want to predict the phytoplankton concentration in the case where there is no suspension feeder.

Figure 8 shows the seasonal variations of calculated values in the present case with the suspension feeder (solid line) and in the case where there is no suspension feeder (broken line). When there is no suspension feeder (ZOO_{n}) in the tidal flat, the nitrogen concen-
Fig. 8. Seasonal variations of calculated values in the present case with the suspension feeder (solid line) and the case where there is no suspension feeder (broken line).

Fig. 9. Annually averaged values of nitrogen standing stocks (KgN) and their fluxes (KgN d\(^{-1}\)) in the case where there is no suspension feeder at the tidal flat. Thick arrows show the main pathway.
trations of phytoplankton \( \text{PHY}_1 \), zooplankton \( \text{ZOO}_1 \) and detritus \( \text{DET}_1 \) in Box 1, and detritus \( \text{DET}_2 \) in Box 2 increase and the nitrogen concentration of nutrient in Box 1 \( \text{DIN}_1 \) decreases.

The nitrogen concentration of phytoplankton \( \text{PHY}_1 \) in Box 1 is about 2.3 times as high as the present case because of the vanishing of

![Diagram](https://via.placeholder.com/150)

**Fig. 10.** Annually averaged values of nitrogen budget (a) and inorganic and organic nitrogen budgets (b) in the present case with the suspension feeder.

![Diagram](https://via.placeholder.com/150)

**Fig. 11.** Annually averaged values of nitrogen budget (a) and inorganic and organic nitrogen budgets (b) in the case where there is no suspension feeder (bivalve).
grazing pressure and the red tide (PHY, concentration of 0.053 mgN L⁻¹ corresponds to 10 μgChl. α L⁻¹ which is the red tide concentration of diatom) may occur.

Figure 9 shows the annually averaged values of nitrogen standing stocks and their fluxes in the case where there is no suspension feeder at the tidal flat. The main pathway of the nitrogen cycling becomes nutrients in Box 1 (DIN) →phytoplankton (PHY) →detritus in Box 1 (DET) →detritus in Box 2 (DET).

**Water quality purification capability**

There are various viewpoints about the purification capability in the coastal sea (e.g. *Nakata* and *Hata*, 1994; *Hata et al.*, 1995; 1996; 2004; *Suzuki et al.*, 1997). In this paper, we define the purification capability as follows. One is the conversion from organic nitrogen to inorganic nitrogen (that is, mineralization). The other is the reduction of suspended matter being transported offshore (that is, removal capability of the suspended matter from the water column). In order to evaluate the purification capability of the tidal flat, we pay attention to the nitrogen budget in this tidal flat (Fig. 10 (a) and Fig. 11 (a)), and divide their budgets into inorganic nitrogen and organic nitrogen in this tidal flat (Fig. 10 (b) and Fig. 11 (b)). Figures 10 and 11 are made from Fig. 7 and Fig. 9, and they show the annually averaged values of nitrogen budget (a) and inorganic and organic nitrogen budgets (b) in the present case with the suspension feeder (Fig. 10) and the case where there is no suspension feeder (Fig. 11) at the tidal flat, respectively.

From the comparison of Fig. 10 (a) with Fig. 11 (a), we can understand that, in the case where there is no suspension feeder (Fig. 11 (a)), the nitrogen flux from the tidal flat to the mud bottom is smaller than that in the present case because the increase of detritus deposition. The detritus which is deposited to the mud bottom causes the degradation of the marine environment in this tidal flat.

To evaluate the water quality purification capability, we pay attention to the nitrogen fluxes from the land to the tidal flat (inflow) and from the tidal flat to the offshore (outflow) in Figs. 10 and 11.

From the comparison of Fig. 10 (b) and Fig. 11 (b), the water quality purification capability of the tidal flat in the case where there is no suspension feeder is lower because the outflow of organic nitrogen increases and that of inorganic nitrogen decreases compared to those in the present case.

**6. Conclusion**

A simple tidal flat model with pelagic and benthic ecosystems was developed in order to analyze the nitrogen cycling in an inter-tidal flat of the Seto Inland Sea, Japan. The main pathway of the nitrogen cycling in the present tidal flat with the suspension feeder is nutrients in the pelagic system →phytoplankton →suspension feeder (bivalve) →nutrients in the pelagic system. When there is no suspension feeder in the tidal flat, the main pathway of the nitrogen cycling in the tidal flat changes into nutrients in the pelagic system →phytoplankton →detritus in the pelagic system →detritus in the benthic system, and the concentration of phytoplankton is about 2.3 times as high as that in the present case with the suspension feeder. It results in the occurrence of red tide in the tidal flat. From the view point of the water quality purification capability of tidal flat, the water quality purification capability of the tidal flat becomes lower in the case without the suspension feeder in the tidal flat because the outflow of organic nitrogen increases compared to that in the present case.

The material cycling in the tidal flat is greatly changed by the change of benthic communities there and at the same time, the water purification capability of the tidal flat will be changed. The suspension feeder plays a very important role in the water purification capability of tidal flat.

**Appendix**

The seasonal variations in 9-component concentrations (mgN L⁻¹ except g L⁻¹ of *ZOOn* and *ZOO*n which are a soft-body dry weight) at Box 1 and Box 2 are given by the following equations. Governing equations and ecosystem processes are based on *Kawamiya et al.* (1995).
\[
\begin{align*}
\frac{d\text{DIN}_{1}}{dt} &= \text{Load from rivers (DIN}_{\text{LAI}}) \\
&= -A_1 \text{ PHY}_1 + B_2 \text{ ZOO}_1 \\
&+ C_1 \text{ DET}_1 + D_1 \text{ DON}_1 \\
&+ V_{12} B_2 \text{ ZOO}_{2s} \\
&- A_{11} \frac{Kv_{12}}{L_{12}} (\text{DIN}_1 - \text{DIN}_2) \\
&- A_{11} \frac{K_{12}}{L_{12}} (\text{DON}_1 - \text{DON}_2) \\
&- A_{11} U_{11} \text{ DON}_1 \\
\end{align*}
\]
\[\text{(A1)}\]

\[
\begin{align*}
\frac{d\text{DON}_{1}}{dt} &= \text{Load from rivers (DON}_{\text{LAI}}) \\
&+ \text{Extracellular excretion (PHY}_1) \\
&+ \text{Decomposition (DET}_1 \rightarrow \text{DON}_1) \\
&- \text{Decomposition (DON}_1 \rightarrow \text{DIN}_1) \\
&- \text{Vertical Diffusion (DON}_1, \text{ DON}_2) \\
&- \text{Horizontal Diffusion (DON}_1, \text{ DON}_2) \\
&- \text{Horizontal Advection (DON}_1) \\
\end{align*}
\]
\[\text{(A2)}\]

\[
\begin{align*}
\frac{d\text{PHY}_1}{dt} &= \text{Photosynthesis (PHY}_1) \\
&- \text{Extracellular excretion (PHY}_1) \\
&- \text{Mortality (PHY}_1) \\
&- \text{Grazing (PHY}_1 \rightarrow \text{ZOO}_1) \\
&- \text{Grazing (PHY}_1 \rightarrow \text{ZOO}_{2s}) \\
&- \text{Horizontal Diffusion (PHY}_1, \text{ PHY}_2) \\
&- \text{Horizontal Advection (PHY}_1) \\
&+ \text{Suspension (PHY}_1) \\
\end{align*}
\]
\[\text{(A3)}\]

\[
\begin{align*}
\frac{d\text{ZOO}_1}{dt} &= \text{Grazing (PHY}_1 \rightarrow \text{ZOO}_1) \\
&- \text{Decomposition (ZOO}_1) \\
&- \text{Egestion (ZOO}_1) \\
&- \text{Mortality (ZOO}_1) \\
&- \text{Horizontal Diffusion (ZOO}_1, \text{ ZOO}_2) \\
&- \text{Horizontal Advection (ZOO}_1) \\
&= V_1 (B_1 \text{ ZOO}_1 - B_2 \text{ ZOO}_2 - B_3 \text{ ZOO}_3) \\
&- b \times c \times V_{21} A_4 \text{ PHY}_2 \\
&- A_{11} U_{11} \text{ ZOO}_1 \\
\end{align*}
\]
\[\text{(A4)}\]

\[
\begin{align*}
\frac{d\text{DET}_1}{dt} &= \text{Load from rivers (DET}_{\text{LAI}}) \\
&+ \text{Mortality (PHY}_1) \\
&+ \text{Egestion (ZOO}_1) \\
&+ \text{Mortality (ZOO}_1) \\
&- \text{Decomposition (DET}_1 \rightarrow \text{DIN}_1) \\
&- \text{Decomposition (DET}_1 \rightarrow \text{DON}_1) \\
&- \text{Horizontal Diffusion (DET}_1, \text{ DET}_1) \\
&- \text{Sinking (DET}_1) \\
&+ \text{Suspension (PHY}_1) \\
&+ \text{Suspension (DET}_1) \\
&+ \text{Egestion (ZOO}_1) \\
\end{align*}
\]
\[\text{(A5)}\]
+ Excretion (ZOOa)
− Vertical Diffusion (DINb, DINs)
− Horizontal Diffusion (DINb, DINs)
− Nitrification (DINs)

\[ V_{21} (A1, B1_{21}, PHY_{31} + C1, DET_{12} + DI_{12}, DON_{12}) \]

\[ + V_{22} (B2_{21}, ZOO_{21}) \]

\[ − A_{21} \frac{K_{V_{21}}}{L_{23}} (DIN_{21} − DIN_{2}) \]

\[ − A_{12} \frac{K_{V_{12}}}{L_{12}} (DIN_{12} − DIN_{1}) \]

\[ − A_{12} DET_{1}, DIN_{2} \]  

(A6)

\[ \frac{dDON_{12}}{dt} = \text{Extracellular excretion (PHY}_{31}) \]

\[ + \text{Decomposition (DET}_{12} → DON_{12}) \]

\[ − \text{Decomposition (DON}_{21} → DIN_{2}) \]

\[ − \text{Vertical Diffusion (DON}_{21}, DON_{12}) \]

\[ − \text{Vertical Diffusion (DON}_{21}, DON_{12}) \]

\[ = V_{21} (A1_{12}, A2_{12}, PHY_{12} + C2_{12}, DET_{1} + DI_{12}, DON_{12}) \]

\[ − A_{21} \frac{K_{V_{21}}}{L_{23}} (DON_{21} − DON_{12}) \]

\[ − A_{12} \frac{K_{V_{12}}}{L_{12}} (DON_{12} − DON_{1}) \]  

(A7)

\[ \frac{dPHY_{31}}{dt} = \text{Photosynthesis (PHY}_{31}) \]

\[ − \text{Extracellular excretion (PHY}_{31}) \]

\[ − \text{Mortality (PHY}_{31}) \]

\[ − \text{Suspension (PHY}_{31}) \]

\[ − \text{Grazing (PHY}_{31} → ZOO_{31}) \]

\[ = V_{21} (A1_{12}, PHY_{31} − A1_{1}, A2_{1}, PHY_{3} − A3, PHY_{3} + A4; PHY_{4}) \]

\[ − V_{21} (B1_{31} + ZOO_{31}) \]  

(A8)

\[ \frac{dZOO_{31}}{dt} = \text{Grazing (PHY}_{31} → ZOO_{31}) \]

\[ + \text{Grazing (DET}_{12} → ZOO_{31}) \]

\[ − \text{Excretion (ZOO}_{31}) \]

\[ − \text{Egestion (ZOO}_{31}) \]

\[ − \text{Mortality (ZOO}_{31}) \]

\[ = V_{21} (B1_{31} + ZOO_{31} + B1_{32} + ZOO_{32}, \]

\[ − B2_{31} ZOO_{31} + B3_{31} ZOO_{31} + B4_{31} ZOO_{31}, \]

\[ (A9) \]

\[ \frac{dZOO_{32}}{dt} = \text{Grazing (PHY}_{31} → ZOO_{32}) \]

\[ + \text{Grazing (PHY}_{31} → ZOO_{32}) \]

\[ − \text{Excretion (ZOO}_{32}) \]

\[ = V_{21} (B1_{32} + ZOO_{32} + B1_{32} + ZOO_{32} + B2_{32} + ZOO_{32}, \]

\[ − B3_{32} ZOO_{32} + B4_{32} ZOO_{32} \]

\[ (A10) \]

\[ \frac{dDET_{12}}{dt} = \text{Mortality (PHY}_{31}) \]

\[ − \text{Decomposition (DET}_{12} → DIN_{12}) \]

\[ − \text{Decomposition (DET}_{12} → DON_{12}) \]

\[ − \text{Suspension (DET}_{12}) \]

\[ − \text{Grazing (DET}_{12} → ZOO_{31}) \]

\[ + \text{Egestion (ZOO}_{31}) \]

\[ + \text{Mortality (ZOO}_{31}) \]

\[ + \text{Mortality (ZOO}_{31}) \]

\[ + \text{Sinking (DET}_{12}) \]

\[ − \text{Sediment (DET}_{12}) \]

\[ = V_{21} (A3_{12}, PHY_{31} − C1_{1}, DET_{1} + C2_{1}, DET_{1} − 0.5 A4_{1}, DET_{1}) \]

\[ − V_{21} (− B1_{31} + ZOO_{31} + B3_{31} ZOO_{31} + B4_{31} ZOO_{31} + B5_{31} ZOO_{31} + B6_{31} ZOO_{31}) \]

\[ + A_{12} \frac{w_{a}}{L_{12}} DET_{1} \]

\[ − A_{12} S_{i2} DET_{1} \]  

(A11)

Here \( dt \) is the time step in second. \( V \) is the volume in liter, subscript 1, 21 and 22 denote 0 to 1 m water depth in Box 1, 0 to 0.5 cm sediment depth in Box 2 and 0 to 10 cm sediment depth in Box 2, respectively. \( A \) is the sectional area in \( m^2 \), \( L \) is the distance in meter, \( U \) is the current velocity in \( m \ s^{-1} \), \( Kh \) is the horizontal eddy diffusivity in \( m^2 \ s^{-1} \), \( Kv \) is the vertical eddy diffusivity in \( m^2 \ s^{-1} \), subscript 12 denotes between Box 1 and Box 2, subscript 23 denotes between Box 2 and Box 3, subscript 14 denotes between Box 1 and Box 4. \( w_{a} \) is the sinking speed of detritus in \( m \ s^{-1} \), \( s_{i} \) is the sedimentation speed of detritus in \( m \ s^{-1} \). Subscript LA1 denotes the load from rivers.

A1 is photosynthesis by primary producer and is represented by the following equation:

\[ A1_t = Vm_{11} \left( \frac{DIN_{11}}{DIN_{11} + Kh_{11}} \right) \times \exp \left( k_{1}T_{1} \right) \]

\[ \times \frac{L_{1}}{lopt_{1}} \exp \left( 1 - \frac{L_{1}}{lopt_{1}} \right) \]

(A12)

\[ A1_t = Vm_{11} \left( \frac{DIN_{12}}{DIN_{12} + Kh_{12}} \right) \times \left( 0.081 \times T_{2} + 1.48 \right) \]

\[ \frac{3.83}{3.83} \]
\[
\frac{(7.85 - \text{TANH} \left( \frac{0.0785 - I_s}{7.85} \right))}{8.84} \quad (A13)
\]

where subscripts 1 and 2 denote Box 1 (or phytoplankton in Box 1) and Box 2 (or microphytobenthos in Box 2), respectively. The function of temperature and light in the photosynthesis equation by microphytobenthos (that is, the second and third term in right-hand side of Eq. (A13)) is experimental equation of Montani et al. (2003). \( V_m \) (d:\(^{-1}\)) is the maximum photosynthesis speed of primary producer, \( K_n \) (mgN L:\(^{-1}\)) is a half saturation constant for DIN, \( k_i \) (\(^\circ\)C:\(^{-1}\)) is the temperature dependency of photosynthesis, \( T \) (\(^\circ\)C) is water temperature, \( I \) is the average light intensity and \( I_{opt} \) (cal m:\(^{-2}\) d:\(^{-1}\)) is optimum light intensity for photosynthesis. \( I_i \) (converted into cal m:\(^{-2}\) d:\(^{-1}\)) and \( I_s \) (converted into \( \mu \)E m:\(^{-2}\) d:\(^{-1}\)) and \( I_r \) (converted into MJ m:\(^{-2}\) d:\(^{-1}\)) \( = 4.52 \text{ E m}^{-2} \text{ d}^{-1} \) are the average light intensity reaching the Box 1 and Box 2, respectively. They were calculated using the following equation:

\[
I_i = I_0 \times d \quad (A14)
\]
\[
I_s = I_0 \times d \times r \quad (A15)
\]

where \( I_0 \) (MJ m:\(^{-2}\) d:\(^{-1}\)) is the total surface radiation observed at the Takamatsu Meteorological Observatory. \( d \) is the percentage of irradiance reduction through the water column and is calculated using the following exponential equation (Montani et al., 2003):

\[
d = \frac{95.2}{H_1} \int_{0}^{H_1} 10^{(-0.143Z_i)} \, dZ_i \quad (A16)
\]

where \( H_1 \) (m) is the water depth. \( r \) is the percentage of light reduction through the sediments and is calculated using the following exponential equation (Montani et al., 2003):

\[
r = \frac{100}{H_2} \int_{0}^{H_2} 10^{(-1.483Z_s)} \, dZ_s \quad (A17)
\]

where \( H_2 \) (mm) is the sediment depth.

\( A2 \) is the ratio of extracellular exertion of DON accompanying photosynthesis and is given by the constant value (Table 1).

Subscripts 1 and 2 denote phytoplankton in Box 1 and microphytobenthos in Box 2, respectively.

\( A3 \) is the mortality of primary producer and is represented by the following equation:

\[
A3_i = Mpo_i \exp (hmp \times T) \quad (A18)
\]
\[
A3_s = Mpo_s \exp (hmp \times T) \quad (A19)
\]

where subscripts 1 and 2 denote Box 1 (or phytoplankton in Box 1) and Box 2 (or microphytobenthos in Box 2), respectively. \( Mpo \) (L mgN:\(^{-1}\) d:\(^{-1}\)) is the mortality rate of primary producer at 0\(^\circ\)C, \( hmp \) (\(^\circ\)C:\(^{-1}\)) is temperature coefficient for mortality.

\( A4 \) is the suspension speed of microphytobenthos and detritus caused by wind waves and is represented by the following equation:

\[
A4 = a \times W^2 \quad (A20)
\]

where \( a \) is coefficient, \( W \) (m s:\(^{-1}\)) is the wind speed. \( b \) and \( c \) are a coefficient about suspension of microphytobenthos (PHY\(_s\)). The suspended PHY\(_s\) is assumed as follows. All of the suspended PHY\(_s\) becomes a target as food of suspension feeder ZOO\(_s\), however, the suspended PHY\(_s\) not eaten by suspension feeder ZOO\(_s\) becomes PHY\(_s\) (b percent) and DET\(_s\) (1\( - b \) percent). \( c \) is a coefficient and is represented by the following equation:

\[
c = 1 - \frac{0.5 \times V_{z_s} \times CR_{z_s} \times ZOO_{z_s}}{V_1} \quad (A21)
\]

\( B1 \) is the grazing by secondary producer. \( B1_i \) is the grazing PHY\(_i\) by zooplankton and is represented by the following equation:

\[
B1_i = a \times \left\{ 1 - \exp \left( \lambda (PHY^*_s - PHY_{s_i}) \right) \right\} \exp (k_i T_i) \quad (A22)
\]

where subscript 1 denote Box 1 (or zooplankton in Box 1). \( a \) (d:\(^{-1}\)) is the maximum grazing speed at 0\(^\circ\)C, \( \lambda \) ((mgN L:\(^{-1}\)):\(^{-1}\)) is Ivlev’s constant, PHY\(_*\) (mgN L:\(^{-1}\)) is the threshold of grazing (that is, when the concentration of phytoplankton is lower than PHY\(_*\), the grazing by zooplankton becomes zero). \( k_i \) (\(^\circ\)C:\(^{-1}\)) denotes the temperature dependency of grazing. The PHY\(_s\) and DET\(_s\) grazing by deposit feeder are based on the grazing by suspension feeder (Nakamura, 2004) and are represented by the
following equation, respectively:
\[
B_{1a-1} = 0.5 \times CR_{a} \times PHY_{2} \quad (A23)
\]
\[
B_{1a-1} = 0.5 \times CR_{a} \times DET_{2} \quad (A24)
\]
where subscripts 2, 2d, 2d-1 and 2d-2 denote Box 2, deposit feeder in Box 2, the PHY$_{2}$ grazing by deposit feeder in Box 2, the DET$_{2}$ grazing by deposit feeder in Box 2, respectively. CR$_{a}$ is the clearance rate by deposit feeder and is represented by the following equation:
\[
CR_{a} = 2.41 \times w_{a}^{0.32} \times f(T_{a}) \quad (A25)
\]
\[
f(T_{a}) = \frac{-0.0549 \times T_{a}^{2} + 2.67 \times T_{a} - 11.2}{18.9} \quad (A26)
\]
where $w_{a}$ (g ind.⁻¹) is soft–body dry weight of deposit feeder, $f$ is the function of temperature. The PHY$_{1}$ and PHY$_{2}^{'}$ grazing by suspension feeder are represented by the following equation (NAKAMURA, 2004), respectively:
\[
B_{1s-1} = 0.5 \times CR_{s} \times PHY_{1} \quad (A27)
\]
\[
B_{1s-1} = 0.5 \times CR_{s} \times PHY_{2}^{'} \quad (A28)
\]
\[
PHY_{2}^{'} = \frac{V_{b} \times A_{s} \times PHY_{s}}{V_{i}} \quad (A29)
\]
where subscripts 2s, 2s-1 and 2s-2 denote suspension feeder in Box 2, the PHY$_{1}$ and PHY$_{2}^{'}$ grazing by suspension feeder in Box 2, respectively. PHY$_{2}^{'}$ is the suspended PHY$_{2}$ in Box 1. CR$_{s}$ is the clearance rate by suspension feeder and is represented by the following equation:
\[
CR_{s} = 2.41 \times w_{s}^{0.32} \times f(T_{s}) \quad (A30)
\]
\[
f(T_{s}) = \frac{-0.0549 \times T_{s}^{2} + 2.67 \times T_{s} - 11.2}{18.9} \quad (A31)
\]
where $w_{s}$ is soft–body dry weight of suspension feeder, $f$ is the function of temperature.

$B_{2}$ is the excretion generation speed of secondary producer and is represented by the following equation:
\[
B_{2a} = \alpha_{a} B_{1a} \quad (A32)
\]
\[
B_{2a} = \alpha_{a} (B_{1s-1} + B_{1s-2}) \quad (A33)
\]
\[
B_{2a} = \alpha_{a} (B_{1s-1} + B_{1s-2}) \quad (A34)
\]
where subscripts 1, 2d and 2s denote zooplankton in Box 1, deposit feeder in Box 2 and suspension feeder in Box 2, respectively. $\alpha$ is assumed to be proportional to the grazing $B_{1}$.

$B_{3}$ is the egestion generation speed of secondary producer and is represented by the following equation:
\[
B_{3} = \beta B_{1} \quad (A35)
\]
\[
B_{3a} = \beta_{a} (B_{1a-1} + B_{1a-2}) \quad (A36)
\]
\[
B_{3a} = \beta_{a} (B_{1s-1} + B_{1s-2}) \quad (A37)
\]
where subscripts 1, 2d and 2s denote zooplankton in Box 1, deposit feeder in Box 2 and suspension feeder in Box 2, respectively. $\beta$ is assumed to be proportional to the grazing $B_{1}$.

$B_{4}$ is the mortality speed of secondary producer at 0°C and is represented by the following equation:
\[
B_{4a} = M_{zo} \exp (kmz_{i} T_{i}) \quad (A38)
\]
\[
B_{4a} = M_{zo} \exp (kmz_{s} T_{s}) \quad (A39)
\]
\[
B_{4a} = M_{zo} \exp (8.5 - \exp (kmz_{s} T_{s})) \quad (A40)
\]
where subscripts 1, 2d and 2s denote zooplankton in Box 1, deposit feeder in Box 2 and suspension feeder in Box 2, respectively. $M_{zo}$ (L mgN⁻¹ d⁻¹) is the mortality of secondary producer at 0°C, $kmz$ (°C⁻¹) is the temperature dependency of mortality of secondary producer.

$C_{1}$ and $C_{2}$ are decomposition of detritus to give DIN and DON, respectively. $C_{1}$ and $C_{2}$ are represented by the following equation:
\[
C_{1} = V_{ni} \exp (kvni T_{i}) \quad (A41)
\]
\[
C_{1} = V_{ni} \exp (kvni T_{s}) \quad (A42)
\]
\[
C_{2} = V_{no} \exp (kwno T_{i}) \quad (A43)
\]
\[
C_{2} = V_{no} \exp (kwno T_{s}) \quad (A44)
\]
where subscripts 1 and 2 denote Box 1 and Box 2. $V_{ni}$ ('d⁻¹) is decomposition speed of detritus to DIN at 0°C, $V_{no}$ ('d⁻¹) is decomposition speed of detritus to DON at 0°C, $kvn$ (°C⁻¹) is temperature dependency of decomposition of detritus to DIN, $kwn$ is temperature dependency of decomposition of detritus to DON.

$D_{1}$ is decomposition of DON to DIN and is represented by the following equation:
\[
D_{1} = V_{di} \exp (kvdi T_{i}) \quad (A45)
\]
\[
D_{1} = V_{di} \exp (kvdi T_{s}) \quad (A46)
\]
where subscripts 1 and 2 denote Box 1 and Box 2. $V_{di}$ ('d⁻¹) is decomposition speed of DON to DIN at 0°C, $kvdi$ (°C⁻¹) is temperature dependency of decomposition of DON to DIN.

$E_{1}$ is denitrification speed from Box 2 and is
represented by the following equation, based on Koike (1991):

\[ E_t = V_{de_t} \exp (k_{de_t} \cdot T) \]  \hspace{2cm} (A47)

where \( V_{de_t} \) (d\(^{-1}\)) is denitrification speed, \( k_{de_t} \) (°C\(^{-1}\)) is temperature dependency of denitrification.

References


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Growth and reproduction of the pillumnid crab *Benthopanope indica* (Decapoda: Brachyura) in Tateyama Bay, Japan

Wataru DOI, Masashi YOKOTA and Seiichi WATANABE

**Abstract:** The growth and reproduction of the pillumnid crab, *Benthopanope indica*, were examined from April 2001 to March 2002 in Tateyama Bay, central Japan. Ovigerous females were mainly observed from June to August, whereas small juveniles were recruited from August to January. After settlement, juveniles (carapace width, CW, of less than 2 mm) grew to and exceeded the mature size (CW 5.80 mm in males and 4.54 mm in females) by the following April. Although large males had considerably larger major chelipeds, their relative growth did not correspond to sexual maturity. The relative growth rate of the male abdominal width decreased at the puberty molt. Enlargement of the abdomen occurred in the mature females, but it was difficult to distinguish postpubertal females from prepubertal females on the basis of abdominal width only, because some females had intermediate abdominal widths, between those of pre- and postpubertal females. Brood size correlated positively with CW, ranging from 120 to 1,700 eggs. After the reproductive season, many large individuals died of senescence, with a longevity of almost one year. However, from size frequency distributions and growth rate analysis, it is likely that some individuals survived until the next reproductive season.

**Keywords:** *Benthopanope indica*, Pilumnidae, growth, reproduction

1. **Introduction**

   The pillumnid crab *Benthopanope indica* (Decapoda, Brachyura) is a small species that attains a carapace width (CW) of approximately 11 mm. It inhabits the branches or roots of the brown alga *Sargassum thunbergii* and under calcareous algae in the intertidal zone. It has been recorded from the temperate to subtropical region of the Indo–West Pacific Ocean (Sakai, 1976; Miyake, 1998). Davie (1989) transferred this species from the genus *Pilumnopeus* (Sakai, 1976; Miyake, 1998) to the new genus *Benthopanope* established by him. *Benthopanope* is distinguished from other genera by its postlarval morphological characteristics. Ko (1995) described the complete larval development of *B. indica* and confirmed Davie’s classification. The crab of this genus recorded in Japan is *B. indica* only (Davie, 1989).

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The growth and reproduction of Xanthoidea have frequently been investigated, especially those of Menippidae (e.g., Tweedale et al., 1993), Xanthidae (e.g., Knudsen, 1960), Panopeidae (e.g., McDonald, 1982), and Eriphiidae (e.g., Tomikawa and Watanabe, 1992). No such studies of the Pilumnidae have been performed until recently, although there are 400 pillumnid species all over the world (Ng and Huang, 2002). The limited references to the Pilumnidae include reports of their embryonic and postembryonic development (Wear, 1967; Clark and Ng, 2004), agonistic behavior (Lindberg and Frydenberg, 1980), fecundity (Almaca, 1987), size at sexual maturity (Kuhlmann and Walker II, 1999), feeding (Kyomo, 1999), reproductive behavior (Kyomo, 2001), reproductive cycle (Kyomo, 2002; Litulo, 2005a), and population structure (Litulo, 2005a, b).

The mouth of Tokyo Bay is by the side of the Kuroshio Current and many aquatic organisms exist in this coastal area. Various crab species including warm-water species, also live on the
reef. Therefore, basic ecological studies of these crabs have been undertaken: the majids *Tiarinia corningera* (Tsuchida and Watanabe, 1991) and *Pugettia quadridens quadridens* (Fuseya and Watanabe, 1993; Fuseya et al., 2001), the xanthid *Leptodius exaratus* (Watanabe et al., 1990), the eriphiid *Eriphia smithii* (Tomikawa and Watanabe, 1992), the plagiudiid *Plagusiida dentipes* (Tsuchida and Watanabe, 1997; Samson et al., 2007), the hymenosomatid *Rhynchoplax coralica* (Gao et al., 1994), the portunids *Thalamita sima* (Norman, 1996) and *Thalamita pelisarti* (as T. prymna; Norman et al., 1997). Although *B. indica* is one of the dominant crabs in this area (personal observation), its life history has not yet been investigated.

In this study, monthly sampling over one year and the morphometric analysis of several body parts of the collected samples were used to clarify the patterns of growth and reproduction and size at sexual maturity. The life history of *B. indica* was inferred from the data.

### 2. Materials and Methods

Samples were collected monthly between April 2001 and March 2002 at upper intertidal zone on the rocky shore near the Tateyama Marine Station, Field Science Center of Tokyo University of Marine Science and Technology, located near the tip of Boso Peninsula, Chiba Prefecture, Japan (Fig. 1). Crabs attached to the roots of the brown alga *S. thunbergii* or hidden below the calcareous algae were collected by hand and forceps during the day (April–October) or at night (November–March) during low tide. Sampling was performed in those algae associations randomly selected until up to about one hundred individuals were collected but the sample size could not reach the purpose in April and May in 2001. The specimens were preserved in 10% formaldehyde–sea water. The crabs were sexed based on the form of the pleopods and the location of the gonopores. The females were checked for the presence or absence of attached eggs in the pleopods. Ovigerous females were separated into those bearing early developing (nonpigmented–eyed) eggs and those with pigmented–eyed eggs. Carapace width (CW) to the nearest 0.01 mm was measured with digital calipers in all specimens and CW frequency distributions by sex for 1 mm intervals were constructed for each month.

Carapace width and the following body parts were measured to the nearest 0.01 mm with digital calipers and under a stereomicroscope using a micrometer: propodus length (PL) and height (PH) of the major chelipeds and the width of the fifth abdominal segment (AW). Cheliped handedness was determined by the size and dentition of the cheliped.

To detect quantititative morphological changes, the growth of some body parts
Fig. 2. Monthly changes in the size frequency distribution of *Benthopanope indica* from April 2001 to March 2002. Figures at the right side of each box indicate the number of individuals in each category.
relative to the CW was analyzed with regression lines. If a morphological change in a body part does not occur during growth, the relationship between the body part and CW is usually described by a single regression line. Conversely, when a morphological change occurs in a body part, two or more regression lines are possible. If the ranges of CW of the two regression lines do not overlap, we can estimate the parameter of the regression lines by searching statistically for the inflection point. We used the Akaike’s information criterion (AIC) method (Akaike, 1973) as the criterion for detecting the best-fit inflection point between two regression lines (see Doi et al., 2007). The inflection point was estimated by the stepwise calculation of each 0.10 mm. In the case of overlapping CW ranges in the regression lines, we tried to distinguish them using the body part/CW ratio.

The total numbers of external eggs (NE) attached to the pleopods of all ovigerous females were counted under a stereomicroscope. To evaluate the relationship between CW and NE, a power function was fitted by the nonlinear least square methods using Solver, a nonlinear optimization tool in Excel 2003 (Microsoft, Tokyo, Japan). To estimate mean egg diameter, the longest and shortest diameters closest to 0.025 mm were measured using a micrometer under a binocular microscope.

3. Results

Growth

The total number of crabs sampled was 1,128, consisting of 572 males, 548 females, eight small individuals of unidentified sex, and two intersex individuals. The CW ranged from 1.29 to 11.32 mm for males and from 1.32 to 9.51 mm for females. The CW frequencies were relative uniformly distributed over the entire size range from April to July (Fig. 2). The size frequency distribution showed that the population was composed of two size groups larger and smaller than ca 7.00 mm CW in June and July. The small crabs (CW<7.00 mm) grew during this period. Whereas those adults comprised the main group in August, they almost disappeared and juveniles (CW<4.00 mm) became the main group in September. The recruits began to occur in August and comprised most of the population from September to March. Although alteration of the cohorts (year class) was clearly observed between August and September, few larger crabs of the previous cohort were observed to have survived.

Reproduction

A total of 44 ovigerous females were collected during the study and their sizes ranged from 4.54 to 9.51 mm CW (mean ± SD, 6.37 ± 1.26) (Fig. 2). Ovigerous females were found from June to September. Their frequency was low in June (7.6%), but increased abruptly to > 30% in July (32.8%) and August (47.6%). Only one specimen was sampled in September (2.1%). Females bearing eyed eggs were collected except in June and their frequencies were 12.1% and 14.3% in July and August, respectively. The mean CW (± SD) of ovigerous females in those months were 8.30 ± 0.93 mm, 6.82 ± 1.23 mm, and 5.63 ± 0.50 mm in June, July, and August, respectively, and the CW of one ovigerous female in September was 5.06 mm.

Relative growth

AIC analysis of two relative size relations (PL to CW, PH to CW) produced two regression lines in males (Fig. 3, Table 1). The inflection points of PL and PH were at CW values of 7.50 mm and 7.60 mm, respectively. The secondary sexual characteristic, elongation of the cheliped, was more clearly observed in the PL value. The relative growth of AW in males was divided into two lines at the CW value of 5.80 mm (Fig. 4; Table 1). The gradient of the upper line was smaller than that of the lower line. There was no marked increase of the cheliped in females. The increase in both PL and PH relative to CW was fitted to a single straight line (Table 1). The female abdominal segment showed considerable enlargement by the puberty molt (Fig. 5). An overlap of the mature, immature, and transition groups was observed from CW larger than 3.00 mm. Therefore, a single straight line representing the growth of AW relative to CW was fitted only for ovigerous females (Fig. 5, Table 1).

The minimum AW/CW value in ovigerous females was 0.293. Assuming this value to be the
Fig. 3. Growth of propodus length relative to carapace width in male *Benthopanope indica*.

Table 1. Regression lines $y = a + bx$ for the morphometric analysis of *Benthopanope indica*. Asterisk indicates that the slope ($b$) is significant (* t test; * $P<0.001$). Dagger indicates that the slope ($b$) is significantly different between sexes (ANCOVA; † $P<0.001$). AIC, Akaike’s information criterion; AW, fifth abdominal segment width; CW, carapace width; IP, inflection point; NA, not applicable; PH, propodus height of the major cheliped; PL, propodus length of the major cheliped.

<table>
<thead>
<tr>
<th>Sex</th>
<th>No. regression lines</th>
<th>AIC</th>
<th>IP (mm, CW)</th>
<th>CW range</th>
<th>Intercept ($a$)</th>
<th>Slope ($b$)</th>
<th>N</th>
<th>R</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male</td>
<td>1</td>
<td>536</td>
<td>1.47-11.32</td>
<td>1.47-11.32</td>
<td>-1.150</td>
<td>1.057</td>
<td>480</td>
<td>0.979</td>
<td>NA†</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>442</td>
<td>7.50</td>
<td>1.47-7.47</td>
<td>0.75</td>
<td>0.939</td>
<td>431</td>
<td>0.970</td>
<td>NA†</td>
</tr>
<tr>
<td>PH</td>
<td>1</td>
<td>-54</td>
<td>NA</td>
<td>1.47-11.32</td>
<td>-2.372</td>
<td>1.247</td>
<td>49</td>
<td>0.879</td>
<td>NA†</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>-113</td>
<td>7.60</td>
<td>1.47-7.57</td>
<td>-0.636</td>
<td>0.629</td>
<td>435</td>
<td>0.967</td>
<td>NA†</td>
</tr>
<tr>
<td>AW</td>
<td>1</td>
<td>-1374</td>
<td>NA</td>
<td>1.29-11.32</td>
<td>0.094</td>
<td>0.181</td>
<td>570</td>
<td>0.980</td>
<td>NA†</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>-1447</td>
<td>5.80</td>
<td>1.29-5.79</td>
<td>0.004</td>
<td>0.205</td>
<td>421</td>
<td>0.965</td>
<td>NA†</td>
</tr>
<tr>
<td>Female</td>
<td>1</td>
<td>NA</td>
<td>1.32-9.41</td>
<td>1.32-9.41</td>
<td>0.232</td>
<td>0.803</td>
<td>459</td>
<td>0.973</td>
<td>* NA</td>
</tr>
<tr>
<td>PH</td>
<td>1</td>
<td>NA</td>
<td>1.32-9.41</td>
<td>1.32-9.41</td>
<td>-0.124</td>
<td>0.459</td>
<td>460</td>
<td>0.970</td>
<td>* NA</td>
</tr>
<tr>
<td>AW</td>
<td>1</td>
<td>NA</td>
<td>4.54-9.51</td>
<td>4.54-9.51</td>
<td>0.270</td>
<td>0.367</td>
<td>44</td>
<td>0.975</td>
<td>* NA</td>
</tr>
</tbody>
</table>

puberty point, we distinguished nonovigerous females at two stages: postpuberty $\geq 0.293$ and prepuberty $<0.293$ (Fig. 6). There were not only postpubertal females with broad abdomens, but also those with extremely narrow abdomens between June and September. Although the change of generations occurred after the main reproductive season (June to August), postpubertal and mature-sized females were found with a mean CW that was greater than that of ovigerous females (6.37 mm CW). Whereas the postpubertal females were included in the group with large CW in most months, females at the postpuberty that were smaller than the smallest ovigerous female (4.54 mm CW) were found in December,
Fig. 4. Growth of fifth abdominal segment width relative to carapace width in male *Benthopanope indica*.

Fig. 5. Growth of fifth abdominal segment width relative to carapace width in female *Benthopanope indica*. Open and closed circles indicate nonovigerous and ovigerous females, respectively.
Fig. 6. Monthly changes in the relationship between carapace width (CW) and abdominal width (AW), AW/CW, in female Benthopanope indica from April 2001 to March 2002. Closed circles, open circles, and crosses indicate ovigerous females, nonovigerous females with wide abdomens (AW/CW ≥ 0.293), and nonovigerous females with narrow abdomens (AW/CW < 0.293), respectively. Solid and dashed vertical lines indicate the smallest (4.54 mm) and mean CW of ovigerous females (6.37 mm), respectively. Horizontal lines indicate the puberty point (AW/CW = 0.293).
March, and especially in April. Sexual dimorphism in growth rates relative to CW was found for all parameters evaluated (Table 1).

**Brood size and egg size**

The numbers of eggs of the 44 ovigerous females (4.54–9.51 mm CW) ranged from 120 to 1,739. Egg number increased with CW (Fig. 7), and large females had large numbers of eggs. The relationship between brood size (number of eggs, NE) and CW is described as follows: \( NE = 2.003CW^{2.946} \) \((N = 44, R^2 = 0.895, P < 0.05)\). The mean diameter of noneyed eggs was 0.38 ± 0.03 mm \((N = 300, 10\) broods), and was significantly smaller than that of eyed eggs, with a mean diameter of 0.42 ± 0.03 mm \((N = 360, 12\) broods) \((t\) test, \(P < 0.01)\).

**4. Discussion**

Newly settled crabs \((CW < 2.00\ mm)\) were found from August, and the smallest males and females \((CW 1.32\ mm\ and\ CW 1.29\ mm,\ respectively)\) were collected in September. From these results, we infer that the beginning of recruitment of the small crabs occurred in August or early September. KO (1995) reported that the period from the first zoea to the first juvenile crab of *B. indica* was at least 24–28 days \((20–25\ \degree C)\) and that the size of the megalopa was 0.87 mm. QUINTANA (1986) showed that the CWS of the megalopa and the first-, second-, and third-stage crabs in the related pilumnid, *Parapilumnus trispinosus*, were 0.83, 1.28, 1.58, and 1.77 mm, respectively. Therefore, these small crabs of *B. indica* might constitute the first postlarval stage one month after hatching, and the earliest hatching females might be from the preceding June or early July. This corresponds to the earliest month \((June)\) in which we collected ovigerous females (Fig. 2).

It is difficult to estimate the final reproductive season from our current data because of inconsistencies in the results. Ovigerous females were collected until September, whereas several crabs of the small size group were sampled in January (Fig. 2). If the period from hatching to recruitment was also one month in the final reproductive season, the small crabs of the final season would have been born around December or late November. However, it was only...
three months before we collected the final ovigerous females. This inconsistency is remarkable. There are three possible explanations of this discrepancy. First, the recruits could be transported from the southern populations with the longer reproductive season through the warm oceanic current. For instance, the tropical and sub-tropical hermit crabs, Calcinus spp., could be collected in this area (Murata et al., 1991). The larval transportation through the oceanic current would play an important role in the source of the recruits of B. incica in this area. Second, the actual pelagic larval period could be longer because the described period was measured in the warmer season. Further research into the relationship between larval development and environmental conditions should clarify this. Third, samples of ovigerous females would not have been caught later in the reproductive season because the main reproductive season had already finished. As we will explain in a later section, this species has two forms of life history. Thus, several mature or mature-like females do not die out, but live beyond the main reproductive season. Occasionally, the surviving females produce eggs until the end of autumn. These results lead us to hypothesize that the reproductive season of this species extends at least from June to September (three months), or slightly longer, until October or November in this area. This seasonality and the duration of the reproductive period are similar to those of the xanthid crab Leptodius exaratus (Watanabe et al., 1990), the eriphiid crab Eriphia smithii (Tomikawa and Watanabe, 1992), the majid crab Tiaria
cornigera (Tsuchida and Watanabe, 1991), the portunid crab Thalamita pelsarti (Norman et al., 1997), and the hymenosomatid crab Rhynchoplax coralicola (Gao et al., 1994) in the same study area. B. indica and these five species are warm-water species and the present study area is the northern limit in their distributions except for R. coralicola (Sakai, 1976; Miyake, 1998). The reproductive season of all warm-water species are limited in about three warmer months in this area. In contrast, other temperate species with the northward distribution have longer reproductive period and/or different seasonality in this area: February–August in the majid crab Pugettia quadridens quadridens (Fuseya and Watanabe, 1993), October–December in the plagusiid crab Plagusia dentipes (Tsuchida and Watanabe, 1997). These patterns of reproductive seasons are possibly related to physiological difference between warmer and temperate species.

In September 2001, a considerable number of small crabs appeared and grew. In the same month, the number of large crabs decreased, although they had comprised the major proportion of the population in previous months. Most individuals that have completed their reproductive activity probably die from senescence. Therefore, their longevity is almost one year. However, some crabs might live for more than one year. From September onwards, a few large crabs were distinguishable from the juveniles recruited in August. To confirm the age of those large crabs, we analyzed their growth rates as follows. We assumed that all the crabs settled on September 1 and calculated the growth rate (∆CW),

Table 2. Growth rate (∆CW) analysis based on the assumption that all crabs were recruited on September 1, 2001, in Benthopanope indica. ∆CW is calculated as follows, ∆CW = CWn − CWi−1, where ∆CW and CW are the growth rate and carapace width of individual i in month t, respectively. CW is the mean carapace width in month t−1. Individuals with − ∆CW were excluded from the analyses because they hatched after September 1, 2001.

<table>
<thead>
<tr>
<th>Month</th>
<th>Male ΔCW (≥ 0)</th>
<th>Female ΔCW (≥ 0)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>Range</td>
</tr>
<tr>
<td>Oct.</td>
<td>1.61</td>
<td>0.04–5.70</td>
</tr>
<tr>
<td>Nov.</td>
<td>1.35</td>
<td>0.01–4.79</td>
</tr>
<tr>
<td>Dec.</td>
<td>1.57</td>
<td>0.01–5.43</td>
</tr>
<tr>
<td>Jan.</td>
<td>1.25</td>
<td>0.06–4.22</td>
</tr>
<tr>
<td>Feb.</td>
<td>1.50</td>
<td>0.13–5.03</td>
</tr>
<tr>
<td>Mar.</td>
<td>1.25</td>
<td>0.19–3.98</td>
</tr>
</tbody>
</table>
\[ \Delta CW_i = CW_a - CW_{i-1}, \]

where \( \Delta CW_i \) and \( CW_a \) are the growth rate and CW of individual \( i \) in month \( t \). \( CW_{i-1} \) is the mean CW in month \( t-1 \). \( \Delta CW_i \) values that were <0 were excluded from the analysis because those individuals had hatched after September 1, 2001. Although the mean \( \Delta CW \) ranged from 1.17 to 1.88, the maximum \( \Delta CW \) showed a considerably higher value (3.34–5.70) in each month (Table 2). Individuals with extremely high \( \Delta CW \) could have been members of the previous year class that had survived after the reproductive season. However, their size frequency distributions were unclear because the sample size was small. The presence of two longevity forms is similar to those of the majid crabs *T. corniger* (TSUCHIDA and WATANABE, 1991) and *P. quadridentis quadridens* (FUSEYA and WATANABE, 1993) in the same study area.

The relative growth rates of male PL and PH increased at the inflection points of 7.50 mm and 7.60 mm CW, respectively. Although both inflection points were close, it is doubtful that these changes reflect physiological maturity. The growth of Brachyura displays two patterns relative to the timing of the pubertal molt: one in which the pubertal molt is the terminal molt and the other in which molts occur more than once after the pubertal molt (HARTNOLL, 1985). In the former type, considerable changes in relative growth were observed at the pubertal molt, but in the latter type, these changes are not clear. *Benthopanope indica* is the latter type, like most xanthoid crabs (HARTNOLL, 1985), because the ovigerous females molt after larval hatching in captivity.

In panopeid crabs such as the male *Panopeus australnesus*, the growth of the cheliped dimensions relative to CW provides a much higher estimate of the mature sizes than that calculated with gonad analysis. The measurement of the length of the first gonopod is consistent with gonad development (NEGRIEIRO–FRANZOZO and FRANZOZO, 2003). Moreover, the pattern of relative growth of the first gonopod length corresponds to the relative increase in AW (HARTNOLL, 1974). Therefore, the inflection point for the male AW (5.80 mm CW) probably indicates the size at physiological maturity in *B. indica* males.

For the relative growth of female AW, a straight line could only be fitted to data from ovigerous females. It was difficult to rigidly divide nonovigerous females into immature and mature groups because many females had a transitional AW.

Morphologically mature females with broad abdomens were found throughout the year. However, our limited data do not show whether the females that survived into the second reproductive season had already spawned in the first reproductive season. We did not examine their ovaries because their body size was small. In future studies, histological observation will be required to confirm their reproductive cycle. Females with narrow abdomens were observed, which exceeded the mean CW of ovigerous females during and after the reproductive season. These females may not have attained sexual maturity. A parasitic epicaridean isopod, *Xanthion spadix*, causes the narrowing of the abdomen of female *L. exaratus* and inhibits their reproductive ability (MIZOGUCHI et al., 2002). It must be confirmed in a future study whether *B. indica* females with narrow abdomens are parasitized by epicaridean isopods. Some small females with broad abdomens were found in December, March, and April, indicating that the pubertal molt also occurs during winter and spring, before the reproductive season in females.

Our study area is located at the extreme northern limit of the distribution of *B. indica* (SAKAI, 1976; MIYAKE, 1998). In female *Panopeus herbstii*, the size at sexual maturity, the mean size of the mature crabs, and the proportion of large crabs were less in the northern part of its distribution than in southern areas (HINES, 1989). HINES (1989) attributed this to the cessation of the molt during the cold season. This interpretation may explain why there are two longevity forms and so much variation in size at maturity in *B. indica*.

Brood size was positively related to body size. The relationship between the number of the eggs per brood and CW in crabs that have the same reproductive season as *B. indica* at Banda are as follows: 610–10,110 (11.80–26.20
Fig. 8. Scheme of the life history of *Benthopanope indica*. In August–January, juveniles are recruited. The carapace width of juveniles increases to above 6.00 mm by June. From June to early September, these crabs start to spawn and incubate their eggs. After the reproductive season, most individuals die. Part of the population survives until the next reproductive season. (*Ko (1995)*)

mm) in *L. exaratus* (WATANABE et al., 1990), 5,293–73,501 (25.10–52.60 mm) in *E. smithii* (TOMIKAWA and WATANABE, 1992), 1,000–2,000 (17.00–25.00 mm) in *T. cornigera* (TSUCHIDA and WATANABE, 1991), and 23–230 (2.65–3.90 mm) in *R. coralicola* (GAO et al., 1994), respectively. The mean number of eggs of *B. indica* is relatively smaller than that of these species because its body size is smaller (HINES, 1982; REID and COREY, 1991). *B. indica* and the latter two species with the relative smaller brood size inhabit in colonies of the algae, while the former two species occur under cobbles and inside crevices. The habitat stability (FUKUI and WADA, 1986) and complexity (LOHRER et al., 2000) are related to the different reproductive effort of the brachyurans and opportunistic species adapt unstable and low complex habitats (FUKUI and WADA, 1986; LOHRER et al., 2000). The habitat characteristic of the colonies of the algae is still unknown, but they may contribute to the low mortality of crabs inhabiting them. It is necessary to investigate the survival rates of such crabs living in the algae. The accurate number of spawnings per female in the annual reproductive season is still unknown, and must be clarified before the reproductive efforts of these species can be compared. *B. indica* has relative small brood size and restricted spawning season in this area. Further studies are
needed to clarify that how degree do the population of Tateyama Bay and that of the southern area contribute to the maintenance of the population of this area.

The life history of B. indica can be deduced from previously published data and the results of this study (Fig. 8). In August–January, the juveniles appear after the larval stage in the colony of brown algae and under calcareous algae. Juveniles with CWs of around 3 mm reach the size of morphological maturity for males (CW 5.80 mm) and the minimum size of ovigerous females (CW 4.54 mm) by the following April. During the reproductive season, from June to early September, the mature females spawn 127–1,739 eggs at a time. Thereafter, most individuals die out, but a few survive into the second year after recruitment and reproduce.

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References


Lindberg, W.J. and R.B. Frydendall (1980) : Resource centered agonism of Pilumnus sayi (Brachyura, Xanthidae), an associate of the


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Distribution of the density ratio in the North Pacific

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Abstract: We estimated the spatial distribution of the density ratio \( R_s \) in the upper 1000 db of the North Pacific from the WOCE data set. The mode value of \( R_s \) was equivalent to those reported in former studies \((3\sim4)\), meaning that the double diffusive convection is moderate or weak; however, the “hot spots” of double diffusive convection were found off eastern Hokkaido and at the formation region of the ESTMW (Eastern Subtropical Mode Water). The vertical eddy double diffusive flux of the density there is up-gradient, where the eddy diffusivity was negative: \(-\langle 9\sim8 \rangle \times 10^{-3} \text{ m}^2/\text{s} \) in the area off eastern Hokkaido and \(-\langle 8\sim4 \rangle \times 10^{-3} \text{ m}^2/\text{s} \) in the ESTMW region. This result means the importance of double diffusive convection to the water mass formation in certain regions. While lower \( R_s \) of the ESTMW region is related to the lateral mixed layer density ratio \( R_w \) estimated in the former studies, the mechanism maintaining large \( R_s \) in other regions still remains to be a topic of future study.

Keywords: Density ratio, Mode Water, Vertical eddy diffusivity, Water mass structure

1. Introduction

World ocean density ratio distributions were first investigated by INGHAM (1966). Here, the density ratio is defined as \( R_s = \alpha \bar{\theta}_s + \beta \bar{S}_s \), where \( \bar{\theta}_s \) and \( \bar{S}_s \) are mean vertical gradients of potential temperature and salinity, respectively.

\[
\alpha = \frac{1}{\rho} \frac{\partial \rho}{\partial \bar{\theta}} \quad \text{and} \quad \beta = \frac{1}{\rho} \frac{\partial \rho}{\partial \bar{S}}
\]

are the thermal expansion and the haline contraction coefficients, respectively. The TURNER angle \( (Tu) \) is defined as a function of \( R_s \), i.e., \( Tu = \tan^{-1} \left( \frac{R_s + 1}{R_s - 1} \right) \) (RUDDICK, 1983). When \( R_s \) is larger than 1 \((Tu \text{ ranges between } 45^\circ \text{ and } 90^\circ)\), the salt finger convection occurs, and when \( R_s \) ranges between 1 and 0 \((Tu \text{ ranges between } -45^\circ \text{ and } -90^\circ)\), the diffusive convection occurs. The activity of both type of convection is intensified as \( R_s \) becomes closer to unity. Especially when \( R_s \) ranges between 1 and 2, the salt finger convection is so active that salt and heat are efficiently transported downwards and that for \( R_s \) ranging between 0.5 and 1, the diffusive convection is active to transport heat and salt upward.

INGHAM (1966) showed that \( R_s \) is constant \((\approx 2)\) in the main thermocline of the Central Waters in world ocean subtropical gyres. SCHMITT (1981, 1990) explained that salt finger convection is a major mechanism of the formation of the Atlantic Central Water maintaining such a constant value. Later on, mapping of \( R_s \) in the world ocean has been tried by FIGUEROA (1996) and YOU (2002) using the Levitus data set. FIGUEROA (1996) then pointed out that \( R_s \) in the main thermocline is less than 2 in most of the ocean except in the Central Waters in the North Pacific where \( R_s \) is larger than 3\sim4.

The double diffusive convection occurs when relatively warm and salty water overlies cooler and fresher water, or vice versa. Such areas are generally found in various oceans; if a certain oceanic area has such lower values of \( R_s \) around unity, it should be called as a “hot spot” of double diffusive convection, where effective vertical mixing should take place.

It has been suggested that enhanced vertical

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mixing can produce significant effects on various large scale features of the ocean, and such effects have driven active studies and researches on this subject. Bryan (1987) investigated the sensitivity of meridional overturning (MOT) and associated meridional heat flux by using a coarse resolution basin-scale model to \( K_v \) (the vertical eddy diffusivity of density). By varying \( K_v \) from \( 1 \times 10^{-5} \) to \( 5 \times 10^{-4} \) m/s, he reported that the magnitude of meridional mass transport in the model increased by an order of 4–fold. If, however, “hot spot” of double diffusive convection is ubiquitous in the world ocean, the effect of associated differential flux of heat and salt and negative flux of density may not be negligible. Garrett and Holloway (1992) used the same model domain and forcing used by Bryan (1987), but taking such a differential flux into account, with heat \( (T) \) and salinity \( (S) \) as separate fields having different diffusivities. By varying the ratio of diffusivity of \( S \) and \( T \) defined as \( d = K_s / K_v \), they showed that the magnitude and the direction of MOT and the mean steady state distribution of \( T \) and \( S \) are sensitive to this parameter \( d \).

Recent observations, however, revealed the enhanced vertical diffusivities over rough topography (e.g., Polzin et al., 1997) due to the tidal effects near the boundary regions. If turbulent diffusivities are indeed enhanced in the deep ocean, such boundary mixing processes might affect the modification of water masses and the circulation pattern of world oceans (Saenko and Merryfield, 2005), and the relative importance of double diffusive convection will be smaller, given that \( R_p \) in the deep ocean are not significantly smaller than those in the upper ocean (You, 2002). The result of these observations may limit the effect of double diffusive convection in the deep ocean, but the double diffusive convection still remains important in the upper ocean where turbulent diffusivities are only of the order of \( 10^{-4} \) m/s and the diffusivities of \( T \) and \( S \) differ significantly (St. Laurent and Schmitt, 1998).

Recently, the concept of lateral mixed layer density ratio (hereafter referred to as \( R_p = \alpha \Delta T_s / \beta \Delta S_s \), where \( \Delta T_s \) and \( \Delta S_s \) are the horizontal temperature and salinity differences between the successive mixed layers several tens of kilometers apart) is introduced to explain the mechanism maintaining the main thermocline \( R_p \) value through the salt finger convection. These studies are motivated by the regulator theory proposed by Stommel (1993) and Stommel and Young (1993). They found \( R_p \) over the basin scale is close to 2 in the temperature range between 7 and 17 °C and assumed a certain process, such as a random rainfall at sea surface controls the temperature and salinity field in the mixed layer to maintain this particular temperature and salinity

\[ R_p \approx 3.6 \]

\[ R_p \approx 1.9 \]
relation. Subsequently, CHEN (1995) used the Levitus climatological data set to show $R_s$ in the same temperature range is less than 2 which supports the STOMMEL’s idea (STOMMEL, 1993). RUDNICK and FERRARI (1999) investigated this lateral changes of temperature and salinity in the mixed layer in more detail in the Northeast Pacific, and obtained a surprising result that lateral changes in temperature and salinity are compensated in density at scales less than O (100 km), and a resulting $R_s$ is close to unity. FERRARI and YOUNG (1997)
Fig. 3. Same as in Fig. 2, but for the designated sigma-theta surfaces. Open circles indicate the hot spots.
explained this low $R_v$ by the slumping of slightly dense water in a surface layer of less dense water, and in the course of this slumping, horizontal density differences are easily disappeared to have $R_v$ close to unity. This model, however, cannot explain the large scale $R_v$ having the value of 2, and the $R_s$ value also having 2 in the main thermocline. Recent idea of explaining this contradiction is given by Schmitt (1999) that such density compensating temperature-salinity anomaly called as "spike" is consumed by the salt finger convection while the upper layer water being subducted, and the $R_s$ is kept 2 in the main thermocline. The problem raised here is the difference in the mode of $R_s$ values between the North Pacific and the other oceans. The examples are shown in Fig. 1 for the WOCE data set (WOCE Global Data Ver.3, 2002, upper 1000 db) in the North Pacific (Fig. 1a) and in the North Atlantic (Fig. 1b). The mode in the North Atlantic is close to 2, while that in the North Pacific is larger than 3. This means that the salt finger convection is not so active in the North Pacific. Is this right? Are there no "hot spots" of double diffusive convection in the North Pacific? This higher value of $R_s$ is usually explained by the fact that average salinity near a surface layer in the North Pacific is lower than that in the North Atlantic caused by strong evaporation over the entire Atlantic. However, this higher value of $R_s$ could not be maintained by the mechanisms explained by the theories above. To solve this problem, we must know the basic water mass structures in the North Pacific through observing the detailed $R_s$ distribution pattern. In the present study, the activity of double diffusive convection in the North Pacific is investigated through the $R_s$ distribution in the upper 1000 db WOCE data set because, below this level, the stratification is usually highly stable.

2. Data processing

Before calculating $R_s$ and $T_u$, all the WOCE CTD casts underwent several processes. Firstly, potential temperature ($\theta$) and salinity were calculated and linearly interpolated at 1 db intervals. The CTD data sets stored at more than 2 db interval were removed for consistency of the quality of data. Secondly, temperature and salinity were vertically smoothed by 11 points (10 db) running mean. Lastly, vertical gradients were calculated by a 10 db least square fit. The $\alpha$ and $\beta$ were calculated by differentiating equation of state (UNESCO, 1981) by temperature and salinity respectively. The occurrence frequencies of $R_s$ values are estimated at each pressure interval (e.g., 0~100 db) or at each designated sigma-theta (hereafter $\sigma_t$) interval (e.g., 21.0~21.5 $\sigma_t$) and the peak values of the $R_s$ are plotted at each 10 degree box in latitude and longitude to analyze the most favorable mode of double diffusive convection.

3. The horizontal distribution at the constant pressure and density surfaces

Shown in Fig. 2 are the horizontal distributions of $R_s$ on pressure surfaces. In higher latitude region beyond 40°N, most fluid columns are stably stratified. In lower latitude region between the equator and 20°N in the layer from the surface to 800 db, the mode values exceed 4, suggesting the salt finger convection is not so active. On the other hand, in the mid-latitude (Subtropical Gyre) between 200 and 500 db, the mode values were between 2 and 4, suggesting the existence of weak salt finger convection. This is in contrast to the North Atlantic where the mode of $R_s$ is less than 2. Looking at the mode value distributions more precisely, we can see that the salt finger convection is active ($R_s < 2$) in the shallower layer between 100 and 300 db in the area off eastern Hokkaido (40~50°N, 140~150°E) and in the eastern sub-tropical North Pacific (20~30°N, 150~130°W). These regions correspond to the region where the North Pacific Intermediate Water (NPIW) and the Eastern Subtropical Mode Water (ESMW) are formed, respectively. The NPIW is defined as a thick salinity minimum around 26.7~26.9 $\sigma_t$ in the western North Pacific (e.g., Qiu and Joyce, 1992). The ESMW is defined as a pycnostad (a minimum of potential vorticity) water around 24.0~25.4 $\sigma_t$ in the eastern North Pacific (e.g., Hanawa and Talley, 2001). Strong modification/formation of water masses are
anticipated in these regions; then, these regions should be "hot spots" of salt finger convection, which should have an important role in the modification formation of these waters. In the area off eastern Hokkaido, weak diffusive convection is expected to occur in the layer below 300 db to 900 db.

$R_s$ distributions on $\sigma_s$ surfaces (Fig. 3) show slight changes in the mode distribution from Fig. 2. In the shallower layers with $\sigma_s$ being less than 24.0, fluid layers are almost statically stable; however, the layers where $\sigma_s$ ranges between 25.0 and 26.5 in the sub-tropical gyre ($2 < R_s < 4$) suggest existence of weak salt finger convection. On the other hand, in the deeper layers in the high latitude, weak diffusive convection is anticipated. Hot spots found in Fig. 2 are also found in density layers with $\sigma_s$ ranging between 24.5 and 25.0 in the eastern sub-tropical North Pacific, but as for in the area off eastern Hokkaido, hot spots become rather ambiguous and undetectable in presented density surfaces. The reason for this phenomenon will be discussed in the next section.

4. Hot spots

To see the vertical profile of $R_s$ together with $\theta$ and $S$ in the area off eastern Hokkaido (Fig. 4, top–left), in the layer between 100 and 300 db (at the top of thermocline), $R_s$ is close to unity ($Iu$ is close to 90°) suggesting the existence of strong salt fingering. However, in the layers deeper than 300 db, salt fingering and diffusive
Fig. 5. Histograms of TURNER angle and θ-S relationship for Central Mode Water (33~40° N, 170~150° W), for Subtropical Mode Water (20~35° N, 120~180° E) and for Eastern Subtropical Mode Water (20~40° N, 120~160° W). All of these Mode Waters are specified by core temperatures, salinities, and by potential vorticity (<2.0 × 10⁻⁶ m⁻¹ s⁻¹).
Convection layers are piled up alternatively suggesting the intrusive features possibly created by double diffusive convection \(\text{(e.g., Ruddick and Turner, 1979)}\). Contrary to this, in the ESTMW region (Fig. 4, right), the salt finger convection favorable layer is found only in the layer between 100 and 200 db \(\text{(at the top of thermocline)}\), and in the deeper layers, the entire fluid column is stably stratified. The occurrence frequency of \(R_s\) and \(\theta - S\) relations in the area off eastern Hokkaido \(\text{(Fig. 4, bottom-left)}\) shows a sharp pointed peak in the salt finger convection regime \(\text{(45}^\circ \text{C} \text{< } T_u \text{< 90}^\circ \text{C)}\), \(R_s \approx 1.3\). The \(\theta - S\) relations aligned along an isopycnal line \(\text{(26.7} \sigma_s\text{)}\) also supports this low \(R_s\) value and it is showing that favorable layers of salt finger convection are confined to a narrow band in the density coordinate \(\text{(around 26.6~26.7} \sigma_s\text{)}\) than in the pressure coordinate \(\text{(100~300 db)}\). It is, thus reasonable that hot spots found in pressure surfaces were rather ambiguous in density surfaces taking interval of \(0.5 \sigma_s\). A relatively small peak is found in the diffusive regime. This should be caused by the temperature inversions commonly observed in this region. As for in the ESTMW region (Fig. 4, bottom-right), a peak value of \(R_s\) is about 1.7, and this also suggests the occurrence of strong salt finger convection; however, the peak is not clearly defined but shows a flat distribution. The \(\theta - S\) relations show a complicated structure contaminated by a certain surface process.

5. Mode Waters in the North Pacific

Two hot spots for double diffusive convection in the North Pacific show different features. Especially at the formation region of ESTMW, the \(\theta - S\) relationship showed a complicated structure. It is thus worth comparing this region with other typical Mode Waters in the North Pacific, such as the Central Mode Water \(\text{(CMW)}\) and the Subtropical Mode Water \(\text{(STMW)}\), and discussing the processes to maintain the thermocline in the North Pacific in this section. The CMW is characterized as a pycnostad \(\text{(minimum of potential vorticity)}\) water centered at 26.2 \(\sigma_s\) surface found at the western coast of the Kuril Islands to 150\textdegree W and between the Kuroshio Extension Front \(\text{(approx. 33}^\circ \text{N)}\) and the Kuroshio Bifurcation Front \(\text{(approx. 40}^\circ \text{N)}\) \(\text{(Suga et al., 1997)}\). The STMW is also a pycnostad water centered at 25.2 \(\sigma_s\) surface found in the Kuroshio region to the International Date Line and is limited between 20\textdegree N and 40\textdegree N. As shown in Fig. 5, the mode values of \(R_s\) are 3.4 for the CMW and 3.9 for the STMW, respectively, suggesting the salt finger convection is not active. However, in the ESTMW region, the mode value is less than
2 (=1.5). This suggests that the mechanism proposed by SCHMIDT (1999) works here indicating the importance of salt finger convection to form the ESTMW. This point is noted by FERRARI and RUDNICK (2000) at the same observation site, however, the mechanism of maintaining such large $R_s$ in the other Mode Waters in the North Pacific is unclear. The salt finger convection is too weak in these locations to maintain large scale constant $R_s$ values larger than 2 in the thermocline (FIGUEROA, 1996 also pointed out this).

6. Vertical diffusivity of density deduced by the formulation by ZHANG et al. (1998)

The important effect of double diffusive convection is the effective downward transport of density. In both types of convection, density gradient is intensified, that is, the sign of eddy diffusivity becomes negative. ZHANG et al. (1998) investigated this effect through parameterizing eddy diffusivities by $R_s$, and pointed out that meridional overturning cell was weakened and deeper temperature and salinity increased in the presence of double diffusive convection. Here, we use their parameterization, and show the horizontal distribution of vertical eddy diffusivity in Fig. 6. Profiles shown here are the averages of vertical diffusivity of density within each $\sigma$ surface ($K_V$) in respective boxes. "Hot spots" can be found in the $\sigma_\theta$ layer around 26.7 in the area off eastern Hokkaido and between in the ESTMW area, respectively. $K_V$ was estimated as $(9\sim8) \times 10^{-3} m^2/s$ in the area off eastern Hokkaido and $- (8\sim4) \times 10^{-3} m^2/s$ in the ESTMW area. These magnitudes are larger than the typical $K_V$ value $1 \times 10^{-2} m^2/s$ in the thermocline (ST. LAURENT and SCHMIDT, 1998) by about an order, showing the importance of double diffusive convection to the water mass formation in respective region.

7. Summary and discussion

We investigated the water mass structure and detailed $R_s$ distribution in the upper 1000 db of the North Pacific by using the WOCE data set. The “hot spots” of double diffusive convection were found in the area off eastern Hokkaido and in the Eastern North Pacific where the NPIW and the ESTMW are formed. Mode values of $R_s$ in these regions are 1.3 and 1.7, respectively. The salt finger convection must be an important process for water mass modification formation in these regions. Although the favorable condition for the onset of salt finger convection was satisfied in most of the mid-latitude (the subtropical gyre) between 200$\sim$500 db or between 25.0$\sim$26.5 $\sigma$ including the CMW and the STMW, the modes of $R_s$ in these regions lie between 3 and 4, suggesting salt finger convection is not so active. The mechanism of maintaining large value of $R_s$ in these regions is still unclear. This higher value of density ratio is usually explained by the fact that the average salinity near the surface layer in the North Pacific is lower than that in the Atlantic where the evaporation is so strong.

The subduction process causing inflow to the main thermocline occurs in winter when the surface mixed layers deepened through surface cooling. In this case, $R_s$ estimated from the Levitus annual mean could not have direct connection with thermocline $R_s$, and the explanation presented by SCHMIDT’s idea of “spiciness” holds true for the Atlantic, but not for the North Pacific except for ESTMW region as was shown in the present study. The observation field in the ESTMW region by RUDNICK and FERRARI (1999) was too limited to discuss the whole basin of the North Pacific; however, RUDNICK and MARTIN (2002) extended their analysis including the Indian and the Atlantic Oceans and concluded that this low value of $R_s$ ($=1$) is a common feature of all the oceans at the scales about O (3$\sim$4km) where the mixed layer depth exceeds about 75 m. Therefore, in order to clarify the maintenance mechanism of thermocline $R_s$ in the North Pacific, we must investigate winter time distribution of $R_s$ more precisely in relation to the mixed layer depth. This problem will remain to be a topic of the future work.

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References

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第45巻第3号掲載欧文論文の和文要旨

野村英明、田村克太、山田美穂子、岡本研、和田実、西村昌彦、吉田明弘、柴田晃、高田秀重、大和田統一：
石油および石炭と分散型石油処理剤添加後にみられた中規模半閉鎖型海洋生態系における植物プランクトン群集の変遷

メソコム（中規模半閉鎖型疑似現状海洋生態系）を用いて、海産植物プランクトン群集に及ぼす低濃度のA重油
（水溶性分画）の影響を調べた。実験は2001年5月23日から6月2日にかけて行った。重油を添加した石油区、
重油に石炭と分散型石油処理剤を添加した石油分散剤区、およびオイルを加えていない海水のみの海水区において、植物プ
ランクトンの出現量、種組成、沈降粒子束、水中石油成分濃度及び水温・塩分などの環境因子をモニターした。実験
開始当初は珪藻、主にChaetoceros属やSkeletonema costatumを主体とした群集構造が形成されていたが、それは
最終的には藻海藻主体の集団に移行した。こうした遷移はどのメソコムタイプにも共通した現象であった。しかし、
ゆるやかに移行した海水区を異なり、油の混入した二つのタイプの珪藻体群は、添加後4日間に大きく減衰しきれ
以後珪藻の増加は見られない一方、藻海藻は急速に増加し、海水区に比べると高密度になった。また、海水区では実
験の後半にも珪藻がマイナスを形成したにもかかわらず、石油の混合したタイプではそれが見られないことに加えて、
沈降粒子束中の珪藻細胞は海水区の20%以下と少なかった。珪藻体群の減衰は、石油成分に暴露されたことによる
成長阻害と考えられた。珪藻体群の縮小は、生食食物網を変質させると共に、底層への有機物フラックスを減じる
ため浮遊系と底生系のカッティングを弱めることがなる。メソコム実験では、自然では水中に存在する物理的
性質である微小な乱流が抑制されることで、植物プランクトン種をそれぞれの物理的活性状況の違いが感じやす
くなる。おそらく水域深水域のような閉鎖あるいは半閉鎖条件の現象で起こっているであろう低濃度の石油汚染による
基礎産生者への影響は、天然では様々な要因が複雑に反映して明らかにならない。こうした低濃度な汚染でも基
礎産生者に影響を与えることが、乱流のないいくつかの環境因子を人為的に取り除くことのできるメソコム実験
群としては観察することができる。

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屋良由美*、柳哲雄、門谷茂、多田邦尚：沿岸海域における物質循環に対する干潟の機能

浮遊・底生結合生態系モデルの簡易な干潟生態系モデルを構築し、瀬戸内海の干潟において窒素循環過程を解析し
た。干潟における観測項目は水質や底生生物に関する項目があり、観測値の季節変動を本モデルの計算結果を再現し
たため、モデルを用いて、干潟の機能を水質浄化機能の観点から評価した。その結果、干潟に懸濁物食者（二枚貝）
が存在する現在の干潟は有機物の無化の割合が大きいことが分かった。さらに、干潟に懸濁物食者が全く存在しな
いと仮定した場合、有機窒素の流出が現在よりも増加するため、干潟の水質浄化能力は低下し、植物プランクトン
による摂餌圧の現象により赤潮の発生することが分かった。

（*〒860-0810 札幌市北区北十条西5丁目 北海道大学大学院地球環境科学研究科地球圈科学部門気候学分野
☎816-8580 福岡県筑紫郡春日野公園6-1 九州大学応用力学研究所力学シミュレーション研究センター野外計測分野
tel: 092-583-7492 E-mail: yara@riam.kyushu-u.ac.jp）

土井 航・横田賢史：館山湾におけるトラノオガニの成長と繁殖

ケガナカ科のトラノオガニの成長と繁殖を明らかにするために、2001年4月から2002年3月までの間、千葉県の
館山湾で月例調査を行ない、抱卵雌は主に6月と8月にかけて出現し、稚ガニの加入は8月から1月にかけてみ
られた。稚ガニは着底後成長し、翌年の4月には成熟サイズを超える。大型の雄は特に大きな足を有するが、そ
の相対成長は性成熟滅は一致しなかった。その一方で、雄の腹節幅の成長率は成熟脱皮後に減少した。雌では成熟個
体で腹節幅の増加がみられた。しかし、成熟脱皮前後の間の大きな腹節をもつ雌になっているために、腹節幅によって未成熟、
成熟個体を区別することはできなかった。一方卵数は甲殻とともに増大し、その範囲は120粒から1,700粒であった。
繁殖期後、大型個体のほとんどは老齢によって死亡し、本種の寿命は約1年と推定された。しかし、甲殻頻度分布と
成長率の解析から、翌年の繁殖期まで生存する個体をもとと考えられる。

（東京海洋大学海洋生物資源学科 〒108-8477 東京都港区南4－5－7、TEL 03-5463-0535、FAX 03-5463-0684、
E-mail: Watanabe@kaiyodai.ac.jp）（渡辺）
嶋田啓資、根本雅生、吉田次郎：北太平洋における密度比の空間分布

北太平洋の上層1000 dbにおける密度比（\( R_n \)）の空間分布をWOCEデータセットから見積もった。これまでの研究と同様に\( R_n \)のモード値は3～4で、二重拡散対流は不活発であることが示されたが、北海道東部沖の海域及び、東部亜熱帯モード水（ESTMW）形成域において二重拡散対流が活発な「hot spot」が存在することが分かった。密度の鉛直渦拡散係数はそれぞれ\((-9.2 \times 10^{-5})\) m\(^2\)/s（北海道東部沖）、\((-5.0 \times 10^{-5})\) m\(^2\)/s（ESTMW形成域）と見積もられた。これらのことを二重拡散対流が氷層の形成に重要な役割を果たしている海域が存在することができる。ESTMW形成域の低い密度比は、これまでの研究で見積もられた表層混合層の密度比との間に関連があることが示されたが、その他の海域の温度躍層に見られる大きな密度比を維持する機構是未だ不明であり、今後の課題として挙げられる。

（東京海洋大学海洋環境学科 〒108-8477 東京都港区港南4-5-7 Eメール：d042010@kaiyodai.ac.jp）
学 会 記 事

1. 2007年6月9日（土）日仏会館会議室において、平成19年度学会学術研究発表が開かれた発表題目と発表者は次のとおり
平成19年度日仏海洋学会学術研究発表会
期日：平成19年6月9日（土）
場所：日仏会館会議室（501号室）東京都渋谷区恵比寿31-9-25
電話03-5421-7641

プログラム
午前（10:00～12:00）
1. 内浦湾における内部潮汐の反射・散乱
………………………・川村有二・北出裕二郎・
松山優治（海洋大）
2. 長崎県形上湾における水温鉱直分布の連続観測
………………………・小林雅人（横浜大・農林業研）・
早川康博（水大校）・
山口仁士・川井仁（長崎環保研）
3. 2006年4月に駿河湾で発生した急潮
…………・水永美雪（海洋大）・久保田雅久（東海大）・
川村有二・松山優治（海洋大）
4. Adeke Land沖における密度逆転の分布と内部波の関係
………………………・平野大輔
北出裕二郎（海洋大）
5. カリフォルニア沿岸亜沼域における沖合い方向への炭素輸送にとフィラメントが果たす役割に関する数値実験
………………………・長井健容（海洋大）
6. 流出水モニタリングのためのヘリコプター搭載型蛍光ライダーの開発
………………………・篠野雅彦・樫富和夫・
山之内博（海技研・運航シス）
午後（14:00～15:00）
7. CO2海洋隔離におけるpH値による生物影響評価の基礎研究
………………………・中村倫明・和田明・
長谷川一幸（日大・院・環境科学）
8. 紅藻ビリヒパ（Corallina pilulifera）の光合成特性
………………………・高原剛・佐藤博雄・
田中準郎（海洋大）
9. 無機懸濁粒子がアサリの受精卵および浮遊幼生に与える影響
………………………・赤塚利之・荒川久幸・
森永勤（海洋大）・瀬戸雅文（福井県大）・
小林篤（千葉県・水総）

2. 2007年6月4日（土）日仏会館において評議員会後
第48回（平成19年度）総会が開かれた
議題は次の通り。

1. 平成18年度事業報告
2）活動状況
会員異動状況

<table>
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<th>会員タイプ</th>
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</table>

2）活動状況
評議員会 1回（18/6/4 日仏会館）
幹事会 2回（18/12/7, 19/4/10 日仏会館）
総会 1回（18/6/4 日仏会館）
学術研究発表会 1回（18/6/4 日仏会館）
学会誌発行 43巻3号～44巻3号

3）編集関係
学会誌「La mer」43(3)・43(4)(41号・44(2)・44(3, 4)発刊

2. 平成18年度収支決算報告
収入の部（備考）
前年度繰越金 763,338
正会員会費 1,000,000 125名
65歳以上会員 132,000 22名
学生会員会費 24,000 6名（4000×6名）
援助会員会費 120,000（7社、12日）
学会誌売上金 58,210
広告料 50,000
別刷り印刷費 442,400
掲載料、超過貢献印刷費 550,000
雑収入 103,146（研究発表会、
学术著作権使用料他）
寄付金 0
合計 3,243,094

La mer 45 : 161-163, 2007
Société franco-japonaise d’oceanographie, Tokyo
支出の部

学会誌印刷費 1,587,250
送料・通信費 159,615
事務費 663,592
交通費 14,700
会議費 4,248
学会賞経費 0 メダル、賞状他
雑費 14,751 郵便・銀行振込手数料他
次年度繰越（銀行残高） 788,938
合 計 3,354,938
原案通り承認された

3．平成19年度事業
1) 総会 学術研究発表会 幹事会 議員会 開催
2) 学会会則の見直し
3) La mer発刊
4) 学会賞のメダルの変更
5) バックナンバーDVD化
6) 仏日シンポジウムの準備
7) その他（平成20．21年度 議員会、会長選出）

4．平成19年度予算

収入の部
正会員会費 800,000 100名×8000円
65歳以上会員 132,000 30名×6000円
学生会員会費 24,000 6名×4000円
援助会員会費 120,000 (7社、12口)
学友誌売上金 60,000
広告料 50,000
別刷り印刷費 480,000
掲載料、超過頁印刷費 800,000 16稿×5000円
雑収入 100,000（要旨集売上、学術著作権使用料他）
17年度繰越（銀行残高） 788,938
合 計 3,354,938

支出の部
学会誌印刷費 2,120,000 4冊×53000円
送料・通信費 100,000
事務費 700,000 人件費、事務用品、封筒他
交通費 20,000
会議費 5,000
学友誌経費 50,000 メダル、賞状他
雑費 25,000 郵便・銀行振込手数料他
予備費 334,938 学会誌バックナンバー

合 計 3,354,938
原案通り承認された

5．平成19年度 学会賞・論文賞受賞候補者推薦委員会
委員
荒川久幸 石丸 隆 今岡明 岩田 磐 奥田邦昭
神田穣太 北白川二郎 河野 博 小林海人 小松輝久
相木幸美 千手智晴 田中祐志 前田昌勲 吉田次郎

6．その他
その後、アトレ恵比寿店ライオンにおいて懇親会がひらかれた。

● 日仏海洋学会会則の改正
平成19年6月9日総会において下記の様に改正され承認されました。

日仏海洋学会会則 新会則（改正条文 下線部分が改正部分）
第3条 上記の目的を達成するために本会は次の事業を行う。
（1）海洋および水産に関する研究会および講演会の開催
（2）定期刊行物、学術上の刊行物の発行
（3）学会賞の授与
（4）日仏両国を主とする海洋および水産に関する共同研究成果の発表、ならびに、技術開発成果の導入および普及
（5）両国の海洋・水産関係者の交流促進および親睦をはかること
（6）その他本会の目的を達成するために必要な事業
第9条 本会は評議員会によって運営される。
評議員の定数は28名以内とし、24名は正会員および学生会員の投票によって選出される。会長は評議員会の同意を得て4名以内の正会員および学生会員を評議員に委嘱することができる。
評議員の任期は2年とする。ただし、重任を妨げない。

第10条 評議員はその内より次の役員を選ぶ。ただし、監事は評議員以外の役員を選択すること。
会長1名、副会長2名、幹事10名以上12名以内、監事2名
役員の任期は2年とする。ただし、重任を妨げない。

第13条 通常総会は毎年1回会長が召集する。
会長は必要に応じて評議員会の決議を経て臨時総会を召集することができる。
総会では評議員会の報告に基づいて、会の重要
問題を審議する。
総会は正会員および学生会員の6分の1以上の出席がなければ成立しない。ただし、出席できない正会員および学生会員は委任状により他の出席会員または議長に決議を委任し、出席会員とみなすことができる。

日仏海洋学会評議員・役員選出規定 改正が検討される項目の改正案
2．評議員の選出は直会員および学生会員の24名連記無記名投票による。
（以下略）

日仏海洋学会賞規定 改正が検討される項目の改正案
3．委員会の委員は9名とする。委員は毎年選の評議員会で選出し、委員長は委員の互選により定める。委員の任期は2年とし、隔年に4名および5名を交代する。会長は委員会が必要と認めた場合、評議員の同意を得て2名まで委員を追加委嘱することができる。ただし、追加委嘱された委員の任期はその年度限りとする。
贊助会員

アレック電子株式会社 神戸市西区井吹台東町7−2−3
株式会社 イー ムス 神戸市中央区東川崎町1−3−3

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財団法人 海洋生物環境研究所 千代田区神田神保町3−29 帝国書院ビル5F
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La mer la mère, l’amour pour la mer!

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Richard Brancker Research（水中ロガーメーカー）
・ 24 ビット分解・RS インタフェース内蔵ロガー
・ 6 項目測定

日本総代理店 ケー・エンジニアリング株式会社
〒111-0053 東京都台東区浅草橋 5-1 4-1 0
TEL 03-5820-8170 FAX 03-5820-8172
www.k-engineering.co.jp sales@k-engineering.co.jp
日仏海洋学会入会申込書
（正会員・学生会員）

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入会申込書送付先：〒150-0013 東京都渋谷区恵比寿3-9-25
（財）日仏会館内

日仏海洋学会

郵便振替番号：00150-7-96503