

Contribution of Benthic and Epiphytic Diatoms to Clam and Oyster Production in the Akkeshi-ko Estuary

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The species composition and dynamics of phytoplankton in the water column and its contribution to clam, *Ruditapes philippinarum*, and oyster, *Crassostrea gigas*, production were studied in the Akkeshi-ko estuary, eastern part of Hokkaido, Japan. A total 128 taxa of diatoms were identified, with 103 and 102 species occurring on the surface sediments and in the water column, respectively. *Amphora* sp., *Bacillaria paradoxa* var *paxilifer*, *Cocconeis scutellum*, *Navicula* sp., *Nitzschia sigma*, *Paralia sulcata*, *Rhoicosphenia curvata*, *Synedra ulna* and *Thalassiosira* sp. were most common and dominant in all stations in both water column and surface sediment. Benthic diatoms were most dominant in both water column and surface sediment. The species composition of epiphytes was, in part, similar to diatom assemblage of the water column and also to that of the surface sediment. The benthic and pelagic ratio in the diatom assemblage of the water column was very high. Benthic diatoms were able to resuspend into water column by turbulence stimulated by wind. Chlorophyll *a* concentration in the water column increased as wind speed increased. Seventy and 67% of the gut contents oysters consisted of benthic diatoms in 2003 and 2004 and also 78 and 87% of clams in 2003 and 2004, respectively. The availability of benthic and epiphytic diatom assemblages contributes significantly to food resources for clam and oyster mariculture due to resuspension by disturbance in the Akkeshi-ko estuary.

Keywords:

- Benthic diatoms,
- pelagic diatoms,
- epiphytic diatoms,
- the Akkeshi-ko estuary,
- clam,
- oyster,
- resuspension.

1. Introduction

Diatoms are unicellular algae, which contribute markedly to primary production in estuarine ecosystems and play an important role in food webs in waters (Pinckney and Zingmark, 1993). Fundamentally, there are two groups of diatoms in estuaries or shallow marine systems, viz., pelagic and benthic species. Benthic diatoms are colonial or unicellular diatoms, free living or attaching to the substratum by gelatinous extrusion. They are mostly associated with substrata throughout their life cycles. Some of them move actively in sediments and sometimes resuspend in the water column, depending on tidal turbulent or other physical factors (Werner, 1977; Schrader and Schuette, 1981). Werner (1977) categorized benthic diatoms into epiphytic (attached to other plants), epipsammic (on sand), epipellic (on sediment), and epilithic (attached to rock surfaces). Pelagic diatoms are

free living (solitary or joined to each other in chains of varying length) and mainly spend their entire life cycles in the water column (Werner, 1977; Schrader and Schuette, 1981).

Diatoms are sensitive to a wide range of environmental variables, and the community structure may quickly respond to changing physical, chemical and biological conditions in the environment (Harrison and Turpin, 1982; Lapointe, 2000; Mitbavkar and Anil, 2002). Diatom abundance is correlated to physical factors, such as sediment character, light and temperature (Colijn and Dijkema, 1981; Nozaki *et al.*, 2002), salinity (Miller and Florin, 1989; Zalat, 1995), depth (Jonsson, 1987), and wave disturbance (Lowe, 1996). Chemical factors such as phosphorus and nitrogen concentrations (Smith, 1982; Hillebrand *et al.*, 2000; Kormas *et al.*, 2001) and biological factors such as grazing pressure by benthic suspension feeders (Mukai, 1992; Yusoff *et al.*, 2002) can affect the community structure of diatoms.

The Akkeshi-ko estuary is the largest estuarine system in the eastern part of Hokkaido (Sawai, 2001a). River inputs and water exchange with the sea, as in most estua-

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rine systems, would affect diatom assemblage in the Akkeshi-ko estuary (Sawai, 2001b). Very little is known about the community structure of diatoms and these environmental factors in such estuaries (Magni and Montani, 1997; Montani *et al.*, 2003). Sawai (2001b) reported that the distribution of living diatoms on the surface sediment near the Kanedasaki salt marsh transect on the northeastern shore of the Akkeshi-ko estuary is correlated to the nature of vegetation and substratum.

Most estuarine areas in Japan are now used for the intensive cultivation of clams and oysters. This activity in Akkeshi-ko has been expanded in the current decade, so the utilization of living material such as diatoms and other phytoplankton, microzooplankton, and so forth, from the water column increased due to overculture of the clam, *Ruditapes philippinarum*, and the oyster, *Crassostrea gigas* (Mukai, unpublished).

It has long been considered that phytoplankton is a main food of benthic filter feeders such as oysters and clams as cultivated in Japanese littoral areas. However, there is a great deal of evidence of shortage of food for these maricultures in many localities in Japan, if we assume that only phytoplankton could form the diet of these bivalves. Some ecosystem models have indicated a discrepancy between what was expected and observations (Kishi *et al.*, 1994; Kasai *et al.*, 2004).

In the present study, the possible components of “phytoplankton” in the water column available for the clam and the oyster is clarified by direct observation to determine the contribution of the benthic diatom assemblage to the clam and oyster mariculture in the Akkeshi-ko estuary.

2. Materials and Methods

2.1 Study sites

The field study was conducted at the Akkeshi-ko estuary, which is located in the eastern part of Hokkaido (43°00' N 144°51' E), northern Japan (Fig. 1). The Akkeshi-ko estuary is almost enclosed but is connected to Akkeshi Bay through a narrow channel. Most of the estuary is covered with extensive eelgrass beds, *Zostera marina* and *Z. japonica*. The estuary is shallow with a mean depth less than 2 m. Surface sediments mostly consist of silt and clay, except for tidal flats near the channel. Water flow in the estuary is driven mainly by tide and wind.

2.2 Field sampling

To collect “phytoplankton” samples from the field, the surface water was sampled monthly at 20 stations for 10 months (March–December 2003). In winter, almost the entire surface of the estuary was covered with ice, making it impossible to sample the water. Sediment sam-

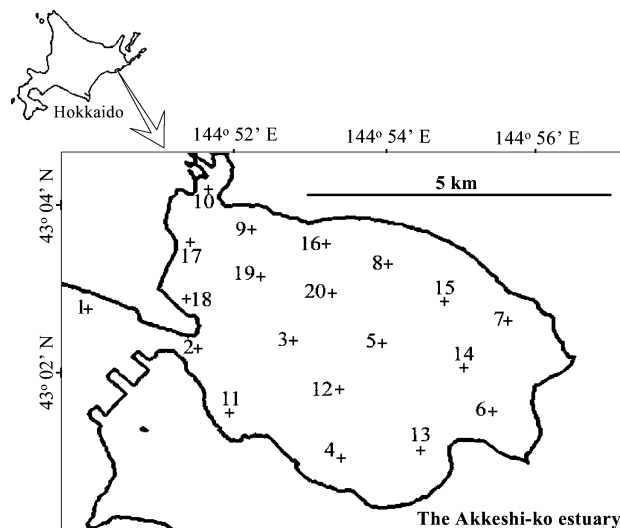


Fig. 1. Sampling stations (Sts. 1–20) in the Akkeshi-ko estuary.

ples were also collected by an Ekman-Birdge grab from the bottom at 20 stations in the Akkeshi-ko estuary. Benthic diatoms were subsampled from the sediment inside the Ekman-Birdge grab by a mini corer (diameter: 3 cm). A roughly 1 cm surface layer of sediment was picked up by cellophane plastic. Observation was restricted to 1 cm of the surface sediments because the vertical difference in species composition of diatom assemblages has been reported (Rathburn *et al.*, 2001).

About 1000 ml water samples were collected monthly at 20 stations in the Akkeshi-ko estuary. The station positions were determined using a shipboard Global Positioning System. Physical parameters such as water temperature and salinity were measured *in situ* by electronic apparatus (“Chlorotec”, Alec Electronic Co.), and surface current was measured by a current-meter (Compact EM, Alec Electronic Co.).

2.3 Sample analysis

For each water sample, 100 ml sub-samples were preserved with 0.2% formaldehyde solution in final concentration. Diatoms in the water samples were condensed to 10 mL volume by centrifugation. For observation samples, 2 mL was pipetted from well-mixed samples and examined under a microscope. Immediately after sampling, surface sediment samples were stored in the dark until analysis. For diatom observation, 2 mL of distilled water was added to 2 mg of frozen sediment. To bleach the diatom cell cytoplasm, 0.2 mL of hydrochloric acid/ethanol (1:99) was added to every sample (0.2 mL distilled water with sub-sample of living diatoms) (Sawai, 2001b). All diatom samples were enumerated under a

microscope (Olympus BX50) examination using phase contrast optics with a 100× objective.

The diatoms from water and sediment samples were identified and counted to the lowest taxonomic level as far as possible. The taxonomic identification of diatoms was carried out using Kato *et al.* (1977); Yamaji (1977); Kawamura and Hirano (1989); Mizuno and Saito (1990); Sawai and Nagumo (2003) and on-line publications: www.marbot.gu.se/sss/diatoms, and www.bio.mtu.edu/jkoyadom/alga_webpage/HOME.html.

2.4 Definition of pelagic-benthic diatom species

Benthic or pelagic diatoms were assigned based on the definition of benthic and pelagic diatoms in Schrader and Schuette (1981) and Werner (1977). The diatoms found in free or attached to a substratum (seagrass, macroalgae, sand or rock) were categorized as benthic diatoms. Free living cells which mainly spent their entire life cycle in the water column were categorized as pelagic diatoms. Although some genera include both pelagic and benthic congeneric species, the present study followed the definition of “pelagic” and “benthic” categories given by other researchers who published a group list of benthic and pelagic diatoms. They categorized genera of *Amphora*, *Aulacosiera*, *Bidulphia*, *Camphylodiscus*, *Cocconeis*, *Cymbella*, *Diploneis*, *Gomphonema*, *Grammatophora*, *Gyrosigma*, *Navicula*, *Nitzschia* (mostly), *Pinnularia*, *Paralia*, *Pleurosigma*, *Rhabdonema*, *Rhicosphenia*, *Rhopalodia*, *Stauroneis*, *Surirella*, *Synedra*, *Triceratium*, *Tryblionella* as benthic diatoms (Kuylenstierna, 1990; Jiang, 1996; Nave *et al.*, 2001; McQuoid, 2005), and genera of *Actinocyclus*, *Aulacosiera*, *Coccinodiscus*, *Chaetoceros*, *Fragilaria*, *Leptocylindrus*, *Melosira*, *Pseudo-nitzschia*, *Rhizosolenia*, *Skeletonema*, *Thalassiosira*, and *Thalassionema* as pelagic ones (Nave *et al.*, 2001; McQuoid, 2005).

2.5 Chlorophyll *a* measurement

Chlorophyll *a* concentration was determined from particles filtered from 100 mL estuary water by 25-mm Whatman GF/F glass fiber filters. Each filter paper with particles was placed in 6 mL DMF, N-N dimethylformamide, and allowed to extract for several hours in the dark. Chlorophyll *a* concentration was measured with a Turner Design model-10 fluorometer and calibrated with a standard solution of pure chlorophyll *a*. Extracts were measured before and after acidification with 0.2 mL of 0.5 N HCl to correct for phaeopigment fluorescence.

In the field, to find evidence of increased chlorophyll *a* concentration in the water column during periods of increasing wind speed and or tidal current, an electronic apparatus (“Chlorotec”, Alec Electronic Co.) was

used for one week of measurements (measured every 2 minutes) at station 5 from 15 to 22 November 2004.

2.6 Chemical analysis

Ammonia (NH₄⁺), nitrate + nitrite (NO₃⁻ + NO₂⁻) and phosphate (PO₄⁻) concentrations in the surface seawater were measured to clarify the influence of chemical parameters on “phytoplankton” assemblages in the Akkeshi-ko estuary. Ammonia concentration was obtained by using a phenol hypochlorite method, as soon as possible and in any case within 4 hours after collection (Strickland and Parsons, 1968). Nitrite and nitrate concentrations were measured with an autoanalyzer (BRAN + LUEBE, TRAACS800, Cd-Cu methods). Phosphate was determined colorimetrically by the method of Murphy and Riley (1962).

2.7 Gut contents analysis of oyster and clam

Twenty to thirty individuals of the oyster (*Crassostrea gigas*) and the clam (*Ruditapes philippinarum*) were collected by hand near St. 11 in the Akkeshi-ko estuary. Body size of oysters was between 72–111 mm length and 21–24 mm length for clams. All the samples were transported to the laboratory and fixed in 10% neutralized formaldehyde seawater solution. In the laboratory, shell length was measured to the nearest 0.1 mm with a caliper. Gut contents from each individual were taken out by dissecting the gut and collection in sample bottles. Diatoms, dinoflagellates, and other organic particles were identified to species level under the microscope, if possible. The analyses followed the water and sediment diatom observations.

2.8 Data analysis

The benthic to pelagic ratio (BPR) of the abundances of diatoms in both water column and sediment was calculated by the following equation,

$$\text{BPR} = \text{B}/(\text{B} + \text{P})$$

where B = cell number of all benthic diatom species and P = cell number of all pelagic diatom species. The BPR is an indicator of the contribution of benthic species. A high BPR shows an assemblage with a high dominance of benthic species.

Statistical analysis was performed with the MINITAB 10 software package. Standard correlation analysis was used to statistically evaluate the data used in this paper.

In addition, correlation analysis was done between chlorophyll *a* concentration and each physical factor (ammonia, nitrate + nitrite and phosphate). The dataset for the chlorophyll *a* was compared with the physical factors at all stations to evaluate their relationship.

3. Results

3.1 Environmental data

Ranges of environmental parameters and diatom densities in each station from March to December 2003 are presented in Table 1. The depths at the stations were generally within 0.3–3.0 m, except for Sts. 2 and 3 (4.7–5.0 m). Salinity was lowest at St. 10 (14.5 psu), which is located in the river mouth, and the highest was in Sts. 2 and 3 (30.5 psu), which are located in or face the narrow channel between Akkeshi Bay and the estuary. There was a pattern of high salinity in the narrow channel and low salinity in the river mouth. Water temperature varied seasonally. The mean water temperatures were 4.9, 15.7 and 9.4°C in spring, summer and autumn, respectively. High water temperatures were recorded in the bay-head areas in spring–summer.

Ammonia and nitrate + nitrite concentrations in the water column ranged from 0.6–2.4 μM and 0.3–5.5 μM in the Akkeshi-ko estuary, respectively. Ammonia concentration was higher at Sts. 10 (5.5 μM), 18 (7.6 μM) and 19 (11.1 μM) than other stations in most seasons. Nitrate + nitrite concentration showed the highest value at Sts. 10 (13.32 μM), 18 (13.63 μM) and 19 (13.84 μM). The nutrients, ammonium and nitrate have similar distribution patterns.

The average concentration of chlorophyll *a* and phaeopigment was 2.8 $\mu\text{g}\cdot\text{L}^{-1}$ and 2.0 $\mu\text{g}\cdot\text{L}^{-1}$, respectively. The highest chlorophyll *a* concentration was observed at St. 6, with a value of 5.0 $\mu\text{g}\cdot\text{L}^{-1}$ and at St. 9 for phaeopigments, with a value of 3.3 $\mu\text{g}\cdot\text{L}^{-1}$. Chlorophyll *a* concentration generally increased in spring and summer at most stations. The distribution pattern of chlorophyll *a* concentration seemed to be opposite to that of nutrients. However, the negative relationships between chlorophyll *a* and ammonia or nitrate + nitrite were not significant.

The 2-minute interval chlorophyll *a* measurements were made with the “Chlorotec” at 10 cm above the sediment surface at St. 5 (the center of the Akkeshi-ko estuary) during one week. The chlorophyll *a* concentration was automatically recorded from 12:00 p.m. on 15 November 2004 to 14:48 p.m. on 22 November 2004. During the measurement, in particular on 15, 16 and 17 November 2004, the wind speed was as high as 14, 11 and 8 $\text{m}\cdot\text{s}^{-1}$, respectively. The high energy wind was followed by an increase of chlorophyll *a* in the water column to 231, 249 and 228 $\mu\text{g}\cdot\text{L}^{-1}$, respectively. In the last days of the measurement on 21 and 22 November 2003, the wind speed decreased to 5 and 2 $\text{m}\cdot\text{s}^{-1}$, respectively. At the same time, low concentrations of chlorophyll *a* of 45 and 48 $\mu\text{g}\cdot\text{L}^{-1}$ were recorded, respectively (Fig. 2).

Table 1. Summary characteristics of the 20 stations in the Akkeshi-ko estuary (nd = no data).

Station	Depth (m)	Salinity (psu)	Temperature (°C)	Current ($\text{cm}\cdot\text{s}^{-1}$)	Diatoms abundance	
					water column ($\text{cell}\cdot\text{L}^{-1}$)	sediment ($\text{cell}\cdot\text{mg}^{-1}$)
1	1.2	27–32	1–17	7–25	5600–12350	5600–26000
2	5.0	28–32	1–14	13–70	3900–11700	nd
3	4.7	28–32	3–15	16–38	4220–12450	nd
4	0.6	23–30	3–21	4–30	3750–16170	6600–23900
5	3.8	26–29	1–20	2–31	7300–14150	8850–25350
6	0.6	22–27	5–16	8–21	9750–12050	8000–15100
7	1.0	19–25	5–15	8–21	10750–15400	7100–12250
8	1.5	22–28	1–18	6–22	4200–19900	8050–42250
9	1.7	16–30	3–21	2–25	3800–19400	10500–26800
10	0.3	6–26	2–18	2–17	3250–14500	8000–27400
11	2.6	25–32	1–16	6–25	4800–13950	6950–14350
12	3.2	25–31	2–16	8–25	3450–13700	8550–22750
13	0.5	22–27	1–21	3–24	6700–14000	7150–22800
14	0.9	22–28	2–19	10–26	3850–13800	6150–17950
15	0.8	21–26	5–17	10–22	6100–12650	4900–15250
16	0.9	22–30	3–19	8–17	3700–15750	12050–36500
17	0.9	22–32	3–18	11–26	2900–14200	4200–20800
18	0.9	23–32	2–15	8–30	3950–13350	4650–13900
19	0.5	25–32	1–17	3–30	3650–12950	10950–25900
20	0.8	26–31	2–14	5–16	8200–16000	10500–29250

3.2 Dynamics of diatom assemblages

From a total of 128 species (taxa) of diatoms identified in the Akkeshi-ko estuary, 103 and 102 species (taxa) occurred on the surface sediments and in the water column, respectively.

Most species were found commonly both on the surface sediment and in the water column. Of these species, 22 species of benthic diatoms and 3 species of pelagic diatoms were common on the surface

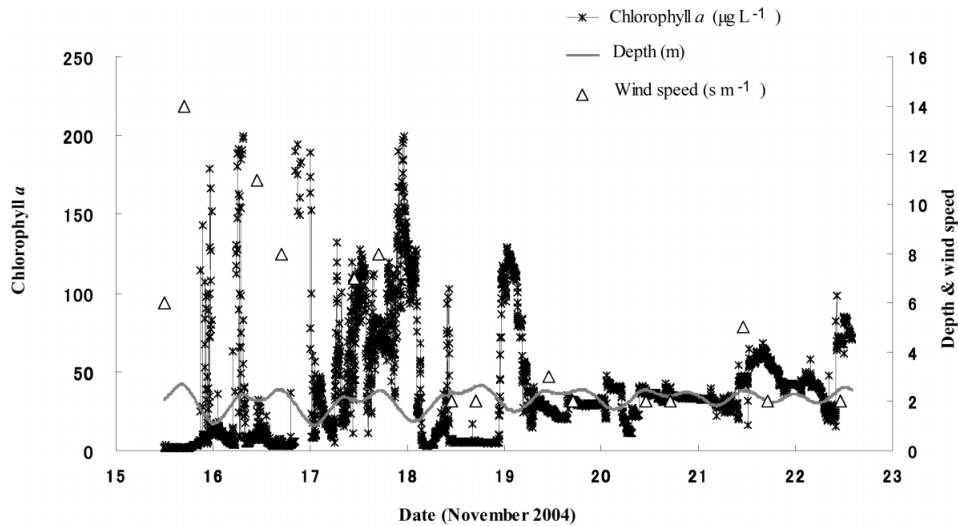


Fig. 2. One-week measurement of chlorophyll *a* concentration with wind speed ($\text{m}\cdot\text{s}^{-1}$) and tidal level (m) above sea floor at St. 5 of the Akkeshi-ko estuary from 15 to 22 November 2004.

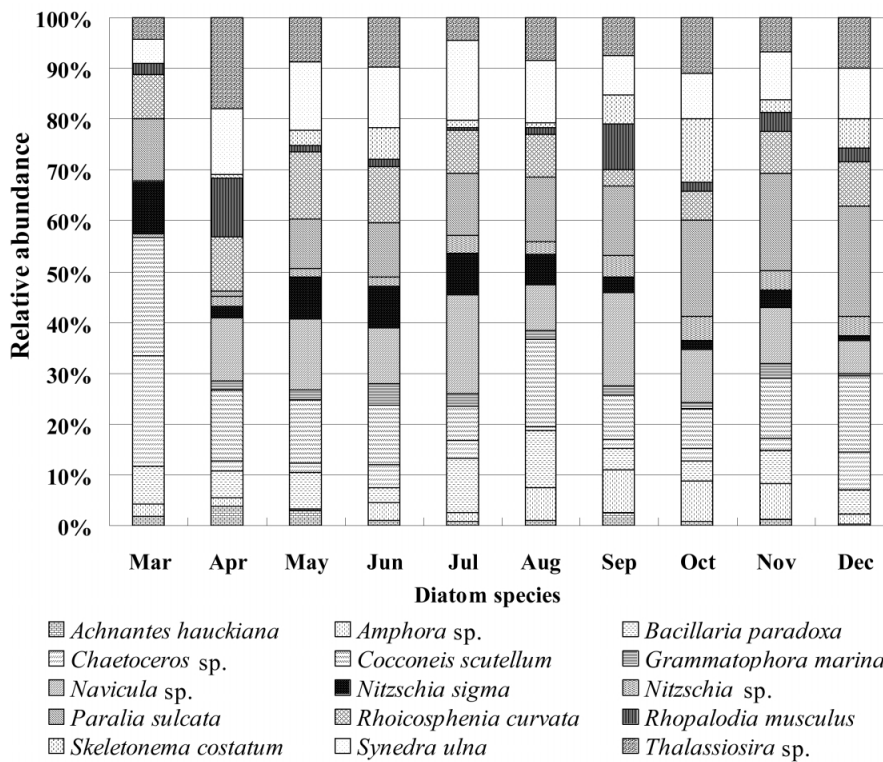


Fig. 3. Species composition of diatom assemblages and its seasonal variation in the Akkeshi-ko water column.

Table 2. List of diatoms recorded in surface sediment and water column in the Akkeshi-ko estuary during 2003 (group codes: B = benthic and P = pelagic). Very rare is <1% of total diatom abundance, rare is 1–3% of total diatom abundance and common is >3% of total diatom abundance.

No.	Name of species	Group	Water column	Surface sediment
1	<i>Achnanthes brevipes</i> Agardh	B	Rare	Rare
2	<i>Achnanthes hauckiana</i> Grunow var. <i>hauckiana</i>	B	Common	Common
3	<i>Achnanthes lanceolata</i> (Van Goor) Hustedt	B		Rare
4	<i>Actinocyclus</i> sp.	B		Rare
5	<i>Actinocyclus</i> sp.	P	Rare	
6	<i>Amphiprora alata</i> Kutzing	B	Very rare	Very rare
7	<i>Amphora helenensis</i> Giffen	B	Rare	Rare
8	<i>Amphora lineolata</i> Ehrenberg	B	Rare	Rare
9	<i>Amphora ovalis</i> Kutzing	B		Very rare
10	<i>Amphora salina</i> W. Smith	B	Rare	Rare
11	<i>Amphora</i> sp.	B	Common	Common
12	<i>Amphora</i> spp.	B	Very rare	Very rare
13	<i>Amphora ventricosa</i> Gregory	B	Common	Common
14	<i>Arachnoidiscus</i> sp.	B		Rare
15	<i>Aulacoseira ambigua</i> (Grunow) Simonsen	P	Common	Common
16	<i>Bacillaria paradoxa</i> var. <i>paxilifer</i> Gmelin	B	Common	Common
17	<i>Bacteriastrium</i> sp.	P	Very rare	
18	<i>Biddulphia obtusa</i> Kutzing	B	Rare	Rare
19	<i>Biddulphia</i> sp.	B	Rare	Rare
20	<i>Caloneis</i> sp.	B	Rare	Rare
21	<i>Campyloneis grevillei</i> (W. Smith) Grunow	B	Very rare	
22	<i>Chaetoceros</i> sp.	P	Rare	
23	<i>Climacosphenia</i> sp.	B	Rare	
24	<i>Cocconeis costata</i> Gregory	B	Common	Common
25	<i>Cocconeis pediculus</i> Ehrenberg	B	Rare	Rare
26	<i>Cocconeis placentula</i> Ehrenberg	B	Very rare	Very rare
27	<i>Cocconeis</i> sp.	B		Very rare
28	<i>Cocconeis scutellum</i> Ehrenberg	B	Common	Common
29	<i>Corethron pelagicum</i> Grunow	P	Rare	
30	<i>Coscinodiscus excentricus</i> Ehrenberg	P	Very rare	
31	<i>Coscinodiscus lecustris</i> Grunow	P	Very rare	Very rare
32	<i>Coscinodiscus marginatus</i> Ehrenberg	P	Rare	
33	<i>Coscinodiscus oculus iridis</i> Ehrenberg	P	Rare	Rare
34	<i>Coscinodiscus</i> sp.	P	Rare	Rare
35	<i>Cosmioneis</i> sp.	B	Rare	Rare
36	<i>Cymbella cuspidata</i> Kutzing	B		Rare
37	<i>Cymbella microcephala</i> Grunow	B	Rare	Rare
38	<i>Cymbella minuta</i> Hilse	B	Common	Common
39	<i>Diatoma elongatum</i> Lingbye	B		Very rare
40	<i>Diatoma hyalina</i> Kutzing	B	Rare	
41	<i>Diploneis fusca</i> (Greg.) Cleve	B	Rare	Rare
42	<i>Diploneis smithii</i> (Brebisson) Cleve	B	Common	Common
43	<i>Diploneis</i> sp.	B	Very rare	Very rare
44	<i>Donkinia</i> sp.	B	Common	Common

sediments and also in the water column at almost all stations (Table 2).

On the surface sediments, only 12 species of benthic diatoms, *Amphora* sp., *Amphora ventricosa*, *Bacillaria paradoxa* var. *paxilifer*, *Cocconeis costata*, *Cocconeis scutellum*, *Navicula rhynchocephala*, *Navicula* sp.,

Nitzschia sigma, *Paralia sulcata*, *Rhabdonema arcuatum*, *Rhoicosphenia curvata*, *Synedra ulna*, and 2 species of pelagic diatoms, *Melosira juergensi* and *Thalassiosira* sp. were most common and dominant at all stations. In the water column, 12 species of benthic diatoms, *Achnanthes hauckiana*, *Amphora* sp., *B. paradoxa* var. *paxilifer*, *C.*

Table 2. (continued).

No.	Name of species	Group	Water column	Surface sediment
45	<i>Entomoneis</i> sp.	B	Rare	Rare
46	<i>Epithemia adnata</i> Kutzing	B	Rare	Rare
47	<i>Eunotia serra</i> Ehrenberg	B	Very rare	Very rare
48	<i>Fragilaria</i> sp.	B	Rare	
49	<i>Frustulia rhomboides</i> Ehrenberg	B	Common	Common
50	<i>Gomphonema acuminatum</i> Ehrenberg	B	Rare	Rare
51	<i>Gomphonema parvulum</i> Kutzing	B	Common	Common
52	<i>Grammatophora</i> sp.	B	Common	Common
53	<i>Gyrosigma balticum</i> (Ehrenberg) Rabh	B		Very rare
54	<i>Gyrosigma scalproides</i> (Rabenhorst) Cleve	B		Rare
55	<i>Gyrosigma</i> sp.	B	Rare	Rare
56	<i>Hantzschia</i> sp.	B		Very rare
57	<i>Leptocylindrus</i> sp.	P	Very rare	
58	<i>Licmophora</i> sp.	B	Rare	Rare
59	<i>Mastoglia</i> sp.	B	Rare	Rare
60	<i>Melosira borrieri</i> Greville	P	Rare	
61	<i>Melosira juergensi</i> Agardh	P	Rare	Rare
62	<i>Melosira nummuloides</i> Agardh	P	Common	Common
63	<i>Melosira</i> sp.	P	Rare	Rare
64	<i>Melosira</i> spp.	P	Rare	
65	<i>Meridion</i> sp.	B	Rare	Rare
66	<i>Navicula cancellata</i> Donk. var <i>Constricta</i> (Ralfs)	B		Rare
67	<i>Navicula cryptotenella</i> Lange-Bertalot	B	Rare	Rare
68	<i>Navicula gregaria</i> Donkin	B	Rare	Rare
69	<i>Navicula marina</i> Ralfs	B	Very rare	Very rare
70	<i>Navicula pseudony</i> Hustedt	B		Rare
71	<i>Navicula pupula</i> Kutzing	B		Very rare
72	<i>Navicula rhynchocephala</i> Kutzing	B	Common	Common
73	<i>Navicula salinarum</i> Grunow	B	Rare	Rare
74	<i>Navicula slevicensis</i> Grunow	B	Rare	Rare
75	<i>Navicula</i> sp.-1	B	Rare	Rare
76	<i>Navicula</i> sp.-2	B	Common	Common
77	<i>Navicula tuscula</i> Form.	B		Very rare
78	<i>Nitzschia closterium</i> W. Smith	B		Rare
79	<i>Nitzschia marginata</i> Grunow	B		Rare
80	<i>Nitzschia punctata</i> Grunow	B	Rare	Rare
81	<i>Nitzschia scalpeliformis</i> Grunow	B	Rare	
82	<i>Nitzschia serriata</i> Cleve	B	Common	Common
83	<i>Nitzschia sigma</i> W. Smith	B	Common	Common
84	<i>Nitzschia</i> sp-1.	B	Rare	Rare
85	<i>Nitzschia</i> sp-2.	B		Very rare
86	<i>Nitzschia</i> sp-3.	B		Rare

scutellum, *Grammatophora marina*, *Navicula* sp., *Nitzschia sigma*, *Nitzschia* sp., *P. sulcata*, *R. curvata*, *Rhopalodia musculus*, and *S. ulna*, and 3 species of pelagic diatoms, *Chaetoceros* sp., *Skeletonema* sp. and *Thalassiosira* sp. were most common and predominant at all stations.

The species composition of diatom assemblages changed slightly seasonally. In the water column, *Thalassiosira* sp., *Navicula* sp. and *C. scutellum* were

abundant in spring. *Skeletonema* sp., *Navicula* sp., *P. sulcata*, *S. ulna*, *C. scutellum* and *B. paradoxa* var *paxilifer* were most abundant in summer and autumn, except *B. paradoxa* var *paxilifer*, which was only abundant in summer (Fig. 3). On the other hand, the species composition of benthic diatoms on the surface sediment was almost similar, particularly in summer and autumn. *C. scutellum*, *Navicula* sp., *P. sulcata* and *R. curvata* were common and dominant in all seasons (Fig. 4). Epiphytic

Table 2. (continued).

No.	Name of species	Group	Water column	Surface sediment
87	<i>Nitzschia</i> spp.	B	Rare	Rare
88	<i>Odontella aurita</i> Greville	B	Rare	Rare
89	<i>Paralia sulcata</i> (Ehrenberg) Cleve	B	Common	Common
90	<i>Pinnularia viridis</i> Ehrenberg	B	Rare	Rare
91	<i>Pinnunavis elegans</i> (W. Smith) Okuno	B		Rare
92	<i>Pleurosigma affine</i> Grunow	B	Rare	Rare
93	<i>Pleurosigma elongatum</i> W. Smith	B	Very rare	Very rare
94	<i>Pleurosigma fasciola</i> Ehrenberg	B	Rare	Rare
95	<i>Pleurosigma intermedium</i> W. Smith	B	Rare	Rare
96	<i>Pleurosigma</i> sp.	B		Rare
97	<i>Pleurosigma rigidum</i> W. Smith	B	Rare	
98	<i>Rhabdonema adriaticum</i> Kutzing	B		Rare
99	<i>Rhabdonema arcuatum</i> Kutzing	B	Common	Common
100	<i>Rhizosolenia alata</i> (Peragallo) Ostensfeld	P	Very rare	
101	<i>Rhizosolenia</i> sp.	P	Very rare	
102	<i>Rhoicosphenia curvata</i> (Kutzing) Grunow	B	Common	Common
103	<i>Rhopalodia gibba</i> (Ehrenberg) Muell	B		Rare
104	<i>Rhopalodia gibberula</i> (Ehrenberg) Muell	B	Rare	Rare
105	<i>Rhopalodia musculus</i> (Kutzing) Muell	B	Common	Common
106	<i>Rhopalodia</i> sp.	B	Rare	
107	<i>Skeletonema</i> sp.	P	Rare	
108	<i>Stauroneis phoenicenteron</i> Ehrenberg	B	Rare	Rare
109	<i>Stephanopyxis</i> spp.	P	Rare	
110	<i>Stigmophora</i> sp.	B	Rare	Rare
111	<i>Surirela gemma</i> Ehrenberg	B		Very rare
112	<i>Surirela</i> sp.	B	Rare	Rare
113	<i>Synedra</i> sp.	B	Rare	Rare
114	<i>Synedra ulna</i> Kutzing	B	Common	Common
115	<i>Thalassionema nitzschioides</i> Grunow	B	Rare	
116	<i>Thalassiosira gravida</i> Cleve	P	Rare	
117	<i>Thalassiosira hyalina</i> Grunow	P	Rare	
118	<i>Thalassiosira nordenskioldi</i> Cleve	P	Rare	
119	<i>Thalassiosira</i> sp.	P	Common	Common
120	<i>Triceratium</i> sp.	B		Rare
121	<i>Tryblionella compressa</i> (Bailey) Mann	B	Rare	
122	<i>Tryblionella granulata</i> Grunow	B	Common	Common
123	<i>Tryblionella lanceola</i> Grunow	B	Rare	Rare
124	<i>Tryblionella levidensis</i> (W. Smith) Grunow	B	Rare	Rare
125	<i>Tryblionella littoralis</i> (Grunow) Mann	B		Rare
126	<i>Tryblionella salinarum</i> (Grunow) Cleve	B		Rare
127	<i>Tryblionella coarctata</i> (Grunow) Mann	B	Rare	Rare
128	<i>Tryblionella</i> sp.	B	Very rare	Very rare

diatom species on seagrass leaves are shown in Fig. 5. The species composition of epiphytes was similar to the assemblage in the water column and also to that of the surface sediment.

In the water column, the densities of benthic and pelagic diatoms at almost all stations doubled in spring and summer, except at St. 10 which increased in autumn (Fig. 6). The density of benthic diatoms on the surface sediment varied seasonally, being high in spring-summer

at most stations except Sts. 10 (near the river-mouth) and 14, which had high densities of benthic diatoms in autumn (Fig. 7).

The benthic to pelagic ratio (BPR) in the diatom assemblage on surface sediment was higher than that in the water column diatom assemblage. The seasonal variations of BPR on the surface sediment and in the water column were high at all stations. During spring, summer and autumn, the BPR was almost 1.0 on the surface sediment,

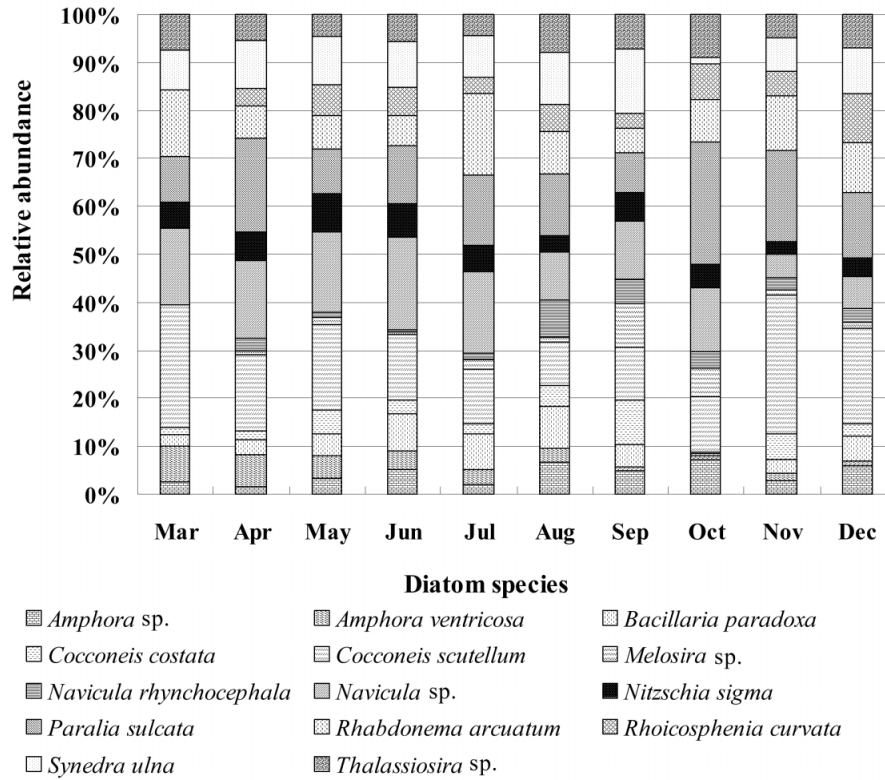


Fig. 4. Species composition of diatom assemblages and its seasonal variation on Akkeshi-ko surface sediment.

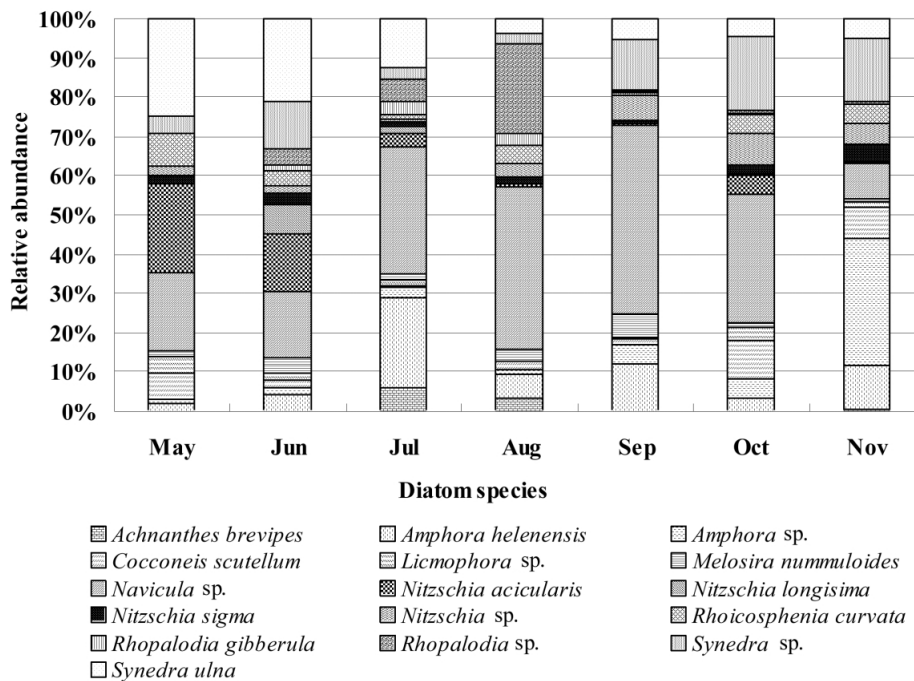


Fig. 5. Species composition of diatom assemblages on the seagrass leaves and its seasonal variation in the seagrass beds of the Akkeshi-ko estuary.

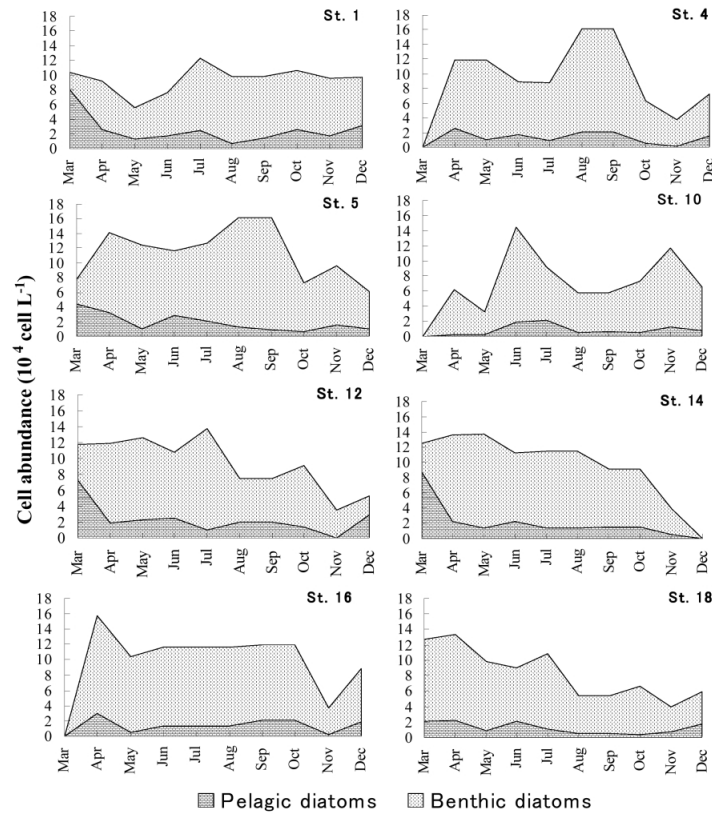


Fig. 6. Seasonal variation of pelagic and benthic diatoms abundance in the water column of the Akkeshi-ko estuary from March to December 2003.

Table 3. The value of Pearson multiple analysis between physical environmental factors and the abundance of benthic and pelagic diatom assemblages in both, surface sediment and water column (BDWC = benthic diatoms in water column, PDWC = pelagic diatoms in water column, BDSed = benthic diatoms on the sediment, and PDSed = pelagic diatoms on the sediment).

	Depth (m)	Salinity (ppt)	Temperature (°C)	Current vel. (m·s ⁻¹)
BDWC	0.244	0.179	0.431	-0.171
PDWC	0.623	0.652	-0.148	0.41
BDSed	-0.502	-0.409	0.248	-0.731
PDSed	-0.469	-0.195	-0.016	-0.622

while in the water column it was up to 0.5 from the total of diatom assemblages.

Correlation analysis between physical environmental factors and abundance of benthic and pelagic diatom assemblages in both the surface sediment and the water column was performed on these data. From these analyses, positive correlations were found between pelagic diatoms in the water column (PDWC) and depth and salinity ($r = 0.623$ and $r = 0.652$, respectively). Correlations between benthic diatom assemblages in the sediment (BDSed) and in the water column (BDWC) and depth and salinity were not significant (Table 3).

3.3 Gut contents of filter feeding bivalves

Gut contents of the clam and the oyster are shown in Fig. 8. All gut contents showed a higher ratio of benthic diatoms than that of pelagic species. Dinoflagellates were also found to some extent in number. These gut contents reflected directly the diatom species composition and BPR in the water column.

4. Discussion

In coastal marine ecosystems, phytoplankton has been recognized as a primary producer besides macroalgae, seagrasses, benthic microalgae, epiphytic

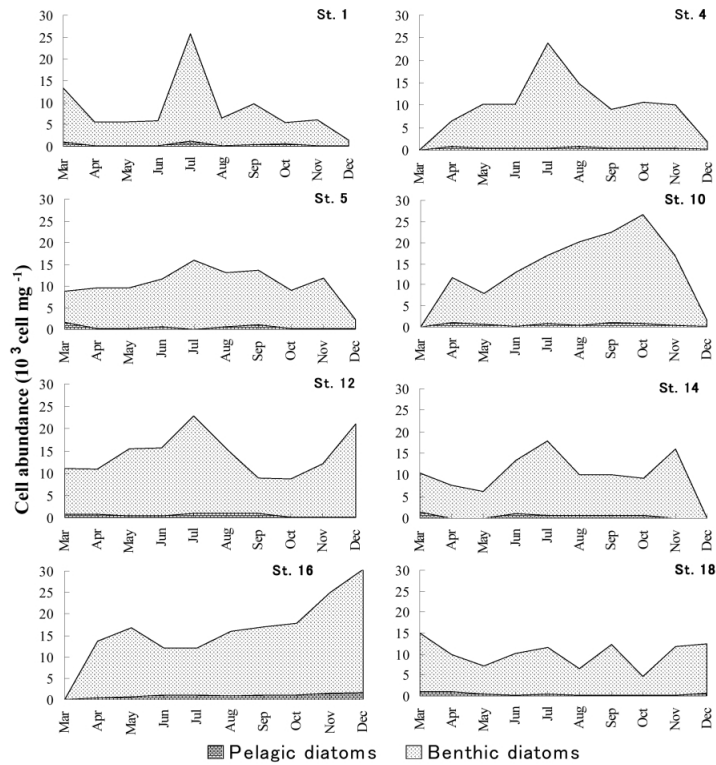


Fig. 7. Seasonal variation of pelagic and benthic diatom abundance on the surface sediment of the Akkeshi-ko estuary from March to December 2003.

micro- and macroalgae, and so on. The importance of phytoplankton in coastal marine ecosystems is relatively small compared with that in pelagic ocean ecosystems. However, it has been considered that phytoplankton may be the sole diet for suspension feeders (Hamamoto and Mukai, 1999), in particular for the clam and the oyster which are popular objects of mariculture in many Japanese estuaries and sand flats.

Hitherto, “phytoplankton” in the coastal water column was believed to comprise pelagic species. Recently the fact that “phytoplankton” includes many benthic diatom species was realized by Montani *et al.* (2003), who discovered the increase of chlorophyll *a* concentration in the estuarine water column in the Seto Inland Sea of Japan, which coincides with the tidal cycle.

The abundance of “phytoplankton” in the water column fluctuates due to many abiotic and biotic factors. It is influenced by light and nutrient availability. Dissolved inorganic nitrogen, as ammonia, nitrate, nitrite, phosphate, silicate and so on, is basically an important factor influencing “phytoplankton” dynamics. These nutrients are supplied fundamentally from rivers. The nutrient concentration and availability to “phytoplankton” would change with seasons and precipitation.

Furthermore, “phytoplankton” may compete for the

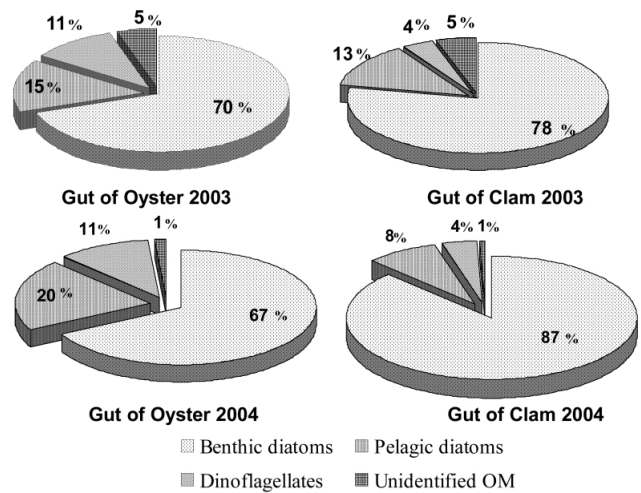


Fig. 8. Gut contents of the Manila clam, *Ruditapes philippinarum*, and the oyster, *Crassostrea gigas* in 2003 and 2004 from the Akkeshi-ko estuary.

nutrients with marine macrophytes, in particular eelgrasses, *Zostera marina* and *Z. japonica*, in the Akkeshi-ko estuary. *Z. marina* may be a strong competitor for “phytoplankton” during spring–summer, because

the biomass and production rate of *Z. marina* is very high in these seasons in the Akkeshi-ko estuary (Mukai *et al.*, unpublished).

On the other hand, the abundance of “phytoplankton” is reduced by feeding of filter feeders such as bivalves, sponges, bryozoans, solitary and compound ascidians, burrowing shrimps, and so on. In the Akkeshi-ko estuary, maricultured bivalve feeding may have the most influence on “phytoplankton” dynamics, due to the great biomass of maricultured bivalves.

In the Akkeshi-ko estuary, the diatom assemblage of the water column was dominated by benthic species, as is the assemblage of surface sediments. Most benthic diatom species in the water column were common with epipelics such as *P. sulcata* and *B. paradoxa* var *paxilifer* and epiphytic species on seagrass leaves such as *Achnantes hauckiana*, *Amphora* sp., *C. scutellum*, *Grammatophora marina*, *Navicula* sp., *Nitzschia sigma*, *Nitzschia* sp., *R. curvata*, *Rhopalodia musculus*, and *S. ulna*. The occupation ratio of epiphytic species in the water column diatom assemblage was about 20% in winter, increasing in May to July with increasing biomass of seagrasses from 54 ± 14 gDW•m⁻² in April to 168 ± 60 gDW•m⁻² in August (Hasegawa, unpublished). On the other hand, some pelagic diatom species were included in diatom assemblages on surface sediments. The most dominant species on the surface sediment were typically epiphytic and epipellic.

Why do these contaminations of pelagic and benthic species occur? The fact that diatom assemblages on surface sediments included pelagic species can be easily understood because, in such shallow estuaries, diatom cells usually sink, so many living pelagic diatom cells can be found on surface sediments at any time. The opposite case would occur due to disturbance by (1) tidal flows and/or (2) wind.

The continuous field measurement showed that chlorophyll *a* concentration in the water column near the bottom increased during periods of high wind velocity (Fig. 2). The increase of chlorophyll *a* concentration in the water column is closely related to the high concentration of diatom assemblages in the water column near the surface sediment. Perrisinotto *et al.* (2002) observed the spatiotemporal dynamics of pelagic and benthic diatoms in Mpenjati Estuary, Kwazulu-Natal, South Africa, and showed that chlorophyll *a* concentration was higher in the open estuary and was directly correlated with strong mixing as a result of strong tidal and riverine flows, thus causing the suspension of benthic diatoms. Benthic and epiphytic diatoms were able to suspend into the water column from the surface sediment by disturbance stimulated by wind and/or tidal currents. Magni *et al.* (2002) described the diurnal fluctuation of nutrients and suspended particulate matter including diatom assemblages

in a shallow estuary area in the Seto Inland Sea of Japan. They considered that the fluctuation was generated by tidal flows.

In the Akkeshi-ko estuary, most of the estuary area is now used intensively for the mariculture of the clam, *Ruditapes philippinarum*, and the oyster, *Crassostrea gigas*. *R. philippinarum* and *C. gigas* are suspension feeders. They take their foods from the water column. The results of this study indicate the availability of benthic diatoms as food sources of *R. philippinarum* and *C. gigas* from the surrounding water column.

There is some evidence for a relationship between diatom availability and suspension feeding. Kamermans (1994) found a close similarity between the species composition of the phytoplankton in water column and phytoplankton species composition in the guts of *Cerastoderma edule*, *Mya arenaria* and *Mytilus edulis*. Cognie *et al.* (2001) observed that *C. gigas* in the estuarine intertidal area of Bourgneu Bay, France, fed only benthic microalgae. Four dominant species of benthic microalgae, which are endemic diatoms characteristic of a tidal mud flat environment, such as *Navicula ammophila* (Grunow), *Navicula rostellata* (Kutzing), *Plagiotropis lepidoptera* (Kuntze), and *Staurophora amphioxys* (Mann), represented more than 95% in cell number of the 16 species in the guts of oysters. The work of Soletchnik *et al.* (2001) on the optimizing of *C. gigas* culture on the French Atlantic coast, showed that a benthic diatom (*Nitzschia* sp.) and a pelagic one (*Skeletonema* sp.) were dominant, preferred foods of *C. gigas*. A correlation between *C. gigas* and their available surrounding food sources was observed by Bougrier *et al.* (1997). Work on selective grazing of *C. gigas* and *M. edulis* in Marenes Oleron (France) showed that *C. gigas* preferentially filtered diatom species more than flagellates. In a natural planktonic community, Dupuy *et al.* (2000) found that the microphytobenthos, in particular benthic diatoms, was the main food source of *C. gigas*. In terms of carbon base, 81% and 15% of the particulate organic carbon (POC) resource came from diatoms and dinoflagellates, respectively. Sorokin and Giovanardi (1995), who reported the foods and feeding activity in the Manila clam, *R. philippinarum*, by using ¹⁴C-labelled algae and bacteria as food sources, found that the diatom (*Nitzschia* sp.) and *Chlorella* form a high proportion of the food source of clams in the Southern Venetian Lagoon. The assimilation rate of green alga and diatoms filtered as food was 50–60%. Nakamura (2001) noticed that *R. philippinarum* actively filtered prey items larger than 2 μm (such as *Nitzschia* spp.) in Nishi-jima Island (Seto Inland Sea of Japan).

In the Akkeshi-ko estuary, the abundance of benthic diatoms was higher than pelagic diatoms in all seasons, as generally reported for several shallow estuarine water

systems (Blackford, 2002; Welker *et al.*, 2002). On the intertidal flat in the Seto Inland Sea of Japan, the biomass of benthic diatoms increased during spring and summer (Montani *et al.*, 2003). The results of the present study show that diatom assemblages on the surface sediment and water column were generally predominated by benthic diatoms, which played a major role throughout the sampling period. The results provide some evidences that the abundance of the benthic diatoms was higher than that of pelagic diatoms. The diatom assemblages were generally composed of *Amphora* sp., *Cocconeis* sp., *Navicula* sp., *Nitzschia* sp., *Pleurosigma* sp. and *Thalassiosira* sp. in all water columns.

In Mpenjati estuary on the Kwanzulu Natal, South Africa, the concentration of benthic diatoms was also always higher than pelagic diatoms in the water column (Perrisinotto *et al.*, 2002). Facca *et al.* (2002) found that the introduction of the clam *R. philippinarum* in Venice Lagoon, Italy, and its harvesting with a hydraulic machine caused suspension of benthic diatoms due to disturbance.

Riaux-Gobin and Bourgoïn (2002) reported that the increase of several benthic diatom species such as *Cocconeis* sp. and *Grammatophora* sp. during summer in Kerguelen Archipelago (Indian Ocean) was strongly related to the dense macroalgal canopy as an important source of these diatoms. Facca *et al.* (2002) found a low diatom concentration in several sites of Venice lagoon, Italy, when macroalgae disappeared in season. This suggests that epiphytic diatoms are important for sustaining "phytoplankton" assemblages in the water column.

Dominant species of benthic diatom assemblage in the Akkeshi-ko estuary occurred adjacent to the seagrass beds, Sts. 8, 9, 13, and 16. Our observations suggest that several species of the benthic diatom assemblage were always associated with the dense seagrass beds. It is interesting that *C. scutellum*, which was most common at all stations, is a typically epiphytic species, attaching to the macrophyte. In Ikuraushi (Southeastern part of Akkeshi-ko) - Kanasaki (Northeastern part of Akkeshi-ko) transect, *C. scutellum* was one of the most abundant living and dead diatom cells in sediment core samples (Sawai, 2001b). Tidal movement was able to tear off this microalga from macrophytes, and the diatom sunk onto the sediment, suffered sedimentary processes, re-suspended into the water column, and was grazed by suspension feeders (Orth and Van Montfrans, 1984; Tuji, 2000; Sawai, 2001b).

The spatial and temporal fluctuation of benthic and pelagic diatoms generally correlates with light and nutrient availability (Kormas *et al.*, 2001; Welker *et al.*, 2002), tidal current (Perrisinotto *et al.*, 2002) and grazing pressure by suspension feeders (Blackford, 2002). Basically, benthic and pelagic diatoms can be controlled by nutrient concentration as bottom-up effects and/or by top-down

effects, such as feeding by suspension feeders (Bennett *et al.*, 2000). In midsummer, the biomass of benthic diatoms was higher than pelagic diatoms at several stations in the Adriatic Sea, with nutrient and light availability being key factors limiting the fluctuation of diatom abundance (Blackford, 2002). The inorganic nutrient concentration in the water column near the sediment surface was an important factor influencing the spatial fluctuation of diatoms. In the Gulf of Trieste (Northern Adriatic Sea), they have significant correlations between diatom abundance and ammonium, silicate and phosphate concentrations. The fluctuation of diatoms in the water column near the surface bottom layer was also influenced not only by the total annual regeneration of ammonium, silicate and phosphate, but also by the sediment characteristic and bioturbation, which may displace diatoms to the water column from the surface layer caused by benthic faunal activity (Welker *et al.*, 2002).

In the Akkeshi-ko estuary, the availability of benthic diatom production is likely to provide significantly enhanced food resources to suspension feeder such as clams and oysters. Blackford (2002), who modelled the relationship between suspension feeders and benthic diatoms, suggested that the suspension feeder was one of the major factors, that controlled the spatial fluctuation of benthic diatom abundance in the estuarine system. Grazing pressure by suspension feeders has a significant effect on the summer population of diatoms. Up to 60% of the standing stock of pelagic and benthic diatoms was lost per day during late summer. The benthic diatoms were the most important food source for clam *R. philippinarum* and oyster *C. gigas* mariculture during spring and summer, when the abundance of the diatoms, including benthic and pelagic diatoms, was high.

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