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Revised Manuscript for *Marine Micropaleontology*

**Development of modern benthic ecosystems in eutrophic coastal oceans: the
foraminiferal record over the last 200 years, Osaka Bay, Japan**

**Akira Tsujimoto^{a*}, Moriaki Yasuhara^b, Ritsuo Nomura^c, Hideo Yamazaki^d,
Yoshikazu Sampei^e, Kotaro Hirose^a, and Shusaku Yoshikawa^a**

^a Division of Biology and Geosciences, Graduate School of Science, Osaka City
University, Osaka 558-8585, Japan

^b Department of Paleobiology, National Museum of Natural History, Smithsonian
Institution, Washington, DC 20013-7012, USA

^c Foraminiferal Laboratory, Faculty of Education, Shimane University, Matsue,
Shimane 690-8504, Japan

^d Department of Life Science, School of Science and Engineering, Kinki University,
Higashiosaka, Osaka 577-8502, Japan

^e Department of Geoscience, Faculty of Science and Engineering, Shimane University,
Matsue, Shimane 690-8504, Japan

* Corresponding author. Tel. and fax: +81-6-6605-3176.

Postal address: Division of Biology and Geosciences, Graduate School of Science,
Osaka City University, 3-3-138 Sugimoto, Sumiyoshi-ku, Osaka 558-8585, Japan

E-mail: tujimoto@sci.osaka-cu.ac.jp (A. Tsujimoto)

1 **Abstract**

2 The ecosystem dynamics of a modern benthic community in Osaka Bay was
3 studied by analyzing sediment cores and fossil foraminifera deposited during the past
4 200 years. The results suggest that the high-density/low-diversity assemblage has
5 appeared in the early 1900s, coinciding with the eutrophication of the bay resulting
6 from the Japanese industrial revolution. This assemblage proliferated during the period
7 1960 to 1970 when the eutrophication and bottom-water hypoxia were most pronounced.
8 The development of the assemblage has been characterized by an increase in the relative
9 and absolute abundance of eutrophication-tolerant species (“*Ammonia beccarii*”,
10 *Eggerella advena*, and *Trochammina hadai*) and a decrease in many other foraminiferal
11 species, such as *Ammonia tepida*, *Elphidium*, *Miliolinella subrotunda*, and *Valvulineria*
12 *hamanakoensis*, that are unable to tolerate low-oxygen conditions. Approximately thirty
13 years after the imposition of discharge restrictions in the 1970s, this assemblage
14 continues to predominate in the inner part of the bay, and *Eggerella advena* is currently
15 found across the entire bay. These records make a significant contribution to
16 understanding the long-term relationship between anthropogenic impact and ecosystem
17 change.

18
19 **Keywords:** benthic foraminifera; ecosystem; eutrophication; hypoxia; Osaka Bay;
20 species diversity

1 **1. Introduction**

2 *1. 1. Urbanization-induced marine eutrophication and benthic response*

3 Marine eutrophication leads to an increase in phytoplankton biomass and
4 hypoxia (Justić et al., 1995; Nixon, 1995; Rabalais et al., 1996; Arai, 2001; Boesch et
5 al., 2001; Cloern, 2001). In its early stage, such eutrophication has a positive impact on
6 the benthic community by increasing the food supply (Pearson and Rosenberg, 1978).
7 However, in the advanced stage, the successive and rapid increase in nutrients leads to
8 oxygen depletion, which is inimical to the survival of many eukaryote benthic
9 organisms that are unable to tolerate low-oxygen conditions. Eutrophication and the
10 resulting hypoxia are characterized by extremely high population densities of a few
11 opportunistic species, such as deposit-feeding small polychaetes, which are resistant to
12 low-oxygen conditions (Pearson and Rosenberg, 1978; Justić, 1987; Beukema, 1991;
13 Gray, 1992; Gray et al., 2002). These unusual benthic communities characterized by
14 extremely high-density/low-diversity are found in eutrophic enclosed coastal seas near
15 metropolises throughout the world (e.g., Beukema, 1991; Llansó, 1992; Rumohr et al.,
16 1996; Wilson et al., 1998; Perus and Bonsdorff, 2004). However, when and how these
17 ecosystem changes have progressed is not always clear. Although biological monitoring
18 is a useful tool for assessing the recovery of aquatic ecosystems from anthropogenic
19 impact (Currie and Parry, 1999; Hawkins et al., 2002; Borja et al., 2006), such
20 assessments are typically based on data collected over the past 20 years, a period during
21 which the anthropogenic impact was already manifested; long-term data sets (e.g., for
22 the past 200 years) are generally not available using this approach. In this context,
23 foraminifera-based paleoecological data recorded in sediment cores can make an
24 important contribution.

25

1 *1. 2. Foraminifera as paleoecological indicators*

2 Many studies has been carried out in many areas using foraminifera as
3 bio-indicators of marine pollution, such as heavy metals (e.g., Yanko et al., 1998; Samir
4 and El-Din, 2001; Frontalini and Coccioni, 2008), oil spill (e.g., Morvan et al., 2004;
5 Ernst et al., 2006), and eutrophication (e.g., Thibodeau et al., 2006; Rabalais et al.,
6 2007; Mojtahid et al., 2008).

7 Among the foraminifera, eutrophication and the resulting hypoxia result in the
8 proliferation of a few opportunistic species (Nagy and Alve, 1987; Alve, 1991a, 1991b,
9 1995a, 1995b; Thomas et al., 2000; Tsujimoto et al., 2006a, b). This selective
10 proliferation increases the absolute abundance and decreases the diversity of benthic
11 foraminiferal assemblage, as well as other members of the benthic community
12 (Mojtahid et al., 2008). Moreover, foraminiferal test preserved in sediment cores can be
13 used to trace environmental changes in benthic communities over periods of decades
14 and centuries (Alve, 1991a; Barmawidjaja et al., 1995; Cearreta et al., 2000; Elberling et
15 al., 2003; Hayward et al., 2004a; Platon et al., 2005; Tsujimoto et al., 2006b). Some
16 authors suggested that the specific index derived from the combination of some
17 foraminiferal species is useful to track the history of anthropogenic eutrophication and
18 resulting hypoxia (e.g., Sen Gupta et al., 1996; Karlsen et al., 2000; Osterman, 2003;
19 Osterman et al., 2008). Thus, the records of fossil foraminifera in sediment cores are
20 useful for compiling long-term data sets designed to identify the appearance of
21 anthropogenically stressed ecosystems, typically characterized by the development of
22 unusual benthic community characterized by extremely high-density/low-diversity.
23 However, there are few studies that addressed the spatiotemporal aspect of the impacts
24 of anthropogenic hypoxia using sediment cores (e.g., Osterman et al., 2008).

25

1 *1. 3. Osaka Bay*

2 Osaka Bay is close to Osaka City, the second largest city in Japan, from which large
3 amounts of pollutants (e.g., household, agricultural, and industrial wastes) are
4 discharged into the bay via the Yodo River (Association for New Social Infrastructure
5 of Osaka Bay, 1996). Yasuhara et al. (2007) assembled published studies concerned
6 with the eutrophication of Osaka Bay and noted that eutrophication first appeared
7 during the 1900s coinciding with the onset of the Japanese industrial revolution; it
8 reached maximum levels between 1960 and 1970 concomitant with the rapid
9 urbanization after World War II. The authors studied the spatiotemporal variations in
10 ostracode fauna over the past 200 years in Osaka Bay using four short sediment cores,
11 and concluded that these two eutrophication events have changed ostracode absolute
12 abundance and faunas. A preliminary study of foraminifera from a short sediment core
13 (core OBY) suggested that foraminiferal absolute abundance and faunas have also
14 changed during much of the same period (Tsujiimoto et al., 2006b). However, detailed
15 spatiotemporal variations of the benthic community in Osaka Bay, including the
16 development of an unusual benthic community characterized by extremely
17 high-density/low-diversity, are still not well understood because fossil ostracodes have
18 become scarce in the inner part of the bay since 1960 and the fact that published fossil
19 foraminiferal data are available from only a single core.

20 The aim of this study was to examine the spatiotemporal relationship between
21 anthropogenic eutrophication and the benthic community, including the development of
22 an unusual benthic community characterized by extremely high-density/low-diversity,
23 using the fossil foraminifera contained in four short sediment cores collected in Osaka
24 Bay.

25

1 2. Environmental setting

2 Osaka Bay is located at the eastern end of the Seto Inland Sea, Southwest Japan; the
3 bay entrance is partially closed by Awaji Island (Fig. 1). The bay is elliptical with a long
4 axis of ~60 km, a short axis of ~30 km, a surface area of ~1500 km², and a mean depth
5 of ~20 m. The surface and bottom-water temperatures of the bay are highest in August
6 and September and lowest in February and March, respectively (Fig. 2). In the inner
7 part of the bay, the surface water salinity fluctuates throughout the year; but, the salinity
8 of the bottom-water is relatively stable (approximately 32) (Figs. 2, 3a; Osaka
9 Prefectural Fisheries Experimental Station, 1998–2000). Consequently, a distinct
10 halocline is formed in the inner part of the bay during the summer season. In the middle
11 part of the bay, the surface and bottom-water salinities are relatively stable throughout
12 the year (Figs. 2, 3a; Osaka Prefectural Fisheries Experimental Station, 1998–2000).

Figure 1

Figure 2

Figure 3

13 The chemical oxygen demand (COD) and phosphorus concentrations are high in the
14 inner part of the Osaka Bay (Figs. 3b, c). Consequently, the productivity of
15 phytoplankton is high in this area, and algal red tides frequently occur (Association for
16 New Social Infrastructure of Osaka Bay, 1996). During the summer, warming of surface
17 waters causes stratification, so that oxygen can not be mixed into the bottom waters.
18 Decomposition of the phytoplankton material deposited to the bottom then causes
19 hypoxia or even anoxia in the inner part of the bay (Association for New Social
20 Infrastructure of Osaka Bay, 1996; Fig. 3d). Thus, the spionid polychaete
21 *Paraprionospio* sp., which is tolerant of low-oxygen conditions, predominates in the
22 inner part of Osaka Bay, where it is characterized by a high biomass and density and
23 forms part of a high-density/low-diversity community (Association for New Social
24 Infrastructure of Osaka Bay, 1996).

25 The population of Osaka City has increased markedly since ~1900, and the

1 discharge of COD, which was calculated on the basis of the statistical data (population,
2 livestock numbers, annual usage of chemical fertilizer, and annual industrial shipment
3 value of the Osaka Prefecture), increased since the early 1900s (Nakatsuji et al., 1998;
4 Osaka City, 2004; Fig. 4). Eutrophication was accelerated by the rapid industrialization
5 and urbanization during the period of high economic growth from the mid 1950s to the
6 early 1970s (Association for New Social Infrastructure of Osaka Bay, 1996).
7 Consequently, the frequency of occurrence of hypoxic bottom-waters and red tides in
8 the innermost part of the bay increased during the 1950s, and reached a maximum in the
9 1970s (Joh, 1986).

Figure 4

10 The “Law Concerning Special Measures for Conservation of the Environment of the
11 Seto Inland Sea” (a sewage treatment program for the Seto Inland Sea) was enacted in
12 1973 in order to reduce the organic pollutant loads (Yamamoto, 2003). As a result, the
13 loads from households, factories, etc., and the occurrences of red tides have decreased
14 since the 1970s (Fig. 4). However, there have been no major further changes in the
15 COD, nitrogen, and phosphorous concentrations over the last 10 years, and red tides
16 still occur frequently (Osaka Prefectural Fisheries Experimental Station, 1973–2002;
17 Fig. 5).

Figure 5

19 **3. Materials and methods**

20 *3. 1. Sampling procedures*

21 Four sediment cores were obtained along a transect from the mouth of the
22 Yodo River to the middle part of Osaka Bay in September 2001 (core OBY; 14 m water
23 depth, mwd,) and June 2003 [cores OS3 (17.8 mwd), OS4 (19 mwd), and OS5 (25
24 mwd)] by scuba divers using an acrylic corer (Fig. 1). Core OBY was the subject of a
25 preliminary study by Tsujimoto et al. (2006b). Sediments in core OS3 consisted of

1 light gray clay with abundant molluscan shell fragments (105–45 cm) overlain by dark
2 gray clay without molluscan shell fragments (45–0 cm). Sediments in core OS4
3 consisted of blue gray clay with molluscan shell fragments (86–35 cm) overlain by light
4 gray clay with molluscan shell fragments (35–0 cm). Core OS5 consisted of
5 homogeneous light gray clay with molluscan shell fragments throughout the core. In the
6 laboratory, core OBY was subsampled in 2 cm slices, and cores OS3, 4, and 5 were
7 subsampled in 2.4 cm slices [see Yasuhara et al. (2007) for detailed subsampling
8 method]. The chronology of the cores was based on the measurements of ^{210}Pb and
9 ^{137}Cs radioactivity in the respective cores, as published in Yasuhara and Yamazaki
10 (2005) and Yasuhara et al. (2007). Depositional ages of more than 100 years were
11 estimated by extrapolation of ages obtained from ^{210}Pb dating of the upper part of the
12 core, thus assuming constant sedimentation rates.

13

14 3. 2. *Geochemical analysis*

15 Sliced subsamples of cores OS3–5 were oven-dried at 50 °C and pulverized to
16 silt size using an agate mortar, after which 10-mg samples were enclosed in a thin Ag
17 film cup. To the samples, 1 M HCl was added, and the samples were then dried at
18 110 °C for 30 min. The dried samples were wrapped in a thin Zn film cup. Total organic
19 carbon (TOC), total nitrogen (TN), and total sulfur (TS) concentrations were measured
20 by the combustion method at 1000 °C and then flashy at ca. 1800 °C using a FISON
21 elemental analyzer EA1108. We calculated the weight ratio of total organic carbon to
22 total nitrogen (C/N), which indicates the source of organic matter (Müller, 1977;
23 Sampei and Matsumoto, 2001). Generally, organic matter derived from planktonic
24 organisms and terrestrial organisms has C/N of 6 to 9 and 15 or higher, respectively
25 (Bordowskiy, 1965a, b). We also calculated the weight ratio of total organic carbon to

1 total sulfur (C/S). Berner and Raiswell (1984) suggested that C/S of >5, 3-5, and <3
2 indicate fresh water conditions, oxic marine to brackish conditions, and reductive
3 marine to brackish conditions, respectively. Hence, a decrease in the C/S indicates the
4 transition toward low-oxygen conditions.

5

6 3. 3. Foraminiferal analysis

7 Sliced subsamples were washed through a 75- or 63- μm sieve (core OBY and
8 cores OS3-5, respectively), after which the residues were oven-dried at 50 °C, and then
9 dry sieved into the >105- μm fractions. We qualitatively scanned 63-105- μm fractions of
10 four samples of core OBY, and confirmed that not many specimens of thin species
11 (*Eggerella advena*, *Buliminella elegantissima*, *Uvigerinella glabra*) that might possibly
12 pass through the 105- μm sieve were present in the smaller size fraction. Foraminiferal
13 assemblages were analyzed in the >105- μm fractions, and samples containing abundant
14 foraminiferal specimens were split into fractions containing approximately 200
15 specimens. Benthic foraminifera were mounted on slides and identified under a
16 stereomicroscope. Absolute abundance of foraminifera (i.e., number of foraminifera per
17 gram of dry sediment) was calculated from the wet weights of samples and the water
18 content. We also calculated the benthic foraminiferal accumulation rates (BFAR;
19 number of specimens/cm²/yr) using the absolute abundance of foraminifera (AAF;
20 number of specimens/g), dry bulk density of sample (DBD; g/cm³), and accumulation
21 rates (AR; cm/yr) as follows [see Yasuhara and Yamazaki (2005) and Yasuhara et al.
22 (2007) for data of DBD and AR]:

23

$$\text{BFAR} = \text{AAF} \times \text{DBD} \times \text{AR}$$

24

25 We determined the number of species in a sample (species richness) and the
Shannon index (species diversity; Shannon and Weaver, 1949) by the software “PAST”

1 (<http://folk.uio.no/ohammer/past/>) (Hammer et al., 2001). The Shannon index takes into
 2 account not only the number of species but also the proportion of each species in a
 3 sample. The Shannon index is given as follows:

$$4 \quad H' = - \sum_{i=1}^S (P_i)(\ln P_i),$$

5 where H' = index of species diversity,

6 S = number of species observed in a sample, and

7 P_i = proportion of each species.

8 A Q-mode CABFAC factor analysis (Imbrie and Kipp, 1971; Klován and
 9 Imbrie, 1971) was performed in order to determine dominant faunal assemblages and
 10 their temporal downcore patterns using the PaleoToolBox and WinTransfer programs
 11 (<http://www.pangaea.de/software/files/Windows/PaleoTools/>; Sieger et al., 1999,
 12 http://www.agu.org/eos_elec/98131e.html). Species comprising more than 3% of the
 13 population in at least two samples were used for the analysis (Akimoto et al., 1999).

14 Tsujimoto et al. (2006b) lumped most of the *Elphidium* species in core OBY
 15 and treated these as a single taxon; therefore, in order to obtain a more accurate estimate
 16 of species richness and diversity, we reidentified all *Elphidium* individuals to the
 17 species level (e.g., Matoba, 1970; Miller et al., 1982; Scott et al., 2000).

18

19 **4. Results**

20 *4. 1. TOC, TN, and TS concentrations, C/N, and C/S*

21 The temporal variations in TOC, TN, and TS concentrations in cores OS3–5.
 22 The TOC and TN concentrations of core OS3 were low and stable before the early
 23 1900s, then gradually increased, and have markedly increased since the 1960s to 1970s
 24 up to 2.3% and 0.29%, respectively. The TOC and TN concentrations in cores OS4 and

Figure 6

1 OS5 gradually increased from the 1880s and the 1900s, respectively (Fig. 6). The TS
2 concentration in all cores gradually increased until the 1960s to 1970s, and then
3 decreased to the present day. The C/N of all cores gradually increased until the 1960s to
4 1970s—although core OS3 was interrupted by a short-term drop of the C/N—and then
5 decreased to the present day. Conversely, the C/S decreased until the 1960s to 1970s,
6 and then increased to the present day, although that in core OS3 generally increased to
7 the present day with the anomalous increase around the 1950s.

8

9 4. 2. *Absolute abundance of foraminifera, BFAR and diversity*

10 Species richness (number of species in a sample) and species diversity (H')
11 were measured in order to assess the spatiotemporal trend in foraminiferal biodiversity
12 (Fig. 7). These two measures of biodiversity are generally higher in the outer part of the
13 bay (cores OS4 and OS5). Although no major changes have occurred in core OS5, the
14 species richness in cores OBY, OS3, and OS4 decreased from around the 1940s to
15 1950s. Species diversity at all sites decreased from the early 1900s. Species richness
16 and species diversity in cores OBY and OS3 increased after the 1970s; however, the
17 richness and diversity in cores OS4 and OS5 are relatively constant after the 1970s.

18 Absolute abundance of foraminifera and BFAR increased notably after the early 1900s
19 in core OBY, and after 1940–1960s in cores OS3, OS4 and OS5. Absolute abundance of
20 foraminifera and BFAR generally decreased from around the 1970s in the inner part
21 (Fig. 8). Although BFAR generally shows a similar trend to the absolute abundance of
22 foraminifera, there are anomalous increases in the cores OS4 and OS5 around the 1960s
23 and 2000s, respectively (Fig. 8).

24

25 4. 3. *Faunal composition*

Figure 7

Figure 8

1 The dominant species from the OBY and OS cores were “*Ammonia beccarii*”
2 (Linné), *Eggerella advena* (Cushman), and *Trochammina hadai* Uchio. “*Ammonia*
3 *beccarii*” of this study has been reported in various Japanese inner bays and coastal
4 areas as *Ammonia beccarii* (Linné) forma 1 or forma A (e.g., Nomura, 1982, 1983,
5 1997). This Japanese “*Ammonia beccarii*” specimens is different from topotype
6 specimens from Rimini, Italy (Nomura and Takayanagi, 2000). In our previous study of
7 core OBY, we dealt with this form as “*Ammonia beccarii*” and showed its morphology
8 in a SEM micrograph (Tsujiimoto et al., 2006b). Therefore, in this study, the taxonomy
9 of *Ammonia* tentatively followed Tsujiimoto et al. (2006b) for better comparison to
10 previous Japanese foraminiferal studies. We will discuss detailed taxonomy of Japanese
11 *Ammonia* elsewhere. Assemblages in cores OBY and OS3 are dominated by “*A.*
12 *beccarii*”, *E. advena*, and *T. hadai*, with subsidiary *Buccella frigida* (Cushman),
13 *Miliolinella subrotunda* (Montagu), *Valvulineria hamanakoensis* (Ishiwada), *Ammonia*
14 *tepida* (Cushman), *Elphidium* spp., and *Reussella aculeata* Cushman (Fig. 9).
15 Assemblages in core OS4 are dominated by “*A. beccarii*”, *E. advena*, and *T. hadai*, with
16 subsidiary *Elphidium* spp., *Pseudononion japonicum* Asano, *Pseudoparella tamana*
17 Kuwano, *Pseudorotalia gaimardii* (d’Orbigny), and *Uvigerinella glabra* Millett (Fig. 9).
18 Assemblages in core OS5 are dominated by *E. advena*, with subsidiary *Gavelinopsis*
19 *praegeri* (Heron-Allen and Earland), *P. japonicum*, *P. tamana*, and *P. gaimardii* (Fig. 9).
20 Raw data are provided in Appendix A. *Eggerella advena* increased in relative
21 abundance and became dominant at all sites after the early 1900s (Fig. 9). “*Ammonia*
22 *beccarii*” or *T. hadai* increased in relative abundance in core OBY after the early 1900s
23 and after the 1950s to 1960s in cores OS3–5 (Fig. 9). These three species reached their
24 maximum levels around the 1970s to 1980s (Fig. 9). In contrast, other species (*A. tepida*,
25 *B. frigida*, *Elphidium* spp., *M. subrotunda*, and *V. hamanakoensis*) decreased in relative

1 abundance notably in core OBY after the early 1900s and after the 1940s to 1960s in
2 core OS3 (Fig. 9). The absolute abundances of all species generally show trends similar
3 to these in relative abundance (data not shown).

4

5 4. 4. *Q-mode factor analysis*

6 Three varimax factors account for 89.3% of the total variance (Appendix B and
7 C; Fig. 10). The first varimax factor explains 35.2% of the total variance. It is
8 characterized by the high positive varimax scores of *Eggerella advena* (score = 0.920).
9 The first varimax factor loading increased in all sites after about the 1900s. This factor
10 increased rapidly in cores OBY and OS3 after 1990 (Fig. 10). The second varimax
11 factor explains 25.7% of the total variance. It is characterized by the high positive
12 varimax scores of *Elphidium excavatum* (Terquem) (0.539), *Ammonia tepida* (0.356),
13 *Valvulineria hamanakoensis* (0.317), *Buccella frigida* (0.278), *Elphidium clavatum*
14 Cushman (0.236), *Miliolinella subrotunda* (0.226), and *Lagenammia* sp. (0.213). The
15 second varimax factor loading decreased in all sites after the early 1900s (Fig. 10). The
16 third varimax factor explains 28.5% of the total variance. It is characterized by the high
17 negative varimax scores of “*Ammonia beccarii*” (−0.883) and *Trochammia hadai*
18 (−0.284). The third varimax factor loading decreased in all sites after the early 1900s,
19 and increased rapidly in cores OBY and OS3 after the 1990s (Fig. 10).

20

21 5. Discussion

22 5. 1. *The history of eutrophication in Osaka Bay*

23 The increase in the concentrations of TOC, TN, and TS and the decrease in C/S
24 in cores (although the trend for the C/S in core OS3 differs from that of the other cores),
25 indicates that eutrophication in the bay commenced some time around 1900.

Figure 10

1 The marked increase in the TOC and TN concentrations in core OS3 after the
2 1950s suggests that eutrophication has strongly influenced the bottom environment in
3 the innermost part of the bay since the 1950s. The reversal of the C/S in cores occurring
4 after the 1970s suggests that eutrophication and the resulting hypoxia gradually
5 weakened as a result of the implementation of discharge restrictions in the early 1970s.
6 However, the reversal of the C/N suggests that primary production has remained largely
7 unaltered after the imposition of restrictions. The steep trend in both the C/S and C/N
8 after the 1990s may be due not to environmental change but instead due to the progress
9 of sulfate reduction by bacteria (*Desulfovibrio*) at a very early stage of diagenesis
10 (Sampei et al., 1997).

11 We document the stepwise changes in eutrophication from the
12 above-mentioned geochemical data (Fig. 6) and from the history of the areas
13 surrounding Osaka Bay (Fig. 4) as follows:

- 14 1. Eutrophication commenced some time around 1900.
- 15 2. Bottom-water hypoxia was restricted to the inner part of the bay during the
16 early stage of eutrophication (~1900s) as indicated by marked increases in the
17 TOC, TN, and TS concentrations in core OS3 after the early 1900s.
- 18 3. Maximum eutrophication and bottom-water hypoxia occurred around the
19 1970s, followed by a decrease in the TS concentration after the 1970s.
- 20 4. Eutrophication and bottom-water hypoxia are severe in the inner
21 part of the bay but are not pronounced in the outer part, as indicated by the fact
22 that marked increases in the TOC and TN concentrations occur only in core
23 OS3.

24

25 5.2. Factor analysis: foraminifera as eutrophication indicators

1 The agglutinated foraminifera *Eggerella advena* and *Trochammina hadai* and the
2 calcareous foraminifera “*Ammonia beccarii*”—dominant species in this study—indicate
3 eutrophic conditions (e.g., Uchio, 1962; Clark, 1971; Thomas et al., 2000; Tsujimoto et
4 al., 2006a, b). “*Ammonia beccarii*” and *T. hadai* dominate in the inner part of Osaka
5 Bay (Tsujimoto et al., 2006a). *Eggerella advena* is one of the most common species in
6 waste discharge regions around the world (see reviews by Alve, 1995a), and is currently
7 found across the entire bay, and has become dominant during the past 100 years
8 (Tsujimoto et al., 2006a, b). Eutrophication and the resulting hypoxia leads to extremely
9 high population densities of a few opportunistic species such as deposit-feeding small
10 polychaetes, which are able to tolerate low-oxygen condition, and the elimination of
11 mollusks and crustaceans (Beukema, 1991). The polychaete *Paraprionospio* sp.
12 dominates in the inner part of Osaka Bay with a high biomass and density and forms a
13 high-density/low-diversity community (Association for New Social Infrastructure of
14 Osaka Bay, 1996). Hence, the spatiotemporal records of eutrophication-tolerant species,
15 such as “*A. beccarii*”, *E. advena*, and *T. hadai*, archived in sediment cores tell us how
16 the present high-density/low-diversity ecosystem originated.

17 The first varimax factor of Q-mode factor analysis is characterized by the high
18 positive varimax scores of *Eggerella advena*, thus this varimax factor is defined as
19 eutrophication assemblage A. The second varimax factor is characterized by the high
20 positive varimax scores of *Elphidium excavatum*, *Ammonia tepida*, *Valvulineria*
21 *hamanakoensis*, *Buccella frigida*, *Elphidium clavatum*, *Miliolinella subrotunda*, and
22 *Lagenammina* sp. Many of these species inhabit the inner bay; however, they are
23 probably susceptible to eutrophic conditions since they are rare in this part of Osaka
24 Bay where eutrophication is serious (Tsujimoto et al., 2006a). Thus, the second varimax
25 factor is defined as the pre-eutrophication assemblage, which dominated Osaka Bay

1 before eutrophication started. The third varimax factor is characterized by the high
2 negative varimax scores of “*Ammonia beccarii*” and *Trochammina hadai*. “*Ammonia*
3 *beccarii*” is ubiquitous in brackish lakes influenced by fresh water and in the areas
4 around river mouths in Japan (e.g., Matoba, 1970; Ikeya, 1970; Kosugi et al., 1991;
5 Nomura and Seto, 2002). In Osaka Bay, this species is abundant in the areas along the
6 shore, and the numbers present generally decrease slightly toward the middle of the bay
7 (Tsujimoto et al., 2006a). *Trochammina hadai* is abundant in organic-rich sediments
8 deposited in brackish waters (Uchio, 1962; Matoba, 1970; Kosugi et al., 1991; Nomura
9 and Seto, 2002). Thus, the third varimax factor is defined as eutrophication assemblage
10 B, which characterizes eutrophication in relatively brackish waters.

11

12 *5. 3. Development of the high-density/low-diversity assemblage over the past 200*
13 *years*

14 Although BFAR and the absolute abundance of foraminifera show a similar tendency
15 to reach high values from the 1960s to the 1980s, BFAR increased very strongly in
16 cores OS4 and OS5 in the 1960s and 2000, respectively, at times of rapid increases in
17 accumulation rates (Fig. 8). These anomalous increases coincide with the rapid
18 increases in the accumulation rates. The accumulation rates of the intervals from 24.9
19 cm to 31.7 cm depth in the core OS4 (= 1960s) and from 0 cm to 12.9 cm depth in the
20 core OS5 (= 2000s) are relatively high, showing 3 cm/yr and 4.57 cm/yr, respectively
21 (Table 1; Yasuhara et al., 2007). The changes in the accumulation rates may cause
22 changes in taphonomy (e.g., transport, degree of preservation). BFAR is an effective
23 measure to estimate the past foraminiferal productivity, but it does not take into account
24 the effect of taphonomic processes (Hayward et al., 2004b). High accumulation rates
25 may cause an accelerated deposition of foraminifera due to better preservation of

Table 1

1 foraminiferal tests. Both accumulation rate and degree of preservation in shallow marine
2 regions fluctuate strongly, so that BFAR as a proxy for foraminiferal productivity
3 should be used with much care. Therefore we use both BFAR and absolute abundance
4 in the discussion below.

5 We discuss spatial and temporal changes in foraminiferal assemblages by sequence in
6 time, using our data combined with regional historical data: 1) before the Japanese
7 industrial revolution (before the early 1900s), 2) Japanese industrial revolution to World
8 War II (the early 1900s to 1940s), 3) high economic growth period (1940s to 1970s),
9 and 4) after the high economic growth period (1970s to 2000s).

10

11 *5.3.1. Before the Japanese industrial revolution (~ early 1900s)*

12 Geochemical and foraminiferal data indicate that the bay environment was
13 stable before the early 1900s.

14

15 *5.3.2. Japanese industrial revolution to World War II (early 1900s to 1940s)*

16 Eutrophication in Osaka Bay commenced some time around 1900 as a result of
17 the Japanese industrial revolution, and bottom water hypoxia was restricted to the
18 innermost part during the early 1900s (Figs. 4 and 6; Yasuhara et al., 2007). The relative
19 abundance of eutrophication assemblage A and eutrophication assemblage B increased
20 and pre-eutrophication assemblage decreased at all sites after that time (Fig. 10).

21 However, the decrease in the species diversity and the increase in BFAR are remarkable
22 innermost part of the bay (Core OBY, figs. 7, 8), to which hypoxia first was restricted
23 (Yasuhara et al., 2007). Specifically, eutrophication-tolerant species such as “*Ammonia*
24 *beccarii*”, *Eggerella advena*, and *Trochammina hadai* increased in relative and absolute
25 abundance as a result of an increase in food supply, but the successive increase in

1 nutrients led to bottom-water hypoxia, producing conditions inimical to the survival of
2 many species unable to tolerate low-oxygen conditions in the innermost part (Figs. 7, 9,
3 and 11).

Figure 11

4 5 5.3.3. High economic growth period (1940s to 1970s)

6 The impact of eutrophication extended from the mouth of the Yodo River to the outer
7 part of the bay as a result of rapid urbanization after World War II as indicated by
8 geochemical data. As a consequence, eutrophication assemblage A and B proliferated
9 and the pre-eutrophication assemblage declined at all sites after the 1940s, resulting in
10 the decrease in the species richness (Figs. 7, 9, and 10). “*Ammonia beccarii*” and
11 *Trochammina hadai* expanded their range to sites OS3 and OS4 (Fig. 9). Concomitant
12 with this proliferation, molluscan shell fragments markedly decreased in cores OS3 and
13 OS4, most likely representing mortality of mollusks by bottom-water hypoxia.
14 Eutrophication had a significant impact on the entire bay and bottom-water hypoxia
15 covered one-third of the bay during the 1970s (Joh, 1986). This was reflected in the
16 geochemical data that shows peaks in the TS concentration and the C/N (Fig. 6).
17 Eutrophication and bottom-water hypoxia were notable in the inner part, as indicated by
18 above-mentioned geochemical data. Coincident with this, “*A. beccarii*”, *Eggerella*
19 *advena*, and *T.hadai* proliferated rapidly, and the pre-eutrophication assemblage
20 virtually disappeared from the inner part of the bay (OBY and OS3) (Figs. 9 and 11). As
21 a consequence, the two measures of diversity in cores OBY, OS3 reached minimum
22 values during the 1970s (Fig. 7).

23 24 5.3.4. After the high economic growth period (1970s to 2000s)

25 The Law Concerning Special Measures for Conservation of the Environment of the

1 Seto Inland Sea was enacted in 1973 in order to reduce the loads of organic pollutants.
2 Fujiwara et al. (2004) analyzed the monitoring data and suggested that the concentration
3 of bottom-water dissolved oxygen in the eastern part of Osaka Bay increased after the
4 1970s. The effect is reflected in the geochemical data that shows reversals in the TS
5 concentration and the C/S and C/N (Fig. 6). Some mesotrophic zooplankton species
6 moved into the innermost part of the bay from the outer parts during the last 20 years,
7 possibly in response to a decrease in primary production or predation pressure or
8 hypoxia (Yamamoto, 2005). A reduction in organic pollution load might lead to a
9 decrease in food supply to the benthos, thus in the abundance of eutrophication-tolerant
10 species (“*A. beccarii*”, *E. advena*, *T. hadai*) and an increase in diversity in the inner part
11 of the bay (Figures 7, 11). *Buccella frigida* rapidly increased in abundance after the
12 period of maximum pollution in the 1970s. This species may be relatively tolerant to
13 eutrophication and bottom-water hypoxia (Schafer, 1973).

14 Eutrophication assemblage A increased and eutrophication assemblage B rapidly
15 decreased in cores OBY and OS3 after the 1990s (Fig. 10). The accumulation rate of
16 “*Ammonia beccarii*” decreased rapidly in the inner part at that time (Fig. 11). Tsujimoto
17 et al. (2006a, b) suggest that these changes might be related to the changes of food
18 supply to the bottom. The change in composition of dominant red tide-causing algae
19 from dinoflagellates (e.g., *Ceratium furca*, *Gymnodium lacustre*, *Olisthodiscus* sp., and
20 *Peridinium* sp.) to diatoms (e.g., *Chaetoceros* spp., *Nitzschia pungens*, and *Rhizosolenia*
21 *fragilissima*) in 1980–1990 may have caused the changes in food supply for
22 detritivorous foraminifera and, consequently, dramatic changes in foraminiferal
23 compositions might have been occurred (Tsujimoto et al., 2006a, b). These changes are
24 restricted to the inner part of the bay (cores OBY and OS3; Fig. 10), possibly because
25 the red tides occur frequently in this part of the bay. Thomas et al. (2004) studied

1 benthic foraminiferal assemblages in nine cores in Long Island Sound, and reported the
2 decrease in the absolute abundance of foraminifera and the increase in the relative
3 abundance of “*A. beccarii*” after the 1960s-1970s. The authors suggested that an
4 increase in N/Si, which leads to blooms in organic-walled primary producers (e.g.,
5 cyanobacteria and dinoflagellates) than diatoms, might cause change from the diatom
6 consuming *Elphidium* to “*A. beccarii*” in Long Island Sound. As mentioned-above, the
7 changes in the food supply, which is mainly caused by the changes in primary producers,
8 might substantially influence benthic foraminifera. However, further work is necessary
9 to confirm the relationship between benthic foraminifera and primary producers.

10

11 The unusual benthic assemblage characterized by extremely
12 high-density/low-diversity has developed since the 1900s, and proliferated during the
13 period 1960 to 1970 when eutrophication and bottom-water hypoxia were most
14 pronounced. The assemblage was characterized by an increase in the relative and
15 absolute abundance of eutrophication-tolerant species (“*Ammonia beccarii*”, *Eggerella*
16 *advena*, and *Trochammina hadai*) and the decrease in many other foraminiferal species
17 that are unable to tolerate the low-oxygen conditions. This assemblage remains
18 dominant in the inner part of the bay even after the imposition of discharge restrictions.
19 This indicates the potential difficulty of restoring ecosystem once they have been
20 anthropogenically heavily impacted. Further study is necessary to fully understand
21 human-induced alteration of coastal ecosystems.

22

23 **6. Conclusion**

24 The ecosystem dynamics of a modern benthic community were elucidated
25 using fossil foraminifers from four sediment cores deposited over the last ~200 years.

1 Our sediment core study demonstrated that the extremely high-density/low-diversity
2 community, which is found in eutrophic enclosed coastal seas near metropolises
3 throughout the world, was caused by eutrophication and the resulting hypoxia after the
4 early 1900s.

5 The formation of the high-density/low-diversity assemblage has been
6 characterized by an increase in the relative and absolute abundance of
7 eutrophication-tolerant species (“*Ammonia beccarii*”, *Eggerella advena*, and
8 *Trochammia hadai*) and a decrease in many other foraminiferal species that are unable
9 to tolerate the low-oxygen conditions. *Eggerella advena* increased over the entire area
10 of Osaka Bay after the 1900s—the period when eutrophication commenced in Osaka
11 Bay as a consequence of the Japanese industrial revolution. After the early 1900s, a
12 marked decrease in species diversity in the innermost part of the bay, and a less
13 pronounced decrease in the middle part of the bay (OS4 and OS5), occurred as a result
14 of the increase in the relative and absolute abundance of “*A. beccarii*”, *E. advena*, and *T.*
15 *hadai*. “*Ammonia beccarii*” and *T. hadai* expanded their range to sites OS3, OS4, and
16 OS5 when the impact of eutrophication extended to the outer parts of the bay (~1950s to
17 1960s). Many other species virtually disappeared from the inner part of the bay (OBY
18 and OS3), as the hypoxic bottom-waters became inimical to their survival of many
19 species. The high-density/low-diversity assemblage proliferated during the period 1960
20 to 1970, when the eutrophication and bottom-water hypoxia were most pronounced. The
21 absolute abundance of “*A. beccarii*”, *E. advena*, and *T. hadai* decreased in the inner part
22 (cores OBY and OS3) after the 1970s when the Law Concerning Special Measures for
23 Conservation of the Environment of the Seto Inland Sea was brought into force. The
24 high-density/low-diversity assemblage might be returning to the pre-eutrophication
25 assemblage in the inner part of the bay following the restrictions on nutrient discharge.

1 These results indicate the necessity for substantial decreases in the amounts of the
2 nutrient input in order to restore former diverse benthic communities. This will lead to
3 the recovery of fishery resources such as shellfish. However, modern assemblages in
4 Osaka Bay are still dominated by eutrophication-tolerant species. This suggests the
5 potential difficulty of restoring ecosystems once they have been anthropogenically
6 destroyed. The long-term records provided by fossil foraminifera emphasize the
7 importance of maintaining a harmonious coexistence between development and
8 environmental quality.

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19

20 **Figure legends**

21 Fig. 1. Index and location maps: (A) showing the location of Osaka Bay; (B) the

22 location of sediment cores and the water survey stations.

23 Fig. 2. Monthly changes in the temperature and the salinity (average of observations
24 from 1996 to 1998; Osaka Prefectural Fisheries Experimental Station, 1998–2000).

25 The locations of the water survey stations are shown in Figure 1B.

- 1 Fig. 3. Present-day distribution of (a) salinity, (b) surface-water chemical oxygen
2 demand (COD), (c) total phosphorus (TP), and (d) bottom-water dissolved oxygen
3 (DO) (3-year average from 2001–2003). Data from Osaka Prefectural Fisheries
4 Experimental Station (2003–2005). Open circles are core locations (see Fig. 1).
- 5 Fig. 4. Secular change in the population size of Osaka City (Osaka City, 2004),
6 discharge of COD from the Osaka Prefecture through the Yodo River (Nakatsuji
7 et al., 1998), and total occurrences of red tides (Osaka Prefectural Fisheries
8 Experimental Station, 1973–2002).
- 9 Fig. 5. Seasonal and interannual variability in (A) dissolved oxygen (DO), (B) chemical
10 oxygen demand (COD), and (C) total phosphorus (TP) at Osaka Bay monitoring
11 site 15 over the past 30 years. Data from Osaka Prefectural Fisheries Experimental
12 Station (1974–2004). The location of the water survey stations are shown in
13 Figure 1B.
- 14 Fig. 6. Temporal distributions of (a) TOC, TN, and TS concentrations and (b) C/N and
15 C/S. (A) OS3, (B) OS4, and (C) OS5.
- 16 Fig. 7. Temporal changes in (A) species richness and (B) species diversity. The
17 minimum of the two diversity measures are recognized only in cores OBY and
18 OS3.
- 19 Fig. 8. Temporal changes in (A) absolute abundance of foraminifera and (B) BFAR.
20 Shadings indicate (a) initial increase (b) peak in absolute abundance of
21 foraminifera and BFAR occurs after the 1970s.
- 22 Fig. 9. Temporal changes in relative abundance of foraminiferal species. (A) OBY, (B)
23 OS3, (C) OS4, and (D) OS5. The solid circles are analyzed horizons. Gray-filled
24 species are eutrophication-tolerant species.
- 25 Fig. 10. Temporal changes of the varimax factor loadings. Factor 1: eutrophication

1 assemblage A; factor 2: pre-eutrophication assemblage; factor 3: eutrophication
2 assemblage B. The scale for factor 3 is reversed. The increase in factors 1 and 3
3 and the decrease in factor 2 indicates the progress of eutrophication and the
4 resulting hypoxia (see text).

5 Fig. 11. Temporal changes in the accumulation rates of “*Ammonia beccarii*”, *Eggerella*
6 *advena*, and *Trochammina hadai*. (A) OBY, (B) OS3, (C) OS4, and (D) OS5.

7

8 **Tables**

9 Table 1 Accumulation rates of the cores. Data from Yasuhara et al. (2007).

10

11 **Appendix Supplementary data**

12 Appendix A.1. Foraminiferal species identified in cores

13 Appendix A.2. Taxonomic list

14 Appendix B. List of the varimax factor scores

15 Appendix C. The varimax factor loadings for samples

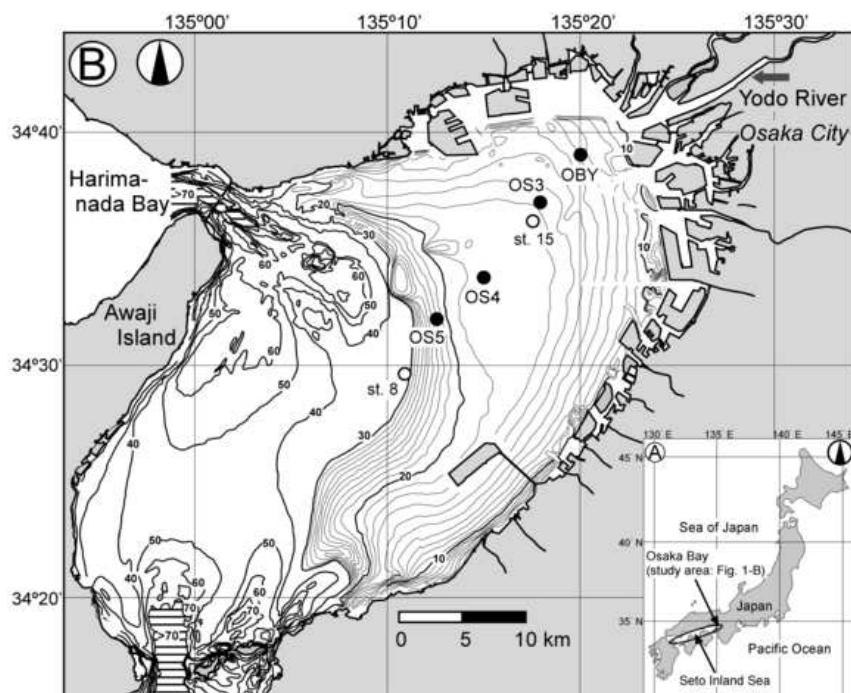


Fig. 1 Tsujimoto et al.

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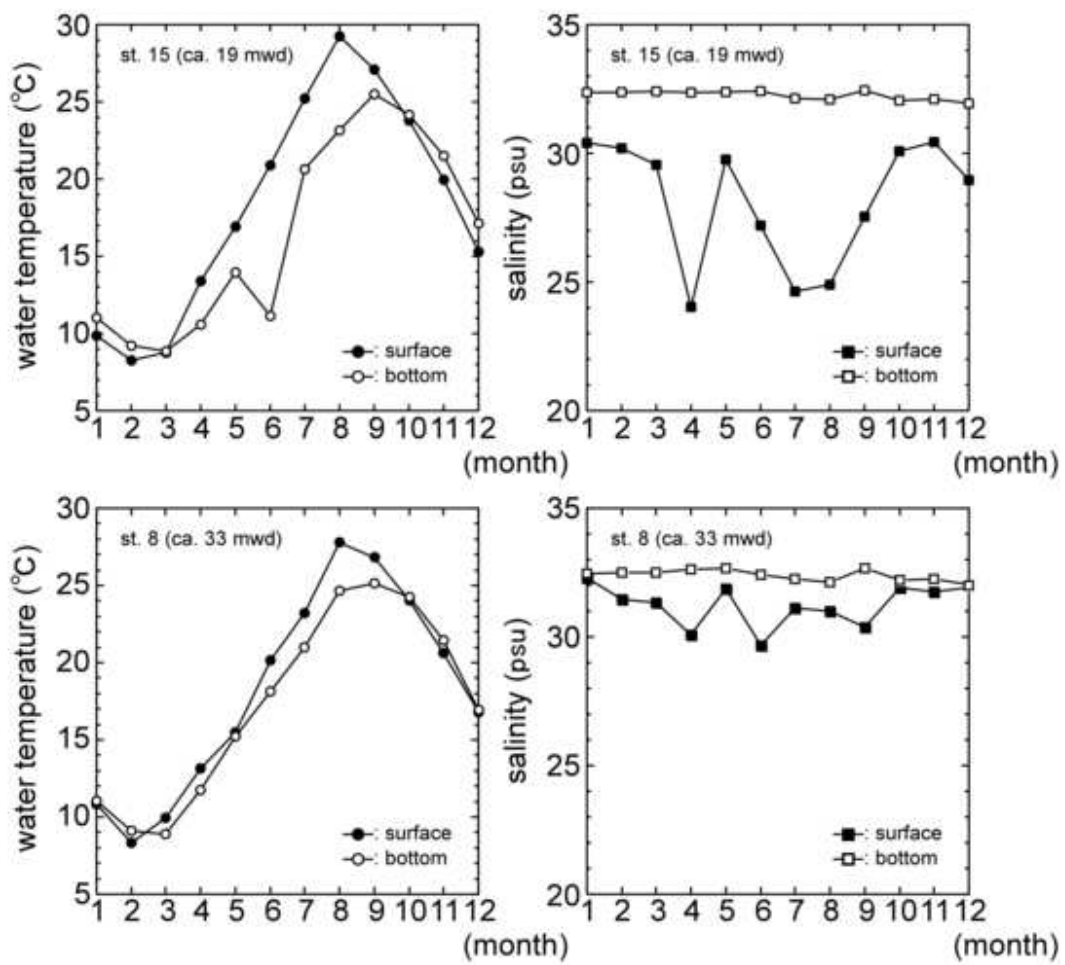


Fig. 2 Tsujimoto et al.

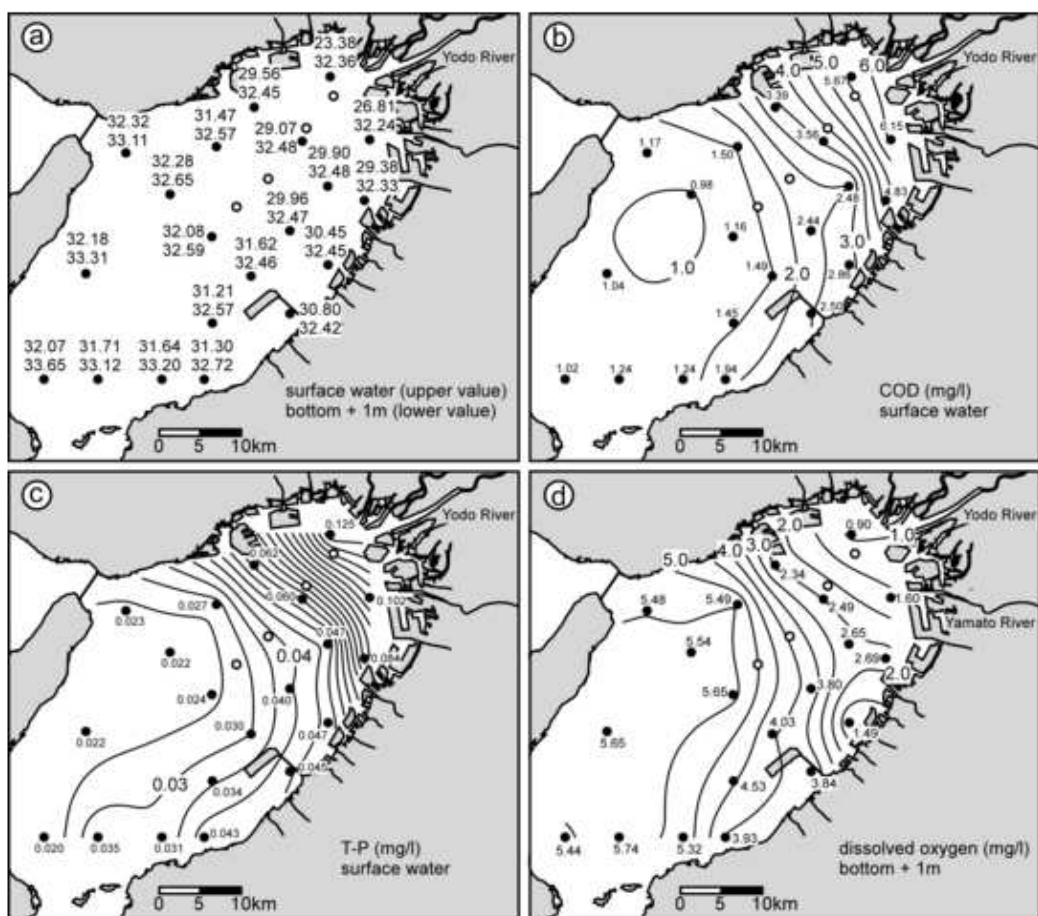


Fig. 3 Tsujimoto et al.

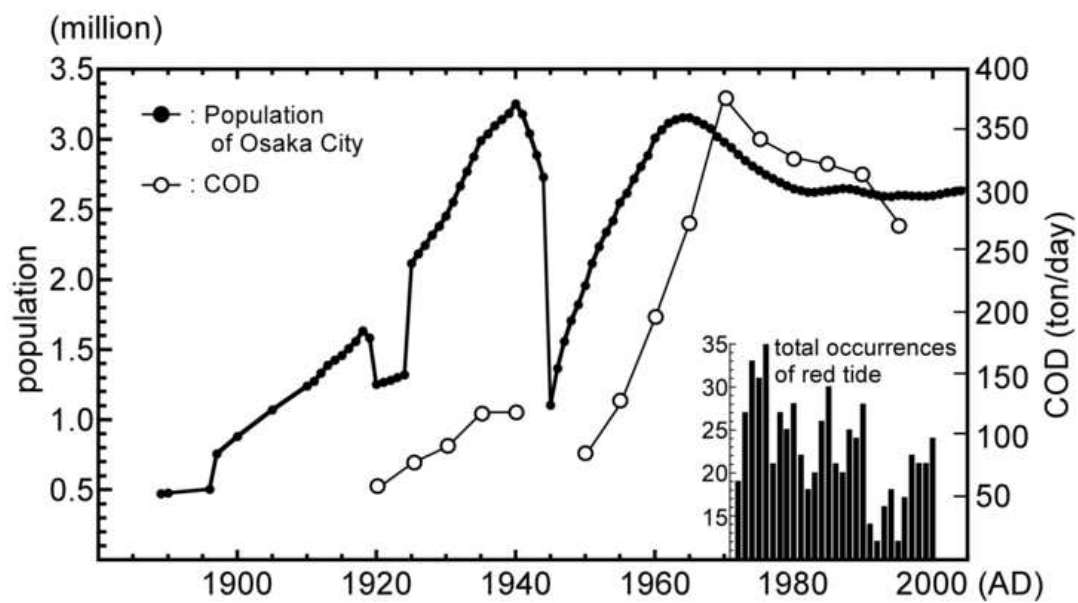


Fig. 4 Tsujimoto et al.

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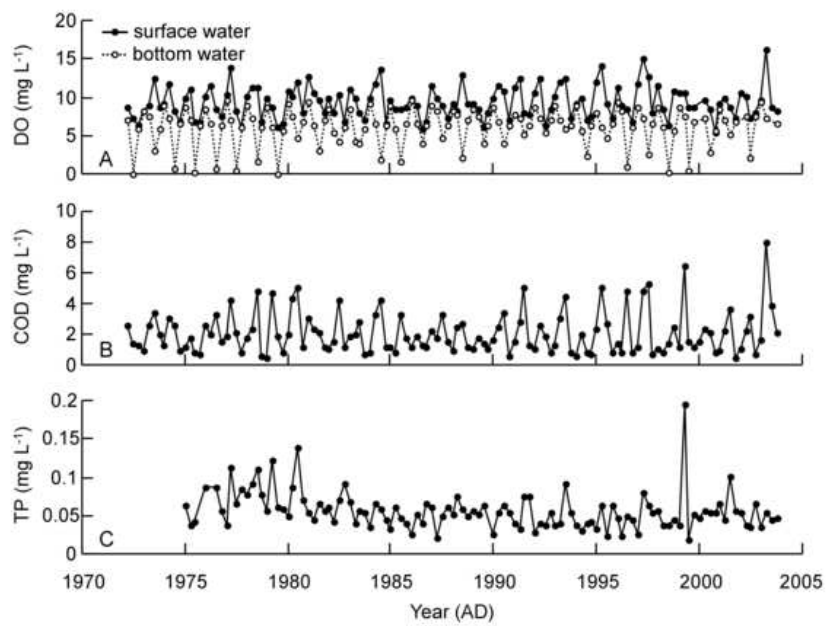


Fig. 5 Tsujimoto et al.

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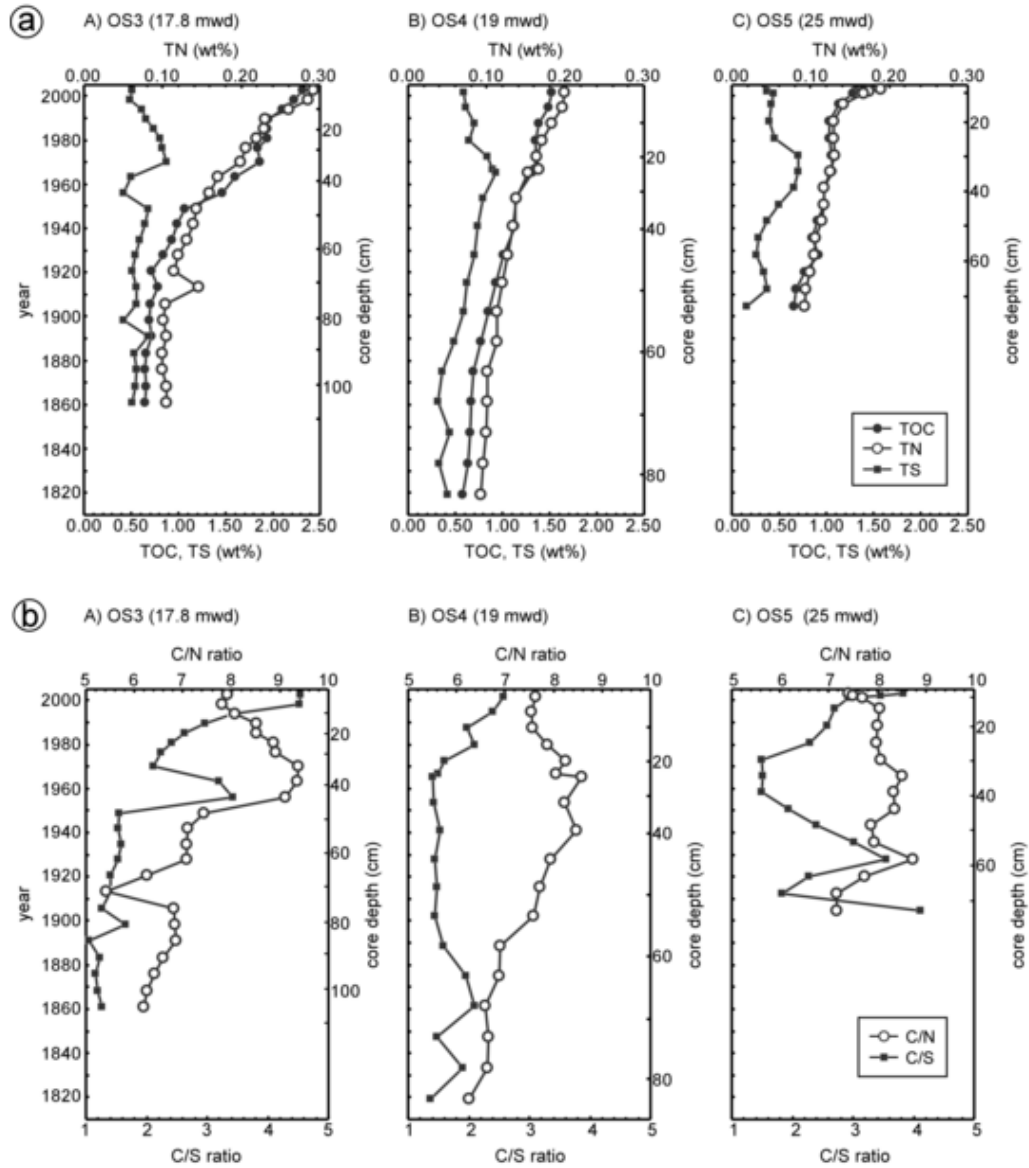


Fig. 6 Tsujimoto et al.

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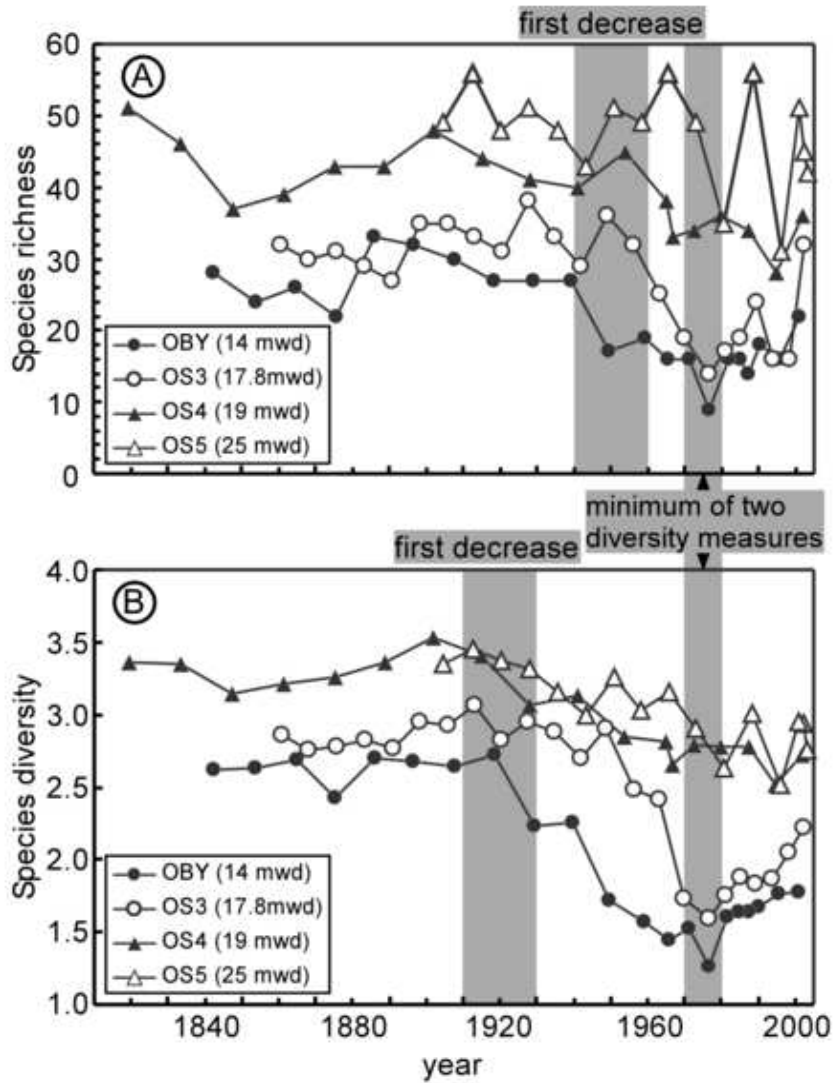


Fig. 7 Tsujimoto et al.

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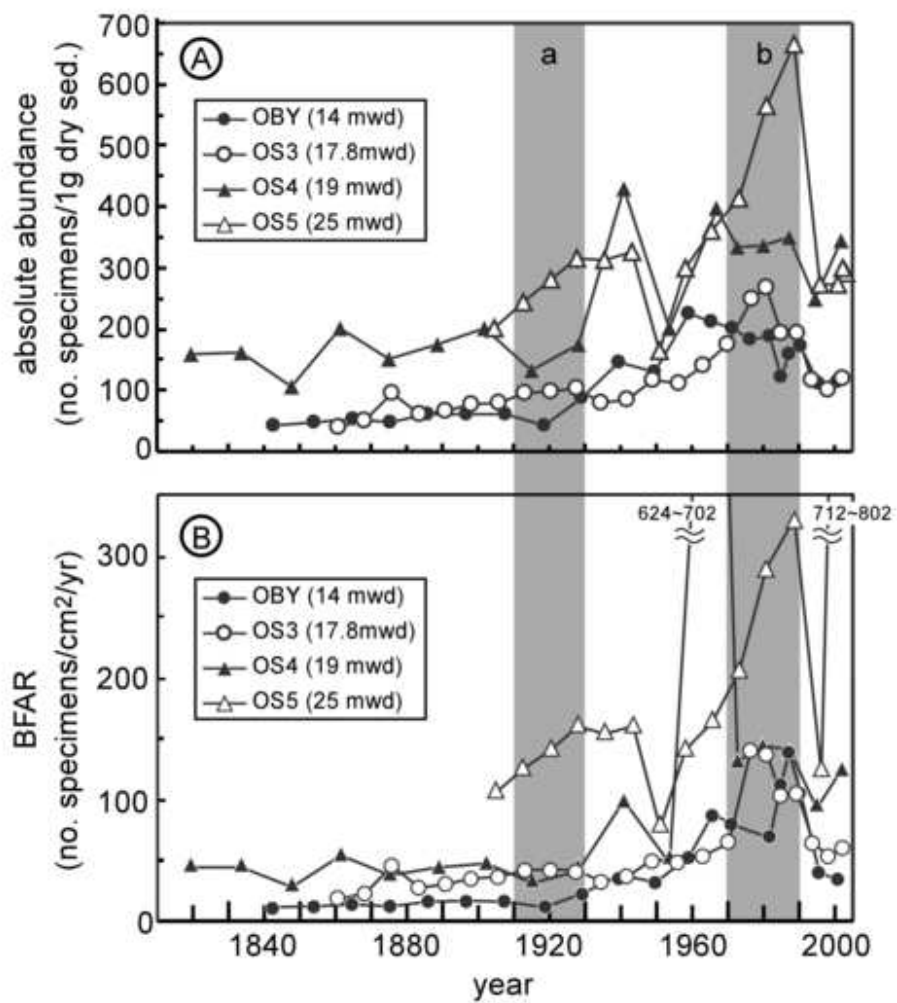


Fig. 8 Tsujimoto et al.

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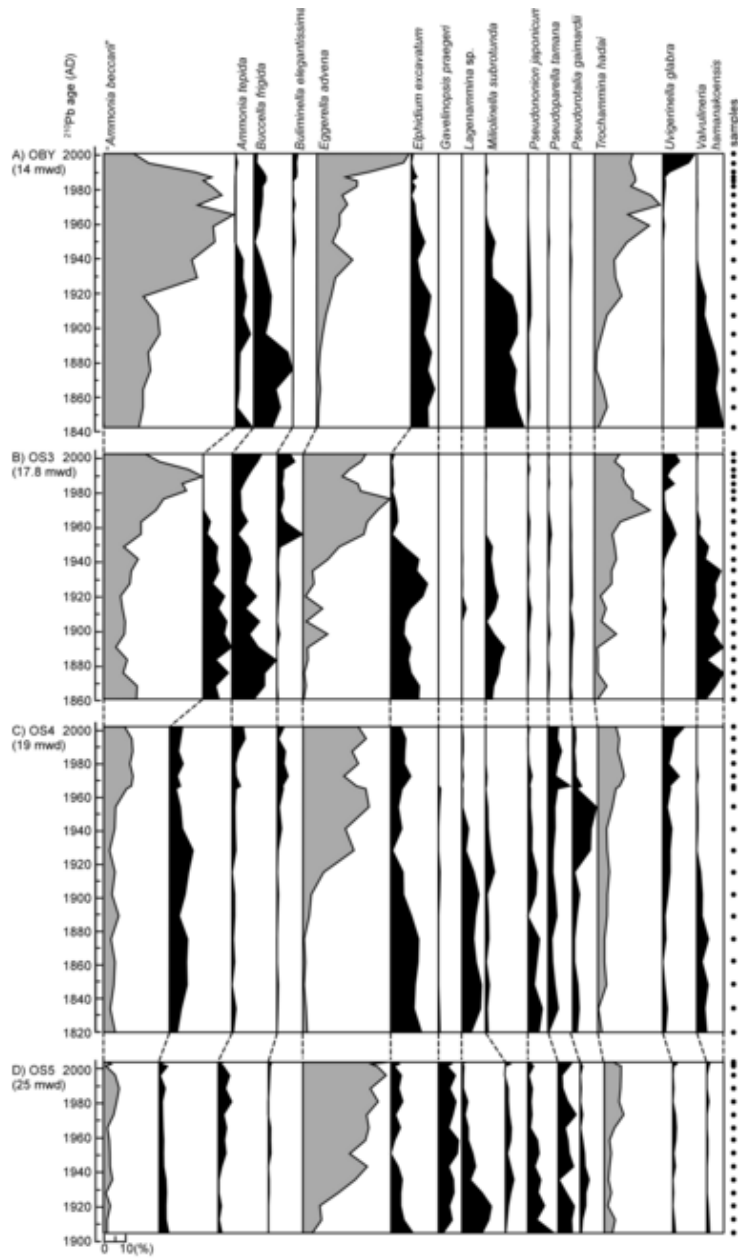


Fig. 9 Tsujimoto et al.

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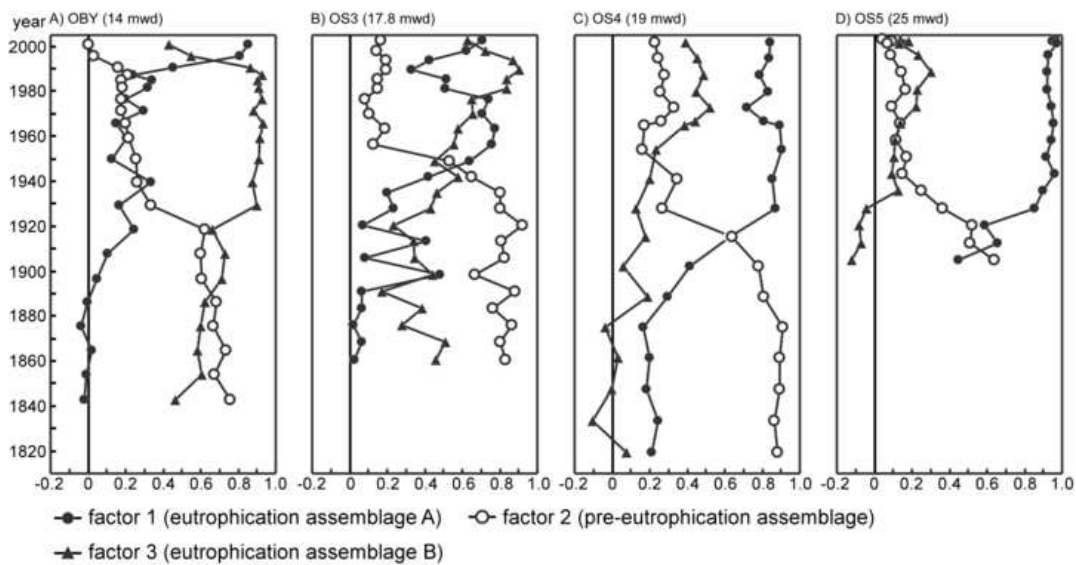


Fig. 10 Tsujimoto et al.

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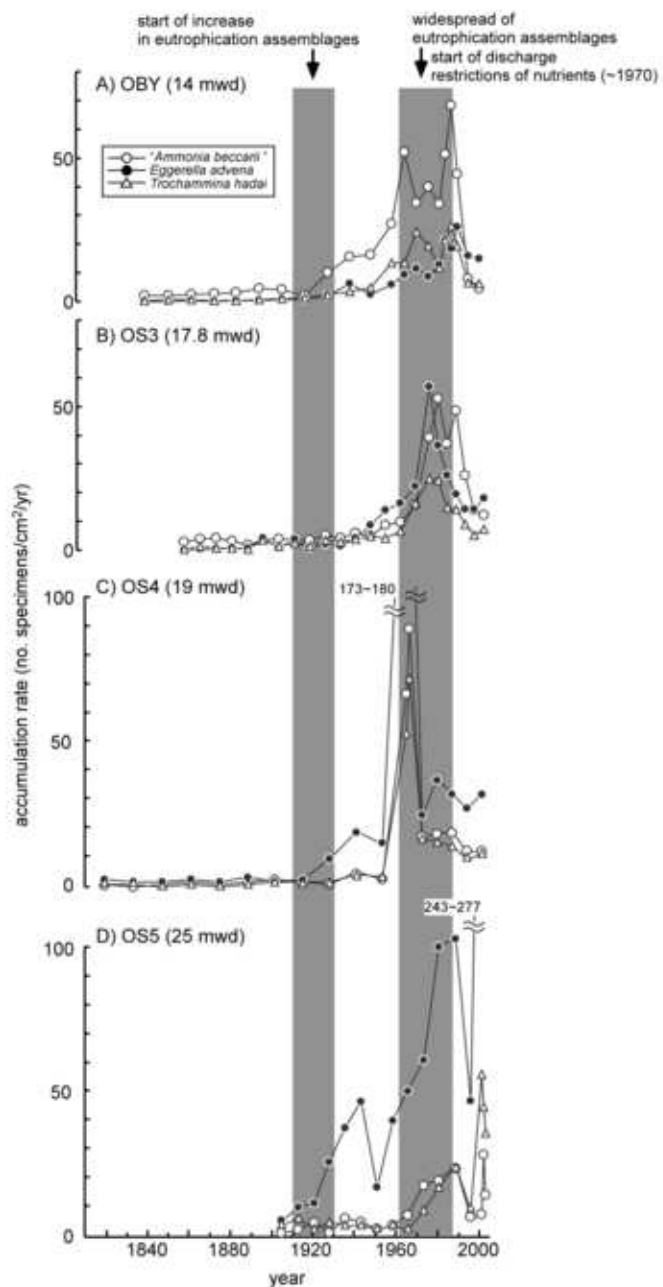


Fig. 11 Tsujimoto et al.

1

1 Table 1

	OBY (14 mwd)		OS3 (17.8 mwd)	OS4 (19 mwd)		OS5 (25 mwd)
interval (cm)	0–10.9	10.9–22.6	0–30.9	0–24.9	24.9–31.7	0–12.9
	22.6–41.6	>41.6	>30.9	>31.7		>12.9
accumulation rate (cm/yr)	0.926	2.029	0.89	0.498	1.105	0.724
					0.683	3 0.39
						4.57 0.709

2