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Benthic Biotic Response to Climate Changes Over the Last 700,000 Years in a Deep Marginal Sea: Impacts of Deoxygenation and the Mid-Brunhes Event

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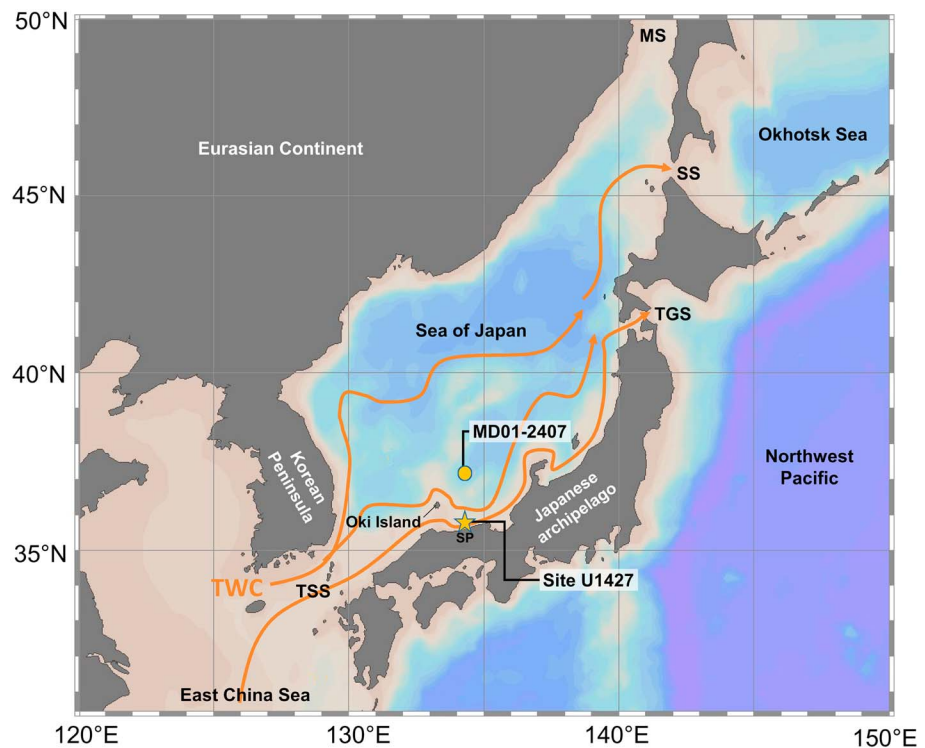
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Abstract The Sea of Japan is a marginal sea, connecting to adjacent seas by four shallow straits (water depths <130 m). Marginal seas are ideal for studying biotic responses to large-scale environmental changes as they often are sensitive to glacial-interglacial and stadial-interstadial climatic cycles. However, only a limited number of studies cover time periods beyond the last two glacial-interglacial cycles. Here we present a 700,000-year record of benthic biotic response to paleoceanographic changes in the southern Sea of Japan, covering the past seven glacial-interglacial cycles, based on ostracode assemblages at the Integrated Ocean Drilling Program (IODP) Site U1427. The results indicate that long-term oxygen variability in the bottom water has been the major control impacting the marginal-sea biota. Five local extirpation events were recognized as barren zones during glacial maxima immediately before terminations I, II, IV, V, and VII, which are probably caused by bottom-water deoxygenation. Results of multivariate analyses indicated clear faunal cyclicity influenced by glacial-interglacial oxygen variability with a succession from opportunistic species dominance through tolerant infauna dominance to barren zone during the deoxygenation processes and the opposite succession during the recovery processes. The Sea of Japan ostracode faunal composition showed distinct difference between the post-MBE and pre-MBE (Mid-Brunhes Event) periods, indicating the MBE as a major disturbance event in marginal-sea ecosystems. The MBE shortened the duration of the extirpation events, fostered dominance of warmer-water species, and amplified the glacial-interglacial faunal cyclicity. Our long-term biotic response study clearly indicates that deep marginal sea ecosystems are dynamic and vulnerable to climate changes.

1. Introduction

Marginal seas are semienclosed systems characterized by relatively small size and simple circulation dynamics. They are sensitive to climate changes in various time scales, typically from millennial to orbital (e.g., Bassetti et al., 2010; Capozzi & Negri, 2009; Gorbarenko et al., 2015; Rohling et al., 2015; Schmiedl et al., 2010; Tada et al., 1999, 2015). Therefore, marginal seas are ideal natural laboratories or mesocosms and have been applied to study biotic responses to large-scale climate changes. For example, in the Nordic Seas, repeated incursions of diverse "Atlantic species groups" from warmer North Atlantic proper are known from warmer periods in Quaternary deep-sea benthic foraminifera (Rasmussen et al., 2003; Yasuhara & Danovaro, 2016). A similar phenomenon is known in the warm deep Mediterranean Sea, in which incursion of diverse "colder water" Atlantic species is known to have occurred during colder periods in nematode long-term time-series records (Danovaro et al., 2004; Yasuhara & Danovaro, 2016). Such incursions of "colder-water" Atlantic species, for example, of shallow-marine and upper-bathyal ostracodes and molluscs, are known as "Northern Guests" in Quaternary Mediterranean fossil records (Cita, 2008; Faranda & Gliozzi, 2011; Pasini & Colalongo, 1996; Ruggieri & Sprovieri, 1977).

Bottom-water deoxygenation events are a typical example of the climate-change influence on marginal seas. These are well known as the sapropels in the eastern Mediterranean Sea, and the distinct dark sediment layers in the Sea of Japan (e.g., Bassetti et al., 2010; Capozzi & Negri, 2009; Gorbarenko et al., 2015; Rohling et al., 2015; Schmiedl et al., 2010; Tada et al., 1999, 2015). However, biotic responses to bottom-water oxygen changes remain insufficiently understood. In particular, long-term records have been sparse in the literature,

Figure 1. Map of the studied region and sites. Map of the Sea of Japan region, Tsushima Warm Current (TWC) and Sites U1427 (35°57.9200′N, 134°26.0604′E, 330 m below sea level) and MD01-2407 (37°04.0000′N, 134°42.1100′E, 932 m below sea level). Abbreviations are as follows: SP: Shimane Peninsula, TSS: Tsushima Strait, TGS: Tsugaru Strait, SS: Soya Strait, and MS: Mamiya Strait. This map was generated with Ocean Data View (Schlitzer, 2016).

and studies of biotic response have been restricted to one or few deoxygenation events, or the last one to two glacial-interglacial cycles (Jorissen, 1999; Rodriguez-Lazaro et al., 2017; Schmiedl et al., 1998, 2003, 2010; Stefanelli et al., 2005).

The Sea of Japan is a marginal sea, where orbital-scale sea level changes, dynamics of ocean circulation, and bottom-water oxygen fluctuation have been the key drivers of paleoenvironmental changes. It is semien-closed by the Eurasian Continent, Korean Peninsula, and Japanese archipelago, connecting to adjacent marine waters through shallow straits (<130 m water depth): to the East China Sea, the Pacific, and the Okhotsk Sea through the Tsushima Strait (sill depth 130 m), the Tsugaru Strait (130 m), and the Mamiya (12 m) and Soya Straits (55 m) respectively (Figure 1). A 150–200 m layer of Tsushima Warm Surface Current (TWC) and the underneath homogenous Japan Sea Proper Water forms a unique circulation system in the Sea of Japan (Talley et al., 2006). The TWC, a mixture of the Kuroshio Current and the East China Sea Coastal Water, is the only major saline water influx to the marginal sea (Gallagher et al., 2015; Talley et al., 2006). The Japan Sea Proper Water mainly originates from the TWC that cools and sinks down in the northern Sea of Japan (e.g., Ikehara & Itaki, 2007; Minoura et al., 2012; Talley et al., 2006). This deepwater formation pro-vides an exceptionally oxygen-rich water to sustain the deep-sea ecosystem (dissolved oxygen concentration of 220–250 μmol/kg; Talley et al., 2006; Minoura et al., 2012). However, the Sea of Japan (sill depth 130 m) was at most completely isolated during low sea level stands (maximum −130 m). The TWC influx was replaced by surface freshening, and convection in the water column was interfered by stratification (e.g., Watanabe et al., 2007). Five modes of water circulation are known to cause euxinic (Mode 1), quasi-anaerobic (Mode 2), anae-robic (Modes 3 and 4), and aerobic conditions (Mode 5) in the bottom water of intermediate depths, respec-tively, in the Sea of Japan (Watanabe et al., 2007). These different modes of circulation caused centimeter- to decimeter-scale alternations of dark- and light-colored layers in basin-wide sediment depositions during the Quaternary (Itaki et al., 2004; Khim et al., 2009; Kido et al., 2007; Tada, 1994; Tada et al., 1992, 1999). Light-colored, bioturbated layers were generally deposited under aerobic condition during interglacial periods.

Thick dark-colored sulfur-rich layers (>20–40 cm thick) were deposited under euxinic condition during glacial maxima with sea level drop >90 m (Kido et al., 2007; Tada et al., 2015; Watanabe et al., 2007).

The above characteristics make the Sea of Japan an ideal location to investigate past biotic response to long-term climate change, given advantages of the well-investigated modern- and paleo-oceanography. Timely, IODP (Integrated Ocean Drilling Program) Expedition 346 (29 July to 27 September 2013) retrieved unprecedentedly long sediment cores from the Japan Sea (Tada et al., 2015). The high-quality cores obtained by the advanced piston coring system of the drilling vessel JOIDES Resolution provided complete sediment sequences with microfossil abundance that enabled a high-resolution reconstruction of ostracode fossil assemblages throughout many glacial-interglacial cycles.

Benthic ostracodes are small bivalved crustaceans (Horne et al., 2002; Rodriguez-Lazaro & Ruiz-Muñoz, 2012), representing an important component of deep-sea meiobenthic communities, with a wide variety of ecological preferences (e.g., Cronin et al., 1999; Yasuhara & Cronin, 2008; Yasuhara et al., 2008; Yasuhara, Hunt, Cronin, et al., 2012; Yasuhara et al., 2017). Ostracodes have excellent fossil records because of their calcite shells, small size, and high abundance (Holmes & Chivas, 2002; Yasuhara et al., 2017). Thus, the ostracode fossil assemblage is an ideal model system to understand metazoan biotic response to paleoclimatic and palaeoceanographic changes (e.g., Cronin & Raymo, 1997; Mesquita-Joanes et al., 2012; Moffitt et al., 2015; Yasuhara et al., 2008, 2009, 2014, 2017; Yasuhara & Cronin, 2008).

Here we present a 700,000-year record of deep-sea benthic biotic response to paleoceanographic changes spanning Marine Isotope Stages (MISs) 1–17 by using ostracode fossil assemblages at Site U1427. We mainly focus on two major climatic aspects during the period, which are the glacial-interglacial oxygen variability and the Mid-Brunhes Event (MBE, ~400–350 thousand years ago [ka]). Although biotic changes associated with glacial-interglacial cycles are well known in general (e.g., Alvarez Zarikian et al., 2009; Cronin et al., 1994; Cronin & Raymo, 1997; Kitamura et al., 1994; Yasuhara et al., 2009), it is important to know more about biotic responses specifically to past oxygen changes in this time scale. This is because human-induced climate and environmental changes are causing serious ongoing deoxygenation in the ocean (Breitburg et al., 2018; Oschlies et al., 2018). Indeed, in the Sea of Japan, the bottom-water oxygen level has declined up to 8–10% in the recent three decades (Gamo, 2011; Kang et al., 2004). The MBE is a major global climatic event that marks the final stage of the Pleistocene climate transition from low-amplitude to high-amplitude glacial-interglacial climatic variability (i.e., Mid-Pleistocene Transition; Cronin, 2010). This fundamental shift in the climate cyclicity involves large-scale changes in the ice shelf development, sea ice volume, global ocean circulation, and potentially marginal sea systems that are sensitive to the climate cyclicity. Recent studies have reported a major faunal shift associated with the MBE in a marginal sea, the Arctic Ocean (Cronin et al., 2014, 2017; deNinno et al., 2015). However, pervasiveness of the ecosystem impacts of this fundamental change in glacial-interglacial cyclicity at the global scale remains uncertain. Thus, our specific research questions are as follows: (1) How has the glacioeustatic-controlled oxygen variability affected the deep marginal sea biota? (2) Did MBE-associated biotic changes occur pervasively beyond the Arctic Ocean, and if so, how have the MBE changed the Sea of Japan deep-sea ecosystem?

2. Methods

2.1. Study Sites and Data Sources

We used the sediment cores from IODP Site U1427 for our ostracode analyses (Figure 1). We also used the dark sediment layer stratigraphy in core MD01-2407 (Kido et al., 2007) and the late Pleistocene sea level stack (Spratt & Lisiecki, 2016) for the comparison with our U1427 ostracode records. Sites U1427 (330 m below sea level) and MD01-2407 (932 m below sea level) are located off the Shimane Peninsula, under the TWC pathway, and within the Japan Sea Proper Water (Figure 1). Sagawa et al. (2018) constructed the age model for Site U1427 based on an integrative chronostratigraphy including oxygen isotope stratigraphy, sediment color, tephrostratigraphy, and planktonic microfossil biostratigraphy. Site U1427 is a relatively shallow site where dark-light layer alternation in the sediment was indistinguishable. Therefore, the nearby deeper site MD01-2407 provides a known stratigraphy of the basin-wide dark layer deposition that indicates Mode-1 water circulation (i.e., euxinic bottom water condition) for the last 640 kyr (Kido et al., 2007; Watanabe et al., 2007). Both of these sites are positioned within the Japan Sea Proper Water. Since the site of core MD01-2407 is in the core of the regional oxygen minimum zone (Tada et al., 2015), it is ideal to represent the oxygenation

history of the Sea of Japan in broad sense. Site U1427 is shallower and lies above the core of the oxygen minimum zone, and thus should have experienced similar but less severe oxygen depletion events.

2.2. Ostracode Analysis

A total of 415 subsamples (standardized 30 ml volume for each) were collected at ~65-cm intervals from the upper 300 m of the Site U1427 composite splice, yielding a sampling resolution of ~1.5 kyr for the millennial-scale ostracode reconstruction of the last 700 kyr. The samples were freeze dried, wet-sieved (63 μm mesh), and finally oven-dried at ~35 °C. All specimens were picked and counted from the >150 μm fraction of the dried residues. In the final census data, one left/right valve and one complete carapace (= two articulated valves) were counted as one and two, respectively. In our results, the number of specimens per sample ranges from 0 to 302. All specimens were identified to the species level mainly by following Ikeya and Suzuki (1992), Ozawa (2003), and Ozawa and Kamiya (2005).

We interpreted ostracode assemblage data, using paleoenvironmental indicators (see section 2.1), community-scale statistics, and three multivariate analyses (see section 2.3). The community-scale statistics include number of ostracode specimens, relative abundance (%) of each species, average frequency of each species, and Simpson index. The average frequency equals to $\Sigma P_i/n$, where P_i is the relative percentage of the species in each sample, and n is the total sample number. Simpson index, which is relatively insensitive to small sample size (Magurran, 2003; Morris et al., 2014), is selected to represent the taxonomic diversity of each sample. The calculation formula follows Simpson (1949): $1-\Sigma P_i^2$, where P_i is relative percentage of a species. The data analyses were done in R version 3.3.3 with R package *vegan* (Oksanen et al., 2017; R Core Team, 2017).

2.3. Multivariate Statistical Analyses

Patterns of species variability were shown by three multivariate statistical analyses, including Non-metric Multidimensional Scaling, Q-mode k-means clustering, and Species Indicator Value. Species relative abundances (%) were used in all multivariate analyses. Certain data selection is required for multivariate analyses on fossil assemblages: we excluded samples with <10 specimens and rare taxa whose 95% cluster confidence interval has a negative lower boundary (Bennington & Rutherford, 1999). Eventually, 208 samples and 13 species that account for 91.82% of the total number of specimens were used in the multivariate analyses.

Non-metric Multidimensional Scaling is an unconstrained ordination method, producing a simplified two-dimensional plot useful for reading the large data set of faunal census (Borcard et al., 2011; Legendre & Legendre, 2012). In this ordination plot, ranking distance relationship among samples and species are well preserved. Unlike other ordination methods (e.g., principal component analysis), it does not extract individual axes by maximizing the variance of data set in the multidimentional space, so axes may arbitrarily be rotated.

Q-mode k-means clustering divides samples into clusters, minimizing the difference of species composition within clusters and maximizing it across clusters (Dimitriadou et al., 2002; Dufrêne & Legendre, 1997). We used Simple Structure Index to decide the optimal number of clusters (i.e., four clusters in our case) for the clustering analysis (Hartigan & Wong, 1979). Also, the nonhierarchical k-means clustering is chosen over the traditional hierarchical dendrogram clustering methods (e.g., complete linkage) because they are more effective in dividing samples of a single site (Vavrek, 2016).
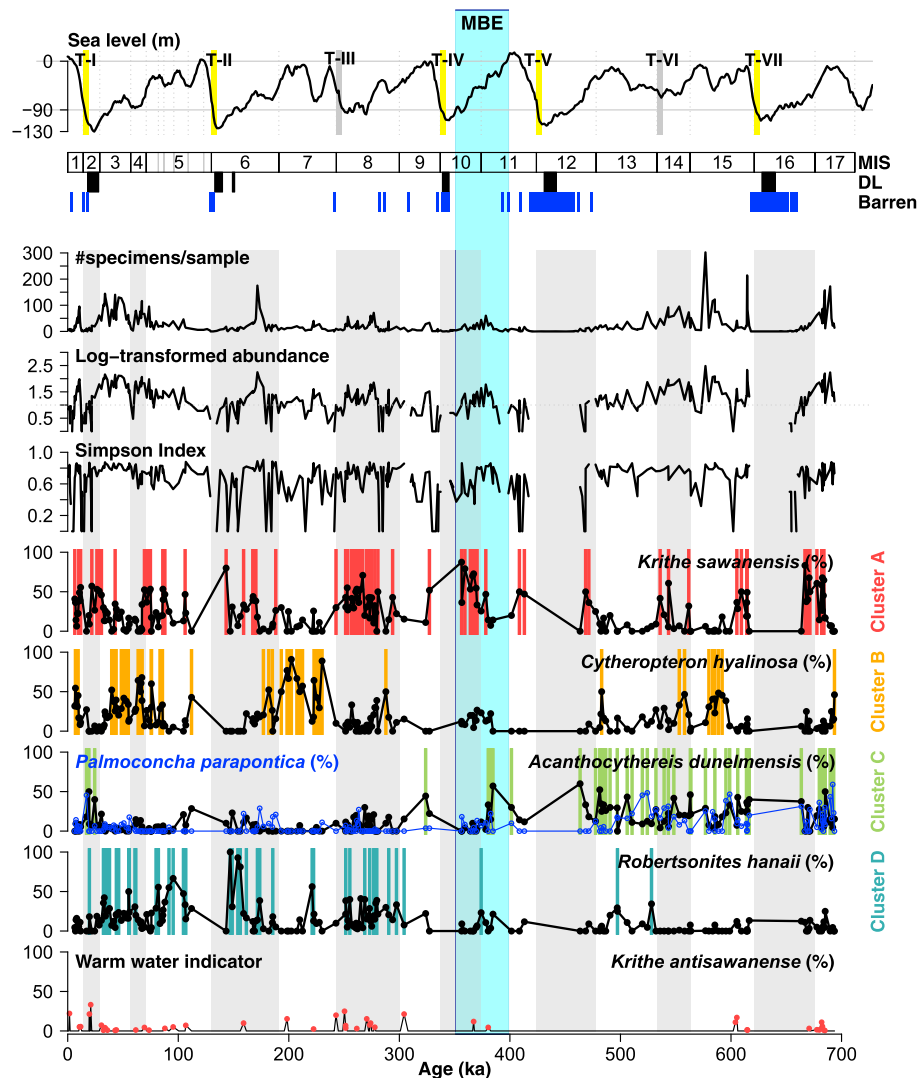
Post-hoc Species Indicator Value method calculates species indicator values of each species for each cluster, identifying the significant species indicators of each cluster with permutation testing (Dimitriadou et al., 2002; Dufrêne & Legendre, 1997; Hartigan & Wong, 1979). The species indicator values are calculated based on relative occurrence frequency of species within a cluster and relative abundance of species across clusters (Dufrêne & Legendre, 1997).

3. Results

3.1. Barren Intervals

We recognized five major ostracode barren intervals at Site U1427. These extirpation events occurred during glacial maxima (i.e., sea level minima) in MISs 2, 6, 10, 12, and 16, immediately before terminations I, II, IV, V, and VII. These periods are represented by deposition of thick dark layers at core site MD01-2407 (Figure 2). Both the dark layers in core MD01-2407 and the major ostracode barren intervals at Site U1427 are absent
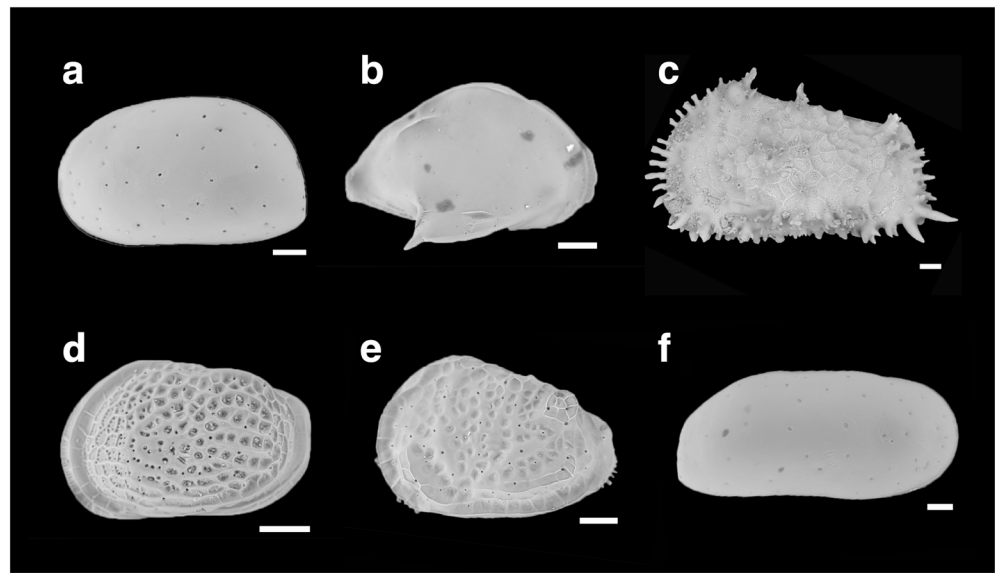
Figure 2. Ostracode faunal variability for the last 700 kyr in Site U1427. Top panels are environmental factors, including a seal level record (Spratt & Lisiecki, 2016), the MIS boundaries (Lisiecki & Raymo, 2005), and the thick dark layers (DL; Kido et al., 2007). Ostracode barren intervals are marked as blue boxes next to the dark layers. Below are the community-scale statistics and clustering results, including total number of ostracode specimens per sample (i.e., 30-cc volume), log-transformed ostracode abundance (base = 10), Simpson index, and relative abundances (%) of six indicator species. Samples in Clusters A to D are shown as color bars in the panels of their corresponding species indicators: Cluster A, red; Cluster B, orange; Cluster C, light green; and Cluster D, cadet blue. In the Cluster C panel, *P. parapontica* is shown in blue. The background gray shadings are even-number Marine Isotope Stages. These data are available in Data Set S1.

during the weak glacial maxima in MISs 8 and 14 before terminations III and VI. During MISs 12 and 16, extremely long barren intervals (~50 kyr) are recorded, and these lasted longer than the periods of the glacial maxima and thick dark layers.

3.2. Ostracod Fauna

In total, the U1427 samples yielded ~9,000 specimens and 55 identified species. The assemblages are overall of low density (up to 300 specimens/30-cc volume) and low diversity (average Simpson index 0.63; Figure 2). Four major species have average frequency over 5%: *Krithe sawanensis* (18%), *Cytheropteron hyalinosa* (11%), *Acanthocythereis dunelmensis* (10%), and *Robertsonites hanaii* (9%). Other common species include *Palmoconcha parapontica*, *Argilloecia* sp. 1, *Loxoconchidea dolgoiensis*, *Acanthocythereis* sp. 1,
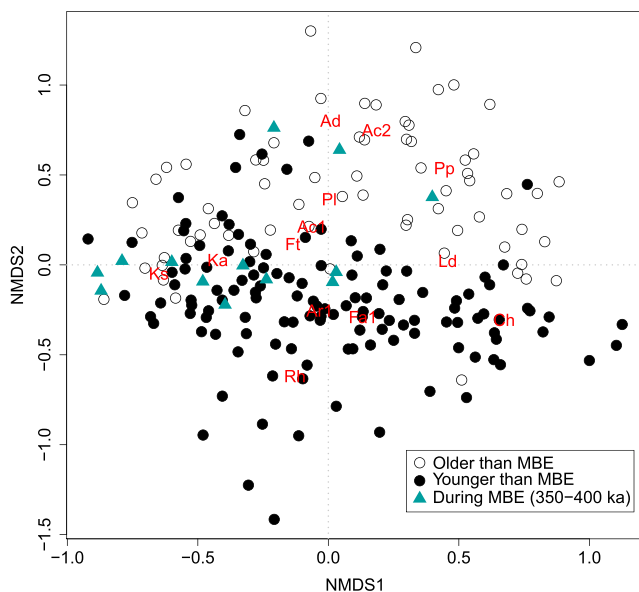
Figure 3. Scanning electron microscopy images of selected species: (a) *Krithe sawanensis* Hanai, left valve, late juvenile; (b) *Cytheropteron hyalinosa* (Hanai), right valve, adult; (c) *Acanthocythereis dunelmensis* (Norman), left valve, adult; (d) *Palmoconcha parapontica* (Zhou), left valve, adult; (e) *Robertsonites hanaii* Tabuki, left valve, late juvenile; and (f) *Krithe antisawanensis* Ishizaki, right valve, adult. The scale bar is 100 μm.

Falsobuntonia sp. 1, *Palmenella limicola*, *Falsobuntonia taiwanica*, *Acanthocythereis* sp. 2, and *Krithe antisawanensis* (Figures 3 and S1).

Figure 4. Non-metric Multidimensional Scaling. The solid circles (younger than the MBE), open circles (older than the MBE), and green triangles (during the MBE) represent samples. Species name abbreviations: Ad: *Acanthocythereis dunelmensis*, Ac1 and Ac2: *Acanthocythereis* sp. 1 and 2, Ar1: *Argilloecia* sp. 1, Ch: *Cytheropteron hyalinosa*, Ft: *Falsobuntonia taiwanica*, Fa1: *Falsobuntonia sp. 1*, Ld: *Loxoconchidea dolgoiensis*, Ks: *Krithe sawanensis*, Ka: *Krithe antisawanensis*, Pp: *Palmoconcha parapontica*, Rh: *Robertsonites hanaii*. The ordination scores are also available in Data Set S1.
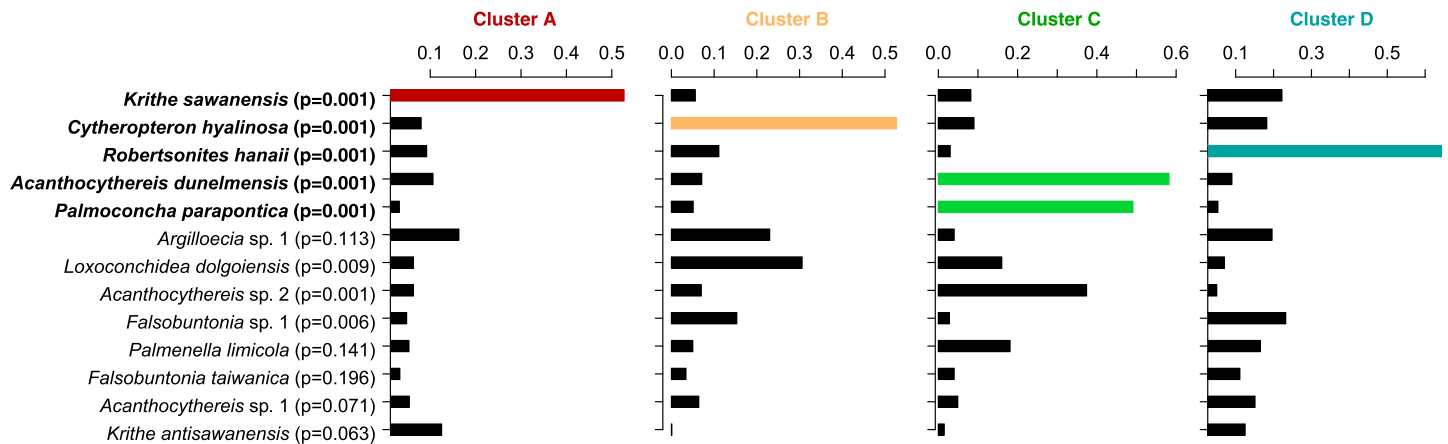
3.3. Multivariate Analyses

Non-metric Multidimensional Scaling shows the relative positions of samples and species in a two-dimensional space, allowing us to read the faunal data at a glance (Figure 4). The two axes are rotatable. Therefore, the positive and negative values along an axis are not absolute, but simply represent the two sides of an axis. Along the horizontal axis, *Cytheropteron hyalinosa*, *Loxoconchidea dogoiensis*, and *Palmoconcha parapontica* occupy the positive range; *Krithe sawanensis* and *Krithe antisawanensis* show closer position on the other side; and *Acanthocythereis dunelmensis* and *Robertsonites hanaii* are at the center. On the vertical axis, *Acanthocythereis dunelmensis* and *Robertsonites hanaii* are clearly separated to opposite directions. The pre-MBE and post-MBE samples are clearly separated into the upper and lower parts, respectively.

Q-mode k-means clustering divides the samples into Clusters A–D, which contain 37, 22, 20, and 20% of samples, respectively (Figure 2). Indicator Value results suggest indicator species for Clusters A–D (Figure 5): Cluster A, *Krithe sawanensis* (score: 0.53, p-value: 0.001); Cluster B, *Cytheropteron hyalinosa* (score: 0.53, p-value: 0.001); Cluster C, *Acanthocythereis dunelmensis* (score: 0.58, p-value: 0.001) and *Palmoconcha parapontica* (score: 0.49, p-value: 0.001); and Cluster D, *Robertsonites hanaii* (score: 0.64, p-value: 0.001). Cluster A (*Krithe sawanensis*) tends to occur during glacial periods, especially during MISs 2, 6, 8, 10, and 14 (Figure 2). In contrast, Cluster B (*Cytheropteron hyalinosa*) tends to occur during interglacials (e.g., MISs 1, 3, 5, 7, and 15) and interglacial-glacial transitions (MISs 5/4, ~100–70 ka; 7/6, ~210–170 ka; 13/12, ~485 ka; and 15/14, ~580–540 ka). Cluster C (*Acanthocythereis dunelmensis* and *Palmoconcha parapontica*) is almost exclusively distributed before the MBE, whereas Cluster D (*Robertsonites hanaii*) prevails after the MBE.

Figure 5. Indicator value scores and *p*-values of the selected species for Clusters A to D. Five species indicators are highlighted by bold. The colors used for the clusters correspond to those in Figure 2. The scores are available in Table S1.

4. Discussion

4.1. Major Extirpation Events

There were five major extirpation events in the deep-sea benthic ostracode community over the last 700 kyr. Each extirpation event corresponds to large-scale sea level reduction during glacial maxima and the basin-wide deposition of thick dark layers in the Sea of Japan (Figure 2). These dark layers indicate a particular water circulation scenario, where the Sea of Japan experienced strong water column stratification due to surface freshening from river runoff (Kido et al., 2007; Watanabe et al., 2007). Due to the cease of convection and formation of stratification, euxinic conditions at greater water depths (>900 m) formed the dark layers, while deoxygenation occurred at intermediate water depths (Kido et al., 2007; Minoura et al., 2012; Watanabe et al., 2007). Besides, crustaceans, including ostracodes, are sensitive to oxygen content (Diaz & Rosenberg, 1995; Yasuhara & Yamazaki, 2005; Yasuhara et al., 2007; Yasuhara, Hunt, Breitburg, et al., 2012). Therefore, the deoxygenation was probably the cause of these extirpation events in ostracodes at intermediate water depths.

Durations of the five major extirpation events show substantial difference between the periods before and after the MBE (Figure 2). Two pre-MBE extirpation events corresponding to the glacial maxima during MISs 12 and 16 are much longer than the post-MBE extirpation events corresponding to the glacial maxima during MISs 2, 6, and 10 (Figure 2). This difference is likely due to the difference in the duration of sea level lowstand. In the Sea of Japan, substantial isolation of the sea and resulting basin-wide bottom oxygen depletion occurred when the sea level dropped more than 90 m (Kido et al., 2007; Minoura et al., 2012). Before the MBE, the duration of the sea level lower than this threshold is ~35 kyr, covering the majority of MISs 12 and 16 (Figure 2). After the MBE, the early glacial stages are characterized by interstadials with moderate sea level peaks (e.g., MIS 3 and early MISs 6 and 10), and the durations of sea level lowstand are restricted to ~25 kyr during the glacial maxima in MISs 2, 6, and 10 (Figure 2). The weak glacial maxima in MISs 8 and 14 without the sea level lowstands substantially greater than −90 m lack major extirpation events (Figure 2).

4.2. Faunal Variability

Glacial/interglacial variability was observed in the abundance and diversity curves (Figure 2). The log-transformed abundance curve shows high similarity with the Simpson index. Ostracodes are overall more abundant and thus slightly more diverse during interglacial periods. Likely, this is the result of the extirpation events during several glacial periods. Indeed, abundance and diversity peaks concentrate in the periods where sea level drop was less than 90 m (Figure 2).

The U1427 ostracode fauna is mainly characterized by the glacial-interglacial alternate dominance of *Krithe sawanensis* and *Cytheropteron hyalinosa* (significant negative correlation: rho = −0.528, *p* < 0.0001). This is clearly shown by the alternations of Clusters A and B throughout the sequence (Figure 2). The alternation between these species probably reflects changes in bottom-water oxygen conditions. *Krithe* is known as an infaunal genus living in the sediment (Coles et al., 1994; Majoran & Agrenius, 1995; McKenzie et al., 1989;

Table 1
Autoecology Summary of the Six Species Indicators

Species name	Cluster	Autoecology	References
Krithe sawanensis	Cluster A	Infaunal and tolerant against low oxygen level (for the genus)	Whatley & Zhao, 1993; Yasuhara & Cronin, 2008; Zhao & Whatley, 1997
Cytheropteron hyalinosa	Cluster B	Carnivorous and presumably demand well-oxygenated water (for the genus)	Hartmann, 1975; Mazzini, 2005
Acanthocythereis dunelmensis	Cluster C	Cryophilic (0–5 °C in the Sea of Japan)	Cronin & Ikeya, 1987; Goto et al., 2014; Irizuki et al., 2007;
Palmoconcha parapontica	Cluster C	Associated with cold and deep water	Yamaguchi & Kamiya, 2007
Robertsonites hanaii	Cluster D	Cool water (2–5 °C)	Ozawa & Kamiya, 2005; Yamada, 2003
Krithe antisawanensis		Warm water (6–20 °C)	Ikeya & Suzuki, 1992; Irizuki et al., 2007

Whatley & Zhao, 1993) and therefore may have higher tolerance for low oxygen condition (Whatley & Zhao, 1993; Yasuhara & Cronin, 2008; Zhao & Whatley, 1997), compared to epifaunal genera, such as *Cytheropteron*. *Cytheropteron* has well-developed alae that are presumably useful for their stable positioning on the sediment surface (Tanaka, 2009; Yamaguchi & Norris, 2012; Table 1 and Text S1). Indeed, *Krithe* tends to be dominant in glacial periods not only in the Sea of Japan (this study) but also in other oceans (Cronin et al., 1996; Yasuhara, Hunt, Cronin, et al., 2012) when less ventilated deep-water is predominant. Therefore, in this study, glacial *Krithe* dominance that tends to occur before and after extirpation events probably reflects moderate oxygen depletion that is not strong enough to cause a faunal extirpation event.

Deep-sea genus *Cytheropteron* is known to be abundant in climatic transitions (Alvarez Zarikian et al., 2009; Cronin et al., 1996, 1999), which is consistent with our result. Furthermore, *Cytheropteron* is considered a carnivorous genus, that is, predator or scavenger on polychaetes (Hartmann, 1975; Mazzini, 2005; Table 1 and Text S1). This autoecological information suggests high metabolic demand or opportunistic nature, which are consistent with our result of *Cytheropteron* dominance in well-oxygenated periods and climatic transitions, respectively. *Cytheropteron* is less abundant during oxygen-depleted glacials, especially during MISs 2, 6, 8, and 14 (Figure 2).

Regarding the long-term trend, a clear faunal transition is found during the MBE at ~400–350 ka. Pre-MBE and Post-MBE samples are clearly divided in the Non-metric Multidimensional Scaling plot (Figure 4). During this transition, the assemblage characterized by high abundance of *Acanthocythereis dunelmensis* is replaced by one with high abundance of *Robertsonites hanaii* (Figure 2). Warmer-water (6–20 °C) species *Krithe antisawanensis* (Table 1 and Text S1) starts to occur more frequently from the same time on (Figure 2). The TWC has been flowing into the Sea of Japan since 1.7 million years ago during every interglacial period, and has been increasingly significant to the paleoceanography of the region (Amano, 1994; Gallagher et al., 2015; Itaki, 2016). Given that *Acanthocythereis dunelmensis* (circumpolar species) prefers a colder environment than *Robertsonites hanaii* (cool-water species) (Table 1 and Text S1), this faunal shift indicates an enhancement in the flow of the TWC during the MBE. Much higher sea level maxima during the interglacial peaks after the MBE (e.g., MISs 1, 5, 9, and 11) than those before that (MISs 13, 15, and 17; see Figure 2) probably strengthened the incursion of the TWC to the Sea of Japan. This interpretation is consistent with molluscan evidence of the "TWC molluscs" occurrence in interglacials after the MBE (i.e., MISs 5, 7, and 9; Gallagher et al., 2015). The higher diversity in the *Robertsonites* dominated period (i.e., after the MBE) than in the *Acanthocythereis* dominated period (i.e., before the MBE; Figure 2) may also imply overall stronger convection and an oxygenated bottom-water environment under a more vigorous TWC. In addition, absence of a significant faunal extirpation event during the relatively weak glacial maximum in MIS 8 may have allowed longstanding success of the endemic species, *Robertsonites hanaii* (Ozawa & Kamiya, 2005; Yamada, 2003; but also see Alvarez Zarikian, 2016; Zhou, 1995) over the widely distributed circumpolar species, *Acanthocythereis dunelmensis* (Brouwers, 1993; Stepanova et al., 2007) (Text S1). In addition, the glacial-interglacial faunal cyclicity (i.e., *Krithe-Cytheropteron* alternation) is more obviously marked after the MBE (Figure 2), probably because of the post-MBE amplification of the glacial-interglacial climatic cycles (Cronin, 2010; Cronin et al., 2017).

5. Conclusion

The Sea of Japan benthic ostracode community has undergone dramatic environmentally induced changes due to the semienclosed nature of the marginal sea. Despite the typical low abundance feature of ostracode

assemblages from the deep Sea of Japan, the influence of orbital climate cycles and the MBE (i.e., the final event marking the emergence of high-amplitude glacial-interglacial variability at ~400–350 ka) on the deep-sea ecosystem is well documented in the ostracode reconstruction in this study. Main conclusions are as follows:

1. The long-term oxygen variability has been a major control of deep marginal sea biota. We discovered five major ostracode extirpation events caused by deoxygenation events during glacial sea level lowstands greater than −90 m. Alternations of dominant faunal components are controlled by glacial-interglacial oxygen variability: *Krithe* dominance during glacial periods before and after the extirpation events is caused by moderate bottom oxygen depletion. *Cytheropteron* dominance during interglacial and interglacial-glacial transition periods represents an oxygenated environment. From MISs 1 to 17, we documented recursive patterns of a succession from opportunistic species dominance (i.e., *Cytheropteron*) through low-oxygen tolerant infauna dominance (i.e., *Krithe*) to hypoxic barren zone and reversed succession (i.e., through *Krithe* to *Cytheropteron*) during the recovery. This observation in the Sea of Japan ostracode fauna is similar with the benthic foraminiferal faunal succession related to Mediterranean deoxygenation, especially the sapropel S1 in intermediate water depths (Jorissen, 1999). The biotic history reconstructed here suggests a general implication on the climatic sensitivity of deep-sea ecosystems in marginal seas (e.g., the Sea of Japan and Mediterranean Sea; this study, and references herein) and oceanic basins (Cannariato et al., 1999; Moffitt et al., 2015; Myhre et al., 2017) characterized by the periodic oxygen depletion.

2. We discovered clear biotic changes associated with the MBE in the Sea of Japan, indicating a more widespread nature of the MBE-associated biotic event beyond the Arctic Ocean (Cronin et al., 2014, 2017; DeNinno et al., 2015). The MBE shortened the duration of the extirpation events, fostered dominance of warmer-water species, and amplified the glacial-interglacial faunal cyclicity through the shorter duration of glacial sea level lowstand < −90 m, enhancement of the TWC with higher interglacial sea level maxima, and amplified glacial–interglacial cycles, respectively. The MBE might have affected deep-sea, especially marginal-sea, ecosystems globally and substantially.

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