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Response of benthic foraminifera (Rhizaria) to anthropogenic environmental changes in the Honjo area of Lake Nakaumi (southwestern Japan) : dispersal potential of neritic benthic foraminifera

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Abstract: We investigated faunal transitions in living (rose Bengal-stained) benthic foraminifera in the Honjo area of Lake Nakaumi (southwestern Japan) through monthly biological monitoring at a fixed station (approx. 8-m depth) to study the dispersal potential of benthic foraminifera. We observed the following transitions in benthic foraminifera: (1) few and sporadic occurrences of benthic foraminifera before November 2007; (2) *Ammonia* “*beccarii*” forma 1 dominant in 2008 and 2009 with occasional occurrences of *Miliammina fusca*; and (3) *Trochammina hadai* dominant from 2010 on, with occasional occurrences of *Elphidium somaense* and *M. fusca*. Young individuals of *A.* “*beccarii*” forma 1 likely settled in the Honjo area in winters of both 2007/2008 and 2008/2009 as a result of widening and deepening of the southwestern channel. The young individuals seemed to grow in spring and summer, but likely died out toward fall, probably because of oxygen deficiency. The channel constructions, opening dikes isolating the Honjo area, in 2007–2008 and May 2009 could explain the dramatic changes in benthic foraminiferal fauna, especially the change in the dominant species from *A.* “*beccarii*” forma 1 to *T. hadai* through a shift in the provenance of the individuals supplied from Lake Nakaumi.

Key words: neritic benthic foraminifera, Honjo area of Lake Nakaumi, dispersal potential, artificial environmental changes

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Introduction

Benthic foraminifera (Rhizaria) are widely distributed in intertidal to deep-sea environments. Because their tests can be preserved in past sediments as fossils, faunal analysis of benthic foraminifera has been a useful approach for considering past environmental conditions. However, because ecological information about benthic foraminifera is still sparse, it is important to study modern benthic foraminifera for precise paleoenvironmental interpretation.

Recently, the dispersal potential of benthic foraminifera has been noted as an important area for study, particularly in neritic environments. Although there are some exceptions, most benthic foraminifera lack a planktonic juvenile stage (see Alve, 1999, and references therein), but propagules (tiny juveniles) are important for benthic foraminiferal ecology (Alve and Goldstein, 2003, 2010) because they may be dispersed long distances during several months of dormancy. Benthic foraminifera may therefore have significant dispersal potential through dispersal and reactivation of propagules. In addition, living (rose Bengal-stained) benthic foraminifera have been found in organic-matter aggregates suspended in the water column of Lake Nakaumi (southwestern Japan) (Nomura and Seto, 2004). Dispersal with organic-matter aggregates also seems plausible for benthic foraminifera.

It is usually difficult, however, to evaluate dispersal mechanisms of benthic foraminifera under natural conditions, including those involving reactivation of propagules, because it is difficult to distinguish new settlements of dispersed individuals from the extant population. For example, faunal transitions of living (stained) benthic foraminifera have been observed in the Honjo area of Lake Nakaumi, southwestern Japan. This lagoon has been modified artificially several times during the last century (Figs. 2 & 3 in Nomura, 2003). In particular, the Honjo area had been largely isolated from the main part of Lake Nakaumi since 1981 by several dikes (e.g., Nomura and Seto, 2002). Benthic foraminifera had almost disappeared in the Honjo area (Nomura and Seto, 2002). Recently (in the late 2000s), new channels were constructed in the southwestern and northeastern parts of the Honjo area, close to the Ohmisaki Dike and through the Moriyama Dike, respectively. As a result, exchange of lagoon waters has resumed between Lake Nakaumi and the Honjo area.

These circumstances make biological monitoring of modern benthic foraminifera in the Honjo area an ideal case study for learning the dispersal potential of neritic benthic foraminifera. In this paper, we report the faunal transition of living (stained) benthic foraminifera at one fixed station in the Honjo area every month from 2006 to 2011.

Study area, materials and methods

Lake Nakaumi is a brackish-water lagoon in southwestern Japan (Fig. 1) with an average water depth of 5.4 m. Its water inputs include oligohaline water, derived mainly from the Hii River and transported through the Ohashi River and Lake Shinji (Fig. 1), and seawater from the Sakai Channel. Its hypolimnion has a salinity of around 27 and experiences a decline in dissolved oxygen content in summer and fall. The lagoon substrate consists mainly of organic-rich muddy sediments (e.g., Sampei et al., 1997; Sakai et al., 2013). The “Honjo area” is located in the northwestern part of Lake Nakaumi (Fig. 1). This area had been separated from the main part of Lake Nakaumi since 1981 by several dikes, except for narrow channels at the southwestern and northern parts (e.g., Nomura and Seto, 2002). In 2007–2008, the southwestern channel near the Ohmisaki Dike was widened and excavated (Fig. 1), and then in May 2009 a new channel was opened through the Moriyama Dike. Nomura et al. (2013) studied the radium isotope ratio ($^{224}Ra/^{228}Ra$) of the lagoon waters in Lake Nakaumi and the Honjo area and reported the general seasonal variations. They recognized perturbation of the seasonal variations in this isotope ratio in the Honjo area, which reflected a new circulation pattern after the opening of the channel through the Moriyama Dike in May 2009.

Environmental profiles of the lagoon water at fixed station M-9 (133°31.53′N, 133°10.79′E, approx. 8 m water depth; Fig. 1) were recorded along with biological monitoring results (K. Seto, unpublished data). The temperature of the hypolimnetic water shows seasonal variations, ranging between 3 and 29 °C (Fig. 2), similar to those of mean air temperature recorded at Sakai Weather Station (approx. 8 km ENE of the Honjo area) (Japan Meteorological Agency: http://www.data.

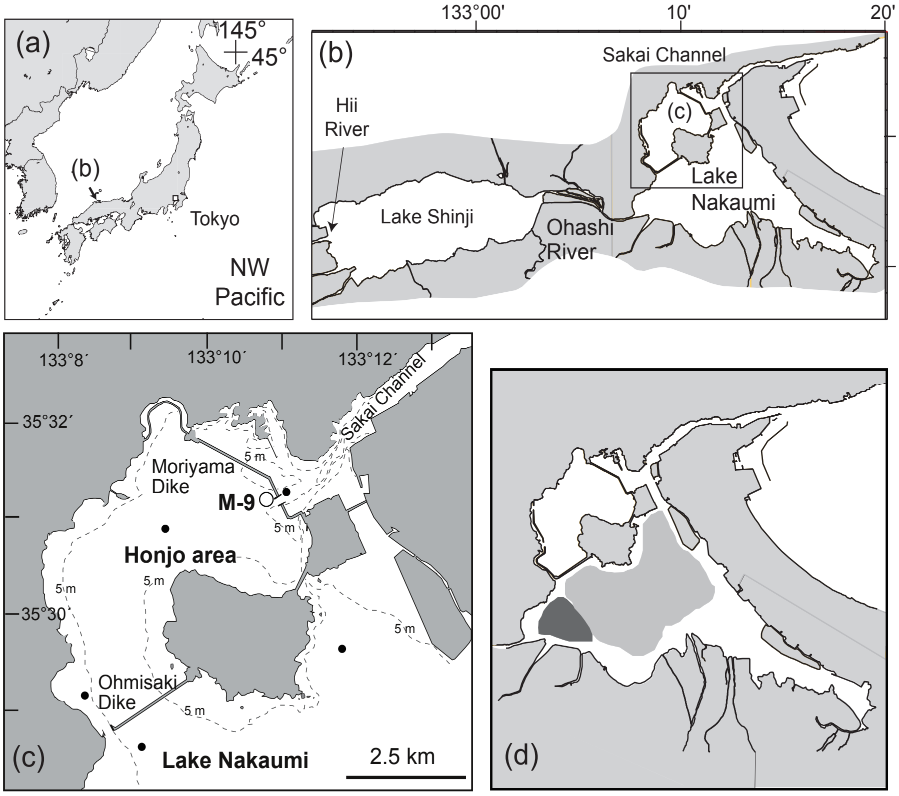

Fig. 1 (a) Locations of our study area, (b) Lake Shinji-Nakaumi system, (c) the Honjo area (modified from Nomura et al., 2015) and (d) recent distributions of *Ammonia* "*beccarii*" forma 1 and *Trochammina hadai* (referring from Nomura et al., 2013). Open and filled circles in (c) show station M-9 and other fixed stations in our study, respectively. Dark and light shading in (d) correspond to the areas of negatively and positively high factor loadings of the *Ammonia* "*beccarii*" assemblage and *Trocammina hadai* assemblage during the 1980s to 1996 in Nomura (2003), respectively.

jma.go.jp/gmd/risk/obsdl/index.php). In contrast, there were no obvious seasonal salinity variations of the hypolimnetic water, although the salinity increased markedly in May 2009 and remained elevated thereafter (Fig. 2). Dissolved oxygen content of the hypolimnetic water showed seasonal variations with lower values in summer and fall (Fig. 2), although the summer and fall values tended to increase beginning in 2009. Thus, there were obvious changes in salinity and dissolved oxygen in the hypolimnetic water at station M-9 beginning in May 2009 after the opening of the northeast channel through the Moriyama Dike.

We used an Ekman-Birge type sampler to collect a surface-sediment sample monthly from the lagoon floor at fixed station M-9 from May 2006 to May 2011. Four replicate meiobenthic (ostracod and foraminiferal) subsamples were taken from the uppermost 1 cm of the sediment surface using an acrylic tube (6-cm inner diameter). The four replicates were combined into a single sample (i.e., 113 cm^3 total volume).

The meiobenthic subsamples were washed through a 250-mesh sieve (62-µm openings). The residues were stained with rose Bengal solution (0.5 g l^{-1}) for 24 hours, after which they were washed with warm water to remove excess dye (Oda, 1978), and dried at 50 °C. Living (stained) foraminiferal specimens were collected from the residues and were identified under a stereo-binocular microscope. Samples from 5 December 2006, 30 January and 26 February 2007, 26 January and 19 February 2008, and 22 February 2009, were not analyzed in this study. Taxonomic assignments followed Matoba (1970) and Nomura and Seto (1992). Generic classification was based on Loeblich and Tappan (1987). The number of specimens per unit volume (# cm^{-3}) was calculated for

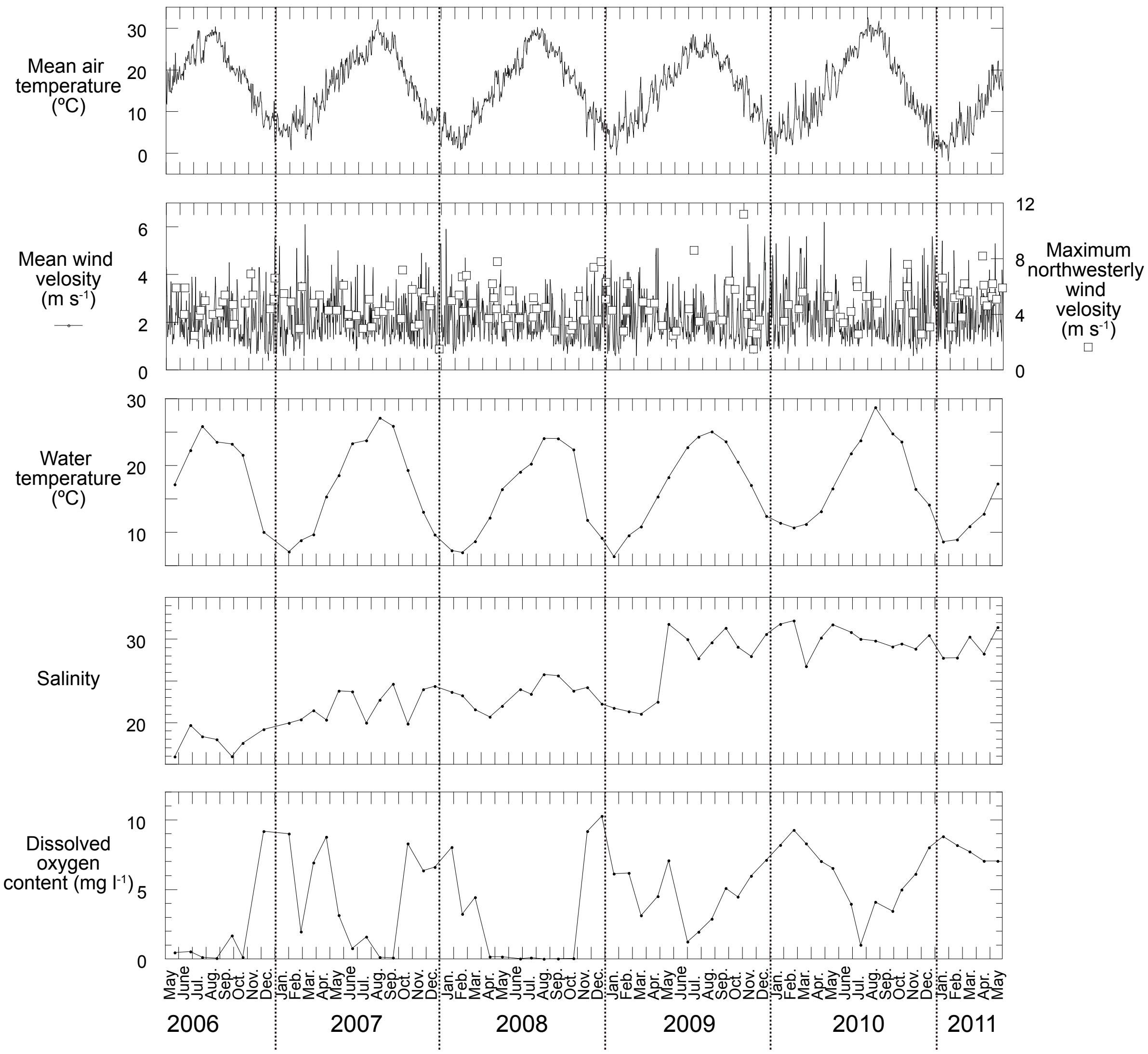

Fig. 2 Daily variations of mean air temperature and mean wind velocity with maximum northwesterly wind velocity at the Sakai Weather Station of the Japan Meteorological Agency (data referred from website of the Japan Meteorological Agency: http://www.data.jma.go.jp/gmd/risk/obsdl/index.php) and seasonal variations of water temperature, salinity and dissolved oxygen content of the hypolimnetic water at station M-9, the Honjo area, Lake Nakaumi.

each species in each sample. The test diameters of living (stained) *Ammonia* "*beccarii*" forma 1 were measured by using a micrometer under a stereo-binocular microscope. Because the foraminiferal tests were sometimes broken, we made separate tallies of perfect and broken tests during size measurements.

Results and discussion

Living (stained) benthic foraminifera were found in most of the samples during our study period. *Ammonia* "*beccarii*" (Linné) forma 1 and *Trochammina hadai* Uchio were common constituents (Fig. 3; Appendix). *Miliammina fusca* (Brady), *Elphidium somaense* Takayanagi and *Ammonia* "*beccarii*" (Linné) forma 2 occurred sporadically at lower numbers during our study interval (Fig. 3; Appendix). All of these species have been commonly reported from Lake Nakaumi and the Sakai Channel (Nomura and Seto, 1992, 2002).

Ammonia "*beccarii*" forma 1 was found almost continuously throughout the study interval (Fig. 4). The occurrence of this species was very low and sporadic

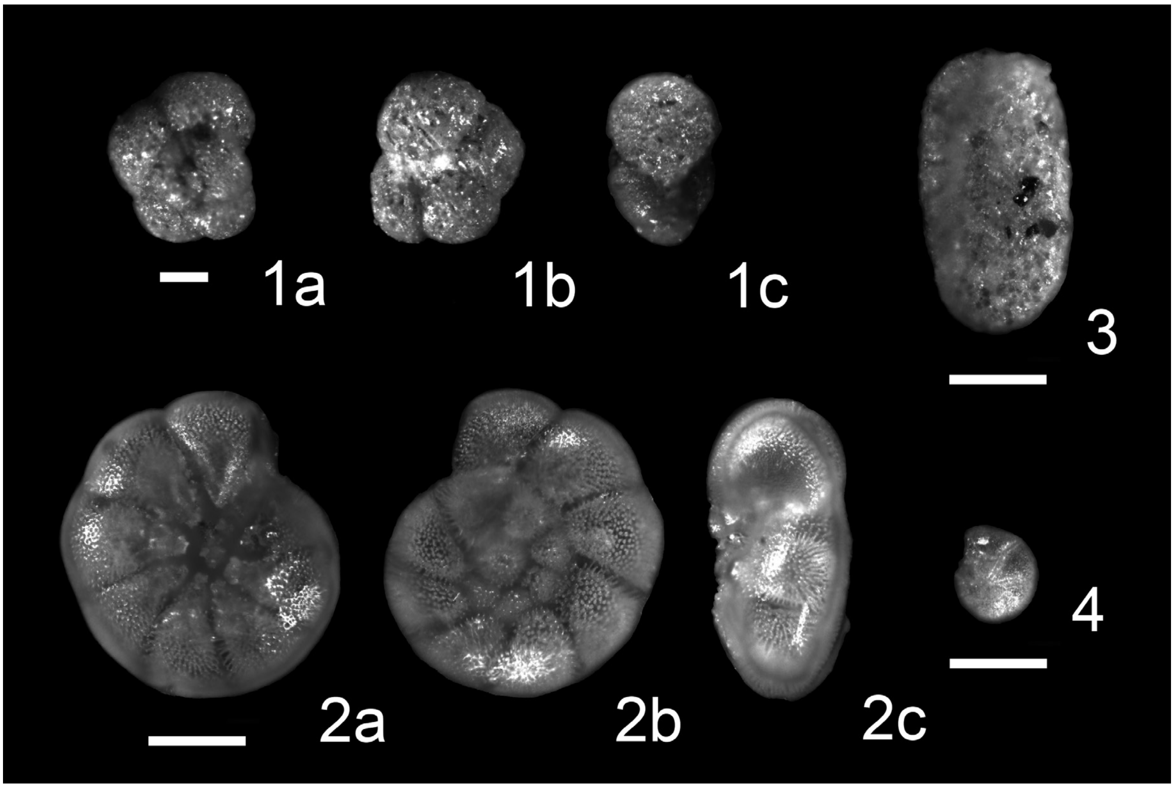

Fig. 3 Light micrographs of benthic foraminifera in the Honjo area, Lake Nakaumi, southwestern Japan. 1a–c. *Trochammina hadai* Uchio; 2a–c. *Ammonia* "*beccarii*" (Linné) forma 1; 3. *Miliammina fusca* (Brady); 4. *Elphidium somaense* Takayanagi. Scale bars = 100 μm.

until November 2007, in agreement with earlier studies by Nomura and Seto (2002) and Nomura (2003), and then it became dominant at station M-9, especially in 2008 and 2009. In addition, the abundance of this species decreased toward fall both in 2008 and 2009 (Fig. 4). In contrast, *T. hadai* became dominant beginning in 2010 (Fig. 4). *Miliammina fusca* was continuously found in the 2008/2009 winter, whereas *E. somaense* was continuously present in the 2009/2010 winter. Thus, the faunal transition of living (stained) benthic foraminifera at station M-9 was as follows: (1) few and sporadic occurrences of benthic foraminifera prior to November 2007, (2) dominant *A.* "*beccarii*" forma 1 during 2008 and 2009 with sporadic occurrences of *M. fusca*, and (3) dominant *T. hadai* from 2010 on with sporadic occurrences of *E. somaense* and *M. fusca*.

There were seasonal variations in the size distribution of living (stained) *A.* "*beccarii*" forma 1 (Fig. 5). Small individuals (<240 μm) were commonly found in December 2007 and March 2008, from December 2008 to March 2009, and in May 2009. In contrast, the number of larger individuals (300–480 μm) increased in May and June 2008, and March and April 2009, decreasing in number within a half year. This pattern is consistent with the trend of decreasing abundance of this species toward fall (Fig. 4). In contrast, the medium-sized individuals (240–300 μm) were continuously common from July to November 2009. Despite the generally low abundance of small individuals in 2010 and 2011, they were common in March 2011.

Based on the abundance and size distribution of living *A.* "*beccarii*" forma 1, we suggest that young individuals of this species settled at station M-9 in the winters of both 2007/2008 and 2008/2009. The young individuals seemed to grow during the following spring and summer seasons, but it is highly probable that the population died out from summer to fall, based on the decreasing abundance (Fig. 4). Hypolimnetic water at station M-9 showed low dissolved oxygen in summer and fall, especially in 2007 and 2008 (Fig. 2). Seasonal oxygen deficiency strongly affects the life history of brackish/shallow-marine benthic foraminifera (e.g., Matsushita

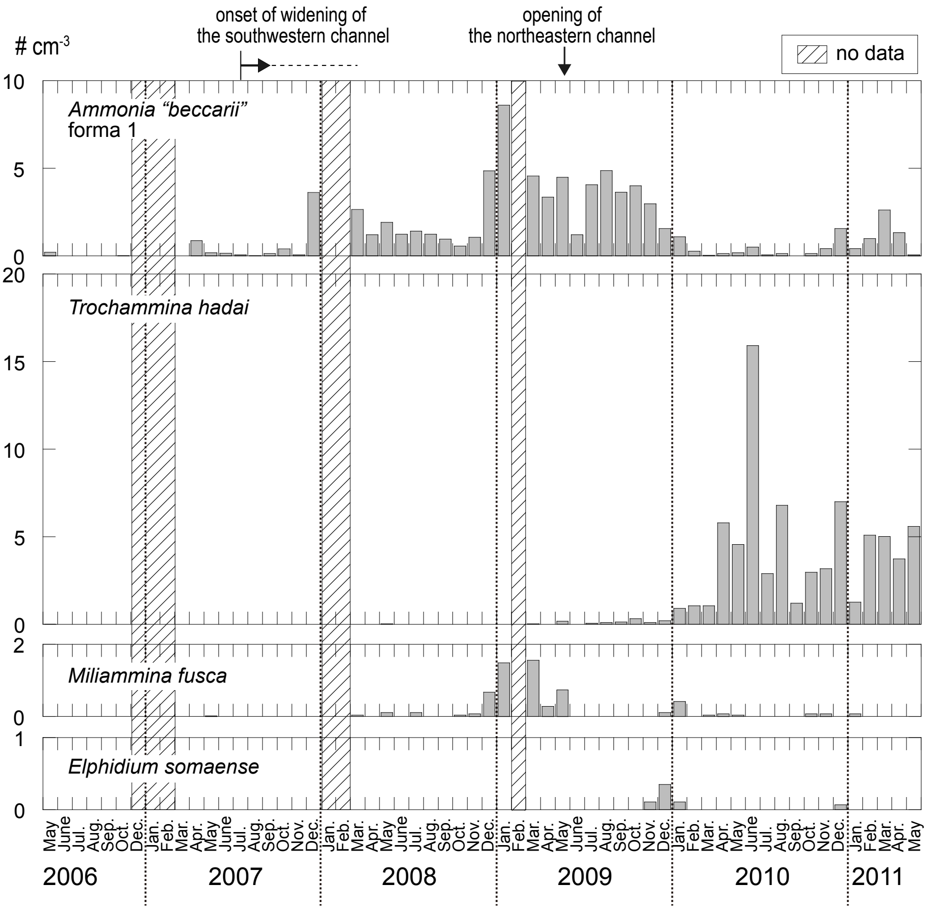

Fig. 4 Seasonal variation of the abundance of selected four benthic foraminifera at station M-9, the Honjo area, Lake Nakaumi.

and Kitazato, 1990). It is reasonable to suppose that the decreasing abundance of *A.* "*beccarii*" forma 1 at station M-9 was affected by the seasonal oxygen deficiency in summer and fall.

Nomura and Seto (2004) reported living (stained) *A.* "*beccarii*" forma 1 and *T. hadai* associated with organic matter aggregates in plankton-tow samples from Lake Nakaumi. In 2010, *A.* "*beccarii*" forma 1 became substantially less abundant compared to the preceding two years. Instead, *T. hadai* became dominant at station M-9. These observations imply that the population of *A.* "*beccarii*" forma 1 was largely maintained by the dispersal of young individuals from other areas rather than by in situ reproduction in the Honjo area during our study period.

In Lake Nakaumi, the channel in the southwestern part of the Honjo area (around the Ohmisaki Dike) was widened and excavated by construction in 2007–2008, whereas another new channel was opened in the northeast part (through the Moriyama Dike) in May 2009. As a result, the circulation pattern of the lagoon water in the Honjo area was also altered, as shown in our water-profile data (Fig. 2). In general, *A.* "*beccarii*" forma 1 had occupied western Lake Nakaumi whereas *T. hadai* had occupied the eastern part (Nomura, 2003; Fig. 1). The widening and deepening of the southwest channel in 2007–2008 can probably explain the dispersal of *A.* "*beccarii*" forma 1 from western Lake Nakaumi and its abundant settlement at station M-9 (Figs. 4 & 5). In addition, *M. fusca* was also found at station M-9 from the 2007 summer with *A.* "*beccarii*" forma 1. Because this species was reported as a tolerant species to oligohaline water in the Lake Shinji-Nakaumi system (Seto et al., 2000), it is reasonable to suppose that *M. fusca* also migrated through the southwest channel.

The northeast channel, in contrast, was opened in May

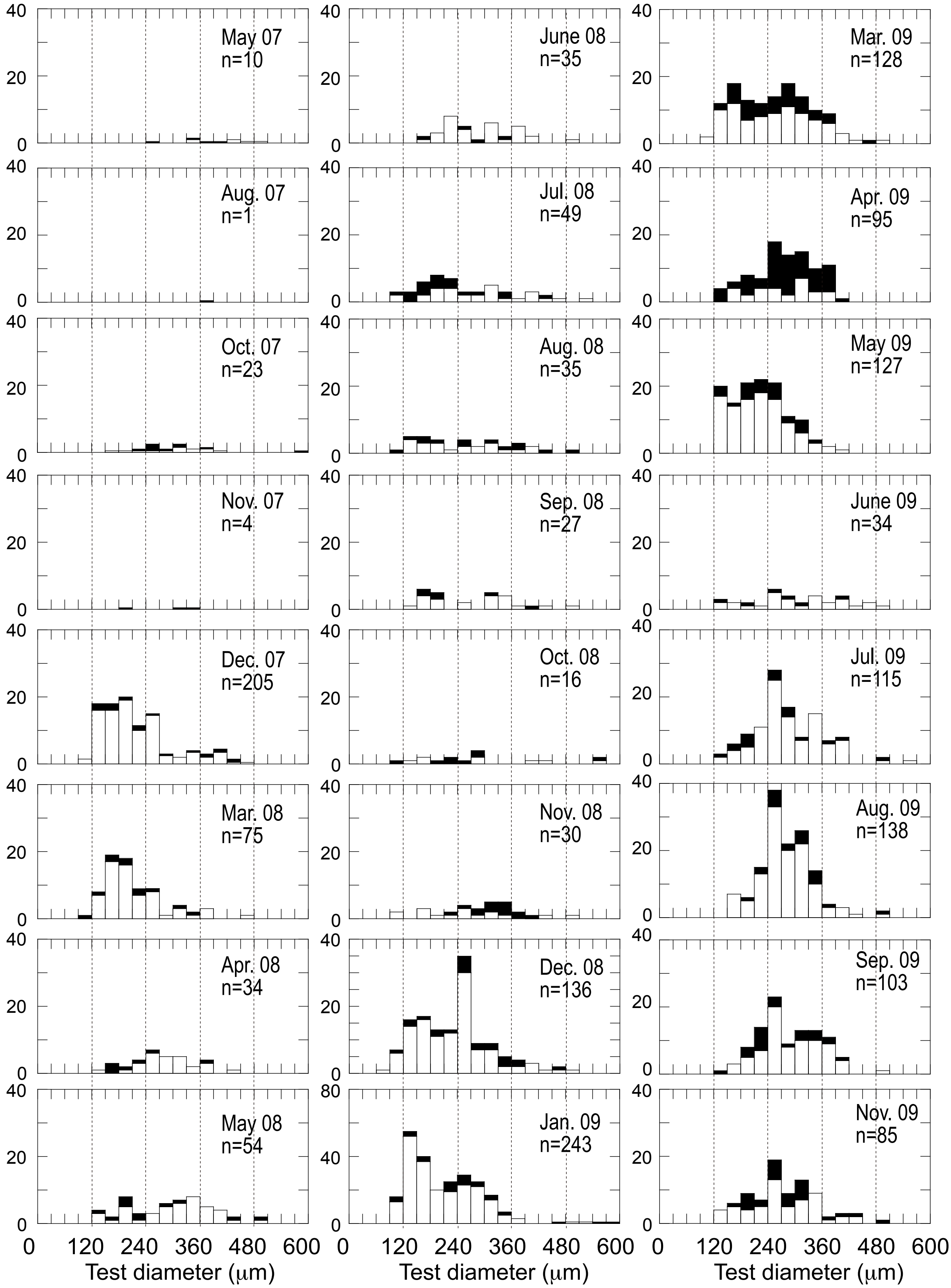

Fig. 5 Seasonal variations of the size distribution of living (stained) *Ammonia* "*beccarii*" forma 1 at station M-9, the Honjo area, Lake Nakaumi. The perfect (unbroken) and broken tests were shown using open and filled boxes, respectively.

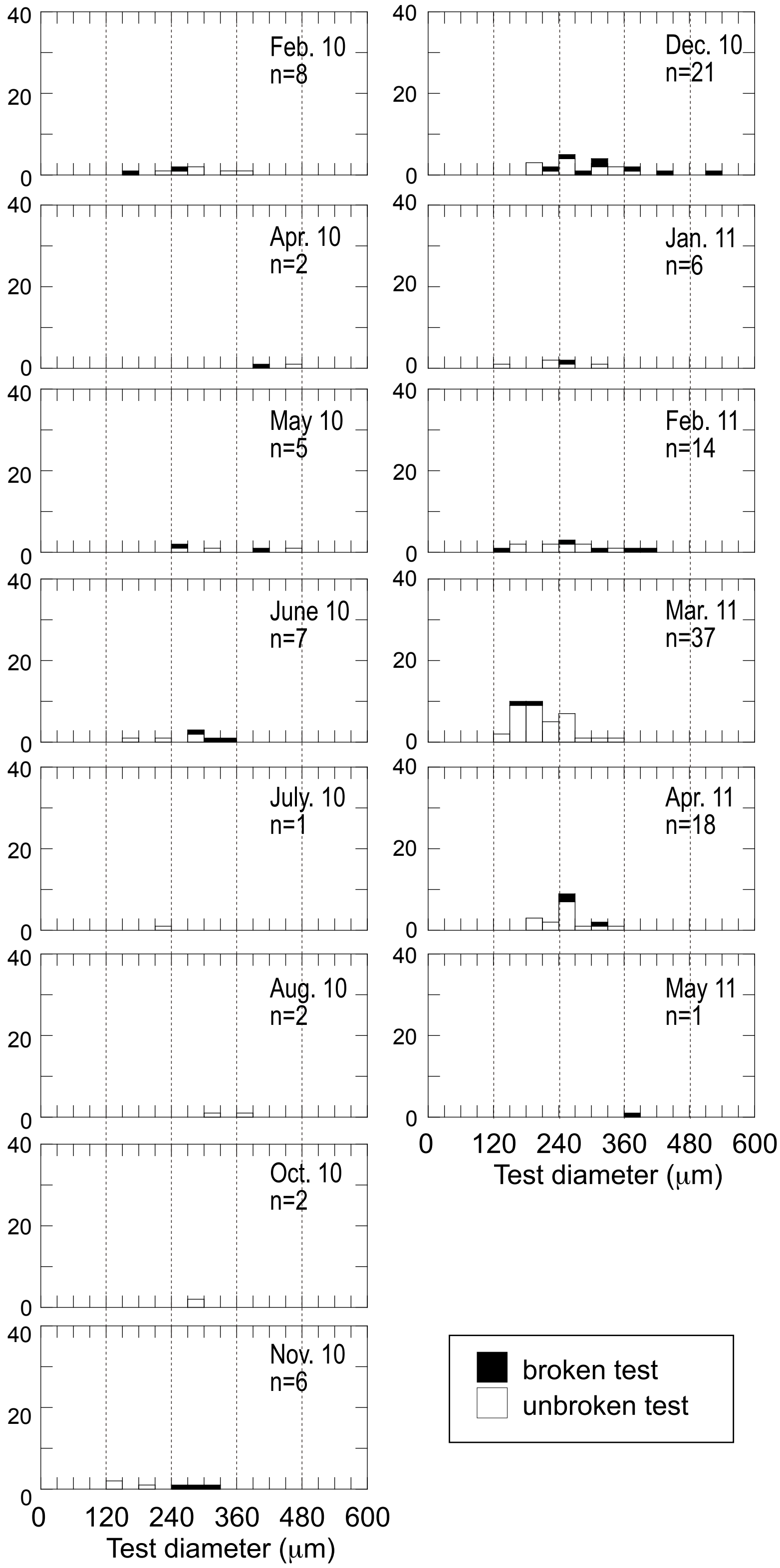

Fig. 5 Continued.

2009, prior to the increase of *T. hadai* at station M-9 beginning in early 2010 (Fig. 4). Radium isotope data ($^{224}Ra/^{228}Ra$) of the lagoon waters in 2011 indicated a westward inflow of the hypolimnetic water from Lake Nakaumi into the Honjo area through the northeast channel (Nomura et al., 2015). Although a detailed discussion of foraminiferal transitions should include the possible influence of other environmental factors, it is reasonable to suppose that the opening of the northeast channel led to the dominance of *T. hadai*, which probably migrated from eastern Lake Nakaumi through this channel. In addition, *E. somaense* is commonly found in the Sakai Channel (Nomura and Seto, 1992), and its first appearance at station M-9 (Fig. 4) in the 2009/2010 winter supports the dispersal of benthic foraminifera from eastern Lake Nakaumi to the Honjo area through the northeast channel after its opening. Thus, the construction of the two channels could explain the faunal transition of benthic foraminifera in our study, especially the change of the dominant species from *A.* "*beccarii*" forma 1 to *T. hadai*, through a shift of the provenance of the individuals supplied from Lake Nakaumi. This scenario also would explain marked decreasing in 2009 and the subsequent few occurrences of *A.* "*beccarii*" forma 1 at station M-9, in spite of improvement of the oxygen deficiency in summer and fall (Fig. 2).

In the 2007/2008 and 2008/2009 winters, *A.* "*beccarii*" forma 1 was abundant and *M. fusca* was common (Fig. 4). In addition, *E. somaense* was present in the 2009/2010 winter (Fig. 4). In particular, occurrences of *M. fusca* and *E. somaense* were common just after periods of relatively strong northwesterly winds (Japan Meteorological Agency: http://www.data.jma.go.jp/gmd/risk/obsdl/index.php) in December 2008 (7.4 and 7.8 m s^{-1}) and November 2009 (11.2 m s^{-1}), respectively (Figs. 2 & 4). The dispersal of these three species in winter might be stimulated by water-column mixing associated with the seasonal northwesterly winds of the East Asian winter monsoon. Suzuki et al. (2019) reported a positive relationship between the abundance of temperate sea bass (*Lateplabrax japonicus*) in Tango Bay, central Japan, and the intensity of the northwesterly winds of the East Asian winter monsoon, through the dispersal of eggs and juveniles. Takata et al. (2019) also suggested that the intensified seasonal northwesterly winds associated with the East Asian winter monsoon might have an important role in the dispersal of some benthic foraminifera in Maizuru Bay, central Japan. Thus, water-column mixing due to the intense seasonal northwesterly winds in winter might also be important dispersal mechanism of benthic foraminifera in Lake Nakaumi in general and in the Honjo area specifically.

Alve (1999) discussed the colonization processes of benthic foraminifera. Subsequently, Weinmann (2018) proposed two classes of possible dispersal mechanisms for benthic foraminifera: (1) propagule dispersal and (2) passive dispersal. These two mechanisms were also described by Alve (1999), as the "release and transport of embryonic juveniles" and the "passive suspension and transport of various growth stages," respectively. Takata et al. (2019) stressed the importance of passive dispersal of benthic foraminifera on floating of organic matter aggregates in Lake Nakaumi, referring to Nomura and Seto (2004) and Nomura et al. (2010). Further biological monitoring of benthic foraminifera and observations of meiobenthic samples from other fixed stations during the same period in Lake Nakaumi and the Honjo area would provide a useful opportunity for studying the dispersal mechanisms of neritic benthic foraminifera under natural conditions. In addition, our results for benthic foraminifera, in combination with those for the macrobenthos and ostracods (e.g., Kurata et al., 2018), will be useful for further understanding of biological monitoring results in Lake Nakaumi and the Honjo area.

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Appedix Occurrences of living (stained) benthic foraminifera at statin M-9, the Honjo area, Lake Nakaumi; shaded samples were not observed in this study; “split” shows the number of splitting of the samples for our observation.

Year	2006						
Date	May, 22	Jun, 26	Jul, 22	Aug, 23	Sep, 26	Oct, 20	Dec, 5
Ammobaculites exiguus							
Lagenammina sp.							
Miliammina fusca							
Textularia earlandi							
Trochammina hadai	1						
Trochammina pacifica							
Quinqueloculia lamarckiana							
Miliolinella circularis							
Cyclogyra planorbis							
Ammonia "beccarii" forma 1	24					1	
Ammonia "beccarii" forma 2							
Ammonia sp. A							
Buliminella elegantissima							
Elphidium somaense							
Rosalina cf. *bradyi*							
Total	25	0	0	0	0	1	-
Split	1	2	1	1	1	1	-

Year	2007											
Date	Jan, 30	Feb, 26	Mar, 26	Apr, 23	May, 21	Jun, 20	Jul, 21	Aug, 20	Sep, 18	Oct, 21	Nov, 24	Dec, 20
Ammobaculites exiguus												
Lagenammina sp.												
Miliammina fusca					1							
Textularia earlandi												
Trochammina hadai												
Trochammina pacifica												
Quinqueloculia lamarckiana												
Miliolinella circularis												
Cyclogyra planorbis												
Ammonia "beccarii" forma 1				25	10	17	8	1	15	23	4	205
Ammonia "beccarii" forma 2												
Ammonia sp. A												
Buliminella elegantissima												
Elphidium somaense												
Rosalina cf. *bradyi*												
Total	-	-	0	25	11	17	8	1	15	23	4	205
Split	-	-	2	4	2	1	1	2	1	2	2	2

Year	2008											
Date	Jan, 26	Feb, 19	Mar, 18	Apr, 20	May, 17	Jun, 26	Jul, 20	Aug, 17	Sep, 18	Oct, 22	Nov, 22	Dec, 24
Ammobaculites exiguus												
Lagenammina sp.												
Miliammina fusca			1		3		3			1	2	19
Textularia earlandi												
Trochammina hadai					1							
Trochammina pacifica												
Quinqueloculia lamarckiana												
Miliolinella circularis												
Cyclogyra planorbis												
Ammonia "beccarii" forma 1			75	34	54	35	40	35	27	16	30	137
Ammonia "beccarii" forma 2												
Ammonia sp. A												
Buliminella elegantissima												
Elphidium somaense												
Rosalina cf. *bradyi*												
Total	-	-	76	34	58	35	43	35	27	17	32	156
Split	-	-	4	4	4	4	4	4	4	4	4	4

Appedix Continued.

Year	2009											
Date	Jan, 20	Feb, 22	Mar, 21	Apr, 27	May, 21	Jul, 2	Jul, 27	Aug, 25	Sep, 25	Oct, 22	Nov, 20	Dec, 24
Ammobaculites exiguus												
Lagenammina sp.									1			
Miliammina fusca	42		44	8	21							3
Textularia earlandi											1	
Trochammina hadai			1		5		2	3	4	9	3	6
Trochammina pacifica												
Quinqueloculia lamarckiana												
Miliolinella circularis												3
Cyclogyra planorbis												
Ammonia "beccarii" forma 1	243		129	95	127	34	115	138	103	113	84	44
Ammonia "beccarii" forma 2												8
Ammonia sp. A									1		2	
Buliminella elegantissima											1	1
Elphidium somaense											3	10
Rosalina cf. *bradyi*												
Total	285	-	174	103	153	34	117	141	109	122	94	75
Split	4	-	4	4	4	4	4	4	4	4	4	4

Year	2010											
Date	Jan, 24	Feb, 23	Mar, 22	Apr, 24	May, 20	Jun, 30	Jul, 21	Aug, 23	Sep, 30	Oct, 20	Nov, 20	Dec, 20
Ammobaculites exiguus												1
Lagenammina sp.												2
Miliammina fusca	12		1	1	1					1	1	
Textularia earlandi		1				1		2				
Trochammina hadai	26	30	30	82	129	225	41	96	17	42	45	99
Trochammina pacifica				1								
Quinqueloculia lamarckiana								3				
Miliolinella circularis	3											
Cyclogyra planorbis					1							
Ammonia "beccarii" forma 1	31	8	1	2	5	7	1	2		2	6	22
Ammonia "beccarii" forma 2	5		1		1							1
Ammonia sp. A		1								1	1	
Buliminella elegantissima												
Elphidium somaense	3											1
Rosalina cf. *bradyi*								1			1	
Total	80	40	33	86	137	233	42	104	17	46	54	126
Split	4	4	4	8	4	8	8	8	8	8	8	8

Year	2011				
Date	Jan, 20	Feb, 20	Mar, 20	Apr, 20	May, 21
Ammobaculites exiguus					
Lagenammina sp.				1	
Miliammina fusca	1				
Textularia earlandi					
Trochammina hadai	18	72	71	53	79
Trochammina pacifica					
Quinqueloculia lamarckiana					
Miliolinella circularis					
Cyclogyra planorbis					
Ammonia "beccarii" forma 1	6	14	37	19	1
Ammonia "beccarii" forma 2					
Ammonia sp. A					
Buliminella elegantissima					
Elphidium somaense					
Rosalina cf. *bradyi*					
Total	25	86	108	73	80
Split	8	8	8	8	8