Seasonal changes in deep-sea benthic foraminiferal populations: Results of long-term observations at Sagami Bay, Japan

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Abstract—To study seasonal changes of deep-sea foraminiferal populations, we have collected sediment samples with an USNEL-type box corer and a multiple corer or using the Submersible “SHINKAI 2000” in situ, at a fixed station (St. SB) in Sagami Bay, since 1991. Seventy-six species belonging to 40 genera of benthic foraminifera have been identified. Seven species of the assemblage are dominant throughout the year. Five of them declined in population density in the summer, resulting in a decrease of the total population density of living foraminifera at that time. Benthic foraminifera migrate vertically in the sediment column over the course of the year, due at least in part to changes in thickness of the oxygenated layer, which thickens in winter. Feeding experiments were also made and the results suggest that shallow infaunal species are likely to respond to deposition of fresh phytodetritus, because deep infaunal species preferred to feed on dried Chlorella, but shallow infaunal species fed only on fresh Chlorella.

INTRODUCTION

The deep-sea is characterized by low temperature, oligotrophy, high hydraulic pressure and darkness throughout the year. Therefore, the deep-sea environment was once thought to be quiet and calm, and to lack in seasonality. Recent researches have revealed that there exists distinct seasonality in the marine life of the deep-sea due to seasonal deposition of phytodetritus exported from the ocean surface (Cole et al., 1987; Gooday, 1988; Thiel et al., 1989). Deep-sea organisms that rely upon this phytodetritus as a food source have corresponding life cycles and fluctuations in abundance and biomass (Billett et al., 1983, 1988; Thiel et al., 1989). Individual taxa vary in their detrital food preferences and life habits (Kitazato, 1994).

Foraminifera, a group of predominantly shelled protists, is one of the major groups of benthic organisms in the deep-sea. They sometimes account for more than 50% of deep-sea biomass (Snider et al., 1984; Gooday et al., 1992). They live within and on the sediment-water interface by consuming various kinds of organic materials (Gooday, 1988; Thiel et al., 1989; Gooday and Turley, 1990; Gooday et al., 1992; Altenbach, 1992). Their distributions reflect species-specific microhabitat preferences (Corliss, 1985; Corliss and Chen, 1988, 1991; Kitazato, 1994). Some species, such as Epistominella exigua and Alabaminella weddelensis, swarm quickly to newly delivered phytodetritus after a spring bloom (Gooday, 1988, 1993; Thiel et al., 1989; Gooday and Turley, 1990). These species are thought to show opportunistic life habits. Such opportunistic feeding habits suggest that
benthic foraminifera may be an important consumer of phytodetritus, and that they should react seasonally in response to delivered organic materials. However, very few studies have been done concerning seasonal occurrences of benthic foraminifera within deep-sea sediments except for some population research based on a few samples collected in different seasons (GOODAY, 1988, 1993, 1994; CORLISS and SILVA, 1993). Time series observations at a fixed station are needed to understand the ecology of foraminifera within deep-sea sediments throughout the year. These observations may be a way to understand the role of benthic foraminifera in deep-sea food chains and the carbon cycle.

To determine the seasonal distributions of benthic foraminifera within deep-sea sediments, we have made periodical samplings of sediments at a fixed station in the Pacific Ocean adjacent to the Japanese Islands for three years from 1991 to 1993. We observed changes both in sediment characteristics and distinct seasonal vertical migrations of benthic foraminifera within the sediments. In this paper, we discuss possible reasons why benthic foraminifera migrate seasonally within the sediments. Culture experiments were also conducted in the laboratory to understand food preferences among benthic foraminiferal species.

METHODS

Samples

We collected bottom sediments from a station, St. SB, located in the central part of Sagami Bay (35°00' N, 139°22.5' E, 1450 m depth; Fig. 1). The station is located on a flat bottom region of the Sagami Trough. Three water masses are recognized in the central part of Sagami Bay (IWATA, 1987). The upper a few hundreds of meters are occupied by relatively saline waters of the Kuroshio current (>34.6‰); the Subarctic Intermediate Water (=Intermediate Oyashio Water; <34.1‰) resides below this water to a depth of about 1000 m, beneath which occurs the Pacific Deep Water (IWATA, 1987). The North Pacific Deep Water overlies the station SB. The bottom water is characterized by temperatures of 2.3 ± 0.1°C, salinities of 34.5 ± 0.2‰, and dissolved oxygen concentration of 1.1 ± 0.2 ml/l. Bottom temperatures in the central part of Sagami Bay do not change throughout the year (MIYA and NEMOTO, 1991). The salinity and dissolved oxygen content also seem to be invariant throughout the year, although data are scarce (Kitazato and Ohga, unpublished data).

We have taken 13 bottom samples from 1991 to 1993 at St. SB using both an USNEL-type box corer (HESSLER and JUMARS, 1974) and a multiple corer (BARNETT et al., 1984). Samples with a well-preserved surface flocculent layer were selected and used for the study. On board, plexiglass subcorers (34 mm in inner diameter) were carefully inserted into the sediment surface of the samplers, in order not to disturb the surface texture at the sediment-water interface. The thickness of the surface oxygenated layer was measured at each sampling occasion. Sediment with a yellowish gray color was judged as the oxygenated layer, because this color is thought to originate from Fe or Mn oxide (BERGER et al., 1979).

Subcores were cut into 1 cm intervals from the surface to 15 cm in depth. The sediments of each core section were fixed for one night at room temperature using
5% buffered formalin concentration and stained using 0.5% rose bengal dissolved in 50% ethyl alcohol-seawater solutions. Samples were then washed over a 250 mesh (63 μm openings) sieve and material retained was dried at 50°C in an electric oven. All specimens for which the cytoplasm was well stained with rose bengal were picked out under a binocular microscope.

*In situ* observation of the sediment surface and undisturbed bottom core samplings were also carried out from the submersible “SHINKAI 2000” at Ocean Bottom Base No. 2 (OBB 2; 35°00′.86″ N, 139°21′.59″ E, depth 1445 m), which is situated about 1 nautical mile north from station SB (KITAZATO and OHGA, 1992).

**Cultures**

We cultured benthic foraminifera that were collected from station SB in a temperature controlled laboratory at 2.5°C. Benthic foraminifera living in sediments above 2200 m can be maintained in a laboratory under 1 atmospheric pressure (KITAZATO, 1989, 1994; LINKE, 1989; HEEGER, 1990). Food preferences of benthic foraminifera were examined in culture bottles where sediments with living foraminifera and seawater were placed. We fed either dried or living *Chlorella* into culture.
bottles such that the sediment surface of each bottle was covered with the *Chlorella*. The feeding experiments were continued for two weeks. We observed living foraminifera continually in culture bottles with a side-mounted binocular microscope (Kitazato, 1981) during the experiments. If food is suitable for the nutrition of a particular foraminiferan, the cytoplasm of the individual changes from dark brown to green because the *Chlorella* are taken into the cytoplasm, enabling determination of food preferences. Techniques and procedures for culturing deep-sea foraminifera are described in detail in Kitazato (1994).

RESULTS

*Seasonal changes of the oxygenated layer*

The bottom sediment at station SB is yellowish gray to dark gray mud. Biogenous calcareous sand grains are present in the mud, together with a small number of volcanic sand grains. The surface oxygenated layer is yellowish gray, and rests upon a dark gray reduced layer. The sediment surface is slightly undulate and fluffy. Many polychaete tubes protrude from the bottom. Hollows made by another polychaete species were scattered on the surface of the sediment. Other macrofauna such as arthropods, gastropods, and ophiuroids are patchily distributed on the surface. Along the sea bottom within one kilometer of the station, which we observed continuously with the submersible, no distinct differences were found in bottom landscapes and sediment characteristics (Kitazato and Ohga, 1992).

The thickness of the oxygenated layer changed drastically between seasons (Fig. 2). During February through June, the oxygenated layer was thin, ranging from 1 to 1.5 cm. Between November and December, the oxygenated layer became 2.5 to 3 cm thick. Characteristics of the surface fluffy layer also changed seasonally. In spring, a 1 to 2 cm thick greenish gray fluffy layer, mainly composed of phytodetritus,
covered the sediment surface. Most of this layer was composed of diatom frustules and/or other plankton remains as already described by Thiel et al. (1989). However, we did not observe any fluffy layer in the winter (Kitazato and Ohga, 1992).

**Seasonal changes of benthic foraminiferal populations**

Seventy-six species belonging to 40 genera of benthic foraminifera have been identified from the station. In terms of abundance the assemblage mainly consists of Textularia kattegatensis, Bolivina pacifica, Fursenkoina rotundata, Fursenkoina sp. 1, Chilostomella ovoidea, Globobulimina affinis, Uvigerina peregrina, U. proboscidea, U. akitaensis, and Bolivina spissa (Kitazato, 1989). These species are commonly present in oxygen-depleted middle bathyal depths in the western Pacific adjacent to the Japanese Islands (Inoue, 1989). The number of living (=rose bengal stained) individuals of benthic foraminifera per 10 cm² changed seasonally at the station SB (Fig. 3). They are abundant in winter and spring, but sparse in summer and autumn except September of 1992. The number of living individuals peaked at 1500 to 2000/10 cm² in winter and spring, and fell to as low as 200 to 500 individuals/10 cm² in summer.

The proportion of each species relative to the total foraminiferal assemblage varies seasonally (Fig. 3), due primarily to fluctuations in population size of a few of the most abundant species; most other species had constant abundance throughout the year. Both Globobulimina spp. and Chilostomella ovoidea increased in November through February. Individuals of Fursenkoina sp. 1 and Bolivina pacifica

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**Sagami Bay**

![Graph showing seasonal changes in the number of living benthic foraminifera per 10 cm² at station SB. Seasonal changes of common species are also drawn in the figure.](image)

Fig. 3. Seasonal changes in the number of living benthic foraminifera per 10 cm² at station SB. Seasonal changes of common species are also drawn in the figure.
Fig. 4. Seasonal changes in the distribution of the total assemblage of benthic foraminifera within the sediment at station SB. Data for December, 1991 and November, 1992 were collected at St. OBB. Results from duplicate samples are also shown in the figure.
increased in abundance mainly in winter and spring. Among them, *Fursenkoina* sp. 1 shows the most distinct increase. Other species did not show any distinct relationship between environmental seasonality and changes in abundance.

The depth distribution at which living foraminifera present varies from species to species (Fig. 5). *Triloculina* sp. and *Bathysiphon* sp. live in the topmost centimeter throughout the year. *Textularia katategensis*, *Fursenkoina rotundata*, *Uvigerina* spp., *Bolivina spissa* and *Fursenkoina* sp. 1 are mainly distributed at 0–2 cm within the sediments. *Globobulimina* spp. and *Chilostomella ovoidea* are concentrated at 0–5 cm. *Bulimina aculeata* shows a different distributional pattern from the other species described here. This species occurs from 0–10 cm. The distribution is not concentrated at a specific depth, but sometimes shows a bimodal pattern, showing maximum concentrations both at 1–3 cm and 5–7 cm depth in the sediments.

The depth distributions within sediments of benthic foraminifera changed seasonally (Figs. 4 and 5). In March, April and May, most foraminifera were concentrated in the top 2 cm. Less than 5% of the total assemblages lived below 5 cm deep in the sediment. In spring, hundreds of *Fursenkoina* sp. 1, *Bolivina pacifica* and *Textularia katategensis* occurred in the top centimeter. In August, November and December, foraminifera were scattered between the surface and 10 cm depth in the sediments. In this season, depth stratification of each species in the sediment was more clearly developed than in the spring.

Laboratory observations of the feeding behaviors of benthic foraminifera show distinct variations in food preferences among species. When we inserted heat-killed *Chlorella* into a culture bottle, *Textularia katategensis*, *Bolivina pacifica* and *Fursenkoina* sp. 1 swarmed over and devoured the fresh food within a day. In contrast, *Globobulimina* spp. and *Chilostomella ovoidea* took most of a week to gather the fresh-food. In contrast, *Globobulimina* spp. and *Chilostomella ovoidea* took dried *Chlorella* more quickly (KITAZATO, 1994).

**DISCUSSION**

Long-term observations of the sediment surface at the permanent station SB in Sagami Bay showed that both the thickness of the surface oxygenated layer of the sediments and the depth distribution of the benthic foraminiferal assemblage changed seasonally. What kinds of environmental factors control such changes? Physico-chemical conditions of the bottom water may not be a main factor, because they do not vary throughout the year. Instead, seasonally delivered organic materials may have triggered seasonality in foraminifera in the deeper part of Sagami Bay.

The change in thickness of the oxygenated layer may be related to the change of the seasonal flux of organic matter, but organic matter flux has not yet been measured directly in Sagami Bay. Both phytodetrital and terrigenous organic materials are supplied to the bottom of the central part of Sagami Bay. Terrigenous organic materials are supplied from the coastal areas to the deeper parts of the bay, although we have no data regarding the temporal pattern of input of terrigenous organic materials. On the other hand, plankton blooms in February through May are recognized in Sagami Bay (THE OCEANOGRAPHICAL SOCIETY OF JAPAN, 1985:...
Fig. 5. Three dimensional blocks show changes in the depth distribution of six selected benthic foraminiferal species within the sediments at station SB. *Triloculina* sp. is an epifaunal species. *Uvigerina* spp. is a very shallow infaunal species. *Fursenkoina* sp. 1 and *Textularia kattegatensis* are shallow infaunal species; *Fursenkoina* sp. 1. increased greatly in number of individuals in the spring. *Globobulimina* spp. is distributed deeply in the sediments. *Bulimina aculeata* shows a bimodal distribution within sediment; we were not able to categorize this species into any current microhabitat models.
Phytodetritus was deposited as a fluffy layer on the sediment surface at the time of the bloom; this fluffy layer is deposited only in spring (Kitazato and Ohga, unpublished data). Decomposition of phytodetritus by aerobic respiration seems to decrease the thickness of the oxygenated layer after the bloom. This scenario is supported by observations in the deep-sea of the Pacific where in dissolved oxygen contents of deep water change with the seasonal rainfall of particulate organic matter through the water column (Smith et al., 1993).

Benthic foraminifera migrated vertically within the sediment on a seasonal basis, concentrating into the shallower part of the sediment in spring. This may also be explained by two factors related to the seasonal delivery of organic matter flux. First, foraminifera that prefer to stay in the oxygenated layer should be concentrated into the thin oxygenated layer during this season. Second, in spring, benthic foraminifera should be distributed in the shallower part of the sediment to take advantage of newly delivered food materials. Which reason is more effective in controlling the distribution of benthic foraminifera, the thickness of the oxygenated layer or the food supply? This likely depends on the microhabitat preferences of each benthic foraminiferal species. The thickness of the oxygenated layer limits the distributional depth of deep infaunal species, while the seasonal deposition of phytodetritus is probably more important to opportunistic species.

Benthic foraminiferal species show depth stratification within the sediment (Corliss, 1985; Kitazato, 1989, 1994), although living depths within sediments are shallower in Sagami Bay than in the Atlantic (Corliss, 1985). Based on current classifications of foraminiferal microhabitats within the sediment (Corliss, 1985; Corliss and Chen, 1988, 1991; Lambshide and Gooday, 1992; Gooday et al., 1992; Kitazato, 1994), the most abundant benthic foraminiferal species in Sagami Bay are classified into microhabitat groups as follows: Triloculina sp. and Bathysiphon sp. are categorized as epifaunal species. Textularia kattegatensis, Fursenkoina rotundata, Uvigerina spp., Bolivina spissa and Fursenkoina sp. 1 are grouped into shallow infaunal species. Globobulimina spp. and C. ovoidea are grouped into deep infaunal species. We are not able to categorize Bulimina aculeata into any group at present.

Several reasons exist for depth stratification. The most common reason is variability in the tolerance of benthic foraminifera to low levels of dissolved oxygen (Corliss, 1985; Bernhard, 1992). Differences in food preference also play a role in stratification. Laboratory observations of feeding behaviors of benthic foraminifera supports this assumption as stated above.

It is apparent that the population size and the depth distribution of benthic foraminifera change in relation to the seasonally formed organic rich layer. It is also probable that life histories of deep-sea benthic foraminiferal species are well linked with seasonally supplied organic detritus (Gooday, 1993, 1994). If foraminifera are responsible for oxidizing a substantial fraction of this detritus, benthic foraminifera may play a critical role in deep-sea food webs, as suggested by Gooday et al. (1992). Irrespective of the size of their role, however, foraminifera are important modern and fossil indicators of ocean flux rates, and we need deeper understanding of their position in deep-sea food webs.
Acknowledgements—We are indebted to Ch. Hemleben, Y. Shirayama and W. Soh for their encouragement during the course of this study. Ch. Hemleben and R. M. Ross critically read the manuscript and made valuable comments. Two anonymous reviewers provided valuable comments on the manuscript. Both the Ocean Research Institute of the University of Tokyo (ORI) and Japan Marine Science and Technology Center (JAMSTEC) kindly gave us opportunities to collect samples at the fixed station in Sagami Bay. Crew members of the R/V Tansei-maru and Hakuho-maru, both of ORI, and the submersible "Shinkai 2000" of JAMSTEC skillfully managed the sampling gear. This research is supported by Grants-in-Aid from the Ministry of Education, Science and Culture of Japan (Scientific Research on Priority Areas, Ocean Fluxes—Their Role in the Geosphere and the Biosphere, nos. 03248205 and 04232211 and Scientific Research Grant no. 02454028 to H.K.).

REFERENCES


