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HYDROBIOLOGY

Unusual Abundance of Macrobenthos and Biological Invasions in the Chukchi Sea

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Abstract—The data from the expedition of the program RUSALCA conducted in 2004 showed unexpectedly high quantitative indices of macrobenthos in the southeastern Chukchi Sea. Extensive areas of the bottom northwest of the Bering Strait were dominated by the bivalve *Macoma calcarea***.** The greatest biomass of benthos in *Macoma*-dominated areas was 4232 g/m^2 with an average of 1382 g/m^2 for the investigated region. Such a high biomass of soft-bottom communities, which is extremely uncommon even in the temperate regions of the oceans, is reported for the Arctic for the first time. The long-term existence (more than 70 years) of highly productive benthic communities dominated by *Macoma calcarea* in one and the same area of the Chukchi Sea can most likely be attributed to gyres, which constantly arise in the region northwest of the Bering Strait. These cyclonic gyres carry nutrient-rich bottom water to the surface and hinder larval transport away from mother populations. They also keep and concentrate major food sources of benthos (live and dead phyto- and zooplankton and fecal pellets) over the benthic community locations. Most likely, a significant proportion of the primary production in the southeastern Chukchi Sea is used by benthos within the investigated *Macoma* community. Findings of three relatively large warm-water Pacific species near Point Hope in the Chukchi Sea are probably indicative of the progressive climate warming during the last century.

Key words: benthos, mollusks, climate warming, biological invasions, Chukchi Sea.
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The Chukchi Sea is located at the interface between two oceans, the Pacific and the Northern Ocean and therefore exerts influence of both these two oceans and the Atlantic, whose weakening warm waters could reach the northern borders of the sea [19]. The significant impact of the Atlantic on the fauna of the Barents Sea gradually becomes weaker toward the east, which is clearly illustrated by depletion of the species composition of invertebrates in the Kara, Laptev and East Siberian seas [33] (Fig. 1).

Despite the fact that investigations of the Chukchi Sea started long ago, viz., in 1878, when the first biological samples were collected by a Swedish expedition from aboard the Research Vessel (RV) *Vega*, the sea is still poorly studied and holds many astonishing mysteries. In 1879 the Vega had to stop for a second winter stay and throughout the winter the scientists of the expedition continued sampling zoological materials. Altogether the samples were collected at 13 stations [36]. The next large expedition was a hydrographic expedition into the Northern Ocean with the RVs *Taimyr* and *Vaigach* that worked in the Chukchi Sea for 5 years, from 1910 to 1914. During the expedition more than 50 trawl samples were collected on the shelf of the Chukchi Sea, which contributed significantly to the knowledge about the fauna of the latter [17–19]. Some small collections were made by a Canadian Arctic expedition in 1913 (in the eastern part of the Chukchi Sea) and a Norwegian expedition aboard the RV *Maud* in 1922 (to the north off Vrangel Island) [37]. In 1929, during an expedition with the F. Litke ice breaker, biologists collected more than 50 trawl samples in the southwestern and central parts of the Chukchi Sea [19]. A rather large water area in the southern and central

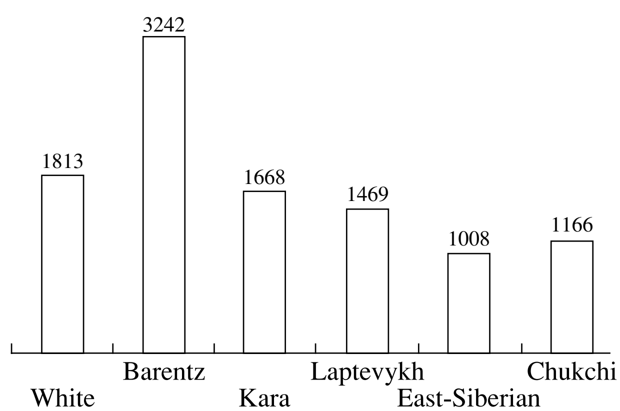

Fig. 1. Distribution of species composition of free-living invertebrates in Eurasian seas of the Northern Ocean (after Sirenko [33]).

parts of the Chukchi Sea was surveyed during expeditions with the Dal'newostochnik and Krasnoarmeets trawlers, in 1932 and 1933 respectively. Twenty-five quantitative samples collected during the cruise of the Krasnoarmeets trawler allowed scientists to identify the dominating species and groups of bottom communities and to determine their qualitative characteristics. Similar sampling (15 qualitative and 34 quantitative samples) was performed during an expedition aboard the Krasin ice breaker in 1935, in the Long Strait, at Vrangel Island, and to the north off the latter. These materials were used by Ushakov in his paper on the bottom fauna of the Chukchi Sea [19]. An expedition with the RV Okhotsk was performed in 1938, when qualitative samples were collected on eight stations located along a transect between the Serdtse-Kamen' and Lisburne capes, and this completed the major investigations in the Chukchi Sea performed prior to the Second World War [19].

Then, after a long-term interruption, in 1946 A.P. Andriyashev collected 18 bottom samples from aboard the Severnyi Polyus ice breaker. In 1976, the scientists of the Zoological Institute of the RAS (ZIN RAS) resumed biological investigations in the Chukchi Sea and collected materials at Schmidt Cape and in coastal areas around the southern and eastern parts of Vrangel Island using the scuba quantitative technique (more than 100 samples) [8, 9]. Investigations in the Chukchi Sea were continued only 12 years later, when, during the joint Soviet–American expedition BERPAC (Program for Long-Term Ecological Research of Ecosystems of the Bering and Chukchi Seas and the Pacific Ocean), aboard the RV *Akademik Korolev*, 43 bottom sampler and 18 trawl samples were collected in the southern Chukchi Sea [34]. The next expedition by ZIN RAS with the *Dmitrii Laptev* freight vessel was performed in 1989. Scuba quantitative technique and traditional sampling methods, using trawls and bottom samplers allowed them to make a significant contribution to the collections of the previous expedition at 54 stations located in the central and western parts of the Chukchi Sea, as well as in the Kolyuchinskaya Guba Bay and at Herald Bank [6, 7]. In 1990, Gagaev, a member of the expedition with the Georgii Maksimov freight vessel, collected samples at four stations located in the Long Strait [4]. In 1995, during a Russian–American expedition aboard the RV Alpha-Helix, materials were collected at 18 stations in the southern part of the Chukchi Sea with bottom samplers and transferred for treatment to the ZIN RAS. Joint investigations of Russian and American scientists initiated in the late 1980s (the BERPAC Program) [29, 34] are continued successively in our own time within the framework of the RUSALCA Program (Russian–American Long-Term Census of the Arctic). These studies have provided new information about the distribution of fauna in surveyed areas of the Chukchi and Bering seas. Some of the data are discussed in this paper.

The major targets of this project were to reveal the reasons for great productivity in the benthic community of the bivalve mollusk *Macoma calcarea* found to the northeast off Sedtse-Kamen' Cape and to provide new information that could corroborate climate warming in the Chukchi Sea.

BRIEF HYDROLOGICAL CHARACTERISTICS OF THE SURVEYED AREA

The major effects on the hydrological regime in the Chukchi Sea are exerted by Pacific waters vigorously streaming northward through the Bering Strait. Three water masses have been distinguished that differ from each other in temperature and salinity: in the western Bering Strait are the waters of the Gulf of Anadyr (the salinity is ≥32.5‰ and the temperature is –1.0 to 1.5°C); in the central part of the strait are the waters of the Bering Sea shelf (salinity is 31.8–32.5‰ and the temperature is 0 to 1.5°C); and in the eastern part of the strait are the Alaskan coastal waters (salinity is ≤31.8‰ and the temperature is ≥4°C) [20, 21, 30]. The salinity and temperature of the bottom waters, determined in the strait at stations 6, 8, and 10 in 2004 were similar or equal to those characteristic of the three water masses as listed above (Table 1).

Moreover, the hydrological situation in the southern Chukchi Sea is significantly affected by Siberian coastal waters streaming from the Eastern Siberian Sea through the Long Strait up to the Bering Strait [15, 21, 30, 38]. According to American scientists, after passing through the Bering Strait, the waters of the Gulf of Anadyr and Bering Sea shelf fuse together to form a solid water mass that is rich in biogenic matter [31]. Warm coastal Alaskan waters that are poor in biogens [31] are running along the western coast of the Arctic Alaska, reaching Cape Barrow in the northeastern Chukchi Sea and pass further to the Beaufort Sea [39]. At the latitude of Point Hope the mixed waters of the Bering Sea shelf and Gulf of Anadyr diverge in two directions, to the northeast, toward the Beaufort Sea and to the northwest, toward Vrangel Island [39]. In the southeastern Chukchi Sea, at the Chukotka Peninsula, these waters meet with cold coastal waters from the Eastern Siberian Sea. As a result of their collision, several large cyclonic gyres arise in that area, to the southwest off the Bering Strait [19, 21, 38]; the greatest one among the latter is located to the north and northeast off Serdtse-Kamen' Cape and Kolyuchinskaya Guba Bay [15]. Thus, the pattern of currents in the Chukchi Sea that was reported by G.E. Ratmanov for the first time does not contradict the modern data. As this is the most detailed scheme of currents for the region that we are interested in, we will try to use it here to explain the existence of a highly productive mollusk community in the southeastern Chukchi Sea.

The bottom water temperature in September 2004 was negative on the beam of the Kolyuchinskaya Guba Bay (Stn. 27) and along the Northern Transect in Her-

Table 1. Benthos stations performed in the Chukchi Sea during the cruise of the RV Professor Khromov in 2004

Station number	Date	Latitude	Longitude	Depth, m	Sampling device	Temperature, °C	Salinity, ‰
6	August 10, 2004	65.40.58 N	168.17.956 W	49.2	Dredge	10.5	30.607
6	August 10, 2004	65.40.667 N	168.17.75 W	50.2	Trawl		
8	August 11, 2004	65.52.69 N	169.05.00 W	48.3	Dredge	3.03	32.55
8	August 11, 2004	65.53.18 N	169.04.67 W	48.2	Trawl		
10	August 11, 2004	66.00.03 N	169.37.40 W	51.7	Dredge	2.35	33.028
11	August 12, 2004	66.56.237 N	170.59.827 W	42	BGS	1.69	33.17
11	August 12, 2004	66.55.63 N	170.59.39 W	43.3	Trawl		
13	August 12, 2004	67.25.92 N	169.37.24 W	51.41	BGS	2.47	32.93
13	August 12, 2004	67.25.78 N	169.38.37 W	52	Trawl		
15	August 13, 2004	67.52.51 N	168.18.87 W	58.7	″	2.77	32.579
15	August 13, 2004	67.52.07 N	168.19.70 W	57.6	BGS		
17	August 13, 2004	68.20.06 N	167.06.06 W	39.7	Trawl		
17	August 13, 2004	68.17.81 N	167.03.06 W	39	BGS		
18	August 14, 2004	68.58.092 N	166.53.116 W	48.2	Trawl	7.95	31.301
18	August 14, 2004	68.57.002 N	166.54.747 W	51.2	BGS		
20	August 14, 2004	69.00.275 N	168.51.642 W	54.3	Trawl	3.69	32.276
20	August 14, 2004	69.00.362 N	168.53.67 W	54.2	BGS		
22	August 15, 2004	68.45.839 N	170.25.27 W	57.5	″	3	32.761
23	August 15, 2004	68.30.9 N	171.28.8 W	56.7	Trawl	2.21	32.907
23	August 15, 2004	68.31.41 N	171.27.74 W	56.4	BGS		
24	August 15, 2004	68.23.00 N	172.20.6 W	57	″	2.05	32.985
25	August 16, 2004	67.51.40 N	172.34.44 W	48.9	Trawl	1.7	33.048
25	August 16, 2004	67.52.209 N	172.33.08 W	49	BGS		
27	August 16, 2004	67.24.42 N	173.38.33 W	34.2	Trawl		
27	August 16, 2004	67.23.845 N	173.39.19 W	35.7	BGS	–1.52	32.869
106	August 18, 2004	70.45.54 N	175.31.27 W	72.7	Trawl	–1.77	33.522
106	August 18, 2004	70.45.586 N	175.32.05 W	71.8	BGS		
085B	August 21, 2004	72.18.95 N	175.59.24 W	103.3	Trawl	–1.41	33.68
085B	August 21, 2004	72.19.036 N	175.59.07 W	104.2	BGS		
073B	August 21, 2004	71.54.109 N	175.29.149 W	71.1	″		
073B	August 21, 2004	71.54.69 N	175.27.10 W	71.5	Trawl	–1.75	33.319
062B	August 22, 2004	71.23.47 N	174.52.23 W	71.6	″	–1.78	33.53

Note: BGS—Bottom grab sampler.

ald Canyon (Stns. 62B, 73B, 85B, and 106). At all other stations the bottom water temperature was positive and to the east (Stn. 18) it was 2–3 times greater than at the west (Stns. 11, 13, 15, 23, 24, and 25) (Table 1).

MATERIAL AND METHODS

The samples collected by the authors in the course of the First Russian–American Joint Expedition RUSALCA, performed in August 10–22, 2004, aboard the RV *Professor Khromov* (Fig. 2A) were used as materials for the project. To analyze the composition and distribution of benthos, 52 samples were chosen that were collected with a bottom sampler at 17 stations, as well as 15 trawl and 3 dredge samples collected at 16 stations in southeastern and southwestern parts of the Chukchi Sea (Table 1). Quantitative samples were collected with a 0.1 m^2 Van Veen grab sampler and 0.25 m^2 Okean grab, with 3 samples taken at each of 17 stations and 2 samples at Stn. 107 respectively. To collect materials we also used a 4 m wide beam trawl and small rectangular dredge with a mouth 22 × 70 cm in size, both made from 1 cm mesh. The samples were rinsed on 1 mm sieves, fixed with 4% buffered formalin and then

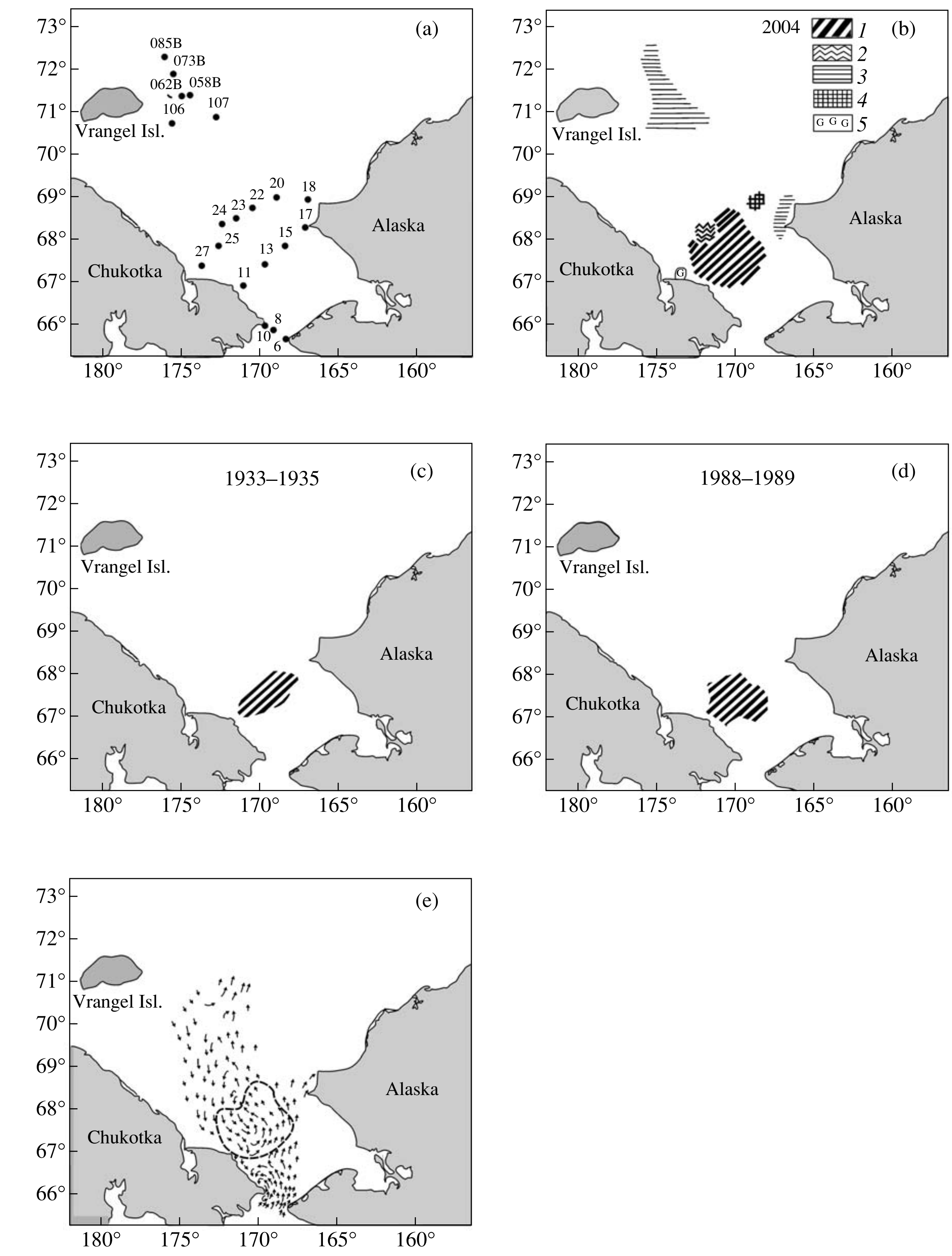

Fig. 2. Scheme of the location of stations performed under RUSALCA Program aboard the RV *Professor Khromov* in 2004 (a); scheme of the distribution of *Macoma calcarea* community after the results of cruises of the RV *Professor Khromov* in 2004 (b); *Krasnoarmeets* trawler and *Krasin* ice breaker in 1933 and 1935 (c); and RV *Akademik Korolev* and *Dmitrii Laptev* freight vessel in 1988 and 1989 (d); a scheme of the current pattern in the Chukchi Sea after the results of the *Krasnoarmeets* trawler in 1933 (after Ratmanov [15]) and distribution of bottom community dominated by *M. calcarea* (interrupted line) after the results of the RV *Professor Khromov* in 2004 (e).

transferred into 75% ethanol. The samples were treated to distinguish and isolate different taxonomic groups; the dominating animals were, if possible, identified at the species or higher level.

To analyze the distribution of benthos (besides bottom grab, trawl and dredge samples) video records were also made at 10 stations by scientists of the VNIIOkeangeologiya (All-Russian Scientific Institute of Ocean Geology) during the cruise aboard the RV *Professor Khromov.*

Taking into account the fact that the materials of the expedition of 2004 were rather limited, only the bottom community dominated by *Macoma calcarea* was identified at six stations. The community was distinguished by the species dominating in biomass [3]. All stations dominated by one or a few species were referred to as belonging to the same community; following the approach of Kuznetsov [12], we also included in this community the stations where the dominating species did not dominate all three samples (however, still being present in a subdominant group), if both the composition of the associated characteristic species and characteristic set of abiotic factors remained the same. To corroborate the position of community borders, we also used partially treated materials of two other expeditions according the RUSALCA program collected by scientists of ZIN RAS in 2005 and 2006, primarily within the area of the *Macoma* community that we revealed.

To determine the changes in the bottom communities, we found data published in the available literature [13, 19, 34] and also some unpublished data from the benthos journal of the expedition performed by ZIN RAS in 1989 aboard the RV *Dmitrii Laptev.* It is pertinent to note that only certain stations sampled in 2004 agreed with the stations of previous expeditions or were located close enough to the latter. In cruises aboard the Krasnoarmeets trawler in 1933 and the Krasin ice breaker in 1935 at each station 1–2 samples were taken with a 0.2 m^2 Petersen grab sampler. In the expedition with the RV *Akademik Korolev* 1–2 samples were collected at each station using a 0.1 m^2 Van Veen grab; while on the Dmitrii Laptev freight vessel 3 samples were taken at each of the surveyed stations using a 0.25 m^2 Okean bottom grab sampler. The biomass is reported here as grams of wet weight of non-fixed animals.

RESULTS

The studies we carried out demonstrated that the western and eastern areas of the southern Chukchi Sea are significantly different from each other in the composition of fauna and in the quantitative characteristics of the latter. In the eastern part of the sea, at Stns. 17 and 18, in depths of 39–51.2 m, in the area of Alaskan coastal waters, the animals were mostly represented by sestonophages (polychaetes and the ascidian *Cheliosoma macleayanum*), showing a relatively small biomass of 86.3 ± 32.8 – 248.8 ± 125.5 g/m^2 (Fig. 2b, Table 2).

To the northeast off Serdtse-Kamen' Cape (Stns. 11, 13, 15, 22, 24, and 25), in depths of 49–57.5 m, in zones of mixed waters of the Gulf of Anadyr and the Bering Sea shelf, as well as in the coastal waters from the Eastern Siberian Sea, the bottom communities were mostly dominated by detritophages–collectors. In these areas the biomass of benthos was an order of magnitude greater and often reached 1000 g/m^2 and more. At Stn. 13 all three samples contained an incredibly large amount of bivalve mollusks, averaging more than 9000 specimens/m^2 (their biomass exceeded 4000 g/m^2) (Table 3). The materials collected from these stations demonstrated the presence of a highly productive community dominated by the bivalve mollusk *Macoma calcarea.* In the surveyed area this is the mollusk species that most often provided the major biomass (Table 3). Among subdominant species we can note the bivalve mollusks *Yoldia hyperborea* and *Ennucula tenuis* and the amphipod *Ampelisca macrocephala.* The preliminary results of treatment of materials collected in 2005 and 2006 within the borders of the revealed community corroborated the domination of *M. calcarea*, not only at stations of the transect between Serdtse-Kamen' Cape and Point Hope (Stns. 11, 13, and 15), but also at stations located between this transect and the transect from Kolyuchinskaya Guba Bay and Cape Lisburne (Stns. 22, 24, and 25).

The examination of video records made at stations 23 and 25 revealed egg clutches looking like mucous balls up to 5 cm in diameter moving along the bottom by the action of currents. The same clutches occurred in a great number in trawl samples from Stns. 13, 15, 23, and 25. The examination of the clutches revealed the presence of bivalve mollusk larvae at the stage of the veliconch, with a shell length of about 350 µm. According to literature data [32], in the species of the genus *Macoma* the pelagic period is very short or even absent entirely, i.e., the larvae are lecitotrophic. According to L. Flyachinskaya (ZIN RAS), these clutches might belong to one of the species of the genus *Macoma.* The samples dominated by *M. calcarea* comprised two more species of the genus *Macoma*, small *M. moesta*, and *M. torelli.* However, both the population density and, especially, the biomass of the two latter species are less than one-tenth as great as those of *M. calcarea.* Taking into account the evident domination of *M. calcarea* in the areas of the stations where mucous egg clutches were registered in abundance, we can suppose that they also belong to *M. calcarea.* Obviously, such a developmental pattern is the most appropriate for mollusks inhabiting areas affected by large-scale cyclonic gyres that do not allow larvae to drift beyond the borders of the parental populations. If so, this could explain the great density of *M. calcarea* populations (6683 ± 927 specimens/m^2 at Stn. 13) comprising specimens of most or all age groups.

Table 2. Population density and biomass of benthos at stations performed during the cruise of the RV Professor Khromov in 2004

Station number	Depth, m	Population density, specimens/m^2	Biomass, g/m^2	Dominating species
11	42.9	3450 ± 360.7	1291.2 ± 94.4	*Macoma calcarea*, *Yoldia hyperborea*, *Ennucula tenuis*, *Ampelisca macrocephala*
13	51.4	11043 ± 113.1	4231.7 ± 574	*M. calcarea*
15	57.6	1886.7 ± 250.9	1081.7 ± 215.2	*M. calcarea*
17	39.0	313 ± 68.9	248.8 ± 125.5	*Nephtys ciliata*, *Cheliosoma macleayanum*
18	51.2	60 ± 12	86.3 ± 32.8	*N. ciliata*
20	54.2	320 ± 42	156.1 ± 46.1	*Ophiura sarsi*, *Nephtys* spp.
22	57.5	933 ± 87.4	260 ± 29.9	*M. calcarea*, *E. tenuis*
23	56.4	1350 ± 87	612.8 ± 10.3	*E. tenuis*
24	57.0	386.7 ± 8.8	491.4 ± 153.6	*M. calcarea*, *E. tenuis*
25	49.0	1476.7 ± 253.8	934.6 ± 110.1	*M. calcarea*, *Y. hyperborea*
27	35.7	680 ± 112	34.7 ± 25.5	*Hippomedon* sp.
58B	58.5	170 ± 4	134.6 ± 56.6	*N. ciliata*, *Maldane sarsi*, *Heliactis arctica*
62B	69.7	510 ± 13	343.1 ± 107	*Nicomache lumbricalis*, *Golfingia margaritacea*
73B	71.1	5697 ± 1182.8	380 ± 90.4	*M. sarsi*
85B	104.2	340 ± 74	231.4 ± 57.6	*M. sarsi*, *Astarte borealis*, *Ctenodiscus crispatus*
106	71.8	110 ± 29	116.9 ± 49.9	*M. sarsi*, *O. sarsi*
107	40.1	300 ± 39	102.5 ± 24.3	*N. ciliata*, *M. sarsi*, *G. margaritacea*

Note: For each station the population density and biomass were calculated from 3 samples.

Table 3. Population density and biomass of benthos in the community of *Macoma calcarea*

Station number	Population density, specimens/m^2		Biomass, g/m^2		Proportion of bivalve mollusks in the total biomass of benthos, %	
	all species of benthos	bivalve mollusks	all species of benthos	bivalve mollusks	all species	the species of the genus *Macoma*
11	3450 ± 360.7	1400 ± 160.1	1291.2 ± 94.4	876.7 ± 86.9	67.9	22.2
13	11043 ± 113.1	9820 ± 1021.6	4231.7 ± 574	4024.3 ± 557.7	95.1	83.1
15	1886.7 ± 250.9	747 ± 198.4	1081.7 ± 215.2	831.7 ± 126.2	76.9	51.6
22	933.3 ± 87.4	703 ± 64.9	260.0 ± 29.9	167.3 ± 25.41	64.2	27.3
24	386.7 ± 8.8	320 ± 40.4	491.4 ± 153.6	414.9 ± 160.4	84.5	40.3
25	1476.7 ± 253.8	1130 ± 196.6	934.6 ± 110.1	741.7 ± 133.7	79.4	47.1

At the edges of the *Macoma*-dominated community, in depths of 35.7–56.4 m, there were areas (Stns. 20, 23, and 27) dominated by the bivalve mollusk *E. tenuis*, the brittle star *Ophiura sarsi*, polychaetes, and amphipods *Hippomedon* sp. The biomass at these stations ranged from 34.7 ± 25.5 to 612.8 ± 10.3 g/m^2 (Table 2).

The Northern Transect (Stns. 58B, 62B, 73B, 85B, 106, and 107), which was mostly performed in Herald Canyon and nearby, in depths of 40.1 to 104.2 m, revealed the domination of the polychaetes *Maldane sarsi, Nicomache lumbricalis*, and *Nephtys ciliata*, the brittle star *O. sarsi*, and sipunculan *G. margaritacea.* At Stns. 85B and 107 of the Northern Transect, in depths of 40–103 m, on silty bottoms, ceriantharians of the *Cerianthus* sp. were recorded that were often arranged in aggregations, with a density of up to 3–4 specimens/m^2. This was found owing to the submarine video recording technique (used in the Chukchi Sea for the first time). However, all attempts to collect these animals at Stn. 107 using the Van Veen grab sampler or heavier Okean sampler failed. The video records showed clearly that these animals could rapidly hide themselves deep in the ground, into sediment layers impenetrable for bottom samplers.

An analysis of samples collected in the Bering Strait using three dredges, in depths of 47–51 m deep (Stns. 6, 8, and 10) showed that these stations are dominated by the sea urchin *Strongylocentrotus pallidus*, the cirripede barnacle *Balanus crenatus* (mostly at Stn. 10), holothurians *Psolus* sp., alcyonarians *Gersemia* sp., actinia, and other animals of the epifauna, which agreed with our earlier data published elsewhere and information available in literature [10, 34].

The trawl samples from Stn. 17, located at the coast of Alaska, from about 40 m deep, were rather rich in fauna. As well as starfish, the brittle star *Gorgonocephalus caryi*, hermit crabs, the crabs *Chionoecetus opilio* and *Hyas coarctatus*, and other members of the epibenthos that are common for the Chukchi Sea, we found three unusual and rather warm-water Pacific species, the bivalve mollusk *Pododesmus macrochisma* (2 specimens) and the crabs *Oregonia gracilis* (1 specimen) and *Telmessus cheiragonus* (3 specimens).

DISCUSSION

A comparison of our data with the results of expeditions carried out earlier allowed us to make some conclusion about the patterns of distribution of bottom communities in the shelf of the Chukchi Sea and their dynamics for the period from 1933 to 2004 (Fig. 2b–2d).

The western and central areas of the southern Chukchi Sea, to the northeast off the Serdtse-Kamen' Cape are occupied by a community of detritophages–collectors that is dominated in biomass by the bivalve mollusk *Macoma calcarea.* At most stations surveyed the proportion of this species exceeds 40–70%, which is evidence that this community is rather stable. In 1933 the biomass of benthos in the *Macoma* community of the southern part of the sea, at 5 stations, equaled 68–1033 g/m^2 (with the average of 306 g/m^2); in 1988, at 8 stations, it was 511–2062 g/m^2 (averaging 1046 g/m^2); and in 2004, at 6 stations, it was 260–4231.7 g/m^2 (averaging 1382 g/m^2).

It is pertinent to note the stability of the *M. calcarea* community that has occupied a vast area in the southern Chukchi Sea until the present, i.e., for at least 70 years. Such a long-term existence of a highly productive benthic community of *M. calcarea* in the southern Chukchi Sea is, in all likelihood, due to water gyres that arise continuously in the area to the northwest of the Bering Sea [15]. The greatest gyre is located exactly above the population of *M. calcarea* that has existed in this area for several decades (Fig. 2e). This gyre involved cooled and somewhat desalinated waters that are rich in biogens of the Eastern Siberian Sea coming from the Long Strait along Chukotka Peninsula and the biogen-rich cooled waters of the Gulf of Anadyr and Bering Sea shelf entering the Chukchi Sea through the eastern part of the Bering Strait [31]. At the exit from the Bering Strait, to the north off Chukotka Peninsula, these currents collide with each other, thus giving rise to water gyres moving in a northwestern direction [5]. Let us mention here that there is no agreement between hydrologists about the movement of the gyres in a northwestern direction. Ratmanov [15] believed that other gyres could arise independently of the great gyre, in the area farther to the northwest. All these gyres are cyclonic; they elevate biogen-rich bottom waters to the surface, which also benefits the increase in primary production. The gyres prevent the drift of larvae beyond the borders of their parental populations and also retain and accumulate the major food items of benthic organisms, living and dead phyto- and zooplankton and fecal masses located above the bottom populations. The bulk of primary production produced by phytoplankton in the southeastern Chukchi Sea is probably consumed by benthos within the above-discussed community of *M. calcarea*, where the mean biomass of the benthos exceeds 1000 g/m^2. In this case, the rich bottom community of *Macoma* functions as an accumulator of organic matter and biogens. The gyres moving to the northwest evidently are already depleted of biogens and phytoplankton, therefore the biomass of the benthos outside the *Macoma* community is significantly smaller and equals 200–300 g/m^2. Unfortunately, we do not have enough data about benthos distribution in the central and western Chukchi Sea to be able to corroborate this idea.

According the data of American colleagues [23], in the northeastern Chukchi Sea many stations were also dominated by bivalve mollusks (mostly *Ennucula tenuis* and *M. calcarea*). However, the population density of these animals did not exceed 880 specimens/m^2, averaging 248 specimens/m^2. In the *Macoma*-dominated area that we surveyed, the population density of mollusks reached 9820 specimens/m^2 (with an average of 2352 specimens/m^2) (Table 3), which is an order on magnitude greater than the values reported by our American colleagues. Such large values of population density and biomass of benthos (at Stn. 13 they exceeded 11000 specimens/m^2 and 4000 g/m^2 respectively) are not characteristic of benthos communities inhabiting soft bottoms, even in temperate zones of the World Ocean, while for the Arctic they were registered for the first time.

Evidently, these are the aggregations of bivalve mollusks that attract walruses to the area. The Pacific walrus *Odobenus rosmarus divergens* mostly feeds on mollusks and *Macoma* occupies the first place in its diet [11] or one of the first places [14]. The same phenomenon was also reported by American biologists for the northeastern Chukchi Sea [27]. Every year, during seasonal migrations, giant schools of walruses migrate in the spring and in early summer from the Pacific, along the northern coast of Chukotka, toward Long Strait and Vrangel Island; the return migration takes place in autumn. During the migrations the walruses perform long-term stops on so-called temporary regular rookeries located at the Serdtse-Kamen' Cape and in the neighboring zones, just in front of the areas occupied by the communities of mollusks. In these areas the animals are battening, diving down more than 50 m deep to feed on mollusks [1].

The findings of relatively warm-water Pacific invaders (the crabs *Telmessus cheiragonus* and *Oregonia gracilis* and bivalve mollusk *Pododesmus macrochisma*) provide evidence in favor of the hypothesis that the warming, which was discussed by Ushakov [19] using materials collected in the early 20th century, still continues in the Chukchi Sea.

The bivalve mollusk *P. macrochisma* is widely distributed in the Northern Pacific, from the Sea of Japan and California to the Commander and Pribylof Islands in the southern Bering Sea, from intertidal zone down to 150 m deep [16]. The first specimen (one waterworn shell valve) of this mollusk from the Chukchi Sea, found in the coastal zone of Wainwright (Northern Alaska, 70°6′N) was deposited in the collections of the Californian Academy of Sciences in San Francisco [22], but unfortunately it has no sampling date. The second specimen was found in 1991 [28] at the coast of Alaska (68°28′N, 166°38′W—from a personal communication of Nora Foster on January 8, 2006). In 2004 two living specimens and one shell valve of *P. macrochisma* were collected with a trawl and bottom grab sampler at Stn. 17 located close to Point Hope. These findings might be considered as putative evidence of climate warming in the eastern Chukchi Sea that benefits the penetration of larvae of Pacific species to the north.

The crab *T. cheiragonus* is widely distributed in the Pacific, from Hokkaido and California to the northern Bering Sea, in depths from 0 to 50 m [2]. In the Chukchi Sea it was registered for the first time in 1976, at several stations in the southeastern part, from the Bering Strait, along the northern coast of the Seward Peninsula, in Kotzebue Sound and to the north, up to Kivalina (68°N) [26]. In 1988 *T. cheiragonus* was captured at the entrance to Kotzebue Sound (Stn. 66, RV *Akademik Korolev*). The third finding comprised 3 specimens found in a sample from Stn. 17, close to Point Hope (68°17′N, RV Professor Khromov), which was farther to the north compared with the previous findings. The latter finding expands the geographic range of this species to the north, which also can be considered as evidence of climate warming in this part of the Chukchi Sea.

The crab *O. gracilis* is widely distributed in the northern Pacific, from northern Japan and California to the Commander Islands and Nunivak Island in the Bering Sea, from the intertidal zone down to 390 m deep [2]. The first finding of *O. gracilis* in the Chukchi Sea, at Point Hope (Stn. 17, RV *Professor Khromov*, 2004) significantly expands the geographic range of this species to the north and can be considered as evidence of climate warming.

It is pertinent to note that along with these three rare and large species, the recent expeditions of 1988, 1989, 1995, and 2004 revealed for the first time in the Chukchi Sea several tens of Pacific polychaetes (the data of S.Yu. Gagaev, ZIN RAS), crustaceans (S.V. Vasilenko, ZIN RAS, pers. comm.), mollusks (the data of B.I. Sirenko), bryozoans (N.V. Denisenko, pers. comm.), and other small animals. Some of these animals could have penetrated into the Chukchi Sea in recent years, which could also be considered as expansion of the geographic ranges of relatively warm-water animals due to climate warming. However, we cannot say with certainty that these animals did not inhabit the Chukchi Sea earlier, as small animals could have been overlooked during earlier investigations. As regards the bivalve mollusk *P. macrochisma* and crabs *T. cheiragonus* and *O. gracilis*, these are rather large animals that can easily be collected with trawls. Judging from the rather dense network of trawling stations performed in the Chukchi Sea around Alaska during the American expeditions of 1970–1974, 1976, 1980, 1986, 1987, and 1991 [24–27, 35], the epifauna of this region should be studied in detail. The presence of the two species mentioned above in a single trawl sample (*P. macrochisma*) or in a few samples collected at the extreme south of the southeastern Chukchi Sea (*T. cheiragonus*) could be evidence of their great rarity in the surveyed region. The absence of the crab *O. gracilis* in all the numerous samples collected prior to 1991 demonstrates, in all likelihood, that this species has penetrated into the Chukchi Sea only in the recent years.

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