

Impaired megabenthic community structure caused by summer hypoxia in a eutrophic coastal bay

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Abstract Eutrophication and hypoxia are major problems affecting the health of coastal ecosystems throughout the world. Tokyo Bay, Japan, is a eutrophic coastal area where the abundance of the megabenthic community has been decreasing. To assess factors associated with the impaired biota, seasonal surveys of the megabenthic community and water and sediment quality were conducted in the bay. Cluster analysis showed a difference in the community structure between the northern and southern parts of the bay. The density of species and species diversity were high throughout the year in the southern part of the bay, whereas in the northern part of the bay species diversity was low and defaunation occurred in August. At this time, bottom hypoxia due to temperature and salinity stratification, and high concentrations of nutrients, chlorophyll *a*, and organic

matter in the water column and/or sediment, dominated the northern part of the bay. In October, bottom hypoxia was less severe but was still present in the northern part of the bay, and recolonization by mobile fishes and sessile mussels occurred. Multivariate analyses of the megabenthic community and environmental parameters in August showed the spatial pattern of the community could be explained by concentrations of dissolved oxygen and particulate organic carbon in the bottom water, and total sulfide and total organic carbon in the sediments. In particular, impairment of the biota in the northern area could be explained by the threshold concentrations of dissolved oxygen $<1.7 \text{ mL L}^{-1}$ and total organic carbon $>20.3 \text{ mg g}^{-1}$.

Keywords Benthic assemblage · Defaunation · Eutrophication · Hypoxia · Organic matter · Tokyo Bay

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Introduction

Productivity in coastal waters is high due to high levels of primary production, which is supported by the supply of nutrients from terrestrial areas (Ryther 1969; Jennings et al. 2001). However, productivity has been impaired by various stressors from human activities, such as eutrophication due to excessive inputs of nutrients and organic matter (Boesch et al. 2001), discharge of toxic pollutants (Stein and Cadien 2009), suspended solids from dredging (Torres et al. 2009), loss of mud and sand flats from land reclamation (Furota 1997), and pressure from commercial or recreational fisheries (Jennings et al. 2001). In addition, bottom hypoxia (with dissolved oxygen [DO] concentration $\leq 2 \text{ mL L}^{-1}$) caused by anthropogenic eutrophication is one of the major environmental stressors in coastal systems throughout the world and is a growing global concern (Diaz and

Rosenberg 1995, 2008). Hypoxia is usually formed in eutrophic systems by excessive nutrient inputs leading to increased primary production, followed by an increase in deposition of organic matter on the bottom. Oxygen is used to decompose this bottom organic matter; however, the supply of oxygen from the surface is hindered when thermal/density stratification occurs, resulting in bottom hypoxia.

To date, various effects of hypoxia on aquatic organisms have been reported at the individual or population level in terms of mortality (Baden et al. 1990; Diaz and Rosenberg 1995), growth (Zhou et al. 2001), reproduction (Thomas et al. 2006, 2007; Thomas and Rahman 2009), settlement (Baker and Mann 1992; Furota 1996), spatial distribution (Pihl et al. 1991; Kodama et al. 2006, 2009), and species interaction (Breitburg et al. 1997; Shoji et al. 2005). Responses to hypoxia differ among taxa. For example, sedentary bivalve species are usually tolerant to hypoxia (Hochachka 1980), and some species can survive even in anoxic conditions for several to dozens of days (Tamai 1992; de Zwaan et al. 2001). Meanwhile, motile animals like fishes, crustaceans, and cephalopods, can evade hypoxic zones, although there are differences among species in the threshold DO level that is tolerated and/or the time when movement away from these conditions begins (Pihl et al. 1991; Das and Stickle 1994; Eby and Crowder 2002). Because coastal benthic communities comprise multiple species in a number of different taxonomic groups, studies of the effects of hypoxia on the health of the coastal system need to assess benthic animals not only at the species/population level but also at the community level. Although coastal macrobenthic and meiobenthic communities have been studied intensively (e.g., Diaz and Rosenberg 1995; Lim et al. 2006; Liu et al. 2008), information on the effects of hypoxia on the megabenthic community is limited.

Tokyo Bay, on the east-central coast of Japan, is a semi-enclosed coastal system with a surface area of 960 km² and an average depth of 15 m (Fig. 1). Water in the bay is exposed to the effects of various anthropogenic activities as a result of the population of about 26 million people in the surrounding catchment area (Furota 1997). Hypoxia was first observed in the bay in 1955 (Ishii et al. 2008) and is one of the major environmental issues affecting the quality of the bay water and sediment. Since 1955, the spatial extent and duration of the low oxygen conditions have been increasing (Ishii et al. 2008). Stock size of the megabenthic assemblage in the bay decreased dramatically in the late 1980s and has since remained low (Kodama et al. 2002). Multivariate analyses of long-term biotic and abiotic data suggest a decreasing trend in bottom DO concentration in the bay as one of the factors causing the stock-size decline of the megabenthic assemblage (Kodama et al. 2002).

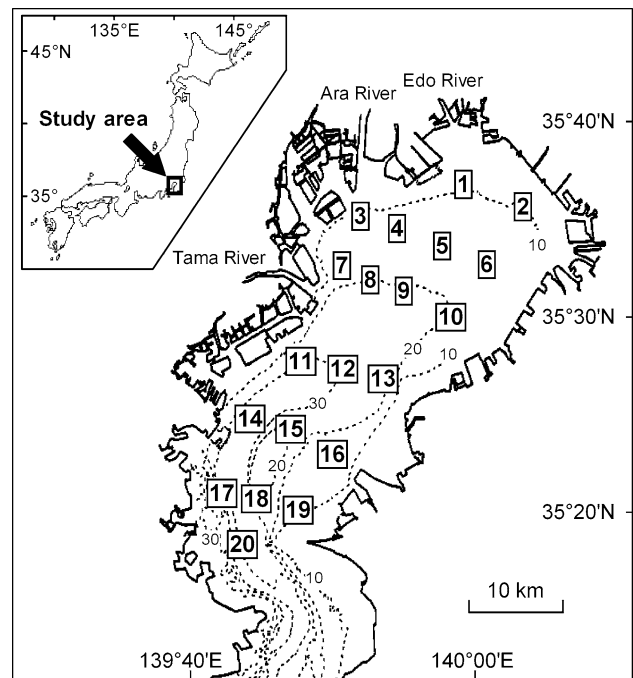


Fig. 1 Locations of 20 sites (numbers in squares) for bottom trawl surveys, water and sediment sampling, and water quality measurement in Tokyo Bay, Japan. Dotted lines with numbers show depth contours in meters

The aim of this study was to describe the spatiotemporal patterns of environmental conditions and the megabenthic community in Tokyo Bay and to evaluate the effects of environmental factors in the bottom waters on disturbance of the megabenthic community structure.

Materials and methods

Field sampling

Bottom-trawl surveys were carried out in 2005 at 20 sampling sites across the bay to collect megabenthos. Sampling occurred four times on a seasonal basis: February 24 (winter), May 12 (spring), August 17 (summer), and October 26 (autumn) (Fig. 1). Surveys were conducted during the day by two 5-t trawlers, each using a trawl with a mouth 5.5 m wide and 0.6 m high. The trawls had a cod-end mesh size of 3 cm and were towed at each station for 10 min at a speed of 2 knots, resulting in a sampling area per station of 3.4×10^{-3} km². The catch included fishes (elasmobranchs and teleosts), crustaceans (decapods and stomatopods), mollusks (bivalves, gastropods, and cephalopods), and echinoderms (echinoids and holothuroids), and these were collected and identified to species level. The number of individuals and the total wet weight (grams) for each species were recorded. Other taxa

(e.g., polychaetes, asteroids, and hydroids) were not collected. The species density in both number of individuals and weight was calculated by dividing the number of individuals and weight, respectively, by the area swept by the trawl at each station.

To monitor water quality, water sampling was conducted at the same 20 sites by two 10-t boats on the same dates as the trawl surveys (Fig. 1). Temperature, salinity, and DO concentrations were measured at the surface (at a depth that was 10% of the total water depth) and bottom layer (at a depth that was 90% of the total depth) using a conductivity, temperature, and depth (CTD) data logger with a DO sensor (model XR-420 CTD Marine, RBR Ltd., Ontario, Canada). DO measurements were not taken for sites 11–20 in February because of equipment problems. Water samples were collected with 8-L Go-Flo bottles (Model 1080, General Oceanics Inc., Miami, FL, USA) at each surface and bottom depth for a total of two samples per site. Water samples were brought back to the laboratory in 500-mL polypropylene bottles on ice.

To understand the spatial characteristics of the sediment during severe summer hypoxia as well as to examine the relationship between disturbance to the megabenthic community in summer and the ambient environment, a sediment sample was collected at each site with a Smith-McIntyre grab sampler (0.05 m²; Rigo, Tokyo, Japan) in August. After each collection, a subsample of the sediment was taken from the surface of the sample in the grab sampler and transported to the laboratory in a 280-mL stainless steel container on ice.

Determination of water and sediment quality

Water samples for chlorophyll *a* (chl *a*) analysis (100 mL) were filtered onto Whatman GF/F glass-fiber filters and the filtrates were collected for nutrient analysis. Pigments were then extracted by placing the filters in 10 mL dimethyl-formamide for 24 h at 35°C. Chl *a* concentrations were determined by fluorometry (model 10-AU, Turner Designs, Sunnyvale, CA, USA). Dissolved nitrite (NO₂⁻), nitrate (NO₃⁻), ammonium (NH₄⁺), and phosphorus (PO₄³⁻) concentrations were measured in the filtered water sample with an auto-analyzer (AACS-II; Bran + Luebbe, Nordstedt, Germany), using standard procedures (Japan Meteorological Agency 1999). Dissolved inorganic nitrogen (DIN) concentration was the sum of NO₂⁻, NO₃⁻, and NH₄⁺ concentrations, and dissolved inorganic phosphorus (DIP) concentration was the PO₄³⁻ concentration.

Water samples for measurements of particulate organic carbon (POC) and particulate organic nitrogen (PON) concentrations were separately filtered through Whatman GF/F glass-fiber filters and analyzed according to established procedures (UNESCO 1994), using a CHN-O

analyzer (Finnigan Flash EA1112; Thermo Electron Corporation, Waltham, MA, USA).

Sediment samples collected in August were measured for grain size, loss on ignition (LOI), and concentrations of total sulfide (TS), total nitrogen (TN), and total organic carbon (TOC). Grain size was measured using the standard sieving and hydrometer procedure (Japan Industrial Standards Committee 2000), and relative percentages of sand (0.075 to <2 mm in diameter), silt (0.005 to <0.075 mm), and clay (<0.005 mm) were determined. LOI was determined according to the procedure by Bale and Kenny (2005) in which pre-weighed dry sediment samples (oven dried at 100°C) were combusted at 450°C for 8 h in a muffle furnace. Concentrations of TN and TOC were determined by a carbon–nitrogen analyzer (CHN-corder model MT-5; Yanaco, Kyoto, Japan), according to the procedure given by the Oceanographic Society of Japan (1986). The concentration of TS was measured by the iodometric titration method, according to the procedure given by the Environmental Agency of Japan (1996).

Data analysis

Prior to analyses, we excluded data on five pelagic species that were incidentally caught during field sampling but were not part of the megabenthic assemblage (three clupeoid fishes: *Engraulis japonicus*, *Konosirus punctatus*, and *Sardinella zunasi*; and two carangid fishes: *Trachurus japonicus* and *Decapterus maruadsi*).

Spatiotemporal patterns in the megabenthic assemblage were investigated through multivariate analyses according to Clarke (1993) and Clarke and Warwick (2001) with the PRIMER 6 software (PRIMER-E, Plymouth, UK). The biotic relationship, in terms of species composition and species density (by number of individuals or by weight), between any two stations was assessed with a zero-adjusted Bray-Curtis similarity index (Clarke et al. 2006). Prior to the calculation of similarity, species density by individuals and weight was logarithmically transformed to reduce the contributions of rare and very common species (Clarke 1993). Spearman's rank correlation coefficient (ρ_s) in the zero-adjusted Bray-Curtis similarity matrices between densities in terms of numbers of individuals and weights within the same month was found to be significant (RELATE routine; $\rho_s = 0.99$ in all months; $P < 0.01$), suggesting that the spatiotemporal pattern is very similar between densities in both number of individuals and in weight. Therefore, in the present study we examined species density by individuals only.

The spatial pattern of the megabenthic community was examined by hierarchical agglomerative clustering with group-average linking on the zero-adjusted Bray-Curtis coefficient (Clarke and Warwick 2001). We applied a

similarity profile (SIMPROF) test for detecting significantly different site groups (Clarke and Gorley 2006; Clarke et al. 2008). Mean and standard deviation of species density, number of species, and the Shannon diversity index (H' ; Clarke and Warwick 2001) were calculated for each site group separated by cluster analysis. We conducted analysis of similarity percentages (SIMPER) to identify dominant species within each site group (Clarke and Warwick 2001). We used two-way analysis of similarities (ANOSIM) to test spatial and temporal differences in assemblage structure (Clarke and Warwick 2001).

To identify water and sediment quality parameters showing a spatial pattern similar to that of the megabenthic assemblage, we applied the BIO-ENV analysis (Clarke and Gorley 2006). In the BIO-ENV analysis, a combination of water and sediment quality parameters is identified whose standardized Euclidean distance matrix shows the highest ρ_s with the biotic Bray-Curtis similarity matrix (Clarke and Ainsworth 1993; Clarke and Warwick 2001). We used data collected in August for the BIO-ENV analysis because sediment data were available only in August. Pairs of variables with a significant Pearson's correlation coefficient ($P < 0.05$) were represented by a single variable, and $\log(1 + x)$ -transformed variables of the bottom water or sediment were used for the BIO-ENV analysis (Clarke and Warwick 2001). To estimate the threshold of environmental variables for separation of site groups, linkage tree (LINKTREE) analysis, a nonparametric modification of De'ath's multivariate regression trees (De'ath 2002), was

performed using the subset of environmental variables identified by BIO-ENV analysis (Clarke and Gorley 2006; Clarke et al. 2008). An absolute measure of group difference (y -axis for the tree) is given by B%, which is the percentage of the average of the between-group rank similarity to the largest rank similarity in the original Bray-Curtis matrix for the megabenthic community data. Split of the tree was accepted if the SIMPROF test showed a significant difference between the divided site groups.

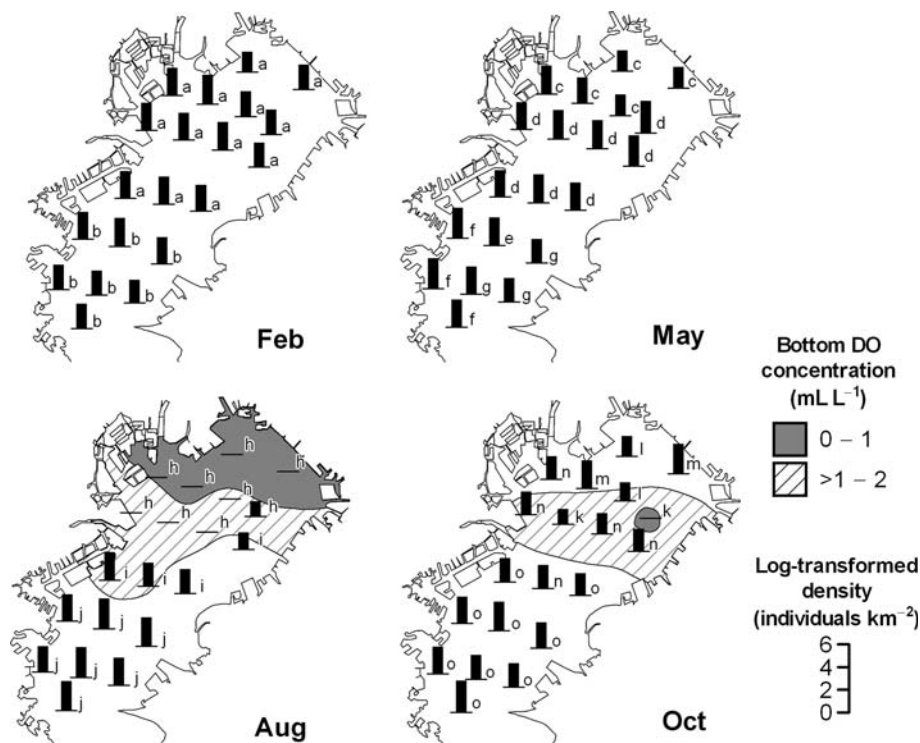
Differences in the monthly mean values of each water quality parameter were tested with nested analysis of variance (nested ANOVA), using R software (version 2.8.1; www.r-project.org). Site groups derived from cluster analysis of the megabenthic community were treated as subgroups within each month in the nested ANOVA. For DO concentrations at the surface and bottom, February data were excluded from the analysis due to the absence of data for sites 11–20 (see Field sampling).

Results

Spatiotemporal patterns in the megabenthic assemblage and hypoxia

Megabenthos was found throughout the bay in all seasons with the exception of two areas in the northern part of the bay where hypoxic bottom water was present: sites 1–5 and 7–9 in August and site 6 in October (Fig. 2). Cluster

Fig. 2 $\log(1 + x)$ -transformed individual densities of the megabenthic assemblage for each site in February, May, August, and October 2005 in Tokyo Bay. Hypoxic areas are displayed by shading (bottom dissolved oxygen [DO] concentration $\leq 1 \text{ mL L}^{-1}$) and hatching ($>1\text{--}2 \text{ mL L}^{-1}$); a–o denote site groups delineated by the SIMPROF test on dendrograms from cluster analysis on the megabenthic community



analysis delineated two site groups in February (groups a and b), five in May (c–g), three in August (h–j), and five in October (k–o) (SIMPROF test, $P < 0.05$; dendrogram not shown). These groupings generally showed a latitudinal gradient from north to south (Fig. 2). The differences in the spatial and temporal patterns of the megabenthic assemblage were supported by the results of the two-way ANOSIM test ($P < 0.01$ for differences among both seasons and sites).

Species density, species number, and species diversity (H') did not indicate large differences between the northern (group a) and southern (group b) parts of the bay in February (Figs. 2 and 3), and both areas were dominated by

various taxa. Fishes (*Pseudopleuronectes yokohamae* and *Repomucenus valenciennei*), crustaceans (*Metapenaeus joyneri* and *Oratosquilla oratoria*), and a mollusk (*Fulvia mutica*) were dominant in the northern part of the bay (Table 1). In the southern part of the bay, an echinoid *Temnopleurus hardwickii* was found in the highest density, and fishes (*R. valenciennei*, *Pennahia argentata*, and *Sillago japonica*), crustaceans (*Pyromaia tuberculata* and *Trachysalambria curvirostris*), and a mollusk (*Loliolus japonica*) were also abundant (Table 1).

In May, although species densities were similar among site groups, species number and diversity showed a decreasing trend in the north-central part of the bay

Fig. 3 Mean and standard deviation (vertical bars) of $\log(1 + x)$ -transformed individual density, number of species, and Shannon's diversity index (H') for the megabenthic community in Tokyo Bay; a–o denote site groups delineated by the SIMPROF test on dendrograms from cluster analysis on the megabenthic community

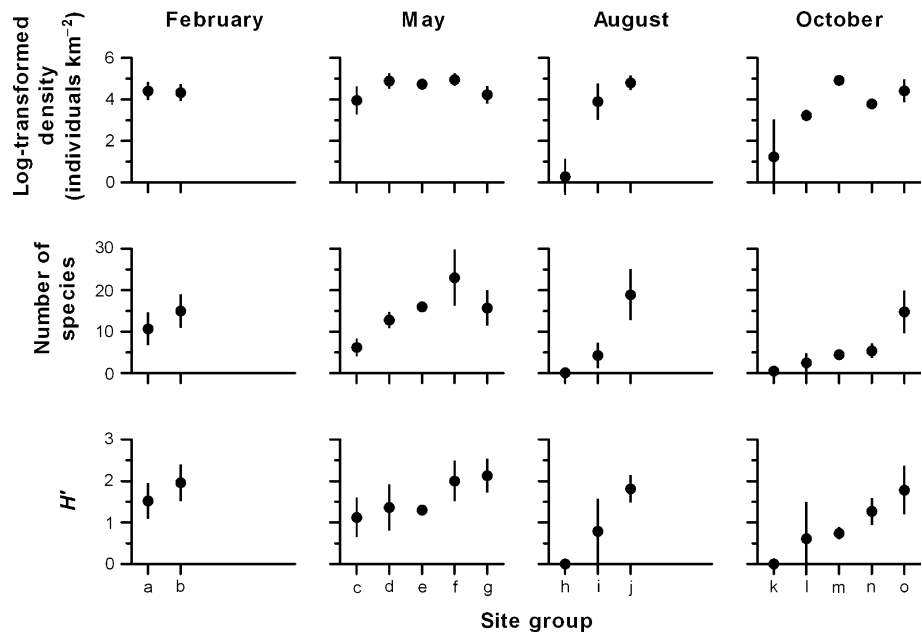


Table 1 Results of SIMPER analysis showing species typifying each site group on the basis of cluster analysis of the megabenthic community in February 2005 from Tokyo Bay. Species accounting for at least 70% of the cumulative contribution for the percentage of the mean Bray-Curtis similarity of species i to the overall mean similarity within a site group (S_i) are presented. F fish; C crustacean; M mollusk; and E echinoid

Site group (sites)	Taxon	Species	Mean density (individuals km ⁻²)	Mean S_i	Cumulative contribution (%)
a (1–13)	F	<i>Pseudopleuronectes yokohamae</i>	1359.3	8.3	16.9
	C	<i>Metapenaeus joyneri</i>	7997.4	8.3	33.7
	M	<i>Fulvia mutica</i>	5369.4	6.9	47.8
	F	<i>Repomucenus valenciennei</i>	3556.9	5.3	58.5
	C	<i>Oratosquilla oratoria</i>	1110.1	4.1	66.8
	C	<i>Pyromaia tuberculata</i>	1064.8	3.9	74.9
b (14–20)	E	<i>Temnopleurus hardwickii</i>	8877.7	7.5	19.8
	C	<i>Pyromaia tuberculata</i>	715.3	4.7	32.1
	F	<i>Repomucenus valenciennei</i>	1093.9	4.4	43.5
	C	<i>Trachysalambria curvirostris</i>	757.3	4.1	54.4
	M	<i>Loliolus japonica</i>	504.9	2.8	61.8
	F	<i>Pennahia argentata</i>	3912.9	1.9	66.9
F	<i>Sillago japonica</i>	504.9	1.7	71.3	

(Figs. 2 and 3). Only two species *P. tuberculata* and *F. mutica* occurred in high densities in the innermost part of the bay (group c; Table 2). Species composition of the dominant species in the north-central area of the bay in May (group d; Table 2) was similar to that found in the northern portion of the bay in February (group a; Table 1). In the mid-southern portion of the bay (group e), densities of echinoids (*T. hardwickii* and *Temnopleurus toreumaticus*) were high (Table 2). Species number and species diversity were high in the southwestern part of the bay (group f; Fig. 3), and the megabenthic community in this area was dominated by fishes (*R. valenciennei*, *Apogon lineatus*, and *P. argentata*), crustaceans (*Crangon* sp., *P. tuberculata*, *T. curvirostris*, *O. oratoria*, and *Charybdis bimaculata*), and a mollusk (*Zeuxis castus*) (Table 2). In the southeastern part of the bay (group g), echinoids (*T. hardwickii* and *T. toreumaticus*) were dominant and elasmobranchs *Dasyatis akajei* and *Okamejei kenojei* were also found in large numbers (Table 2).

In August, defaunation occurred in the northern parts of the bay where bottom hypoxia was present (Fig. 2). Species density, species number, and species diversity

decreased substantially in group h (Fig. 3) where only one species (*O. oratoria*) was collected at site 6 (Fig. 2; Table 3). In the hypoxic edge (group i), species number and species diversity were low, and *Scapharca broughtonii* dominated the species composition (72.1%) (Table 3). Species density, species number, and species diversity were high in the southern part of the bay (group j; Fig. 3) where nine species dominated the megabenthic community, with the highest contribution by *Repomucenus valenciennei* (Table 3).

In October, hypoxia began to abate and recolonization by megabenthos took place in the northern part of the bay (Fig. 2). Some pockets of severe hypoxia (DO concentration less than 1 mL L⁻¹) remained, however, and as a result, no megabenthos was found at site 6 and only *P. yokohamae* was collected at site 8 (group k; Fig. 2; Table 4). In other central and northern areas of the bay (groups l, m, and n), species density recovered from the August defaunation; however, species number and species diversity in these groups were still low compared with group o in the southern part of the bay. Mobile fishes (*Lateolabrax japonicus* and *P. argentata*) and a cephalopod

Table 2 Results of SIMPER analysis showing species typifying each site group on the basis of cluster analysis of the megabenthic community in May 2005 from Tokyo Bay. Species accounting for at least 70% of the cumulative contribution for the percentage of the mean Bray-Curtis similarity of species *i* to the overall mean similarity within a site group (S_i) are presented. SIMPER analysis could not be conducted for group e, which is composed of a single site, therefore the species accounting for at least 70% of the cumulative species density are shown. *F* fish; *C* crustacean; *M* mollusk; and *E* echinoid

Site group (sites)	Taxon	Species	Mean density (individuals km ⁻²)	Mean S_i	Cumulative contribution (%)
c (1–5)	C	<i>Pyromaia tuberculata</i>	2827.4	18.3	49.9
	M	<i>Fulvia mutica</i>	15786.4	8.9	74.1
d (6–13)	F	<i>Repomucenus valenciennei</i>	22604.6	9.2	15.4
	C	<i>Pyromaia tuberculata</i>	6185.0	8.4	29.3
	C	<i>Oratosquilla oratoria</i>	2724.3	7.4	41.5
	C	<i>Metapenaeus joyneri</i>	8578.0	7.3	53.6
	M	<i>Fulvia mutica</i>	54376.1	7.2	65.6
	C	<i>Trachysalambria curvirostris</i>	994.0	5.2	74.2
e (15)	E	<i>Temnopleurus hardwickii</i>	36520.7	–	–
	E	<i>Temnopleurus toreumaticus</i>	8246.6	–	–
f (14, 17, 20)	C	<i>Crangon</i> sp.	43687.4	6.9	10.9
	F	<i>Repomucenus valenciennei</i>	10897.3	6.9	20.0
	C	<i>Pyromaia tuberculata</i>	9621.1	6.9	28.8
	C	<i>Trachysalambria curvirostris</i>	6479.5	6.7	37.3
	F	<i>Apogon lineatus</i>	2847.1	6.9	45.3
	C	<i>Oratosquilla oratoria</i>	4123.3	6.2	52.6
	C	<i>Charybdis bimaculata</i>	1079.9	7.2	59.9
	M	<i>Zeuxis castus</i>	883.6	7.6	66.9
	F	<i>Pennahia argentata</i>	3534.3	8.4	73.5
	g (16,18,19)	E	<i>Temnopleurus toreumaticus</i>	3632.4	7.8
E		<i>Temnopleurus hardwickii</i>	4319.7	6.7	28.4
F		<i>Dasyatis akajei</i>	1079.9	5.9	39.9
F		<i>Repomucenus valenciennei</i>	981.7	5.9	51.5
M		<i>Loliolus japonica</i>	490.9	5.9	63.1
F		<i>Okamejei kenojei</i>	490.9	5.7	74.3

Table 3 Results of SIMPER analysis showing species typifying each site group on the basis of cluster analysis of the megabenthic community in August 2005 from Tokyo Bay. Species accounting for at least 70% of the cumulative contribution for the percentage of themean Bray-Curtis similarity of species *i* to the overall mean similarity within a site group (S_i) are presented. SIMPER analysis could not be conducted for group h, which included only a single species. *F* fish; *C* crustacean; *M* mollusk; and *E* echinoid

Site group (sites)	Taxon	Species	Mean density (individuals km ⁻²)	Mean S_i	Cumulative contribution (%)
h (1–9)	C	<i>Oratosquilla oratoria</i>	32.7	–	–
i (10–13)	M	<i>Scapharca broughtonii</i>	4491.5	26.0	72.1
j (14–20)	F	<i>Repomucenus valenciennei</i>	12412.0	6.6	15.6
	C	<i>Oratosquilla oratoria</i>	3912.9	4.1	25.2
	F	<i>Amblychaeturichthys hexanema</i>	925.6	3.6	33.7
	M	<i>Loliolus japonica</i>	1725.1	3.6	42.0
	C	<i>Pyromaia tuberculata</i>	12832.7	3.4	50.0
	F	<i>Cynoglossus interruptus</i>	1178.1	3.4	57.9
	F	<i>Pseudopleuronectes yokohamae</i>	1556.8	2.8	64.5
	F	<i>Mustelus manazo</i>	1346.4	2.2	69.5
	F	<i>Apogon lineatus</i>	16072.5	1.6	73.3

Table 4 Results of SIMPER analysis showing species typifying each site group on the basis of cluster analysis of the megabenthic community in October 2005 from Tokyo Bay. Species accounting for at least 70% of the cumulative contribution for the percentage of the mean Bray-Curtis similarity of species *i* to the overall mean similarity within a site group (S_i) are presented. SIMPER analysis could not be conducted for group k, which included only a single species. *F* fish; *C* crustacean; *M* mollusk; and *E* echinoid

Site group (site)	Taxon	Species	Mean density (individuals km ⁻²)	Mean S_i	Cumulative contribution (%)
k (6,8)	F	<i>Pseudopleuronectes yokohamae</i>	147.3	–	–
l (1,5)	M	<i>Loliolus japonica</i>	1178.1	44.3	100
m (2,4)	M	<i>Perna viridis</i>	50363.3	28.6	32.7
	M	<i>Mytilus galloprovincialis</i>	35784.4	25.6	62.0
	F	<i>Lateolabrax japonicus</i>	1030.8	18.1	82.7
n (3,7,9,10,12)	M	<i>Loliolus japonica</i>	1708.2	20.0	33.9
	F	<i>Lateolabrax japonicus</i>	530.1	16.4	61.6
	F	<i>Pennahia argentata</i>	2238.4	11.1	80.4
	F	<i>Apogon lineatus</i>	1767.1	4.0	14.5
o (11,13–20)	F	<i>Repomucenus valenciennei</i>	719.9	3.7	28.0
	C	<i>Pyromaia tuberculata</i>	6643.1	3.3	40.1
	M	<i>Loliolus japonica</i>	1178.1	2.5	49.3
	F	<i>Cynoglossus interruptus</i>	229.1	1.8	55.9
	E	<i>Temnopleurus hardwickii</i>	5432.3	1.7	62.0
	F	<i>Pennahia argentata</i>	523.6	1.0	65.7
	F	<i>Okamejei kenojei</i>	556.3	0.9	69.0
	F	<i>Crangon</i> sp.	949.0	0.6	71.3

(*L. japonica*) as well as sessile mussels (*Perna viridis* and *Mytilus galloprovincialis*) were dominant in the northern part of the bay (Table 4) where moderate hypoxia was present (Fig. 2). Meanwhile, the southern part of the bay (group o) was dominated by nine species from various taxa (Table 4).

Temporal changes in water and sediment quality parameters

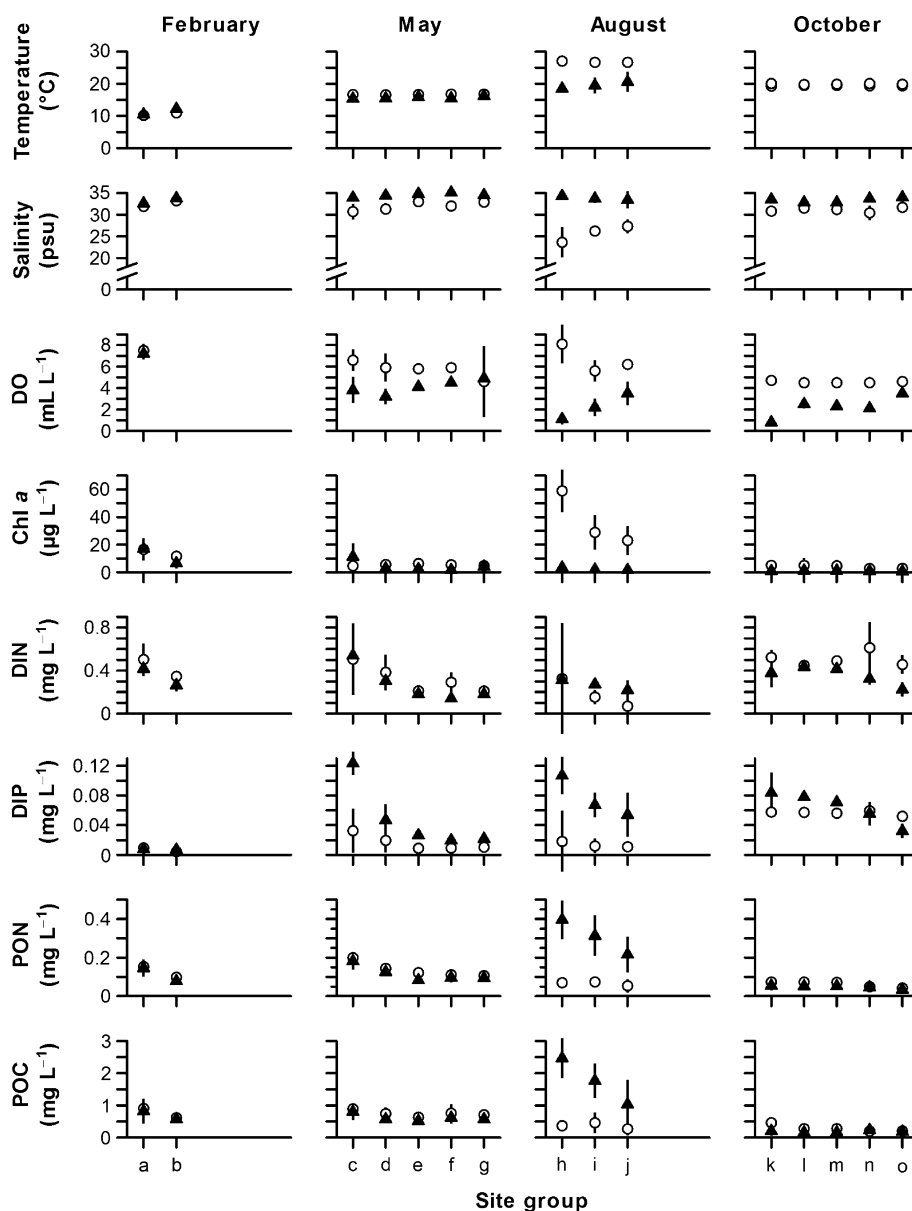
Mean values of water quality parameters at the surface and bottom layers in each site group separated by cluster analysis on the megabenthic community are shown in

Figure 4. All of the monthly mean values for each water quality parameter at both surface and bottom layers showed significant differences between certain times of the year (nested ANOVA; $P < 0.01$ for all water quality parameters). The highest mean surface water temperature occurred in August, as did the greatest difference between surface and bottom mean water temperatures (6.1°C in the southern part of the bay [group j] to 8.6°C in the northern part [group h]). Bottom salinity did not show a large temporal fluctuation, whereas salinity at the surface decreased in August. The difference in salinity between the surface and bottom water in August ranged from 6.1 in the southern part of the bay (group j) to 10.7 in the northern part (group h). Mean DO concentration remained at normoxic conditions at the surface throughout the year, whereas it

decreased substantially at the bottom in the north-central part of the bay in August (groups h and i; Figs. 2 and 4). In October, hypoxia was still present at sites 5–10, although hypoxia abated at the innermost sites 1–4 (Fig. 2). The mean bottom DO concentration remained low in the north-central areas (groups k, l, m, and n; Fig. 4).

Mean concentrations of chl *a*, DIN, DIP, PON, and POC were generally higher in the northern part of the bay than in the southern part (Fig. 4). The surface mean chl *a* concentration was highest in August, while that at the bottom decreased from February to October (Fig. 4). The surface mean DIN concentration was lower in August (Fig. 4). The mean DIP concentration was elevated at the surface in October, whereas it increased from May to October at the bottom, especially in the northern part of the bay (Fig. 4).

Fig. 4 Mean values of temperature, salinity, and concentrations of dissolved oxygen (DO), chlorophyll *a* (chl *a*), dissolved inorganic nitrogen (DIN) and phosphorus (DIP), and particulate organic nitrogen (PON) and carbon (POC) in the surface (white circles) and bottom layer (solid triangles) of Tokyo Bay in 2005. Site groups are derived from cluster analysis on the megabenthic community. Vertical bars indicate standard deviations. No data were obtained for DO at site group b in February



Mean concentrations of PON and POC showed decreasing trends from February to October at the surface, whereas they peaked in August at the bottom (Fig. 4).

In August, the mean concentrations of sediment TS, TOC, and TN as well as LOI were high in the north-central part of the bay (groups h and i) where the sediment consisted primarily of silt and clay (Fig. 5). Mean concentrations of TS, TOC, and TN and LOI were low in the southern part of the bay (group j) where sand was the main constituent of the sediment (Fig. 5).

Effect of water and sediment quality on the megabenthic assemblage

Two sets of environmental variables were used in the BIO-ENV analysis (the first set includes concentrations of DO and POC from the bottom water layer and TS from sediments and the second comprises concentrations of chl *a* from the bottom water layer and TOC from sediments) because these variables did not show a significant correlation with each other within the set ($P > 0.05$). In the BIO-ENV analysis for the first set, the combination of the three variables explained the spatial pattern in the megabenthic community in August ($\rho_s = 0.54$, $P < 0.01$). The LINK-TREE analysis of the megabenthic community based on concentrations of bottom DO, POC, and TS showed that sites could be separated into four groups (SIMPROF test, $P < 0.01$; Fig. 6a), and the grouping was similar to that by cluster analysis using the Bray-Curtis similarity index for the megabenthic community (Table 3). The first split separated sites 1–9 and 11 from sites 10 and 12–20 at $B\% = 94$, with the threshold DO concentration less than 1.7 mL L^{-1} for the former site group and greater than 1.8 mL L^{-1} for the latter (Fig. 6a). The next division separated sites 1–9 from site 11 at $B\% = 73$, with a higher POC concentration in the former sites (Fig. 6a). The southern part of the bay (sites 14–20) was separated from the central area (sites 10, 12, and 13) at $B\% = 72$, with the former sites showing lower concentrations of POC and TS than the latter (Fig. 6a). In the second data set, only TOC concentration was selected by the BIO-ENV analysis ($\rho_s = 0.50$, $P < 0.01$). The LINKTREE analysis of the megabenthic community based on TOC concentration split sites into three groups (SIMPROF test, $P < 0.01$; Fig. 6b). The first split at $B\% = 87$ divided the central-northern part of the bay (sites 1–13 with the exception of site 2; corresponding to group h and i) from the southern part of the bay (sites 14–20; corresponding to group j) at a TOC level around 20 mg g^{-1} (Fig. 6b). The second split differentiated sites 1, 6, 7 and 11–13 (TOC concentration $< 28.9 \text{ mg g}^{-1}$) from sites 3–5 and 8–10 ($> 30.8 \text{ mg g}^{-1}$) at $B\% = 50$ (Fig. 6b).

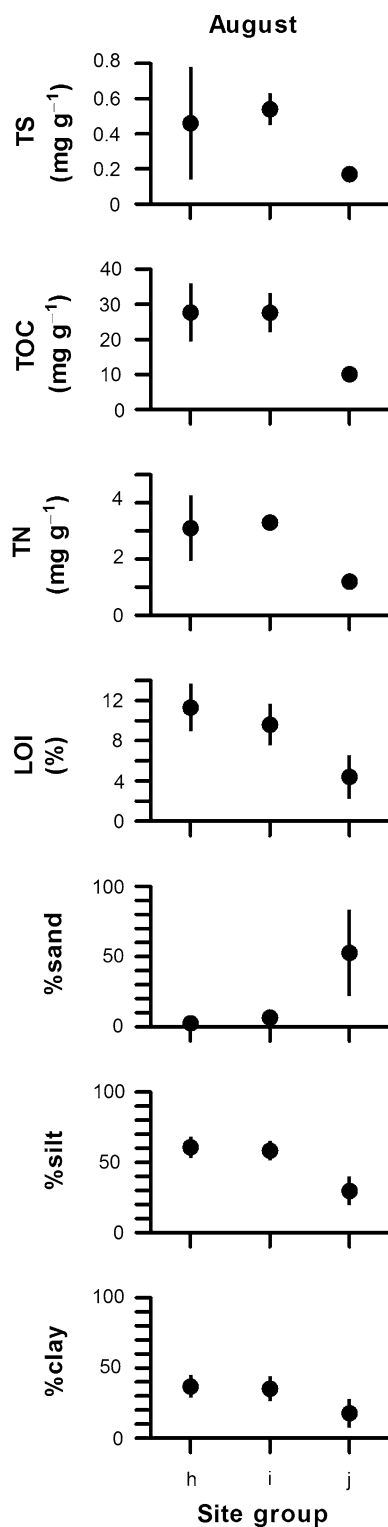
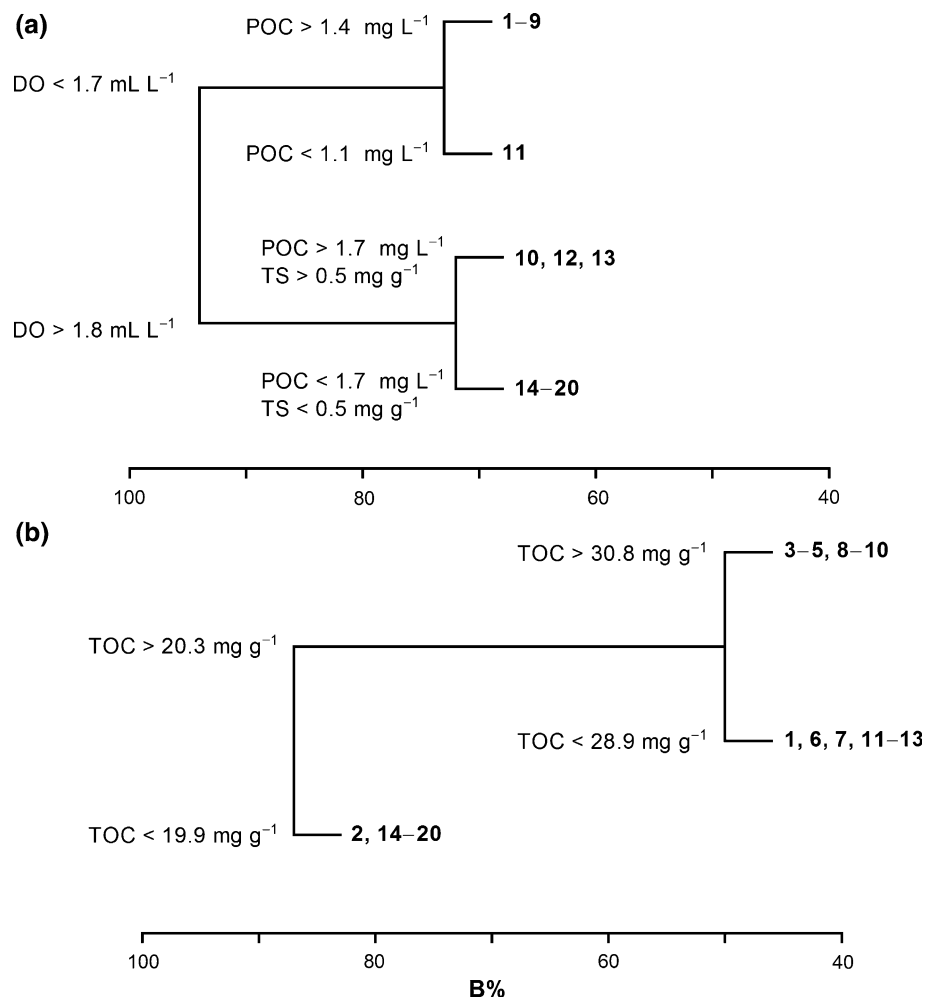


Fig. 5 Mean values of concentrations of total sulfide (TS), total organic carbon (TOC), total nitrogen (TN), loss on ignition (LOI), and relative percentage of sand, silt, and clay in the sediment of Tokyo Bay in August 2005. Site groups are derived from cluster analysis on the megabenthic community. Vertical bars indicate standard deviations

Fig. 6 Results of the LINKTREE analysis from two data sets collected in August 2005 in Tokyo Bay; **a** dissolved oxygen (DO) and particulate organic carbon (POC) in bottom water and total sulfide (TS) in the sediment; and **b** chlorophyll *a* in bottom water (not retained in the LINKTREE analysis) and total organic carbon (TOC) in the sediment. Numbers to the right of each clade indicate sites. Threshold concentrations are shown to the left of each clade



Discussion

In eutrophic coastal systems, formation of hypoxia usually takes place during summer to autumn and is triggered by stratification of the water column, which reduces oxygen supply from the surface to the bottom (Diaz and Rosenberg 2008). In the present study, bottom hypoxia was present in August and October in the northern part of Tokyo Bay. Thermal and salinity stratification was observed in the summer and was prominent particularly in the northern part of the bay. This resulted in hypoxic conditions developing in the bottom layer of Tokyo Bay during this time. Thermal and salinity stratification abated in October; however, hypoxic conditions remained in the northern part of the bay, although the spatial extent of severe hypoxia (DO concentration ≤ 1 mL L⁻¹) decreased. In the Neuse River Estuary (NC, USA), salinity stratification and high water temperature are the main factors causing bottom hypoxia, and hypoxia can occur with a difference in salinity of only 1–2 psu between the surface and bottom water when the temperature exceeds 20°C (Buzzelli et al. 2002). In Tokyo

Bay, the bottom water temperature in October was still around 20°C (Fig. 4) and the difference in salinity between the surface and bottom layers was 3.1 psu in the hypoxic areas (sites 5–10; Figs. 2 and 4). In addition, concentrations of sediment organic matter in the northern part of the bay were higher than in the southern areas (Figs. 2 and 5), suggesting that microbial decomposition of organic matter could have caused the persisting bottom hypoxia, as reported in other coastal systems (Diaz and Rosenberg 2008). The high concentrations of nutrients and sediment organic matter in the northern part of the bay can be attributed to the combination of anthropogenic activities in the adjacent terrestrial areas and to rivers emptying into the bay (Furota 1997). These high nutrient levels most likely caused the increase in phytoplankton production, as suggested by the high chl *a* concentrations that were also found in this area (Fig. 4). Dead phytoplankton that eventually accumulate and decay on the bottom would be one of the major sources of the high concentrations of sediment organic matter in the northern part of the bay. In contrast, bottom hypoxia was not evident in the southern

part of the bay in August, although thermal and salinity stratification was observed in the southwestern area. This absence of hypoxic conditions in the southern part of the bay can be attributed to the low concentration of organic matter in the sediment compared to the northern areas and to the exchange of sea water between the southern part of the bay and the ocean, which provides oxygen-saturated water to the bay and helps prevent the waters from becoming hypoxic (Furota 1997). Similar bottom DO gradients (low in the inner part and high in the outer part) have been reported in other semi-enclosed coastal systems; e.g., Chinhae Bay, Korea (Lim et al. 2006) and Pensacola Bay, FL, USA (Thomas et al. 2007).

Bottom hypoxia affects species density and spatial distribution of megabenthic animals. In the Kattegat, Sweden, species density of demersal fishes decreased substantially when the bottom DO concentration was reduced to less than 2 mL L^{-1} (Baden et al. 1990). In addition, threshold DO levels needed to support megabenthic species have been estimated to be around 1.4 mL L^{-1} in the Neuse River Estuary (Eby and Crowder 2002) and the Gulf of Mexico shelf (Craig and Crowder 2005), and both studies showed contraction of the spatial distribution of demersal species due to bottom hypoxia. In the present study, cluster analysis of the megabenthic community separated sampling sites into 2–5 groups on the basis of differences in species density and species composition. In general, species density, species number, and species diversity were higher in the southern part of the bay than in the northern part. The bottom hypoxia that prevailed in the northern half of the bay in August would have caused a substantial reduction in species density and species diversity; no organisms were found in severely hypoxic areas (DO concentration $\leq 1 \text{ mL L}^{-1}$). In contrast, species density and species diversity of the megabenthos in the southern part of the bay, where a high DO concentration and low POC and TS concentrations were observed in the bottom layer and/or sediment, were high throughout the year. The BIO-ENV analysis for August data showed that concentrations of DO and POC in the bottom water and TS in the sediments were significant factors affecting spatial structure in the megabenthic community. The LINKTREE analysis separated the bay into northern and southern sections at the first split with DO levels between 1.7 and 1.8 mL L^{-1} , suggesting that the presence of megabenthos in the bay was strongly regulated by this threshold DO concentration.

Mortality and behavioral response to hypoxia differ among taxa, with some taxa surviving in hypoxic conditions for a certain period of time. In particular, some bivalve species are tolerant of low DO concentrations, and this tolerance is suggested to be linked to enhanced anaerobic ATP yield as well as a depressed metabolic rate (Hochachka 1980). In the present study, *S. broughtonii*, a

hypoxic-tolerant sessile bivalve species (Watanabe et al. 2005), dominated the hypoxic central area of the bay in August. In October, however, the density of this species decreased substantially and it was no longer dominant, suggesting that *S. broughtonii* could not survive the prolonged exposure to hypoxic conditions, as also reported for other hypoxia-tolerant bivalves (Theede et al. 1969; Altieri 2006; Holmes and Miller 2006). In August, mantis shrimp *O. oratoria* were still present in the northern hypoxic area (site 6), although species density was very low. In a previous study, Pihl et al. (1991) showed that mantis shrimp *Squilla empusa* in the York River, Chesapeake Bay, USA, remained in hypoxic areas until their tolerance was exceeded, at which point they migrated to normoxic water. Pihl et al. (1991) suggested that increased food availability under hypoxic conditions, during which infaunal macrobenthic species come to the sediment surface, would be attractive to hypoxia-tolerant *S. empusa*. In Tokyo Bay, however, the vast majority of *O. oratoria* probably either die or leave the severely hypoxic areas in summer because (1) defaunation of macrobenthic prey species also occurs (Ohkoshi and Furota 1997) resulting in a lack of food for survival, (2) behavioral abnormality (i.e., immobilization) occurs in adult *O. oratoria* at DO concentrations $< 3.1 \text{ mL L}^{-1}$, although the lethal DO concentration is 0.6 mL L^{-1} (Hamano and Yamamoto 2005), and (3) tagged *O. oratoria* released in the northern part of the bay in May were recaptured only in the southern part during the summer (Ohtomi et al. 1989), suggesting that individuals either migrate to the southern part of the bay or die in the northern part. Indirect effects of hypoxia on megabenthic community structure, such as predator-prey interaction, as suggested by Pihl et al. (1991), have not been investigated in Tokyo Bay but should be addressed in future studies.

The result of the LINKTREE analysis showed that bottom TS concentration is one of the factors affecting the megabenthic community structure between hypoxic and normoxic areas in the bay, and this may be related to defaunation in the hypoxic areas as a result of hydrogen sulfide (H_2S) production. H_2S is produced during decomposition of organic matter by anaerobic bacteria, and the production is dependent on temperature and pH (Boyd and Tucker 1998). In August 2005 in the north-central part of Tokyo Bay, bottom water temperatures ranged from 18.5 to 19.5°C in the hypoxic areas (groups h and i; Fig. 4), and pH ranged from 7.7 to 8.6 (National Institute for Environmental Studies, www.nies.go.jp/igreen/index.html). Under these conditions, 3–26% of bottom TS exists as H_2S (Boyd and Tucker 1998). H_2S is toxic to aquatic organisms, inhibiting the electron transport chain in aerobic respiration (Torrans and Clemens 1982). The survival rate of the prawn *Macrobrachium nipponense* under hypoxic conditions has been shown to decrease in the presence of

H₂S compared to prawn exposed to equivalent hypoxic conditions without H₂S (Kang et al. 1995). However, tolerance to hypoxia combined with sulfide differs between species (Diaz and Rosenberg 1995). The bivalve *S. broughtonii* was dominant in the central part of the bay in August, suggesting that this species is tolerant of hypoxic conditions when H₂S is present, as reported for other bivalve species (Theede et al. 1969). In this study, however, it was not possible to estimate the H₂S concentrations in the water from the TS measurements in the sediment, and, additionally, the threshold lethal concentration for H₂S under hypoxic conditions is unknown for the megabenthic animals in the bay. In situ monitoring of H₂S concentrations in the bottom water of Tokyo Bay as well as laboratory experiments to determine lethal H₂S concentrations under hypoxic conditions for each megabenthic species are required to better understand how defaunation occurs in the bay during hypoxic periods.

Sediment TOC concentration represents the amount of organic matter (Magni et al. 2008) and correlates with factors causing ecological stress, such as hypoxia, high ammonia and sulphide, and chemical contamination of sediments (Hyland et al. 2005). Magni et al. (2008) proposed that TOC can be used as a general screening-level indicator for evaluating the likelihood of reduced sediment quality and associated effects on the macrobenthic community in coastal areas. Hyland et al. (2005) have shown impaired macrobenthic communities from seven coastal systems around the world and have suggested that the risk of reduced species richness of the macrobenthic community should be high at TOC values > 35 mg g⁻¹. In the present study, the spatial pattern of the megabenthic community in Tokyo Bay was correlated with that of TOC concentration in the sediment. The LINKTREE analysis divided the central-northern part of the bay (group h and i) from the southern part of the bay (group j) at a TOC level around 20 mg g⁻¹ (Fig. 6), where species density, species number, and species diversity of the megabenthic community in the former sites were lower than in the latter in August. Our results suggest that the critical TOC level may differ among different trophic levels or taxa, and this deserves further examination in order to develop sound management procedures for coastal ecosystems.

Recolonization in defaunated areas occurs after bottom hypoxia abates. The first stage of recolonization, however, does not involve all species of the natural community for the area but rather species that are mobile and/or settlement of pelagic larvae. Recolonization by immigration of mobile demersal species to areas where bottom water hypoxia has abated has been reported in other coastal systems (e.g., Pihl et al. 1991; Eby and Crowder 2002). We attribute the autumn recolonization of the megabenthic assemblage in the northern part of Tokyo Bay to an immigration of the

mobile fish *L. japonicus*, *P. argentata*, and *P. yokohamae* and the cephalopod *L. japonica* and to recruitment of young-of-the-year mussels *P. viridis* and *M. galloprovincialis*. High tolerance of larvae to hypoxic conditions may increase reproductive success and result in rapid recruitment to the northern part of the bay soon after abatement of hypoxia, which may explain the increase in young-of-the-year juveniles of *P. viridis* and *M. galloprovincialis* (mean individual body weights, 1.5 and 2.5 g, respectively). In a closely related mussel (*Mytilus edulis*), larval settlement is not hindered by a low DO concentration of 0.9 mL L⁻¹ (Wang and Widdows 1991).

In conclusion, summer hypoxia in the central-north part of Tokyo Bay caused defaunation of the megabenthos, possibly because of mass mortality and/or migration toward normoxic areas of the bay. In addition to causing defaunation of adult megabenthos, hypoxic conditions may disturb larval settlement of the dominant megabenthic species in the bay. Although extended spawning periods have been reported for the dragonet (*R. valenciennesi*; spring to autumn) and mantis shrimp (*O. oratoria*; spring to summer), the settlement of larvae from the spring spawning does not take place, probably because of the persistence of bottom hypoxia in the settlement grounds (Ikejima and Shimizu 1999; Kodama et al. 2006, 2009). Comprehensive action is needed to reduce hypoxia and to further the recovery of the megabenthic community in the bay. Measures to decelerate eutrophication and hypoxia could include conservation and enlargement of tidal flats, reduction of the influx of inorganic nutrients and organic substances into the bay from terrestrial areas, and removal of organic substances and sludge accumulating on the bay bottom (Council for Renaissance of Tokyo Bay 2003). Implementation of these measures would at least partially facilitate the recovery in stock size of the megabenthic community in the bay.

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