Southward Migration of Arctic Ocean Species During the Last Glacial Period

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Abstract The East Asian winter monsoon (EAWM) is associated with northerly surface winds affecting crop and livestock productivity and social and economic activities across East Asia. However, the relationship between EAWM dynamics and marine biota remains poorly understood. In this study, we analyzed fossil ostracods from sediment cores collected in the northwestern Pacific Ocean to detect the appearance/disappearance of circumpolar species during the late Quaternary. We compared our ostracod records, including dating results, with ice-rafted debris records from the Sea of Japan, and identified two southward migration events of Arctic ostracods at 120–100 ka (Marine Isotope Stage [MIS] 5d stadial) and 30–15 ka (MIS 3 and 2, peak Last Glacial), which corresponded to a strengthened EAWM system. Our results indicate that an intensified EAWM influenced the Yellow Sea Bottom Cold Water formation, lowered the winter water temperatures, and allowed Arctic ostracods to migrate southward into the Yellow Sea.

Plain Language Summary The impacts of climatic conditions on marine ecosystems and the distribution of marine species are major concerns due to ongoing anthropogenic climate change. Fossil records can provide direct evidence of past climate impacts, and the Yellow Sea (YS) is an important location to track changes in cold-adapted marine species, as it is located at the southern end of the distribution of Arctic circumpolar species. In this study, we found that circumpolar ostracod species dominated the YS during distinct stadial and peak glacial periods—120 to 100 and 30 to 15 thousand years ago—intervals that are consistent with the periods of a strengthened East Asian winter monsoon (EAWM) during the Last Glacial Period. We suggest that the stronger EAWM during these periods enhanced the formation of Yellow Sea Bottom Cold Water and/or lowered the winter temperatures of the YS, allowing Arctic ostracods to inhabit more southern regions of the YS.

1. Introduction

The East Asian winter monsoon (EAWM) driven by the thermal contrast between the continent of Asia and the North Pacific Ocean is an important meteorological system in East Asia (Tada et al., 2016). Intensification of the EAWM is often accompanied by strong winds, freezing temperatures, and snowstorms, among other hazards, which cause severe damage across East Asia (Wang, 2006; Zhou et al., 2011). Yet the impacts of EAWM variability on marine biota are poorly understood. The Yellow Sea (YS) has been regarded as an ideal location to study the evolution of the EAWM, as it is sensitive to climate change, and its environment is strongly influenced by the EAWM (Hao et al., 2017; L. Wang, Li, Liu, et al., 2021; L. Wang, Li, Wang, et al., 2021). Furthermore, the YS is also the southern end of the distribution of some circumpolar species in the northwestern (NW) Pacific Ocean (J. Y. Liu, 2013; R. Y. Liu, 2011).
Circumpolar species living in and around the Arctic Ocean have prehistorically changed their distributions in response to climate change, including expanding southward to the Baltic, the Mediterranean, and the North Atlantic during past cooling events (e.g., Crippa et al., 2019; Cronin & Cronin, 2015; Frenzel et al., 2010). Many marine invertebrates that occur further north or in the Arctic are also found in the YS (J. Y. Liu, 2013; R. Y. Liu, 2011), especially in Yellow Sea Bottom Cold Water (YSBCW), a cold-water mass distributed across the central YS at depths >50 m (H. W. Yang et al., 2014). These include ophiuroids, bivalves, decapod crustaceans, and a sponge, many of which are threatened by ongoing climate change (J. Y. Liu, 2013). However, ostracod record indicates that the YS had more cold-water species during certain periods of the Pleistocene, including species that are not currently found in the YS (J. Y. Liu, 2013; Zhao et al., 2014).

Unlike most other crustaceans (or arthropods with chitinous carapaces), ostracods have fully calcified, bivalved carapaces, and thus have been the most common fossil arthropods, which provide an excellent fossil record for detailed paleoecological reconstructions. Previous studies based on multiple subtidal sediment cores from the YS suggested that two distinctive intervals of ostracod assemblages were dominated by circumpolar species (J. Liu et al., 2018; Zhao et al., 2014), including Hemicytherura clathrata, Heterocyprideis fascis, Munseyella hatatatenesis, Rabilitmis septentrionalis, Robertsonites tuberculatus, and Sarsicytheridea bradii. Among these species, only S. bradii is known from the present-day YS, while the others are restricted to and widely distributed in the Arctic Ocean and adjacent seas (Zhao et al., 2014; Zhao & Wang, 1988). One interval was assigned to Marine Isotope Stage (MIS) 5e (peak Last Interglacial) in a previous study (J. Liu et al., 2018). The other interval, dominated by circumpolar species, occurred earlier (Zhao et al., 2014). However, the exact ages of these two intervals remain unclear.

Here, we analyzed ostracod assemblages in a new sediment core (YSZK-1) (Figure S1 in Supporting Information S1) from the South Yellow Sea (SYS) and found two intervals with circumpolar and cold-water ostracods. By comparing our results with the well-dated ostracod data from the Integrated Ocean Drilling Program Expedition Site U1427 in the Sea of Japan (Huang et al., 2018) and other nearby cores from the YS (J. Liu et al., 2010, 2018; Zhao et al., 2014), we determined the ages of these two intervals for the first time. Our results further emphasize the role of the EAWM on the migration of Arctic ostracods.

2. Oceanographic and Geologic Setting

The YS is a marginal sea of the Western Pacific Ocean located between mainland China and the Korean Peninsula (J. Liu et al., 2018). It is separated from the Bohai Sea to the north by the boundary from the Liaodong Peninsula to the Shandong Peninsula and bounded in the south by the East China Sea via a line connecting the Yangtze River Estuary and Cheju Island at the southwestern tip of the Korean Peninsula (J. X. Liu et al., 2016). It is further divided into the North Yellow Sea and the SYS by a line from the Shandong Peninsula to the Korean Peninsula (J. X. Liu et al., 2016). Sediment discharge to the western and central parts of the YS is dominated by the Yellow River and Yangtze River, while the eastern part is dominated by Korean rivers (Choi et al., 2013).

The YS lies on the North and South China Blocks and can be divided into the North and the South Yellow Sea Basins, respectively (J. Liu et al., 2018). Basin development was caused by large-scale interactions between the Pacific, Eurasian, and Indian plates along the West Pacific continental margin during the late Mesozoic and Cenozoic (Ren et al., 2002; Y. C. Zhang et al., 1989). During the Cenozoic, the India–Eurasia collision and/or Pacific subduction drove the tectonic inversion and denudation in the South Yellow Sea Basin and further caused the West Pacific continental margin to change topographically from Cenozoic lowlands to basins below sea level during the late Quaternary (J. Liu et al., 2018; J. Zhang et al., 2019). The Neogene–Quaternary sequences range from 1,000 to 2,000 m in thickness in the South Yellow Sea Basin (Cai, 2005). Quaternary sediments have a mean thickness of ~224 m (Gao et al., 2020; Qin et al., 1989). Since the Quaternary, the sedimentary sequences of the SYS shelf have been strongly influenced by sea-level fluctuations represented by alternating marine and terrestrial deposits (Mei et al., 2016; L. Wang, Li, Liu, et al., 2021; L. Wang, Li, Wang, et al., 2021).

3. Materials and Methods

The studied sediment core (YSZK-1) is ~40 m long and mainly consists of clay, silty clay, silt, mud, and fine sand. Fifty samples (Figure S2 in Supporting Information S1) were collected, 34 of which yielded ostracods. Four accelerator mass spectrometry (AMS) 14C dates based on shell fragments, and two optically
stimulated luminescence (OSL) dates based on quartz grains were obtained from YSZK-1 (Tables S1 and S2 in Supporting Information S1). AMS $^{14}$C dating was performed at Beta Analytic Inc. (USA) and all AMS dates were calibrated to calendar ages using Calib rev. 7.01 (Stuiver & Reimer, 1993) and the Marine13 calibration data set (Reimer et al., 2013). All OSL samples were collected in stainless steel tubes and sealed in black plastic bags. Sample preparation and measurement were then performed under subdued red light in the Luminescence Dating Laboratory of the Qinghai Institute of Salt Lakes, Chinese Academy of Sciences.

Ostracod samples were wet sieved with mesh sizes of 63, 150, and 850 μm, oven dried, and then dry sieved over mesh-size of 150 mm, the standard fraction for fossil ostracod research (Gemery et al., 2017; Yasuhara et al., 2017). We employed the counting method of Yasuhara et al. (2017), who counted each articulated carapace as two specimens and each disarticulated valve as one. Generally, the studied ostracod specimens were well-preserved with translucent valves.

Non-metric multidimensional scaling (NMDS) was used to explore the relationships between ostracod assemblages. This method produced a two-dimensional ordination of our faunal assemblages while preserving the ranks of differences between data points (Borcard et al., 2011; Legendre & Legendre, 2012). We performed NMDS on 19 samples with at least 50 specimens in the R package “vegan” (Oksanen et al., 2019; R Core Team, 2016). The relative abundances (%) of the 11 most abundant taxa (accounting for 83% of all specimens) and Bray–Curtis dissimilarity were used for NMDS.

To improve our understanding of the spatial and temporal patterns of the distributions of circumpolar species in the YS, we compiled the downcore relative abundances of circumpolar species, counts of ice-rafted debris (IRD), and reconstructed sea-level stacks from multiple published studies (Huang et al., 2018; Ikehara & Itaki, 2007; J. Liu et al., 2010, 2018; Zhao et al., 2014; Figure S1 in Supporting Information S1). We used the sea-level stack presented by Spratt and Lisiecki (2016).

The preferred environments of each circumpolar species were used to assist in interpreting the ostracod data. The modern geographical distributions of many circumpolar ostracods have been compiled in the Arctic Ostracod Database, specifically by Cronin et al. (2021) for the Arctic and by Iwatani et al. (2012) for the NW Pacific. Using the coordinates of each site, we queried the World Ocean Atlas for the mean annual temperature and salinity of each site (Locarnini et al., 2018; Zweng et al., 2018). These resources allowed the relative abundance of each species in each environment to be calculated.

4. Results

Forty-three ostracod species belonging to 33 genera were found in YSZK-1 (Table S3). Among them, S. bradii, Cytheropteron nodosoalatum, H. fascis, Rabilimis mirabilis, and R. septentrionalis are considered to be circumpolar species (Cronin & Ikeya, 1987; J. Liu et al., 2018; Stepanova et al., 2003; Zhao et al., 2014); Acanthocythereis mutsuensis is considered to be a cold-water species (Zhao & Wang, 1990); Amphileberis nipponica, Aurila cymba, Bicormucythere bisanensis, Cytheromorpha acupunctata, Cytheropteron donghaiense, Pisticythereis bradyformis, Spinileberis quadriaculeata, and Trachyleberis niitsuensis are regarded as temperate species (Brandão et al., 2013; Hou & Gou, 2007; Yasuhara & Irizuki, 2001; Yasuhara & Seto, 2006); and Albileberis sinensis, Neomonomeratina delicata, Neosinocythere elongata, and Sinocythereidae impressa are treated as subtropical based on their modern distributions (Cao, 1998; Hong et al., 2017, 2019; Hou & Gou, 2007; Irizuki et al., 2009; Niiyama et al., 2019; Yajima et al., 1986; Figure S3 in Supporting Information S1). The autoecologies of the dominant species are summarized in Table S4 in Supporting Information S1.

Among circumpolar and cold-water species, C. nodosoalatum, H. fascis, and R. mirabilis lack a present-day record in the NW Pacific (Figure 1), whereas others (S. bradii, A. mutsuensis, and R. septentrionalis) can be found in both present-day and Pleistocene–Holocene sediments in the Sea of Japan or the YS (Figure 2). The environmental ranges of the latter taxa are generally similar between the Arctic and NW Pacific; however, the environmental conditions in the NW Pacific under which those ostracods live tend to be warmer and more saline, and their distributional peaks occur at greater depths (Figures 1 and 2).
Figure 1.
We used NMDS to explore the relationships between faunal assemblages and to understand species contributing to the differences observed within them. The closeness of plotted data points in NMDS indicates greater similarity (Figure 3). In our plots, positive and negative values had no ecological significance. Rather, on the negative end of the horizontal axis, circumpolar species (S. bradii, H. fascis, and R. mirabilis) formed a group with close spacing along the core (core depths: ∼9–17 m; Figure 3). Temperate and subtropical species characterized several samples, from core depths of ∼22–28 m on the positive end of the horizontal axis. On the positive end of the vertical axis, A. mutsuensis represented one of the oldest samples (core depth: ∼29 m) in this study. Temperate and subtropical species, including N. delicata, S. impressa, and P. bradyformis, occupied the opposite side of the vertical axis.

**Figure 1.** Geographical distribution and environmental ranges of six relevant circumpolar species in the Arctic. In the top panel, six maps show the presence (colored circles) and absence (black circles) of the focal species in Pleistocene (light green), Holocene (dark green), and Modern (purple) intervals. The records are from our study and those compiled from the literature. Available modern records of S. bradii and A. mutsuensis in the Yellow Sea lack coordinates and thus are indicated by hatchings here (Zhao & Wang, 1988). The middle panel is the species index specifying a color scheme used in the bottom panel: S. bradii (red), A. dunelmensis (orange), A. mutsuensis (yellow), and R. septentrionalis (wheat). The bottom panel shows the preferred environment of each species using modern records. We calculated the mean percentage of each species in each bin range of the environmental parameters. The relative abundances of modern ostracods are sourced from Iwatani et al., 2012. Temperature and salinity data for each site are sourced from World Ocean Atlas 2018 (Locarnini et al., 2018; Zweng et al., 2018). Water depth information was provided along with the ostracod data (Iwatani et al., 2012).

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**Figure 2.** Paleobiogeographical distribution and environmental ranges of four relevant circumpolar species in the northwestern Pacific. In the top panel, four maps show the presence of the focal species in Pleistocene (light green), Holocene (dark green), and Modern (purple) intervals. The records are from our study and those compiled from the literature. Available modern records of S. bradii and A. mutsuensis in the Yellow Sea lack coordinates and thus are indicated by hatchings here (Zhao & Wang, 1988). The middle panel is the species index specifying a color scheme used in the bottom panel: S. bradii (red), A. dunelmensis (orange), A. mutsuensis (yellow), and R. septentrionalis (wheat). The bottom panel shows the preferred environment of each species using modern records. We calculated the mean percentage of each species in each bin range of the environmental parameters. The relative abundances of modern ostracods are sourced from Iwatani et al., 2012. Temperature and salinity data for each site are sourced from World Ocean Atlas 2018 (Locarnini et al., 2018; Zweng et al., 2018). Water depth information was provided along with the ostracod data (Iwatani et al., 2012).
5. Discussion

Five circumpolar ostracods were found in the YSZK-1 samples; specifically, S. bradii, C. nodosa, H. fascis, R. mirabilis, and R. septentrionalis, and these species are known to inhabit the central and marginal Arctic Ocean (Figure 1; Cronin & Ikeya, 1987; J. Liu et al., 2018; Stepanova et al., 2003; Zhao et al., 2014). In addition to these taxa, A. mutuensis, a cold-water species recorded in the Sea of Japan that is morphologically similar to A. danelmensis (Ikeya & Cronin, 1993; Zhao & Wang, 1988), was found in the lower part of the studied core (Figure S3 in Supporting Information S1). These changes in faunal compositions are also reflected in the NMDS plot (Figure 3), in which the oldest studied interval (~29 m) was dominated by cold-water species, the middle (~22–28 m) was dominated by temperate and subtropical species, and the youngest interval (~9–17 m) was dominated by circumpolar species. A compilation of the percentages of circumpolar species reported in multiple studies (Huang et al., 2018; J. Liu et al., 2010, 2018; Zhao et al., 2014) and our data showed that these species dominated the SYS during two different periods (Figure 4). During the earlier period (blue shading in Figure 4), the western part of the SYS (SYS-0803, SYS-0701, SYS-0702, CSDP-1) was dominated by S. bradii, H. fascis, and R. mirabilis, whereas cores YSZK-1 and NHH01 were dominated by A. mutuensis (Zhao et al., 2014). During the later period (green shading in Figure 4), the YSZK-1 and NHH01 assemblages were dominated by S. bradii, H. fascis, and R. mirabilis. A continuous ostracod record from an adjacent region in the southern part of the Sea of Japan also yielded two distinct peaks of high circumpolar species abundance.

![Figure 3](image1.png)

Figure 3. Non-metric multidimensional scaling plot of studied YSZK-1 samples (stress < 0.05). Samples are represented as solid circles in green, black, and blue. The core intervals of green and blue samples correspond to those in the same color shadings in Figure 4. Species name abbreviations: AcMu: Acanthocythereis mutuensis, AmNi: Amphileberis nipponica, AuCy: Aurila cynba, BiBi: Bicorncythere biosanensis, CyAc: Cytheromorpha acupunctata, HeFa: Heterocyprideis fascis, NeDe: Neomonomeratina delicata, PiBr: Pistocythereis bradyiformis, RaMi: Rabilimis mirabilis, SaBr: Sarsiocytherea bradii, SiM: Sinocytherea impressa.

![Figure 4](image2.png)

Figure 4. Compiled plots of relevant faunal and proxy records: summed relative abundances of circumpolar taxa from six published Yellow-Sea cores (SYS-0803, SYS-0701, and SYS-0702 data from J. Liu et al. (2010); CSDP-1 data from J. Liu et al. (2018); NHH01 data from Zhao et al. (2014)), our study (YSZK-1), and the Japan-Sea IODP Site U1427 (Huang et al., 2018); counts of ice-rafted debris (IRD from core GH95–1208; Ikehara & Itaki, 2007); and a reconstructed sea-level stack (Spratt & Lisiecki, 2016). In the panels of Yellow-Sea records, the ages determined by accelerator mass spectrometry 14C and optically stimulated luminescence are marked next to the curves (J. Liu et al., 2010, 2018). MISs 1–5 (Lisiecki & Raymo, 2005) are annotated along the age axis of the sea-level stack. We related two peaks of circumpolar species among multiple cores in blue and green shadings, respectively. Note that the list of recorded circumpolar species and cold-water ostracods differs slightly between cores: SYS-0803 includes A. mutuensis, Acanthocythereis sp., H. fascis, Howeina camptocythereoides, R. septentrionalis, and S. bradii; SYS-0701 includes Acanthocythereis sp., H. fascis, and R. septentrionalis; SYS-0702 includes Acanthocythereis sp., H. fascis, R. septentrionalis, and S. bradii; U1427 includes A. danelmensis; NHH01 includes A. mutuensis, S. bradii, H. fascis, R. mirabilis, T. seogwipoensis and R. tuberculatus; YSZK-1 includes A. mutuensis, S. bradii, H. fascis, and R. mirabilis. See Figure S1 in Supporting Information S1 for core localities.
consistent with the stratigraphic positions of the YS (Figure 4). Considering the general consistency in the estimated ages of these peaks across cores, we correlated them between the YS and the Sea of Japan (Figure 4).

The two periods of circumpolar species dominance at Site U1427 are assigned to MIS 5d and MIS 2 according to the continuous sedimentation and a robust integrated age model based on oxygen isotope stratigraphy, tephrostratigraphy, and planktonic microfossil biostratigraphy (Huang et al., 2018; Sagawa et al., 2018). And with the radiocarbon dates from Site YSZK-1, the later period of circumpolar species dominance is considered to be 30–15 ka (MIS 3 and 2, peak Last Glacial). The earlier period of circumpolar species dominance is further constrained by the OSL dates from four cores in the SYS (Figure 4). OSL dating has been shown to provide a reliable and accurate chronometer in regions where there is a lack of suitable materials for radiocarbon ($^{14}$C) dating (Jacobs, 2008). Therefore, the earlier period is considered to be the MIS 5d stadial (120–100 ka). The earlier period was formerly correlated to the MIS 5e (J. Liu et al., 2018) and the later period was not previously well-constrained (Zhao et al., 2014). Caution is warranted when analyzing later periods in the YS because a hiatus exists within this period due to subaerial exposure, as the YS was shallow enough to be exposed by >100-m reductions in sea level, and because the radiocarbon date from Site YSZK-1 is slightly older than the range reported (Figure 4). Therefore, this younger period of circumpolar species dominance in the YS may largely represent late MIS 3, perhaps as old as ~40 ka. The western part of the YS was interpreted to have been deposited in fluvial and deltaic environments (i.e., mostly subaerially exposed) during MIS 3 and 2, and thus lacks the younger peak of circumpolar species dominance (J. Liu et al., 2018; Figure 4).

The appearance of circumpolar ostracods (S. bradii, H. fascis, and R. mirabilis) in the SYS indicates the existence of an ancient YS cold-water mass (J. Liu et al., 2018), known today as YSBCW (e.g., Z. G. Yang et al., 1998; H. W. Yang et al., 2014). Currently, YSBCW is distributed in the lower layer of the central trough of the YS, with a mean depth of 44 m, a temperature of <10°C, and salinity ranging from 32‰ to 33‰ (Oh et al., 2013). The depth, temperature, and salinity ranges of the circumpolar and cold-water ostracod species in the Arctic and NW Pacific Oceans mostly fall within those of YSBCW (Figures 1 and 2). However, currently only A. mutsueensis and S. bradii occur in the central and deeper parts of the YS occupied by the YSBCW (i.e., beyond the 50-m isobath) (Zhao & Wang, 1988).

The main regions of current circumpolar and cold-water ostracod species distribution, such as the Kara and Laptev Seas, are covered with ice that starts from October to November and lasts from May to June, and the bottom water temperature is <0°C nearly year-round (Stepanova et al., 2007). Nevertheless, the modern Arctic Ocean and NW Pacific Ocean are very different environments (Figure 1 and Figure S4 in Supporting Information S1). From 1982 to 2017, sea surface temperatures (SSTs) in the YS ranged from 13 to 18°C (Y. G. Liu, 2017), and based on older records dating from January 1958 to December 2008, the monthly mean temperatures of bottom waters in the YS were ~0–10°C between December and May and ~10–25°C from June to November (Li et al., 2015). Additionally, the mean SST of the Sea of Japan ranged from 5 to 20°C from 1982 to 2018 (Lee & Park, 2019).

Overall, the surface and bottom water temperatures of the NW Pacific Ocean range from 10 to 20°C and 5–15°C, respectively (Figure S4 in Supporting Information S1). The environmental conditions recorded in the fossil record of the circumpolar and cold-water ostracods suggests that the water temperature in the NW Pacific (the SYS and the Sea of Japan) was colder during MIS 5d and MIS 3 and 2, and the development of YSBCW was further strengthened in the YS. Although A. mutsueensis and S. bradii are now known to inhabit the central and deeper parts of the YS (Zhao & Wang, 1988), we did not find these species in the uppermost part of our core (Figure S3 in Supporting Information S1). It remains unknown why YSZK-1, NHH01 and the adjacent cores (SYS-0803, SYS-0701, SYS-0702, and CSDP-1) had different ostracod assemblages during MIS 5d, warranting further investigation.

Intensification of the EAWM leads to stronger northerly winds in winter, significantly controlling winter SSTs in the NW Pacific (Hanawa et al., 1989; Z. Liu et al., 2019; Matsuzaki et al., 2020; Sagawa et al., 2014). These stronger winds enhance the formation of YSBCW (H. W. Yang et al., 2014) and the EAWM has been shown to affect marine ecosystems in the NW Pacific (e.g., Chiu et al., 2017). For instance, Ikehara and Itaki (2007) found distinct peaks in the EAWM during the late Quaternary using IRD records from the northern Sea of Japan. Some of these peaks (~110–100 ka and 30–20 ka) are consistent with the peaks of the two circumpolar species-dominant periods identified from Site U1427 (Figure 4) and evidence from the Loess Plateau in China also shows that there was a stronger EAWM during MIS 2 and MIS 5d (Chen et al., 1999; Xiao et al., 1992).
Thus, we suggest that a stronger EAWM (i.e., stronger northerly winds) during these two periods strengthened the YSBCW formation and/or lowered the winter water temperature in the YS, allowing the circumpolar species to abundantly inhabit the SYS.

6. Conclusions

Thirty-three genera and 43 species of marine ostracods were identified from a 40-m long sediment core (YSZK-1) in the SYS. Five circumpolar and one cold-water species were found in the studied core—*S. bradii, C. nodosotalatum, H. fascis, R. mirabilis, and R. septentrionalis*, respectively. Combining the ostracod records from core YSZK-1 and adjacent cores in the YS, *S. bradii, H. fascis, and R. mirabilis* were found to dominate during two distinct periods, which could be correlated with the ostracod records of Site U1427 in the Sea of Japan. Subsequently, two periods of the circumpolar species dominance were identified at 120–100 ka (MIS 5d stadial) and 30–15 ka (MIS 3 and 2, peak Last Glacial). The presence of circumpolar ostracods during MIS 5d and MIS 3 and 2 indicates that the formation of YSBCW was strengthened (i.e., made colder) by strong northerly winds, which in-turn were influenced by the EAWM. The timing of these two periods coincided with periods of distinctively stronger EAWMs based on independent (terrestrial) records. We suggest that the intensified EAWM during MIS 5d and MIS 3 and 2 influenced the development of YSBCW and/or lowered the winter water temperatures in the YS, and thus controlled the distribution of circumpolar ostracods in the YS.

Conflict of Interest

The authors declare no conflicts of interest relevant to this study.

Data Availability Statement

All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Materials. Supporting Information have been uploaded in Dryad (https://doi.org/10.5061/dryad.9zw3r22hr) and Zenodo (https://doi.org/10.5281/zenodo.7030572).

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