

Correlation of *Virgulinitella fragilis* Grindell & Collen (benthic foraminiferid) with near-anoxia in Aso-kai Lagoon, central Japan

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ABSTRACT – The distribution of *Virgulinitella fragilis* and the hydro-environment of Aso-kai Lagoon, central Japan, were studied to clarify the foraminifer's adaptation to low-oxygen conditions. The hypolimnion of the lagoon is oxygen-poor during much of the year. Two faunas (A and B) are recognized, based on cluster analysis. Cluster A fauna consists of species common in brackish lagoons, such as the genera *Trochammina* and *Ammonia*, and occurs in seasonally oxygenated waters. *Virgulinitella fragilis*, the predominant species of Cluster B fauna, dominates the central part of the lagoon. This species can tolerate more severe oxygen deficiencies than the typical brackish foraminifers (e.g. *Trochammina* spp.) and can adapt to long periods of oxygen-poor conditions in coastal lagoon environments, as well as in pelagic to hemi-pelagic settings. In order to survive in the near-anoxia of Aso-kai Lagoon, *V. fragilis* may have adapted to environments in which little reactive iron is available in the sediment, leaving pore-water and bottom-water sulphide available for symbionts, or may utilize sulphur denitrification processes. *J. Micropalaeontol.* 24(2): 159–167, October 2005.

KEYWORDS: *Virgulinitella fragilis*, Aso-kai Lagoon, hydrography, near-anoxia, oxygen deficiency

INTRODUCTION

Aso-kai Lagoon (c. 4.9 km² and 15 m maximum water depth) is a brackish lake, lying along the coast of Miyazu Bay, central Japan (Fig. 1). It is separated from Miyazu Bay by a sand bar ('Amano-hashidate') and is connected to the bay through a narrow channel (Fig. 1). The lagoon's hypolimnion (the deep layer of lagoonal water) is oxygen-poor for long periods during the year (Nakanishi *et al.*, 1979), because the exchange of water between the lagoon and the bay is limited.

The benthic foraminiferid, *Virgulinitella fragilis* Grindell & Collen (Fig. 2), is common in Aso-kai Lagoon (Takata *et al.*, 2003). This species has been reported in a number of marine dysoxic to anoxic environments (Altenbach *et al.*, 2002; Bernhard, 2003). It has been suggested that *V. fragilis* may adapt to severe oxygen deficiency via symbiosis (Bernhard,

2003). The study of the adaptation of benthic foraminifers to oxygen-poor environments is important in both foraminiferal ecology and palaeoceanographic studies. Aso-kai Lagoon is an ideal location for investigating how benthic foraminifers adapt to near-anoxia because of easy accessibility and the presence of much steeper environmental gradients in comparison with the open marine environment. The object of this study is to clarify: (1) the ecology of *V. fragilis* and other species in a coastal lagoon environment; and (2) the adaptation of *V. fragilis*

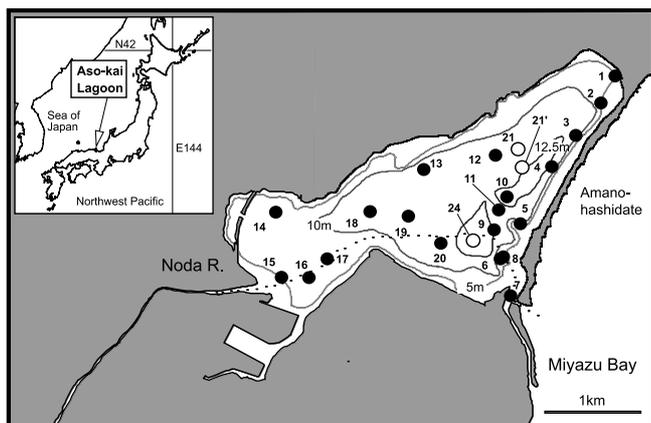


Fig. 1. Study area and sampling localities (shaded circle: surface sediment collections; open circle: seasonal water sample collections).

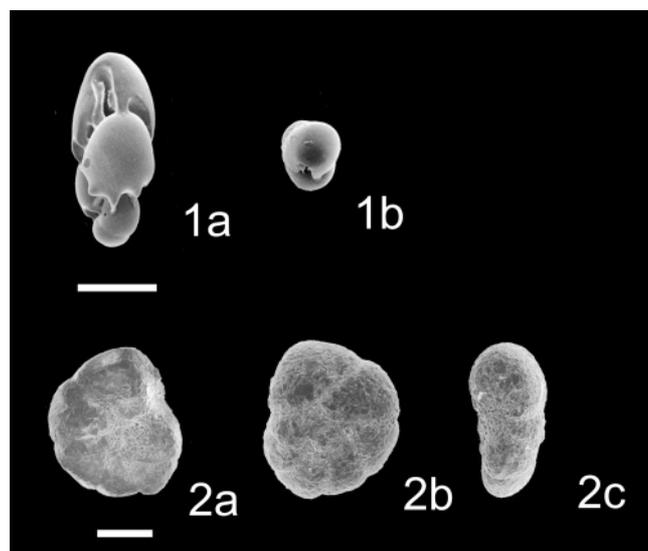


Fig. 2. Scanning electron micrographs of benthic foraminifers in Aso-kai Lagoon. (1a, b) *Virgulinitella fragilis* Grindell & Collen: (a) side view; (b) apertural view. (2a–c) *Trochammina* cf. *japonica* Ishiwada: (a) spiral view; (b) umbilical view; (c) edge view. Scale bar=100 µm.

to near-anoxia, based on assemblage analysis of modern benthic foraminifers in Aso-kai Lagoon.

METHODS

Samples were collected from 20 localities (Aso-1 to -20) in Aso-kai Lagoon on October 26, 2001, using an Eckmannbergetype sampler (Fig. 1). Sediment samples for geochemical and sedimentological/micropalaeontological analyses were collected from the uppermost few millimetres and the upper centimetre of surface sediment, respectively. A thinner layer of the uppermost sediment was used for geochemical analysis than was used for foraminifers because it represents better the chemical processes at the sediment–water interface.

Sediment samples for geochemical analysis were dried at 70°C and crushed and thoroughly homogenized in an agate mortar. Total organic carbon (TOC) and total sulphur (TS) contents were analysed using a FISON CHNS-elemental analyser E.A. 1108 at the Research Center for Coastal Lagoon Environments, Shimane University, using the technique of Sampei *et al.* (1997). From each sediment sample 10 mg was taken in a thin silver film container and 1N-HCl added twice and dried at 110°C for four hours. The dried sample was wrapped with thin tin film. BBOT (2, 5-Bis-(5-tert-butylbenzoxazol-2-yl)-thiophen) was used for standard to employ standard regression line method for quantitative analysis.

Samples for sedimentological/micropalaeontological analyses were divided into two subsamples for analysis of water content and foraminifers. Water content was calculated by weighing pre- and post- drying at 70°C. We calculated the dry weight of the foraminiferal analysis subsample based on its wet weight and the water content of each sample. Subsamples for foraminiferal analysis were washed on a 200 mesh (75 µm opening) sieve. Residues were stained with 0.5% Rose Bengal solution containing 70% methanol for 24 h. The residues were washed with hot water to remove excess dye and dried at 70°C. Foraminiferal specimens were picked using a stereo-binocular microscope, identified and classed as living or dead by the presence of staining. Relative abundance and individual number per dry sediment weight ($n g^{-1}$) were calculated for each species in each sample.

Q-mode cluster analysis was carried out on the total (living (stained) and dead) foraminiferal fauna. The total fauna was used for the analysis since living (stained) individuals were not common in the samples studied. The data matrix consisted of 28 taxa for which at least three individuals occurred in each sample, and 17 samples containing more than 50 specimens (stations Aso-4, -15 and -16 were excluded because of their small number of specimens). Horn's index of overlap (Horn, 1966) was applied to determine the similarity between samples:

$$\text{Overlap } (R_o) = \frac{\sum(xi + yi) \log(xi + yi) - \sum xi \log xi - \sum yi \log yi}{(X + Y) \log(X + Y) + X \log X + Y \log Y}$$

where, xi and yi are the number of individuals per unit weight of sediment of i th taxa in samples x and y , respectively, and X and Y are the total number of individuals in samples x and y per unit weight of sediment, respectively. The clustering was carried out by using the unweighted pair group method, with arithmetic average in a FORTRAN program (Davis, 1973).

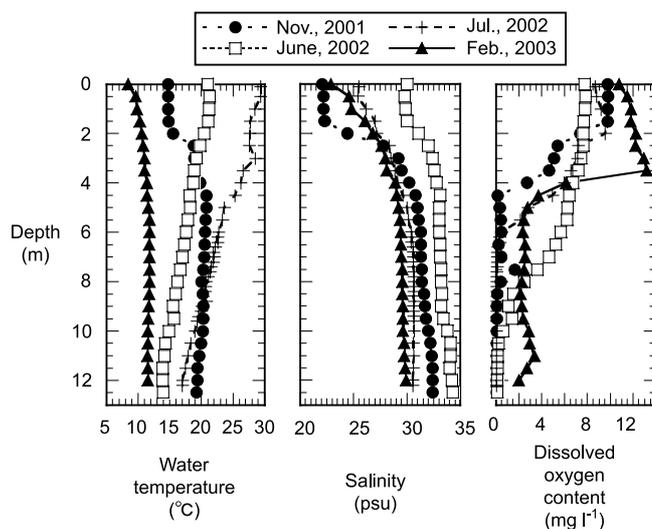


Fig. 3. Water temperature, salinity and dissolved oxygen content of lagoon water in Aso-kai Lagoon. November 2001 data from station Aso-21, other data from station Aso-21'.

Water temperature, salinity and dissolved oxygen content were recorded using a 'Quanta' multiparameter probe from Hydrolab Inc., at stations Aso-21 and Aso-21' on November 12, 2001, June 2, July 25, 2002 and February 26, 2003. Additionally, bottom water samples for hydrogen sulphide concentration were collected at stations Aso-21 and Aso-21' on November 12, 2001 and June 2, July 25, 2002, based on the procedure of Sakai *et al.* (2004). Hydrogen sulphide concentrations were measured based on the methylene blue method (Cline, 1969).

RESULTS

Hydrography

Seasonal change in water temperature, salinity and dissolved oxygen content at stations Aso-21 and Aso-21' are shown in Figure 3. These data are highly variable on a seasonal basis in the epilimnion (the surface layer of lagoonal water), whereas in the hypolimnion there is very little change. Dissolved oxygen content below 10 m water depth is nearly 0 mg l⁻¹, except in February. Similar oxygen-limitation (<10% oxygen saturation) of hypolimnetic water was also reported below 8–10 m water depth during at least eight months (April–November) in Aso-kai Lagoon in the study of Nakanishi *et al.* (1979), who measured the oxygen content of lagoonal water at five stations two decades ago. Thus, below 10 m depth the lagoon water is nearly anoxic during long periods of the year (probably eight months), although an inflow of oxygen-rich seawater occurs during the winter season. Additionally, even in February 2003 some stations show near-anoxia in bottom waters (stations Aso-16 and -17), while stations Aso-24 and Aso-21 have higher oxygen concentrations (Figs 3, 4). This observation indicates that the renewal and oxygenation of deep water in winter is restricted to locations adjacent to the sand bar, and that the hypolimnion of the lagoon's interior, especially the south-western part, is nearly anoxic throughout the year.

The hydrogen sulphide concentration of bottom water is commonly very low, nearly 0 mM at station Aso-21' in June (0 µM) and July (0.36 µM), 2002, although a high concentration

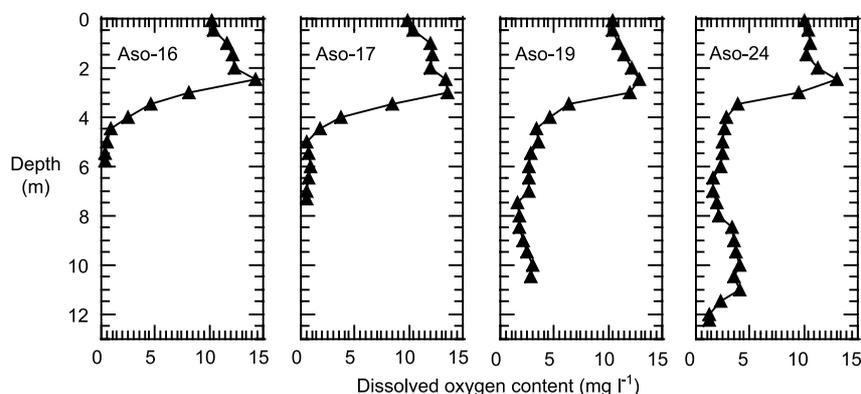


Fig. 4. Dissolved oxygen content at four localities in Aso-kai Lagoon, February 2003.

(0.79 mM) was observed on one occasion at station Aso-21 in November 2001. This observation is consistent with the results of Nakanishi *et al.* (1979), in which hydrogen sulphide concentration of hypolimnetic water is lower than $10 \mu\text{g-S l}^{-1}$ ($0.31 \mu\text{M}$) from late November to July.

Benthic foraminifers

In this study 32 genera and 67 species are recognized (Table 1). *Virgulinema fragilis* Grindell & Collen and *Trochammina cf. japonica* Ishiwada are common constituents in Aso-kai Lagoon; they are associated with Miliolids, *Ammonia cf. Ammonia beccarii* (Linné) forma 1, *Rosalina* spp. and *Elphidium* sp. A. There are no obvious differences in the distributions of living (stained) and total specimens of *Trochammina cf. japonica* (Fig. 5). There is thus no reason to suspect that the tests of these species are transported any significant distance after death. Living (stained) individuals of *V. fragilis* occurred only in the inner lagoon, whereas dead specimens were also found in locations near the sand bar. These differences are significant in the deeper portions of the lagoon (e.g. stations Aso-3, -9, -10 and -14). Since both living and dead tests occur together in the central portion of the lagoon, this species clearly lives in the inner lagoon, although one cannot dismiss the transportation of dead tests to other areas (Fig. 5).

The cluster analysis recognizes two clusters (A and B). Cluster A occurs in the north-eastern and south-eastern parts of the lagoon, in locations adjacent to the sand bar (seven localities) (Fig. 6). Cluster B dominates the central to inner part of the lagoon (ten localities) (Fig. 6). Cluster A does not show a marked association with water depth, whereas the distribution of Cluster B is restricted to depths below 7.6 m (Table 2). Cluster A fauna is characterized by an abundance of *T. cf. japonica* or *Rosalina* spp. (Fig. 6). Subordinate taxa in Cluster A are Miliolids, *A. cf. A. beccarii* forma 1 and *Elphidium* sp. A. The composition of these subordinate taxa varies at each locality. Cluster B fauna is characterized by a predominance of *V. fragilis* and associations of Miliolids and *Rosalina* spp. (Fig. 5).

Although stations Aso-4, -15 and -16 were excluded from the cluster analysis because of low abundances, *V. fragilis* is found at stations Aso-4 and -16, whereas *Ammonia* spp. and *Valvulineria hamanakoensis* occur at station Aso-15. Scarcity of foraminifers at these stations is probably due to dilution with

large amounts of coarse-grained terrigenous materials derived from the river or sand bar.

Total organic carbon and total sulphur content

The results of geochemical analyses are shown in Table 2. High TOC and TS contents ($>3.27\%$ and $>2.20\%$, respectively) occur in surface sediments in the central portion of the lagoon (e.g. stations Aso-11 to -13 and Aso-17 to -20). In this area, TS content is relatively constant (2.20–3.01%), while TOC content is more variable (3.27–5.84%) (Fig. 7).

DISCUSSION

Distribution of faunas in Aso-kai Lagoon

Virgulinema fragilis, the predominant species of Cluster B fauna, has been reported only rarely in coastal environments, whereas characteristic taxa of the Cluster A fauna, namely *Trochammina*, *Ammonia*, *Rosalina* and *Elphidium*, are common foraminifers in brackish waters. The discussion of *V. fragilis* and *T. cf. japonica*, the characteristic species of cluster A and B faunas, respectively, is limited to living (stained) specimens only because environmental inferences based on living occurrences are more reliable than those based on total specimen occurrence in understanding of foraminiferal habitat (e.g. Murray, 2000). The inferences about the ecology of *V. fragilis* and *T. cf. japonica* are based on the comparison of both species relative to TOC and TS content of the surface sediment and the dissolved oxygen content of lagoon water.

Living (stained) *V. fragilis* are restricted to locations with higher TOC and TS contents than that of *T. cf. japonica* (Fig. 7). This is most likely due to the greater oxygen deficiency in the water column at locations associated with *V. fragilis*, than at locations where *T. cf. japonica* occurs. This assumption is based on the suggestion of Berner (1984), that low oxygen levels are responsible for high TOC and TS content in sediment. The area hosting *V. fragilis* is restricted to water depths greater than 11.1 m in the central to north-eastern part of the lagoon (stations Aso-11, -12, -13, -18, -19 and -20) and to 7.6 m water depth in the south-western part of the lagoon (station Aso-17) (Table 2), a depth that coincides with the near-anoxia that occurs during long portions of the year (Figs 3, 4). Therefore, it is concluded that the distribution of *V. fragilis* is related closely to significant periods of oxygen deficiency during the year. On

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
<i>Allanaccockia?</i> sp.	T								0.79											
<i>Ammonia beccarii</i> (Linne) forma 1	L		0.18											0.11						
<i>Ammonia</i> cf. <i>A. beccarii</i> (Linne) forma 1	T		0.18											0.11						
<i>Ammonia</i> cf. <i>A. beccarii</i> (Linne) forma 2	L	47.95 2.28	2.98																	
<i>Ammonia japonica</i> (Hada)	L				1.52				0.79											
<i>Ammonia</i> sp. A	L				1.52				0.79											
<i>Ammonia?</i> sp. indet.	T				1.52															
<i>Bolivina striata</i> Cushman	L	2.28	0.39																	
<i>Bolivina tokiokai?</i> Uchio	L			0.18																
<i>Bolivina</i> sp. A	T		0.13																	
<i>Bolivina</i> sp. B	L			0.20																
<i>Brizalina seminuda</i> (Cushman)	L				0.32					0.69	0.24									
<i>Bulimina elegantissima</i> (d'Orbigny)	L				0.21					0.35	0.71	0.20	0.16							
<i>Cassidulina</i> sp.	T									0.35	0.24									
<i>Cibicides lobatulus</i> (Walker & Jacob)	L							1.16		0.94										
<i>Cibicides</i> cf. <i>lobatulus</i> (Walker & Jacob)	L							1.16	0.79	0.24										
<i>Cibicides subdepressus</i> Asano	T					3.03	0.02			0.79	0.35									
<i>Cibicides</i> sp. indet.	L						0.01			0.35										
<i>Cibicides</i> sp.	T		0.13																	
<i>Cyclogure planorbis</i> (Schultze)	L							2.33												
<i>Cymbalopolletta</i> sp. A	L			0.20	0.11	6.07	0.07	4.65	1.57			0.20								
<i>Eggerelloides advena</i> (Cushman)	L			0.11	0.11	1.52	0.06		1.57											
<i>Elphidium advenum?</i> (Cushman)	L							2.33												
<i>Elphidium crispum</i> (Linne)	L			1.52																
<i>Elphidium jenseni</i> (Cushman)	L			0.43	1.52			3.49	0.79	0.35										

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
<i>Elphidium kushiroense</i> Asano	T					4.55					0.24									
<i>Elphidium</i> cf. <i>subarcticum</i> Cushman	L							3.49												
<i>Elphidium subincertum</i> Asano	L	0.13							0.79											
<i>Elphidium</i> sp. A	T	2.28	0.13																	
<i>Elphidium</i> sp. B	L	2.28	3.76	0.20	0.86			2.33	2.36	0.69	0.71									
<i>Elphidium</i> sp. C	L	2.28	0.39					1.16												
<i>Elphidium</i> sp. D	L							1.16												
<i>Elphidium</i> sp. E	T							0.79												
<i>Gavelinopsis?</i> sp.	L										0.24									
<i>Glabratella</i> sp. A	L	4.57			0.11	0.01	0.01	2.33		1.16	1.57	0.35	0.71			0.14	0.14			0.21
<i>Glabratella</i> sp. B	L		0.39									0.16								
<i>Hanzawaia nipponica</i> Asano	L						0.01													
<i>Haynesina</i> sp.	T					4.55				0.35										
<i>Hyaline?</i> sp.	L										0.71									
<i>Massilina?</i> sp.	T																			
<i>Massilina?</i> sp.	L				0.11	1.52		1.16	1.57	0.35	0.71									
<i>Mitilinea</i> sp.	L										0.24									
<i>Nonionella stella</i> Cushman & Moyer	T																			
<i>Nonionella?</i> sp.	L										0.24									
<i>Paracassidulina?</i> sp.	L										0.24									
<i>Pararotalia?</i> sp.	L										0.24									
<i>Planoglabratella suboecularis</i> (Asano)	L																			
<i>Quinqueloculina</i> sp. A	T	13.70		0.20	0.32		0.02	5.82	4.72	1.73	1.88	0.39		0.42						
<i>Quinqueloculina</i> sp. B	L						0.02													
<i>Quinqueloculina</i> sp. C	T	4.57	2.72	1.46	0.41	9.10	0.02	0.02	0.69	3.30	3.30		0.49	0.21					0.49	0.41
<i>Quinqueloculina</i> sp. D	L	6.85	0.52	0.18	0.64	4.55	0.02	1.16					0.16							
<i>Quinqueloculina</i> sp. D	L			0.37					3.15											

Table 1. Abundance of foraminifers per weight ($n\ g^{-1}$) in Aso-Kai Lagoon.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
<i>Quinqueloculina</i> sp. E	T	0.13																		
<i>Quinqueloculina</i> sp. F	L	0.13																		
<i>Quinqueloculina</i> sp. G	T							1.16												
<i>Quinqueloculina</i> sp. H	L								0.79											
<i>Quinqueloculina</i> sp. I	T							4.65												
<i>Rosalina bradyi</i> (Cushman)	L							3.49												
	T							1.16												
<i>Rosalina</i> sp. A	L	6.85			1.07	24.28	0.35	26.76	8.65	3.46	5.42									
	T				0.54		0.33			1.04										
<i>Rosalina</i> sp. B	L									1.04										
	T				0.52					1.04										
<i>Rosalina</i> sp. C	L								0.07											
	T								0.06											
<i>Rosalina</i> sp. indet.	L									3.03										
	T																			
<i>Textularia</i> sp.	L																			
	T																			
<i>Tiphotrecha kelletiae</i> (Thalman)	L										0.24									
	T																			
<i>Trifarina</i> sp.	L																			
	T																			
<i>Tritoculina</i> sp.	L								0.79											
	T																			
<i>Trochammina</i> cf. <i>japonica</i> Ishiwada	L	84.49	7.25	0.37	0.20	0.64	97.10	107.03	21.23	0.35	2.12	0.20	0.16			0.06	0.28			0.41
	T	31.97	0.65			6.07		5.82	2.36		0.47	0.20								0.21
<i>Trochammina inflata?</i> (Montagu)	L																			
	T																			
<i>Trochammina pacifica</i> Cushman	L									0.20										
	T									0.20										
<i>Trochammina</i> sp. A	L									0.11										
	T									4.65										
<i>Valvulineria hamanaoensis</i> (Ishiwada)	L	11.42	1.04													0.45				
	T	2.28																		
<i>Virgulineria fragilis</i> Gridell & Collen	L		4.02	5.48	2.05				5.50	6.23	10.84	38.37	14.15	15.41		0.28	9.00	23.07	20.77	10.78
	T		0.13						1.18	0.79	0.49					0.06	1.25	3.03	1.48	0.83
Miscellaneous	L	9.13	0.78	0.37		0.54	10.62	0.04	13.96	4.72	1.38	1.88	0.79							
	T					0.04			0.35											0.33

Abundance of living (stained) and total (living+dead) specimens are shown in columns 'L' and 'T', respectively.

Table 1. Continued.

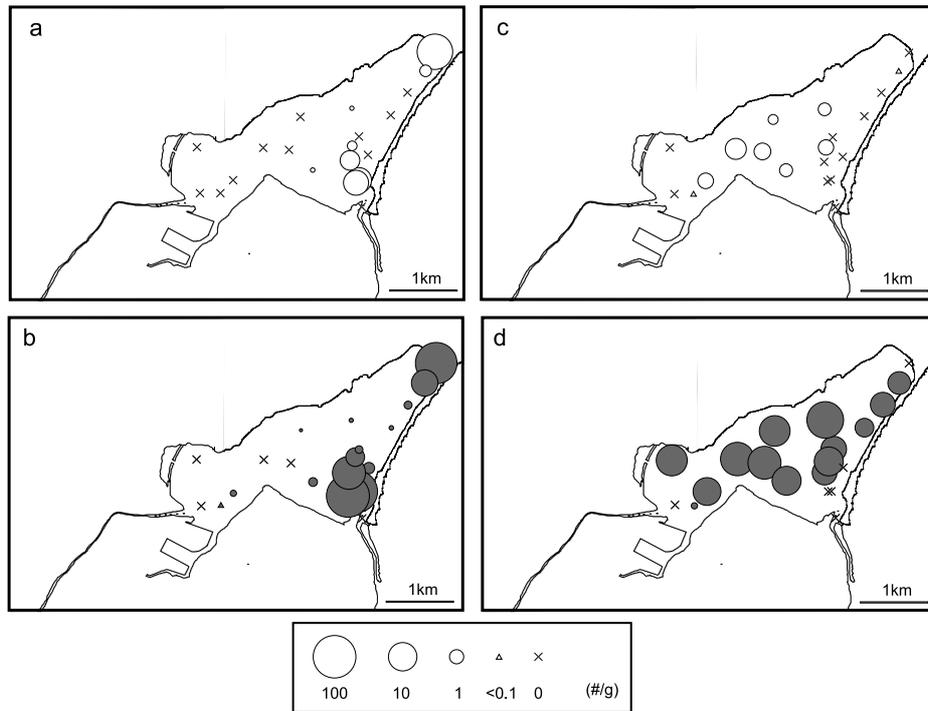


Fig. 5. Geographical distribution of abundance of living (stained) and total (living (stained) + dead) specimens of (a, b) *Trochammina cf. japonica*: (a) living (stained); (b) total; and (c, d) *Virgulinea fragilis*: (c) living (stained); (d) total.

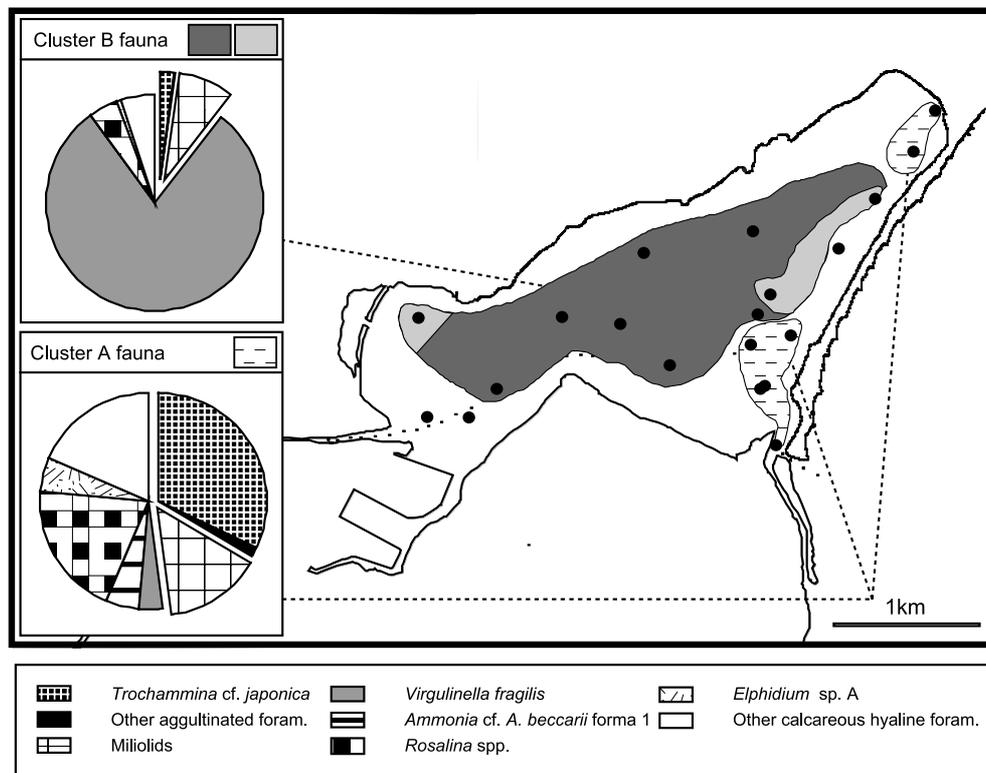


Fig. 6. Distribution and average faunal composition of Clusters A and B. Distribution of Cluster B with living (stained) and only dead (empty) tests of *V. fragilis* is shown as dark- and light-shaded pattern, respectively.

Station	Water depth (m)	TOC (%)	TS (%)	Cluster	<i>Virgulinema fragilis</i>
1	5.7	3.25	0.99	A	
2	7.9	4.29	2.58	A	+
3	11.1	4.39	2.93	B	+
4	12.3	4.64	3.01	—	
5	3.3	0.15	0.14	A	
6	6.3	0.27	0.18	A	
7	2.0	0.15	0.04	A	
8	8.7	0.80	0.51	A	
9	12.7	3.40	2.11	A	+
10	12.8	5.18	2.62	B	+
11	12.6	5.83	2.92	B	++
12	12.0	4.05	3.01	B	++
13	11.5	3.89	2.60	B	++
14	8.8	3.27	2.52	B	+
15	4.1	4.74	0.44	—	
16	6.2	3.64	1.64	—	+
17	7.6	3.70	2.20	B	++
18	11.1	4.85	2.74	B	++
19	11.4	4.81	2.71	B	++
20	12.2	4.25	3.01	B	++

++: containing living (stained) specimens; +: only dead specimens or rare living (stained) specimens.

Table 2. Summary among 20 stations of water depth, total organic carbon content (TOC), total sulphur content (TS), cluster and occurrence of *Virgulinema fragilis*

the other hand, the distribution of *T. cf. japonica* coincides with localities where relatively oxygen-rich bottom water was observed adjacent to the sand bar in February, 2003 (Fig. 4). From this, one can infer that this species is restricted to areas that are well oxygenated for at least a portion of the year. *Trochammina hadai* (probably equivalent to *T. cf. japonica* here) thrive in seasonally oxygen-poor settings, adopting a life history strategy that allows individuals to tolerate oxygen-poor periods, although oxygenated conditions are required for reproduction and growth (Matsushita & Kitazato, 1990; Kitazato, 1994). This agrees with the hypothesis concerning the restricted distribution of *T. cf. japonica*. The present observations indicate that *V. fragilis* tolerates more intensive and a longer duration of oxygen-poor conditions than does *T. cf. japonica*, which is restricted to regions in which low-oxygen conditions are seasonally replaced by well-oxygenated waters.

Adaptation of *Virgulinema fragilis* to oxygen deficiency in Aso-kai Lagoon

Virgulinema fragilis has been reported from some marine dysoxic to anoxic environments. Bernhard (2003) reported the predominance of this species in the bathyal zone of the Cariaco Basin, which is characterized by year-round anoxia and abundant hydrogen sulphide. Altenbach *et al.* (2002) reported the occurrence of this species on the upper shelf off Namibia, which is characterized by oxygen-poor conditions (<0.32 ml l⁻¹). Thus, *V. fragilis* can adapt to severe oxygen deficiency in pelagic to hemi-pelagic settings. The results of this study indicate that *V. fragilis* can also live in conditions of severe oxygen-deficiency for a long duration in a shallow-water setting. This contradicts the suggestion of Grindell & Collen (1976) that this species also lives

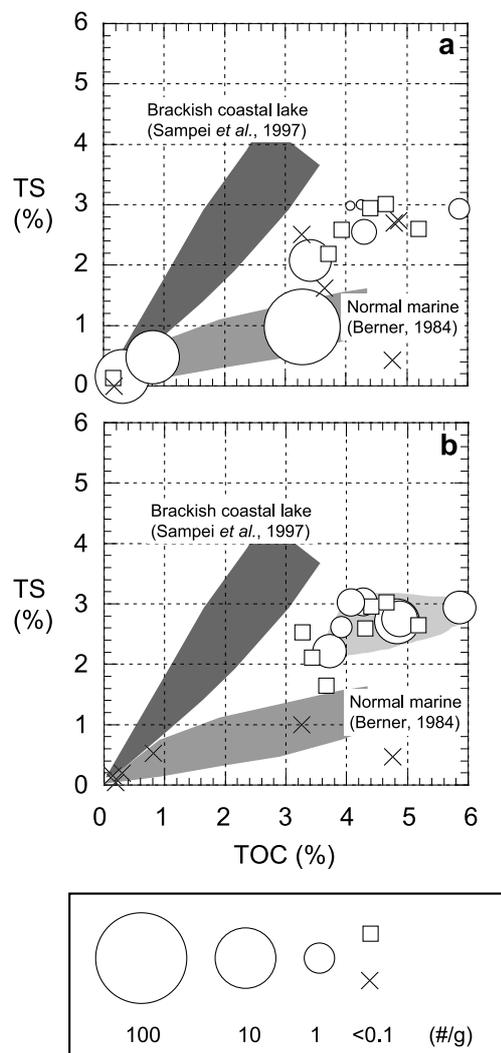


Fig. 7. Relationship between total organic carbon (TOC) vs. total sulphur (TS) contents of surface sediments and abundance per unit weight (individual number per gram) of living (stained) individuals of (a) *Trochammina cf. japonica* and (b) *Virgulinema fragilis*. The occurrence of dead tests only is shown by open squares. Absence of any tests of the species is indicated by 'X'. Data taken from Sampei *et al.* (1997), Bernier (1984) and this study.

in a relatively well-oxygenated environment (7.18–12.63 mg l⁻¹) in Wellington Harbour (New Zealand). This conclusion was based on the water chemistry of Booth (1975), but the dissolved oxygen content data came from the outer part of the bay where *V. fragilis*, especially living (stained) specimens, were not observed; oxygen content was not measured at locations where *V. fragilis* was present. Therefore, it is concluded that *V. fragilis* can adapt to near-anoxia in a coastal lagoon setting, as well as in pelagic to hemi-pelagic settings.

How *V. fragilis* adapts to these oxygen-poor conditions is still not well known. Bernhard (2003) suggested one possible adaptation of this species to severe oxygen deficiency. She found that *V. fragilis* accommodates two symbionts, a chloroplast and a sulphide-oxidizing bacterium, and implied that this species may be resistant to anoxic and sulphide-rich conditions through symbiosis.

To see if there is a particular relationship between TOC and TS content in the surface sediments of the inner and central Aso-kai Lagoon hosting living (stained) *V. fragilis*, these data were compared with the TOC and TS contents of other environments, because TOC and TS contents in surface sediments record long-term (multi-season) environmental conditions. TS content is weakly positively correlated with TOC content in Aso-kai Lagoon (Fig. 7), although TOC and TS contents commonly show a positive correlation in many brackish and bay sediments, such as 'normal marine sediments' (Berner, 1984) and 'brackish coastal lake sediments' (Sampei *et al.*, 1997). This feature is similar to that of 'euxinic (Black Sea) sediments' (Berner, 1984, fig. 8). It is suggested that the oxygen-poor circumstances that lead to this relationship between TOC content and TS content in the sediment also contribute to the distribution of *V. fragilis* in the study area.

One possible explanation for this pattern is the low levels of reactive iron in the sediment. Pyrite (FeS₂) is the major constituent of sulphide in most sediments. The amount of detrital reactive iron controls the concentration of sulphide (pyrite) in deep basin sediments of the Black Sea (Lyons & Berner, 1992). The scarcity of reactive iron may lead to available sulphide which can be utilized by the symbionts of *V. fragilis*. Another process allowing survival under anoxic conditions may be sulphur denitrification. Altenbach *et al.* (2002) noted the relationship between the abundance of *V. fragilis* and denitrification, in which sulphur-denitrifying bacteria (*Thiobacillus*, *Beggiatoa* and others) consume sulphide and nitrate under anoxic conditions (Hasegawa & Hanaki, 2001). *Beggiatoa*, one bacterium of this type, is commonly associated with the habitat of *V. fragilis* (Bernhard, 2003). The processes by which *V. fragilis* may have adapted to oxygen deficiency clearly need further study.

ACKNOWLEDGEMENTS

The authors thank Shun-suke Murakami (Shimane University) for help in the field survey and sample processing, and Kaoru Hirono and Ju-zou Naitou (Miyazu Fishery Cooperative) for help during field work. They are also indebted to Ritsuo Nomura and Toshiaki Irizuki (Shimane University) for kind assistance with electron micrographs. Thanks are also due to David L. Dettman (University of Arizona & Shimane University) for improving the English in this manuscript. Alexander Altenbach (Tübingen University) and an anonymous reviewer are thanked for their helpful comments on the manuscript. This work was partly supported by a grant-in-aid (Satoshi Tanaka, no. 12740282) for scientific research from the Ministry of Education, Science and Culture of Japan.

Manuscript received 13 February 2004

Manuscript accepted 10 January 2005

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