

UDC 574.587.015(268.45)

## BARENTS SEA MEGABENTHOS: SPATIAL AND TEMPORAL DISTRIBUTION AND PRODUCTION

© 2020 D. V. Zakharov<sup>1,2</sup>, L. L. Jørgensen<sup>3</sup>, I. E. Manushin<sup>1</sup>, and N. A. Strelkova<sup>1</sup>

<sup>1</sup>Polar branch of VNIRO (“PINRO” named after N. M. Knipovich), Murmansk, Russian Federation

<sup>2</sup>Murmansk Marine Biological Institute RAS, Murmansk, Russian Federation

<sup>3</sup>Institute of Marine Research, Tromsø, Norway

E-mail: [zakharden@yandex.ru](mailto:zakharden@yandex.ru)

Received by the Editor 11.10.2019; after revision 07.05.2020;  
 accepted for publication 26.06.2020; published online 30.06.2020.

This long-term observation of the faunal composition within the Barents Sea provides a benchmark for monitoring community changes caused by oceanographic variability, fishery activities, and crab predators (*Chionoecetes opilio*, *Paralithodes camtschaticus*), whose populations have been rapidly growing and spreading in recent years. In the Arctic systems, megabenthic communities comprise a significant part of benthic biomass and play an important role in carbon cycling on continental shelves. The gradual accumulation of knowledge on megabenthos may make it possible to assess their role in the ecosystem and ultimately contribute to a more rational management of the Barents Sea resources. This article represents an important series of long-term megabenthic observations in the Barents Sea. The main goal of our research is to identify spatial patterns and temporal trends in the megabenthic part of communities, including changes in the biomass and production values. As a part of the joint Norwegian-Russian ecosystem surveys, benthic experts have been identifying the invertebrates (megafauna) collected by bottom trawls during annual assessments of commercial stocks, such as Atlantic cod (*Gadus morhua*) and northern shrimp (*Pandalus borealis*). The sampling equipment used was a Campelen 1800 bottom trawl, rigged with rockhopper ground gear and towed on double warps, and standardized to a fixed sampling effort (equivalent to a towing distance of 0.75 nautical miles (nm), or 1.4 km). The processing of the biological material was conducted in accordance with standardized procedures, following the retrieval of each trawl. This work represents data from 5016 stations from 2005 to 2017, with a total sampled biomass of 238.4 tons and 14.9 million individual organisms. In total, 694 megabenthic species (1058 taxa) have been recorded, with the greatest diversity observed in the depth range of 100–400 m, while the largest mean catches were taken between depths of 600–800 m. The biomass (B) and production (P) values of the benthic megafauna were approximately stable during the 9 years of investigation, although there was a decreasing trend after 2014. The annual production P/B ratio of megabenthos was calculated to be at 0.3. The distribution, contribution to production, and gross biomass values of the megabenthos had been underestimated in the previous studies of zoobenthos. The results from this research show that, in the current warm period, the majority of the Barents Sea is in an intermediate state between the Arctic and boreal regions due to the wide distribution of boreal species toward the north. The dynamics of the mean biogeographical index (the border between areas of the dominance of boreal and Arctic species) within the central-southern part of the Barents Sea suggests that a large part of the area can be characterized as predominantly boreal intermediate since 2013.

**Keywords:** Arctic, Barents Sea, megabenthos, climate, Atlantic Current, production, species distribution

The effects of global climate change have been particularly noticeable in the Arctic, causing a restructuring of Arctic ecosystem [19 ; 25 ; 33] and a northward shift of biogeographical boundaries as a consequence of warming [5 ; 6 ; 10 ; 12 ; 18 ; 21].

In the Arctic systems, megabenthic communities comprise a significant part of benthic biomass [7 ; 30] and play an important role in carbon cycling on continental shelves [23 ; 32]. Marine benthic communities are well-suited for long-term comparative investigations, as comprising species have a relatively long lifespan and either are sessile or have low motility. These traits make it possible to measure the effects of environmental change on communities over time. The potential impact of climate change on the marine environment may be acute, but it is difficult to register due to the lack of baseline data. A recent analysis showed that 34–59 % of Arctic megafauna taxa have yet to be documented [45].

The Barents Sea is a continental shelf sea with an average depth of 230 m (Fig. 1a); it is characterized by a transitional zone from warm Atlantic waters to cold Arctic ones (Fig. 1b) [43 ; 44]. Substantial climatic changes have been observed during the last four decades [8 ; 47]. Water temperatures in the subarctic Barents Sea during the past decade have reached the highest rates over the period observed [8]. Ice coverage has declined by about 10 % [4], while water temperature has risen by approximately 1.5 °C [35]. The area covered by the warmer Atlantic water has increased [28] due to northward shifts in the polar front, where Atlantic and Arctic water masses meet [43].

Analysis of Barents Sea benthic megafauna shows clear biogeographical patterns, with an Arctic productive community dominating in the northeast [11] and occasionally in the northwest, and an Atlantic warm water community in the southwest [29 ; 30]. A deep-cold-water community is found in the northwestern part of the Barents Sea shelf. A shallow bank community is predominant on the Spitsbergen Bank located southwards of Spitsbergen and in the southeastern Barents Sea. This shallow bank community is also found sporadically west and north of Spitsbergen [30].

It has been suggested that climate change is causing a northward shift of biogeographical boundaries in the northern hemisphere due to the warming process [21]. The number of boreal species has increased, while the number of arctic species have declined [31]. The range of some species has expanded, and new boreal-subtropical species have appeared in the Arctic [52 ; 53].

The gradual accumulation of knowledge on megabenthos may make it possible to assess its role in the ecosystem and ultimately contribute to a more rational management of Barents Sea resources. This article presents an important series of long-term megabenthic observations in the Barents Sea. The main goal of our research is to identify spatial patterns and temporal trends in the megabenthic part of communities, including changes in biomass and production values.

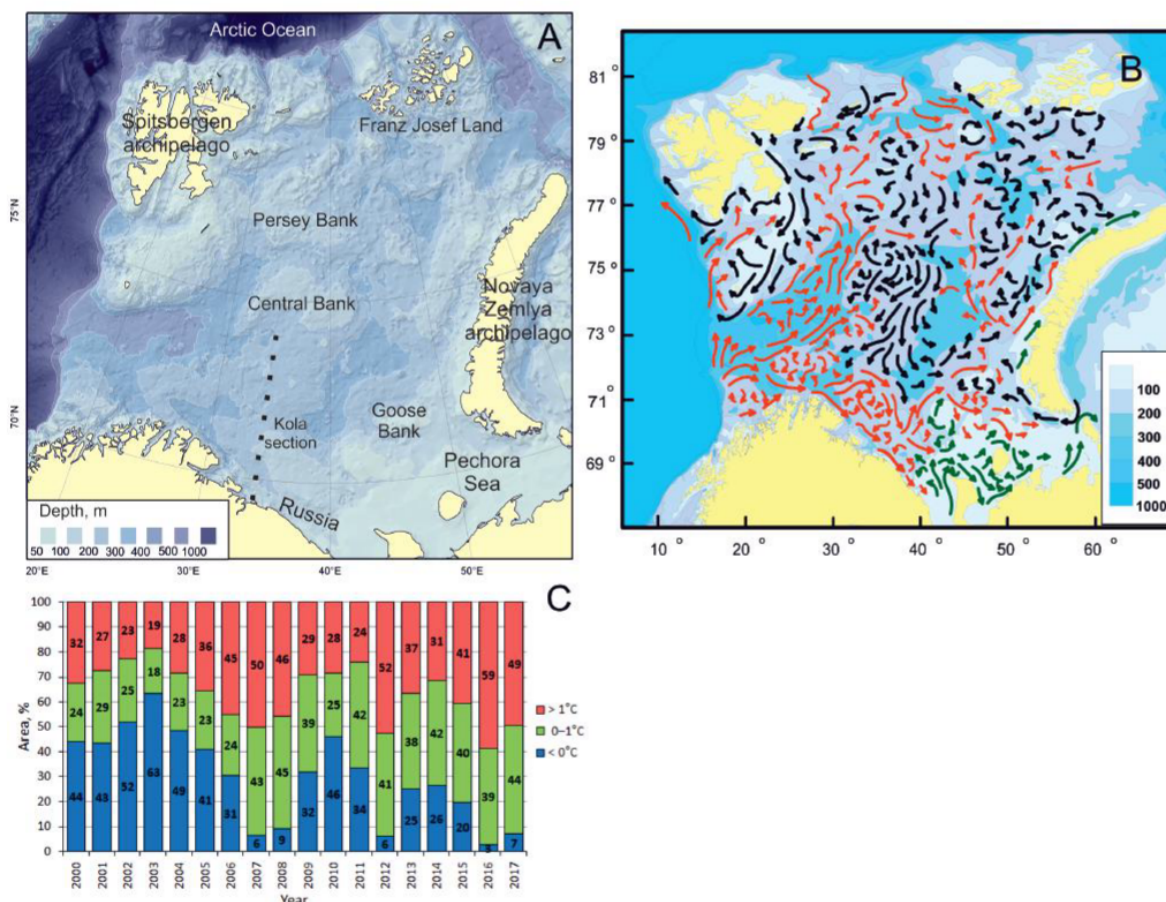
## MATERIAL AND METHODS

**Benthos sampling.** Norwegian and Russian ships were used to survey the Barents Sea annually August to November. Sampling stations were established at fixed positions along a regular grid (around 35 nautical miles between each station), covering an area of about 1.5 million km<sup>2</sup>. The sampling equipment used was a Campelen 1800 bottom trawl, rigged with rockhopper ground gear, towed on double warps, and standardized to a fixed sampling effort (equivalent to a towing distance of 0.75 nautical miles, or 1.4 km). The horizontal opening was 15 m, and the vertical one was 5 m. The mesh size was 80 mm (stretched) in the front and 22 mm in the cod end, allowing capture and retention of vertebrates (fishes) and large invertebrates (megabenthos) from the seabed. All catch data presented in the article have been standardized to 1 nautical mile (hereinafter nm).

**Data.** Benthos specialists from the Polar branch of VNIRO (Russian and Norwegian ships), Institute of Marine Research, Murmansk Marine Biological Institute, and other international institutions (Norwegian ships) were involved in the processing and identification of benthos collected by the scientific trawl during the annual Norwegian-Russian Ecosystem Survey [1].

The processing of the biological material was conducted in accordance with standardized procedures, following the retrieval of each trawl [30]. The invertebrates were separated from the vertebrate catch in the onboard fish laboratory. Depending on catch weight, the material was processed in total or as a subsample. Records were made using paper datasheets, to be entered into a database afterward.





**Fig. 1.** The Barents Sea, with: A – a map showing place names and depth contours; B – a map of bottom water currents with arrows showing: 1) the main streams of Atlantic water (red), 2) coastal currents (green), and 3) cold Arctic currents (black) [49]. C – % of areas covered by water with different bottom temperatures in the Barents Sea (N71–79°, E25–55°) (August to September in 2000–2017) [26]

**Рис. 1.** Баренцево море: А — карта с указанием топографических названий и глубин; В — карта придонных течений, красные стрелки показывают основные потоки Атлантического течения, зелёные — прибрежные течения, чёрные — холодные арктические течения [49]. С — соотношение площади дна с различной придонной температурой воды в Баренцевом море (71–79° с. ш., 25–55° в. д.) в августе — сентябре 2000–2017 гг. [26]

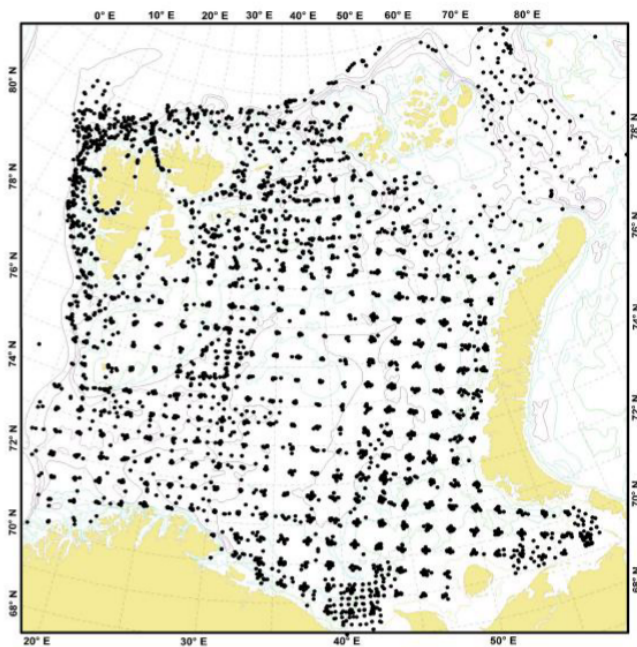
The total subsample weight was used to determine the adjustment factor in order to represent the full catch. All large (> 100 g) species, as well as rare megabenthic ones, were taken from the total catch, while the remaining species were extracted only from the subsample.

Most of the taxonomic processing was undertaken onboard to the lowest possible taxon. In cases of identification difficulties, the species were photographed and/or preserved for further processing by taxonomic specialists on land. In order to develop standardized species identification across all involved ships and throughout the entire research period, the naming of all the species was checked using photographs of each processed catch since 2013.

Following identification, the number of individuals of each species or taxon was counted, and wet weight was measured on electronic balances ( $\pm 0.5$  g).

Totally, 5016 stations were sampled between 2005 and 2017 (Fig. 2). The total sampled biomass of benthic megafauna was 238.4 tons, consisting of over 14.9 million individuals. Some individuals were assigned to the genus or higher taxonomic level due to difficulties with their species identification. The final

list included 1058 taxa, of which 694 were identified to species onboard (Table 1). As the Campelen trawl is designed to catch northern shrimp (*Pandalidae* family), this semipelagic shrimp could be overestimated in the data, and therefore it was excluded from the analysis and used only for megabenthic data smoothing. Similarly, all pelagic species, such as jellies (Scyphozoa), were also excluded from the analysis. Values are presented as mean  $\pm$  standard error (hereinafter *SE*) unless otherwise stated.



**Fig. 2.** Location of 5016 trawl stations covered during 2005–2017 by the joint Norwegian-Russian Ecosystem Survey

**Рис. 2.** Положение 5016 донных траловых станций, выполненных в ходе проведения норвежско-российских экосистемных съёмок в 2005–2017 гг.

**Table 1.** Summary of the analyzed megafauna from the joint Norwegian-Russian Ecosystem Survey (2005–2017)

**Таблица 1.** Объём материала, проанализированного в экосистемных съёмках 2005–2017 гг., и его основные характеристики

Year	Number of stations	Total		Average abundance (ind.·nm <sup>-1</sup> )	Average biomass (kg·nm <sup>-1</sup> )	Amount	
		Abundance (ind.)	Biomass (tons)			species	taxa
2005	224	107,114.0	2.6	522.5	12.7	142	218
2006	637	964,569.0	25.9	1576.0	42.1	261	388
2007	551	633,761.5	22.9	1240.2	44.6	222	351
2008	431	901,885.1	14.8	2183.7	35.7	157	244
2009	378	769,129.3	15.9	2056.4	42.2	283	391
2010	319	285,322.8	8.6	900.0	27.3	273	360
2011	391	1,333,887.2	13.4	3411.4	34.3	282	442
2012	443	4,345,807.4	55.6	9832.1	125.5	354	513
2013	487	1,888,138.0	34.8	3885.0	71.7	362	538
2014	165	463,108.6	6.0	2806.7	36.7	220	333
2015	334	606,272.4	6.6	1815.1	19.9	398	599
2016	317	1,340,958.8	11.5	4230.1	36.3	266	423
2017	339	1,277,828.3	19.8	3769.4	58.6	319	500
<b>Total</b>	<b>5016</b>	<b>14,917,782.4</b>	<b>238.4</b>	<b>2940.7*</b>	<b>45.2*</b>	<b>694</b>	<b>1058</b>

**Note:** \* indicates the mean value across all years.

**Примечание:** \* — среднее значение за все годы.



To determine whether there were any temporal differences in abundance and smoothed mean biomass among megabenthic fauna across the Barents Sea, the mean values per grid cell (N0.5°, E2°) were calculated both for early (2005–2011) and late (2012–2017) time periods of the study (see Figs 8 and 9).

**Data smoothing.** An examination of megabenthic biomass values in the Barents Sea indicated extensive inter-annual variations (Table 1). Therefore, the following steps were taken to minimize the chances of a possible sampling error and a distortion of results: 1) data collection was restricted to the area between N68–80°, E15–62° in order to exclude sectors covered only occasionally; 2) catches of > 1 ton were excluded; 3) shrimps of the Pandalidae family were excluded from the overall calculations and analyzed separately because all species of this family are benthopelagic, and the Campelen trawl possesses high catchability for such shrimps [51].

A smoothing function was constructed using a second-degree polynomial equation that was considered to minimize fluctuations in megafauna data. This was done for both Russian and Norwegian data samples, followed by a merge into a consolidated database. The smoothing procedure was conducted in three steps: 1) smoothing Pandalid data; 2) smoothing sessile epifauna data; 3) smoothing data of two other ecological groups (mobile epifauna and infauna).

The smoothing of Pandalid shrimp annual biomass data showed that the majority of shrimp biomass values had insignificant variations when compared to the smoothing curve. From the adjusted Pandalid values, correction coefficients were used to adjust the sampled biomass data of other taxa.

After this process, the megabenthic biomass was divided into three categories: “sessile epifauna”, “mobile epifauna”, and “infauna”. Because epifauna biomass fluctuated more than biomass of Pandalid shrimps, a second correction coefficient derived from the second-degree polynomial equation was calculated in the same way as for Pandalid shrimp biomass.

For mobile epifauna and infauna, the real values were divided by the second correction coefficient. Thereafter, modified biomass values of the mobile epifauna and infauna were smoothed in the same way. Smoothed data were used for further analysis in special cases, which are discussed below.

**Production** was calculated by multiplying taxon biomass by production to biomass (P/B) ratio. Two types of P/B ratio were used. The first was calculated for the major taxonomic groups from Degen *et al.* [11], and the second was calculated from the Manushin formula [37] (Table 2), except for taxa Porifera, Cnidaria, and Bryozoa, that were taken from Degen *et al.* [11]. Community production was calculated from the summarized production value of each taxon/species per station.

**Table 2.** Equations describing the dependence of the P/B ratio on mean body weight ( $\bar{W}$ , g of wet weight) for different taxa

**Таблица 2.** Уравнения, описывающие зависимость коэффициента P/B от средней массы тела ( $\bar{W}$ , г сырой массы) для разных таксонов

Taxon	Equation
Annelida	$P / B = 0.365 \times \bar{W}^{-0.377}$
Arthropoda	$P / B = 2.190 \times \bar{W}^{-0.276}$
Chordata	$P / B = 0.073 \times \bar{W}^{-0.579}$
Echinodermata	$P / B = 0.730 \times \bar{W}^{-0.342}$
<b>Total</b>	$P / B = 0.694 \times \bar{W}^{-0.390}$

**Biogeographical analysis.** The biogeographical status of the Barents Sea can be assessed by determining the boundary lines between the Arctic and boreal communities at different points in time. The fluctuation of these boundary lines over time reflects the effects that water temperature changes have on benthic fauna. Here the Biogeographical Indices (hereinafter BGI) [38] are used to show the ratio between the boreal and Arctic components of the fauna:

$$BGI = \frac{Bb - Ba}{Bb + Ba}, \quad (1)$$

where Bb and Ba are biomasses of the boreal and Arctic species, respectively.

Each species from the stations was placed into one of three biogeographical categories: “boreal”, “Arctic”, or “boreal-Arctic” [50]. Afterwards, all species classified as “boreal-Arctic” were excluded from further analyses, leaving only pure “boreal” and “Arctic” species to be used in the calculation of the boreal-Arctic ratio per station [46]. The station value of the BGI varied from  $-1$  (only Arctic species) to  $+1$  (only boreal species). In the case of absence or equal amounts of boreal and Arctic species, the BGI for a station is zero. The stations with such BGI values represent the hypothetical boundary line between the Atlantic boreal and Arctic biogeographical regions.

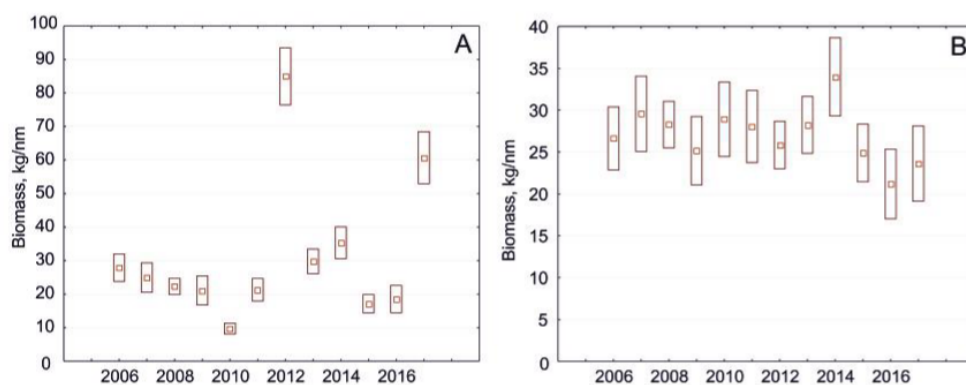
To illustrate the BGI distribution, the Barents Sea and adjacent waters were divided into grid cells ( $10^\circ$  long.,  $1^\circ$  lat.), and the mean values of all stations per grid cell over a 3-year period were calculated and used as input for the map.

To show the distributional dynamics of borderlines between areas dominated by either boreal or Arctic species (*i. e.*,  $BGI = 0$ ) 2005 to 2017, the centroid of each grid cell was used to plot the BGI in Map Viewer (Golden Software) [20]. The inverse distance to a power method was performed for gridding, and the moving average method was used for calculating the time series. Henceforth, the name “**boreal-Arctic boundary**” is used for the hypothetical boundary lines ( $BGI = 0$ ) between the Atlantic boreal and Arctic biogeographical regions.

Dynamics of boundary shifts in the region of  $N69-76^\circ$ ,  $E20-55^\circ$  2005 to 2017 was described using the BGI per cell over a 3-year period and calculated using the moving average method. The area delimited by  $N69-76^\circ$ ,  $E20-55^\circ$  was chosen for the analysis because it provided the most informative annual station coverage during the research period, with the exceptions being 2005 and 2014 due to the lack of data from the Norwegian participants of the study.

## RESULTS

**Biomass dynamics.** The mean biomass 2006 to 2017 was estimated to be  $31 \text{ kg}\cdot\text{nm}^{-1}$ . The mean biomass varied year to year, with the highest mean observed in 2012 ( $54 \text{ kg}\cdot\text{nm}^{-1}$ ) and the lowest one registered in 2010 ( $22 \text{ kg}\cdot\text{nm}^{-1}$ ) (Fig. 3A). The smoothed annual biomass reduced the maximum values of 2012 and 2017 considerably, resulting in a relatively stable curve, although variability increased after 2013, with the lowest biomass means observed in 2016 and 2017 (Fig. 3B). The average smoothed biomass 2006 to 2017 was estimated at  $27 \text{ kg}\cdot\text{nm}^{-1}$ , with annual means varying  $-6 \text{ kg}\cdot\text{nm}^{-1}$  in 2016 to  $+7 \text{ kg}\cdot\text{nm}^{-1}$  in 2014.

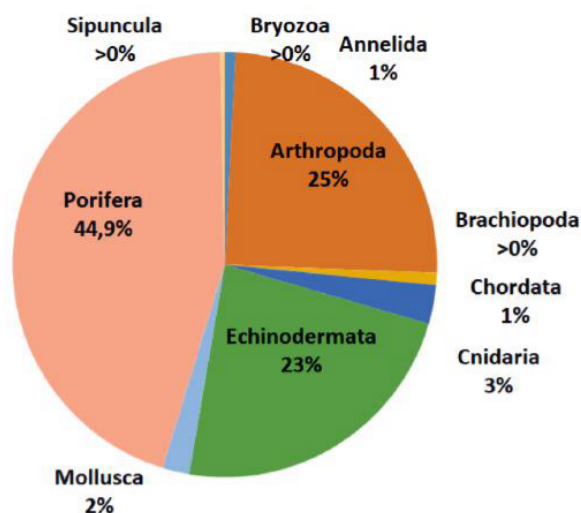


**Fig. 3.** Inter-annual variations in mean ( $\pm SE$ ) biomass ( $\text{kg}\cdot\text{nm}^{-1}$ ) in the Barents Sea for observed (A) and smoothed (B) data (2006–2017)

**Рис. 3.** Межгодовые изменения средней ( $\pm SE$ ) биомассы (кг на морскую милю) в Баренцевом море для наблюдаемых (А) и сглаженных (В) данных (2006–2017)



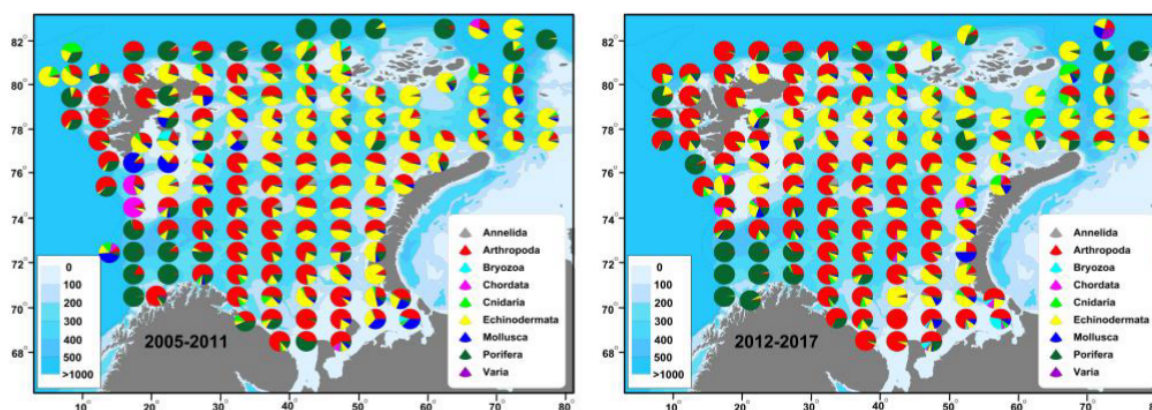
**Biomass of different taxa.** The surveys in the Barents Sea have revealed patterns in the distribution of the megabenthic fauna. For the region as a whole, Porifera biomass dominated the fauna, followed by that of Arthropoda and Echinodermata (Fig. 4).



**Fig. 4.** Biomass distribution of the main megabenthic groups from 2005–2017 trawl surveys in the Barents Sea

**Рис. 4.** Соотношение биомассы основных групп мегабентоса в Баренцевом море по результатам траловых съёмок 2005–2017 гг.

Patterns were also noted in the spatial distribution in phyla biomass within the survey area (Fig. 5). Porifera was predominant in the western and northern peripheral areas; Arthropoda was predominant in the central and northwestern areas, while Echinodermata dominated mostly at the northern stations of the Barents Sea. Cnidaria dominated in the deep stations in the northern periphery but also had a noticeable presence in several locations in the central Barents Sea. Chordata (mainly Ascidiacea) biomass was dominant sporadically but with no apparent pattern. Areas with even phyla distribution were particularly prevalent in the shallow areas of the Novaya Zemlya Bank (eastern Barents Sea), Spitsbergen (northwestern Barents Sea) and other bank areas, due to the diversity of biotopes and environmental conditions there.

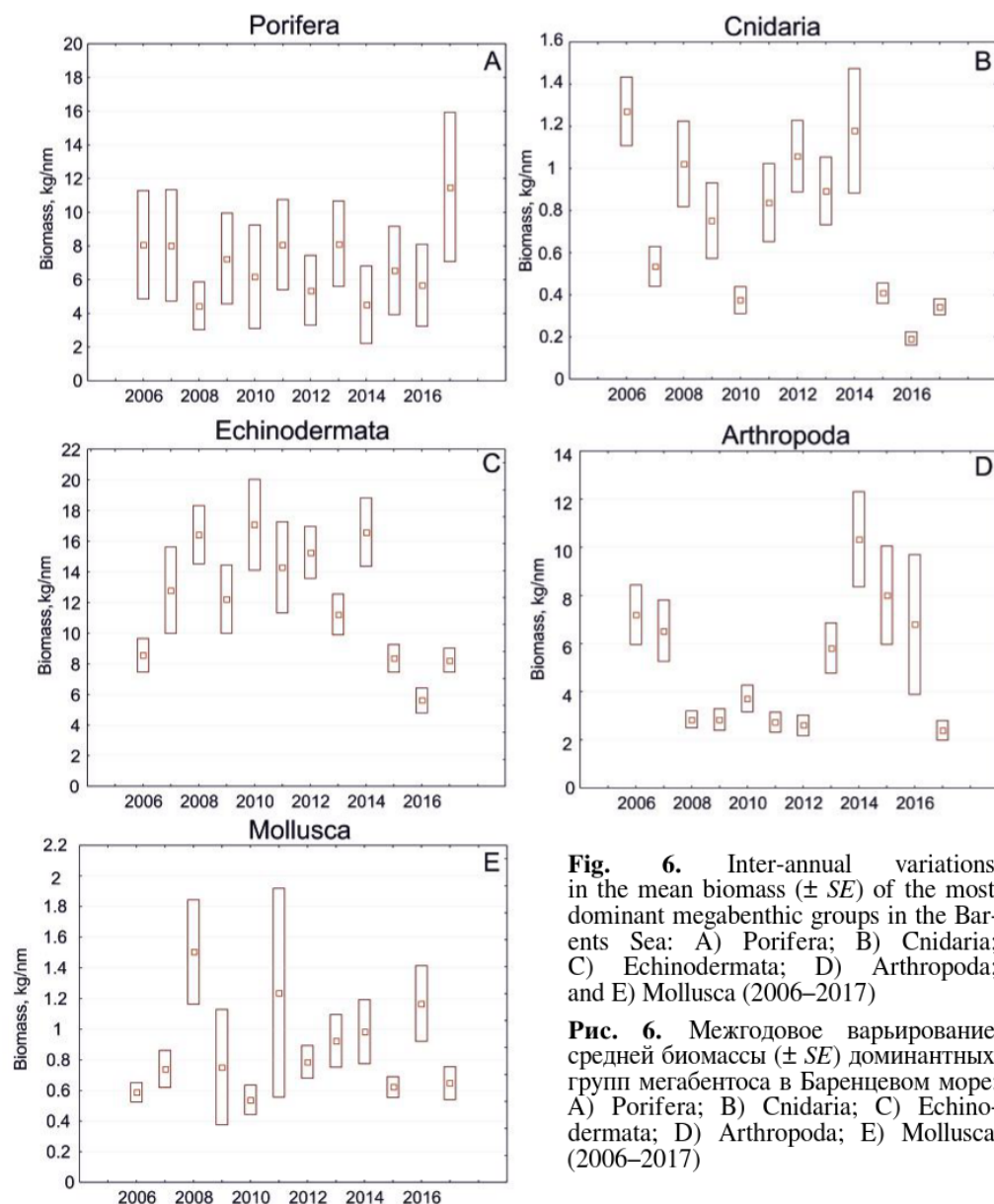


**Fig. 5.** Biomass distribution of the main phyla (Arthropoda, Echinodermata, Mollusca, and Porifera) and other groups (Annelida, Bryozoa, Sipuncula, Cnidaria, Chordata, and Brachiopoda) shown as mean values per grid cell (N1°, E5°) in 2005–2011 and 2012–2017

**Рис. 5.** Соотношение биомассы основных типов (Arthropoda, Echinodermata, Mollusca и Porifera) и других групп (Annelida, Bryozoa, Sipuncula, Cnidaria, Chordata и Brachiopoda) в генерализованном квадрате (N1°, E5°), данное в виде средних значений в 2005–2011 и 2012–2017 гг.

Several changes were observed in phyla dominance from the early period (2005–2011) to the late one (2012–2017). The northernmost stations, adjacent to the Arctic Ocean, shifted from being dominated by either Arthropoda or Echinodermata to becoming almost entirely dominated by Porifera. Along the west coast of Novaya Zemlya, the previously high diversity of phyla changed to domination by Arthropoda. Meanwhile, the central-eastern Barents Sea (N72–77°, E40–50°) has shifted from mostly Arthropoda to being dominated by Echinodermata.

Inter-annual variation in biomass (smoothed values) of five most dominant taxa revealed that Porifera remained relatively stable, except in 2017 when the biomass increased. The biomass of Cnidaria and Echinodermata experienced rapid decreases from 2015, while Arthropoda and Mollusca were more variable, ending with low values in 2017 (Fig. 6). Arthropoda and Echinodermata biomass were inversely related (linear regression is as follows: Echinoderm biomass =  $-1.4 \times$  Arthropod biomass + 19.1;  $R^2 = 0.64$ ).

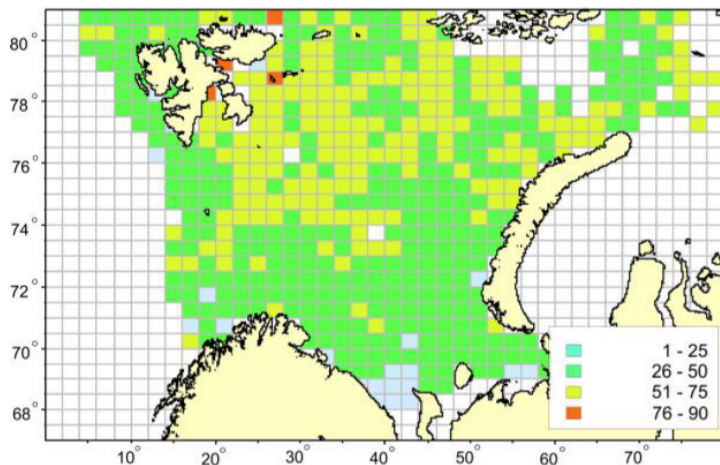


**Fig. 6.** Inter-annual variations in the mean biomass ( $\pm SE$ ) of the most dominant megabenthic groups in the Barents Sea: A) Porifera; B) Cnidaria; C) Echinodermata; D) Arthropoda; and E) Mollusca (2006–2017)

**Рис. 6.** Межгодовое варьирование средней биомассы ( $\pm SE$ ) доминантных групп мегабентоса в Баренцевом море: A) Porifera; B) Cnidaria; C) Echinodermata; D) Arthropoda; E) Mollusca (2006–2017)



**The number of species.** Species of the Barents Sea, presented as the mean number of species recorded during 2005–2017 (Fig. 7), had the highest values around Spitsbergen, while the lowest value was found in the northeastern region, which had the poorest coverage during the research period. However, low species diversity was also recorded in the southern areas of the Barents Sea that had experienced regular coverage as in the western and central areas of the sea.

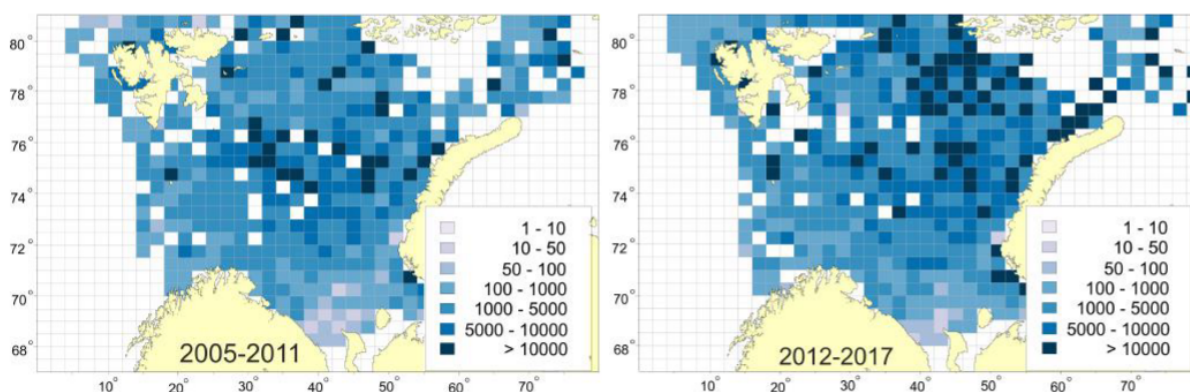


**Fig. 7.** Mean number of megabenthic species in the Barents Sea per grid cell (N0.5°, E2°) across the research period (2005–2017)

**Рис. 7.** Среднее количество видов мегабентоса в Баренцевом море в генерализованном квадрате (N0.5°, E2°) за период исследования (2005–2017)

**Abundance and biomass distribution during two time periods (2005–2011 and 2012–2017).** The mean abundance was generally similar for both periods (the early one –  $(5489 \pm 226)$  ind.·nm<sup>-1</sup>; the late one –  $(5023 \pm 363)$  ind.·nm<sup>-1</sup>). However, the maximum catch nearly doubled between the early and late periods: 388,000 to 793,000 ind.·nm<sup>-1</sup>. *F*-test shows that the differences between periods are statistically significant ( $F_{fact} (0.38) < F_{crit} (0.93)$ ; *p*-value = 0.0).

For both the early and late periods (Fig. 8), high mean abundances (up to 50,000 ind.·nm<sup>-1</sup>) were recorded in the central region of the Barents Sea. However, in the late period, high abundances were also frequently noted in the northeastern region. The lowest abundances were observed in the southern area, particularly around Cape Kanin Nos that had regular coverage, but also in the northwest in the early period with poor coverage.

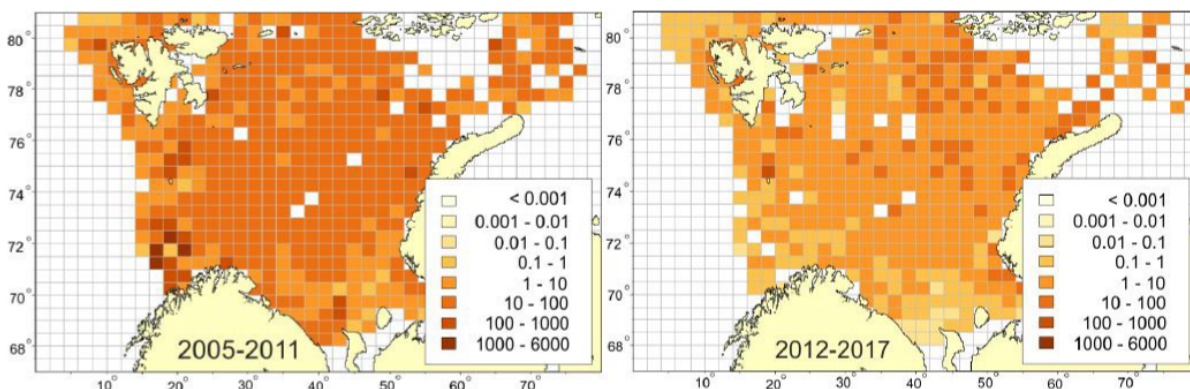


**Fig. 8.** Mean abundance (ind.·nm<sup>-1</sup>) per grid cell (N0.5°, E2°) for the early (2005–2011) and late (2012–2017) research periods

**Рис. 8.** Средняя численность (экз. на морскую милю) в генерализованном квадрате (N0.5°, E2°) для раннего (2005–2011) и позднего (2012–2017) периодов исследования

The smoothed mean biomass decreased both in the early and late periods:  $(70.6 \pm 6.6)$   $\text{kg} \cdot \text{nm}^{-1}$  in the earlier period to  $(63.0 \pm 6.2)$   $\text{kg} \cdot \text{nm}^{-1}$  in the later one (Fig. 9).  $F$ -test showed that these differences were statistically significant ( $F_{\text{fact}} (1.12) > F_{\text{crit}} (0.07)$ ;  $p$ -value = 0.0025). Meanwhile, the maximum catch increased  $8.5 \text{ t} \cdot \text{nm}^{-1}$  in the early period to  $9.8 \text{ t} \cdot \text{nm}^{-1}$  in the late one.

In the early period, the largest catches ( $> 1$  ton) were obtained in the southwestern part of the Barents Sea (Fig. 9) due to the abundant sponge fields in this area; these were intentionally avoided in the late period due to the risk of damage to the bottom fauna and the gear. While relatively large catches have been made within a large area of the central Barents Sea in the early period, similar catches were mostly observed in the northeastern part of the Barents Sea during the late period. Late period data showed that large areas of the southeastern Barents Sea had the lowest biomass amounts ( $< 1 \text{ kg} \cdot \text{nm}^{-1}$ ).



**Fig. 9.** Mean biomass ( $\text{kg} \cdot \text{nm}^{-1}$ , smoothed values) per grid cell ( $\text{N}0.5^\circ$ ,  $\text{E}2^\circ$ ) across 2005–2011 and 2012–2017

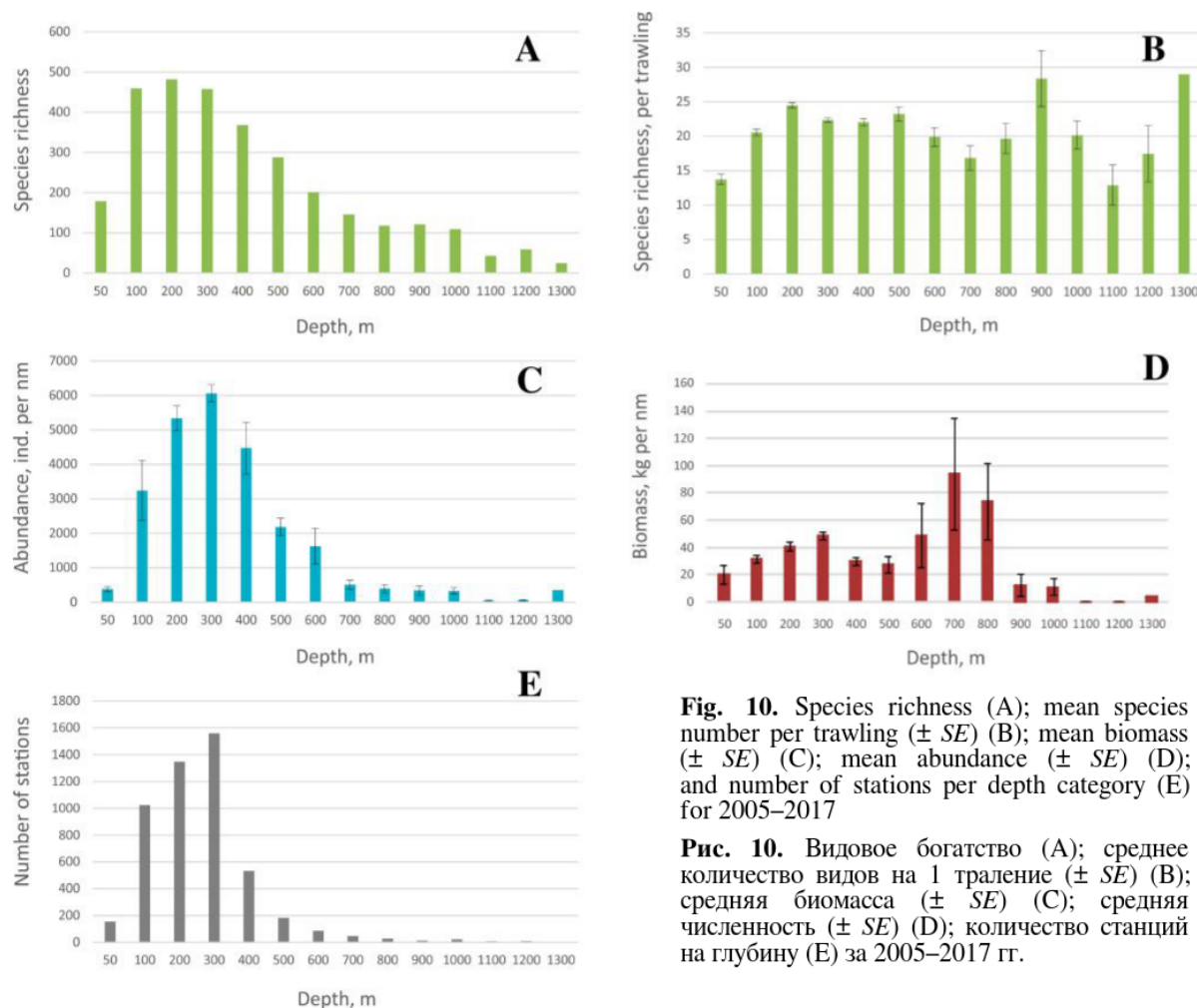
**Рис. 9.** Средняя биомасса (кг на морскую милю,глаженные значения) в генерализованном квадрате ( $\text{N}0.5^\circ$ ,  $\text{E}2^\circ$ ) в 2005–2011 и 2012–2017 гг.

The depth-related species richness, abundance, and biomass are shown in Fig. 10A, and a sampling frequency – in Fig. 10E. The highest sampling frequency and, therefore, more robust results were observed at 100–400-m depth. Stations shallower than 50 m or deeper than 600 m were less frequently sampled. In terms of species richness, the greatest diversity was seen at depths of 100–400 m (642 species), with lower richness on stations at  $\leq 50$  m (179 species) and a steady decline in richness at 500 m and deeper ( $\leq 347$  species). The largest biomasses (average catch  $> 100 \text{ kg} \cdot \text{nm}^{-1}$ ) were caught at 700-m depth, while the lowest biomasses ( $< 20 \text{ kg} \cdot \text{nm}^{-1}$ ) – at  $\geq 900$  m. The highest abundances were noted at 200–300-m depth (more than  $5000 \text{ ind} \cdot \text{nm}^{-1}$ ), while the lowest (less than  $500 \text{ ind} \cdot \text{nm}^{-1}$ ) took place at  $\leq 50$  m and  $\geq 700$  m.

**Production.** When comparing the results for calculating production (see Fig. 11), the inter-annual variation showed similar trends between two methods, but at different scales, with the Manushin values being almost twice as large as those obtained with using the Degen *et al.* method (Fig. 11). Inter-annual variations of average megabenthic production in the Barents Sea in 2006–2017 reached the highest in 2008 and 2014 and the lowest in 2017. Most years showed a range  $3\text{--}4 \text{ kg} \cdot \text{nm}^{-1} \cdot \text{year}^{-1}$  (Fig. 11A) with a mean of  $(3.6 \pm 0.6) \text{ kg} \cdot \text{nm}^{-1} \cdot \text{year}^{-1}$  or  $7\text{--}10 \text{ kg} \cdot \text{nm}^{-1} \cdot \text{year}^{-1}$  with a mean of  $(8.1 \pm 0.1) \text{ kg} \cdot \text{nm}^{-1} \cdot \text{year}^{-1}$  (Fig. 11B).

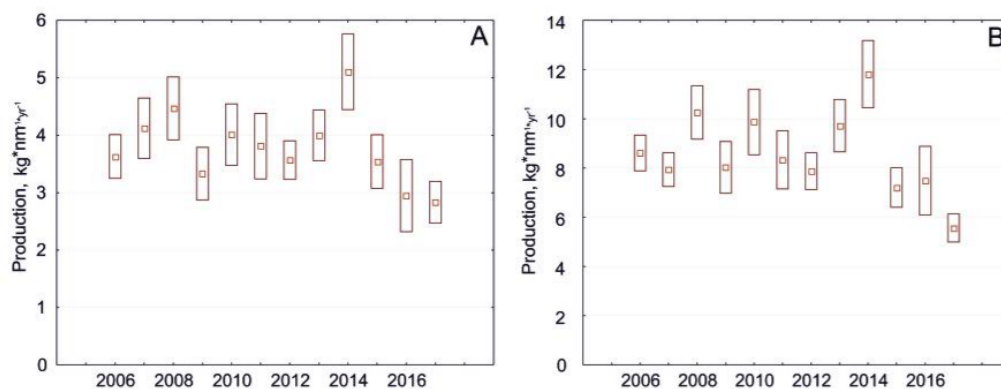
**The distribution of the Arctic versus boreal taxa of the Barents Sea.** The distribution of the BGI values (see “Material and Methods”) in the Barents Sea during 2005–2017 showed Arctic species dominating in the northern and eastern sectors of the Barents Sea, while the southern and western areas were dominated by the boreal species. These two regions are separated by a boreal-Arctic boundary line that has varied over time (Fig. 12).





**Fig. 10.** Species richness (A); mean species number per trawling ( $\pm SE$ ) (B); mean biomass ( $\pm SE$ ) (C); mean abundance ( $\pm SE$ ) (D); and number of stations per depth category (E) for 2005–2017

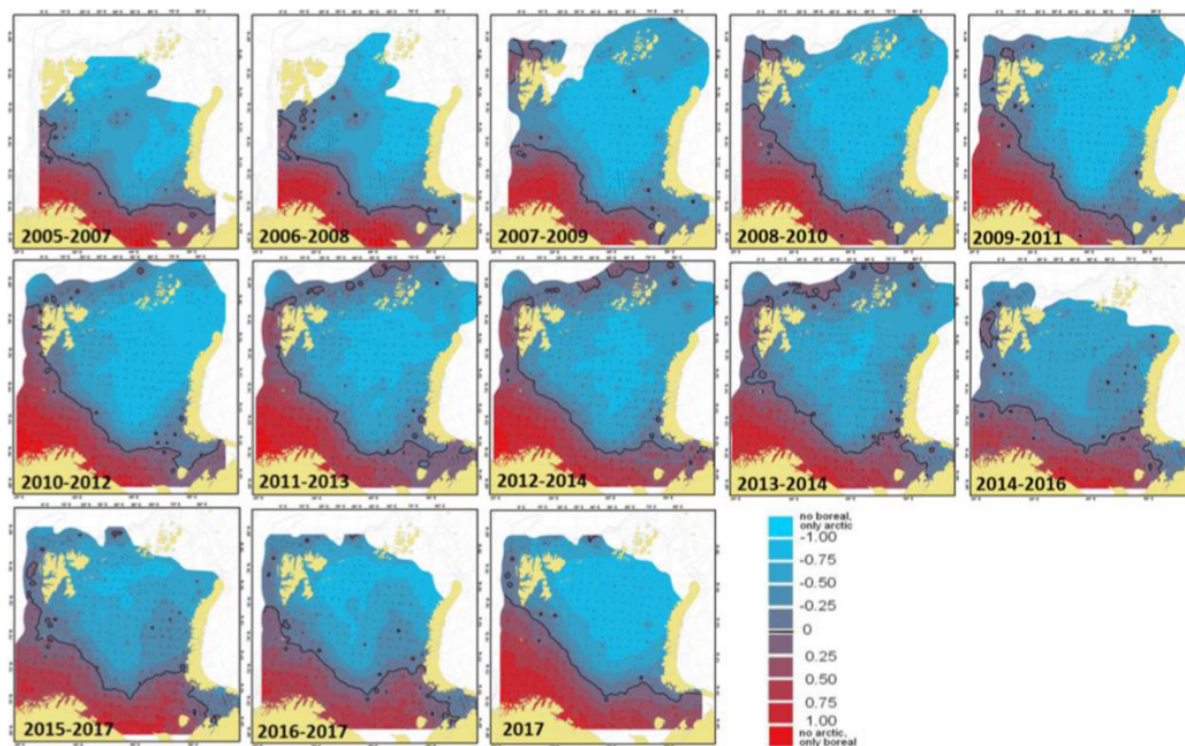
**Рис. 10.** Видовое богатство (A); среднее количество видов на 1 траление ( $\pm SE$ ) (B); средняя биомасса ( $\pm SE$ ) (C); средняя численность ( $\pm SE$ ) (D); количество станций на глубину (E) за 2005–2017 гг.



**Fig. 11.** Inter-annual variation of mean megabenthic production ( $\pm SE$ ) in the Barents Sea in 2006–2017 calculated with two different P/B ratios: A) Degen *et al.* [11] and B) Manushin [37]

**Рис. 11.** Варьирование продукции мегабентоса ( $\pm SE$ ) в Баренцевом море в 2006–2017 гг., рассчитанной с использованием двух разных коэффициентов P/B: A) по Degen с соавторами [11]; B) по Манушину [37]

The location of the boreal-Arctic boundary line closely follows three main currents of Atlantic water in the Barents Sea: along the western slope of the Barents Sea shelf, to the Central Bank, and along the western shelf of the Novaya Zemlya archipelago (see also Fig. 1A).



**Fig. 12.** Temporal distribution of the Arctic (blue) and boreal (red) areas of the Barents Sea (2005–2017). The black line shows the position of the boreal-Arctic boundary

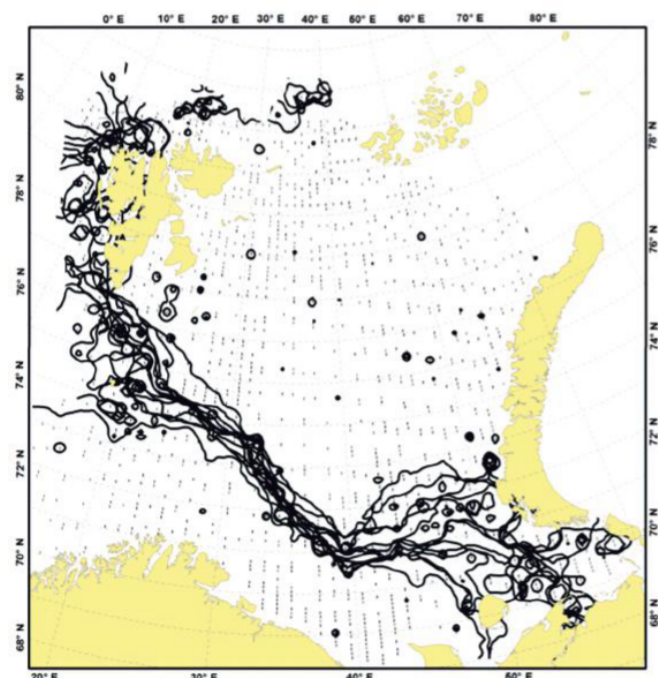
**Рис. 12.** Временное распределение арктических (синие) и boreальных (красные) областей в Баренцевом море в 2005–2017. Чёрная линия показывает положение boreально-арктической границы

The position of the boreal-Arctic boundary ( $BGI = 0$ ) varied between years and locations (Fig. 13). In the southeastern part of the sea, the positions of the boundary have changed spatially by approximately 150–200 nm during 2005–2017, around 150 nm on the Spitsbergen Bank, and less than 50 nm in the central part of the sea.

The inter-annual fluctuation in the boreal-Arctic boundary position is most distinctive in the southeastern part of the Barents Sea. The results show that the boundary moved towards the southwest (upper five pictures in Fig. 12) during 2006–2010, indicating a prevalent distribution of Arctic species over boreal, while over the course of the next six years (2011–2016) it moved back in a northwards direction.

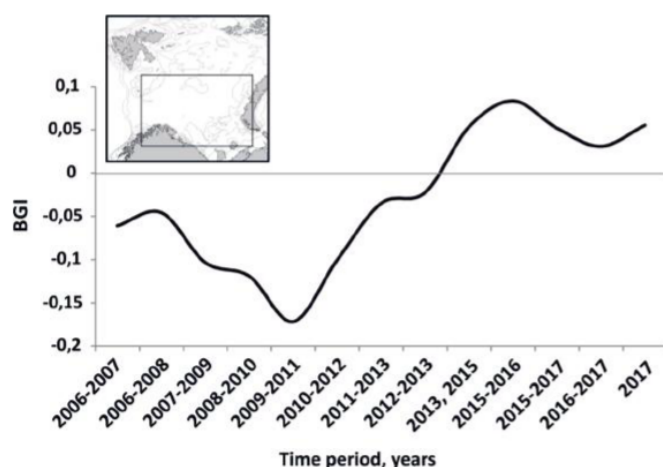
An area-based mean BGI for the central-southern part of the Barents Sea (Fig. 14) demonstrated a prevalence of Arctic species during 2007–2014, with a minimum value in 2010, followed by a prevalence of boreal species during 2014–2017. The years 2005 and 2014 are excluded from the calculation due to the lack of Norwegian data. The lowest and highest presence for boreal species in the constrained area is observed in 2010 and 2015–2016, respectively. Values below zero indicate the dominance of Arctic biomass, while values above zero indicate boreal dominance in the defined area (see embedded map in Fig. 14).





**Fig. 13.** Annual position of the boreal-Arctic boundary (BGI = 0) calculated 2005 to 2017

**Рис. 13.** Положение бореально-арктической границы (биогеографический индекс BGI = 0) в 2005–2017 гг.



**Fig. 14.** Temporal variation of the mean BGI calculated for the central-southern Barents Sea constrained by N69–76°, E20–55° (map embedded) (2006–2017)

**Рис. 14.** Варьирование среднего значения биогеографического индекса BGI, рассчитанного для акватории Баренцева моря, ограниченной N69–76°, E20–55° (карта встроена) (2006–2017)

## DISCUSSION

Throughout 13 years (2005–2017) of annual monitoring of the benthic megafauna, 21 % of 3245 species previously known [36] from Barents Sea, have been recorded. More than 5000 stations, 200 tons, and 14 million individuals of megafauna have been sampled. This achievement has become possible with using existing annual stock surveys, already being conducted by national governmental institutions, with the addition of benthic expertise, thereby making it possible to identify and evaluate the benthic by-catch from the commercial fish/shrimp trawl. It has proven to be a time- and cost-efficient approach for conducting long-term monitoring of the benthic habitats without additional seabed impact.

As the surveys were carried out using a trawl, animals in the catch were characterized by size as megabenthos [1]. Previous studies of zoobenthos mainly used material collected by grabs [15], but trawls and dredges of various design are better suited for sampling large invertebrates [17]. This was confirmed when studying the echinoderm fauna in the Kara Sea [2]. Taking into account the fact that the distribution,

contribution to production, and gross biomass of 694 species (1058 taxa) studied here have been previously undervalued, it is therefore assumed that zoobenthos in previous studies had not been fully taken into account.

In 2005–2014 (the first nine years of investigation), the mean biomass and production values of the benthic megafauna were mostly stable, but they tended to decline after 2014.

The spatial distribution of the biomass showed that the highest values of megabenthos were recorded on the continental slope in the areas of hydrological fronts where water masses meet [39 ; 40 ; 42]. Similar results have previously been obtained for macrobenthos in the Barents Sea [2 ; 9 ; 14 ; 15 ; 34 ; 41], indicating that the same environmental factors are structuring these two faunal components. Prior to the ecosystem survey of the Barents Sea, however, there was no data on the distribution of megabenthic organisms in the Barents Sea, thus making it difficult to compare megabenthic and macrobenthic parts of the communities.

The depth range of 100–300 m accounted for 65 % of sea area [34] and included 79.5 % of the total number of stations used in the ecosystem survey, meaning that the investigated area was approximately evenly covered by bottom trawling. The highest species variety was observed in the 100–400-m depth layer, and a reduction in the number of species coincided with an increase in depth. This is also in accordance with prior investigations of macrobenthos [24], and has previously been explained by the depletion of food resources [34]. However, the mean numbers of species per trawling (Fig. 10B) show that species diversity in general is remarkably high in both shallow coastal areas and deep sea of the investigated parts of the Barents Sea.

The largest average catches of megabenthic fauna were taken at a depth range of 600–800 m, along the continental slope of the western and northern parts of the Barents Sea. Communities of high benthic biomass (predominantly sponges) have previously been reported [9 ; 34] in the area of the warm Atlantic Current of the West-Spitsbergen branch [39 ; 40 ; 42] and in Saint Anna Trough near Franz Josef Land [22] where they filtrate water current for food particles.

The average biomass of Arthropoda was at its highest in 2006–2007, coinciding with the introduction of red king crab (*Paralithodes camtschaticus*) to the southern part of the Barents Sea, and in 2013–2016, when the population of snow crab (*Chionoecetes opilio*) rose dramatically in the eastern part of the Barents Sea. The decrease in crustacean catches in recent years is most likely related to the spreading of snow crab over a larger area and the beginning of fishing in the areas of its maximum concentrations in the eastern part of the Barents sea in 2016 [48], where up to 8,000 tons of crab are caught annually.

It can be suggested that the decline observed in the biomass of Cnidaria and Echinodermata after 2014, was caused by predation and competition from the snow crab. Echinoderms and cnidarians are frequently found in crab stomachs [54], which may indicate feeding on these animals by large populations of snow crab.

Apart from a few exceptions, the Mollusca biomass tended to increase until 2016. Taking into account only the area populated by snow crab, the average biomass of Mollusca has increased, while across the Barents Sea as a whole, biomass was stable, which suggests that snow crabs may have only a small influence on the Mollusca biomass.

Molluscs are one of the main macrobenthic groups in snow crab diet [54]. However, large molluscs with strong shells, that could be caught by trawls, were not present in its diet, which suggests that the biomass of large molluscs is driven by other factors.

Both methods used to calculate the inter-annual variation of the megabenthic production in the Barents Sea showed similar trends; however, the use of Manushin formula doubled the resulting values of production. Using the mean biomass ( $27 \text{ kg} \cdot \text{nm}^{-1}$ ), the annual P/B ratio was calculated to be 0.14 [11] and 0.3 [37]. There is a difference between the P/B ratio calculated by the Degen *et al.* method in this paper (0.14) and the value in the original article (0.15) [11]. This difference is explained by the selection of area of the Barents Sea (see “Material and Methods”), exclusion of catches > 1 ton, and the longer research period. It is assumed that the values obtained from the calculation with using the Manushin method [37]

are more realistic because his formula is based on taxonomic status and an individual average body weight of ectothermic animals. It could be suggested that Degen *et al.* [11] calculations had not taken into account small-sized groups of animals, due to the low catchability of small animals by the Campelen trawl. In Manushin formula [37], this underestimation is minimized because both available materials and author's own data are used to create production equation for a wide size range of animals. Similar results were obtained in a study of scallop (*Chlamys islandica*) near the Kola Peninsula, being a similar megabenthos size group, where P/B ratio was estimated to be 0.25 [13]. Comparing P/B ratio of macrobenthos (0.2–5.3; mean  $(1.44 \pm 0.06)$  [54]) and megabenthos (0.3), the level of megabenthic production seems to be realistic.

The boreal-Arctic boundary line in the Barents Sea (also called the biogeographical border between the Arctic and boreal regions) has been known since the mid-XIX century, but without general consensus of its position due to different criteria for setting the biogeographical boundaries [27].

The results from this research show that, in the current warm period, the majority of the Barents Sea is in an intermediate state between the Arctic and boreal regions due to the wide distribution of boreal species toward the north. Dynamics of BGI mean value within the central-southern part of the Barents Sea (see Fig. 14) suggests that since 2013, a larger part of the Barents Sea could be characterized as a predominantly boreal intermediate area. Moreover, it is suggested that the shift in the boundary line between the Arctic and boreal areas toward its most southern position in 2009–2011 may have been caused by the coldest year prior to the research period (2003, *i. e.*, six to eight years beforehand), resulting in the largest negative anomaly for the megabenthos biomass.

**Acknowledgement.** We acknowledge the joint Norwegian-Russian Ecosystem Survey of IMR and PINRO and all colleagues and staff on the ships, in the laboratories, and in the offices. We appreciate the help of Claude Nozères (Maurice Lamontagne Institute) and Stephen Long (Zoological Society of London) who made valuable corrections and remarks to the manuscript. We would like to thank the anonymous reviewers of the manuscript for useful comments.

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## МЕГАБЕНТОС БАРЕНЦЕВА МОРЯ: ПРОСТРАНСТВЕННО-ВРЕМЕННОЕ РАСПРЕДЕЛЕНИЕ И ПРОДУКЦИОННАЯ ХАРАКТЕРИСТИКА

Д. В. Захаров<sup>1,2</sup>, Л. Л. Йоргенсен<sup>3</sup>, И. Е. Манушин<sup>1</sup>, Н. А. Стрелкова<sup>1</sup>

<sup>1</sup>Полярный филиал ФГБНУ «ВНИРО» («ПИНРО» имени Н. М. Книповича),  
Мурманск, Российская Федерация

<sup>2</sup>Мурманский морской биологический институт РАН, Мурманск, Российская Федерация

<sup>3</sup>Институт морских исследований, Тромсё, Норвегия  
E-mail: [zakharden@yandex.ru](mailto:zakharden@yandex.ru)

Представлены результаты программы мониторинга мегабентоса Баренцева моря и сопредельных акваторий, выполняемой Россией и Норвегией с 2005 г. Мегабентос является одним из важнейших компонентов донной составляющей экосистемы Баренцева моря, формируя значительную долю живого вещества, включённого в пищевые цепи и систему экологических взаимоотношений. В частности, организмы мегабентоса играют существенную, а зачастую и определяющую роль в питании донных рыб и ракообразных Баренцева моря, в том числе важнейших промысловых видов: трески, пикши, камчатского краба, краба-стригуна опилио и др. Нередко представители данной группы формируют специфические биотопы, определяющие условия существования множества других видов животных. Постепенное накопление знаний о мегабентосе позволит оценить его роль в экосистеме и в конечном итоге поспособствует рациональному управлению ресурсами Баренцева моря. Основная цель нашего исследования — описать пространственное распределение и выявить динамику биомассы и продукции мегабентоса в Баренцевом море. С 2005 г. в рамках оценки запасов промысловых видов рыб и беспозвоночных проводится обработка прилова мегабентоса из донных тралений. За 2005–2017 гг. выполнено 5016 траловых станций, обработано 238,4 т валовой биомассы мегабентоса, просмотрено около 14,9 млн экз. животных. Материал собирали с помощью донного трала Campelen 1800 — низкоселективного активного сетного орудия лова, выполненного из капроновой дели с шагом ячеи 125 мм, с мелкоячеистой сетной кутовой вставкой с размером ячеи 22 мм и резиновым грунтопом типа «рокхоппер» с диаметром катков 40 см. Для удобства сравнительного анализа количественные параметры, представленные в статье, рассчитывали на стандартную дистанцию траления в 1 морскую милю (nm). Обработку материала проводили на борту судна непосредственно между постановками тралов. В ходе исследования зарегистрировано 694 вида мегабентоса; высокое видовое разнообразие зафиксировано



на глубинах 100–400 м, наибольшие средние значения биомассы и численности отмечены на глубинах 600–800 м. Биомасса (В) и продукция (Р) мегабентоса были стабильны на протяжении первых девяти лет исследований, но после 2014 г. появилась тенденция к их снижению. Значение коэффициента Р/В для мегабентоса оценивается на уровне 0,3. Предполагается, что предыдущие исследования бентоса в Баренцевом море недооценивали вклад как минимум 694 видов из группы мегабентоса в видовое богатство, валовую биомассу, численность и продукцию. Динамика биогеографического индекса (граница между бореальной и арктической зонами) в южной части Баренцева моря позволяет предположить, что с 2013 г. большую часть моря можно охарактеризовать как бореальную промежуточную область.

**Ключевые слова:** Арктика, Баренцево море, мегабентос, климат, Атлантическое течение, продукция, видовое богатство