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Spatial pattern of macrobenthic communities along a shelf-slope-basin transect across the Bering Sea

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Abstract

Due to its unique geological location, the Bering Sea is an ideal place to investigate the water exchange and ecosystem connectivity of the Pacific Ocean–Arctic Ocean and subarctic–Arctic region. Based on a number of summer surveys (July to September, 2010, 2012 and 2014), macrobenthic communities and their spatial-temporal patterns are exhibited for the majority of the Bering Sea (53°59′–64°36′N). The results show that the macrobenthic communities were dominated by northern cold-water species and immigrant eurythermic species, and the communities assumed a dispersed and patchy distribution pattern. Polychaetes (*Scoloplos armiger*), crustaceans (*Ceradocus capensis*) and sea urchins (*Echinarachnius parma*) were the main dominant groups in the shallow shelves; the sea star (*Ctenodiscus crispatus*) and the brittle star (*Ophiura sarsii*) were the main dominant groups in the continental slope; whereas small polychaetes (*Prionospio malmgreni*) dominated the basin area. Sediment type, water depth, and currents were the major factors affecting the structure and spatial distribution of the macrobenthic communities. Compared with other seas, the shallow areas of the Bering Sea showed an extremely high-standing biomass. In particular, the northern shelf area (north of St. Lawrence Islands and west of 170°W), which is primarily controlled by Anadyr Water, is an undersea oasis. In contrast, a deficiency in the downward transport of particulate organic carbon has resulted in a desert-like seabed in the basin area. By comparing our results to previous studies, we found that macrobenthic communities of the Bering Sea have undergone significant structural changes in recent decades, resulting in a decrease in abundance and an increase in biomass. In addition, populations of amphipods and bivalves in the northern shelves have decreased significantly and have been gradually replaced by other species. These changes might be associated with advanced seasonal ice melting, changes in organic carbon input, and global warming, indicating that large-scale ecosystem changes have been occurring in the Bering Sea.

Key words: macrobenthos, community structure, Arctic, Bering Sea, environmental drivers

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1 Introduction

The Bering Sea is the only link between the Arctic Ocean and the Pacific Ocean. Due to its unique geographical location, this sea area is an ideal place to investigate the water exchange and ecosystem connectivity of the Pacific Ocean–Arctic Ocean and subarctic–Arctic region (Clement et al., 2005; Woodgate and Aagaard, 2005). Although located at a high latitude with 7–8 months of seasonal snow cover, the Bering Sea remains one of the world's most productive regions (Berger et al., 1987; Grebmeier et al., 1988; Piepenburg, 2005; Wang et al., 2014a; Lin et al., 2016). The Bering Sea is rich in fishery resources, especially in fish and crabs, which support a plurality of higher predators such as cetaceans, seals, elephant seals, and sea birds that migrate to the area for feeding (Springer et al., 1996; Moore et al., 2003; Lovvorn et al., 2003; Ray et al., 2006; Dehn et al., 2007). In the continental slope region at the junction of the basin and the shelf of the Bering Sea, the Bering Sea Green Belt has a primary productivity and a seabed habitat secondary productivity (calculated by carbon) of 175–275 g/(m^2·a) (Okkonen et al., 2004) and (4.2±1.8) g/(m^2·a) (Lin et al., 2016), respectively.

Macrobenthos play an important role in polar marine ecosystems. Because these organisms have a slow growth rate and a long life cycle, they are resistant to interannual change and small fluctuations in water column productivity (Carey, 1991). Thus, macrobenthos are good indicators of potential changes in ecosystems. Changes in the macrobenthic communities at a times-

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cale of years to decades can predict long-term changes in ecosystems caused by climate effects (Dunton et al., 2005). The retreat of sea ice and increased glacial melt caused by global warming have seriously affected biodiversity and the community structure in the Bering Sea (Wlodarska-Kowalczuk and Weslawski, 2001; ACIA, 2004; Perovich et al., 2015). In the last 25 years, the biomass of the benthic Greenland halibut (*Greenland turbot*) has decreased by more than 80%, whereas that of pelagic fishes, such as cod, has increased by approximately 400%. An abrupt change in snow crab biomass is believed to be closely associated with the sea ice retreat caused by rising temperatures (Siddon and Zador, 2017). Human activities are also a major cause of interference in the region; both business development and overfishing have led to sharp changes in the macrobenthic population and community structure of the Bering Sea and surrounding waters. For example, marine mammals on the top of the food chain (such as sea lions) decreased by more than 50% between the 1950s and the 1980s, and the population of harbor seals decreased by 90% since the 1970s (Pitcher, 1990).

The shallow shelves and slope of the Bering Sea are critically influenced by water column production, organic carbon cycling, and pelagic-benthic coupling. Short food chains and shallow depths are characteristic of high-productivity areas in this region, and thus, changes in lower trophic levels can rapidly impact higher trophic organisms, including pelagic- and benthic-feeding marine mammals and seabirds (Grebmeier et al., 2006a).

The latest research shows that the amplified Arctic warming over the past decade has significantly contributed to a continual global warming trend (Huang et al., 2017), hence there is a critical need for biological, geological, and chemical comprehensive analysis and time series comparison to observe and evaluate the changing Arctic ecosystem. Using data acquired in the Bering Sea during the 4th, 5th, and 6th Chinese National Arctic Research Expeditions (CHINAREs) combined with previous survey data and literature, this study aims to answer the following questions: (1) What is the spatial variability of macrobenthic communities in the Bering Sea along the shelf-slope-basin transect? (2) What is the change in benthic macrobenthic communities of the Bering Sea in the context of climate change? (3) Is there a quantifiable relationship between the spatial differences in macrobenthic communities and environmental factors? Answering these questions will allow us to investigate the dynamics of the macrobenthic communities of the subarctic seas and its response to environmental change. Our quantitative data on macrobenthos will improve our understanding of benthic production processes and ecosystem dynamics in the context of rapid climate change.

2 Methods

2.1 *Survey area*

The Bering Sea is the northernmost marginal sea on the coast of the Pacific Ocean, and connects the Arctic Ocean in the north through the Bering Strait to the Pacific Ocean in the south across the Aleutian Islands. The Bering Sea has a complex seabed terrain with extensive variation. Deep-sea basins are found in the south and west, and large shelf areas exist in the north and east. The key currents of this region were the more saline, nutrient-rich Anadyr Water (AW) transiting northward on the western side, and fresher, more nutrient-limited Alaska Coastal Water (ACW) flowing northward on the eastern side, and intermediate salinity, nutrient-rich Bering Shelf Water (BSW) lies between AW and ACW. Much of the northern Bering Shelf is ice-covered in winters but ice-free in summers, and the growth of ice over southern deep water is limited by warm water in the central basin.

2.2 *Sampling methodology*

Macrobenthic samples were collected at 46 stations in the Bering Sea (Fig. 1) while aboard the R/V Xuelong during the 4th CHINARE (July to September 2010), 5th CHINARE (July to September 2012), and 6th CHINARE (July to September 2014). Thereinto, 33 stations at depths ranging from 19 m to 105 m were located on the Bering Shelf, which were divided into three sectors comprising the northern (NB), eastern (EB) and western (WB) Bering Shelf; seven stations were located on the Bering Slope (BS) at depths ranging from 119 m to 258 m; six stations were located on the Bering Basin (BB) at depths ranging from 2 603 m to 3 873 m. To facilitate discussion, abbreviations for specific regions were adopted.

One sample was collected at each station using a 0.25 m^2 box corer (50 cm×50 cm×60 cm). Each sample was rinsed through 0.5-mm mesh sieves, and the residue containing the macrobenthos was fixed in 7% formaldehyde for processing. Macrobenthos were identified to the lowest possible taxonomic level, and individuals within each taxon were counted and weighed. Taxon names were cross checked against the World Register of Marine Species (http://marinespecies.org/).

Environmental variables, including bottom temperature and salinity at the base of the water column, were quantified at each station using a Sea-Bird Electronics (SBE911 Plus) CTD system. Grain analysis (percentage of sand, silt and clay) of the filtered sub-samples was performed at each station using a Malvern Mastersizer laser particle sizer according to Yao et al. (2014). The median particle diameter (Md) and sorting values were also calculated. The total organic carbon (TOC) and total nitrogen (TN) contents in the sediments were measured with a CHN analyzer (Vario EL III) after the samples were freeze-dried according to Qiao et al. (2011). The environmental factors measured are summarized in Table 1.

2.3 *Data treatment and analysis*

PRIMER 6.0 was used to calculate the Bray-Curtis similarity coefficients, on which the similarity matrix and the cluster analysis were constructed. To mitigate the effects of rare and opportunistic species on the macrobenthic structure analysis, a pretreatment was performed on the raw data to exclude species with a relative abundance of less than 0.5%. Species with a relative abundance greater than 3% at any given station were retained. To balance the roles of the dominant and rare species in the macrobenthic structure, the abundance data were subjected to fourth root conversion and standardization. To identify the characteristic species for each of the macrobenthic groups, we used similarity profile (SIMPROF) to test different groups based on the similarity percentage (SIMPER) to sort the inter-group percentages of the average similarity contribution.

We analyzed the relationship between the environmental variability and the macrobenthic communities using direct gradient analysis. The unimodal ordination method of canonical correspondence analysis (CCA) was chosen based on a preliminary detrended correspondence analysis on macrobenthic communities, which indicated that the longest length of gradient (20.269 3) was longer than 4, suggesting that the majority of taxa exhibited a linear response to environmental variation (Lepš and Šmilauer, 2003). The collinearity between environmental factors and macrobenthic communities was tested to prevent over interpretation

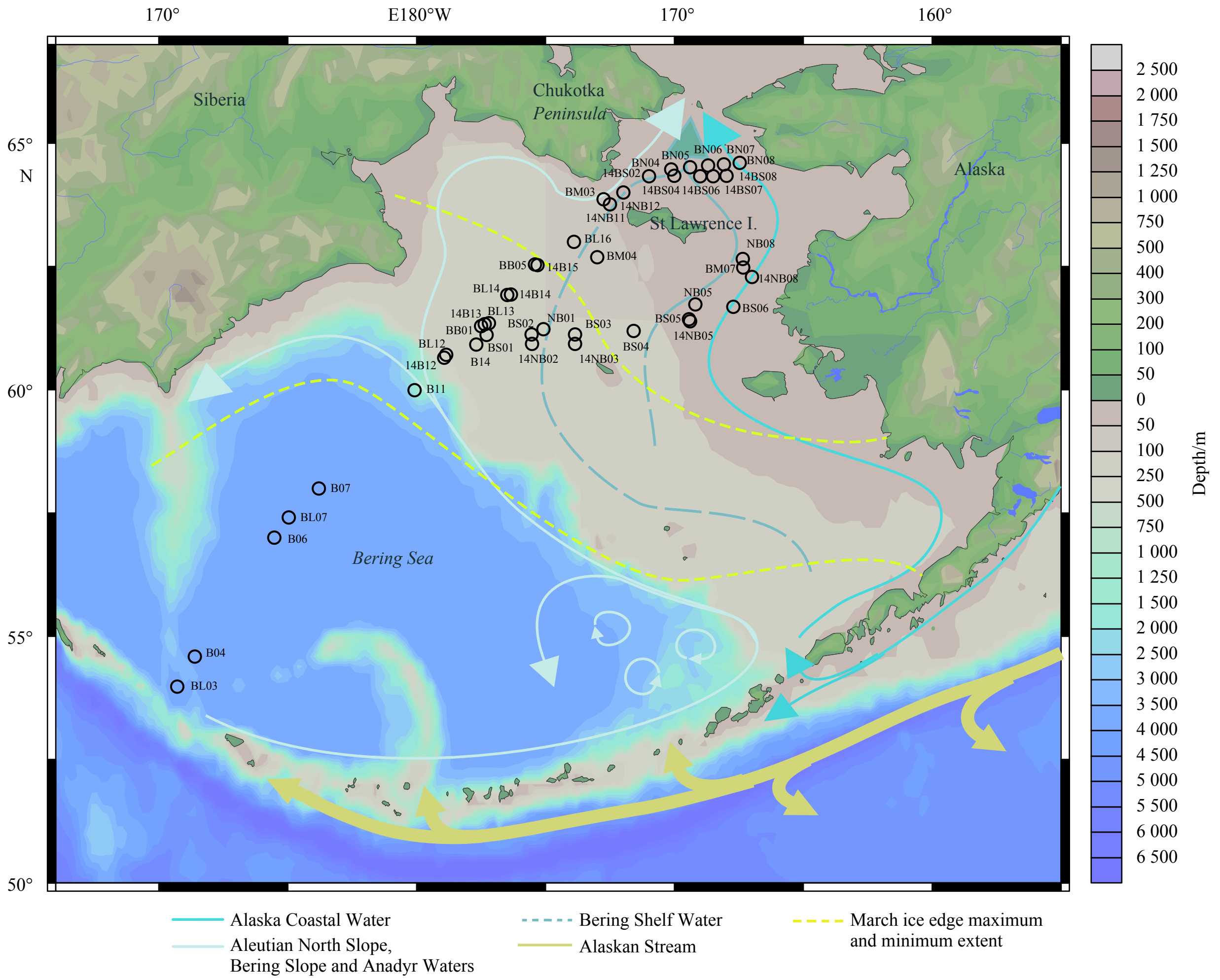

Fig. 1. Map of the Bering Sea showing the sampling locations, water mass types and extent of sea ice (modified from the map provided by Tom Weingartner and Seth Danielson, University of Alaska Fairbanks).

(Blanchet et al., 2008; Borcard et al., 2011), followed by a Monte Carlo permutation test (999 permutations under reduced model). The results showed that the correlation between environmental factors and macrobenthic communities was reliable (Pseudo-F=1.230 984, Significance=0.004). The above analysis was performed using R 3.4.2 and the vegan library (Oksanen et al., 2017).

3 Results

3.1 *Species composition and distribution*

A total of 12 phyla and 239 species of macrobenthos were identified from the obtained samples, of which polychaetes were the most abundant (with a total of 110 species), whereas crustaceans, mollusks and echinoderms represented 49, 44 and 12 species, respectively (Fig. 2). The dominant species in the shelves of the Bering Sea included *Scoloplos armiger*, *Ceradocus capensis*, and *Echinarachnius parma*; those in the slope area included *Ctenodiscus crispatus*, *Ophiura sarsii*, and *Eudorella pacifica*; and those in the basin area included *Prionospio malmgreni*, *Dasybranchethus fauveli*, and *Ampelisca brevicornis*.

3.2 *Distribution of abundance and biomass*

The average abundance of macrobenthos of all the stations was (727±1 320) ind./m^2, and the average densities of the five sectors were as follows: NB ((1 027±2 156) ind./m^2) > EB ((926±1 001) ind./m^2) > WB ((700±602) ind./m^2) > BS ((572±752) ind./m^2) > BB ((28±29) ind./m^2). The average abundance of the NB was characterized by crustaceans, whereas polychaetes were more abundant in the other areas (Fig. 3).

The mean biomass was (597.2±1 603.6) g/m^2, and the average biomass of the five sectors were as follows: NB ((1 435.4±2 762.6) g/m^2) > WB ((357.8±343.8) g/m^2) > BS ((332.6±223.1) g/m^2) > EB ((107.6±108.5) g/m^2) > BB ((0.4±0.4) g/m^2). The average biomasses of the NB and BS were characterized by echinoderms, whereas the EB and WB were characterized by mollusks. The average biomass of the BB was characterized by polychaetes (Fig. 4).

3.3 *Community structure*

The macrobenthic data collected from the 44 stations (two of which showed no presence of organisms) were subjected to cluster analysis (Fig. 5). The macrobenthic communities were divided into 16 groups with a 16% similarity threshold. The compositions were significantly different among the groups (R=0.847, p=0.001). Using SIMPER, species in each group (excluding the groups that only had one station) that had an accumulated contribution rate of 80% (Table 2) and had a significant inter-group contribution rate were used as characteristic species to describe the macrobenthic communities. The geographical distributions of the groups are shown in Fig. 6.

Table 1. Water depth, sediment type, bottom water temperature and salinity, and sampling time of the sampling sites

Sector	Station	Depth/m	Sediment type	Bottom temperature/°C	Bottom salinity	Sampling time
NB	4BS02	41	sand	0.41	32.21	2010-07-19
NB	BM03	55	clayey silt	−0.16	32.94	2012-07-17
NB	BN04	37	sand	−0.07	32.77	2012-07-17
NB	BN05	33	sand	−0.25	32.53	2012-07-17
NB	BN06	37	sand	0.28	32.46	2012-07-17
NB	BN07	27	sand	0.29	32.28	2012-07-17
NB	BN08	22	sand	−0.34	33.11	2012-09-11
NB	14NB11	55	clayey silt	0.50	32.60	2014-07-26
NB	14NB12	54	clayey silt	0.98	32.71	2014-07-26
NB	14BS02	40	sand	1.70	32.80	2014-07-26
NB	14BS06	40	sand	2.56	32.10	2014-07-27
NB	14BS07	40	sand	1.90	31.90	2014-07-27
NB	14BS04	40	sand	1.90	32.30	2014-07-27
NB	14BS08	36	sand	0.63	32.10	2014-07-27
EB	NB05	40	sandy silt	−1.00	32.12	2010-07-17
EB	NB08	35	silty sand	0.54	32.66	2010-07-18
EB	BM07	30	sand	4.28	31.51	2012-07-11
EB	BS05	32	silty sand	3.16	31.38	2012-09-10
EB	BS06	19	sand	8.42	31.02	2012-09-10
EB	14NB05	38	silty sand	1.70	30.90	2014-07-24
EB	14NB08	32	sand	5.20	30.60	2014-07-24
WB	BB05	79	sandy silt	−1.10	32.12	2010-07-16
WB	NB01	92	silt	−0.74	31.89	2010-07-17
WB	BL16	68	silt	−0.38	32.46	2012-07-15
WB	BS04	49	silty sand	−1.24	31.41	2012-07-16
WB	BL14	95	clayey silt	−0.21	32.50	2012-07-16
WB	BM04	55	sandy silt	−1.34	32.03	2012-07-16
WB	BS03	70	sandy silt	−1.34	31.80	2012-09-11
WB	5BS02	91	sandy silt	−0.21	32.42	2012-09-11
WB	14NB02	105	sandy silt	0.80	32.40	2014-07-23
WB	14NB03	74	sandy silt	0.62	32.00	2014-07-23
WB	14B14	102	clayey silt	−0.12	32.27	2014-07-25
WB	14B15	79	sandy silt	−1.40	32.10	2014-07-26
BS	B14	130	sandy silt	2.11	32.88	2010-07-15
BS	BB01	130	sandy silt	1.96	32.80	2010-07-15
BS	BS01	119	sandy silt	0.60	32.83	2012-07-16
BS	BL13	124	sandy silt	0.14	32.71	2012-07-20
BS	BL12	223	silty sand	1.82	33.14	2012-09-11
BS	14B12	258	silty sand	3.70	33.60	2014-07-22
BS	14B13	130	sandy silt	1.60	32.70	2014-07-23
BB	B04	3 873	clayey silt	1.57	34.67	2010-07-11
BB	B06	3 780	clayey silt	1.60	34.67	2010-07-12
BB	B07	3 743	clayey silt	1.61	34.67	2010-07-13
BB	B11	2 603	sandy silt	1.67	34.63	2010-07-14
BB	BL03	3 613	clayey silt	1.70	34.63	2012-07-13
BB	BL07	3 770	clayey silt	1.69	34.63	2012-09-11

3.4 *Relationship between macrobenthos and environmental factors*

The total interpretation of CCA for the macrobenthos was 24.6% (Fig. 7). Among the environmental variables, Md (r^2=0.759 7, p=0.001), sand% (r^2=0.571 0, p=0.002), silt% (r^2=0.428 4, p=0.008), clay% (r^2=0.340 7, p=0.032), TOC (r^2=0.505 7, p=0.002), and TN (r^2=0.524 0, p=0.001) were significantly related to the community structure. For example, Group 2 was significantly positively correlated with sand%, and Groups 9 and 10 were significantly positively related to clay% and TOC.

4 Discussion

The results showed that the macrobenthic communities in the Bering Sea were characterized by northern cold-water species and immigrant eurythermic species. Most of the species were distributed in a wide range, whereas the indigenous species were rare. For example, the large crab *Chionoecetes opilio* is widely distributed in the Arctic Ocean, Barents Sea, northern Atlantic Ocean and St. Lawrence Bay. The small amphipod *Ceradocus capensis* was found in the South China Sea. The macro echinoderm *Echinarachnius parma* was found in the Arctic

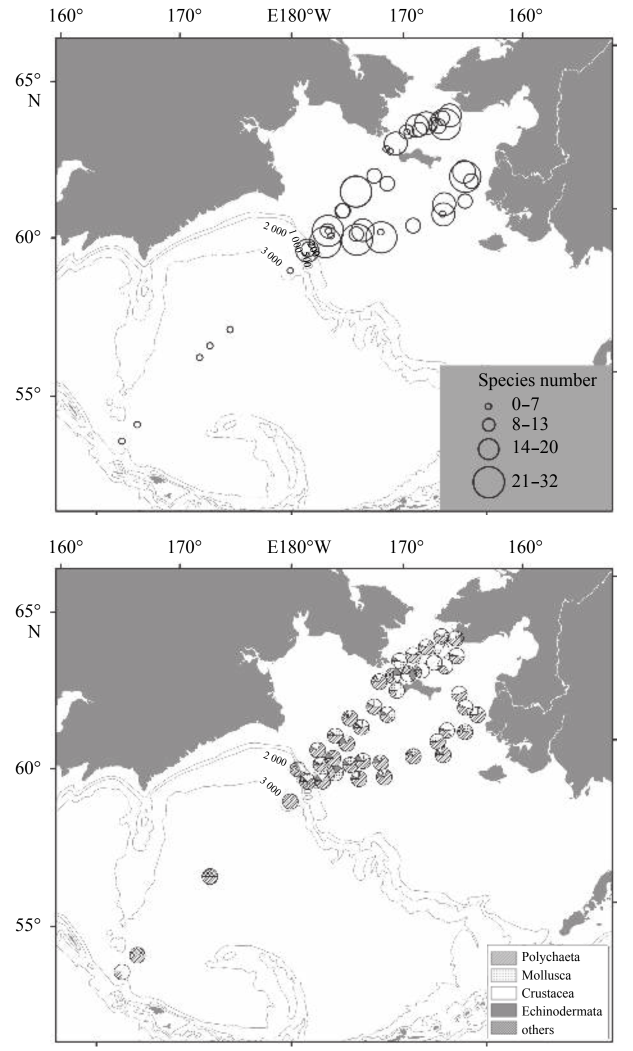

Fig. 2. Species number and composition of macrobenthos in the Bering Sea.

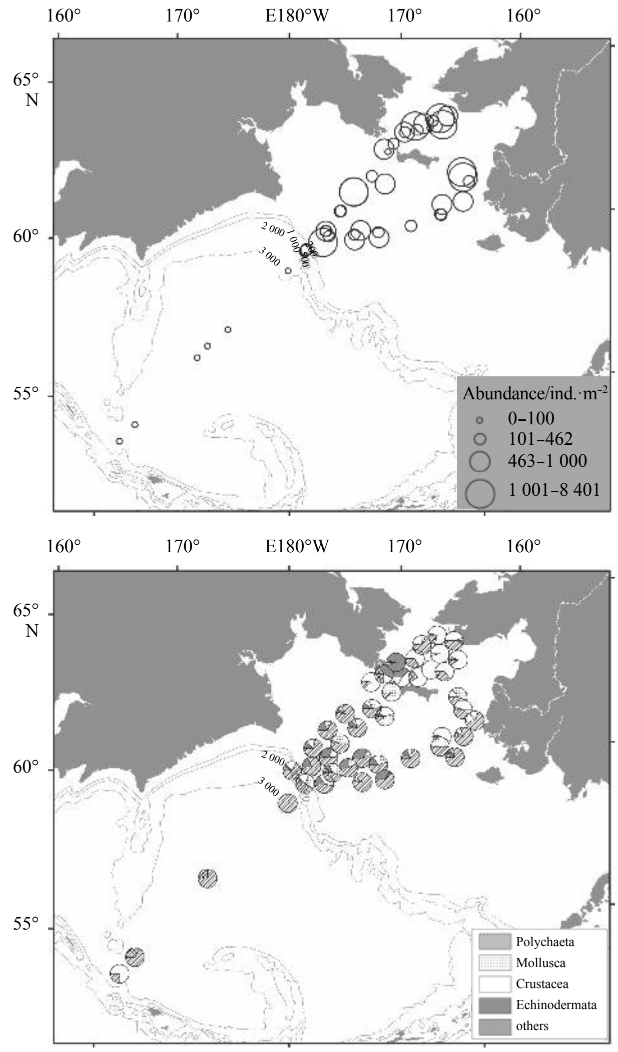

Fig. 3. Spatial distribution of macrobenthos abundance in the Bering Sea.

Ocean, the North Atlantic Ocean, and the waters near Canada. *Ctenodiscus crispatus*, a characteristic species of continental slope, is widely distributed in the Sea of Japan, the northern Atlantic Ocean, the Okhotsk Sea, the Barents Sea, and the waters around Canada and the United States. *Ophiura sarsii*, which is one of the major characteristic species of the Bering Sea and the Arctic Ocean, has a distribution range extending to the northern Atlantic Ocean, the northern Pacific Ocean, the Sea of Japan, the St. Lawrence Bay, the Gulf of Mexico, the Yellow Sea, and the waters around Europe. Moreover, polychaetes such as *Scoloplos armiger* and *Heteromastus filiformis* are distributed in the Arctic Ocean, the northern Atlantic Ocean, the northern Pacific Ocean, the Mediterranean Sea, the North China Sea, and the East and South China Seas. Mollusks such as *Nuculana pernula* and *Megayoldia thraciaeformis* are distributed in the North Atlantic, the Barents Sea, and the waters around Canada (GBIF Secretariat, 2017; WoRMS, 2017; Huang and Lin, 2012a, b).

Similar to the macrobenthos of the western Arctic Ocean, but significantly different from those in the Southern Ocean (Brey and Gerdes, 1998; Wang et al., 2014b; Lin et al., 2016), the macrobenthic communities in the Bering Sea were not a typical local community but contained diverse community structures derived from spatial heterogeneity. The Bering Sea is a marginal sea of the Pacific Ocean and is located in the subarctic region. Nutrient-rich warm waters of the Pacific Ocean pass the Bering Strait and enter the Arctic Circle, allowing species exchange between the Bering Sea and other northern seas (Piepenburg, 2005). The macrobenthic communities in the Bering Sea were exhibited a dispersed and patchy distribution pattern.

The *Chionoecetes opilio*-*Echinarachnius parma* group (Group 2) was primarily distributed in the sandy NB (with a water depth of approximately 40 m) and exhibited a simple composition. The large animals *Chionoecetes opilio* and *Echinarachnius parma* were the major characteristic species and had average densities of 13 ind./m^2 and 156 ind./m^2, respectively, and average biomasses of 257.1 g/m^2 and 3 660.5 g/m^2, respectively. The *Ctenodiscus crispatus*-*Cyclocardia crebricostata*-*Megayoldia thraciaeformis* group (Group 7) was mainly distributed in the BS with sandy silt, was found at a water depth of 119–130 m, and displayed a simple community structure. *Ctenodiscus crispatus* was the characteristic species and had an average abundance and biomass of 16 ind./m^2 and 255.6 g/m^2, respectively. The *Nuculana pernula*-*Tharyx* sp.-*Ophiura* sp. group (Group 9) was primarily distributed in the WB (32–102 m water depth) in sandy silt sediment. *Nuculana pernula* was the characteristic species, with an average abundance and biomass of 30 ind./m^2 and 23.9

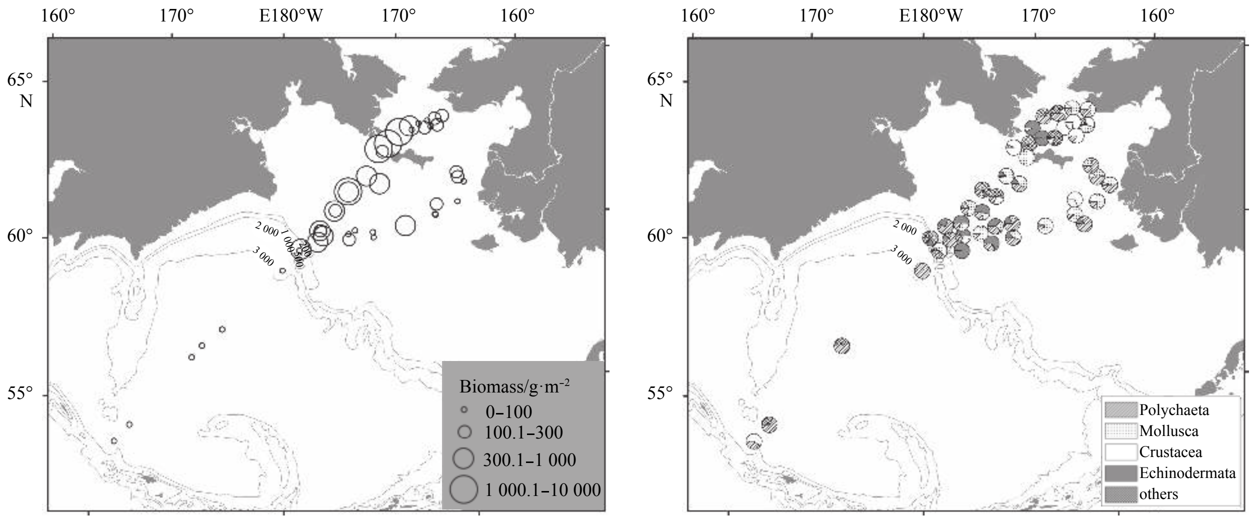

Fig. 4. Spatial distribution of macrobenthos biomass in the Bering Sea.

g/m², respectively. The *Heteromastus filiformis-Praxillella praetermissa-Nephtys ciliata-Ophiura sarsii* group (Group 10) was rich in species, complex in structure, and wide in distribution. *Heteromastus filiformis* and *Ophiura sarsii* were the characteristic species and were observed in the WB and BS at 35–258 m in silty sand or sandy silt sediment. The *Scoloplos armiger-Glycinde wireni-Sternaspis scutata* group (Group 11) was simple in structure. The polychaete *Scoloplos armiger* was the characteristic species and was distributed in the EB and WB at a depth of 32–49 m in a sandy or silty sediment. The *Ceradocus capensis-Scoloplos armiger-Nephtys caeca-Byblis gaimardii* group (Group 12) was characterized by small amphipods and polychaetes, was distributed in the NB and EB, and was found at a water depth of 19–40 m in sandy sediment.

The environmental factors affecting macrobenthic communities are complex and diverse (Robertson, 1979; Cusson and Bourget, 2005; Grebmeier et al., 2006a; Bolam and Eggleton, 2014; Lin et al., 2016). Blanchard et al. (2013a, b) found that the sharp change in the water depth from the shelves to the basin and the differences in sediment conditions and organic matter supply were the main factors resulting in differences in the macrobenthic distribution. Grebmeier et al. (2006a) argued that the nutrient-rich warm waters of the Pacific Ocean and the violent pelagic-benthic coupling were the major factors influencing the macrobenthic distribution in the Arctic regions. Additionally, the impact of the pelagic-benthic coupling on the macrobenthos of the Arctic was much greater than that on the macrobenthos of temperate and tropical waters (Petersen and Curtis, 1980). Comprehensive analysis revealed that, among the data obtained by simultaneous observation, the sediment type, water depth and sedimentary organic matter content were the major factors affecting the community structure and spatial distribution of the

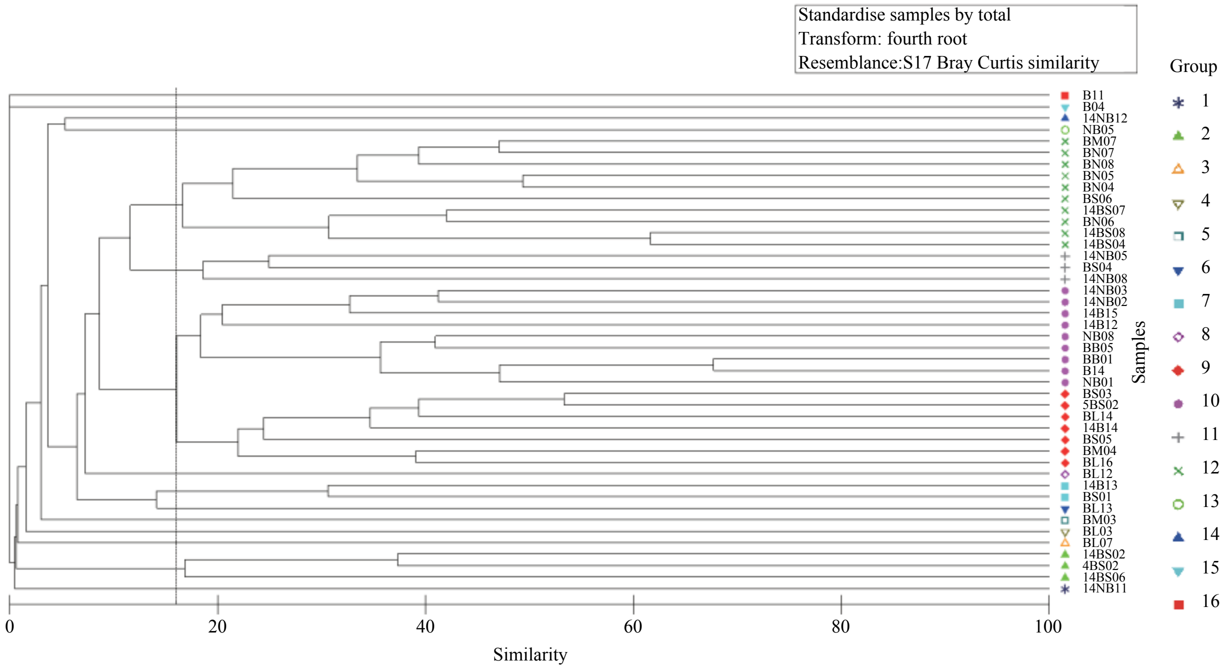

Fig. 5. Bray-Curtis similarity cluster analysis of macrobenthic communities in the Bering Sea.

Table 2. Simper similarity analysis based on the macrobenthic communities composition of the Bering Sea

Group	Total similarity	Species	Average abundance	Average similarity	Contribution rate/%	Cumulative percentage/%
2	23.68	*Chionoecetes opilio*	1.66	15.62	65.95	65.95
		Echinarachnius parma	1.87	8.06	34.05	100
7	30.61	*Ctenodiscus crispatus*	1.78	11.06	36.12	36.12
		Cyclocardia crebricostata	1.64	9.78	31.94	68.06
		Megayoldia thraciaeformis	1.91	9.78	31.94	100
9	28.24	*Nuculana pernula*	1.95	11.96	42.36	42.36
		Tharyx sp.	1.25	3.96	14.01	56.38
		Ophiura sp.	1.09	3.21	11.37	67.75
		Heteromastus filiformis	0.86	2.55	9.02	76.77
		Scoloplos armiger	0.76	1.49	5.29	82.06
		Melinna cristata	0.76	1.46	5.17	87.23
		Barantolla sp.	0.78	1.35	4.8	92.03
10	26.49	*Heteromastus filiformis*	1.27	4.42	16.67	16.67
		Praxillella praetermissa	0.92	2.87	10.83	27.5
		Nephtys ciliata	0.78	2	7.55	35.04
		Ophiura sarsii	1.06	1.98	7.47	42.51
		Scoloplos armiger	0.99	1.88	7.1	49.61
		Aphelochaeta pacifica	0.72	1.5	5.67	55.28
		Eudorella pacifica	0.83	1.48	5.57	60.85
		Leitoscoloplos pugettensis	0.88	1.29	4.88	65.73
		Barantolla sp.	0.64	0.93	3.51	69.24
		Aricidea nolani	0.62	0.92	3.46	72.7
		Nephtys caeca	0.6	0.87	3.29	76
		Nuculana pernula	0.43	0.67	2.53	78.53
		Harpiniopsis vadiculus	0.57	0.64	2.42	80.95
		Macoma calcarea	0.56	0.61	2.29	83.24
		Lumbrineris sp.	0.52	0.52	1.98	85.22
		Ennucula tenuis	0.57	0.5	1.89	87.1
		Ctenodiscus crispatus	0.41	0.47	1.77	88.87
		Micronephthys minuta	0.47	0.45	1.69	90.56
11	20.74	*Scoloplos armiger*	2.2	10.3	49.66	49.66
		Glycinde wireni	1.6	7.92	38.21	87.87
		Sternaspis scutata	1.11	2.51	12.13	100
12	24.66	*Ceradocus capensis*	1.67	6.38	25.85	25.85
		Scoloplos armiger	1.21	2.98	12.07	37.93
		Nephtys caeca	0.87	2.45	9.93	47.86
		Byblis gaimardii	0.93	1.81	7.34	55.19
		Ampelisca eschrichtii	0.84	1.7	6.91	62.1
		Paraphoxus tomiokaensis	0.77	1.63	6.59	68.69
		Maldanidae und.	0.67	1.16	4.71	73.4
		Glycinde wireni	0.54	0.92	3.74	77.14
		Photis sp.	0.47	0.72	2.92	80.06
		Iphinoe tenera	0.46	0.62	2.51	82.57
		Tryphosella horingi	0.44	0.55	2.24	84.81
		Eudorella pacifica	0.46	0.53	2.15	86.96
		Ampelisca brevicornis	0.56	0.47	1.91	88.87
		Cerebratulus sp.	0.37	0.4	1.63	90.5

macrobenthos in the Bering Sea.

The sediment type is an important factor that affects the natural distribution of macrobenthos, and is the result of the long-term natural selection of the macrobenthos (Hopcroft et al., 2008; Bolam et al., 2010). The sediment of the shelf and slope areas of the Bering Sea is dominated by silty sand/sandy silt, whereas the basin area is characterized by clayey silt. The diversity and standing biomass of the macrobenthos from areas with coarser sediment were higher than those from areas with muddy habitats. The higher standing biomass observed in the coarser habitats with reduced organic matter may indicate that macrobenthos in these regions is driven by other factors, for example, increased hydrodynamic activity.

Water depth and currents determine the downward transport of available particulate organic carbon (POC) from the upper waters for macrobenthos, as well as the pelagic-benthic coupling strength. The NB is at the intersection of the Alaska Coastal Water (ACW), Anadyr Water (AW), and Bering Sea Slope Water

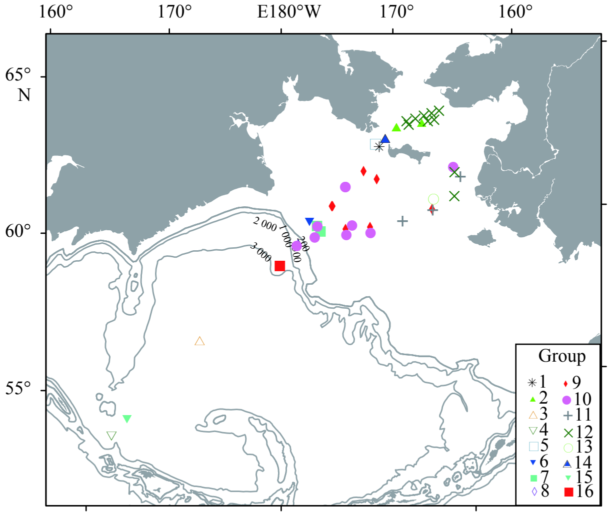

Fig. 6. Spatial distribution patterns of macrobenthic communities in the Bering Sea.

(BSW). Due to tight pelagic-benthic coupling and the high primary and secondary productivity of the water column (Grebmeier et al., 1988), a high-standing biomass is present in this area, compared with other seas (e.g., the Barents Sea, the UK continental shelf, the English Channel, the North Sea, the Weddell and Lazarev Sea, Porsangerfjord of Northern Norway, the Beaufort Sea, and the Arctic Ocean) (Brey and Gerdes, 1998; Cooper et al., 2008; Bolam et al., 2010; Kędra et al., 2013; Fuhrmann et al., 2015; Lin et al., 2016). In the Asian continent facing side of the northern Bering Sea (west of 170°W, north of St. Lawrence Island), where the nutrient-rich AW and a strong upwelling present, the average abundance and biomass of macrobenthos reach (1 505±3 062) ind./m^2 and (2 774.3±3 513.9) g/m^2, respectively, which can be called a “Bering benthic oasis”. However, on the side facing Alaska (east of 170°W), where the nutrient-limited ACW dominant, the average abundance and biomass of macrobenthos are much lower, at (551±405) ind./m^2 and (96.5±75.7) g/m^2, respectively.

Unlike the slope area of the Chukchi Sea, the Bering Slope is an another oasis with high water column production, which

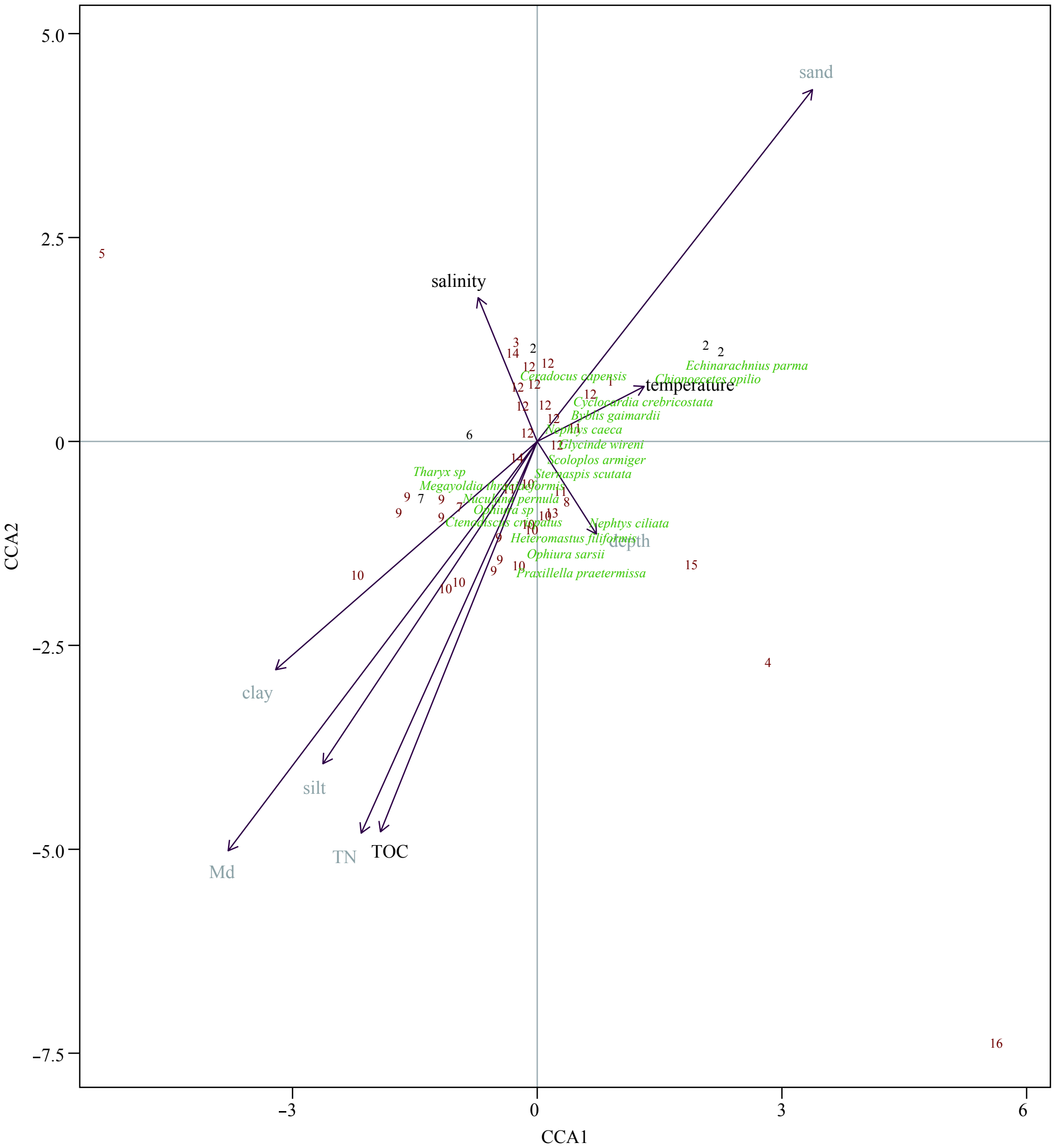

Fig. 7. CCA ordination diagram of macrobenthos and environmental variables.

forms the "Bering Sea Green Belt" and has a primary production between 175 and 275 g/(m²·a). Tidal mixing at the shelf-break front and transverse circulation in the Bering Slope Current, which includes eddies near the shelf edge, result in vertical transport of pelagic nutrients to the seafloor (Springer et al., 1996). Rich food sources have resulted in high-standing benthic biomass in this area. The deep Bering Basin, which accounts for nearly half of the Bering Sea, exhibits typical high-nutrient, low-chlorophyll (HNLC) properties (Banse and English, 1999). The water depth has become an inhibitor for the transfer of POC in water column to seafloor. The deficiency in food sources has resulted in a desert-like seabed.

Previous studies have shown that the average abundance and biomass of macrobenthos were 4 752 ind./m² and 300–400 g/m² (Grebmeier and McRoy, 1989), respectively, and amphipods and bivalves were the dominant taxa (Grebmeier and McRoy, 1989; Grebmeier and Cooper, 1995; McCormick-Ray et al., 2011). In particular, Ampeliscid amphipods dominated in vast areas of the northern Bering Shelf, with high values of mean abundance and biomass at 4 606 ind./m² and 263.5 g/m² (the conversion factor of wet weight to dry weight is 0.2) (Highsmith and Coyle, 1990), respectively, and were the primary prey of the migratory California gray whale. However, compared with results obtained from previous studies, the macrobenthic communities of the Bering Sea have undergone significant structural changes.

Despite amphipods remained one of the dominant groups, a significantly reduced abundance was exhibited in the northern Bering Shelf. A shift in gray whale feeding sites was reported from the northern Bering Sea to Barrow off of the northern slope of Alaska (Moore et al., 2003, 2006). Furthermore, the abundance of mollusks was significantly decreased, and no longer a major group in the northern Bering Shelf. The results showed that the average abundance of macrobenthos in the northern Bering Shelf significantly declined (1 028 ind./m²) in recent decades, whereas the biomass significantly increased (1 435.4 g/m²). In addition, this similar trend was found in the Bering Slope compared with the results of an investigation conducted in the summer of 1999 (Lin et al., 2016). Recent studies indicate a decline in the organic carbon supply and bivalve biomass, which has been interpreted as a consequence of seasonal sea ice retreat and increasing temperatures (Grebmeier and Dunton, 2000; Lovvorn et al., 2003; Grebmeier et al., 2006b). All of these changes support the hypothesis that a large-scale ecosystem change is underway.

5 Conclusions

Based on multiyear biological, chemical, hydrological and geological surveys, this study analyzed the community structure and the temporal and spatial patterns of the macrobenthos in the Bering Sea and their relationships to environmental factors. The macrobenthic communities of this region were dominated by northern cold-water species and immigrant eurythermic species, and exhibited a dispersed and patchy distribution pattern. Combined influenced by the sediment type, water depth, and currents, the northern Bering Shelf and Bering Slope exhibited a high-standing biomass. In recent decades, the macrobenthos of the Bering Sea has undergone significant structural changes, exhibiting a decline in abundance and an increase in biomass. In addition, amphipods and bivalves have been gradually replaced by other taxa, indicating that these benthic ecosystems have been undergoing large-scale structural changes, likely due to seasonal ice melting; changes in organic carbon input; and climate change.

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