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LIVING (STAINED) DEEP-SEA FORAMINIFERA OFF HACHINOHE (NE JAPAN, WESTERN PACIFIC): ENVIRONMENTAL INTERPLAY IN OXYGEN-DEPLETED ECOSYSTEMS

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ABSTRACT

Live (Rose-Bengal stained) deep-sea foraminiferal faunas have been studied at five stations between 500–2000-m depth along the NE Japanese margin (western Pacific) to understand how complex environmental conditions (e.g., oxygen depletion, organic matter) control their structure (i.e., diversity, standing stocks, and microhabitats). All stations are characterized by silty sediments with no evidence of recent physical disturbances. The three stations located between 760–1250 m are bathed by dysoxic bottom waters (<45 µmol/L). Although high organic-carbon contents are recorded at all stations (>2.2% DW), only the oxygen-depleted sites are characterized by higher concentrations of sugars, lipids, and enzymatically hydrolysable amino acids (EHAA). Sedimentary contents in chlorophyllic pigments decrease with water depth without any major change in their freshness (i.e., [Chl *a*/(Chl *a* + Pheo *a*)] ratios). Both *Uvigerina akitaensis* and *Bolivina spissa* are restricted to the stations bathed by dysoxic waters, proving their oxygen-depletion tolerance. In such conditions, both phytophagous taxa are obviously able to take advantage of labile organic compounds (e.g., lipids and EHAA) contained in phytodetritus. *Nonionella stella* and *Rutherfordoides cornuta* survive in oxygen-depleted environments probably via alternative metabolic pathways (e.g., denitrification ability) and a large flexibility in trophic requirements. At stations where oxygen availability is higher (i.e., >70 µmol/L in bottom water) and where bioavailable organic compounds are slightly less abundant, diversity indices remain low, and more competitive species (e.g., *Uvigerina curticosta, U.* cf. *U. graciliformis*, *Nonionella globosa*, *Nonionellina labradorica*, and *Elphidium batialis*) are dominant.

INTRODUCTION

In deep-sea ecosystems, both spatial and temporal dynamics of benthic foraminifera are constrained by various physico-chemical parameters (e.g., Gooday, 2003; Jorissen et al., 2007). The bioavailability of sedimentary organic matter at the seafloor is a major ecological factor in controlling foraminiferal diversity, standing stocks, and microhabitats (e.g., Jorissen et al., 1998; Kitazato et al., 2000; Fontanier et al., 2002, 2003; Langezaal et al., 2006; Duchemin et al., 2007; Koho et al., 2008; Larkin & Gooday, 2009; Gooday et al., 2010; Duros et al., 2011, 2013). In eutrophic settings, high organic-matter flux can also limit the development of the benthic community by inducing either temporary or long-term hypoxia in the surface sediment (i.e., oxygen-minimum zones; Sen Gupta & Machain-Castillo, 1993; Jannink et al., 1998; Bernhard & Sen Gupta, 1999; Gooday et al., 2000; Kurbjeweit et al., 2000; Schumacher et al., 2007; Woulds et al., 2007; Glud et al., 2009; Mallon et al., 2012). Under hypoxic conditions, foraminiferal faunas are indeed characterized by low diversity and higher standing stocks due to the dominance of stress-tolerant species. In these settings, foraminiferal survival may rely on alternative metabolic pathway (e.g., nitrate respiration; Risgaard-Petersen et al., 2006; Høgslund et al., 2008; Glud et al., 2009; Piña-Ochoa et al. 2010; Koho et al., 2011; Bernhard et al. 2012a, b; Glock et al., 2012). Therefore, both oxygen and nitrate concentrations may influence foraminiferal communities. However, as these parameters are all strongly interrelated, it is difficult to detangle whether benthic foraminifera observed under hypoxic environments echo distribution of electron acceptors or whether they respond to organic-matter flux (e.g., Gooday, 2003; Jorissen et al., 2007). Other influences, which may play an important role in foraminiferal ecology, are hydro-sedimentary processes, such as sediment gravity flows and bottom nepheloid layers (e.g., Hess et al., 2005; Koho et al., 2007, 2008; Hess & Jorissen, 2009; Duros et al., 2011; Fontanier et al., 2013). These processes may either hinder the development of benthic communities by inducing physical disturbances at the seafloor or enhance the trophic regime by supplying organic matter by lateral advection to the deep ocean (e.g., Hess et al., 2005; Koho et al., 2007, 2008; Hess & Jorissen, 2009; Duros et al., 2011; Fontanier et al., 2013). Foraminiferal faunas are thus characterized by various stages of recolonization, depending on the frequency of

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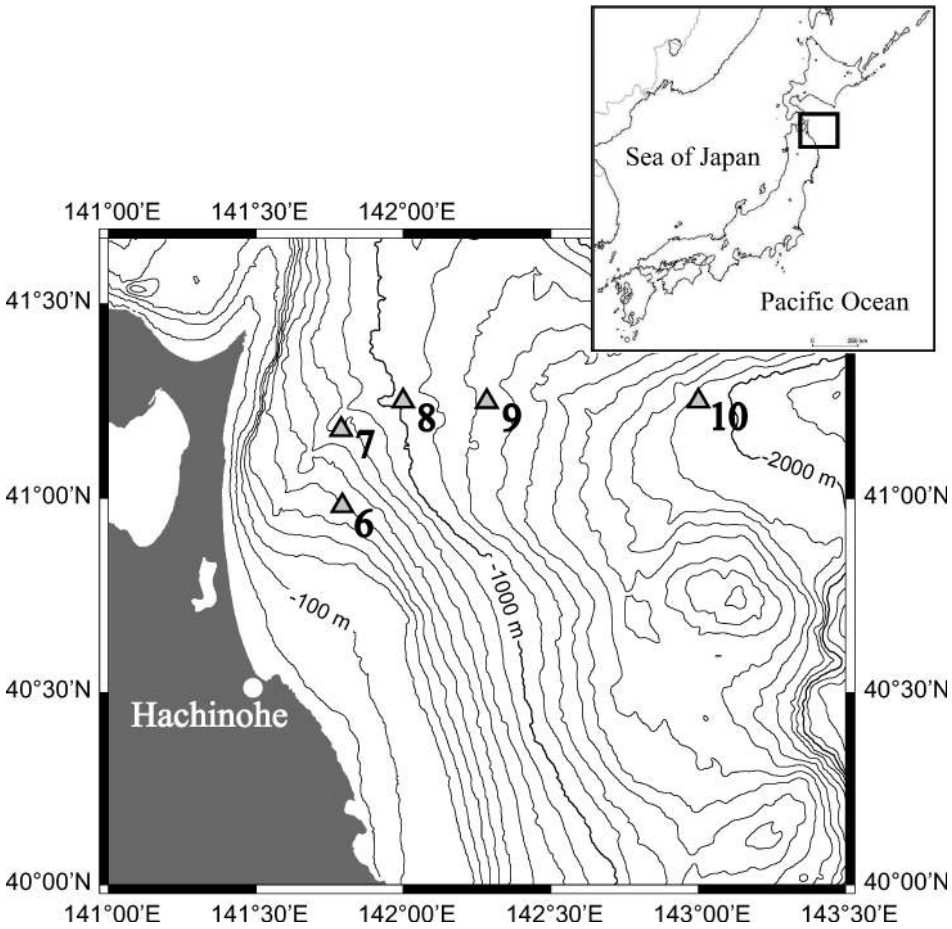

FIGURE 1. Bathymetry and location of the five investigated stations in the study area off Hachinohe (Japan, western Pacific). Station depths and geographic positions are listed in Table 1.

physical disturbance (e.g., turbidite), or by more stable equilibrium phases related to continuous focusing of organic matter (e.g., eutrophication). The overall structure of a living foraminiferal community is, therefore, a function of complex multifactorial constraints, which makes foraminifera very useful in biomonitoring studies and paleoenvironmental reconstructions, providing that their responses to individual environmental variables are soundly assessed.

In this study, we present an ecological investigation of foraminiferal faunas at five deep-sea stations along the Japanese margin off Hachinohe, NE Japan (Fig. 1; Table 1). They describe a bathymetric transect between 496–1963 m (Fig. 1). The study area is of high interest since it is characterized by a so-called oxygen-minimum zone (OMZ) at intermediate depths (700–1500 m). This OMZ results from a combination of high productivity and poor ventilation of upper intermediate waters (Nagata et al., 1992; Saino et al., 1998). Moreover, this area may be affected by sedimentary instability resulting from seismic and volcanic activities (Itou et al., 2000). Ikeya (1971) has already investigated living (stained) foraminiferal faunas off Hachinohe (NE Japan) along the shelf and the upper slope.

TABLE 1. Location of the five investigated stations. At each site, physico-chemical parameters were measured, including BWT (bottom-water temperature), BWS (bottom-water salinity), and BWO (bottom-water oxygen), and the number of multi-corer deployments is shown. A single asterisk (*) indicates that a core was collected on the second deployment for radionuclide analysis (see Material-and-Methods section). The double asterisks (**) indicate that BWT, BWS, and BWO (at station 7) were inferred from the CTD cast performed at station 10.

Stations	Multi-corer Deployment(s)	Latitude (N)	Longitude (E)	Depth (m)	BWT** (°C)	BWS**	BWO (μmol/L)
Station 6	2*	40°58.891′	141°47.572′	496	3.5	33.9	112
		40°58.904′	141°47.625′	498			
Station 7	1	41°10.647′	141°47.348′	760	3.3	34.2	42**
Station 8	2*	41°15.003′	142°00.028′	1033	2.9	34.3	36
		41°15.003′	141°59.965′	1026			
Station 9	1	41°14.982′	142°16.969′	1249	2.6	34.4	33
Station 10	2*	41°14.918′	142°59.989′	1963	2.0	34.6	70
		41°15.182′	143°00.101′	1963			

This work described different faunal zones in relation to bathymetry, but largely ignored the ecological relationships linking living communities and environmental factors. Paleoenvironmental studies were performed on fossil benthic foraminifera in long cores collected in this study area (e.g., Ohkushi et al., 2003, 2005; Hoshiba et al., 2006; Ikehara et al., 2006; Shibahara et al., 2007). These studies provided critical information on the relative strengths of the intermediate-water circulation and the OMZ, as well as ventilation and surface-water productivity during the Late Quaternary. Noticeably, Shibahara et al. (2007) proposed paleoenvironmental interpretations based on the distinction of Kaiho's (1994) three oxygen-indicative foraminiferal groups: oxic (>67 μmol/L), suboxic (13–67 μmol/L), and dysoxic (4–13 μmol/L). These works suggest that ventilation of intermediate waters changed throughout the Quaternary in relation to climatic oscillation. However, no close attention was paid to the possible role of organic detritus availability in controlling community structure. Recent in situ experimental works based on living faunas have demonstrated that ingestion rates and trophic requirements differ among foraminiferal taxa from the oxygen-depleted Japanese margin (Nomaki et al., 2005a, b, 2006, 2009, 2011). For instance, although phytophagous species feed on fresh phytodetritus (e.g., *Uvigerina akitaensis* Asano, *Bolivina spissa* Cushman), others also ingest detritus and bacteria [e.g., *Globobulimina affinis* (d'Orbigny), *Chilostomella ovoidea* (Reuss)]. All these works suggest that organic-detritus quality and foraminiferal structure are strongly interrelated.

In this study, we have investigated the living (stained) foraminiferal communities along the NE Japanese margin in relation to physico-chemical conditions at and below the sediment-water interface. Foraminiferal standing stocks, diversity, and microhabitats were studied at the five selected stations. Geochemical conditions (oxygen, nitrate, ammonia, organic compounds) and sediment properties (grain-size distribution and total ^{210}Pb activities) were also precisely described. We examined many descriptors of organic matter (OC, C/N atomic ratio, δ^{13}C in organic carbon, lipids, carbohydrates, amino acids, chlorophyllic pigments) to get an overall description of both qualitative and quantitative changes in sedimentary organics. The aim of this ecological investigation is to assess the role played by the concentrations of dissolved oxygen (in pore and bottom waters) and sedimentary organic matter (qualitatively and quantitatively) in controlling the structure of living foraminiferal faunas in view of unraveling their potential as proxies for past redox (or bottom-water oxygen) conditions and detrital organic matter inputs. Please note that we have followed the nomenclature defined by Bernhard & Sen Gupta (1999) to qualify oxygenation levels (i.e., oxic >44.6 μmol/L, dysoxic between 4.5–44.6 μmol/L, microxic <~4.5 μmol/L, anoxic = 0 μmol/L).

MATERIALS AND METHODS

Study area

The five stations investigated in this paper were sampled during the KT11-20 cruise in August 2011, aboard the R/V *Tansei-Maru* (Atmosphere and Ocean Research Institute, University of Tokyo/JAMSTEC). This scientific cruise took place off Hachinohe (NE Japan, western Pacific), five months after the Tōhoku-oki earthquake (Mw = 9.0) and tsunami that struck the eastern coast of Japan (Fig. 1). Three major currents dominate surface waters in this region: the Tsugaru Warm Current, Kuroshio Current, and Oyashio Current. The Tsugaru Warm Current is an extension of the Tsushima Current that flows northward through the Sea of Japan, and in turn is a branch of the warm, saline waters of the Kuroshio Current. The Tsugaru Warm Current supplies warm waters eastward through the Tsugaru Strait into the Pacific Ocean over a sill at 130-m depth. The maximum depth of the Tsugaru Warm Current is <200 m. As a result, cool waters of the Oyashio Current (originating from the subpolar region) underlie those of the Tsugaru Warm Current where they intersect. The Kuroshio Current transports warm (>15°C), saline, and oligotrophic waters northeast along the southeast coast of Japan (Nagata et al., 1992). The convergence of these three surface waters generates hydrological fronts that are very productive, especially during the so-called "Yakumizu" bloom of late winter and spring diatoms (Saino et al., 1998; Itou et al., 2000).

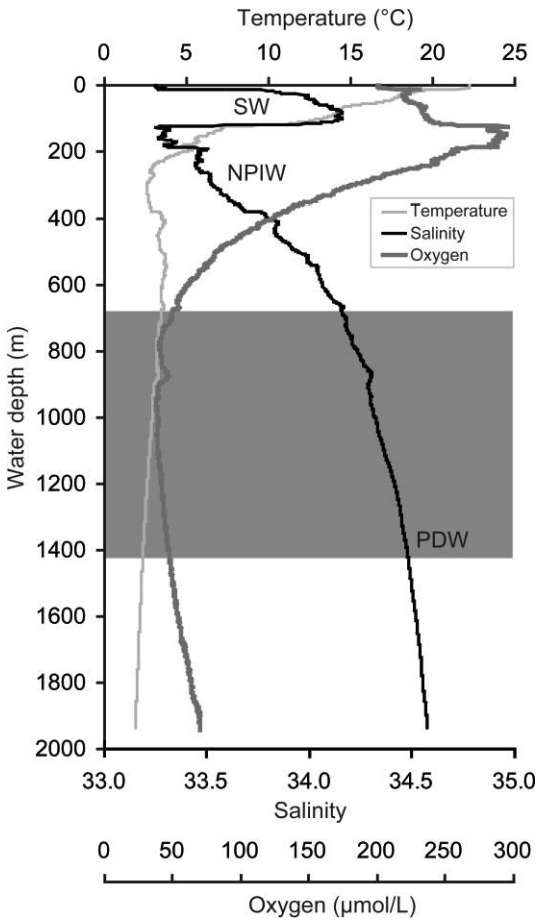

FIGURE 2. Temperature, salinity, and oxygen profiles from the water column in the study area. These data were gathered by CTD cast at station 10. The shaded area defines the bathymetric zone where bottom-water oxygen is dysoxic (<45 μmol/L according to Bernhard & Sen Gupta, 1999). SW = Surface Waters; NPIW = North Pacific Intermediate Water; PDW = Pacific Deep Water.

Below the surface waters, the North Pacific Intermediate Water (NPIW), formed in the NW Pacific (Talley, 1991; Yasuda, 1997; Fig. 2), is defined by the salinity minimum at depths below 200 m. Deeper, the NPIW mixes gradually with the more saline Deep Pacific Water (DPW), which usually occurs between 800–3000-m depth within temperate latitudes (Bostock et al., 2010). An oxygen-depleted water mass exists at intermediate depths (generally around 700–1500 m) in the front area off Hachinohe because of reduced intermediate-water ventilation and high surface-water primary production (through mineralization of sinking organic particles; Nagata et al., 1992; Fig 2). In many studies (e.g., Ohkushi et al., 2003, 2005; Hoshiba et al., 2006; Ikehara et al., 2006; Shibahara et al., 2007), this oxygen-depleted water mass is defined as an oxygen-minimum zone (OMZ), even if oxygen concentration does not fall below the 22 μmol/L threshold defined by Helly & Levin (2004) to characterize a classical OMZ. In our study area, station 6 (496-m depth) is located in the upper NPIW (Figs. 1 and 2; Table 1). Stations 7 (760 m), 8 (1033 m), and 9 (1249 m) are located in the oxygen-depleted water mass, where dissolved oxygenation is <45 μmol/L (Fig. 2; Table 1). Station 10 (1963 m) is bathed by the PDW.

Sampling Strategy

Sediment samples were collected with a Barnett-type multi-corer equipped with eight Plexiglas tubes (82-mm internal diameter; Barnett et al., 1984). The multi-corer allowed sampling of the upper decimeter of the sediment column, the overlying bottom waters, and a comparatively undisturbed sediment-water interface. It was deployed once at stations 7 and 9, and twice at stations 6, 8, and 10. At the latter stations, the core dedicated only to radionuclide (total ^{210}Pb) analysis was gathered on the second deployment (Table 1). At each station, a first core was sliced horizontally every 0.5 cm from the sediment-water interface to a 4-cm depth, every 1 cm between 4–6-cm depth and then every 2 cm down to 10 cm in the sediment column. Each sediment slice was divided into four subsamples and immediately frozen (-80°C) on board. Back at the laboratory, three of them were freeze-dried and analyzed for sedimentary organic matter (OC, C/N atomic ratio, lipids, carbohydrates, amino acids, δ^{13}C in organic carbon) and grain size. The fourth subsample was used for chlorophyllic pigment analysis. Please note that δ^{13}C was analyzed only in the first 0.5 cm, whereas amino acids were processed in the first centimeter of sediment. At stations 6, 8, and 10 a second core (collected on the first multi-corer deployment) was used for oxygen microprofiles. A third core was assessed for pore-water extraction (e.g., nitrate, ammonium) and solid phase treatment, and the last core from each station was processed for foraminiferal investigation.

Geochemical Analysis

Bottom-Water Oxygen Concentration and In-Sediment Oxygen Profiles

Bottom seawater was collected in Niskin bottles installed on a rosette system equipped with a CTD (Conductivity, Temperature, and Depth). Oxygen concentrations in the water at each station (except for station 7) were determined by Winkler titration. Oxygen microprofiles within sediment cores collected at stations 6, 8, and 10 were developed using a handmade incubation chamber and a microprofile system commercialized by Unisense A/S. After opening the lid of the core sampler, a subcore was quickly collected using a piston device made from a 50-ml syringe. The subcore was put in the incubation chamber filled with the Niskin bottle seawater collected above the sea floor, and left for more than nine hours, while keeping the water temperature and oxygen concentration the same as in the original bottom water. Fluctuation of oxygen concentration in the chamber was <0.5 μmol/L. After the incubation, oxygen was measured with an OX-50 microsensor and a motor controller.

Pore-Water Nitrate and Ammonium

Immediately upon arrival on board, bottom water overlying the core dedicated to pore-water extraction was sampled with a syringe, and the related core was transferred to an N_2-purged glove bag. Following the removal of the remaining overlying water, the core was sliced at discreet intervals (top 2 cm every 0.5 cm, from 2–10 cm every 1 cm, and between 10–20 cm every 2 cm). Sediment slices were placed in 50-ml centrifuge tubes, which were closed in an N_2 atmosphere. The samples were subsequently centrifuged for 20–30 minutes at 2800 rpm outside the glove bag and then transferred back into it. Under the N_2 atmosphere, the supernatant was removed and filtered over 0.45-μm Teflon™ filters. In some cases where no or little pore water was extracted, the samples were combined with adjacent ones to allow further analyses. Both the solid phases and pore-water samples were immediately frozen (-20°C) to await further analyses. Back at the laboratory, the pore-water nitrate concentration was measured by a Bran-Luebbe AA3 autoanalyzer, and ammonium by spectrophotometry, using phenol-hypochlorite (Helder & De Vries, 1979).

Organic-Matter Analyses

Total nitrogen, total carbon, and organic-carbon concentrations (TN, TC and OC, respectively) were measured using the freeze-dried sediment subsamples (~280 mg DW). Homogenized, weighted samples were analyzed in an automatic CN-analyzer Elementar VarioMax after acidification with 2M HCl at 40°C overnight to remove carbonates. Precise measurements of about 2% and 0.3% DW were recorded for TN and OC, respectively. Total lipids were measured using a colorimetric method after extraction of 150 mg DW sediment subsample(s) with a 2/1 (V:V) chloroform-methanol mixture. Absorbances were measured at 520 nm using a Beckman® UV spectrophotometer (10% precision; Barnes & Blackstock, 1973). Total carbohydrates (''sugars'') were measured using a colorimetric method on a 200-mg DW fraction hydrolyzed by 3M H_2SO_4. Absorption of the products resulting from the anthrone-sulfuric acid reaction was measured at 625 nm using a Beckman® UV spectrophotometer (8% precision; Brink et al., 1960).

TABLE 2. Geochemical and sedimentological features of the five investigated stations. Abbreviations are explained in the Materials-and-Methods section.

	Geochemical features				
Stations	OC(% DW)	C/NAtomic Ratio	$\delta^{13}C$(‰)	TCHO(mg/g DW)	Lipids(mg/g DW)
Station 6	2.2±0.3	8.5±0.8	−22.06	2.9±0.4	2.0±0.4
Station 7	2.6±0.1	8.5±0.1	−22.20	3.3±0.3	2.8±0.4
Station 8	2.5±0.1	8.7±0.3	−22.03	3.3±0.6	2.4±0.3
Station 9	2.7±0.2	8.6±0.2	−21.74	3.7±0.7	2.5±0.3
Station 10	2.2±0.1	8.8±0.1	−22.07	3.0±0.1	2.3±0.6
	Geochemical features				
Stations	THAA(nmol/mg DW)	EHAA(nmol/mg DW)	EHAA/THAA (%)	Chl *a*(μg/g FW)	[Chl *a*/(Chl *a*+Phe *a*)](%)
Station 6	63.29±0.54	8.83±0.74	13.9±1.3	2.15±0.86	9.8±1.5
Station 7	102.88±6.05	10.84±4.02	10.4±3.3	1.86±0.97	8.4±1.4
Station 8	69.90±1.60	11.11±0.69	15.9±0.6	1.03±0.31	6.3±0.9
Station 9	96.88±3.97	14.44±3.04	14.8±2.5	1.23±0.40	7.4±0.6
Station 10	62.69±2.75	7.60±0.02	12.1±0.6	1.00±0.24	7.5±0.8
	Sedimentological features				
Stations	D_{10}(μm)	D_{50}(μm)	D_{90}(μm)	Lithology	SML(cm)
Station 6	5±0	24±1	116±4	Sandy silt	~5
Station 7	5±0	22±1	73±6	Silt	< 1
Station 8	4±0	20±1	76±1	Silt	< 1
Station 9	5±0	20±0	53±2	Silt	~5
Station 10	5±0	19±1	68±6	Silt	~5

Stable carbon isotopes ($\delta^{13}C$) were measured from samples treated with HCl (2M) to remove carbonate, and then, subsequently rinsed with cold deionized water to remove chloride before freeze-drying (Schubert & Nielsen, 2000). A few milligrams of the resulting powdered material were put in tin cups and placed in the automated sample carousel of the elemental analyzer (EA 3000 Eurovector) coupled to an Isotopic Ratio Mass Spectrometer (IR/MS, GVI Isoprime). The standard deviation for replicates of internal standards is less than ±0.2‰ for isotopic ratios.

Total hydrolysable amino acids (THAA) and enzymatically hydrolysable amino acids (EHAA) were assessed in the first centimeter of the freeze-dried sediment subsamples. Bulk sediment was first crushed and passed through a 200-μm mesh. THAA and EHAA were assayed according to Mayer et al. (1995). Approximately 15-mg DW of sediment were mixed with 500 μL of 6M HCl (100°C) and kept under vacuum for 24 h. Hydrolyzed subsamples (100 μL) were neutralized with 100 μL of 6M NaOH, and buffered with 2 mL of H_3BO_3 (0.4 M, pH = 10). Fluorescent derivatives were obtained by adding 200 μL of an orthophtaldialdehyde (OPA) solution (100 mg OPA/1 mL methanol, 100 mL buffer pH = 9.8, and 0.05 mL mercaptoethanol) and 2 mL of phosphate buffer (pH = 8) to 200 μL of those samples. Total hydrolysable amino acids were quantified 2½ min after OPA addition through florescence measurements (340-nm excitation wavelength and 453-nm emission wavelength) taken with a Perkin Elmer LS55 fluorescence spectrometer. Enzymatically hydrolysable amino acids (EHAA) were extracted following a biomimetic approach (Mayer et al., 1995). Approximately 100 mg of DW sediment were poisoned with a 1-mL solution containing sodium arsenate (0.1 M) and pentachlorophenol (0.1 mM) within a sodium phosphate buffer (pH = 8), and were incubated for 1 h at room temperature to prevent the bacterial utilization of amino acids released after the addition of 100 μL of proteinase K solution (1 mg/mL). Sediment was then incubated for 6 h at 37°C. After centrifugation, 75 μL of pure trichloroacetic acid were added to 750 μL of supernatant to precipitate macromolecules, which are considered to be unsuitable for absorption. After another centrifugation, 750 μL of the supernatant were hydrolyzed and processed as described for THAA. A blank accounting for possible degradation of the enzyme was carried out. Enzymatically hydrolysable amino acids were then quantified using the procedure described above for THAA. The EHAA/THAA percentage ratios were computed for each station (Rosenberg et al., 2003; Grémare et al., 2005; Pastor et al., 2011; Table 2). This ratio is indicative of the lability of amino acids.

For chlorophyll *a* and pheophytin *a* analysis, 0.5–3.7 g of frozen (–80°C) sediment subsamples were extracted overnight at 4°C with 90% acetone (final concentration taking into account the sediment-water content). They were then centrifuged and their supernatant was used to assess chlorophyll *a* and pheophytin *a* through the [Chl *a*/(Chl *a* + Pheo *a*)] ratios of Neveux & Lantoine (1993) that were computed in percent for each station (Table 2). This ratio is indicative of the freshness of plant material.

SEDIMENT PROPERTIES

Grain-Size Analysis

Grain size was analyzed with a Malvern® Diffraction Particle Size Laser. Before measuring, bulk (not decarbonated) sediments were immersed in water and moderately stirred with a plastic stick. Table 2 presents the mean values of the 10th, 50th, and 90th percentiles (D_{10}, D_{50}, and D_{90}, respectively). Mean values are calculated for all sediment intervals along the 10-cm core at each site.

Total ^{210}Pb Radionuclide Activity

Total ^{210}Pb activity is measured to determine the mixed-layer thickness below the sediment-water interface. The mixing may be related to biological and/or physical processes affecting the surface sediments. At each station, the sediment core dedicated to radionuclide analysis was sliced horizontally every 0.5 cm from the sediment-water interface to 4-cm depth, every 1 cm between 4–6-cm depth and then every 2 cm down to the bottom of the core. Sediment samples were stored in plastic bags at ambient temperature. Radionuclide activity at stations 6, 8, and 10 were measured at the Japan Agency for Marine-Earth Science and Technology (JAMSTEC). Sediment samples were transferred into plastic cubes in constant volume to measure water contents. After measuring the total weight, the plastic cubes were put in an oven at 80 °C and left for two days. Then, dry weight was measured and sediments were subsequently ground in a mortar. Two grams of powdered samples were transferred to plastic tubes and sealed hermetically. The samples were left for more than two months to wait for secular equilibrium between ^{226}Ra and ^{222}Rn. Gamma-ray spectra were measured with a gamma-ray analysis system equipped by SEIKO EG&G, consisting of an ORTTEC 12030 well type germanium detector and a MCA-7800 spectrum analyzer. The peaks of ^{210}Pb (46.5 keV) were calculated by Gaussian curve fitting using KaleidaGraph 4.1 software (Synergy Software, USA). Radionuclide activities were quantified and corrected for the respective counting efficiencies as determined by standard materials (CANMET DL-1a uranium-thorium ore). Applied counting times ranged from 1–3 days. Activity of ^{210}Pb in cores gathered at both stations 7 and 9 were measured by alpha spectrometry of its granddaughter ^{210}Po at the CEREGE laboratory (France). Samples were dissolved in a mixture of HCl, HNO_3, and HF in the presence of ^{209}Po as a yield tracer, and were plated spontaneously from the 1.5N HCl solution onto Ag disks. Uncertainties were calculated by standard propagation of the 1-sigma counting errors of samples and blanks.

Benthic Foraminiferal Analysis

Each core gathered for foraminiferal study on the first multi-corer deployment was sliced horizontally every 0.5 cm from the sediment-water interface to 4-cm depth, every 1 cm between 4–6-cm depth, and then every 2 cm down to 10-cm deep in the sediment column. The corresponding samples were transferred on board ship into 500-cm^3 bottles, which were filled with 95% ethanol containing 1 g/L Rose Bengal stain, commonly used to identify live foraminifera (Walton, 1952; Murray & Bowser, 2000). All samples were gently shaken for several minutes to obtain a homogeneous mixture. At the laboratory, they were sieved through both 63 and 150-μm screens, and the sieve residues were stored in 95% ethanol. The 63–150-μm fraction is not discussed in this paper, because we prefer to focus on the larger size fraction which is widely used for paleoceanography. Stained foraminifera belonging to the >150-μm fraction were sorted in wet samples and stored in Plummer slides. One problem with this technique is that Rose Bengal may stain the protoplasm of dead foraminifera that may be relatively well-preserved for long time periods under the generally anoxic conditions prevailing deep in sediments (Corliss & Emerson, 1990; Bernhard, 2000). We therefore applied very strict staining criteria (i.e., all chambers except the last one stained bright pink), and compared doubtful individuals to perfectly stained ones of the same species found in the superficial sediment layers. Non-transparent agglutinated and miliolid taxa were broken on many occasions to inspect the interior of the test. Most stained foraminifera were identified to species level (see Appendix 1 for taxonomic references of major species). Census data are presented in Appendix 2. Because samples were preserved and sorted in ethanol, many soft-shelled foraminiferal species may have shrunk and become unrecognizable during picking. Thus, our counts probably underestimate the soft-shelled foraminiferal group. We obtained digital photographs of major species using a Jeol® 6301F scanning electron microscope at the Service Commun d'Imageries et d'Analyses Microscopiques at Angers University (Fig. 3). For each station, we calculated different indices to assess diversity (Table 3). First, we calculated simple diversity (S), representing the number of taxa identified at least to the genus level. Because S diversity does not take into account taxa abundance and is highly sensitive to sample size, we also determined the E(S_{100}) value in relation to the rarefaction curve (Table 3). This value represents the number of taxa identified after picking 100 specimens. As an information-statistic index, we also calculated the Shannon index, H′ (log base *e*; Equation 1 in Appendix 3), complemented by the Evenness index, E (Hayek & Buzas, 1997; Equation 2 in Appendix 3), as described in Murray (2006).

A Canonical Correspondence Analysis (CCA) was performed with PAST© (Hammer et al., 2001) to decipher the complex nature of relations between species and the different environmental parameters at the five stations. Because important environmental parameters (i.e., oxygen-penetration depth, pore-water nitrate, and ammonium) were only available at three stations (6, 8, and 10), we were obliged to limit our statistical treatment to a comparison of major organic descriptors (OC, C/N atomic ratio, δ^{13}C, EHAA, THAA, EHAA/THAA ratio, Chl *a*, [Chl *a*/(Chl *a* + Pheo *a*)] ratio), bottom-water oxygenation, and sediment D_{90} with major (at least >2.5% at one site) foraminiferal species.

RESULTS

Bottom- and Pore-Water Geochemistry

Bottom-water oxygen (BWO) content ranges between 33 μmol/L at station 9 (1249 m) and 112 μmol/L at station 6 (496 m; Table 1). Both stations 7 (760 m) and 8 (1033 m) are characterized by dysoxic conditions (<45 μmol/L). Oxygen-penetration depth (OPD) at station 6 (496 m) is around 2 mm (Fig. 4). The bottom-water nitrate concentration is 36 μmol/L and falls to concentrations <5 μmol/L below the sediment-water interface (SWI; Fig. 4). At station 8 (1033 m), BWO concentration is 36 μmol/L (Fig. 4) with an OPD close to 3 mm. Bottom-water nitrate concentration is 42 μmol/L and is depleted (<4 μmol/L) below the SWI. At station 10 (1963 m), BWO is ~70 μmol/L with an OPD of ~5 mm. Nitrate concentration in bottom

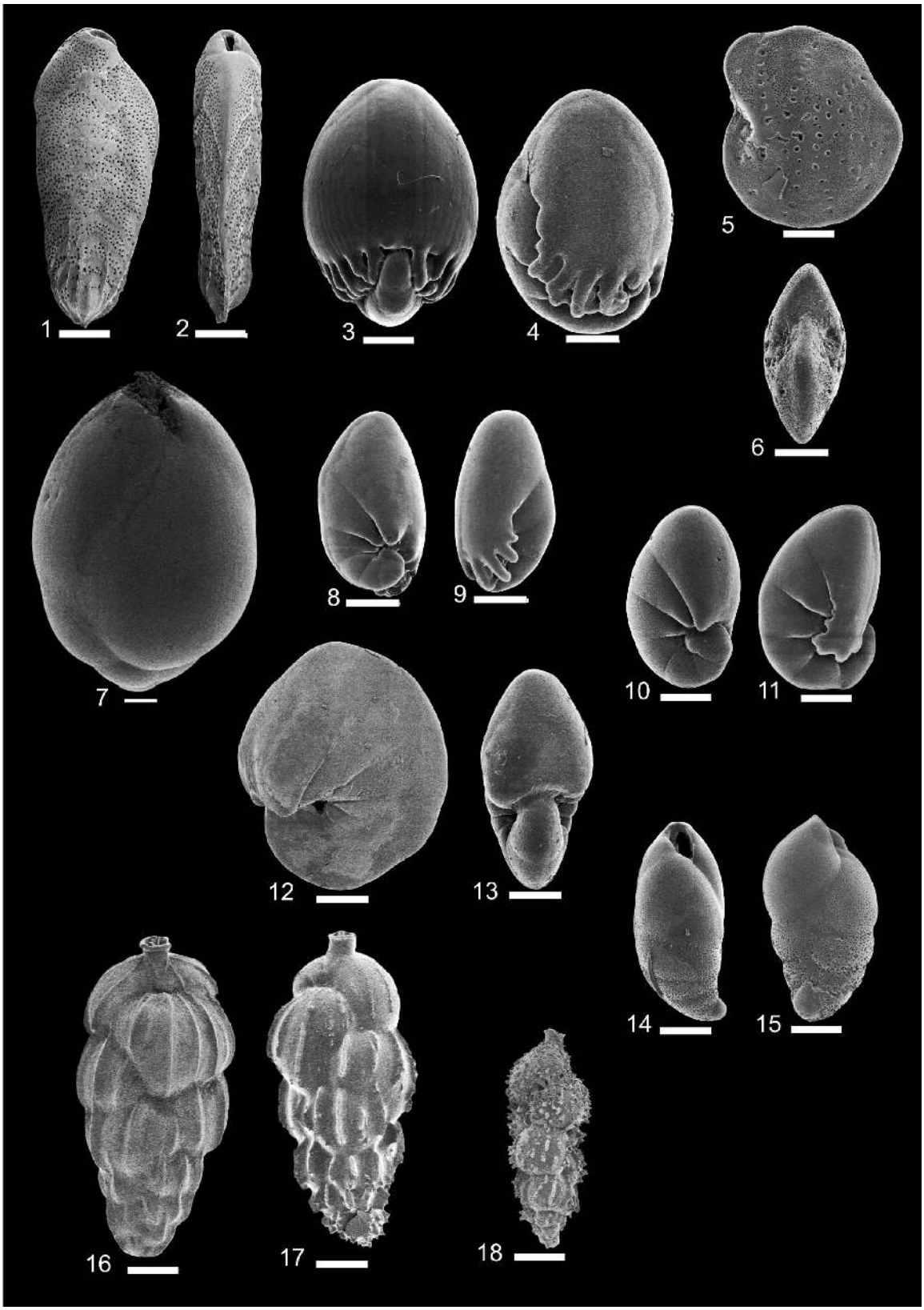

FIGURE 3. SEM images of the main foraminiferal taxa observed along the bathymetric transect; scale bars = 100 μm. **1, 2** *Bolivina spissa* (station 9). **3, 4** *Chilostomellina fimbriata* (station 10). **5, 6** *Elphidium batialis* (station 10). **7** *Globobulimina pacifica* (station 9). **8, 9** *Nonionella globosa* (station 6). **10, 11** *Nonionella stella* (station 7). **12, 13** *Nonionellina labradorica* (station 10). **14, 15** *Rutherfordoides cornuta* (station 7). **16** *Uvigerina akitaensis* (station 8). **17** *Uvigerina curticosta* (station 10). **18** *Uvigerina* cf. *U. graciliformis* (Station 6).

TABLE 3. Foraminiferal density and measures of assemblage diversity for the five investigated stations. Standing stocks are normalized for a 100-cm^2 surface area. Ecological indices [S, H′, E, E(S_{100})] are explained in the Materials-and-Methods section.

Stations	Standing stock (No. Ind./100 cm^2)	Simple Diversity (S)	Shannon index (H′)	Evenness index (E)	Rarefaction E(S_{100})
Station 6	1030	18	1.78	0.33	12.17
Station 7	3119	21	1.75	0.27	10.45
Station 8	11513	24	1.57	0.20	9.97
Station 9	1657	13	1.68	0.41	10.01
Station 10	256	9	1.81	0.68	8.48

water is close to 41 μmol/L and is depleted in surficial sediments. A subsurface nitrate peak of ~20 μmol/L is, however, recorded at the 2–3 cm interval, which may be related to a burrow. At stations 6, 8, and 10, bottom-water ammonia concentrations are <6 μmol/L. The highest value is recorded at dysoxic station 8. Below the sediment-water interface, pore-water ammonia contents are >12 μmol/L.

SEDIMENTARY FEATURES

Station 6 (496 m) is characterized by sandy silts (D_{50} = 24 ± 1 μm; D_{90} = 116 ± 4 μm; Table 2; Fig. 4). Large particles (in sieved residues >150 μm) are made of pellets, diatom frustules, and some volcanic debris. A 5-cm mixed layer is observed at the surface with a total ^{210}Pb activity of ~900 Bq/kg (Fig. 4). At stations 7, 8, and 9 (760 m, 1033 m and 1249 m, respectively), the sediment contains fine silt with a limited contribution of fine sand (D_{90} < 76 μm). There, sandy particles >150 μm are made of diatom frustules and foraminiferal tests. At both stations 7 and 8, the profiles of total ^{210}Pb activity decrease quite regularly, indicating a very shallow mixed layer, probably <1-cm thick (Fig. 4). At station 9, we observe a 5-cm thick mixed layer. At station 10 (1963 m), fine silt dominates (Table 2), and an ~5-cm thick mixed layer is also found.

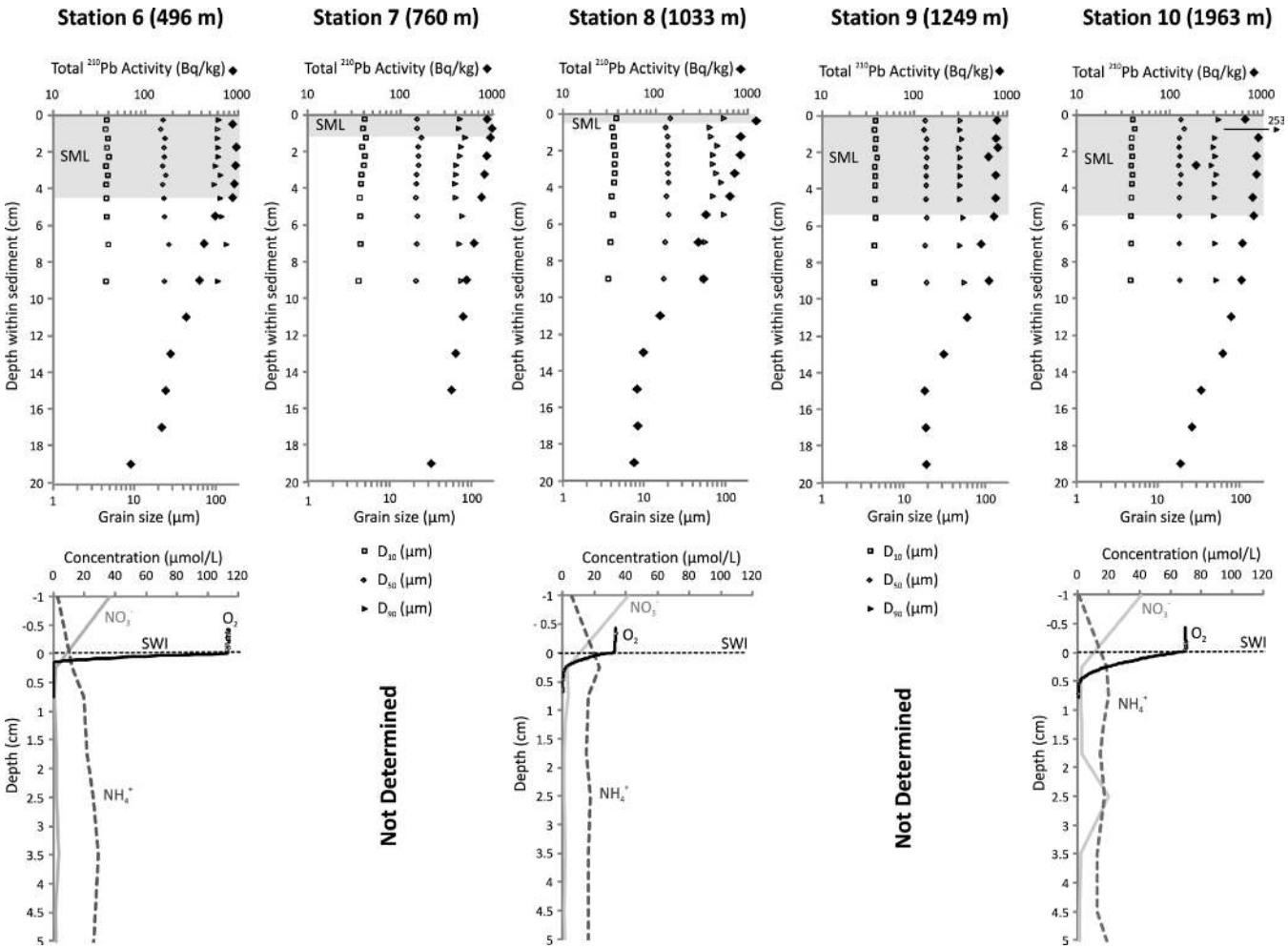

FIGURE 4. Vertical profiles of total ^{210}Pb activity for the five sampling stations. The shaded box corresponds to the SML (= Sediment Mixed Layer). The 10th, 50th, and 90th percentiles (D_{10}, D_{50}, and D_{90}, respectively) are also pictured on the same graphs (upper panels). Dissolved oxygen (O_2), nitrate (NO_3^-), and ammonia (NH_4^+) concentrations above and below the sediment-water interface (SWI) at stations 6, 8, and 10 are presented in the lower panels. Note the change of vertical scales between the upper and the lower panels.

Sedimentary Organic Matter

Sedimentary OC content ranges between 2.2 ± 0.3% DW at station 6 (211 m) and 2.7 ± 0.2% DW at station 9 (1249 m; Table 2). Higher values (>2.5% DW) are recorded at stations 7, 8, and 9, where bottom water oxygenation is <45 μmol/L. The C/N ratio shows only small changes along the overall bathymetric transect with values between 8.5 ± 0.1 (station 7) and 8.8 ± 0.1 (station 10). A relative constancy is observed for organic $\delta^{13}C$, with values ranging between −21.74 (station 9) and −22.20‰ (station 7). Lipids concentrations are low at station 6 (2.0 ± 0.4 mg/g DW) and maximal at station 7 (2.8 ± 0.4 mg/g DW). Higher concentrations are recorded at the oxygen-depleted sites (stations 7, 8, and 9). Sugar content is also low at station 6 (2.9 ± 0.4 mg/g DW) and maximal at station 9 (3.7 ± 0.7 mg/g DW). Here again, sugar concentrations are greater at stations 7, 8, and 9 compared to more oxygenated sites (Table 2). In the first centimeter of sediment, total hydrolysable amino acids (THAA) range between 62.6 ± 2.7 nmol/mg DW at station 10 to 102.9 ± 6.1 nmol/mg DW at station 7. EHAA values are high (>10 nmol/mg DW) at stations 7, 8, and 9, which are bathed by dysoxic water. EHAA/THAA ratios are quite low, with values ranging between 10.4–15.9%. Chl *a* content roughly decreases with water depth, with a maximum value of 2.15 ± 0.86 μg/g at station 6 and a minimum value of 1.00 ± 0.24 μg/g at station 10. The [Chl *a*/(Chl *a* + Pheo *a*)] ratios are quite constant along the bathymetric transect with values ranging between 6–10%.

Live (Stained) Foraminiferal Faunas

Standing Stocks and Diversity

Foraminiferal standing stocks vary between 256 individuals/100 cm^2 at station 10 (1963-m depth) and ~11,500 individuals/100 cm^2 at station 8 (1033-m depth; Table 3). Highest abundances (>1600 individuals/100 cm^2) are recorded at the three stations bathed by dysoxic waters (<45 μmol/L). When considering the vertical distribution of foraminiferal faunas within the sediment at all sites, the highest density is recorded in the first centimeter (Fig. 4). Simple diversity (S) ranges between 9 (station 10)–24 taxa (station 8). Conversely, the Shannon index (H′) is low at station 8 (1.57) and higher at station 10 (1.81). Evenness (E) is maximal at station 10 (0.68) and minimal at station 8 (0.20). The rarefaction index, $E(S_{100})$, shows only limited variability (between 9–13 taxa) in relation to the overall bathymetric transect.

Foraminiferal Composition and Microhabitat

At station 6 (496 m), *Nonionella globosa* (44%) and *Uvigerina* cf. *U. graciliformis* (22%) are both dominant species (Fig. 5). Their abundances are maximal in the first 0.5 cm of the sediment column, as is usually the case for shallow-infaunal taxa. *Nonionellina labradorica* (12%) lives preferentially between 1–3 cm. It is considered an intermediate-infaunal species. *Globobulimina pacifica* (5%) occupies the deep-infaunal microhabitat.

At station 7 (760 m), *Uvigerina akitaensis* (40%) and *Bolivina spissa* (27%) dominate the living fauna (Fig. 5). *Uvigerina akitaensis* is a shallow-infaunal species and its highest density is recorded in the first 0.5 cm of the sediment column. *Bolivina spissa* has an intermediate vertical distribution with a density maximum recorded in the 1–1.5-cm interval. *Rutherfordoides cornuta* (9%) and *No. labradorica* (7%) occupy the topmost 2 cm. *Reophax micaceus* (7%) and *Nonionella stella* (4%) are considered as intermediate-infaunal species.

At station 8 (1033 m), *B. spissa* (44%) and *U. akitaensis* (33%) dominate the living fauna (Fig. 5). They present the same microhabitat patterns as at station 7. *Chilostomellina fimbriata* (6%) and *No. labradorica* (4%) occupy deep-infaunal habitat with density maxima recorded in the 4–5-cm interval. *Reophax micaceus* (4%) shows an intermediate-infaunal distribution.

At station 9 (1249 m) *U. akitaensis* (41%) and *B. spissa* (24%) are dominant (Fig. 5). Both taxa occupy the same microhabitats previously described for them. *Chilostomellina fimbriata* is a secondary species (16%), which occupies the deep-infaunal microhabitat, as does *N. globosa* (5%).

At station 10 (1963 m), *No. labradorica* is dominant (32%), but with an erratic vertical distribution within the sediment column. *Elphidium batialis* (22%) and *Uvigerina curticosta* (16%) are relatively abundant in the first centimeter and behave like shallow-infaunal species (Fig. 5). *Chilostomellina fimbriata* (11%) is a deep-infaunal taxon with a mode between 6–8 cm.

Canonical Correspondence Analysis

The CCA has revealed two major axes explaining more than 87% of data variability (Fig. 6). Stations 7, 8, and 9 and *U. akitaensis*, *B. spissa*, *Ru. cornuta*, and *R. micaceus* (among others) are grouped together along the negative side of Axis 1. This cluster is grouped by environmental vectors related to high sedimentary content in labile organic compounds (e.g., lipids, EHAA) and organic-matter-enriched sediments (OC). On the opposite side, station 6 is characterized by *N. globosa*, *G. pacifica*, *U.* cf. *U. graciliformis*, and *Cibicidoides pseudoungerianus.* This cluster is notably defined by high bottom-water oxygenation (BWO), coarser sediments (D_{90}), and a smaller contribution of labile organic matter. Between both of these clusters, Station 10 is pulled up along Axis 2, where it is grouped with *E. batialis*, *No. labradorica*, and *U. curticosta*.

DISCUSSION

Questioning the Sedimentary Instability

Surface sediments at all stations are characterized by fine sediments dominated by silt. Biogenic compounds, such as intact diatom frustules, radiolarians, pellets, and dead benthic and planktonic foraminifera, are abundant in the larger grain-size class (>150 μm). They are likely related to vertical transport by aggregation through the water column. Although northern Japan (Hokkaido) has intense volcanic activity, the contribution of volcanic tephras (e.g., volcanic glass, pumice) at our sites is minor compared to shelf and shelf-break areas (unpublished data of Ki-ichiro Kawamura and Minami Fujii). Grain-size analyses (Fig. 4; Table 2) and complementary CT-scan observations (unpublished data of Arito Sakaguchi and Masafumi

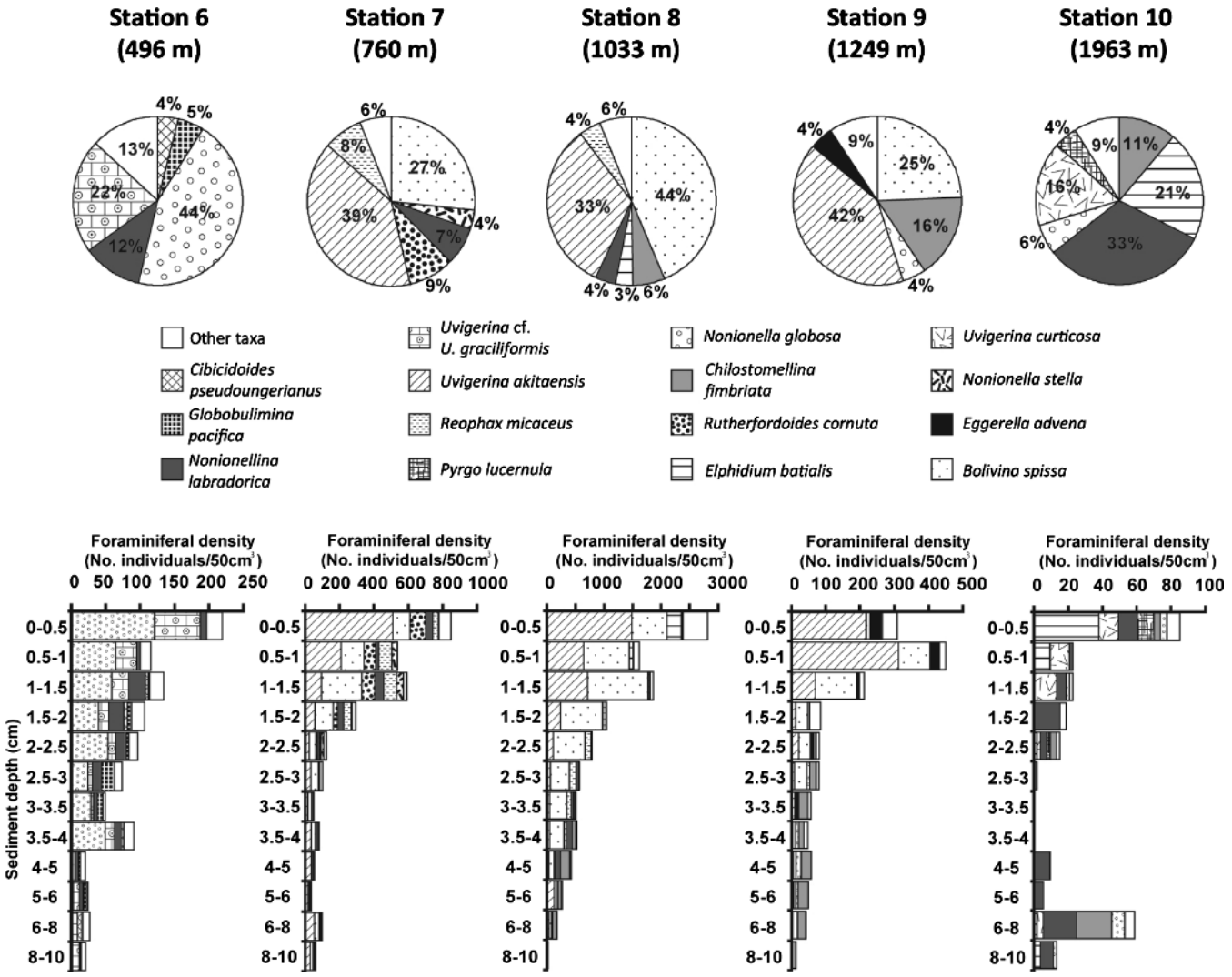

FIGURE 5. Composition of selected live benthic foraminifers along the five-station bathymetric transect (in % total fauna). Only taxa with relative abundances >2.5% in one of the cores are pictured. Lower panels correspond with down-core distribution of live benthic foraminifers (number of individuals belonging to the >150-μm fraction found in each level, standardized for a 50-cm³ sediment volume). As above, only taxa with relative abundances >2.5% in one of the cores are shown. Note the change of density scale between the graphs.

Murayama) have revealed neither fining-up deposits (e.g., a Bouma sequence) nor an erosional surface in the topmost decimeter of sediment. Moreover, higher ^{210}Pb activities recorded in the topmost mixed layer (>750 Bq/kg) and gradual radioactive decay observed within the sediment at all sites confirm sediment accumulation without major physical disturbances (Fig. 4). Overall, our data suggest that no major gravity-flow event has affected our sampling stations.

A Complex Interplay Between Organic Matter and Oxygenation

Sedimentary organic contents recorded at the five stations are high (>2.2% DW). Even if we include the potentially high contribution of reworked organic matter by lateral advection from upper slope and adjacent shelves, this confirms that the open marine region off Hachinohe (NE Japan) is one of the most productive oceanic areas in the world (Saino et al., 1998). This study area is indeed located at the convergence of Oyashio surface waters and the Tsugaru and Kuroshio streams (Nagata et al., 1992). The hydrological fronts there between surface currents are characterized by enhanced primary production (Sanio et al., 1998). The C/N atomic ratios ranging between 8.5–8.8 suggest that sedimentary organic matter is mainly related to marine phytodetritus, presumably made of microphytoplankton and bacterioplankton (Nakatsuka et al., 2003). The δ^{13}C (with values around −22‰) also support a preeminent marine source for organic detritus (Nakatsuka et al., 2003; Darnaude et al., 2004). Land-derived particulate organic carbon presents a lighter δ^{13}C signature close to −27‰ (Ogawa & Ogura, 1997; Barth et al., 1998). Nevertheless, fresh phytodetritus produced mainly during the spring bloom has a higher δ^{13}C (−19 to −20‰) and a lower C/N ratio (5.5–7.5; Kitazato et al., 2000; Nakatsuka et al., 2003). It seems, therefore, that organic matter from sediment samples gathered in August 2011 is moderately degraded (with a plausible contribution of continental matter).

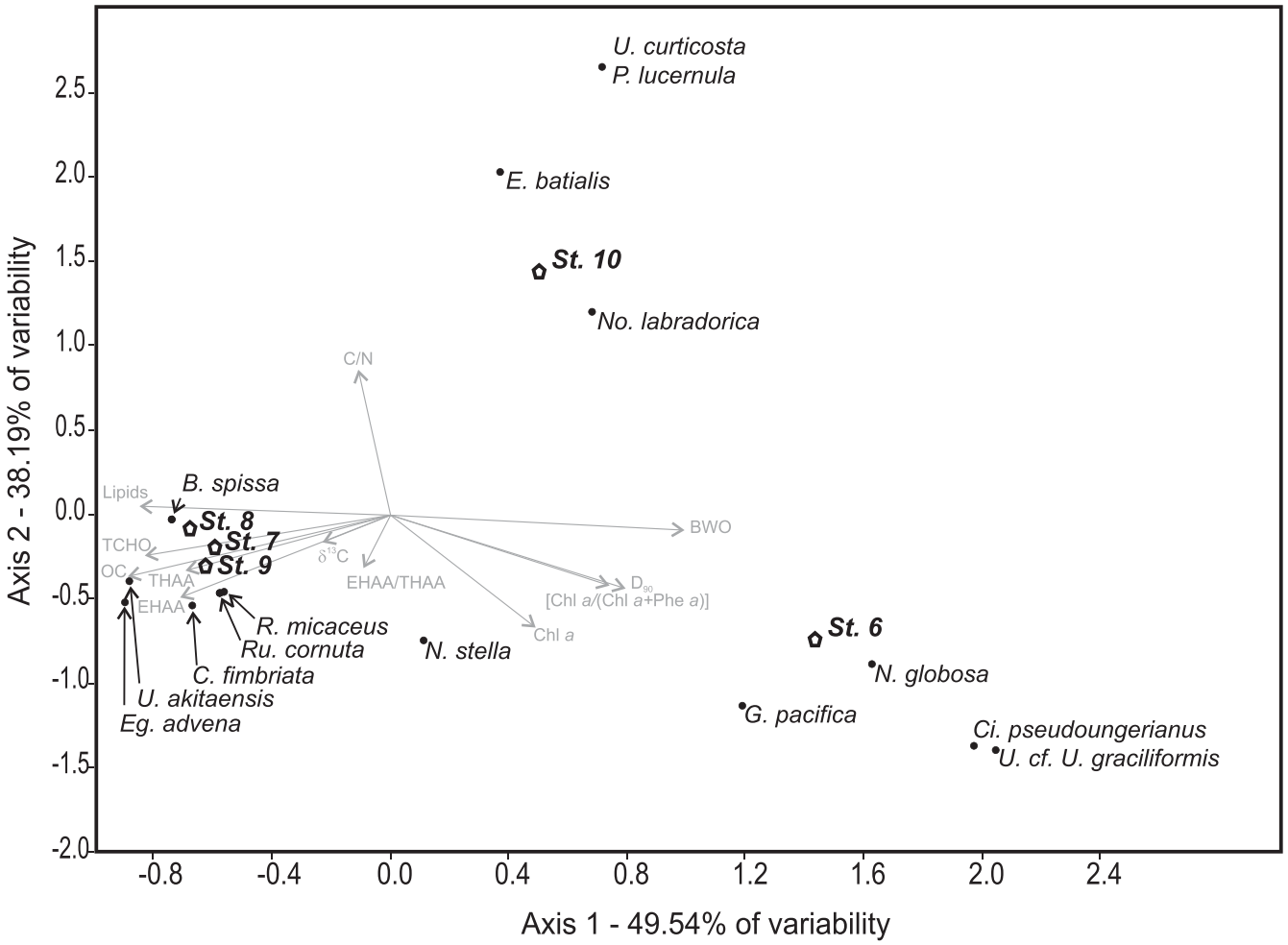

FIGURE 6. Graphical representation of Canonical Correspondence Analysis. The five sampling stations and all major foraminiferal species (>2.5% at least at one station) are plotted according to both axes 1 and 2. Environmental vectors are pictured in grey. Labels are explained in the Materials-and-Methods section.

The high primary productivity and degradation of organic compounds throughout the water column is largely responsible for the presence of an oxygen-minimum zone. Further, the progressive decrease in oxygenation level from 200–1000-m depth is likely related to a gradual mixing between the well-oxygenated NPIW and the underlying oxygen-depleted layer. In all cases, dysoxic conditions prevail between 700–1300-m depth (<45 μmol/L) with oxygenation dropping down to ~30 μmol/L at 1200-m depth. The dysoxia seems to favor both accumulation and preservation of organic detritus in the topmost sediment (OC > 2.5% DW). Furthermore, carbohydrates and lipids are more concentrated at dysoxic stations 7, 8, and 9 compared to stations 6 and 10. Therefore, if we consider lipids and EHAA as relevant descriptors of bioavailable organic matter (Grémare et al., 2003), these kinds of compounds are more abundant in dysoxic ecosystems. The freshness of chlorophyllic pigments depicted by [Chl *a*/(Chl *a* + Pheo *a*)] ratios is very low (<10%) at all sites and thus unrelated to water depth. However, we note that phytopigments (in μg/g) are representative of only a minor contribution to the overall sedimentary organic pool. Below the SWI, the overall mineralization (aerobic and anaerobic) of organic compounds is intense, as underlined by the very shallow oxygen-penetration depths (<5 mm) recorded at stations 6, 8, and 10. At all investigated stations, NO_3^- concentrations are depleted below the first centimeter of sediment, suggesting that denitrification is likely an important process of mineralization within the very surficial sediments (e.g., Glud et al., 2009), although alternative reactions may not be excluded [e.g., oxidation of dissolved Mn(II); Deflandre et al., 2002; Hyacinthe et al., 2001]. Accordingly, NH_4^+ production is effective immediately below the SWI with concentrations ≤40 μmol/L in the first 5 cm. To summarize, our results suggest that eutrophic conditions prevail overall along the bathymetric transect with a preferential burial of bio-available organic compounds at the stations bathed by dysoxic bottom waters.

Foraminiferal Communities off Hachinohe: Between Stress Tolerance and Metabolic Plasticity

Our observations show fairly low foraminiferal diversity as compared to other bathyal ecosystems from either eutrophic or oligotrophic oxygenated basins (e.g., Schmiedl et al., 2000; Fontanier et al., 2002, 2008, 2013; Koho et al.;

2007, 2008; Duros et al., 2011, 2013). As reviewed by Gooday (2003), dissolved oxygen plays an important role in the control of foraminiferal diversity, which is depressed within an OMZ relative to adjacent well-oxygenated environments. For example, a tight relationship between foraminiferal diversity and bottom-water oxygenation has been documented across the Oman and Pakistan margins with extremely low species richness in the OMZ core as compared to communities underlying a well-ventilated water mass (e.g., Hermelin & Shimmield, 1990; Jannink et al., 1998; Gooday et al., 2000; Schumacher et al., 2007). The causes of diversity depression in oxygen-depleted environments are complex. On the one hand, only species with alternative metabolic pathways and specific ecological adaptations (e.g., denitrification ability, detoxification by P-ER complexes, mutualism with prokaryotes) are able to thrive under adverse conditions in hypoxic environments (Sen Gupta & Machain-Castillo, 1993; Bernhard & Bowser, 1999, 2008; Bernhard & Sen Gupta, 1999; Bernhard, 2000, 2003; Risgaard-Petersen et al., 2006; Høsglund et al., 2008; Piña-Ochoa et al., 2010; Koho et al., 2011; Bernhard et al., 2012a, 2012b). On the other hand, opportunistic taxa can benefit from the lack of competition for food and space, and therein proliferate close to the sediment-water interface under such conditions (e.g., Sen Gupta & Machain-Castillo, 1993; Bernard & Sen Gupta, 1999).

Living (Stained) Faunas Typical of Oxygen-Depleted Environments

Within our study area, both *Uvigerina akitaensis* and *Bolivina spissa* are strictly dominant in samples from the oxygen-depleted stations, where bottom-water oxygenation is <45 μmol/L and where relatively labile organic materials (as defined by lipids and EHAA contents) are most available (Fig. 6). *Uvigerina akitaensis* is common in the OMZ from the Japanese margin (e.g., Ishiwada, 1964; Ikeya, 1971; Inoue, 1989; Nishi, 1990; Ohga & Kitazato, 1997; Kitazato et al., 2000; Nomaki et al., 2005a; Glud et al., 2009). In situ tracer experiments in Sagami Bay (with the ^{13}C-labelled green alga *Dunaliella tertiolecta* Butcher) have shown that this shallow-infaunal species features higher carbon assimilation rates than deep-infaunal taxa such as *Chilostomella* spp. and *Globobulimina* spp. (Nomaki et al., 2005b). *Uvigerina akitaensis* can ingest up to 40% of its own biomass within nine days (Nomaki et al., 2011). Because it feeds selectively on fresh phytodetritus (i.e., the diatom *Chaetoceros sociale* Lauder and the green alga *D. tertiolecta*), this species is considered a strict ''phytophagous'' species (Nomaki et al., 2005b, 2006). In this study, its dominance in shallow-infaunal microhabitats confirms that this taxon is probably the most opportunistic species across the Japanese OMZ (Fig. 5; Appendix 2). Even though Nomaki et al. (2007) have demonstrated that *U. akitaensis* has an aerobic metabolism (with oxygen respiration rate of ~6 nmol O_2/day/individual), its absence in oxic environments (at stations 6 and 10) may be related either to the relative scarcity of high-nutritional-value detritus at both sites or to microaerophile behavior as defined in Bernhard & Sen Gupta (1999). Alternatively, *U. akitaensis* may not be able to compete for food when more efficient ''oxyphilic'' competitors (*Uvigerina* cf. *U. graciliformis*, *Nonionella globosa*, *Uvigerina curticosta*, *Elphidium batialis*) occupy shallow-infaunal microhabitats. It should be stressed that *U. akitaensis* is morphologically very similar to *Uvigerina* ex gr. *U. semiornata*, which is dominant in the Indo-Pakistan OMZ core (Schumacher et al., 2007). The latter taxon dominates the uptake of fresh organic matter when bottom-water oxygenation is very low (close to 5 μmol/L), whereas larger metazoan benthos are more efficient in food acquisition when oxygenation is higher (Woulds et al., 2007). Therefore, if *U. akitaensis* and *U.* ex gr. *U. semiornata* are genetically (and physiologically) related, it is not surprising that *U akitaensis* is the major opportunistic taxon at the most oxygen-depleted stations on the Japanese slope.

Bolivina spissa has been recorded in the OMZ from the Pacific Ocean (Ishiwada, 1964; Ikeya, 1971; Douglas & Heitman, 1979; Ingle et al., 1980; Mullins et al., 1985; Quinterno & Gardner, 1987; Inoue, 1989; Mackensen & Douglas, 1989; Ohga & Kitazato, 1997; Bernhard & Sen Gupta, 1999; Kitazato et al., 2000; Glud et al., 2009; Mallon et al., 2012). It feeds preferentially on fresh algae and is thereby considered as a ''phytophagous'' species (Nomaki et al., 2005b, 2006). Its oxygen respiration rate is lower than *U. akitaensis* (~3 nmol O_2/day/individual; Nomaki et al., 2007). On the other hand, *B. spissa* has not been documented yet as a denitrifying species. In our study area, its microhabitat within the sediment is slightly deeper compared to *U. akitaensis*. Maximal abundances are indeed recorded below the top 0.5 cm of sediment, where strongly hypoxic (~dysoxic to anoxic) conditions prevail (Fig. 5; Appendix 2). *Bolivina spissa* may well be a microaerophile or have metabolic adaptations such as denitrification ability to survive in such an adverse microhabitat. Alternatively, *B. spissa* may be excluded from the topmost sediment, because *U. akitaensis* can better exploit highly available and labile organic substrate.

Rutherfordoides cornuta and *Nonionella stella* are both relatively abundant at station 7, where BWO is close to 45 μmol/L and where sedimentary lipids and THAA contents are the highest. There, *Ru. cornuta* occupies the topmost sediments, whereas *N. stella* behaves like an intermediate-infaunal species (Fig. 5; Appendix 2). *Rutherfordoides cornuta* was described in the OMZ from the California inner borderland basins, thriving in dysoxic to microxic environments (2–15 μmol/L; Douglas & Heitman, 1979; Bernhard et al., 1997, 2012a; Bernhard, 2000). It was also documented in the bathyal oxygen-depleted environments from the Japanese margin (Sagami Bay; Nomaki et al., 2005a). On the basis of TEM observations, this species is considered to be a detritus feeder and a symbiont-free bacteriovore (Bernhard et al., 2012a). Moreover, this taxon is capable of denitrification (Bernhard et al., 2012a). *Nonionella stella* has been documented in anoxic sediments from shelf environments (Ikeya, 1971; Leutenegger, 1984; Kitazato, 1994) and in dysoxic to anoxic sediments from several OMZs in the Pacific Ocean (0–15 μmol/L; Phleger & Soutar, 1973; Bernhard et al., 1997, 2012a; Mallon et al., 2012). The species was also assayed for both denitrification and oxygen respiration (Risgaard-Petersen et al., 2006; Høsglund et al., 2008; Piña-Ochoa et al., 2010). Accordingly, chloroplasts that are sequestered in its cytoplasm may

provide nitrate reductase indispensable for nitrate respiration (Bernhard & Bowser, 1999; Grzymski et al., 2002; Bernhard et al., 2012a). Overall, it is likely that *Ru. cornuta* and *N. stella* are both facultative anaerobes.

Other Dominant Species

At station 6, the most oxygenated with $O_2 > 110$ μmol/L, *N. globosa* and *U.* cf. *U. graciliformis* are both dominant. The presence of *N. globosa* was also documented by Ikeya (1971) along the oxygenated upper slope of our study area. This species was also identified by Nishi (1990) in the Japanese OMZ (Sagami Bay) where it presented a polymodal distribution vertically within the sediment column, thereby suggesting it could perform anaerobic metabolism. At station 6, *N. globosa* is fairly abundant in the first 0.5 cm and occurs down to 5-cm depth. It is also present in low abundances at all other stations, especially at station 9, where it occupies a deep-infaunal microhabitat with a density peak between 4–5-cm depth (Appendix 2). Overall, *N. globosa* occupied several microhabitats, suggesting flexibility in terms of metabolic pathways. That species (like *N. stella*) may be a facultative anaerobe using plastids for denitrification (Bernhard & Bowser, 1999; Grzymski et al., 2002; Bernhard et al., 2012a). Moreover, it may feed on more-or-less degraded organic detritus. Finally, its dominance at station 6 could be related to its ability to compete for food in relatively well-oxygenated sediments (noticeably when reactive species such as *U. akitaensis* and *B. spissa* are dismissed from the struggle for food sources). *Uvigerina* cf. *U. graciliformis* is present only at station 6 where it dominates shallow infaunal microhabitat. It is considered a seasonal phytophagous taxon with a preferential aerobic metabolism. In any case, further in situ and laboratory experiments are necessary to assess food preferences and metabolic adaptations in both *N. globosa* and *U.* cf. *U. graciliformis.*

At the deepest station 10, where oxic conditions prevail at the sediment-water interface ($O_2 > 70$ μmol/L), *E. batialis* and *U. curticosta* are relatively abundant, although total foraminiferal abundance is the lowest (~250 individuals/100 cm^2) recorded during the present study. Both taxa occupy a shallow-infaunal microhabitat. Therefore, they may rely on aerobic metabolism and behave as seasonal phytophagous taxa, as defined by Nomaki et al. (2005b, 2006). However, *E. batialis* is most abundant (in absolute value) in the first 0.5 cm at station 8 (1000-m depth), where dysoxia prevails, suggesting that this species can also tolerate low-oxygen conditions.

Nonionellina labradorica is relatively abundant at oxic or dysoxic stations. Its highest abundance is recorded at station 8 where it occupies a deep-infaunal microhabitat. It also occupies an intermediate-infaunal habitat at stations 6 and 7, and has been described off Hachinohe between 500–1100-m depth (Ishiwada, 1964; Ikeya, 1971). Kitazato (1989) and Nishi (1990) also documented it as a shallow- and intermediate-infaunal species at bathyal stations along the Japanese margin. Therefore, it was proposed to belong to both aerobic and anaerobic groups (Nishi, 1990). In other ocean regions, Alve (1990), Cedhagen (1991), and Bernhard & Bowser (1999) described this taxon in fjords from Sweden. Corliss & Emerson (1990) documented *Florilus labradoricus* (= *No. labradorica*) in deep-infaunal microhabitats from the NE Atlantic, where the species is a eurybathic taxon with a wide geographical distribution. As far as *No. labradorica* sequesters chloroplasts (Cedhagen, 1991; Bernhard & Bowser, 1999), it may use them for denitrification. This putative metabolic flexibility would be equivalent to those of *N. globosa* and *N. stella*. Overall, its various microhabitats reflect a preference for organic detritus, whether degraded or fresh.

Globobulimina pacifica and *Chilostomellina fimbriata* occupy deep-infaunal microhabitats (several centimeters below SWI; Appendix 2; Fig. 5), and they are obviously able to survive in anoxic sediment. *Globobulimina pacifica* was documented as a eurybathic species by Sen Gupta & Machain-Castillo (1993), and it occurred from dysoxic to anoxic environments (Phleger & Soutar, 1973; Douglas & Heitman, 1979; Mackensen & Douglas, 1989; Nishi, 1990; Bernhard, 1992; Glud et al., 2009). Accordingly, it is considered (with other *Globobulimina* species) as a facultative anaerobe that can store a high concentration of nitrate in its large test for respiration (Risgaard-Petersen et al., 2006; Glud et al., 2009; Koho et al., 2011). *Globobulimina* can ingest fresh phytodetritus and also degraded organic detritus (Goldstein & Corliss 1994; Kitazato & Ohga, 1995; Nomaki et al., 2005a, 2006); therefore, it is considered to be a "seasonal phytophagous" taxon, switching from fresh algae when available in the sediment to degraded organic matter (Nomaki et al., 2006). Little literature information is available concerning the ecology of *C. fimbriata*. Off Hachinohe, Ikeya (1971) identified it between 700–1000 m. This large-sized species (which appears as an intriguing morphological mix between *Chilostomella ovoidea* and *N. globosa*) is abundant at stations 8 and 9. There, deep in the sediment column, it may store nitrate for respiration and feed on degraded organic detritus.

From Modern Calibration to Past Reconstruction

The ecological features for all potentially fossilizing taxa recorded in our study are summarized in Table 4 and pictured in Figure 7. Intentionally, we have not described agglutinated species such as *Reophax micaceus* and *Eggerella advena*, which do not readily fossilize. Our assumptions regarding both the trophic and metabolic preferences of dominant taxa (e.g., *No. labradorica, N. globosa*) should be carefully tested through in situ experiments, laboratory incubation, and TEM observations. It should also be noted that the reliability of paleoecological interpretations for those calcareous species (belonging to the >150-μm size fraction) may be limited by taphonomic losses in upper sediments. Indeed, postmortem physical destruction and/or dissolution of thin-shelled species (i.e., *N. globosa, N. stella, G. pacifica, C. fimbriata, Ru. cornuta*) may severely alter the composition of dead faunas during fossilization. During sampling, pH of the pore water at stations 8 and 10 was lower than 7 (Oguri Kazumasa, unpublished data), which through dissolution can generate major discrepancies between living and fossil foraminiferal faunas. Moreover, lateral advection of allochthonous foraminifera by seismogenic/tsunamogenic

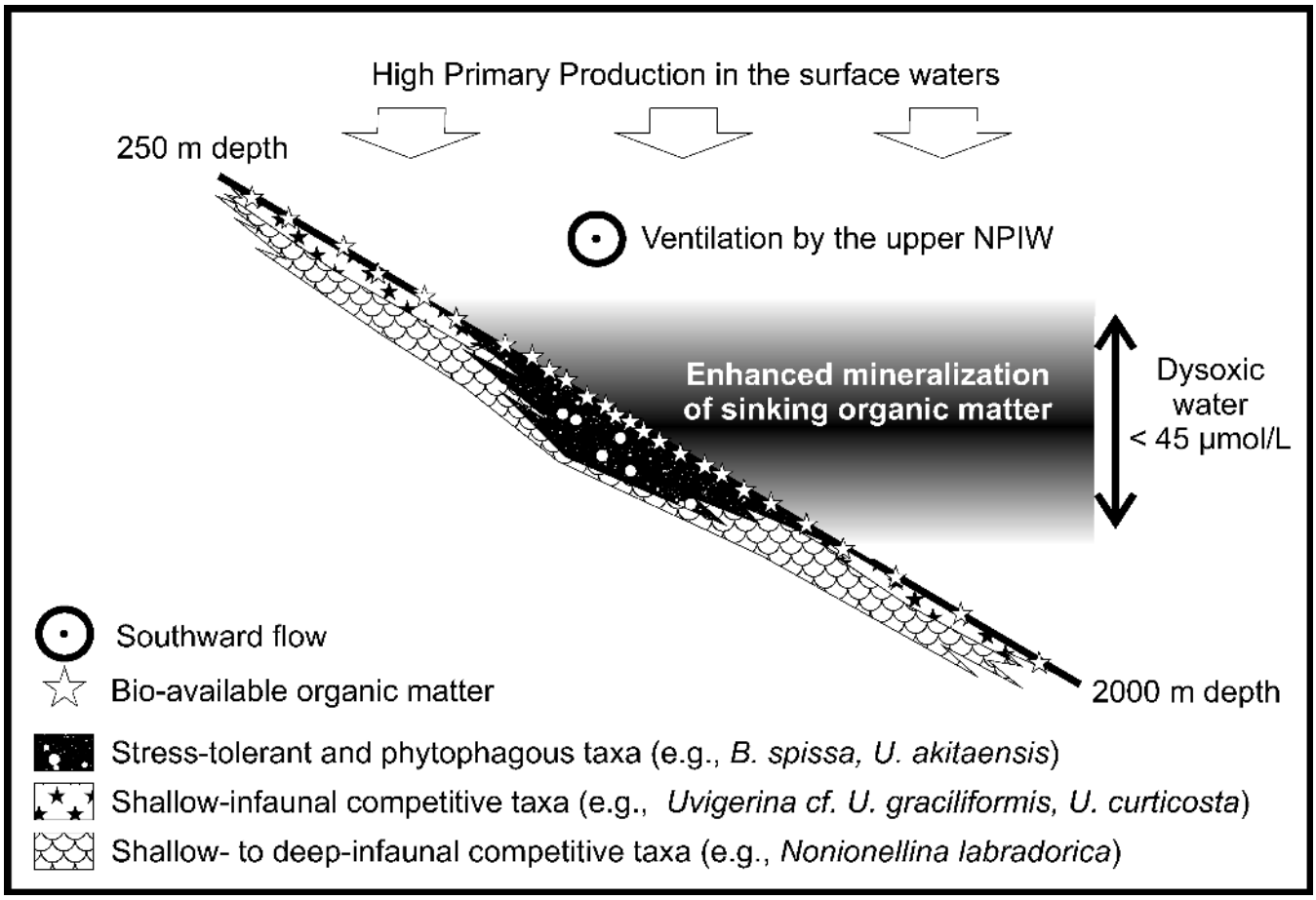

FIGURE 7. Conceptual scheme illustrating the ecological constraints (biotic and abiotic) on the foraminiferal faunas in our study area. High primary production in surface waters sinks toward the seabed and becomes potentially bio-available organic matter for the benthic community. Between 700–1300-m depth, dysoxic conditions (<45 µmol/l) prevailing in the NIPW leads to an enhanced deposition of bio-available organic matter. In these conditions, stress-tolerant and phytophagous taxa tend to dominate the foraminiferal community.

turbidity currents may also interfere with the autochthonous foraminiferal record. It is likely that small-sized and easily transportable foraminiferal taxa (e.g., *Epistominella*, *Cassidulina*, *Buliminella*) are more subject to these types of taphonomic processes. An ongoing study dedicated to a comparison of living and dead faunas in our study area will provide critical information on the fossilization processes.

If we neglect the potential biases mentioned above, our data suggest that assemblages of large-sized (>150-µm size fraction) foraminifers can provide instructive information on past records regarding the complex interplay between organic-matter flux and oxygenation. For instance, both *U. akitaensis* and *B. spissa* are relevant indicators for oxygen-depleted settings. They thrive indeed in dysoxic ecosystems (<45 µmol/L), where labile organic matter (enriched in lipids and EHAA) is abundant. *Uvigerina* cf. *U. graciliformis*, *U. curticosta*, and *E. batialis* correspond to benthic environments bathed by more oxygenated bottom waters (>70 µmol/L), where degraded detritus with intermediate nutritional value accumulates. If we consider species presumably capable of denitrification (i.e., *N. stella*, *N. globosa*, *No. labradorica*, *Ru. cornuta, G. pacifica*), the overall sum of their relative contribution correlates surprisingly well ($N = 5$; $r = 0.98$; $p < 0.01$) with bottom-water oxygenation (Fig. 8). Because of their putative metabolic plasticity (oxygen respiration and denitrification), these competitive species may replace *U. akitaensis* and *B. spissa* when food quality decreases and oxygen level increases at the sediment-water interface. Of course, such an interpretation would be invalid if *U. akitaensis* and *B. spissa* (as dominant taxa from the OMZ) are also denitrifying taxa.

Previous paleoenvironmental studies were performed off Hachinohe (our study area) to assess the historical change of the so-called OMZ throughout the Quaternary (Ohkushi et al., 2003, 2005; Uchida et al., 2004; Hoshiba et al., 2006; Ikehara et al., 2006; Shibahara et al., 2007). In light of our ecological results, it seems that some adjustments should be made to the paleoecological interpretations discussed in these valuable works. For instance, Shibahara et al. (2007) grouped *U. akitaensis* and *N. globosa* in the same paleoecological group (namely "suboxic"—between 13–67 µmol/L). However, our data clearly show that both species differ in terms of bathymetrical distribution and survival strategies (e.g., facultative anaerobe vs. opportunism). *Nonionellina labradorica* was classified as an "oxic" taxon (>67 µmol/L) by Shibahara et al. (2007), although our data suggest that this species is able to survive in anoxic

TABLE 4. Ecological characteristics for the main (fossilizing) calcareous taxa observed along the bathymetric transect. Reference studies cited in parentheses: 1 = Nomaki et al. (2006); 2 = Nomaki et al. (2007); 3 = Bernhard et al. (2012a); 4 = Piña-Ochoa et al. (2010); 5 = Risgaard-Petersen et al. (2006); 6 = Høsglund et al. (2008); 7 = Bernhard & Reimers (1991).

Fossilizing calcareous species	Preferential bathymetric distribution (our study)	Microhabitat within the sediment (our study)	Oxygenation level (our study)
Uvigerina cf. *U. graciliformis*	Above the oxygen-depleted water mass (>45 μmol/L)	Shallow infaunal	Oxic
Nonionella globosa	Above and below the oxygen-depleted water mass (>45 μmol/L)	Shallow to deep infaunal	Oxic to anoxic
Globobulimina pacifica	Above the oxygen-depleted water mass (> 45 μmol/L)	Deep infaunal	Anoxic
Uvigerina akitaensis	Oxygen-depleted water mass (<45 μmol/L)	Shallow infaunal	Dysoxic to anoxic
Bolivina spissa	Oxygen-depleted water mass (<45 μmol/L)	Shallow to intermediate infaunal	Dysoxic to anoxic
Rutherfordoides cornuta	Oxygen-depleted water mass (<45 μmol/L)	Shallow infaunal	Dysoxic to anoxic
Nonionella stella	Oxygen-depleted water mass (<45 μmol/L)	Intermediate to deep infaunal	Dysoxic to anoxic
Chilostomellina fimbriata	Within and below the oxygen-depleted water mass	Deep infaunal	Anoxic
Elphidium batialis	Within and below the oxygen-depleted water mass	Shallow infaunal	Oxic to dysoxic
Uvigerina curticosta	Below the oxygen-depleted water mass (>45 μmol/L)	Shallow infaunal	Oxic
Nonionellina labradorica	Overall bathymetric transect	Intermediate to deep infaunal	Oxic to anoxic

Fossilizing calcareous species	Oxygen respiration	Nitrate respiration	Food preferences	Symbionts
Uvigerina cf. *U. graciliformis*	No data	No data	Putatively seasonal phytophagous	No data
Nonionella globosa	Putatively yes (*Nonionella* group)	Putatively yes (*Nonionella* group)	Putatively deposit feeder (*Nonionella* group)	No data
Globobulimina pacifica	Putatively yes (*Globobulimina* group)	Putatively yes (*Globobulimina* group)	Seasonal phytophagous (1)	Putative endosymbionts
Uvigerina akitaensis	Yes (2)	No data	Phytophagous (1)	No data
Bolivina spissa	Yes (2)	No data	Phytophagous (1)	No data
Rutherfordoides cornuta	No data	Yes (3)	Deposit feeder, bacteriovore (3)	No (3)
Nonionella stella	Yes (4)	Yes (4, 5, 6)	Putatively deposit feeder (*Nonionella* group)	Putative ectosymbionts (7)
Chilostomellina fimbriata	No data	No data	Putatively deposit feeder	No data
Elphidium batialis	No data	No data	Putatively seasonal phytophagous	No data
Uvigerina curticosta	No data	No data	Putatively seasonal phytophagous	No data
Nonionellina labradorica	No data	Putatively yes (chloroplasts)	Putatively deposit feeder	No data

sediments as well. *Elphidium batialis* was considered as a "suboxic" taxon by Shibahara et al. (2007), but we show that this species was dominant at the relatively well-ventilated station 10. Overall, it is fairly unrealistic and quite awkward to limit the ecological meaning of one species to a simplistic single-parameter nomenclature. The occurrence of a given species indeed results from the complex interplay among: 1) the oxygen and nitrate levels at and below the sediment-water interface, 2) the organic matter bioavailability, and 3) the competition for habitat and resources among all foraminiferal taxa.

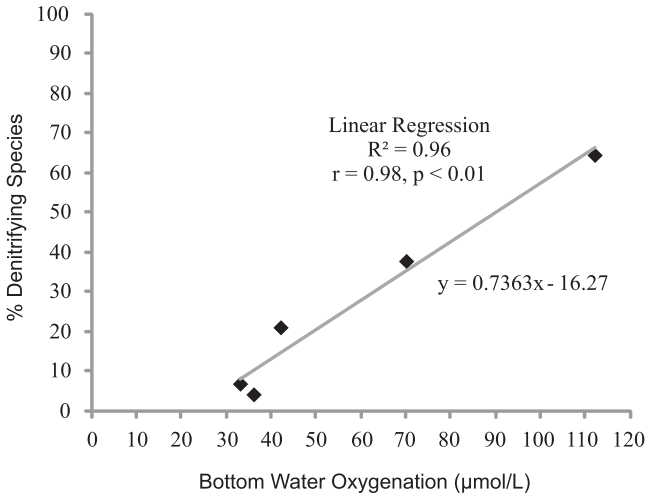

FIGURE 8. Comparison of the bottom-water oxygenation (μmol/L) and the sum of percentages of presumably denitrifying species (i.e., *Nonionella stella*, *N. globosa*, *Nonionellina labradorica*, *Rutherfordoides cornuta*, *Globobulimina pacifica*).

CONCLUSIONS

Live (Rose-Bengal stained) foraminiferal faunas show changes in community structure across the oxygen-depleted intermediate water mass from the NE Japanese margin (western Pacific). Those changes are obviously related to environmental and (presumably) interspecific constraints. *Uvigerina akitaensis* and *Bolivina spissa* are restricted to oxygen-depleted environments indicating their tolerance of anoxia. Under such dysoxic to anoxic conditions (<45 μmol/L), both phytophagous taxa take advantage of labile organic phytodetritus (rich in lipids and EHAA). *Nonionella stella* and *Rutherfordoides cornuta* likely survive by using alternative metabolism (i.e., denitrification) with flexible trophic requirements. At more oxygenated (i.e., >70 μmol/L in bottom water) stations, *Uvigerina curticosta*, *Uvigerina* cf. *U. graciliformis*, *Nonionella globosa*, *Nonionellina labradorica*, and *Elphidium batialis* are dominant. Those species, presumably less opportunistic than *U. akitaenis* and *B. spissa*, may compete efficiently for bioavailable organic detritus in the upper sediments. Even if a relevant distinction can be recognized along our bathymetric transect between dysoxic and oxic taxa (with an oxygen concentration threshold between 45–70 μmol/L), it seems difficult to differentiate foraminiferal taxa on the sole basis of oxygen levels. Indeed, nitrate concentration,

nutritional values of organic detritus, and interspecific competition for shallow-infaunal habitat should also be carefully considered as other potential limiting ecological factors.

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APPENDIX 1. Species of benthic foraminifera recognized along the five-station bathymetric transect off Hachinohe, with reference to plates and figures in the literature. Only species with relative abundances >1% are described.

Species (> 1%)	References
Bolivina spissa Cushman, 1926	Matoba & Yamaguchi, 1982, pl. 1, figs. 22a, b
Cassidulina carinata Silvestri, 1896	Jones, 1994, pl. 54, fig. 3
Cibicidoides pseudoungerianus (Cushman, 1922)	Ishiwada, 1964, pl. 8, figs. 115a, b
Chilostomellina fimbriata Cushman, 1926	Ishiwada, 1964, pl. 7, figs. 110a, b
Eggerella advena (Cushman, 1922)	Jones, 1994, pl. 47, figs. 8, 10
Elphidium batialis Saidova, 1961	Ishiwada, 1964, pl. 3, figs. 48, 49
Globobulimina pacifica Cushman, 1927	Jones, 1994, pl. 50, fig. 9
Nonionella globosa Ishiwada, 1950	Ishiwada, 1964, pl. 3, fig. 40
Nonionella stella Cushman & Moyer, 1930	Matoba & Yamaguchi, 1982, pl. 4, figs. 4a, b
Nonionellina labradorica (Dawson, 1860)	Ishiwada, 1964, pl. 3, fig. 33
Pyrgo lucernula (Schwager, 1866)	Jones, 1994, pl. 2, fig. 5
Reophax micaceus Earland, 1934	Uchio, 1960, pl. 1, fig. 8
Rutherfordoides cornuta (Cushman, 1913)	Matoba & Yamaguchi, 1982, pl. 3, fig. 9a, b
Uvigerina akitaensis Asano, 1950	Ishiwada, 1964, pl. 5, fig. 70
Uvigerina curticosta Cushman, 1927	Cushman, 1927, pl. 4, fig. 1
Uvigerina cf. *U. graciliformis* Papp & Turnovsky, 1953	van der Zwaan et al., 1986, pl. 21, figs. 6, 8

APPENDIX 2

Census data for live benthic foraminifera in the >150-μm fraction for the five sampling stations. This table can be found on the Cushman Foundation website in the JFR Article Data Repository (http://www.cushmanfoundation.org/jfr/index.html) as item number JFR_DR 2014005

APPENDIX 3

Equations for 1) the Shannon index (H′) and 2) the Evenness index (E).

Equation 1:

$$H' = -\sum_{i=1}^{S} (p_i \times \ln(p_i))$$

where p_i is the probability of presence for the species i (i.e., % value/100).

Equation 2:

$$E = e^{H'} \Big/ S$$

where H' is the Shannon index and S is the simple diversity (i.e., the count number of taxa).