1871
ИнБЮМ – IBSS

Морской биологический журнал
Marine Biological Journal
2024, vol. 9, no. 1, pp. 32–50
https://marine-biology.ru

UDC 594.58-15(268.45)

IMPACT OF THE RED KING CRAB AND THE SNOW CRAB ON THE BARENTS SEA MEGABENTHIC COMMUNITIES

© 2024 **D. Zakharov[1], I. Manushin[2], L. Jørgensen[3], and N. Strelkova[2]**

[1]Zoological Institute of Russian Academy of Sciences, Saint Petersburg, Russian Federation
[2]Polar branch of VNIRO (“PINRO” named after N. M. Knipovich), Murmansk, Russian Federation
[3]Institute of Marine Research, Bergen, Norway
E-mail: *zakharden@yandex.ru*

The work is devoted to problems of mutual adaptation of two invasive commercial crab species, the red king crab *Paralithodes camtschaticus* and the snow crab *Chionoecetes opilio*, and the recipient ecosystem of the Barents Sea. Data on the distribution of megabenthic communities obtained for 2006–2020 are provided. The dynamics of invasive crab populations is analyzed, and related changes that occurred in the Barents Sea bottom communities during this period are studied. Mechanisms of the impact of crab species on bottom communities and prospects for their colonization of the Barents Sea are discussed. The research is based on the results of quantitative and taxonomic analysis of bycatch in 6,010 bycatches with a Campelen 1800 trawl performed in the Barents Sea in 2006–2020 during the joint Russian–Norwegian ecosystem survey on RV of the Polar branch of VNIRO and the Institute of Marine Research. The expansion of the range and increase in abundance of the red king crab since the early 1990s led to its colonization of the vast area of the southern Barents Sea. In 2006–2010, this species dominated in megabenthic communities around the Murmansk Rise and Kaninskaya Bank. In 2016–2020, the red king crab spread north and east – up to the Kolguev Island and the southern slope of the Goose Bank. An increase in abundance of the snow crab resulted in its colonization of a huge area in the Barents Sea: from the Pechora Sea to the Franz Josef Land archipelago and from the Novaya Zemlya archipelago to the Spitsbergen archipelago. In 2006–2010, the snow crab abundance started to increase in the Novaya Zemlya archipelago area; there, it was a subdominant species in communities of soft sediments of the Goose Bank. In 2011–2015, the snow crab began to dominate in communities of the Goose and Novaya Zemlya banks and the northern Central Bank. At the same time, it continued to increase its role as a subdominant species in almost all megabenthic communities near the Novaya Zemlya archipelago. Later, in 2016–2020, this species dominated in benthic communities on the boundary with the Kara Sea between the Novaya Zemlya and Franz Josef Land archipelagos, on the slopes of the Novaya Zemlya Bank, near the Central Bank, and in the Southern Novaya Zemlya Trench. Its range increased and covered the area from the Franz Josef Land and Novaya Zemlya archipelagos to the Perseus Bank in the west and to the Pechora Sea in the south. As shown, under current climatic conditions, the red king crab will remain part of megabenthic communities in the southeastern Barents Sea. The snow crab will continue to migrate from the east to the western Barents Sea, up to the Spitsbergen archipelago, where similar benthic communities exist; in case of colder conditions, its migration will occur faster. A scenario is possible in which shallow waters of the Spitsbergen archipelago will be a new reproductive center of the snow crab population in the Barents Sea, along with the current center near the Novaya Zemlya archipelago.

Keywords: Barents Sea, megabenthos, bottom communities, red king crab, *Paralithodes camtschaticus*, snow crab, *Chionoecetes opilio*

Most benthic communities of large marine ecosystems, such as the Barents Sea, are subject to spatial and temporal transformation. Some of the key factors affecting their restructuring are climate fluctuations, interspecific competition, and anthropogenic load.

In the Barents Sea, such changes are studied for quite a long time and identified on the example of macrozoobenthos against the impact of climate and bottom trawling [Denisenko, 2003, 2007, 2013; Manushin, 2021a, b] and pressure from introduced species [Manushin et al., 2021; Strelkova et al., 2021; Zakharov et al., 2021b, 2022b]. Long-term data on bycatch of bottom invertebrates during ichthyological trawling are available, and differences are revealed between this part of the community and macrozoobenthos investigated using bottom grabs and dredges [Zakharov et al., 2021a]. So, the question arises on its response to external effects. In literature, benthos caught in ichthyological trawls is predominantly called megabenthos [Atlas of the Megabenthic Organisms, 2018; Gutt, Starmans, 1998; Jørgensen et al., 2022; Rybakova et al., 2019; Zakharov et al., 2020]; less commonly, it is called trawl macrobenthos [Kolpakov et al., 2018; Shuntov, Volvenko, 2015].

Recently, the emergence of new species on the Barents Sea shelf has become fairly common [Zakharov, Jørgensen, 2017]. As a rule, these are single findings, and the impact of such invaders on native communities is mostly local and limited. The exceptions are the red king crab *Paralithodes camtschaticus* (Tilesius, 1815) and the snow crab *Chionoecetes opilio* (Fabricius, 1788). Due to their size, these species can be classified as megabenthos; so, the investigation of their bycatch in trawl benthos is of certain interest when studying both their acclimatization and associated dynamics of benthic communities in the Barents Sea.

The introduction of the red king crab into the Barents Sea occurred more than 60 years ago [The Red King Crab, 2021]; the introduction of the snow crab, more than 25 years ago [Kuzmin et al., 1998; Snow Crab *Chionoecetes opilio*, 2016]. The expansion of the range and increase in the abundance of the red king crab since the early 1990s resulted in the fact that this species colonized a vast site of the southern Barents Sea. The range of the snow crab rose from the Goose Bank (one finding in 1996) to a broad area in the Barents and Kara seas and adjacent waters.

The nutrition of the red king crab and snow crab was properly analyzed, and this allowed both to describe their food spectrum in the Barents Sea and identify the most intensively consumed groups of animals [Manushin, 2021b; Snow Crab *Chionoecetes opilio*, 2016; Zakharov et al., 2021b, *etc.*]. With bycatch data from ichthyological trawls, one can assess the distribution of invasive crabs, their biomass in new areas, and possible effect on other megabenthic species. In this regard, the aim of this study is to reveal changes in the structure of megabenthic communities that have occurred over the past 15 years under the impact of the red king crab and the snow crab.

MATERIAL AND METHODS

Material for this work was sampled during annual Russian–Norwegian ecosystem survey in August–November 2006–2020 (Fig. 1A). The research covered the entire Barents Sea, the northwestern Kara Sea, the eastern sites of the Norwegian and Greenland seas, and adjacent areas of the Arctic Ocean. Trawls were mainly carried out within nodes of the standard grid of stations, with a distance between stations of about 40 nautical miles (Fig. 1B).

The material was sampled with a Campelen 1800 trawl [Atlas of the Megabenthic Organisms, 2018]. Within 2006–2020, 6,010 stations were performed. The material was processed onboard the RV by a unified technique [Zakharov et al., 2020, 2022a]. In total, 1,182 taxa were identified; out of them, 747 taxa were identified down to the species level. Animals were taxonomically identified to the lowest level possible. Material on the snow crab and red king crab was sampled since 2004. Data on nutrition of crabs were taken from previously published works [Manushin, 2021a; Zakharov et al., 2021b].

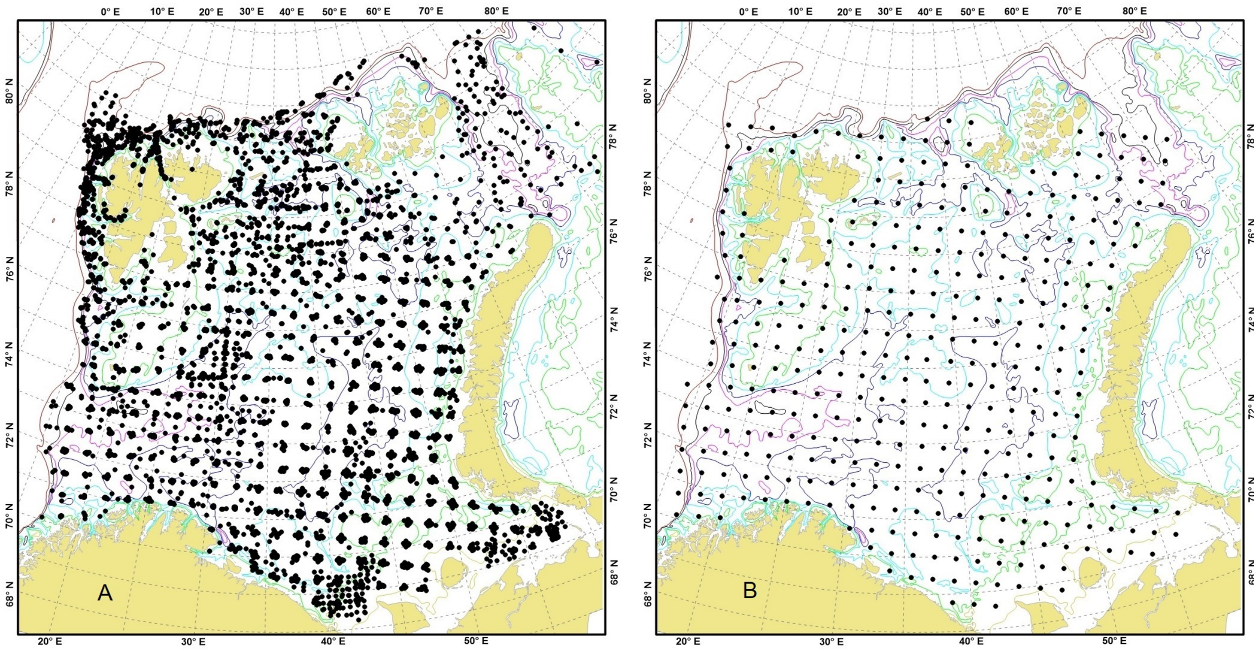

Fig. 1. Position of bottom trawls in 2006–2020 (A) and the standard grid of stations (B) in the joint Russian–Norwegian ecosystem survey

For comparative analysis, biomass values provided in this paper were calculated for a standard trawling distance of 1 nautical mile. Pelagic and benthopelagic species, *e. g.*, the northern shrimp *Pandalus borealis* Krøyer, 1838, were excluded from the dataset.

To estimate the changes in megabenthic communities over 15 years, this period was divided into three ones: 2006–2010, 2011–2015, and 2016–2020. Stations performed during each period and located at a distance of < 35 nautical miles from nodes of the standard grid (Fig. 1B) were combined for subsequent analysis. Stations situated at longer distances and not covered by the standard grid were excluded from the dataset. Each trawl point matched only one node of the standard grid of stations. The variation in depths between stations at nodes of the standard grid for each period averaged about 5 m.

The material obtained in different years during cruises of several RV and processed by researchers of various qualifications differed in the detail of taxonomic processing. Accordingly, to standardize the initial data and analyze it properly, part of the material was not used or was taxonomically grouped. Species and taxa recorded only once during the entire study period were excluded from the dataset. Supraspecific identification of widespread and easily identifiable species was ruled out as well [*e. g.*, *Hyas* sp. against the backdrop of occurrence of two well-recognized species, *Hyas araneus* (Linnaeus, 1758) and *Hyas coarctatus* Leach, 1815]. Animals identified down to the phylum, class, and order levels were excluded from the analysis due to their low abundance or negligible contribution to total biomass. Species with low biomass (bryozoans, hydroids, and amphipods) and difficult to taxonomically identify (sponges and polychaetes) were grouped within family rank.

For each group of stations united within nodes of the standard grid of trawling, a total list of taxa was made, and their ratios in the total biomass were determined. The obtained data were processed by *k*-means clustering using the Bray–Curtis dissimilarity as a station-by-station similarity measure.

The number of clusters was determined for each period based on testing their optimal number by various statistical techniques: elbow method, gap statistic, silhouette method, and clustree.

The data were statistically processed in R applying the following libraries: geosphere, tidyr, tidyverse, ggplot2, clustree, vegan, factoextra, and cluster. Also, MS Office Excel was used. Maps were constructed in Golden Software MapViewer 8.

The names of the morphostructures of the Barents Sea are taken from the publication of A. Zinchenko [2001].

RESULTS

Monitoring which we have begun in 2004–2005 showed that the snow crab and the red king crab were recorded in the survey area at 1% of stations. Then, their occurrence changed. For the snow crab, it increased sharply and rose almost by 30 times by 2020. For the red king crab, it remained almost at the same level of 2% until 2013, started to increase in 2014, and finally reached the value of 4–5% (Fig. 2). This reflects different stages of acclimatization for crab populations during the study period. Specifically, the red king crab was at the last stages of naturalization, while the snow crab was actively exploring the recipient ecosystem expanding its range and increasing the abundance.

In 2004, the distribution area of the snow crab was 20 thousand km^2; that of the red king crab was 28 thousand km^2. By 2020, the range of the snow crab increased by more than 40 times and reached the value of 831 thousand km^2, while that of the red king crab rose only by 6 times, up to 176 thousand km^2. The rates of increase in both the frequency of occurrence and range for the snow crab were significantly higher than those for the red king crab (Fig. 2).

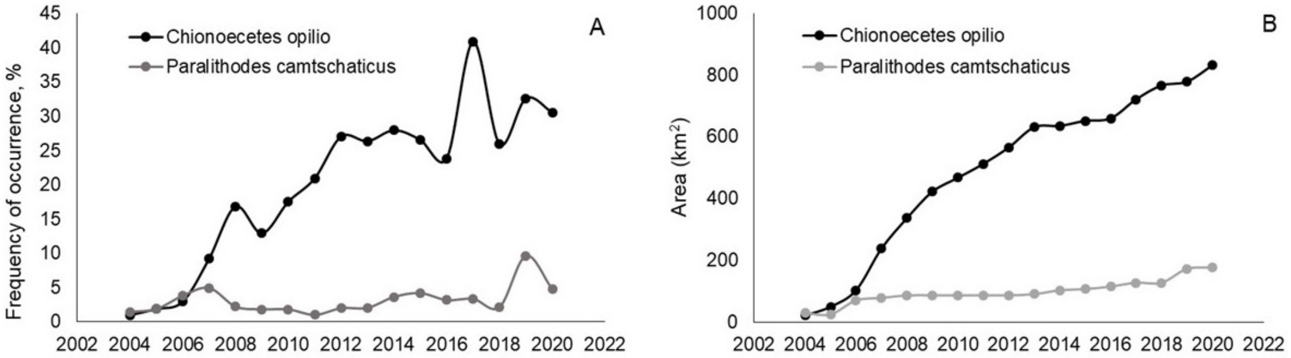

Fig. 2. Frequency of occurrence (%) (A) and range area (km^2) (B) of the snow crab and the red king crab in 2004–2020

To analyze the fluctuations in the composition of megabenthos over 15 years, we selected nodes of the standard grid of stations (Fig. 1B) where the snow crab and the red king crab were encountered during the entire study period. The proportion of the snow crab in the total biomass of bycatch in its habitat gradually increased from 0.2% in 2006 to 2% in 2011. In 2012, it rose to 5%; by 2013, the value increased sharply to 15%. In subsequent years, the relative biomass stabilized, varied slightly at one level, and reached 20.6% by 2020. In 2008–2013, the relative biomass of the red king crab in the survey area varied at the level of 1–2%; since 2014, it increased sharply; and by 2020, it amounted to 28.9% (Fig. 3).

In general, in the distribution area of considered invaders, the proportion of almost all megabenthic groups decreased since 2006: ascidians, from 5 to 0.1% in 2020; cnidarians (mainly, sea anemones), from 7 to 1%; crustaceans (excluding introduced species), from 6 to 3%; and molluscs, from 5.2 to 1.3%. The proportion of echinoderms dropped significantly: from 62% in 2006 to 36% in 2020. No changes were recorded in the relative biomass of polychaetes (Annelida in Fig. 3), nemerteans, priapulids, *etc.* (Varia in Fig. 3). At the same time, an increase in the proportion of sponges was noted in bycatches: from 5 to 10% (Fig. 3).

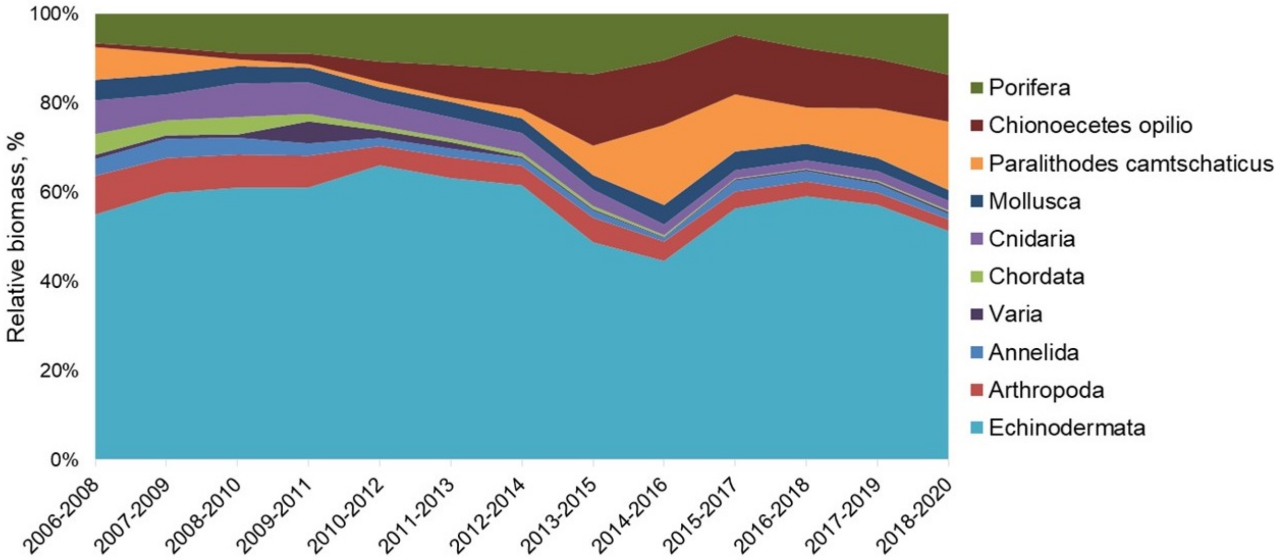

Fig. 3. Dynamics of the ratio of biomass of the main megabenthic groups and two invasive species in their range in the Barents Sea (three-year moving averages)

The dynamics of the relative biomass of the snow crab showed a statistically significant positive trend ($R^2 = 0.69$; $p = 0.0015$) (Fig. 4). When ruling out the data for 2018 and 2019, when the snow crab aggregations were under-surveyed [ICES Working Group, 2020], the coefficient of determination increased to 0.79.

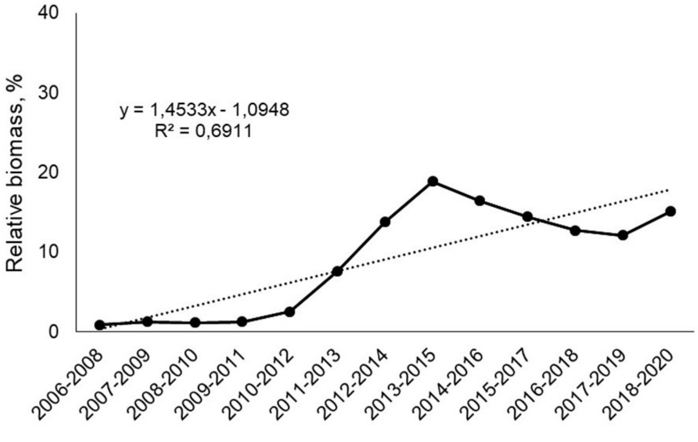

Fig. 4. Dynamics of the snow crab relative biomass in its range. The solid line represents three-year moving averages; the dotted line, linear trend

The moving average of the dynamics of the relative biomass for the snow crab within its distribution area is characterized by a rise, with a slight decrease in recent years (Fig. 4). However, this trend is not typical for all sites of the range. Thus, in the Goose Bank, the linear trend in the dynamics of the relative biomass for the snow crab in 2006–2020 is negative (Fig. 5A); in the Central Bank area and Novaya Zemlya shallows, it is positive (Fig. 5B–D).

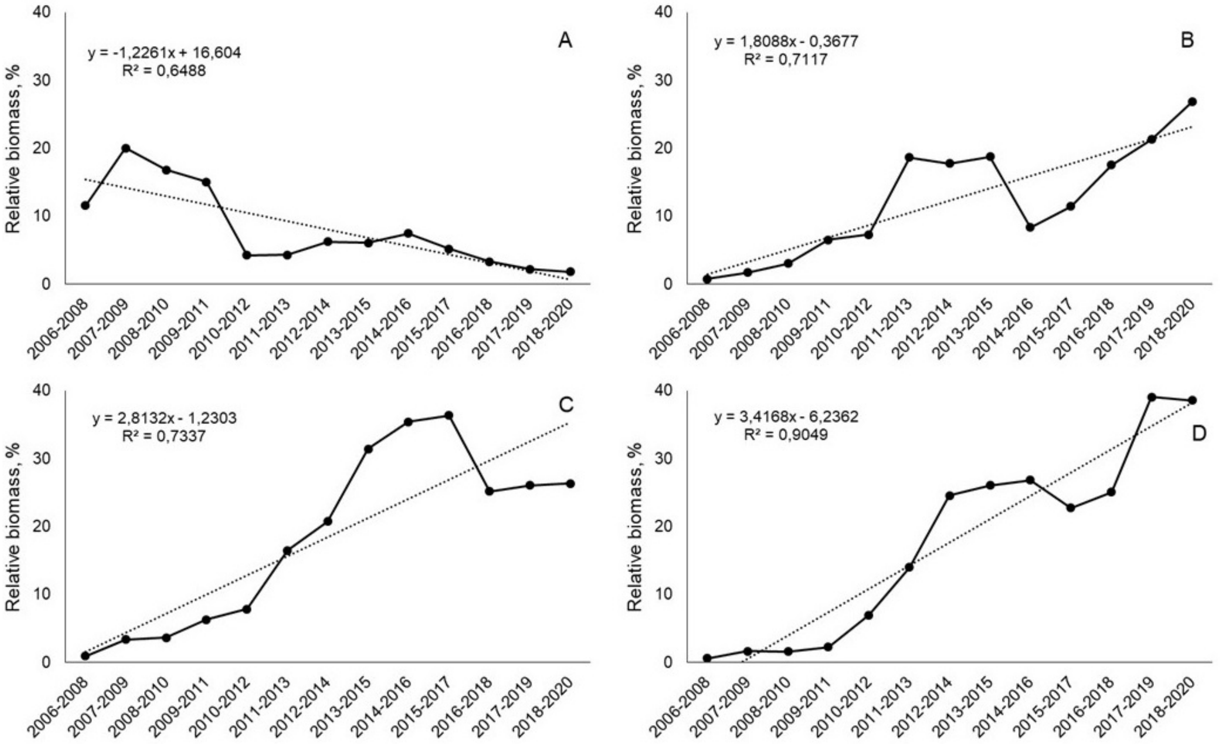

Fig. 5. Dynamics of the snow crab relative biomass in the Goose Bank (A), Central Bank (B), southern Novaya Zemlya Bank (C), and northern Novaya Zemlya Bank (D). The solid line represents three-year moving averages; the dotted line, linear trend (data from all catches in the area are used)

Until 2015, the proportion of the red king crab in the total biomass of megabenthos within its range rapidly increased; then, it stabilized at a fairly high level, with a slight downward trend (Fig. 6). For the red king crab, the trend of the dynamics of the relative biomass was statistically significant ($R^2 = 0.81$; $p = 0.0012$).

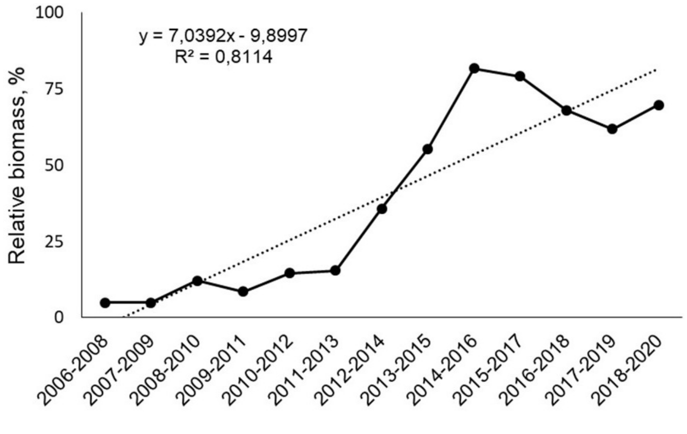

Fig. 6. Dynamics of the red king crab relative biomass in its range

According to the results of *k*-means clustering, 11 clusters were identified in the first analyzed period; 11 clusters were revealed in the second one; and 12 were defined in the third one (Fig. 7, Table 1).

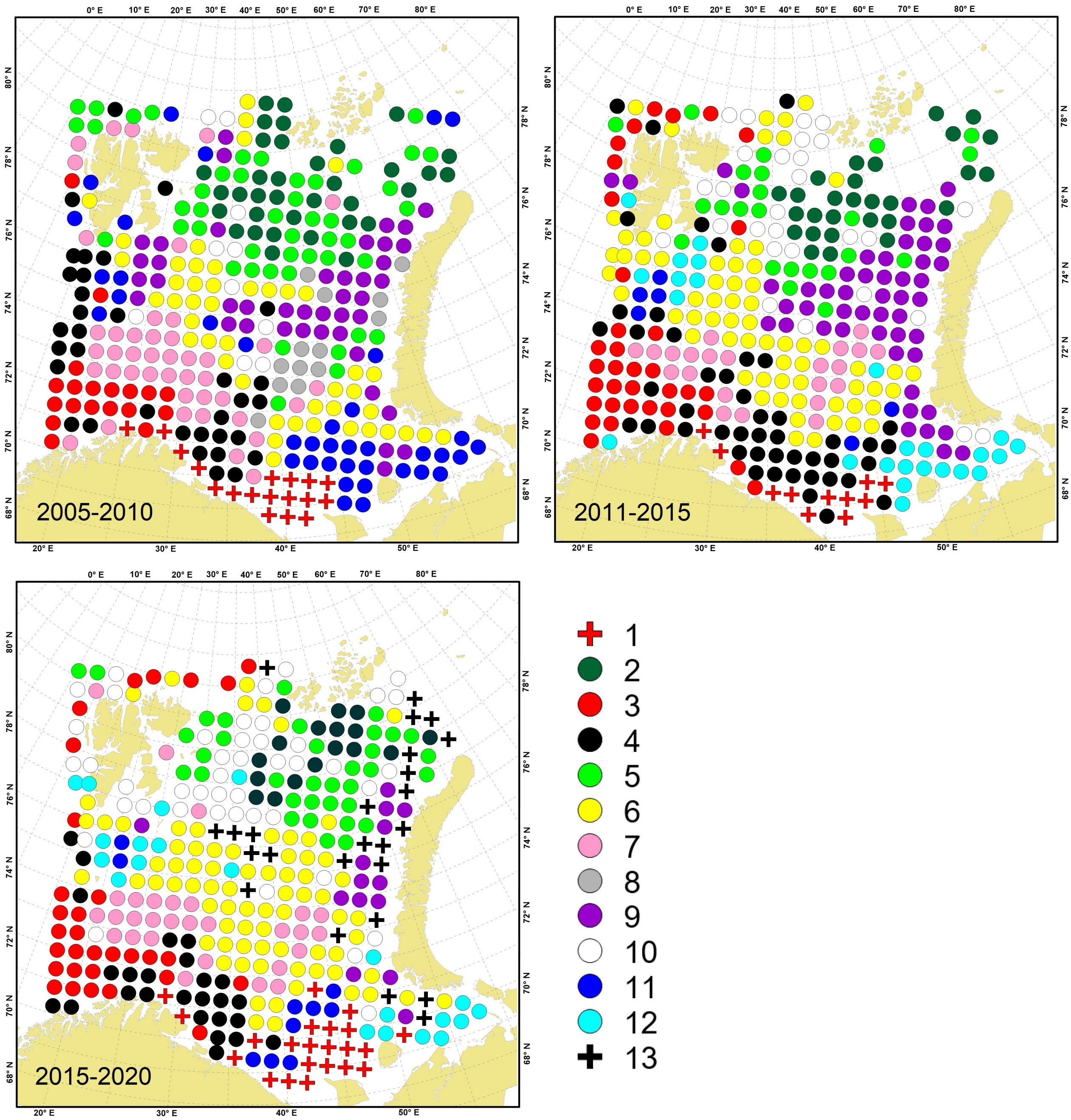

Fig. 7. Megabenthic communities in the Barents Sea and adjacent waters based on the surveys of 2006–2010, 2011–2015, and 2016–2020. Designations of the communities are given in Table 1

In 2006–2010, the biomass of the snow crab rapidly increased in the southeastern Barents Sea. This species became a subdominant one [against the backdrop of the prevalence of the starfish *Ctenodiscus crispatus* (Bruzelius, 1805)] in soft-soil communities in the Goose Bank area [community No. 6 in Fig. 7 and Table 1]. By 2010, the snow crab already locally dominated in the biomass of megabenthic catches in this site [Lyubin et al., 2010a].

Table 1. Megabenthic communities in the Barents Sea based on the surveys of 2006–2010, 2011–2015, and 2016–2020. Designations of the communities are the same as in Fig. 7. Dominant and subdominant species are given with relative biomass indicated (%)

2006–2010		2011–2015		2016–2020	
Community	Dominant and subdominant species	Community	Dominant and subdominant species	Community	Dominant and subdominant species
1 ✚	***Paralithodes camtschaticus*** (55.0) Geodiidae (1.9) *Hippasteria phrygiana* (1.7)	1 ✚	***Paralithodes camtschaticus*** (41.7) Suberitidae (1.8)	1 ✚	***Paralithodes camtschaticus*** (61.2)
2 ●	*Gorgonocephalus* (14.8) *Ophiopleura borealis* (9.7) *Umbellula encrinus* (7.6) *Heliometra glacialis* (7.3) *Ophiacantha bidentata* (5.8)	2 ●	*Ophiopleura borealis* (21.0) *Gorgonocephalus* (12.9) *Molpadia* (6.6) *Ophiacantha bidentata* (5.6) *Ophioscolex glacialis* (4.5)	2 ●	*Ophiopleura borealis* (24.3) ***Chionoecetes opilio*** (4.9) *Molpadia* (4.0) *Gorgonocephalus* (3.7)
3 ●	Geodiidae (75.4) *Parastichopus tremulus* (1.4)	3 ●	Geodiidae (67.2) Ancorinidae (4.9)	3 ●	Geodiidae (70.2) Ancorinidae (4.9)
4 ●	Actiniaria (57.4) Alcyonacea (7.0) Hormathiidae (5.1) *Hippasteria phrygiana* (3.5)	4 ●	Hormathiidae (8.7) Actiniaria (6.5) *Urasterias lincki* (6.2) *Ctenodiscus crispatus* (5.0)	4 ●	*Bolocera tuediae* (10.1) *Hippasteria phrygiana* (10.1) *Parastichopus tremulus* (8.2) Hormathiidae (5.0) *Molpadia* (4.5)
5 ●	*Gorgonocephalus* (48.8) Actiniaria (2.9) *Heliometra glacialis* (2.8) *Ctenodiscus crispatus* (2.5)	5 ●	*Gorgonocephalus* (45.9) *Ctenodiscus crispatus* (4.2) *Sabinea septemcarinata* (3.1) ***Chionoecetes opilio*** (2.1)	5 ●	*Gorgonocephalus* (37.6) ***Chionoecetes opilio*** (13.0) *Ophiopleura borealis* (4.2) *Ophioscolex glacialis* (4.1)
6 ●	*Ctenodiscus crispatus* (23.7) ***Chionoecetes opilio*** (7.7) *Urasterias lincki* (7.0) *Icasterias panopla* (6.7)	6 ●	*Ctenodiscus crispatus* (39.6) *Icasterias panopla* (18.6) *Urasterias lincki* (10.0) *Sabinea septemcarinata* (8.7) Hormathiidae (5.8)	6 ●	*Ctenodiscus crispatus* (23.1) *Urasterias lincki* (9.6) *Icasterias panopla* (6.9) Polymastiidae (5.0) ***Chionoecetes opilio*** (4.4)
7 ●	Polymastiidae (10.6) Actiniaria (8.3) *Molpadia* (7.5) *Ctenodiscus crispatus* (6.2) Theneidae (4.1)	7 ●	*Molpadia* (24.8) *Ctenodiscus crispatus* (11.2) Polymastiidae (3.6) Theneidae (3.6)	7 ●	*Molpadia* (22.9) *Ctenodiscus crispatus* (12.3) *Bathyarca glacialis* (7.6) Polymastiidae (7.1)
8 ●	*Ciona intestinalis* (13.7) *Molpadia* (11.5) *Ctenodiscus crispatus* (4.3) *Strongylocentrotus* (4.3)				
9 ●	*Strongylocentrotus* (35.1) *Sabinea septemcarinata* (5.7) *Gorgonocephalus* (5.5) *Ctenodiscus crispatus* (3.6)	9 ●	*Strongylocentrotus* (34.4) ***Chionoecetes opilio*** (18.0) *Ctenodiscus crispatus* (9.2) *Urasterias lincki* (4.6) *Gorgonocephalus* (3.6)	9 ●	*Strongylocentrotus* (37.9) ***Chionoecetes opilio*** (9.9) *Gorgonocephalus* (1.7)

Continue on the next page…

2006–2010		2011–2015		2016–2020	
Community	Dominant and subdominant species	Community	Dominant and subdominant species	Community	Dominant and subdominant species
10 ○	*Heliometra glacialis* (27.6) Actiniaria (6.0) *Sabinea septemcarinata* (3.7)	10 ○	*Gorgonocephalus* (7.9) *Sabinea septemcarinata* (6.4) *Heliometra glacialis* (6.1) *Ophiacantha bidentata* (5.0) *Strongylocentrotus* (4.4) *Ctenodiscus crispatus* (4.1)	10 ○	*Heliometra glacialis* (7.6) *Sabinea septemcarinata* (6.0) *Ctenodiscus crispatus* (5.6) *Chlamys islandica* (5.0) *Ophiacantha bidentata* (4.7) *Gorgonocephalus* (4.5)
11 ●	*Sabinea septemcarinata* (15.4) *Cucumaria frondosa* (12.7) *Sclerocrangon boreas* (7.0) *Hyas araneus* (6.4) *Balanus* (5.8) *Strongylocentrotus* (5.4)	11 ●	*Cucumaria frondosa* (32.0) *Microcosmus glacialis* (4.7) *Balanus* (1.9)	11 ●	*Cucumaria frondosa* (21.2) ***Paralithodes camtschaticus*** (13.8) Suberitidae (7.0) Hormathiidae (2.3)
		12 ◍	*Strongylocentrotus* (13.8) *Balanus* (10.4) *Chlamys islandica* (6.9) *Alcyonidium gelatinosum* (5.6) *Hyas araneus* (4.7)	12 ◍	*Strongylocentrotus* (16.2) *Balanus* (9.1) *Chlamys islandica* (6.9)
				13 ✚	***Chionoecetes opilio*** (35.3) *Ctenodiscus crispatus* (4.1) *Gorgonocephalus* (3.3)

In 2011–2015, the snow crab became a subdominant species in the Novaya Zemlya shallows (community No. 9 in Fig. 7 and Table 1) and the northern Central Bank (No. 5). During this period, it was a subdominant species in almost all communities of the Novaya Zemlya archipelago. The area of several communities shifted. Specifically, for sea urchins, the area decreased (No. 9), and for the mud star *C. crispatus* (No. 6), it increased. The snow crab populations were unstable (see Fig. 5). Thus, the dense aggregation in the Goose Bank dropped greatly, and this is associated with the redistribution of aggregations in general. The snow crab aggregations that moved to the areas of the Central Bank and the southern Novaya Zemlya Bank were increasing their proportions in communities since 2006, and in the northern Novaya Zemlya shallows, since 2009.

In 2016–2020, the snow crab prevailed in communities (No. 13 in Fig. 7 and Table 1) between the Novaya Zemlya and Franz Josef Land archipelagos on the border with the Kara Sea, on the slopes of the Novaya Zemlya shallows and in the Central Bank, and in the Southern Novaya Zemlya Trench. The area of communities with the subdominance of this hydrobiont increased and covered the area from the Franz Josef Land and Novaya Zemlya archipelagos to the Perseus Bank, as well as the northern Pechora Sea (No. 2, 5, and 9). To the south of the Franz Josef Land archipelago, the snow crab was a subdominant species in the community of the brittle star *Ophiopleura borealis* Danielssen & Koren, 1877 (No. 2). In the Novaya Zemlya Bank, in the community dominated by sea urchins of the genus *Strongylocentrotus* Brandt, 1835 (No. 9), mainly *Strongylocentrotus pallidus* (G. O. Sars, 1871), the snow crab was the second most dominant species. In the eastern sea, in the community of brittle stars of the genus *Gorgonocephalus* Leach, 1815 (No. 5) and *O. borealis* (No. 2), the snow crab was on the second position.

In 2006–2010, the red king crab prevailed among megabenthic organisms in coastal waters of the Kola Peninsula, in the Murman Rise, and in waters off the Kanin Peninsula (community No. 1 in Fig. 7 and Table 1). In the community of sponges (No. 3) in the Eastern Murman and warm-water species (No. 4) in the Western Murman, it was a subdominant species.

In 2011–2015, it still dominated in the North Cape area and Eastern Murman waters, but became less common in bycatches in the coastal Western Murman and Murmansk Rise. Dense aggregations of the red king crab on the southern slope of the Kaninskaya Bank expanded eastward, to the Kanin Peninsula.

In 2016–2020, the area of the red king crab dominance expanded noticeably to the northeast: this species prevailed in communities around the entire Kanin Peninsula, north and west of Kolguev Island, off the Kaninskaya Bank, and in the Goose Bank. In the community of the orange-footed sea cucumber *Cucumaria frondosa* (Gunnerus, 1767) (No. 11 in Fig. 7 and Table 1), the red king crab was the first subdominant in the areas of the southern Murmansk Rise, on the slopes of the Kaninskaya Bank, and in the southern Goose Bank. To a limited extent, it was also found in communities of sponges of the genus *Geodia* Lamarck, 1815 (No. 3), warm-water species (No. 4), and shallow-water species (No. 12) in the Pechora Sea. Moreover, it was recorded in the community of the snow crab (No. 13) at the southern tip of the Novaya Zemlya (see Fig. 1 and Table 1).

DISCUSSION

Studies of the dynamics of macrozoobenthic communities in the Barents Sea showed that their alterations under the impact of climatic factors and bottom trawling are registered with a delay of approximately four years [Denisenko, 2013; Lyubina et al., 2012, 2016]. In the case of larger and longer-lived megabenthic organisms, the delay in the recorded response to stress or shifts in environmental conditions should be longer. For these reasons, to analyze changes in the structure of the megabenthic component of benthic communities, we considered not annual data, but data over five-year periods.

In different areas of the Barents Sea, communities are undergoing transformations according to various scenarios (depending on the strength of the effect of prevailing factors).

In the southern Barents Sea, the key factors affecting benthic communities are as follows: the influx of warm Atlantic waters [Denisenko, 2003, 2007, 2013; Zakharov et al., 2022b], active bottom trawling [Lyubin et al., 2010b], predation by the red king crab [Manushin, 2021a, b], and predation by demersal fish (mostly haddock and flounder) [Eriksen et al., 2020]. Importantly, over the past few decades, none of the listed factors has prevented the active acclimatization of the red king crab in the southern Barents Sea, increase in its abundance, and expansion of its range.

The long period of positive temperature anomalies observed in the sea since the late XX century [Boitsov et al., 2012; Trofimov et al., 2018] contributed to the distribution of the crab not only westward, along the coast of Norway, but also eastward, along the Kola Peninsula coast up to the White Sea Gorlo Strait and the Murmansk and Northern Kanin Rise [The Red King Crab, 2021].

Active bottom fishing in the southern Barents Sea has an extremely negative impact on megabenthos [Lyubin et al., 2010b, 2011; Løkkeborg, Fosså, 2011; Zakharov, Luybin, 2012], but affects the red king crab to a lesser extent. Current fishing regulations in the Russian Federation are aimed at maximum protection of this species – a valuable commercial resource. Bycatch of more than 10 crabs *per* 1 ton of catch is prohibited. If this level of bycatch is exceeded, the vessel must change its position by 5 nautical miles. All caught crabs, regardless of number, sex, and size, must be immediately returned to their habitat; this is strictly controlled by regulatory agencies. Poaching is localized mostly in coastal waters and has minimal impact on dense commercial aggregations in the open sea. Moreover, bottom trawling provides additional food for crabs (waste from onboard fish processing and discards of substandard parts of the catch) [Manushin, 2021a]. Also, animals injured by trawls become attractive and easy prey [Kedra et al., 2017].

Out of the above-listed factors, the only negative one can be competition with bottom fish. However, commercial fishing actively reduces its pressure on bottom communities, and fish consumption of adult crabs is extremely insignificant [Dolgov, Benzik, 2021]. So, in recent years, in the open, southern Barents Sea, very favorable conditions have developed for the red king crab distribution.

A weakly expressed increase in the frequency of occurrence (see Fig. 2) and distribution area of the red king crab during the study period, compared to indicators of the snow crab, is due to the smaller range area and the fact that a noticeable part of its population is concentrated off the coast. Moreover, trawl catches of the red king crab in open waters (with a rather sparse grid of ecosystem survey stations) are mostly random because of the high mobility of aggregations of large sexually mature males: those perform long and extensive migrations both to find food and reach breeding sites [Berenboim, 2003]. A significant proportion of the red king crab in the total biomass of megabenthos is also explained by the fact as follows: in the southern Barents Sea, the trawl bycatch of megabenthos is quite low, and one of its possible reasons seems to be the long-term negative impact of active trawling [Lyubin et al., 2010b]. Thus, even one commercial male weighing several kilograms caught by trawling can cause the total biomass of megabenthos in the bycatch to be exceeded.

The main groups of macrozoobenthos most actively consumed by the red king crab are echinoderms and molluscs [Strelkova et al., 2021]. Within the distribution area of this species, out of megabenthic organisms, the relative biomass of sea anemones, crustaceans, and ascidians also decreased during the study period. At the same time, an increase in the relative biomass of sponges was noted, the biomass of which negatively correlates with the distribution density of the red king crab. Specifically, in the Western Murman waters (part of the coast west of the Kola Bay), after a drop in the distribution density of the red king crab, a rise in the relative biomass of sponges was recorded – up to formation of local communities with their dominance.

A change in the structure of the benthic population, with the replacement of part of the benthic community by sponges, was previously recorded in the Svyatonos settlement of the Icelandic scallop *Chlamys islandica* (O. F. Müller, 1776), in the area of mass development of the seston-feeding fauna [Nosova et al., 2018; Zolotarev, 2016]. The factor mostly affecting the change in the composition of the community in this area was the long-term fishery of the Icelandic scallop. As a result of overfishing and consequent epizootic, the dominant species, *i. e.*, the Icelandic scallop, was replaced by other seston-feeders, mainly sponges. Unlike more highly organized animals, those are weakly susceptible to pressure from predators, infectious diseases, and damage by commercial dredges. Importantly, after mechanical disruption of the integrity of the sponge body, new individuals can be formed from the body fragments. Under artificial conditions, a fragment of the sponge *Geodia barretti* Bowerbank, 1858 (a species widespread in the Barents Sea) completely regenerated the structure of its body within a year and increased its mass by 40% [Hoffmann et al., 2003]. To date, the probability of a reverse process – a competitive replacement of sponges by scallops when their fishing ceases – is not clear. Apparently, degradation of the scallop population under the impact of fishing is irreversible; therefore, restoration of the stock of this valuable species to its previous level is impossible. However, for other hydrobionts, this factor can be a positive one: by forming dense settlements, sponges ensure a favorable habitat for many animal species [Kedra et al., 2017; Khalaman, Komendantov, 2011].

A similar picture was noted in areas with mass settlements of the orange-footed sea cucumber in shallow waters of the northwestern and southeastern Barents Sea (the Spitsbergen, Goose, and North Kaninskaya banks and Moller Plateau). In 2006–2010, its community was not isolated during clustering, but was combined with a community characteristic of shallow waters of the southeastern sea and part of the Spitsbergen Bank. In 2011–2015, the relative biomass of *C. frondosa* in the southern sea increased (see Table 1) which may be due to a gradual consumption of certain benthic groups by the red king crab and a restructuring of the community. Previously, similar structural changes – a decrease in the number of main components (taxa) of the red king crab food spectrum and an increase in the abundance of their trophic competitors not consumed by this crab – were recorded in the macrobenthic communities of Motovsky Bay [Strelkova et al., 2021]. A similar picture was registered in several other water basins with the appearance of invaders [Alimov et al., 2000].

The ethological aspects of the biology of the red king crab and snow crab differ significantly. The first species, whose breeding and feeding areas are spatially separated, performs long and extensive migrations. As already mentioned, this mainly concerns sexually mature males of commercial size. Females and juveniles are more sedentary and stick to a narrow coast almost all year round [The Red King Crab, 2021]. So, in the open, southern Barents Sea, the bycatch is dominated by large male red king crabs – grazing predators. In contrast, the snow crab has noticeably less pronounced migratory activity. Throughout its range, catches include individuals of both sexes and all age groups with slight differentiation by depth [Zakharov et al., 2021b].

The growth of the snow crab population has led to its colonization of a huge area in the eastern and northern Barents Sea: from the Pechora Sea to the Franz Josef Land archipelago and from the Novaya Zemlya archipelago to Spitsbergen. In general, its distribution largely copies the distribution within the Barents Sea of Pacific-origin species, *e. g.*, whelks [Zakharov, 2013]. To date, Pacific species are recorded throughout the Barents Sea, but they form a stable faunal complex in the Novaya Zemlya, Kanin–Pechora, and Medvezhin–Nadezhdin shallows only. The faunal similarity of the benthic population indicates the similarity of living conditions in these remote areas.

The habitat of the snow crab continues to expand westward, to the Spitsbergen archipelago. There, the benthos is similar in terms of species composition and quantitative characteristics to communities widespread in the area of the densest concentrations of the snow crab.

However, modern data indicate that the expansion of its range westward is much slower than eastward, into adjacent areas of the Kara Sea [Zalota et al., 2018, 2019, 2020; Zimina, 2014]. Apparently, the main factor inhibiting its westward distribution is now the warming of the Barents Sea waters observed in the last few decades [ICES Working Group, 2022]. Obviously, in case of a cold snap, colonization of the snow crab in the western sea may accelerate [Bakanev, 2017], and a new center of its reproduction may be formed in the Spitsbergen archipelago area – in addition to the existing one off the Novaya Zemlya archipelago.

In some years within 2006–2010, in the Goose Bank, the bycatch of the snow crab reached 30–40% of the catch mass. In subsequent years, there were a decrease in its abundance in this site and formation of new dense settlements much further north, in the area of the Novaya Zemlya Bank and eastern slopes of the Central and Perseus banks. A drop in the abundance of the snow crab and its importance in the megabenthic part of the benthic community in the Goose Bank area may be associated both with the impact of warm waters of one of the North Cape Current branches and with a decrease in the food supply after the explosive growth in the abundance of the invader.

Interestingly, in 2006–2010, in the Central Basin area, there was a community dominated by the ascidian *Ciona intestinalis* (Linnaeus, 1767) (No. 8 in Fig. 7 and Table 1). During next two periods, it was no longer distinguished: it was absorbed by a community dominated by holothurians of the genus *Molpadia* Cuvier, 1817. This may be partly due to the fact that the growing population of the snow crab feeds on ascidians. Their large size, soft cylindrical body with no protective shell, and attached lifestyle – apparently, all these characteristics made ascidians vulnerable to the invasive predator occurring in mass, in contrast to *Molpadia* representatives burrowing into the ground.

Undoubtedly, as mentioned above, against the backdrop of a cold snap, the frequency of occurrence and range of the snow crab will increase [Bakanev, 2017]. However, a rise in the abundance of the invader in already explored areas is unlikely, since the main limiting factor in this case is not the ambient temperature, but the food supply. Apparently, after the colonization of certain areas, there will be a redistribution of aggregations into adjacent communities suitable for the species and a reduction in the abundance of the invader down to an optimal level. To date, a similar picture is observed in the Goose Bank and partly in the southern Novaya Zemlya Bank, where the growth in the abundance of the invasive species is slowing down or has already stopped. Most likely, new productive generations will arise locally in areas that are being explored by the invader for the first time, for example, off the Spitsbergen and Franz Josef Land archipelagos and in elevations of the northern and central Barents Sea.

Like the red king crab, the snow crab displaces or replaces native species by consuming them or competing for food. However, due to its smaller size, the snow crab seems to be unable to eat larger individuals of megabenthos; so, this species affects *via* eating their juveniles. The pressure from the invader on megabenthos may be partially reduced by the consumption of macrozoobenthos by the crab.

In recent years, the proportion of the snow crab in catches within the area it has explored long ago remains at a level of about ⅕ of the total biomass of trawl megabenthos. It can be assumed as follows: under conditions of the Barents Sea, this proportion is optimal, and in the future, it will be maintained within the entire area inhabited by this species.

Obviously, the occurrence of the snow crab and red king crab in the Barents Sea ecosystem does not lead to an increase in the total bioproductivity of the water basin, since the latter is completely determined by the level of food resources available to bottom population [Zenkevich, 1970], *i. e.*, primary production. In case of the invaders considered, we are talking only about the redistribution of energy flows and an increase in their biomass due to native species. Being exclusively carnivores, these two species do not introduce new or uninvolved sources of nutrients into the food pyramid (for example, unclaimed detritus or plankton); those just exploit and transform existing benthic communities [Biological Invasions, 2004; Shadrin, Anufriieva, 2019].

Under current conditions, both crab species will definitely continue to expand their ranges against the backdrop of comfortable conditions and availability of sufficient food supply. The red king crab will continue to integrate into the communities of the Pechora Sea and adjacent waters. However, its distribution northward will most likely be limited to the Goose Bank and Moller Plateau, and eastward, to shallow waters subject to winter cooling. The range of the snow crab will cover the entire northern and eastern sea, with the exception of areas under the impact of warm Atlantic waters. Its distribution will not be uniform, but the area of megabenthic communities with its dominance will increase. Apparently, competition between invaders will be minimal; it will be observed only at the junction of habitats. With climate fluctuations, the ranges of crabs will change in antiphase: with warming, the range of the red king crab will expand, and the range of the snow crab will decrease, and *vice versa*.

Thus, the benthic communities of the Barents Sea are currently in a state of transformation caused by a long period of warming and emergence of new invasive species. The presented results suggest as follows: while the red king crab and the snow crab explore accessible waters, the bottom population of the Barents Sea will undergo significant structural changes within the entire distribution area.

The material for this work was sampled within the framework of the state research assignments of the Polar branch of VNIRO (Murmansk) and Institute of Marine Research (Bergen). The paper was prepared within the framework of the state research assignment of the Zoological Institute of the Russian Academy of Sciences No. 122031100275-4.

Acknowledgement. We are grateful to all colleagues and staff onboard the RV, in laboratories, and in offices for their work in the joint Russian–Norwegian ecosystem survey of the Barents Sea. We are extremely grateful to the reviewers for their comments and positive final assessment of our paper.

REFERENCES

1. Alimov A. F., Orlova M. I., Panov V. E. Posledstviya introduktsii chuzherodnykh vidov dlya vodnykh ekosistem i neobkhodimost' meropriyatii po ikh predotvrashcheniyu. In: *Vidy-vselentsy v evropeiskikh moryakh Rossii* : sbornik nauchnykh trudov. Apatity : Izd-vo Kol'skogo nauchnogo tsentra RAN, 2000, pp. 12–23. (in Russ.)
2. *Atlas of the Megabenthic Organisms of the Barents Sea and Adjacent Waters.* Murmansk : PINRO, 2018, 534 p. (in Russ.)
3. Bakanev S. V. Prospects of snow crab *Chionoecetes opilio* fishery in the Barents Sea. *Voprosy rybolovstva*, 2017, vol. 18, no. 3, pp. 286–303. (in Russ.)
4. Berenboim B. I. Sezonnye migratsii kamchatskogo kraba v Barentsevom more. In: *Kamchatskii krab v Barentsevom more.* Murmansk : PINRO, 2003, pp. 70–78. (in Russ.)
5. *Biological Invasions in Aquatic and Terrestrial Ecosystems* / A. F. Alimov, N. G. Bogutskaya (Eds). Moscow ; Saint Petersburg : KMK Scientific Press Ltd., 2004, 436 p. (in Russ.)
6. Denisenko S. G. Mnogoletnie izmeneniya donnoi fauny Barentseva morya i gidrologicheskie flyuktuatsii vdol' razreza "Kol'skii meridian". In: *Materialy simpoziuma, posvyashchennogo 100-letiyu okeanograficheskikh nablyudenii na razreze "Kol'skii meridian" (Murmansk, 1999).* Murmansk : Izd-vo PINRO, 2003, pp. 65–76. (in Russ.)
7. Denisenko S. G. Zoobentos Barentseva morya v usloviyakh izmenyayushchegosya klimata i antropogennogo vozdeistviya. In: *Dinamika morskikh ekosistem i sovremennye problemy sokhraneniya biologicheskogo potentsiala morei Rossii.* Vladivostok : Dal'nauka, 2007, pp. 418–511. (in Russ.)
8. Denisenko S. G. *Biodiversity and Bioresources of Macrozoobenthos in the Barents Sea: Structure and Long-Term Changes.* Saint Petersburg : Nauka, 2013, 284 p. (in Russ.)
9. Dolgov A. V., Benzik A. N. Kamchatskii krab kak ob"ekt pitaniya donnykh ryb. In: *The Red King Crab in the Barents Sea* : 3rd edition, revised and expanded. Moscow : VNIRO, 2021, pp. 347–359. (in Russ.)

10. Zakharov D. V. *Raspredelenie, ekologiya i promyslovoe znachenie mollyuskov semeistva Buccinidae v Barentsevom more i sopredel'nykh vodakh*. (dissertation). Murmansk, 2013, 162 p. (in Russ.)
11. Zakharov D. V., Luybin P. A. Fauna, ecology and distribution of molluscs Buccinidae (Mollusca, Gastropoda) in the Barents Sea and adjacent waters. *Vestnik Murmanskogo gosudarstvennogo tekhnicheskogo universiteta*, 2012, vol. 15, no. 4, pp. 749–757. (in Russ.)
12. Zakharov D. V., Manushin I. E., Strelkova N. A. Sravnitel'nyi analiz bentosnykh materialov, sobrannykh raznymi orudiyami lova v vostochnoi chasti Barentseva morya. In: *Chteniya pamyati K. M. Deryugina* : materialy XXII yubileinogo nauchnogo seminara "Kafedre ikhtiologii i gidrobiologii 90 let". Saint Petersburg : St Petersburg University, 2021a, pp. 52–68. (in Russ.)
13. Zakharov D. V., Manushin I. E., Strelkova N. A., Zimina O. L., Khacheturova K. S., Blinova D. J., Jørgensen L. L. Guidance for the assessment of the megabenthos bycatch in the bottom trawl in the course of research surveys. *Voprosy rybolovstva*, 2022a, vol. 23, no. 3, pp. 179–192. (in Russ.). https://doi.org/10.36038/0234-2774-2022-23-3-179-192
14. Zakharov D. V., Strelkova N. A., Manushin I. E., Khacheturova K. S., Blinova D. Yu., Kudryashova A. S. Changes in benthic communities in the Kola Peninsula bays in the 21st century. In: *Marine Research and Education (MARESEDU-2022)* : proceedings of the XI International Conference. Tver : PoliPRESS, 2022b, vol. 3 (4), pp. 102–105. (in Russ.)
15. Zenkevich L. A. Donnaya fauna okeana. In: *Programma i metodika izucheniya biogeotsenozov vodnoi sredy. Biogeotsenozy morei i okeanov*. Moscow : Nauka, 1970, pp. 213–227. (in Russ.)
16. Zinchenko A. G. Geomorfologicheskaya osnova kompleksnykh landshaftno-geoekologicheskikh issledovanii Barentseva morya. In: *Opyt sistemnykh okeanologicheskikh issledovanii v Arktike*. Moscow : Nauchnyi mir, 2001, pp. 476–481. (in Russ.)
17. Zolotarev P. N. *Biology and Fishery of the Icelandic Scallop Chlamys islandica in the Barents and White Seas*. Murmansk : PINRO, 2016, 289 p. (in Russ.)
18. *The Red King Crab in the Barents Sea* : 3rd edition, revised & expanded. Moscow : VNIRO, 2021, 712 p. (in Russ.)
19. Kolpakov N. V., Korneichuk I. A., Nadtochy V. A. Current data on composition and distribution of trawl macrozoobenthos in the Russian waters of the Japan Sea. *Izvestiya TINRO*, 2018, vol. 193, pp. 33–49. (in Russ.). https://doi.org/10.26428/1606-9919-2018-193-33-49
20. *Snow Crab Chionoecetes opilio in the Barents and Kara Seas*. Murmansk : PINRO, 2016, 242 p. (in Russ.)
21. Lyubin P. A., Anisimova N. A., Jørgensen L. L., Manushin I. E., Prokhorova T. A., Zakharov D. V., Zhuravleva N. E., Golikov A. V., Morov A. V. Megabentos Barentseva morya. In: *Nature of the Shelf and Archipelagos of the European Arctic. Complex Investigations of the Svalbard Archipelago Nature* : proceedings of the International Scientific Conference, Murmansk, 27–30 October, 2010. Moscow : GEOS, 2010a, iss. 10, pp. 192–199. (in Russ.)
22. Lyubin P. A., Anisimova N. A., Manushin I. E., Zhuravliova N. E. Additional catch of macrozoobenthos in the ichthyological over-trawling as a mark of trawling intensity. *Vestnik Murmanskogo gosudarstvennogo tekhnicheskogo universiteta*, 2010b, vol. 13, no. 4 (spec. iss.), pp. 641–646. (in Russ.)

23. Lyubina O. S., Strelkova (Anisimova) N. A., Lubin P. A., Frolova E. A., Dikaeva D. R., Zimina O. L., Akhmetchina O. Yu., Manushin I. E., Nekhaev I. O., Frolov A. A., Zakharov D. V., Garbul E. A., Vyaznikova V. S. Modern quantitative distribution of zoobenthos along on the transect "Kola Section". *Trudy Kol'skogo nauchnogo tsentra RAN*, 2016, no. 2 (36), pp. 64–91. (in Russ.)
24. Manushin I. E., Zakharov D. V., Strelkova N. A., Lyubin P. A., Zhuravfleva N. E., Vyaznikova V. S., Nosova T. B., Blinova D. Yu., Khacheturova K. S. Otsenka vozdeistviya kamchatskogo kraba na bentos raionov Vostochnogo Murmana. In: *The Red King Crab in the Barents Sea*. Moscow : VNIRO, 2021, pp. 651–660. (in Russ.)
25. Manushin I. E. Pitanie kamchatskogo kraba v yuzhnoi chasti Barentseva morya. In: *The Red King Crab in the Barents Sea*. Moscow : VNIRO, 2021a, pp. 283–337. (in Russ.)
26. Manushin I. E. Potreblenie pishchi kamchatskim krabom. In: *The Red King Crab in the Barents Sea*. Moscow : VNIRO, 2021b, pp. 337–342. (in Russ.)
27. Nosova T. B., Manushin I. E., Zakharov D. V. Structure and long-term dynamics of zoobenthos communities in the areas of scallop *Chlamys islandica* beds at Kola Peninsula. *Izvestiya TINRO*, 2018, vol. 194, pp. 27–41. (in Russ.). https://doi.org/10.26428/1606-9919-2018-194-27-41
28. Strelkova N. A., Manushin I. E., Zakharov D. V., Vyaznikova V. S. Otsenka vozdeistviya kamchatskogo kraba na bentos raionov Zapadnogo Murmana. In: *The Red King Crab in the Barents Sea*. Moscow : VNIRO, 2021, pp. 600–650. (in Russ.)
29. Trofimov A. G., Karsakov A. L., Ivshin V. A. Climate changes in the Barents Sea over the last half century. *Trudy VNIRO*, 2018, vol. 173, pp. 79–91. (in Russ.)
30. Shadrin N. V., Anufriieva E. V. Lake ecosystems and invasive species: All are not so simple. In: *Lakes of Eurasia: Problems and Solutions* : proceedings of the II International Conference, 19–24 May, 2019. Kazan : Izd-vo Akademii nauk Respubliki Tatarstan, 2019, pt 2, pp. 355–359. (in Russ.)
31. Shuntov V. P., Volvenko I. V. Generalized assessments of composition, quantitative distribution and biomass of benthic macrofauna on the shelf and slope in the North-West Pacific. *Izvestiya TINRO*, 2015, vol. 182, no. 3, pp. 3–22. (in Russ.). https://doi.org/10.26428/1606-9919-2015-182-3-22
32. Boitsov V. D., Karsakov A. L., Trofimov A. G. Atlantic water temperature and climate in the Barents Sea, 2000–2009. *ICES Journal of Marine Science*, 2012, vol. 69, iss. 5, pp. 833–840. https://doi.org/10.1093/icesjms/fss075
33. Eriksen E., Benzik A. N., Dolgov A. V., Skjoldal H. R., Vihtakari M., Johannesen E., Prokhorova T. A., Keulder-Stenevik F., Prokopchuk I., Strand E. Diet and trophic structure of fishes in the Barents Sea: The Norwegian–Russian program "Year of stomachs" 2015 – establishing a baseline. *Progress in Oceanography*, 2020, vol. 183, art. no. 102262 (17 p.). https://doi.org/10.1016/j.pocean.2019.102262
34. Hoffmann F., Rapp H. T., Zöller T., Reitner J. Growth and regeneration in cultivated fragments of the boreal deep-water sponge *Geodia barretti* Bowerbank, 1858 (Geodiidae, Tetractinellida, Demospongiae). *Journal of Biotechnology*, 2003, vol. 100, iss. 2, pp. 109–118. https://doi.org/10.1016/s0168-1656(02)00258-4
35. ICES Working Group on the Integrated Assessments of the Barents Sea (WGIBAR). *ICES Scientific Reports*, 2020, vol. 2,

iss. 30, 206 p. https://doi.org/10.17895/ices.pub.5998

36. ICES Working Group on the Integrated Assessments of the Barents Sea (WGIBAR). *ICES Scientific Reports*, 2022, vol. 4, iss. 50, 235 p. https://doi.org/10.17895/ices.pub.20051438
37. Jørgensen L. L., Logerwell E. A., Strelkova N. A., Zakharov D. V., Roy V., Nozères C., Bluhm B. A., Ólafsdóttir S. H., Burgos J. M., Sørensen J., Zimina O., Rand K. International megabenthic long-term monitoring of a changing arctic ecosystem: Baseline results. *Progress in Oceanography*, 2022, vol. 200, art. no. 102712 (20 p.). https://doi.org/10.1016/j.pocean.2021.102712
38. Kedra M., Renaud P. E., Andrade H. Epibenthic diversity and productivity on a heavily trawled Barents Sea bank (Tromsøflaket). *Oceanologia*, 2017, vol. 59, iss. 2, pp. 93–101. https://doi.org/10.1016/j.oceano.2016.12.001
39. Khalaman V. V., Komendantov A. Y. Structure of fouling communities formed by *Halichondria panicea* (Porifera: Demospongiae) in the White Sea. *Russian Journal of Ecology*, 2011, vol. 42, no. 6, pp. 493–501. https://doi.org/10.1134/S1067413611050080
40. Kuzmin S. A., Akhtarin S. M., Menis D. T. The first findings of snow crab *Chionoecetes opilio* (Decapoda, Majidae) in the Barents Sea. *Zoologicheskii zhurnal*, 1998, vol. 77, no. 4, pp. 489–491.
41. Gutt J., Starmans A. Structure and biodiversity of megabenthos in the Weddell and Lazarev seas (Antarctica): Ecological role of physical parameters and biological interactions. *Polar Biology*, 1998, vol. 20, iss. 4, pp. 229–247. https://doi.org/10.1007/s003000050300
42. Lyubin P. A., Anisimova N. A., Manushin I. E. Long-term effects on benthos of the use of bottom fishing gears. In: *The Barents Sea: Ecosystem, Resources, Management. Half a Century of Russian–Norwegian Cooperation* / T. Jakobsen, V. K. Ozhigin (Eds). Trondheim : Tapir Academic Press, 2011, pp. 768–775.
43. Lyubina O. S., Frolova E. A., Dikaeva D. R. Current zoobenthos monitoring at the Kola Transect in the Barents Sea. In: *Arctic Marine Biology: A Workshop Celebrating Two Decades of Cooperation Between Murmansk Marine Biological Institute and Alfred Wegener Institute for Polar and Marine Research* / G. Hempel, K. Lochte, G. Matishov (Eds). Bremerhaven : Alfred Wegener Institute for Polar and Marine Research, 2012, pp. 177–189. (Berichte zur Polar- und Meeresforschung = Reports on Polar and Marine Research ; no. 640).
44. Løkkeborg S., Fosså J. H. Impacts of bottom trawling on benthic habitats. In: *The Barents Sea: Ecosystem, Resources, Management. Half a Century of Russian–Norwegian Cooperation* / T. Jakobsen, V. K. Ozhigin (Eds). Trondheim : Tapir Academic Press, 2011, pp. 760–767.
45. Rybakova E., Kremenetskaia A., Vedenin A., Boetius A., Gebruk A. Deep-sea megabenthos communities of the Eurasian Central Arctic are influenced by ice-cover and sea-ice algal falls. *PLoS One*, 2019, vol. 14, iss. 7, art. no. e0211009 (27 p.). https://doi.org/10.1371/journal.pone.0211009
46. Zakharov D. V., Jørgensen L. L. New species of the gastropods in the Barents Sea and adjacent waters. *Russian Journal of Biological Invasions*, 2017, vol. 8, iss. 3, pp. 226–231. https://doi.org/10.1134/S2075111717030146
47. Zakharov D. V., Jørgensen L. L., Manushin I. E., Strelkova N. A. Barents Sea megabenthos: Spatial and temporal distribution and production. *Morskoj biologkcheskij zhurnal*, 2020, vol. 5, no. 2, pp. 19–37. https://doi.org/10.21072/mbj.2020.05.2.03

48. Zakharov D. V., Manushin I. E., Nosova T. B., Strelkova N. A., Pavlov V. A. Diet of snow crab in the Barents Sea and macrozoobenthic communities in its area of distribution. *ICES Journal of Marine Science*, 2021b, vol. 78, iss. 2, pp. 545–556. https://doi.org/10.1093/icesjms/fsaa132
49. Zalota A. K., Spiridonov V. A., Vedenin A. A. Development of snow crab *Chionoecetes opilio* (Crustacea: Decapoda: Oregonidae) invasion in the Kara Sea. *Polar Biology*, 2018, vol. 41, iss. 10, pp. 1983–1994. https://doi.org/10.1007/s00300-018-2337-y
50. Zalota A. K., Zimina O. L., Spiridonov V. A. Combining data from different sampling methods to study the development of an alien crab *Chionoecetes opilio* invasion in the remote and pristine Arctic Kara Sea. *PeerJ*, 2019, vol. 7, art. no. e7952 (25 p.). https://doi.org/10.7717/peerj.7952
51. Zalota A. K., Spiridonov V. A., Galkin S., Pronin A. A. Population structure of alien snow crabs (*Chionoecetes opilio*) in the Kara Sea (trawl and video sampling). *Oceanology*, 2020, vol. 60, iss. 1, pp. 83–88. https://doi.org/10.1134/S0001437020010257
52. Zimina O. L. Finding the snow crab *Chionoecetes opilio* (O. Fabricius, 1788) (Decapoda: Majidae) in the Kara Sea. *Russian Journal of Marine Biology*, 2014, vol. 40, iss. 6, pp. 490–492. https://doi.org/10.1134/S1063074014060224

ВЛИЯНИЕ КАМЧАТСКОГО КРАБА И КРАБА-СТРИГУНА ОПИЛИО НА СООБЩЕСТВА МЕГАБЕНТОСА БАРЕНЦЕВА МОРЯ

Д. В. Захаров[1], И. Е. Манушин[2], Л. Л. Йоргенсен[3], Н. А. Стрелкова[2]

[1]Зоологический институт Российской академии наук, Санкт-Петербург, Российская Федерация
[2]Полярный филиал ФГБНУ «ВНИРО» («ПИНРО» имени Н. М. Книповича),
Мурманск, Российская Федерация
[3]Институт морских исследований, Берген, Норвегия
E-mail: *zakharden@yandex.ru*

Работа посвящена проблемам взаимной адаптации двух чужеродных видов промысловых крабов — камчатского краба *Paralithodes camtschaticus* и краба-стригуна опилио *Chionoecetes opilio* — и реципиентной экосистемы Баренцева моря. Представлены данные о распределении сообществ мегабентоса, полученные за период с 2006 по 2020 г. Проанализированы динамика численности крабов и связанные с ней изменения, произошедшие в донных сообществах Баренцева моря за указанные годы. Проведено обсуждение механизмов воздействия крабов на донные сообщества и перспектив освоения ими акватории Баренцева моря. Исследование основано на результатах количественно-таксономического анализа прилова беспозвоночных в 6010 тралениях стандартным учётным тралом Campelen 1800, выполненных в акватории Баренцева моря в 2006–2020 гг. в ходе проведения совместной российско-норвежской экосистемной съёмки на судах Полярного филиала ФГБНУ «ВНИРО» и Института морских исследований (Institute of Marine Research, Bergen, Trømso). Расширение ареала и увеличение численности камчатского краба с начала 1990-х гг. привели к его расселению в обширной акватории южной части Баренцева моря. В 2006–2010 гг. камчатский краб доминировал в сообществах мегабентоса Мурманской и Канинской банок. К 2016–2020 гг. область его доминирования расширилась на север и восток — до острова Колгуев и южного склона Гусиной банки. Рост численности краба-стригуна опилио привёл к заселению им огромной акватории в Баренцевом море — от Печорского моря до архипелага Земля Франца-Иосифа и от архипелага Новая Земля до архипелага Шпицберген. В 2006–2010 гг. численность краба-стригуна опилио начала расти у архипелага Новая Земля, где он выступал в качестве субдоминанта в сообществах мягких грунтов Гусиной банки.

В 2011–2015 гг. краб-стригун опилио стал доминировать в сообществах Гусиной банки, Новоземельской банки, северной части Центральной возвышенности. В то же время он продолжал увеличивать свою роль как вид-субдоминант практически во всех сообществах у архипелага Новая Земля. Позднее, в 2016–2020 гг., краб-стригун опилио доминировал в бентосных сообществах на границе с Карским морем между архипелагами Новая Земля и Земля Франца-Иосифа, на склонах Новоземельской банки, у Центральной банки и в Южно-Новоземельском жёлобе. Его ареал увеличился и в итоге охватил акваторию от архипелагов Земля Франца-Иосифа и Новая Земля до возвышенности Персея на западе и до Печорского моря на юге. Показано, что камчатский краб будет и дальше входить в состав сообществ юго-восточной части Баренцева моря. Краб-стригун опилио продолжит миграцию с востока в западную часть моря вплоть до архипелага Шпицберген, где существуют сходные сообщества бентоса; в случае похолодания миграция пойдёт более быстрыми темпами. Возможен сценарий, при котором мелководье архипелага Шпицберген станет новым центром воспроизводства популяции краба-стригуна опилио в Баренцевом море вместе с нынешним центром у архипелага Новая Земля.

Ключевые слова: Баренцево море, мегабентос, донные сообщества, камчатский краб, *Paralithodes camtschaticus*, краб-стригун опилио, *Chionoecetes opilio*