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Response of deep-sea benthic foraminifera to paleoproductivity changes on the Shatsky Rise in the northwestern Pacific Ocean over the last 187 kyr

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Abstract. We studied the deep-sea benthic foraminiferal fauna from core NGC108 (36°36.85′N, 158°20.90′E; 645 cm long, recovered from 3,390 m water depth) collected from the Shatsky Rise in the central northwestern Pacific Ocean, to determine the relationship between benthic foraminifera and paleoproductivity in the transitional zone between the subtropical Kuroshio Extension and the subarctic current over the last 187 kyr. *Cassidulina reniforme*, *Eilohedra levicula*, and *Epistominella exigua* were the most abundant species. The relative abundance of *C. reniforme* was positively correlated with biogenic opal and organic carbon contents, which are proxies for paleoproductivity. The relative abundance of *E. exigua* was negatively correlated with biogenic opal and organic carbon contents, and the relative abundance of *E. levicula* had no correlation with biogenic opal and organic carbon contents. We conclude that *C. reniforme* and *E. exigua* are indicative of high and low productivity, respectively. The high relative abundances of *C. reniforme* reflect high paleoproductivity during glacial periods [oxygen isotope stages (OISs) 6, 3, and 2], indicating a southward advance of the Subarctic Front during global cooling. The high relative abundances of *E. exigua* reflect low paleoproductivity during the interglacial and postglacial periods (OISs 5 and 1). Faunal changes in the deep-sea benthic foraminifera on the Shatsky Rise suggest a direct response to orbital-scale paleoproductivity changes.

Key words: benthic foraminifera, late Quaternary, northwestern Pacific Ocean, paleoproductivity, Shatsky Rise

Introduction

The abundance of deep-sea foraminifera, as reflected by both the biomass of living populations and the accumulation rate of dead tests, is closely related to the flux of organic matter to the sea floor (e.g. Corliss and Emerson, 1990; Thomas *et al.*, 1995; Thomas and Gooday, 1996). In addition, organic carbon flux to the sea floor has a strong influence on the taxonomic composition of modern deep-sea foraminifera (Gooday, 1993, 2003; Jorissen *et al.*, 2007; Fontanier *et al.*, 2002, 2003, 2008; Duros *et al.*, 2012). In intermediate water depths in upwelling regions and semi-closed basins, such as the Santa Barbara Basin, depletion of dissolved oxygen is the most important factor controlling benthic foraminiferal distribution (Cannariato and Kennett, 1999; Caulle *et al.*, 2014; Abu-Zied *et al.*, 2008; Moffitt *et al.*, 2015). In contrast, oxygen levels in deep waters are increased by both the effects of ventilation of oxic deep-water masses and the poor respiration activity of organisms due to a restricted supply of organic matter settling from the ocean surface. Thus, deep-sea benthic foraminifera are mainly limited by food supply. Faunal changes in benthic foraminifera would be closely related to changes in surface paleoproductivity in oligotrophic and mesotrophic environments. However, the relationship between paleoproductivity and faunal changes remains poorly understood for the Pacific Ocean during the Quaternary (Ohkushi *et al.*, 2000; Ujiié, 2003). Deep-sea benthic foraminifera are valuable for investigating the biotic response to climate change because of their high fossilization potential and their presence in the same cores and samples that are used to infer changes in climate, allowing for direct comparisons (Yasuhara *et al.*, 2012, 2017).

The Shatsky Rise, which is located about 1,600 km east of Japan, is centered in the middle latitudes of the northwestern Pacific Ocean (Figures 1, 2). It is an important area for reconstructing biological productivity changes

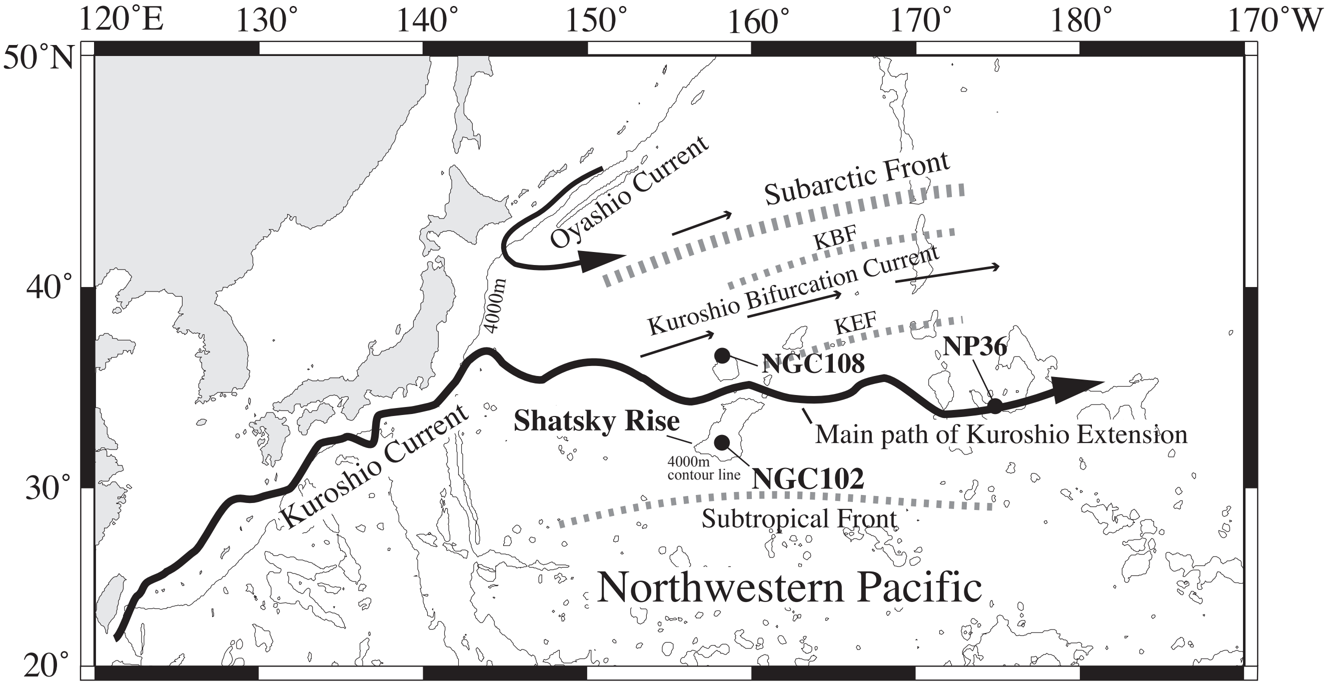

Figure 1. Location map of the sampling site of core NGC108 in the northwestern Pacific Ocean. The sampling site locations of cores NGC102 and NP36 referred to in this study are also shown. The position of the main path of the Kuroshio Extension is based on Mizuno and White (1983). The positions of the Subarctic Front, the Kuroshio Bifurcation Front (KBF) and the Kuroshio Extension Front (KEF) are based on Zhang and Hanawa (1993).

related to the latitudinal migration of water mass fronts between subarctic and subtropical waters during the late Quaternary. The Subarctic Front consists of the water mass between the subtropical (Kuroshio Extension) and subarctic waters and is centered near 41°N–43.5°N (Kawahata, 2002; Kawahata *et al.*, 1998). The subarctic water mass shows higher primary productivity than the subtropical water mass, with higher biogenic opal flux in the sinking particles (Kawahata, 2002; Kawahata *et al.*, 1998). In contrast, the subtropical water mass is characterized by oligotrophic conditions, which include low primary productivity due to the permanent thermocline in the surface water. The southward advance of the Subarctic Front in this region during glacial periods increased paleoproductivity compared with interglacial periods (Kawahata *et al.*, 1999, 2000, 2002; Maeda *et al.*, 2002).

Changes in climate have resulted in shifts in the position of the Subarctic Front (Thompson and Shackleton, 1980; Thompson, 1981; Kawahata *et al.*, 2000). Increases in the relative abundances of subarctic water species, such as the planktonic foraminiferan *Neogloboquadrina pachyderma*, indicated that the Subarctic Front migrated southward during oxygen isotope stages (OISs) 2 and 6, and that it reached latitudes of 32°N–35°N during OIS 6 (Thompson and Shackleton, 1980). Total organic carbon and biogenic opal contents in a southern site (core NGC102; Figure 1) and a northern site (core NGC108) in the Shatsky Rise suggest increased paleoproductivity during the glacial periods (Kawahata *et al.,* 1999; Maeda *et al.*, 2002). The surface water at core site NGC108 seems to have been more influenced by subarctic water over time, whereas core site NGC102 was more affected by subtropical water. The transition zone between the subarctic and subtropical waters was narrower in latitude at the OIS 2/3 boundary and during OISs 4 and 6. Ohkushi *et al.* (2000) documented glacial–interglacial changes in the benthic foraminiferal fauna in core NGC102 over the last 298 kyr. They concluded that fluctuations in the dominant species reflected changes in surface productivity related to the latitudinal shift of the Subarctic Front, and that assemblages dominated by the phytodetritus-feeding species *Epistominella exigua* increased during some interglacial periods. Similar foraminiferal results over the last 370 kyr were obtained from core NP36 (34°11′N, 179°15′E, recovered from 2,664 m water depth; Figure 1) from the Hess Rise (Ujiié, 2003).

Modern Atlantic foraminiferal studies (e.g. Sun *et al.*, 2006) have suggested that the cosmopolitan deep-water species *Epistominella exigua* is an indicator of the seasonality of phytodetritus flux settling from the surface water

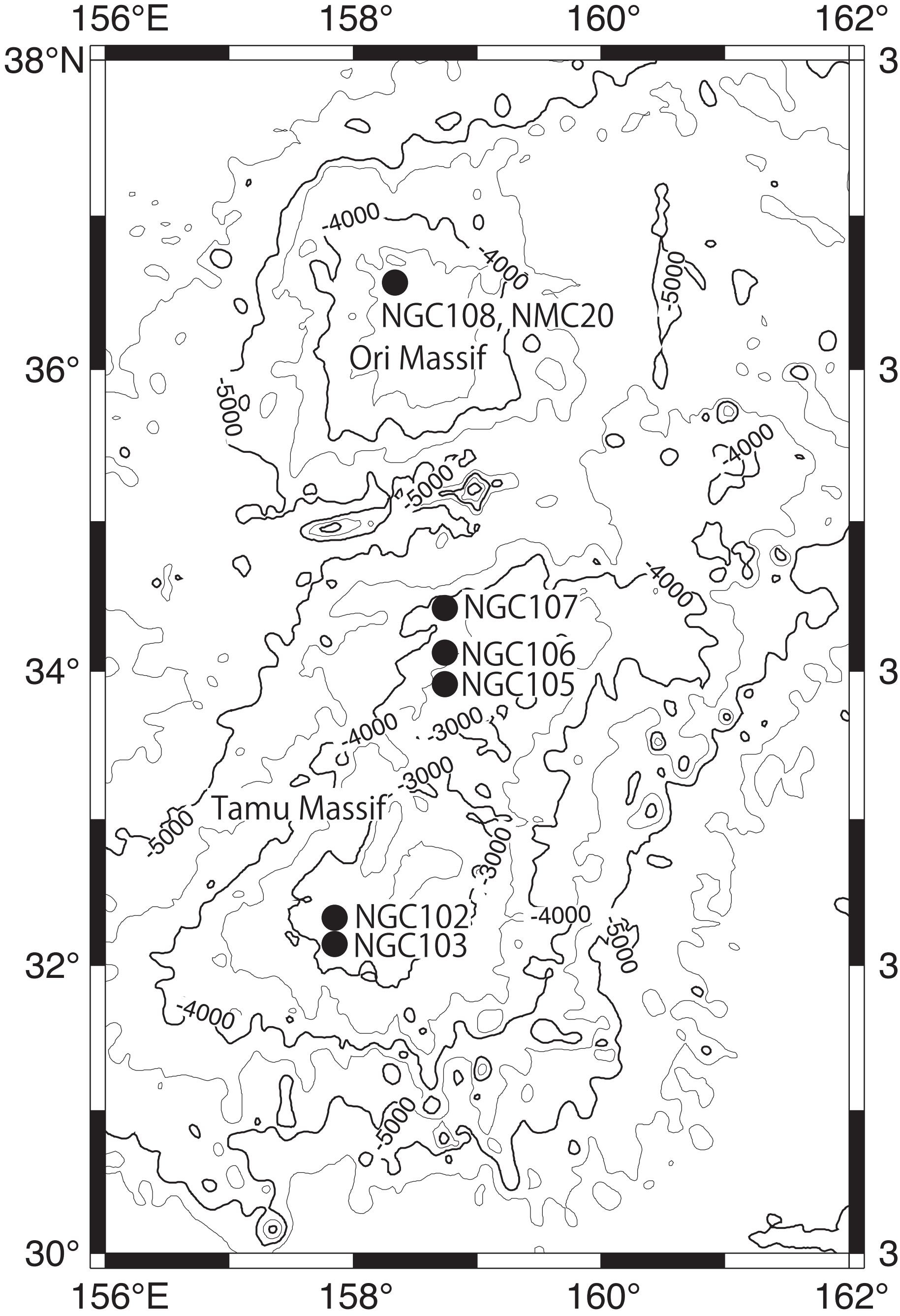

Figure 2. Location map of the surface sediment samples for the modern benthic foraminifera studied in the Shatsky Rise.

to the deep-sea floor; this species is abundant between 30°N and ~60°N and is associated with relatively high primary productivity. In contrast, fossil data from a southern site (core NGC102) in the Shatsky Rise suggested that this species may be associated with reduced productivity (Ohkushi *et al*., 2000). Thus, the paleoceanographic interpretations of the presence and abundance of this species are still inconsistent between the Pacific and Atlantic oceans. Detailed data for the spatio-temporal structure of cosmopolitan deep-sea foraminifera, as well as productivity data in global ocean basins, will be needed to resolve this issue.

It is difficult to obtain sediment cores suitable for assessing faunal changes in deep-sea benthic foramin-

Table 1. Locations of the surface sediment samples for the modern benthic foraminifera studied in the Shatsky Rise. PC, pilot corer; MC, mutiple corer.

Sample no.	Latitude	Longitude	Water depth (m)	Instrument	Description
NGC102	32°19.84′N	157°51.00′E	2,612	PC	calcareous nannofossil ooze
NGC103	32°08.86′N	157°50.80′E	2,743	PC	calcareous nannofossil ooze
NGC105	33°56.63′N	158°45.40′E	3,382	PC	siliceous rich calcareous nannofossil ooze
NGC106	34°09.93′N	158°45.10′E	3,713	PC	siliceous rich calcareous nannofossil ooze
NGC107	34°28.41′N	158°44.90′E	4,117	PC	siliceous rich calcareous nannofossil ooze
NGC108	36°36.85′N	158°20.90′E	3,390	PC	siliceous rich calcareous nannofossil ooze
NMC20	36°36.87′N	158°21.00′E	3,392	MC	siliceous rich calcareous nannofossil ooze

ifera because of the poor preservation of calcareous fossils, especially in the carbonate-corrosive abyssal plain of the North Pacific Ocean. The Shatsky Rise is an oceanic plateau elevated 5–6 km above the vast abyssal plain of the central North Pacific and in consequence this makes the collection of rare carbonate sediments from abyssal depths possible. Thus, the Shatsky Rise provides a rare opportunity for insight into the survival history of calcareous foraminiferal fauna in a remote abyssal site located far from other habitable areas that are shallower than the carbonate compensation depth (CCD) of around 4 km.

We studied the late Quaternary deep-sea benthic foraminiferal records from core NGC108 (recovered from 3,390 m water depth) sampled from the northern site in the Shatsky Rise. The main purpose of this study was to describe the characteristics of the abyssal foraminiferal fauna from the deepest site in the Shatsky Rise, which is about 800 m deeper and shows relatively higher primary productivity than that of an earlier core, NGC102 (recovered from 2,612 m water depth; Ohkushi *et al*., 2000). In addition, we discussed the relationships among the three most abundant species (*Cassidulina reniforme*, *Eilohedra levicula*, and *Epistominella exigua*) in this core and determined the paleoproductivity.

Oceanographic setting

In the modern North Pacific, the deep bottom waters, which are characterized by highly uniform properties and sourced from other basins, are located below 2,500 m depth (Pickard and Emery, 1990). Based on GEOSECS data (Craig *et al*., 1981), the dissolved oxygen content in the North Pacific is about 130–150 μmol l^{-1} at 3 km depth, the temperature is 1.5°C, and salinity is about 34.7 psu. According to Berger *et al*. (1987), modern annual primary productivity is approximately 35–60 gC m^{-2} yr^{-1} around the Shatsky Rise. Based on the amounts of organic carbon in core NGC108, Maeda *et al.* (2002) estimated that paleoproductivity varied from 57 to 100 gC m^{-2} yr^{-1} over the last 180 kyr.

Material and methods

Core sample

Core NGC108 (36°36.85′N, 158°20.90′E; 645 cm long, recovered from 3,390 m water depth) was collected from the northwestern plateau (Ori Massif) of the Shatsky Rise (Figures 1, 2; Table 1) using a gravity corer during the R/V *Hakurei-maru* cruise NH95-1 as part of the Northwest Pacific Carbon Cycle Study (NOPACCS) program. This sediment core is mainly composed of gray to olive gray silica-rich calcareous nannofossil ooze. The planktonic foraminiferal δ^{18}O, organic carbon, biogenic opal, and inorganic element data for the core were previously reported by Maeda *et al.* (2002) (Figure 3). We established the stratigraphic framework for core NGC108 based on the δ^{18}O record of the planktonic foraminiferan *Globorotalia inflata*. A total of 86 samples (2-cm slices) were taken for δ^{18}O analysis at approximately 8-cm intervals, for an average sample temporal interval of around 2.3 kyr (Maeda *et al*., 2002). OIS determination and the subsequent conversion into numerical ages followed the global benthic LR04 stack curve (Lisiecki and Raymo, 2005) time scale. The record of this core extends back to 187.6 ka, in OIS 6 (Figure 3, Table 2). Moreover, the age model in the upper 50 cm of the core was established based on the radiocarbon ages of the planktonic foraminifera (Ohkushi *et al*., 2017) (Table 3). The radiocarbon ages were calibrated using CALIB 7.1 (Stuiver *et al*., 2017). ΔR (116 ± 79) was calculated from reservoir values reported from the middle latitude northwestern Pacific margin in the Marine Reservoir Correction Database

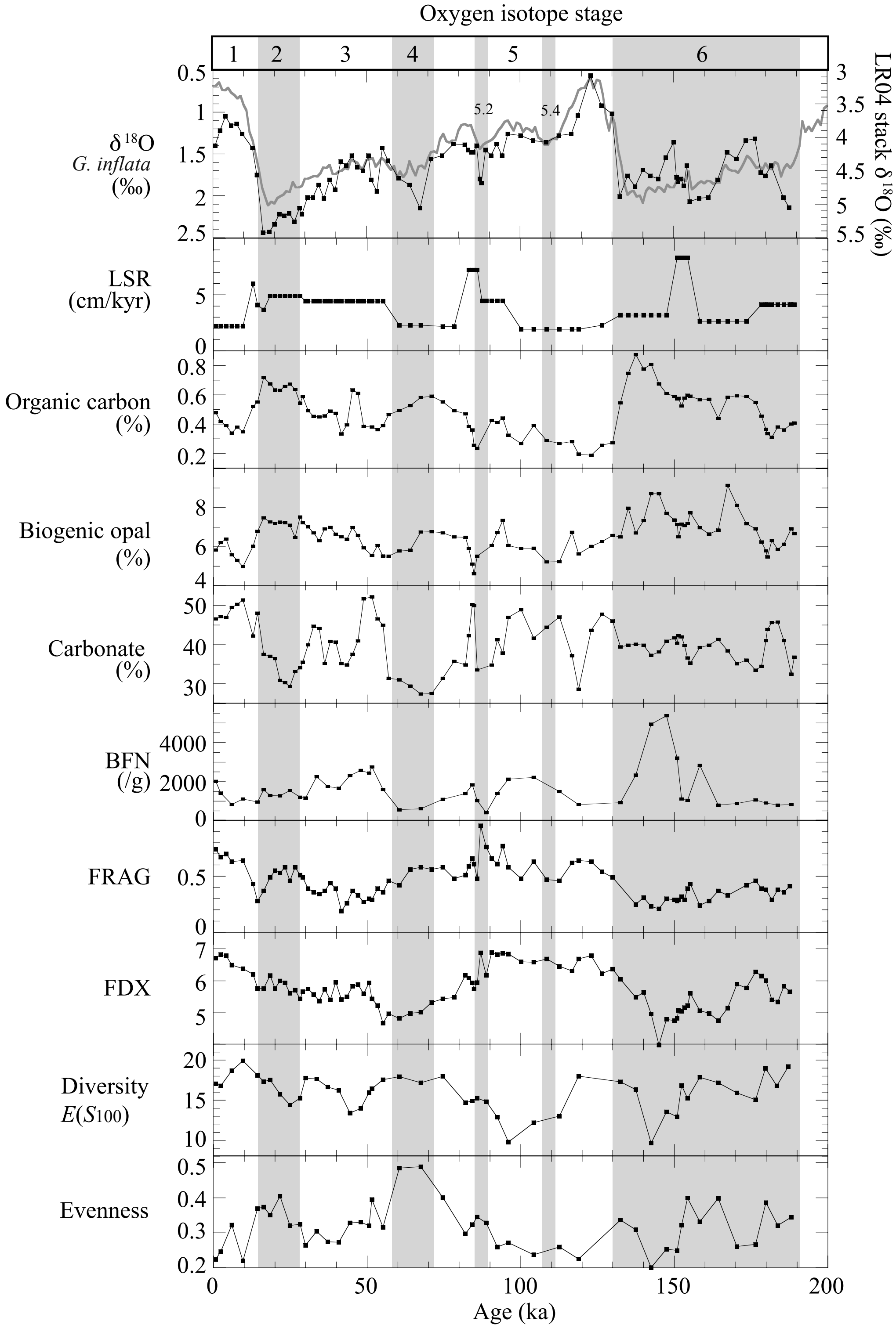

Figure 3. Time series plots of δ^{18}O of the planktonic foraminiferan *Globorotalia inflata* with δ^{18}O of LR04 global stack (a gray line) (Lisiecki and Raymo, 2005), linear sedimentation rate (LSR), organic carbon content, biogenic opal content, carbonate content (Maeda *et al*., 2002), benthic foraminiferal number, fragmentation ratio of the planktonic foraminifera (FRAG) (de Silva, 1999), planktonic foraminiferal dissolution index (FDX) (de Silva, 1999), benthic foraminiferal species diversity index $E(S_{100})$, and evenness in core NGC108. Gray shaded areas mark oxygen isotope stages (OISs) 2, 4, 5.2, 5.4, and 6.

Table 2. Tie points of $\delta^{18}O$ in core NGC108 with the LR04 isotopic event.

Sample no.	Depth in core (cm)	LR04 isotopic event	Age (ka)
3-0	104	3.0	29.0
4-24	228	4.0	57.0
4-56	260	5.0	71.0
4-80	284	5.1	82.0
5-16	320	5.2	87.0
5-56	360	5.3	96.0
6-8	412	5.5	123.0
6-24	428	6.0	130.0
6-88	492	6.3	150.0
7-32	536	6.4	155.3
7-88	592	6.5	176.5
cc94	640	6.6	187.6

(Stuiver *et al*., 2017; Shishikura *et al*., 2007; Yoneda *et al*., 2007). The linear sedimentation rate (LSR) estimated by this model ranged from 1.9 to 8.3 cm kyr^{-1}, and averaged 3.4 cm kyr^{-1} (Figure 3).

Sample processing

In the laboratory, samples (about 1 g of sediment each) for foraminiferal study were dried at about 50°C for 2 days, weighed, washed through a 63-μm sieve, and dried again at 50°C. Benthic foraminiferal analysis was performed on 46 samples. The average temporal sample interval was approximately 4 kyr. We used a microsplitter to obtain sample aliquots estimated to contain at least 200 specimens of benthic foraminifera. All benthic foraminifera picked from the aliquot were identified and counted.

Faunal analysis

The number of benthic foraminiferal specimens per gram of dry sediment (BFN) was calculated to evaluate the relative changes in foraminiferal abundance (Figure 3; Appendix). Species diversity $E(Sn)$ was also calculated from the benthic foraminiferal census (Hurlbert, 1971; Yasuhara *et al*., 2012). $E(Sn)$ estimates the number of species in a sample of individuals reduced to a common size (n). We set n at 100, well below the lowest number of specimens counted in a sample. Evenness (E) is used to describe how individuals are divided among species (Murray, 2006). Species diversity values increase either by the addition of unique species or by greater species evenness (E). These two indices were calculated using PAST software version 2.16 (Hammer *et al*., 2001).

Cluster analyses were performed to determine sample groups (Q-mode clusters) and species groups (R-mode clusters). The relative frequencies of benthic foraminiferal taxa were used for these analyses. The Q-mode cluster analysis was performed for all samples. Squared Euclidean distance was used to measure the distance between samples. A dendrogram was generated using an average linkage method between the groups. Twenty-four taxa were used for R-mode cluster analysis, and the similarities among the taxa were measured by Pearson's correlation. A dendrogram was again generated using an average linkage method.

Results

Occurrences of major species

In total, 58 genera and 157 species were identified in the 46 samples (Appendix). Micrographs of selected benthic foraminiferal species are shown in Figure 4. Twenty-four taxa occurred with a relative abundance of more than 4% in at least one sample (Figures 5, 6). *Cassidulina reniforme*, *Epistominella exigua*, and *E. levicula* were the dominant species throughout the core, but showed large fluctuations in relative abundance, between 0% and 76%, 0% and 61%, and 1% and 43%, respectively. High abundances of *C. reniforme* occurred in middle and late OIS 6, the middle of OIS 5, and from late OIS 3 to OIS 2. *Epistominella exigua* was abundant during the interglacials (OIS 5 and OIS 1), and decreased in OIS 6, in the middle of OIS 5 and OIS 4, and in the last part of OIS 3 to OIS 2. The relative abundance of *E. levicula* increased in the middle of OIS 6 and OIS 5, at the end of OIS 3, and in early OIS 2.

In addition to the three most dominant species, three other benthic taxa had relative abundances greater than 10% in at least one sample. *Brizalina pacifica* had maximum abundance values up to 11%. These high peaks were in OIS 2 and at the end of OIS 6. *Porogavelinella ujiiei* was common, with an abundance range of 0–10%. This species was relatively abundant in OISs 4 and 6. The maximum relative abundance (13%) of *Globocassidulina subglobosa* occurred around 21 ka.

Uvigerina peregrina had a maximum abundance value (6%) at 58 ka, which occurred around the OIS 1/2, 3/4, and 5/6 boundaries. *Triloculina frigida* and *Ehrenbergina trigona* both increased in abundance during glacial stages (OISs 2, 4, and 6). *Fontbotia wuellerstorfi* increased in abundance during OIS 1 and OIS 5. *Planulina* aff. *subinflata* was present at 10 ka in early OIS 1 and at 80–90 ka in OIS 5. *Pullenia okinawaensis* had a limited presence at 20–30 ka in OIS 2, and at 60–80 ka in OIS 4–5.

Table 3. Radiocarbon ages of planktic foraminifera *Globorotalia inflat* in core NGC108.

Depth in core	Sample no.	Planktic foraminifera	Calibrated age (1 sigma range) by Calib rev7.10	Median probability	ΔR
(cm)		(^{14}C age)	(cal BP)	(cal BP)	(years)
0–2	NGC108 TOP	1280±50	635–810	724	116±79
24–26	NGC108 2-20	11090±70	12368–12637	12490	116±79
32–34	NGC108 2-28	12470±60	13707–13955	13827	116±79
40–42	NGC108 2-36	13680±170	15498–16071	15779	116±79
48–50	NGC108 2-44	15290±80	17828–18124	17973	116±79

Stainforthia sp. was present only in OIS 2. *Triloculina tricarinata* had a relative abundance of 4% only in OISs 2 and 3. *Pullenia quinqueloba* had low abundances (1–5%) from OIS 5 to OIS 1. *Fursenkoina complanata* occurred frequently with low abundances of 0–4% throughout the core. *Pacinonion lateralis* had a limited occurrence at 50 ka in OIS 3 and 65 ka in OIS 4. *Oridorsalis umbonatus* increased in abundance from OIS 4 to OIS 2. The occurrence of *Pacinonion minutus* was restricted to 120–140 ka and 170 ka, from OIS 6 to early OIS 5. *Pacinonion novozealandicum* mainly occurred in OIS 3 and OIS 6. *Hansenisca soldanii* occurred only rarely in OISs 1, 3, and 5. *Gyroidina lamarckiana* occurred around the OIS 1/2 and 5/6 boundaries.

BFN

BFN fluctuated between 407 and 5,376 individuals g^{-1}, with an average value of 1,590 individuals g^{-1} (Figure 3). Although there was no clear contrast in the BFN values between glacial and interglacial periods, the highest values were from the glacial horizons. The highest values occurred at the end of OIS 6 (147.5 ka and 142.5 ka), but other peaks occurred in the middle of OIS 3. However, the peak in OIS 6 was twice as high as the other peaks.

Species diversity and evenness

$E(S_{100})$ fluctuated between 9.6 and 19.9, with an average value of 16.0 (Figure 3). Species diversity calculated using $E(S_{100})$ was low at the end of OIS 6 and in the middle of OIS 5, and high in the early Holocene (OIS 1). Evenness fluctuated between 0.2 and 0.5, with an average value of 0.32. Evenness was high in OIS 2, OIS 4, and middle OIS 6, and low in late OIS 6, middle OIS 5, and OIS 1.

R-mode cluster analysis

Based on a rescaled distance (18) for clustering, 24 taxa were classified into seven clusters (Figure 7; Table 4), designated as species groups A through G. Species Group A consists of *Cassidulina reniforme*, *Epistominella* sp., *Triloculina frigida*, and *Melonis balreeanus*. Species Group B consists of *Eilohedra levicula*, *Pacinonion novozealandicum*, *Porogavelinella ujiiei*, and *Triloculina tricarinata*. Species Group C consists of *Globocassidulina subglobosa*, *Pullenia okinawaensis*, and *Pullenia quinqueloba.* Species Group D consists of *Gyroidina lamarckiana*, *Planulina* aff. *subinflata*, *Hansenisca soldanii*, and *Pacinonion minutus.* Species Group E consists of *Epistominella exigua*, *Fontbotia wuellerstorfi*, *Oridorsalis umbonatus*, and *Pacinonion lateralis*. Species Group F consists of *Ehrenbergina trigona* and *Stainforthia* sp. Species Group G consists of *Brizalina pacifica*, *Uvigerina peregrina*, and *Fursenkoina complanata*.

Q-mode cluster analysis

Based on a rescaled distance (7) for clustering, 45 samples were classified into four clusters (Figure 8): Clusters 1 through 4. Here, "OIS# [sample depth] cm" was used for each sample name. Cluster 1 was mainly observed in the interglacial horizons. Cluster 3 was distributed in both glacial and interglacial horizons, except for peak warm intervals such as the Eemian (isotope event 5e) and the Holocene. Clusters 2 and 4 were mainly observed in the glacial assemblages.

Cluster 1 consists of samples from OIS 5, early OIS 3, and OIS 1. This cluster is characterized by abundant *Epistominella exigua*. Cluster 2 mainly consists of samples from OIS 6 and late OIS 3 to OIS 2. This cluster is characterized by abundant *Cassidulina reniforme*, with common *Eilohedra levicula*. Cluster 3 consists of samples from OIS 6, OIS 5, early OIS 3, and late OIS 2 (the last deglacial). This cluster is characterized by the co-occurrence of *C. reniforme*, *Ei. levicula*, and *Ep. exigua*. Cluster 4 consists of only three samples: OIS6_500 cm, OIS6_484 cm, and OIS6_468 cm, from late OIS 6. This cluster is dominated by *C. reniforme* with accompanying *Ei. levic-*

Figure 4. Scanning electron micrographs of selected benthic foraminiferal species. **1,** *Brizalina pacifica* (Cushman and McCulloch) from Sample 2-32; **2,** *Cassidulina reniforme* Nørvang from Sample 6-96; **3,** *Eilohedra levicula* (Resig) from Sample 3-36; **4,** *Epistominella exigua* (Brady) from Sample 2-0; **5,** *Fontbotia wuellerstorfi* (Schwager) from Sample 5-80; **6,** *Ehrenbergina trigona* Goës from Sample 2-16; **7,** *Globocassidulina subglobosa* (Brady) from Sample 2-64; **8,** *Gyroidina lamarckiana* (d'Orbigny) from Sample 2-16; **9,** *Oridorsalis umbonatus* (Reuss) from Sample 3-96; **10,** *Planulina* cf. *subinflata* (Bandy) from Sample 2-16; **11,** *Fursenkoina complanata* (Egger) from Sample 2-48; **12,** *Porogavelinella ujiiei* Kawagata from Sample 4-48; **13,** *Pacinonion novozealandicum* (Cushman and Edwards) from Sample 3-96; **14,** *Pullenia quinqueloba* (Reuss) from Sample 4-80; **15,** *Uvigerina peregrina* Cushman from Sample 4-16; **16,** *Triloculina frigida* (Lagoe) from Sample 7-72.

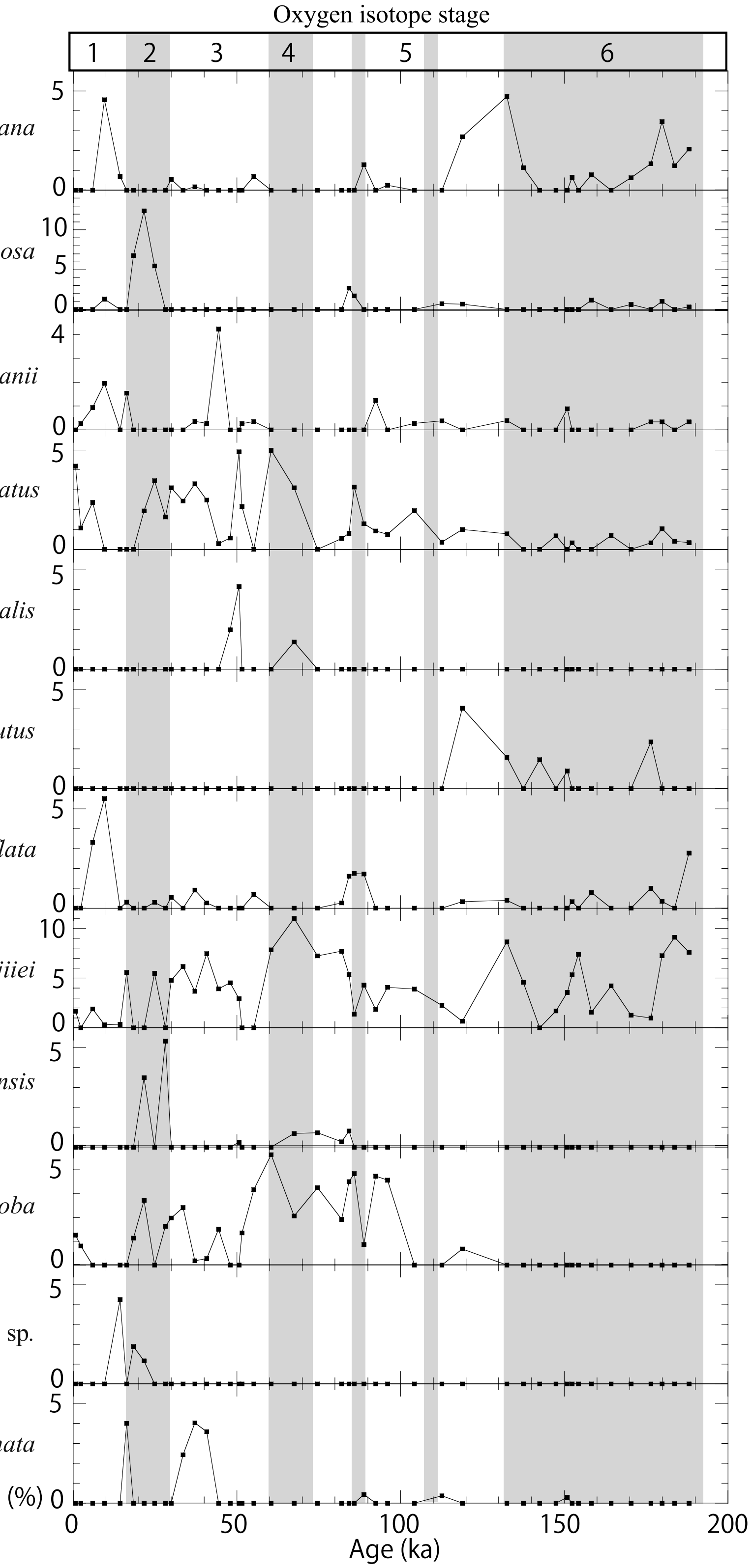

Figure 5. Time series plots of the relative abundances of the benthic foraminiferal taxa in core NGC108. Numerals along the top of the graphs represent oxygen isotope stages (OISs).

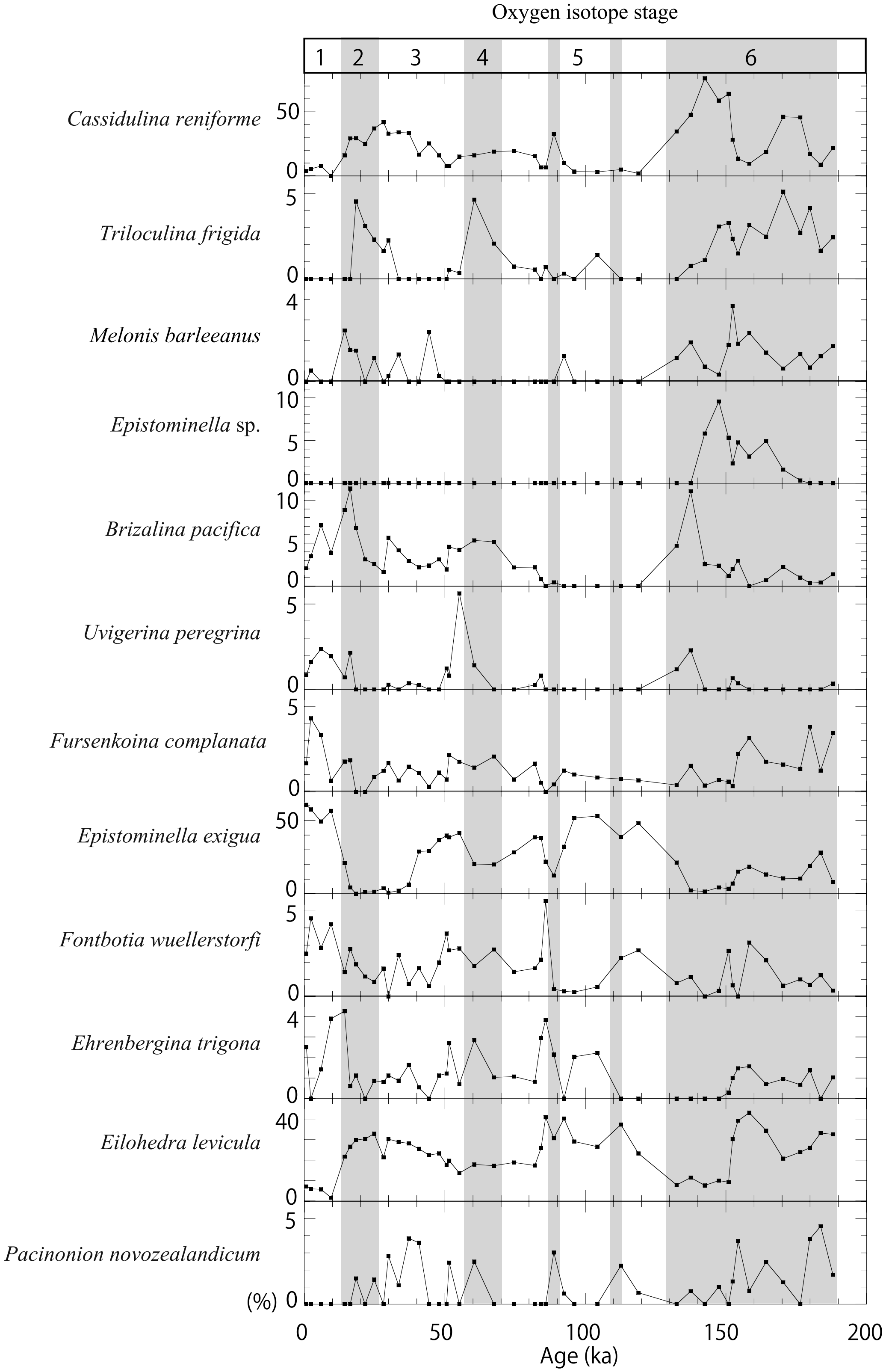

Figure 6. Time series plots of the relative abundances of the benthic foraminiferal taxa in core NGC108. Numerals along the top of the graphs represent OISs.

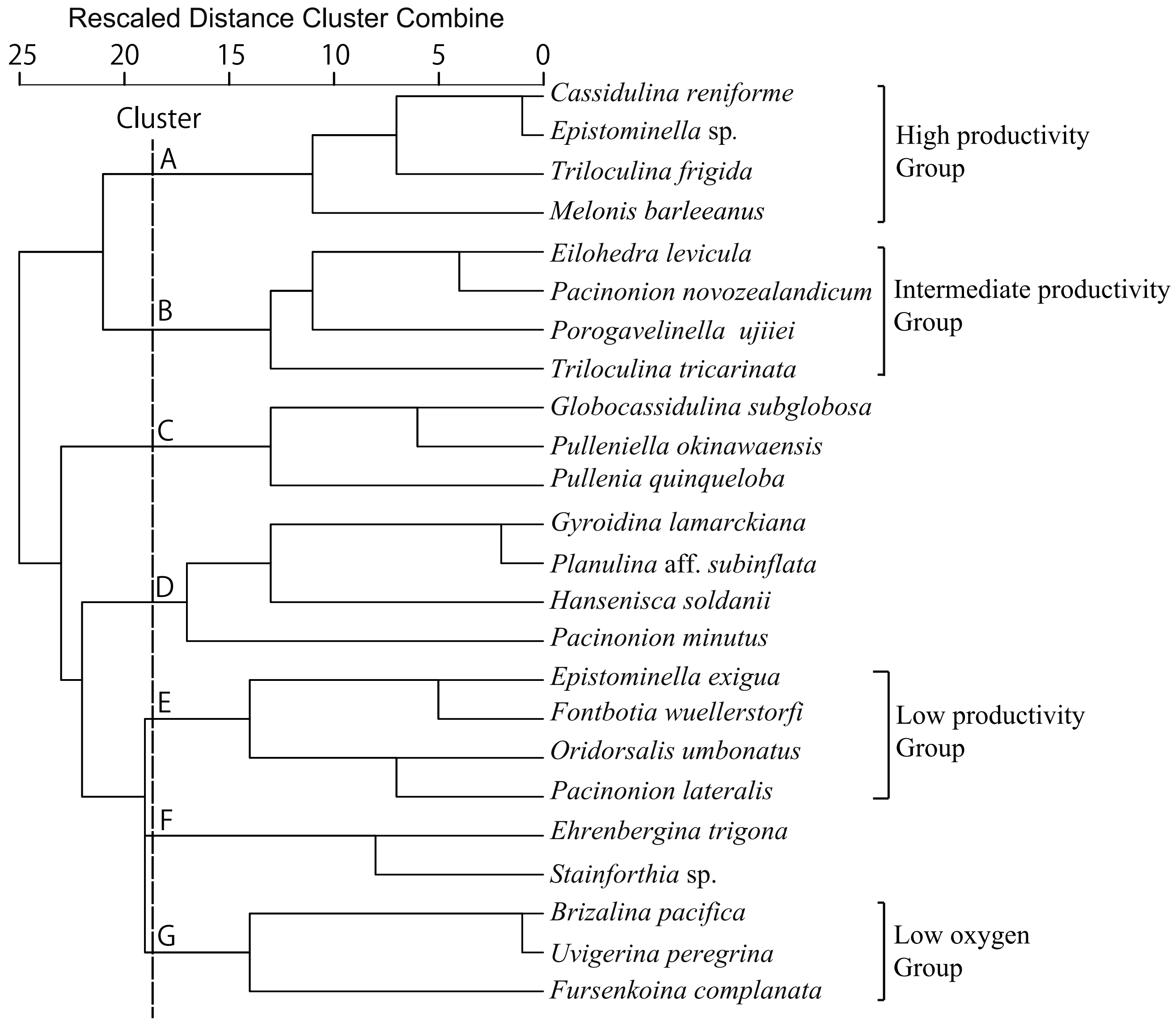

Figure 7. Result of R-mode cluster analysis of 24 selected taxa from core NGC108 recovered from the northwestern Pacific Ocean.

ula and *Epistominella* sp.

Bathymetric distributions of benthic foraminifera on the Shatsky Rise

The bathymetric distributions of the six characteristic species of calcareous benthic foraminifera from 2,612–4,117 m depths on the Shatsky Rise are illustrated in Figure 9 (Ohkushi, 1998). The data show the relative abundances of the benthic foraminiferal species in seven surface sediment samples recovered at approximately 32–36°N and 158–159°E. Six pilot core samples (NGC102, 103, 105, 106, 107, and 108) and one multiple core sample (NMC20) were used for the analyses (Figure 2; Table 1). The Shatsky Rise is largely situated beneath the subtropical Kuroshio Extension (Roden, 1975). This subtropical front is located between 28°N and 35°N in the central North Pacific (Figure 1). In contrast, the Subarctic Front is normally encountered between 40°N and 45°N. Thus, the NGC108 and NMC20 core sites are located just beneath the main path of the Kuroshio Extension. The NGC102 and NGC103 core sites are located near the southern limb of the Kuroshio Extension. The degree of $CaCO_3$ saturation and the depths of the lysocline and CCD affect both living and fossil foraminifera. The calcite saturation horizon above the Shatsky Rise is near a depth of 800 m (Chen *et al*., 1988). The calcite lysocline

Table 4. Correlation of the occurrence of the benthic foraminifera with biogenic opal, organic carbon, and carbonate contents, FRAG and FDX (data from de Silva, 1999), δ^{18}O, and species diversity $E(S_{100})$ in core NGC108.

Cluster (Interpretation)	Species	Biogenic opal		Organic carbon		Carbonate		FRAG		FDX		δ^{18}O		$E(S100)$	
		r (*N*=36)	*P*-value	*r* (*N*=36)	*P*-value	*r* (*N*=36)	*P*-value	*r* (*N*=37)	*P*-value	*r* (*N*=39)	*P*-value	*r* (*N*=37)	*P*-value	*r* (*N*=45)	*P*-value
Cluster A (High productivity)	*Cassidulina reniforme*	0.79	<0.001	0.75	<0.001	−0.35	0.036	−0.46	0.004	−0.47	0.003	0.41	0.012	−0.35	0.019
	Epistominella sp.	0.54	0.001	0.33	0.051	−0.03	0.847	−0.48	0.003	−0.56	<0.001	0.07	0.690	−0.45	0.002
	Triloculina frigida	0.45	0.006	0.35	0.039	−0.44	0.007	−0.37	0.024	−0.43	0.007	0.44	0.006	−0.10	0.524
	Melonis barleeanus	0.45	0.007	0.45	0.006	0.02	0.920	−0.56	<0.001	−0.32	0.044	0.40	0.014	−0.09	0.550
Cluster B (Intermediate productivity)	*Eilohedra levicula*	0.03	0.841	−0.16	0.343	−0.22	0.196	−0.08	0.652	0.00	0.976	0.18	0.287	−0.22	0.143
	Pacinonion novozealandicum	−0.09	0.613	−0.10	0.555	0.06	0.726	−0.20	0.228	−0.24	0.148	0.11	0.511	0.01	0.935
	Porogavelinella ujiiei	−0.07	0.697	0.09	0.615	−0.27	0.117	−0.01	0.964	−0.24	0.137	0.21	0.205	0.03	0.825
	Triloculina tricarinata	0.17	0.317	0.23	0.177	−0.04	0.811	−0.09	0.611	0.00	0.986	0.34	0.040	0.21	0.173
Cluster C	*Globocassidulina subglobosa*	0.12	0.484	0.19	0.270	−0.27	0.107	0.11	0.507	0.11	0.513	0.43	0.008	0.12	0.419
	Pullenia okinawaensis	0.22	0.200	0.13	0.466	−0.28	0.103	0.14	0.421	−0.06	0.703	0.34	0.041	0.05	0.732
	Pullenia quinqueloba	−0.30	0.077	−0.28	0.096	−0.17	0.334	0.35	0.031	0.05	0.740	−0.11	0.530	0.08	0.620
Cluster D	*Gyroidina lamarckiana*	−0.28	0.097	−0.19	0.268	0.11	0.532	0.08	0.652	0.19	0.256	−0.11	0.510	0.21	0.162
	Planulina aff. *subinflata*	−0.46	0.005	−0.34	0.045	0.34	0.041	0.31	0.064	0.21	0.195	−0.34	0.041	0.40	0.007
	Gyroidinoides soldannii	−0.21	0.224	−0.13	0.436	0.34	0.045	0.13	0.437	0.25	0.129	−0.10	0.557	0.05	0.761
	Pacinonion minutus	0.04	0.804	−0.11	0.528	−0.32	0.055	0.04	0.792	0.16	0.333	−0.23	0.167	−0.19	0.210
Cluster E (Low productivity)	*Epistominella exigua*	−0.76	<0.001	−0.74	<0.001	0.53	0.001	0.55	<0.001	0.58	<0.001	−0.73	<0.001	0.10	0.510
	Fontbotia wuellerstorfi	−0.50	0.002	−0.41	0.013	0.17	0.326	0.12	0.464	0.10	0.546	−0.15	0.377	0.45	0.002
	Oridorsalis umbonatus	−0.30	0.080	−0.20	0.246	−0.22	0.193	0.24	0.150	0.10	0.552	−0.01	0.972	0.32	0.032
	Pacinonion lateralis	0.05	0.793	0.10	0.576	−0.31	0.064	−0.14	0.420	−0.02	0.889	0.01	0.952	0.08	0.590
Cluster F	*Ehrenbergina trigona*	−0.45	0.006	−0.32	0.056	0.32	0.061	0.19	0.268	0.11	0.491	−0.16	0.334	0.37	0.012
	Stainforthia sp.	0.14	0.415	0.17	0.312	0.10	0.558	−0.16	0.349	0.05	0.767	0.25	0.140	0.28	0.065
Cluster G (Low oxygen)	*Brizalina pacifica*	0.16	0.362	0.53	0.001	0.05	0.763	−0.25	0.141	−0.15	0.375	0.45	0.005	0.54	<0.001
	Uvigerina peregrina	−0.33	0.052	−0.02	0.913	0.35	0.035	−0.08	0.629	−0.12	0.465	−0.10	0.556	0.42	0.004
	Fursenkoina complanata	−0.14	0.419	−0.10	0.553	0.25	0.138	−0.06	0.721	0.03	0.867	−0.09	0.585	0.29	0.057

in the northwestern Pacific is near a depth of 3,200 m and the CCD is around 4,400 m (Berger *et al.*, 1976). Thus, all the samples used for this study were collected from depths above the lysocline or between the lysocline and the CCD.

Epistominella exigua was the most dominant species between 2,612 and 4,117 m depths, accounting for a total of 16–65% of the calcareous specimens (Figure 9). The highest value (65%) was observed in core NMC20 from the northernmost part of the Shatsky Rise. However, the distribution of *E. exigua* does not show bathymetric dependence within the depth range of 2,612 to 4,117 m (Figure 9). *Epistominella exigua* occurred at depths ranging from 500 to 4,500 m in the northwestern Pacific benthic foraminiferal assemblages. It is especially common at depths below 2,000 m beneath the Kuroshio Current off southwest Japan (Inoue, 1989), as well as at depths from 2,300 to 3,500 m near the Emperor Seamounts located around 50–55°N (Saidova, 1961). However, this species has not yet been observed in the high productivity conditions of the northwestern Pacific subarctic marginal ocean settings, such as those in the Oyashio Current

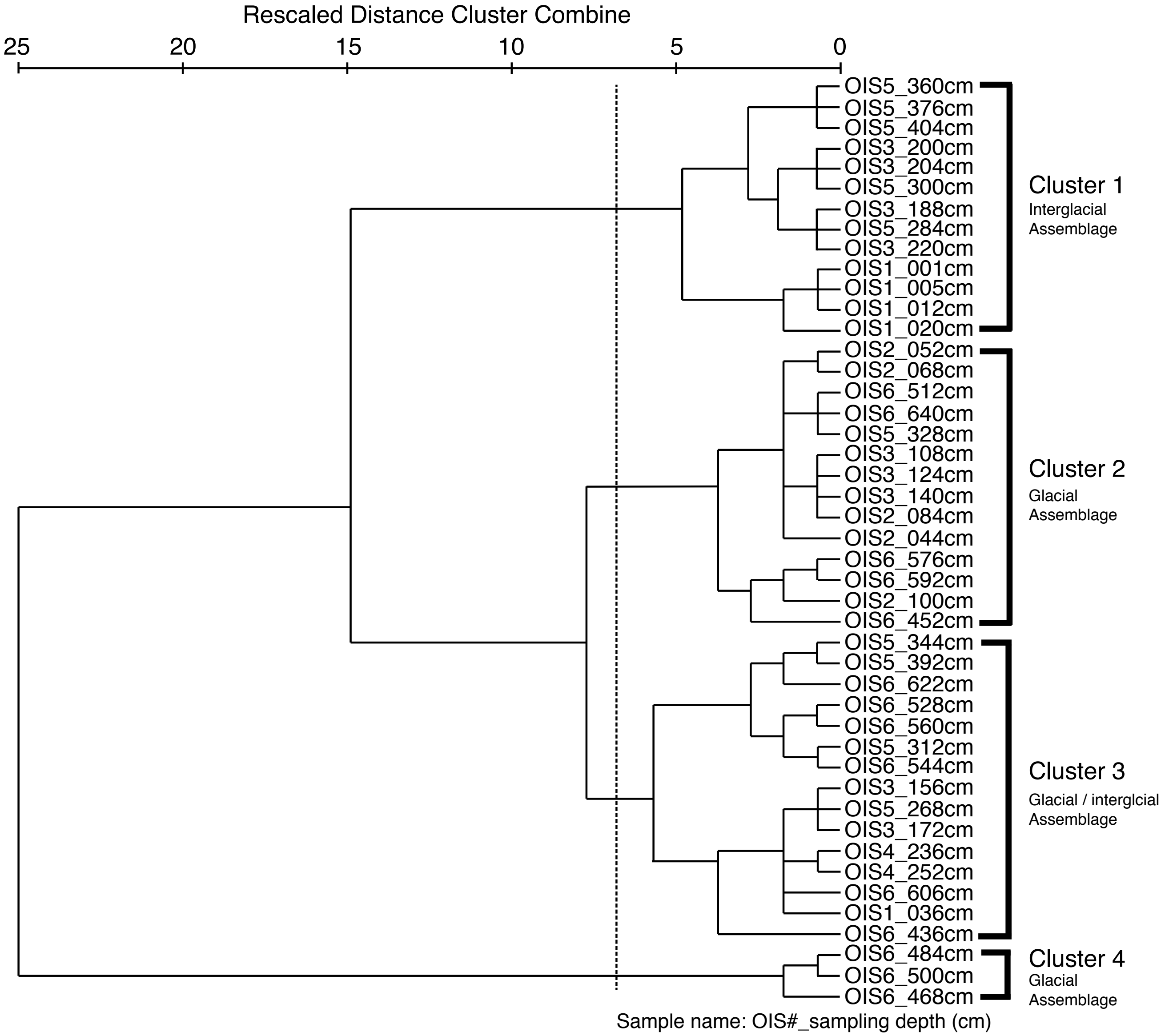

Figure 8. Result of Q-mode cluster analysis of 45 samples from core NGC108 recovered from the northwestern Pacific Ocean.

region and the Sea of Okhotsk (Figure 1), (Matoba, 1976; Saidova, 1961; Thompson, 1980). Primary productivity and biogenic silica production of surface waters generally increases with latitude in the northwestern Pacific. Thus, the present distribution of *E. exigua* may be related to the low flux of organic materials.

Eilohedra levicula commonly occurred between 2,612 and 4,117 m depths, accounting for 2–11% of the total calcareous benthic foraminifera. The maximum abundance (11%) of this species was observed at a depth of 2,743 m (core NGC103). The bathymetric preference of this species is not clear, although its peak abundance was observed at a shallower depth.

Uvigerina peregrina was dominant at a depth of 2,612 m (core NGC102), accounting for 16% of the total calcareous benthic foraminifera. Thus, *U. peregrina* exhibited maximum abundance at the shallowest site and decreased in abundance below the lysocline. Based on the distributional patterns of recent benthic foraminifera on the northwest African continental margin, Luzte and Coulbourn (1984) observed that high abundances of *U. peregrina* were associated with a wide range of bottom-water dissolved oxygen, but with relatively high organic carbon weight percentages of > 2.0%. Likewise, Miller

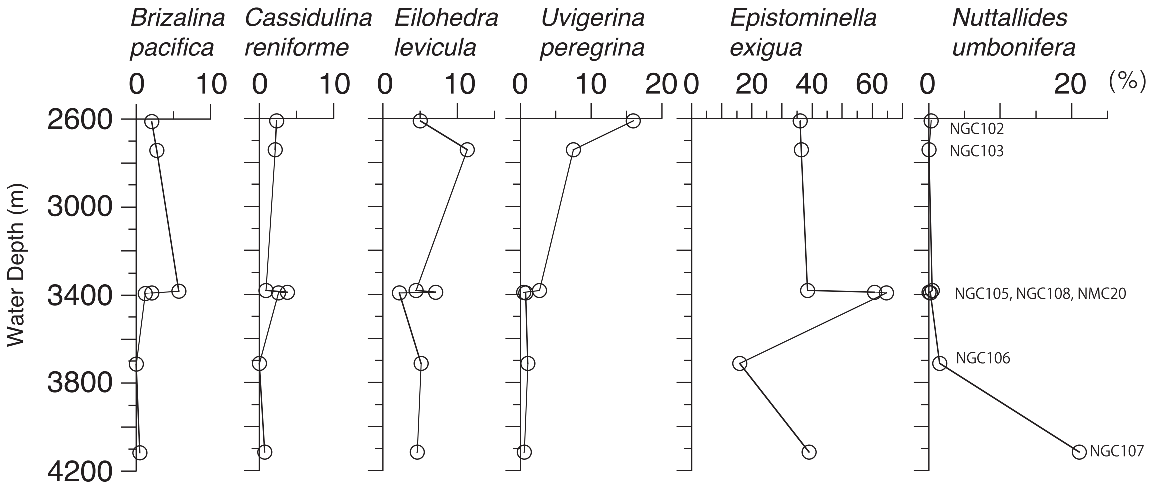

Figure 9. Bathymetric distribution of the relative abundances of the characteristic benthic foraminiferal species in the Shatsky Rise. Data from Ohkushi (1998).

and Lohmann (1982) observed that the highest abundances of this species coincided with the maxima of organic carbon and silt within the sediments on the United States continental slope and rise. Wahyudi and Minagawa (1997) reported that high abundances of *U. peregrina* coincided with high accumulation rates of organic carbon in the Okinawa Trough during the last glacial maximum. Thus, this species may be an indicator of stable high productivity in environments associated with intense upwelling, such as ocean margins.

Cassidulina reniforme had low abundances ranging from 0 to 3.7%, occurring extremely rarely in deeper sites (cores NGC106 and 107) at depths of 3,713 m and 4,117 m. Likewise, *B. pacifica* had low abundances ranging from 0 to 5.8%, occurring extremely rarely in the two deeper sites.

Nuttallides umbonifera increased in abundance below the lysocline and reached a maximum abundance of 21% in the deepest sample (4,117 m). *Nuttallides umbonifera* became the dominant species slightly above the CCD (4,117 m). *Nuttallides umbonifera* has been reported throughout the ocean by many researchers. In the Atlantic, this species is the most characteristic component of the fauna affected by the Antarctic Bottom Water (AABW). According to Lohmann (1978), this species becomes the dominant benthic foraminiferan below 4,000 m in the western South Atlantic. In the Pacific, Burke (1981) reported that this species, as well as *Epistominella exigua*, occurs abundantly from depths below the lysocline (3,500 m) to 4,200 m in the western Equatorial Pacific. The abundance of *N. umbonifera* in the Shatsky Rise near the CCD is consistent with these previous findings. This implies that this species is strongly influenced by the physical and chemical properties of deep water or bottom water, as observed in the Atlantic Ocean where it is closely associated with the AABW. Several studies have suggested the importance of the undersaturation of $CaCO_3$ as an ecological influence on *N. umbonifera* (Lohmann, 1978; Corliss, 1979; Bremer and Lohmann, 1982). In particular, Bremer and Lohmann (1982) showed that some Atlantic benthic foraminifera, such as *N. umbonifera*, are consistently correlated with the degree of $CaCO_3$ saturation in sea water. The ecology of this species appears to show strong resistance to carbonate dissolution. In the Atlantic, this species occurs more abundantly in interglacial sediments than in glacial sediments (Schnitker, 1979). Yasuda (1995) similarly observed greater abundance of this species during interglacials in the western Pacific.

Discussion

Carbonate dissolution

The current lysocline depth at the Shatsky Rise is approximately 3,200 m (Berger *et al.*, 1976; Chen *et al.*, 1988; Maeda *et al.*, 2002) and the sea floor depth at core site NGC108 is 3,390 m. Pacific deep water was less corrosive during glacial periods than in interglacial periods, as interglacial carbonate contents were significantly reduced in the equatorial Pacific (Farrell and Prell, 1989). However, carbonate contents during OISs 1 and 5 in interglacial periods (45–50%) were higher than during glacial periods in OISs 2, 4, and 6 (30–40%) in core NGC108 (Maeda *et al.*, 2002). This may be due to an increase in sinking carbonate particles from the ocean surface during interglacials, as carbonate content is higher in subtropical waters than in subarctic waters (Kawahata *et al.*, 1998). In core NGC108, de Silva (1999) documented that carbonate dissolution during interglacial periods was more intense than during glacial periods, based on the planktonic foraminiferal dissolution index (FDX) and the fragmentation ratio (FRAG) (Figure 3). *Epistominella exigua* has a positive correlation with both dissolution indices (Table 4). In contrast, *Cassidulina reniforme*, *Melonis barleeanus*, *Triloculina frigida*, and *Epistominella* sp. have negative correlations with both dissolution indices (Table 4). The high interglacial abundance of *E. exigua* may reflect the influence of corrosive deep water of Atlantic origin. However, there is no clear relationship between the dissolution indices and other indices, such as foraminiferal diversity and BFN (Figure 3). Thus, we conclude that the post-depositional dissolution effect in core NGC108 was not a primary factor affecting changes in the benthic foraminifera.

Productivity and benthic foraminifera

Mass accumulation rates of organic carbon reflect primary productivity in the surface water rather than the influence of decomposition by dissolved oxygen in the bottom water, if the organic carbon originates from marine primary production (Jahnke, 1990). Diatoms, an important component of phytoplankton, are the main source of biogenic opal. Therefore, biogenic opal also could serve as an important indicator of primary productivity. In this paper, we use the content data rather than the accumulation rate data to prevent any artifacts from the sedimentation rate estimate. Maeda *et al.* (2002) analyzed organic carbon and biogenic opal contents in core NGC108 and estimated the primary productivity. High productivity occurred in OISs 2 to 4 and in late OIS 6, whereas the minima were observed in OIS 1 and early OIS 5. Organic carbon content was correlated with biogenic opal content in core NGC108 ($r = 0.7$) (Figures 3, 10).

BFN is not an accurate proxy for surface productivity compared with opal and organic carbon, because BFN on the Shatsky Rise is not only influenced by changes in paleoproductivity, but also by factors such as dissolved oxygen and carbonate saturation. However, the highest BFN values were also observed during glacial periods, reflecting higher productivity during these times.

Comparisons of the organic carbon and biogenic opal contents with the relative abundance of the three dominant benthic foraminifera are shown in Figure 10. The relative abundance of *Cassidulina reniforme* is positively correlated with the weight percents of biogenic opal and organic carbon ($r = 0.79$ and 0.75, respectively; both $p < 0.001$). These correlations suggest that changes in the abundance of *C. reniforme* reflect increases in food delivery to the sea floor and high export productivity. The relative abundance of *Epistominella exigua* is negatively correlated with the weight percents of biogenic opal and organic carbon ($r = -0.76$ and -0.74, respectively; both $p < 0.001$). The relative abundance of *Eilohedra levicula* has no clear correlation with these two parameters ($r = 0.03$, $p = 0.841$ and $r = -0.16$, $p = 0.343$). *Eliohedra levicula* and *Ep. exigua* belong to a group of benthic foraminifera that rapidly colonize phytodetrital organic material (Gooday, 1993; Smart *et al.*, 1994). This opportunist behavior (r-strategist) is an adaptation to a fluctuating food supply that allows rapid growth and reproduction in the presence of phytodetritus. However, the different abundance patterns between these two species in this study indicate that they have different environmental preferences, and suggest that *Ei. levicula* prefers a higher food supply than *Ep. exigua*. The abundances of *Ep. exigua* and *Ei. levicula* are not positively correlated in other locations [e.g. Yasuda (1997) in the western equatorial Atlantic; Loubere (1998) in the Indian Ocean; Thomas *et al.* (1995) in the northern Atlantic; Ohkushi *et al.* (2000) in the northwestern Pacific; and Ujiié (2003) in the central North Pacific Ocean]. King *et al.* (1998) demonstrated that *Ei. levicula* was more common than *Ep. exigua* in dense, laminated diatom mats in the Neogene equatorial Pacific. This suggests that the high relative abundance of *Ep. exigua* indicates the lowest productivity in core NGC108.

In Figure 10, the visual distribution of the cluster assemblages in the order of clusters 1–3–2–4 roughly matches the *Cassidulina reniforme* abundance pattern. The Cluster 1 assemblage, dominated by *Epistominella exigua*, is mainly linked with interglacial stages, indicating the lowest paleoproductivity. The Cluster 3 assemblage is associated with transitional environments (from glacial to interglacial), with a common occurrence of *C. reniforme*, *Ep. exigua*, and *Ei. levicula*. The Cluster 2 assemblage is associated with the higher productivity of glacial periods, with high abundances of *C. reniforme* and *Ei. levicula.* The Cluster 4 assemblage is characterized by the exceptional dominance of *C. reniforme* and *Epistominella* sp. and is restricted to only the highest productivity intervals in OIS 6.

Comparison of the R-mode cluster analysis with the Q-mode analysis results indicates that species groups A and E are lower and higher paleoproductivity indicators, respectively (Figures 8, 10, Table 4). Thus, the epifaunal species *Fontbotia wuellerstorfi* is closely tied to *Epistominella exigua*, *Oridorsalis umbonatus*, and *Pacinonion lateralis*, and is indicative of lower productivity. *Epistominella* sp., *Melonis barleeanus*, and *Triloculina frigida* are interpreted to be indicative of higher productivity. In contrast, environmental factors indicated by species group B, which is composed of *Eilohedra levicula*, *Fursenkoina complanata*, *Pacinonion novozealandicum*, *T. tricarinata*, and *Porogavelinella ujiiei*, are still

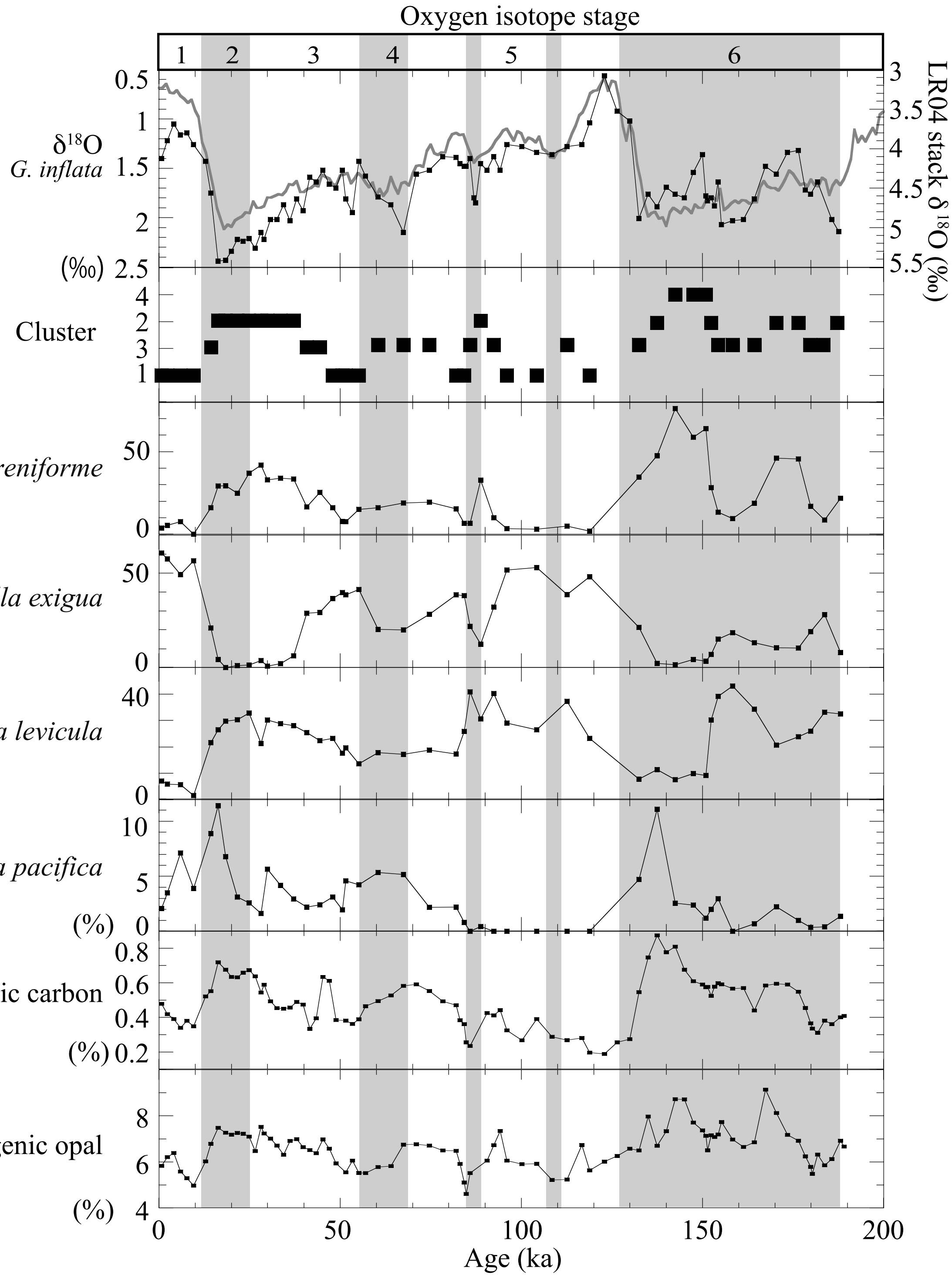

Figure 10. Temporal changes of δ^{18}O of the planktonic foraminiferan *Globorotalia inflata* with δ^{18}O of LR04 global stack (gray line) (Lisiecki and Raymo, 2005), sample groupings (clusters 1–4) of the Q-mode cluster analysis of benthic foraminiferal assemblages, the relative abundances of four benthic foraminiferal species (*Cassidulina reniforme*, *Eilohedra levicula*, *Epistominella exigua*, and *Brizalina pacifica*), and organic carbon and biogenic opal contents (Maeda *et al.*, 2002) in core NGC108.

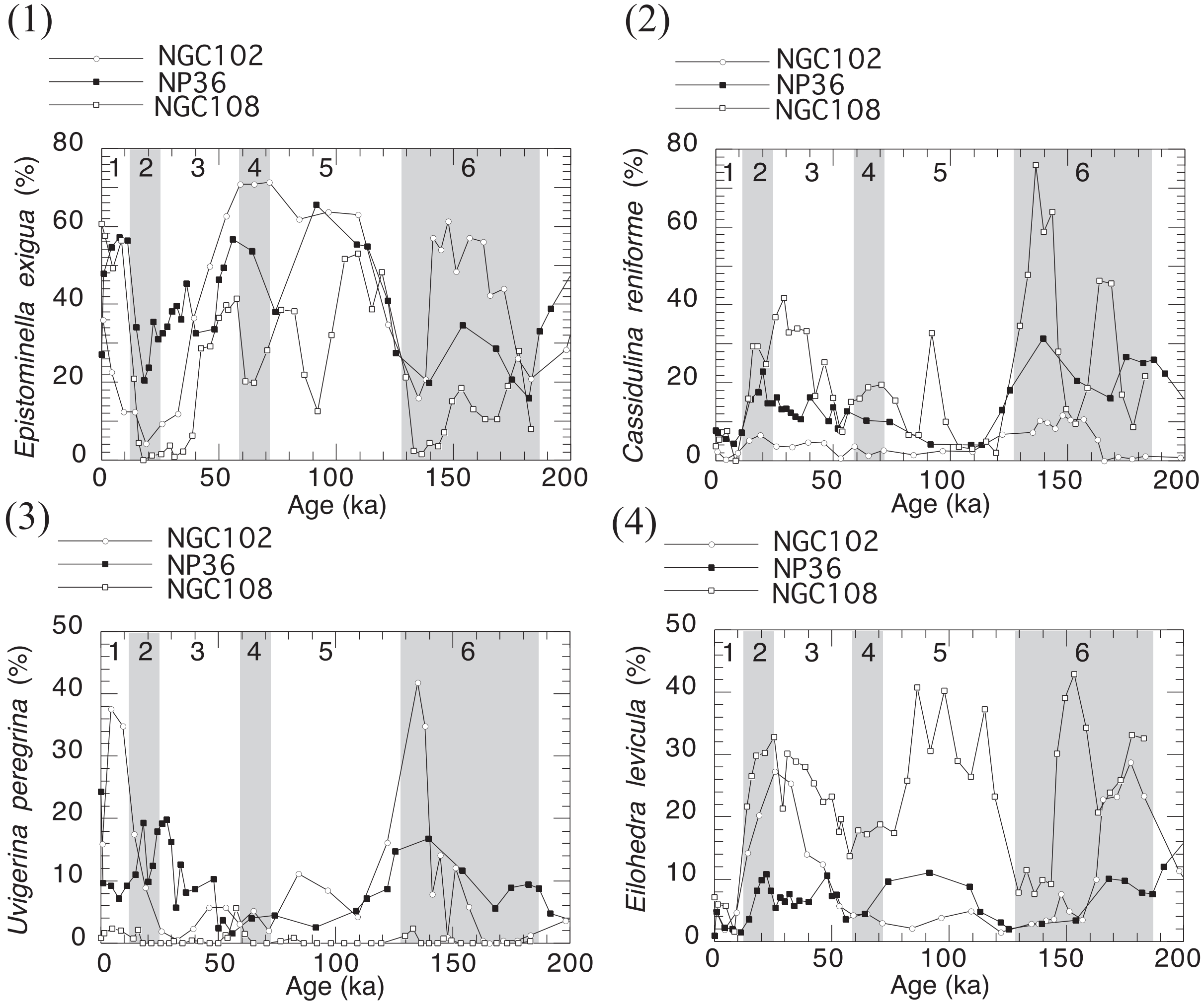

Figure 11. Temporal changes in the relative abundances of the benthic foraminiferal taxa in cores NGC108, NGC102 (Ohkushi *et al.*, 2000), and NP36 (Ujiié *et al.*, 2003). **1,** *Epistominella exigua*; **2,** *Cassidulina reniforme*; **3,** *Uvigerina peregrina*; **4,** *Eilohedra levicula*.

unclear, as these species have no correlation with paleoproductivity indices. However, species group B may be indicative of intermediate productivity, as *Ei. levicula* prefers a higher food supply than *Ep. exigua* and a lower food supply than *C. reniforme*.

Species group G may reflect high-productivity-low-oxygen sea floor environments, as *Brizalina pacifica*, *Fursenkoina complanata*, and *Uvigerina peregrina* are typical species indicative of low oxygen and high organic contents. Thus, *B. pacifica* and *U. peregrina* abundances may indicate an organic-rich and oxygen-poor sea floor during the glacial maximum in OISs 2 and 6, or the last deglaciation.

Comparison of benthic foraminiferal assemblages among cores NGC108, NP36, and NGC102

We compared benthic foraminiferal assemblages among cores NGC108, NP36 (Ujiié, 2003), and NGC102 (Ohkushi *et al.*, 2000) (Figures 1, 11). Planktonic foraminiferal assemblages in the Hess Rise indicate that the Subarctic Front did not reach core site NP36 (Ujiié, 2003). Changes in the position of the front may have caused differences in benthic faunal patterns among these sites, because organic matter flux to the sea floor would be greatly affected by the migration of the front. The average benthic foraminiferal accumulation rate for core NGC108 was 3,527 individuals cm^{-2} kyr^{-1}. That of core NGC102 was 1,217 individuals cm^{-2} kyr^{-1}. Similarly, organic carbon data indicate that the estimated primary productivity at core site NGC102 was always lower than at NGC108 (Maeda *et al.*, 2002), meaning that the productivity at core site NGC108 was higher than that at NGC102. Although productivity levels were different at the two sites, the peak values at each site both occurred in OIS 6, OIS 4, and late OIS 2.

The dominant species in core NGC102 were *Epistominella exigua*, *Eilohedra levicula* (= *Alabaminella weddellensis*), and *Uvigerina peregrina*, whereas in core NP36 *Cassidulina reniforme*, *Ei. levicula*, *Ep. exigua*, and *U. peregrina* were dominant. Ohkushi and Natori (2001) reported on the living benthic foraminifera from the Suiko Seamount and Hess Rise and noted that *Ei. levicula* and *Ep. exigua* constituted the most abundant species in those regions. These data indicate that these species commonly occur in many regions of the northwestern Pacific, and that these four common species were probably key components in the Quaternary deep-sea assemblages in the central northwestern Pacific.

We compared the time series patterns of these four dominant species among the three sites (Figure 11). The relative abundance of *Epistominella exigua* was interpreted as indicative of low productivity. The relative abundance of *Ep. exigua* in core NGC108 is quite different from the other sites, reflecting the substantial differences in productivity. However, the abundance patterns of *Ep. exigua* between cores NGC102 and NP36 are generally similar, except for the OIS 4 horizon, which shows high abundance of this species. In addition, the abundance of *Ep. exigua* in core NGC108 was low in OISs 6 and 2, and was high in OISs 5 and 1. The fluctuations in productivity estimated from *E. exigua* in core NGC102 are more similar to those in core NP36 than those in NGC108. This suggests that the subarctic water only affected core site NGC108, and that the other two core sites were under subtropical waters during glacial times.

Cassidulina reniforme is an abundant species in core NGC108, but not in cores NGC102 or NP36, where *Uvigerina peregrina* is the most abundant species. *Uvigerina peregrina* is relatively abundant in water depths of 2,600–2,700 m on the Shatsky Rise and decreases in abundance below 2,700 m (Ohkushi, 1998; Ohkushi and Natori, 2001). The present distributional pattern of *U. peregrina* suggests that the water depth at core site NGC108 is too deep for this species to thrive. *Cassidulina reniforme* and *U. peregrina* have been reported from similar environments characterized by high productivity and low oxygen (Miller and Lohman, 1982; Lutze and Coulbourn, 1984; Sen Gupta and Machain-Castillo, 1993). In core NGC108, high abundances of *C. reniforme* occurred in the middle and late parts of OIS 6. In cores NGC102 and NP36, *U. peregrina* abundances were high in the latest part of OIS 6 and at the OIS 1/2 boundary (the last deglaciation). If *U. peregrina* abundance peaks closely correspond with deglaciation, the deglacial expansion of the oxygen minimum zone, which was documented in the intermediate depths of marginal seas in the subarctic Pacific (Moffitt *et al.*, 2015), may affect deeper depths in the Shatsky Rise. Unfortunately, however, the time resolution for core NGC102 is relatively poor on a millennial scale and, therefore, a high-resolution study of the deglacial horizons in the Shatsky Rise is needed.

Cassidulina reniforme in core NGC108 and *Uvigerina peregrina* in core NGC102 both had their highest peak abundance at around 130 ka. Moreover, similar abundance peaks of these species were observed in the Hess Rise at around 136 ka. The high abundances of these species at around 130–136 ka indicate the highest productivity. Planktonic foraminiferal studies (e.g. Thompson, 1981) have indicated a regional strong cooling event in late OIS 6 in the Shatsky Rise. The highest productivity during late OIS 6 would have been caused by the southward migration of the productive subarctic front.

Species diversity of benthic foraminifera in core NGC108

Among the ecological hypotheses proposed to explain global variation in species diversity, the species–energy hypothesis has emerged as a leading contender (Hawkins *et al.*, 2003; Hunt *et al.*, 2005; Willing *et al.*, 2003). The species–energy hypothesis predicts a positive correlation between species diversity and available energy, measured in forms such as temperature or biological productivity. Based on deep-sea benthic foraminiferal fossil data, Hunt *et al.* (2005) suggested that temperature, but not paleoproductivity, is a significant predictor of species diversity during the late Quaternary. Corliss *et al.* (2009) suggested that the species diversity of modern deep-sea foraminifera is controlled by the seasonality of productivity in the North Atlantic. However, Yasuhara and Danovaro (2016) rejected this hypothesis by reanalyzing the data and instead showed a significant effect of temperature. Productivity control of deep-sea diversity is suggested not only by foraminifera, but also by other organisms such as deep-sea molluscs (Tittensor *et al.*, 2011; McClain *et al.*, 2012). Thus, these studies suggest that the fundamental factors controlling deep-sea diversity seem to be temperature and/or biological productivity as a food source.

In our study, no significant relationships were found between species diversity and paleoproductivity proxies, such as organic carbon and biogenic opal contents. However, in the two lowest diversity horizons, one horizon in OIS 6 corresponded to a biogenic opal peak (Figure 3). The other lowest diversity horizon in the middle of OIS 5 corresponded to horizons of low biogenic opal and organic carbon. The low peak of species diversity in OIS 6 resulted from the exclusive dominance of *Cassidulina* *reniforme*, which is indicative of high paleoproductivity. The primary cause of the exclusive dominance of *C. reniforme* is still unclear. This low abyssal diversity may be a complex response to several factors, including not only high paleoproductivity, but also deep-water cooling or oxygen decrease. Planktonic foraminiferal studies (e.g. Thompson, 1981) have indicated a strong regional cooling event in late OIS 6 in the northwestern Pacific. A sustained decrease in bottom-water temperature may have influenced the diversity decrease observed during the late glacial period (Hunt *et al.*, 2005; Yasuhara *et al.*, 2012).

In contrast, the low species diversity peak in the middle of OIS 5 resulted from the exclusive dominance of *Epistominella exigua*, which is indicative of low paleoproductivity. A seasonally restricted supply of phytodetritus would lead to the dominance of this phytodetritus-feeding species. Thus, poor food supply to the abyssal sea floor would result in the low diversity observed.

Evenness values are higher during glacial periods. Higher evenness may generally be associated with high productivity. In addition, high species diversity around the transition from glacial to interglacial periods may be associated with high productivity and deep-water warming synchronized with a deglacial low oxygen event, such as expansion of the oxygen minimum zone at intermediate depths in the subarctic North Pacific (Moffitt *et al.*, 2015).

Overall, we cannot adequately explain the relationship between species diversity and faunal changes, as the reason for the greater fluctuation in diversity during OIS 6 is unclear. Several environmental factors, including productivity, temperature, oxygen, and carbonate saturation would be associated with diversity changes on the glacial–interglacial scale. It will be necessary to obtain higher resolution diversity data with multi-proxy data, including productivity and temperature, from the abyssal Pacific to address this problem effectively.

Conclusions

Faunal changes in deep-sea benthic foraminifera on the Shatsky Rise suggested a direct response to orbital-scale paleoproductivity changes. The benthic foraminiferal assemblages on the Shatsky Rise and Hess Rise were closely related to changes in export productivity during the last 187 kyr. Four species, *Cassidulina reniforme*, *Eilohedra levicula*, *Epistominella exigua*, and *Uvigerina peregrina*, which were dominant on the Shatsky Rise and Hess Rise, were key components of the Quaternary deep-sea assemblages and are useful for determining paleoenvironments in the central northwestern Pacific. *Cassidulina reniforme* and *U. peregrina* increased in relative abundance with higher productivity, and the abundance of *Ep. exigua* increased under lower productivity conditions. In addition, paleoproductivity may be one of the most important factors affecting the processes regulating species diversity in deep-sea communities during the late Quaternary. In summary, deep-sea benthic foraminiferal assemblages reflect the glacial–interglacial history of long-term changes in a direct pelagic–benthic coupling.

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Faunal reference list of foraminiferal species in this study (in alphabetical order)

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Cassidulina reniforme Nørvang. *Cassidulina crassa* d'Orbigny var. *reniforme* Nørvang, 1945, p. 41, fig. 6.

Ehrenbergina trigona Goës. *Ehrenbergina serrata* Reuss var. *trigona* Goës, 1896, p. 49; *Ehrenbergina trigona* Goës: Jones, 1994, p. 61, pl. 55, figs. 2–3, 5.

Eilohedra levicula (Resig). *Epistominella levicula* Resig, 1958, p. 304, fig. 16; *Eilohedra levicula* (Resig): Lipps, 1965, p. 124.

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Globocassidulina subglobosa (Brady). *Cassidulina subglobosa* Brady, 1881; *Globocassidulina subglobosa* (Brady): Ujiié, 1990, p. 39, pl. 21, figs. 4–7.

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71, pl. 5, fig. 31; *Pullenia quinqueloba* (Reuss): Ujiié, 1990, p. 43, pl. 23, figs. 5–7; pl. 24, figs. 1–5.

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Uvigerina peregrina Cushman, 1923, p. 166, pl. 42, figs. 7–10. Lamb and Miller, 1984, p. 6, pl. 8, figs. 1–6; pl. 9, figs. 1–5.

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Author contributions

M. H. carried out the preparation of foraminiferal samples and identification of foraminiferal specimens. N. N. and K. O. checked her foraminiferal identification. In addition, K. O. carried out the numerical analysis. All authors contributed to the writing of the paper.

Appendix. Census data of benthic foraminifera in core NGC108.

Depth in core (cm)	1	5	12	20	36	44	52	68	84	100	108	124	140	156	172	188	200	204	220	236	252	268
Age (ka)	0.7	2.3	5.9	9.6	14.3	16.3	18.4	21.6	24.9	28.2	29.9	33.5	37.1	40.7	44.4	48.0	50.7	51.6	55.2	60.5	67.5	74.7
Sample number	Top	2-0	2-08	2-16	2-32	2-40	2-48	2-64	2-80	2-96	3-04	3-20	3-36	3-52	3-68	3-84	3-96	4-0	4-16	4-32	4-48	4-64
Astacolus sp.																						
Biloculinella depressa (d'Orbigny)			2		2						1			1					1			
Bolivinellina transrusens (Phleger and Parker)										1							2					
Brizalina pacifica (Cushman and McCulloch)	5	13	15	12	25	37	18	8	9	4	20	19	16	8	8	11	8	17	12	15	15	6
Brizalina sp.							8		1										1			
Fursenkoina complanata (Egger)	4	16	7	2	5	6			3	3	6	3	8	4	1	4	3	8	5	4	6	2
Cassidulina reniforme Nørvang	9	20	16		45	95	78	64	128	102	117	154	182	60	84	57	32	28	43	45	55	54
Cassidulina sp.																						
Chilostomella cushmani Chapman													1									
Chilostomella oolina Schwager	1					4	1	2	1	2	1	9	5	1	4	2					2	
Cibicidoides cicatriocosus (Schwager)												2				1						
Cibicidoides mundulus (Brady, Parker and Jones)											1											
Cibicidoides pachyderma (Rzehak)		1					1															
Cibicidoides robertsoniana (Brady)													4									
Cibicidoides sp.				4				1														
Dentalina communis d'Orbigny														1						1		1
Dentalina sp.														1								
Eggerella bradyi (Cushman)	1			1							1			2			6		1	2	3	2
Ehrenbergina trigona Goës	6		3	12	12	2	3		3	2	4	4	9	2		4	5	10	2	8	3	3
Eilohedra levicula (Resig)	17	22	12	5	61	86	79	78	114	52	107	131	153	92	74	82	72	73	39	50	50	52
Epistominella exigua (Brady)	145	214	104	174	59	14		3	5	9	3	10	34	104	97	129	162	143	118	57	58	78
Epistominella sp.																						
Eponides sp.			1		17		10	16		31								26	10			
Eusphaeroidina inflata Ujiié		4	1																			
Evolvocassidulina bradyi (Norman)																						
Evolvocassidulina sp.																						
Evolvocassidulina ? sp.																						
Favulina hexagona (Williamson)		1																				
Fissulina quadricarinata (Sidebottom)														1								
Fissurina alveolata (Brady)						1													1		2	6
Fissurina atlantica Jones																						
Fissurina barkeri Ujiié					1																	
Fissurina collifera (Buchner)																					1	
Fissurina crebra (Matthes)				2													1					
Fissurina cucurbitasema Loeblich and Tappan																						
Fissurina exsculpta (Brady)																						
Fissurina fimbriata (Brady)										2			1						1			
Fissurina laevigata Reuss										1												
Fissurina periperforata Ujiié									1													
Fissurina radiata Seguenza																						
Fissurina wiesneri Barker																	1					
Fissurina spp.		5						1			2	11	9	3			6	8		4		
Fissurina ? sp.							5									3						
Fontbotia wuellerstorfi (Schwager)	6	17	6	13	4	9	5	3	3	4		11	4	6	2	7	15	10	8	5	8	4
Francesita advena (Cushman)														1	1			2	4	1		
Fursenkoina cedrosensis (McCulloch)				8								1										
Fursenkoina shreibersiana (Czjzek)																					1	6
Fursenkoina sp.															1							
Glandulonodosaria calomorpha (Reuss)												1										
Globobulimina sp.																						
Globocassidulina sp.				3																		
Globocassidulina subglobosa (Brady)				4			18	32	19													
Gyroidina lamarckiana (d'Orbigny)				14	2						2		1						2			
Gyroidina neosoldanii (Brotzen)										2					2							
Gyroidinoides kawagatai (Ujiié)																						
Gyroidinoides orbicularis (d'Orbigny)		6	1																		11	5
Gyroidinoides sp.		1			2							12										8
Hansenisca soldanii (d'Orbigny)		1	2	6		5							2	1	14			1	1			
Heteromorphina calomorpha (Reuss)																						
Hoeglundina elegans (d'Orbigny)	1				2		1	1														
Hormosinella guttifera (Brady)	1																					
Ioanella tumidulus (Brady)		2									1											
Karreriella hanzawai (Takayanagi)	1			2	1																	
Karreriella sp.		1																				
Laevidentalina curta (Ujiié)												1										
Lagena alticostata (Cushman)																						1
Lagena apiopleura Loeblich and Tappan																			1			
Lagena foliformia (Buchner)																						
Lagena gracillima (Seguenza)	1																					
Lagena hispidula Cushman												1								1		
Lagena nebulosa Cushman			1	3								1		1								
Lagena substriata Williamson	1				1		2				2	1										
Lagena sp.				1																		
Lenticulina limbosa (Reuss)																						
Lernella sp.					1																	

Appendix. *Continued 1.*

Depth in core (cm)	284	300	312	328	344	360	376	392	404	436	452	468	484	500	512	528	544	560	576	592	606	622	640
Age (ka)	82.0	84.2	85.9	88.8	92.4	96.0	104.3	112.6	118.8	132.5	137.5	142.5	147.5	151.0	152.4	154.3	158.3	164.4	170.4	176.5	179.7	183.4	187.1
Sample number	4-80	4-96	5-08	5-24	5-40	5-56	5-72	5-88	6-0	6-32	6-48	6-64	6-80	6-96	7-08	7-24	7-40	7-56	7-72	7-88	c/c 60	c/c 76	c/c 92
Astacolus sp.																							1
Biloculinella depressa (d'Orbigny)									1														
Bolivinellina transrusens (Phleger and Parker)									3	5													
Brizalina pacifica (Cushman and McCulloch)	8	3		1						12	29	7	7	4	6	8		2	7	3	1	1	4
Brizalina sp.				1				1					3	1			1			2	1		1
Fursenkoina complanata (Egger)	6	2		1	4	4	3	2	2	1	4	1	2	2	1	6	8	5	5	4	11	3	10
Cassidulina reniforme Nørvang	56	25	19	76	32	14	11	13	6	88	125	209	172	215	84	36	24	53	145	135	49	21	63
Cassidulina sp.																							
Chilostomella cushmani Chapman																							
Chilostomella oolina Schwager			1	5							1	1	2					1	4	1			3
Cibicidoides cicatriocosus (Schwager)																							
Cibicidoides mundulus (Brady, Parker and Jones)																							
Cibicidoides pachyderma (Rzehak)																							
Cibicidoides robertsoniana (Brady)		1					2		4		1						1					1	
Cibicidoides sp.																							
Dentalina communis d'Orbigny																							
Dentalina sp.																							
Eggerella bradyi (Cushman)							2	2	7													2	2
Ehrenbergina trigona Goës	3	11	11	5		8	8							1	3	4	4	2	3	2	4		3
Eilohedra levicula (Resig)	63	96	117	71	129	114	95	99	69	20	30	21	29	31	90	106	109	97	65	71	75	80	94
Epistominella exigua (Brady)	140	142	63	29	103	203	190	103	143	54	6	4	13	12	21	41	47	37	33	31	55	68	23
Epistominella sp.												16	28	18	7	13	8	14	5	1			
Eponides sp.		7			8	7	7	10	2	1	1	4	9	2	10		2	14	1	3	4		4
Eusphaeroidina inflata Ujiié																							
Evolvocassidulina bradyi (Norman)																			1				
Evolvocassidulina sp.										1													
Evolvocassidulina ? sp.						1																	
Favulina hexagona (Williamson)										2													
Fissulina quadricarinata (Sidebottom)																							
Fissurina alveolata (Brady)																					1		
Fissurina atlantica Jones								1															
Fissurina barkeri Ujiié																							
Fissurina collifera (Buchner)																							
Fissurina crebra (Matthes)			2						1														
Fissurina cucurbitasema Loeblich and Tappan																2	2						
Fissurina exsculpta (Brady)																	1						
Fissurina fimbriata (Brady)																							
Fissurina laevigata Reuss																						1	
Fissurina periperforata Ujiié																			1				
Fissurina radiata Seguenza																						1	
Fissurina wiesneri Barker	1																						
Fissurina spp.			3		1		1		1							1		1			3		
Fissurina ? sp.																							
Fontbotia wuellerstorfi (Schwager)	6	8	16	1	1	1	2	6	8	2	3		1	9	2		8	6	2	3	2	3	1
Francesita advena (Cushman)			8	2	1				2														2
Fursenkoina cedrosensis (McCulloch)																							
Fursenkoina shreibersiana (Czjzek)																							
Fursenkoina sp.																							
Glandulonodosaria calomorpha (Reuss)										2	2												
Globobulimina sp.																			1	3			
Globocassidulina sp.																							
Globocassidulina subglobosa (Brady)		10	5					2	2								3		2		3		1
Gyroidina lamarckiana (d'Orbigny)				3		1			8	12	3				2		2		2	4	10	3	6
Gyroidina neosoldanii (Brotzen)									4	1													
Gyroidinoides kawagatai (Ujiié)															1								
Gyroidinoides orbicularis (d'Orbigny)			1												2								
Gyroidinoides sp.	2																						
Hansenisca soldanii (d'Orbigny)					4		1	1		1				3						1	1		1
Heteromorphina calomorpha (Reuss)															1			1					
Hoeglundina elegans (d'Orbigny)										3	7												
Hormosinella guttifera (Brady)																							
Ioanella tumidulus (Brady)									1		1												
Karreriella hanzawai (Takayanagi)																							
Karreriella sp.																							
Laevidentalina curta (Ujiié)																							
Lagena alticostata (Cushman)																							
Lagena apiopleura Loeblich and Tappan																							
Lagena foliformia (Buchner)															1								
Lagena gracillima (Seguenza)	1	1	1																				
Lagena hispidula Cushman																							
Lagena nebulosa Cushman		1										1						1					
Lagena substriata Williamson				2	1								1										
Lagena sp.															1				1				
Lenticulina limbosa (Reuss)									1														
Lernella sp.																							

Appendix. *Continued 2.*

Depth in core (cm)	1	5	12	20	36	44	52	68	84	100	108	124	140	156	172	188	200	204	220	236	252	268
Age (ka)	0.7	2.3	5.9	9.6	14.3	16.3	18.4	21.6	24.9	28.2	29.9	33.5	37.1	40.7	44.4	48.0	50.7	51.6	55.2	60.5	67.5	74.7
Sample number	Top	2-0	2-08	2-16	2-32	2-40	2-48	2-64	2-80	2-96	3-04	3-20	3-36	3-52	3-68	3-84	3-96	4-0	4-16	4-32	4-48	4-64
Marginulina sp.							1															
Marginulina cf. *obesa* Cushman							1															
Marginulina obesa Cushman			1																			
Martinottiella sp.			1																			
Melonis barleeanus (Williamson)		2			7	5	4		4		1	6			8	1						
Melonis sphaeroides Voloshinova						4						2	3									
Melonis sp.						1																
Melonis ? sp.																						
Nodellum membranaceum (Brady)														1								
Oolina globosa (Montagu)			1			3					1	2	1	1	1		1					1
Oolina sp.																						
Ophthalmidium acutimargo (Brady)										1												
Oridorsalis tenera (Brady)		4		1	4							1			2							
Oridorsalis umbonatus (Reuss)	10	4	5					5	12	4	11	11	18	9	1	2	20	8		14	9	
Oridorsalis sp.						4																
Pacinonion lateralis (Cushman)																7	17				4	
Pacinonion minutus (Ujiié)																						
Pacinonion novozealandicum (Cushman and Edwards)							4		5		10	5	21	13				9		7		
Pandaglandulina torrida (Cushman)					1																	
Parafissurina buckneri Ujiié																						
Parafissurina fornasini (Buchner)																						1
Parafissurina lateralis (Cushman)									3													
Parafissurina sp.				1											1							
Parafissurina subcarinata (Parr)				1																		
Parafissurina tectulostoma Loeblich and Tappan																						
Planulina aff. *subinflata* (Bandy)			7	17		1			1		2		5	1					2			
Planulina sp.																			2			
Porogavelinella ujiiei (Kawagata)	4		4	1	1	18			19		17	28	20	27	13	16	12			22	32	20
Porogavelinella sp.																						
Pseudofissurina mccullochae Jones																						
Pullenia bulloides (d'Orbigny)	2			1							5						1	2	1	2	4	4
Pullenia malkinae Coryell and Mossman				2																		
Pullenia miocenica Kleinpell		2												1			16					
Pullenia okinawaensis Ujiié								9		13							1				2	2
Pullenia quadriloba (Reuss)			1	1		1	1		6				3	1		8						
Pullenia quinqueloba (Reuss)	3	3					3	7		4	7	11	1	1	5			5	9	13	6	9
Pullenia sp.	8	7	8	2	1			3		1	5	4	2	1	1			5		1		5
Pullenia ? sp.									1							1	4					
Pulleniella asymmetrica (Ujiié)																1						
Pyrgo lucernula (Schwager)								1														
Pyrgo murrhina (Schwager)				1		3			1	1			1				1	3	2			1
Pyrgo oblonga (d'Orbigny)											1			1	1							
Pyrgo serrata (Bailey)					1		2															
Pyrulina angusta (Egger)					1																	
Pyrulina fusiformis (Roemer)								5														
Pyrulina sp.												1										
Pytine paradoxa (Sidebottom)		1											1									
Quadrimorphina glabra (Cushman)			1			1																
Quinqueloculina polygona d'Orbigny																						
Quinqueloculina venusta Karrer	1			1				2														
Quinqueloculina weaveri (Rau)													2	1					1			
Quinqueloculina sp.																	1					
Rotamorphina minuta (Schubert)		12				1	1															
Rutherfordoides rotundiformis (McCulloch)											1											
Rutherfordoides sp.																				1		
Rutherfordoides tenius (Phleger and Parker)											3		1	1		3		4	1	6		
Seabrookia earlandi (Wright)											2							2				
Siphotextularia catenata (Cushman)	1		2	1																		
Siphotextularia flintii (Cushman)		3								1										1		4
Sphaeroidina bulloides d'Orbigny				3																		
Stainforthia sp.					12		5	3														
Triloculina frigida (Lagoe)							12	8	8	4	8							2	1	13	6	2
Triloculina lucernula (Schwager)	1				3										9	5	1			1		
Triloculina tricarinata d'Orbigny						13						11	22	13								
Triloculina sp.						1																
Turrilina brevispira Ten Dam					2																	
Uvigerina canariensis d'Orbigny							1															
Uvigerina hispida Schwager							1															
Uvigerina peregrina Cushman	1	6	5	5	2	6					1		2	1					1	4		
Uvigerina proboscidea Schwager			1	1		2											4	2	11			
Uvigerina sp.	1																1	1	4			
Valvulineria minuta (Schubert)	3															2					5	
Unidentified specimens	5	4	3	3	7	1		6			12		14		1	7	15	2		3	8	
Total number of specimens	239	372	211	308	282	324	265	258	347	244	355	454	546	362	331	353	408	371	285	281	291	277
Number of species	24	25	25	31	28	25	25	20	21	21	29	28	29	32	21	20	24	21	26	24	21	24
Benthic foraminiferal number (specimens g^{-1})	2016	1414	829	1110	961	1590	1288	1272	1539	1206	1156	2256	1751	1659	2310	2575	2442	2748	1600	564	605	1093
Hurlbert species diversity $E(S_{100})$	17.1	16.8	18.7	19.9	18.1	17.3	17.5	15.8	14.4	15.3	17.8	17.7	16.6	16.3	13.4	14.0	16.0	16.4	17.6	18.0	17.2	18.0
Shannon species diversity $H(s)$	1.68	1.82	2.05	1.94	2.34	2.19	2.17	2.09	1.86	1.92	2.04	2.14	2.07	2.14	1.93	1.89	2.04	2.11	2.07	2.45	2.33	2.26
Evenness e^H/S	0.22	0.25	0.31	0.22	0.39	0.36	0.35	0.42	0.31	0.32	0.27	0.30	0.28	0.26	0.33	0.34	0.32	0.38	0.29	0.49	0.51	0.40

Appendix. *Continued 3.*

Depth in core (cm)	284	300	312	328	344	360	376	392	404	436	452	468	484	500	512	528	544	560	576	592	606	622	640
Age (ka)	82.0	84.2	85.9	88.8	92.4	96.0	104.3	112.6	118.8	132.5	137.5	142.5	147.5	151.0	152.4	154.3	158.3	164.4	170.4	176.5	179.7	183.4	187.1
Sample number	4-80	4-96	5-08	5-24	5-40	5-56	5-72	5-88	6-0	6-32	6-48	6-64	6-80	6-96	7-08	7-24	7-40	7-56	7-72	7-88	c/c 60	c/c 76	c/c 92
Marginulina sp.																							
Marginulina cf. *obesa* Cushman																							
Marginulina obesa Cushman																							
Martinottiella sp.																							
Melonis barleeanus (Williamson)					4					3	5	2	1	6	11	5	6	4	2	4	2	3	5
Melonis sphaeroides Voloshinova											1												
Melonis sp.																							
Melonis ? sp.																2							
Nodellum membranaceum (Brady)																							
Oolina globosa (Montagu)													2										
Oolina sp.		2																					
Ophthalmidium acutimargo (Brady)																							
Oridorsalis tenera (Brady)						1																	
Oridorsalis umbonatus (Reuss)	2	3	9	3	3	3	7	1	3	2			2		1			2		1	3	1	1
Oridorsalis sp.																							
Pacinonion lateralis (Cushman)																							
Pacinonion minutus (Ujiié)									12	4		4		3						7			
Pacinonion novozealandicum (Cushman and Edwards)				7	2			6	2		2		3		4	10	2	7	4		11	11	5
Pandaglandulina torrida (Cushman)																							
Parafissurina buckneri Ujiié	1																						
Parafissurina fornasini (Buchner)			1					1	1														
Parafissurina lateralis (Cushman)																							
Parafissurina sp.				1	1					1													
Parafissurina subcarinata (Parr)								1															
Parafissurina tectulostoma Loeblich and Tappan																					2	3	
Planulina aff. *subinflata* (Bandy)	1	6	5	4					1	1					1		2			3	1		8
Planulina sp.																							
Porogavelinella ujiiei (Kawagata)	28	20	4	10	6	16	14	6	2	22	12		5	12	16	20	4	12	4	3	21	22	22
Porogavelinella sp.																1							
Pseudofissurina mccullochae Jones																						2	
Pullenia bulloides (d'Orbigny)	3	2			1	1	1							3		1					5		
Pullenia malkinae Coryell and Mossman																							
Pullenia miocenica Kleinpell																							
Pullenia okinawaensis Ujiié	1	3																					
Pullenia quadriloba (Reuss)	11						4	1															
Pullenia quinqueloba (Reuss)	7	13	11	2	12	14			2														
Pullenia sp.	3	1	3		1	2	2	6	4		1	1	1			3	2	6	1	2	6	3	9
Pullenia ? sp.							1				9												
Pulleniella asymmetrica (Ujiié)									1						7	1	1		1	1	1	3	4
Pyrgo lucernula (Schwager)																							
Pyrgo murrhina (Schwager)		1																			1	2	1
Pyrgo oblonga (d'Orbigny)				2	1							1	1	2	2	6	5	5	4		1		1
Pyrgo serrata (Bailey)																							
Pyrulina angusta (Egger)			1																				
Pyrulina fusiformis (Roemer)									1														1
Pyrulina sp.																							
Pytine paradoxa (Sidebottom)							1																
Quadrimorphina glabra (Cushman)										4	4												
Quinqueloculina polygona d'Orbigny	1																						
Quinqueloculina venusta Karrer																							
Quinqueloculina weaveri (Rau)																	1				2	1	
Quinqueloculina sp.	2																						
Rotamorphina minuta (Schubert)																		1					
Rutherfordoides rotundiformis (McCulloch)																							
Rutherfordoides sp.																							
Rutherfordoides tenius (Phleger and Parker)					3			1													1		
Seabrookia earlandi (Wright)																		3					
Siphotextularia catenata (Cushman)									1														
Siphotextularia flintii (Cushman)																	3					1	
Sphaeroidina bulloides d'Orbigny																							
Stainforthia sp.																							
Triloculina frigida (Lagoe)	2		2		1		5				2	3	9	11	7	4	8	7	16	8	12	4	7
Triloculina lucernula (Schwager)																							
Triloculina tricarinata d'Orbigny				1				1						1									
Triloculina sp.	1									1												1	
Turrilina brevispira Ten Dam																							
Uvigerina canariensis d'Orbigny																							
Uvigerina hispida Schwager																							
Uvigerina peregrina Cushman	1	3								9	6				1	1							1
Uvigerina proboscidea Schwager																		2	2				
Uvigerina sp.			1							1			1		1				2				
Valvulineria minuta (Schubert)																							
Unidentified specimens	13	11	3	5	2	3	2	2	2	8	7		1	1	16					4		1	5
Total number of specimens	363	372	287	232	321	393	359	266	297	261	262	275	293	337	299	271	254	283	314	297	289	242	289
Number of species	24	22	21	20	21	15	19	20	29	25	22	14	20	18	25	20	24	23	25	22	28	24	28
Benthic foraminiferal number (specimens g^{-1})	1389	1835	1023	407	1397	2130	2218	1495	816	924	2334	4944	5376	3213	1108	1040	2841	798	877	1057	905	797	825
Hurlbert species diversity $E(S_{100})$	14.7	14.9	15.3	14.8	12.9	9.8	12.2	13.0	18.0	17.3	16.3	9.6	13.5	12.9	16.8	15.2	17.9	17.2	15.9	15.1	19.0	16.8	19.2
Shannon species diversity $H(s)$	1.92	1.92	1.98	1.88	1.69	1.41	1.51	1.65	1.88	2.09	1.92	1.04	1.62	1.50	2.04	2.08	2.07	2.22	1.88	1.77	2.38	2.04	2.27
Evenness e^H/S	0.30	0.32	0.35	0.33	0.26	0.27	0.24	0.26	0.23	0.35	0.32	0.20	0.25	0.25	0.33	0.40	0.33	0.40	0.26	0.27	0.39	0.32	0.35