ICES Journal of
Marine Science

ICES Journal of Marine Science (2021), 78(2), 545–556. doi:10.1093/icesjms/fsaa132

Diet of snow crab in the Barents Sea and macrozoobenthic communities in its area of distribution

Denis V. Zakharov [1,2]*, Igor E. Manushin[1], Tatiana B. Nosova[1], Natalya A. Strelkova[1], and Valery A. Pavlov[1]

[1]Polar branch of VNIRO («PINRO» named after N.M. Knipovich), Murmansk, Russia
[2]Murmansk Marine Biological Institute RAS (MMBI RAS), Murmansk, Russia

*Corresponding author: tel. +7 9021357253; e-mail: zakharden@yandex.ru.

Zakharov, D. V., Manushin, I. E., Nosova, T. B., Strelkova, N. A., and Pavlov, V. A. Diet of snow crab in the Barents Sea and macrozoobenthic communities in its area of distribution. – ICES Journal of Marine Science, 78: 545–556.

Received 7 February 2020; revised 1 July 2020; accepted 2 July 2020; advance access publication 10 October 2020.

This article investigates the diet of the snow crab (*Chionoecetes opilio*) and its feeding intensity in the Barents Sea. Data show that snow crab has a diverse diet that includes almost all types of benthic invertebrates living in the Barents Sea. There are differences between the diets of females and males and of juveniles and adults. Juveniles and females typically occupy shallow areas with communities of bivalve molluscs, while males typically live deeper on slopes and depressions where polychaetes and crustaceans are the most abundant groups. Stomach contents were analysed to determine the species composition and frequency of occurrence of various benthic taxa. Consumption of food was estimated and compared with data from the Russian seas of the Pacific region. The total annual consumption of macrozoobenthos by snow crab was calculated in accordance with its current distribution in the Barents Sea. Snow crab consumes at least 30 000 tonnes of benthos annually, which amounts to 0.1–0.2% of the total macrozoobenthic biomass in the investigated area. The population of snow crab causes the largest impact on the benthic communities in the northeastern part of the Barents Sea and near the south side of the Novaya Zemlya archipelago.

Keywords: Barents Sea, communities, consumption, distribution, feeding, invasion, macrozoobenthos, snow crab (*Chionoecetes opilio*), species composition

Introduction

In recent decades, there have been active processes of populating the eastern waters of the Barents Sea and adjacent sections of the Kara Sea by the snow crab (*Chionoecetes opilio*, O. Fabricius, 1788). The hydrological conditions for the existence of snow crab are close to optimal over almost the entire area of the Barents and Kara seas, with extensive living spaces and suitable food supply (Bakanev, 2015, 2017). In association with these factors, the crab's population is steadily increasing, with new areas of the seabed becoming inhabited on a regular basis.

It is the largest biological invasion in the Barents Sea since the introduction of the red king crab (*Paralithodes camtschaticus*). Expansion patterns suggest that snow crab can be expected to exert a greater influence on the species inhabiting the bottom of the Barents Sea than the red king crab. The red king crab resides in a rather narrow area of the southern Barents Sea, with its distribution limited to warm waters (the average for the red king crab being 3.2–5.5°C; Stevens, 2014), whereas snow crab possesses the ability to settle onto almost the entire Barents Sea shelf. The future dynamics of snow crab abundance will most likely be regulated by food supply and pressure from fishing and predation.

With an increase in the abundance of snow crab in the Barents Sea, a significant increase in its competition with other local benthos-consuming species, primarily demersal fish, should be expected.

Studies on snow crab diet have been made on stocks in traditional areas of the North Pacific (Kun and Mikulich, 1954; Tarverdieva, 1981; Nadtochij *et al.*, 2001; Chuchukalo *et al.*, 2011a, b, 2012; Kolts *et al.*, 2013; Divine *et al.*, 2017) and Northwest Atlantic basins (Brêthes *et al.*, 1982; Lovrich and Sainte-Marie, 1997; Squires and Dawe, 2003). There is minimal published information on snow crab in the Barents Sea (Pavlov, 2007; Tankovskaya (Nosova) and Pavlov, 2014; Nosova, 2016), and only recently have the first data started to appear regarding snow crab diet in the Barents Sea and its potential impact on benthic communities (Zakharov *et al.*, 2016).

In the process of the establishment of the snow crab population in the Barents Sea, the question of how the trophic relationships between snow crab and endemic fauna deserves special attention. The gradual accumulation of knowledge on the nutritional demands of snow crab may make it possible to assess the degree of its impact on the ecosystem and ultimately contribute to more rational management of the Barents Sea fishery resources.

The purpose of this research was to analyse the food base of the snow crab and the characteristics of its diet in the eastern part of the Barents Sea. The following tasks were set to (i) present data on the quantitative and qualitative characteristics of the macrozoobenthos within the portions of the Barents Sea inhabited by snow crab; (ii) identify the main benthic communities being intensively consumed by snow crab; (iii) conduct a taxonomic composition study of invertebrates that are preyed upon by snow crab and their variability depending on population demographics associated with different habitats; (iv) evaluate the intensity of crab consumption of invertebrates in the region; and (v) estimate the annual macrozoobenthos consumption by snow crab within its habitat range in the Barents Sea.

Methods

Benthic community composition

To characterize the macrozoobenthic communities in the areas inhabited by snow crab, data obtained during benthic surveys of the Barents Sea in 2003–2006 were used (Anisimova *et al.*, 2011). The materials sampled at 145 stations were analysed, thus almost completely covering the areas of the Barents Sea with the largest populations of snow crab (Figure 1a). Benthic samples were taken with a van Veen grab with a capture area of 0.1 m^2 in fivefold replications at each station. The samples were washed with seawater in a conical washing sieve made of nylon with a mesh size of 0.5 mm. Materials were fixed in a 4% formaldehyde solution neutralized with sodium tetraborate. All subsequent processing of benthic samples was conducted onshore in a VNIRO laboratory. During the sorting and preparation of samples for taxonomic processing, animals were placed into 75% ethanol. All the biomass values given in this work are represented by the "ethanol" (i.e. wet) weight. Sampled animals were classified, if possible, down to the species level.

The Shannon diversity index was used as a generalized indicator of biodiversity (Shannon, 1948). Discrete classifications of benthic communities were identified by average linkage hierarchical clustering. Czeckanovski's (1909) quantitative index was used as a measure of similarity between stations. In this article, we used the number of species and their production at the station as abundance:

$$\text{Czekanowski's quantitative index}_{ij} = \frac{2\sum_{k=1}^{S}\min(x_{ik},\ x_{jk})}{\sum_{k=1}^{S}(x_{ik}+x_{jk})}, \tag{1}$$

where S = number of species and x_{ik} = production of species k in sample i.

The value of annual species production was estimated by (2) (Manushin, 2008):

$$P = B \times 0.0019 \times (B/N)^{-0.39} \times 365, \tag{2}$$

where P = annual production of a species/taxon (g $m^{-2}year^{-1}$), B = species/taxon biomass (g m^{-2}), N = species/taxon abundance (no. m^{-2}), 0.0019 = daily production of an individual weighing 1 g, and 365 = number of days per year.

Snow crab diet composition

Specimens for analysis of snow crab diet were collected in the period 2000–2019 from VNIRO bottom-trawl surveys in the eastern part of the Barents Sea (Figure 1b). Crabs taken for diet analysis were collected within a geographic area ranging from 30–65°E to 69–78°N in a depth range of 38–371 m.

The survey trawl was a Campelen-1800 shrimp trawl featuring a horizontal footrope opening of 25 m, a vertical opening of 5 m, and a codend liner of 22-mm mesh. Tow duration was 15 min at a speed of 3.1–3.3 knots. In total, crabs were selected opportunistically from 221 tow catches. Crabs selected for diet investigation were subjected to biological analysis: they were weighed, measured for length and width of the carapace, and carapace stage registered (Nizyaev *et al.*, 2006). Stomachs and intestines were removed from study specimens and stored in a 10% solution of neutralized formalin for subsequent laboratory examination. In total, the stomach contents of 971 crabs were analysed, of which 626 were males (carapace widths 22–143 mm) and 345 were females (carapace widths 19–91 mm; Figure 2).

Processing of stomach contents was conducted in a laboratory using the method of quantitative weight analysis (Borutsky *et al.*, 1974). The taxonomic affiliation of the food lump fragments was determined with the highest possible accuracy. The classification of snow crab diet items was conducted in accordance with the World Register of Marine Species (WoRMS) (2020). Unfortunately, due to the strong grinding of food by crabs, it was difficult to determine not only the genus and species of the specimens, but sometimes even the higher taxonomic level. Amorphous material (flaky material of various compositions) was classified as "detritus", and all polychaete tubes of *Spiochaetopterus typicus* were classified as "living biomass".

The constituents of the food lumps were dried on filter paper and weighed to 0.1 mg precision. The frequency of a particular food component occurrence, expressed as a percentage, was determined as the ratio of the number of stomachs in which a diet item was located to the total number of stomachs containing food.

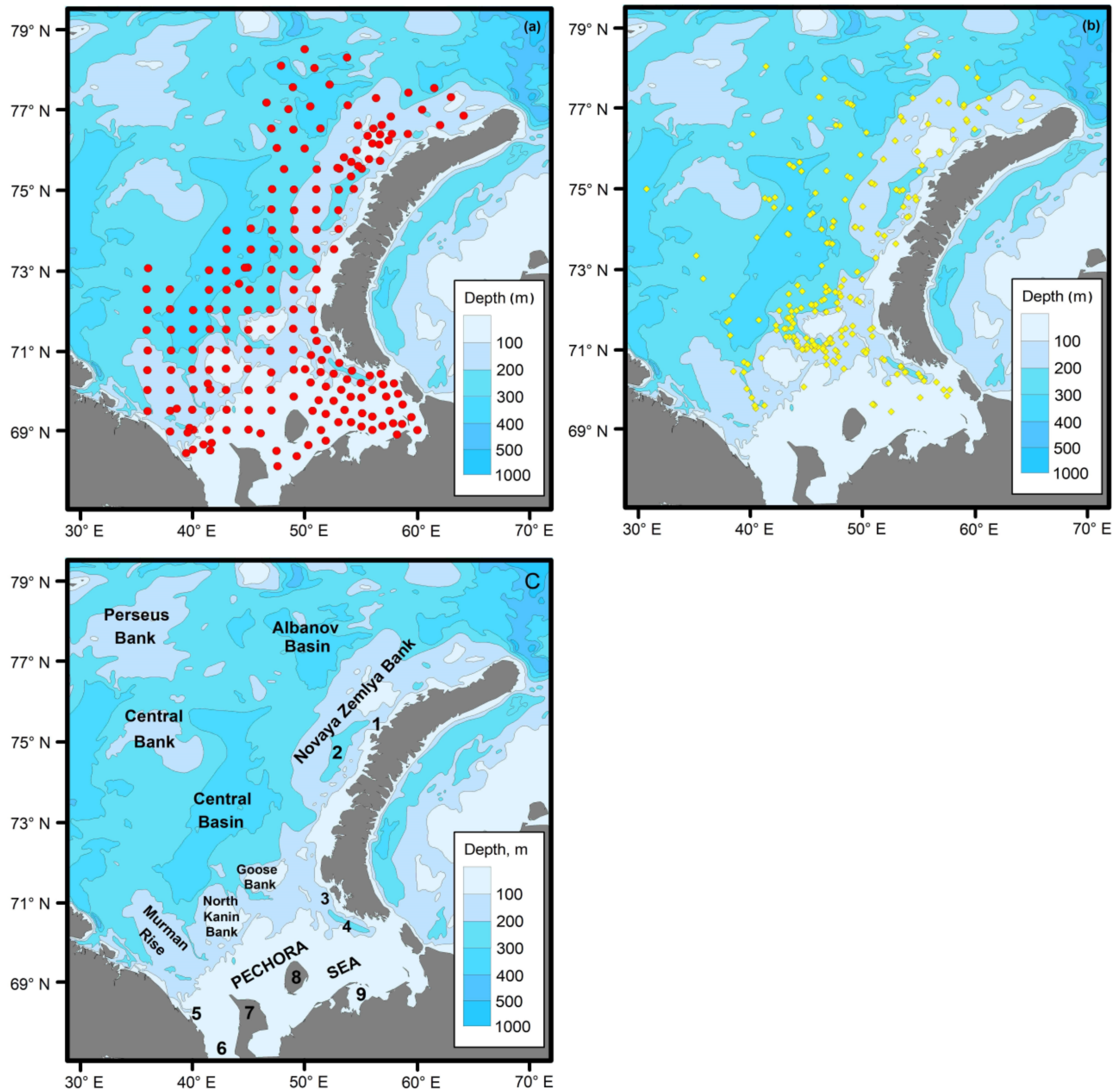

Figure 1. (a) Location of stations used in 2003–2006 benthic survey sampling; (b) locations of snow crab specimen collections for stomach content analysis (2000–2014); and (c) main bathymetric features of the Barents Sea referenced in this study (Zinchenko, 2001): 1—the Admiralty Peninsula; 2—Novozemelsky Trench; 3—Mezhdasharsky Island; 4—South Novozemelsky Trench; 5—the Svyatoy Nos Cape; 6—the White Sea Throat; 7—Kanin Peninsula; 8—Kolguyev Island; and 9—Pechora Bay.

Impacts of consumption by snow crab

To assess the intensity of nutrition, the stomach fullness index (SFI), defined as the ratio of the entire food weight to the total weight of the crab in prodecymille (%), was used. To assess the role of a particular item in the overall diet composition, the partial stomach fullness index (PSFI), calculated as the ratio of the food component's weight to the crab weight of the crab in prodecymille, was used. A mean SFI of stomach fullness was calculated with empty stomachs and mean PSFI without empty stomachs.

Results

Benthic community composition

In the analysed grab samples, 1309 taxa belonging to 15 types, 36 classes, 125 orders, and 328 families of marine bottom invertebrates were distinguished. Out of the 1309 taxa, 1018 were determined to the species level, which constituted 78% of the total taxonomic list. The largest number of species in the researched area was represented by Arthropoda types—275 species (27% of the total species list), Annelida—247 (24%), Mollusca—162 (16%), and Bryozoa—159 species (16%). The total proportion of

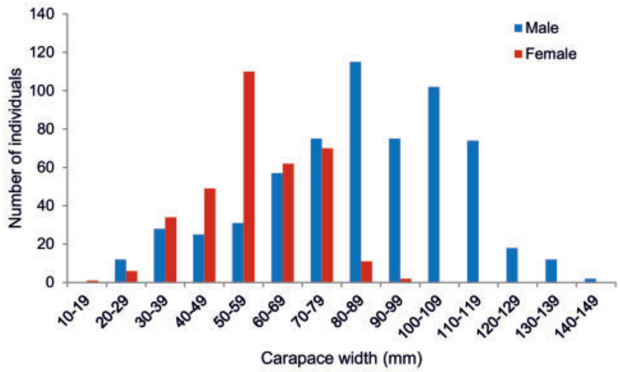

Figure 2. Size composition of male and female snow crab specimens taken for diet analysis.

representatives of other types of animals did not exceed 17% of the total species composition.

Despite being diverse, the benthic community was spatially patchy in distribution in terms of overall abundance. The species variety at different stations ranged from 31 to 212 taxa. The mean species density in the region was 106 ± 3 taxa $0.5\,m^{-2}$. Three regions were observed with a high level of biodiversity: the northern part of the Pechora Sea, the Admiralty Peninsula, and near the Svyatoy Nos Cape (Figure 3a).

The taxonomic structure of the macrozoobenthos in the snow crab's inhabited areas is relatively homogeneous. The largest number of species was represented by worms (mainly polychaetes), molluscs (mainly bivalves and gastropods), and crustaceans. In relatively shallow areas, such as the Novaya Zemlya Bank, the Pechora Sea, and the Murman Rise, the proportion of bryozoans and hydroids increased due to the abundance of solid substrates necessary for the attachment and development of colonies.

Benthic biomass at the sites of the research stations ranged from 1.6 to $2569.2\,g\,m^{-2}$, with a mean of $192.7 \pm 19.4\,g\,m^{-2}$, in the studied area, which is estimated as a considerably large value for the Barents Sea. Previous studies showed that the mean biomass of macrozoobenthos in different periods of the last century ranged from 80 to $147\,g\,m^{-2}$ (Anisimova *et al.*, 2011). Areas with high values of the total benthic biomass—$>200\,g\,m^{-2}$—were observed at the southern end of the Novaya Zemlya archipelago, on the Novaya Zemlya Bank, and on the border with the White Sea Throat (Figure 3b and d). The area of maximum abundance of snow crab coincides roughly with areas of high macrobenthic biomass numbers. This suggests that the rapid increase in the crab population is supported by a rich forage base concentrated in these areas.

Around the Novaya Zemlya Bank, the main clusters of snow crab are concentrated in the habitats of bottom-dwelling communities with a predominance of bivalve mollusc *Macoma calcarea*, barnacle *Balanus*, and sea cucumber *Psolus phantapus*. Concentrations of crabs at the southern end of the Novaya Zemlya archipelago coincide with the location of mass settlements of bivalves *M. calcarea* and *Astarte borealis*. The area around the Svyatoy Nos Cape is characterized by dense settlements of bryozoans and the bivalve *Chlamys islandica*. In this area, the snow crab population is absent; however, yet another invasive species—the red king crab—was present.

The biomass ratio of the main macrozoobenthic groups in the studied region is heterogeneous. Main concentrations are located in the southeastern part of the Barents Sea (e.g. south of the Novaya Zemlya archipelago) and at relatively shallow stations on the Novaya Zemlya Bank. These densest concentrations of macrozoobenthos are dominated by bivalve molluscs. At deep-sea stations in the central part of the region, polychaete worms are the most widespread, among which the seminal polychaeta *S. typicus* predominates, forming up to 90% of the total biomass. In the northern and eastern parts of the researched area, the number of echinoderms in the composition of the bottom population showed a noticeable increase. Stations with a predominance of crustaceans were found mainly in the shallow areas with depths of <100 m, with the main biomass-forming species mainly being the barnacles *Balanus balanus* and *Balanus crenatus*.

The abundance of macrobenthic organisms in the eastern part of the Barents Sea varied from 197 to 10 676 no. m^{-2}, averaging 2912 ± 141 no. m^{-2}. In the northeastern part of the Sea, a region with low density and a minimum abundance of species (182 no. m^{-2}) was found close to the Albanov Basin (Figure 3c). A gradual increase in abundance up to 6930 no. m^{-2} occurs as the depth decreases towards the shores of the Novaya Zemlya archipelago. Thus, along the coast, a belt of increased macrozoobenthic organism density is formed. The highest abundance in the northeastern part of the researched area was recorded for the brittle star *Ophiura robusta* (up to 2000 no. m^{-2}). Significant abundances of benthic organisms were also observed at the Murman Rise and Kanin Bank.

In the southeast part of the study area, a lower density of benthic settlement was noted in the estuary of the Pechora Bay and to the northwest of Kolguyev Island, and an increased density in the southeastern shallow waters of the Pechora Sea. The maximum density (10 676 no. m^{-2}) of macrozoobenthic organisms was recorded to the east of the Pechora Bay.

At the majority of stations in the observed region, polychaete worms predominated. To the east of the Kanin Peninsula, stations with a high density of hydroids were noted, mainly *Obelia longissima* and representatives of the Sertulariidae family. The Novaya Zemlya Bank was represented by stations with a high abundance of *O. robusta*, and bivalve molluscs of the Thyasiridae and Arcidae families dominate in the Albanov Basin.

To identify the key forage species that form the basis of the snow crab food base, the distribution of macrozoobenthic communities in the eastern part of the Barents Sea was mapped. Cluster analysis revealed 17 relatively discrete benthic community types, the characteristics of which are given in Table 1 and the distribution shown in Figure 4. Table 1 shows only 11 main communities associated with snow crab.

Several stations were characterized by the single dominance of such species as *C. islandica* (Ch), *Pelonaia corrugata* (Pc), *Brisaster fragilis* (Bf), *Dacrydium vitreum* (Dv), *Ctenodis cuscrispatus* (Cc), and various bryozoans (Bry). Along with widespread biocenoses in the southeastern part of the sea, with the dominance of *Galathowenia oculata* (Go) and *Serripes groenlandicus* (S), these local communities are not currently included in the habitat area of snow crab.

Snow crab diet composition

The distribution of snow crab overlaps most directly with major concentrations of benthos in the northwestern and southern parts

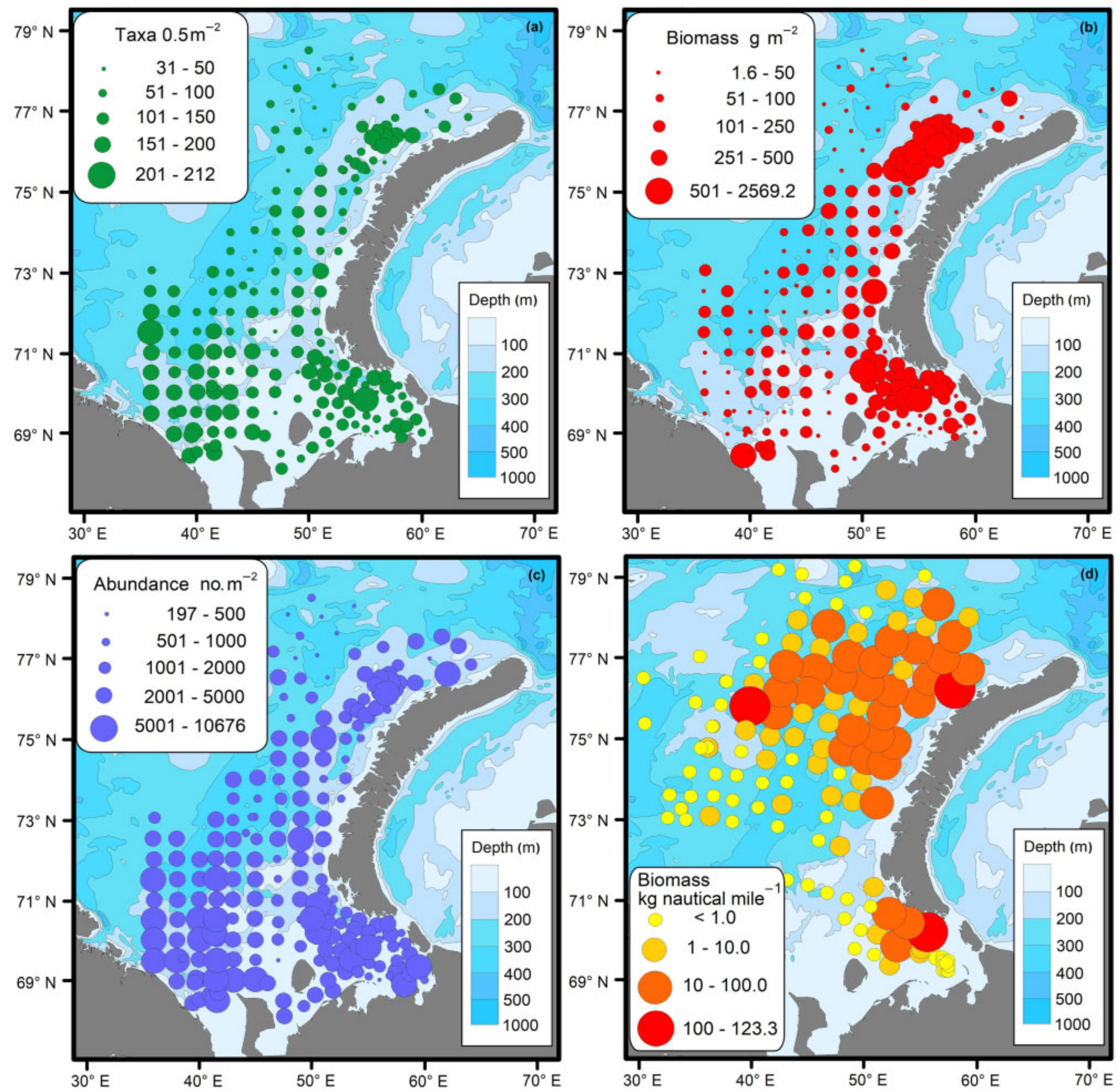

Figure 3. Distribution of macrozoobenthic taxa (taxa 0.5 m^{-2}) (a), biomass (g m^{-2}) (b), abundance (no. m^{-2}) in 2003–2006 (c), and biomass of snow crab (kg nautical mile^{-1}) in 2017 (d).

of Novaya Zemlya, on and near the Novaya Zemlya Bank, and near the South Novozemelsky Trench (Figure 3d).

Individuals within different components of the snow crab population are stratified spatially by depth. Females and small crab are distributed in shallower water and generally on rougher substrates than large adolescents and adult males (Figure 5); the same distribution was observed near Newfoundland (Mullowney *et al*., 2018).

The taxonomic composition of the snow crab diet was quite extensive and included 14 types of free-living invertebrates, 19 classes, 30 orders, 55 families, and 137 taxa, of which 45 taxa were classified up to a species rank (Table 2).

In addition to free-living invertebrates, the remains of algae, fragments of organs, tissues, and fish parasites, as well as detritus and sand, were found in the stomachs of the snow crab.

An analysis of the frequency of occurrence of specific items in the diet of both male and female snow crabs indicated that molluscs (48% of males and 69% of females), annelids (66% for both), arthropods (41 and 31%, respectively), and echinoderms (25 and 28%, respectively) were most often present in the stomachs (Figure 6).

Among the molluscs found in the stomachs of snow crab, bivalves were the most common (in 40% of males and 64% of females); among annelids, polychaetes (in 66% of both sexes);

Table 1. Parameters of the main communities in the eastern part of the Barents Sea according to 2003–2006 (names of columns same as names of communities in Figure 4).

Parameter	Community										
	Ac	Bg	S	Sk	Mc	Ab	St	C	P	B	Go
Depth (m)	193.3 ± 27.2 (112–335)	263.3 ± 11.9 (238–294)	37.1 ± 6.3 (10–37)	268.0 ± 20.6 (212–303)	127.2 ± 8.4 (86–213)	81.2 ± 4.9 (8–132)	235.8 ± 7.8 (126–366)	112.1 ± 22.8 (18–240)	132.2 ± 8.8 (117–147)	76.3 ± 4.2 (52–107)	176 ± 9.2 (143–200)
Total number of taxa	354	170	395	218	549	722	783	432	208	597	401
Species density (taxon 0.5m^{-2})	74.1 ± 15.6 (31–157)	71.8 ± 8.8 (41–90)	86.8 ± 9.3 (34–154)	101.0 ± 10.8 (85–133)	105.3 ± 8.2 (38–160)	120.0 ± 5.7 (42–200)	96.1 ± 4.9 (35–212)	113.3 ± 15.2 (34–188)	103.6 ± 16.0 (74–129)	126.7 ± 9.5 (51–164)	150.8 ± 2.0 (145–158)
Biomass (g m^{-2})	49.6 ± 29.4 (1.6–281.7)	101.5 ± 25.5 (31.8–187.6)	90.6 ± 28.5 (4.6–385.8)	46.9 ± 17.6 (14.6–85.2)	377.2 ± 63.3 (13.1–896.3)	242.1 ± 38.1 (5.3–1 253.1)	97.2 ± 9.4 (13.6–321.6)	148.7 ± 13.8 (94.3–206.5)	637.1 ± 101.5 (458.6–810.2)	531.0 ± 183.9 (58.4–2 569.2)	39.4 ± 7.7 (16.7–59.6)
Abundance (no. m^{-2})	1 078 ± 374 (204–3 072)	1 662 ± 478 (346–2 986)	2 694 ± 743 (272–10 676)	2 270 ± 685 (1 123–3 896)	2 392 ± 285 (700–4 700)	3 227 ± 305 (316–9 292)	2 828 ± 252 (444–10 162)	3 719 ± 725 (512–6 204)	2 684 ± 362 (2 276–3 408)	3 314 ± 492 (773–6 926)	5 244 ± 417 (3 636–6 384)
Dominant species by biomass	*Astarte crenata*	*Bathyarca glacialis*	*Serripes groenlandicus*	*Polymastia grimaldii*	*Macoma calcarea*	*Astarte borealis*	*Spiochaetopterus typicus*	*Clinocardiumciliatum*	*Psolus phantapus*	*Balanus balanus*	*Brisaster fragilis*
Dominant species by abundance	*A. crenata*	*Galathowenia oculata*	*G. oculata*	*Spiophanes kroeyeri*	*Ophiura robusta*	Nematoda	*S. typicus*	*G. oculata*	*Philomedes globosus*	*O. robusta*	*G. oculata*
Dominant species by production	*A. crenata*	*B. glacialis*	*S. groenlandicus*	*S. kroeyeri*	*M. calcarea*	*A. borealis*	*S. typicus*	*C. ciliatum*	*P. phantapus*	*B. balanus*	*G. oculata*
Shannon index (biomass)	3.2 ± 0.3	2.3 ± 0.1	2.5 ± 0.3	3.4 ± 0.5	3.1 ± 0.1	2.7 ± 0.1	3.0 ± 0.1	3.4 ± 0.1	2.2 ± 0.1	2.9 ± 0.2	4.8 ± 0.3
Shannon index (abundance)	4.8 ± 0.2	4.6 ± 0.1	4.7 ± 0.1	5.0 ± 0.2	5.1 ± 0.1	5.1 ± 0.1	4.5 ± 0.1	4.9 ± 0.2	4.8 ± 0.1	5.1 ± 0.2	5.5 ± 0.2

The mean values are given with a standard error; the variation range of the parameters is indicated in parentheses.

among arthropods, higher crustaceans (29 and 17%, respectively); and among echinoderms, brittle stars (18% in both sexes; Figure 7). Of the bivalve molluscs, the most common crab prey was *Nuculana pernula*, *Ennucula tenuis*, *Ciliatocardium ciliatum*, and *Macoma* sp. Among polychaetes, *S. typicus* and representatives of Terebellida (from the genera *Mellina* and *Pectinaria*) were more often preyed upon. Higher crustaceans were primarily represented by the order Decapoda: shrimps (*Sabinea septemcarinata*, *Sclerocrangon ferox*, *Pandalus borealis*), crabs (*C. opilio*, *Hyas araneus*), and hermit crab (*Pagurus pubescens*).

Impacts of consumption by snow crab

The frequency of an object's occurrence in the digestive system does not always give a complete picture of its role in the nutrition of the studied species. A weight analysis of components of the stomach's contents allows a fuller characterization of the nutritional characteristics. A quantitative weight analysis of the contents of the stomachs of different categories of crabs showed that the intensity of females' feeding was significantly higher than that of males (Table 3). The mean SFI value for females was 14.0 ± 1.4%, while for males, it was only 8.6 ± 0.6%. In this case, the difference in the mean sizes of males and females does not matter—even if males and females belonging to the same size range were taken into account, the mean SFI value for males would increase to only 10.0 ± 0.9%.

The differences noted are statistically significant for both the general consumption of food (SFI), as well as for most of its components, with the exception of crustaceans and polychaetes (PSFI; Table 3).

The SFI showed a reliable correlation with the carapace width both for males [F_{fact} (2.85) > F_{crit} (1.80), $p = 0.0012$], but not for females [F_{fact} (1.25) > F_{crit} (2.13), $p = 0.28$; Table 4]. The SFI of males decreased with the crabs' growth, reflecting a decrease in physiological needs. In females, the picture is less clear and probably requires more samples.

A comparison of the SFI values did not reveal significant differences with changes in depth of sampling for both females and males. There were also no significant differences in SFI values in relation to depth for both sexes.

Concerning the spatial distribution of the mean values of the benthic PSFI, it can be concluded initially that its higher values occur on the edges of slopes of underwater banks (Figure 8).

Discussion

Benthic community composition

The areas of high snow crab density coincide with that of communities dominated by *M. calcarea* (Mc), *A. borealis* (Ab), *S. typicus* (St), *Clinocardium ciliatum* (C), *P. phantapus* (P), and barnacles of the genus *Balanus* (B) (Figure 4).

A community dominated by the bivalve detritus clam *M. calcarea* occupies the entire northern part of the Novaya Zemlya Bank, the area of the Southern Novaya Zemlya Trench, and near Mezhdasharsky Island. Clay and silty-sandy sediments mixed with stones are typical in these areas, with depths of ~100–150 m (Lepland *et al.*, 2014). The *M. calcarea* community is characterized by high productivity and biodiversity indices. *Macoma calcarea* accounts for about half of the community's gross biomass and about one-third of its total production. In addition to *M. calcarea*, the community is characterized by

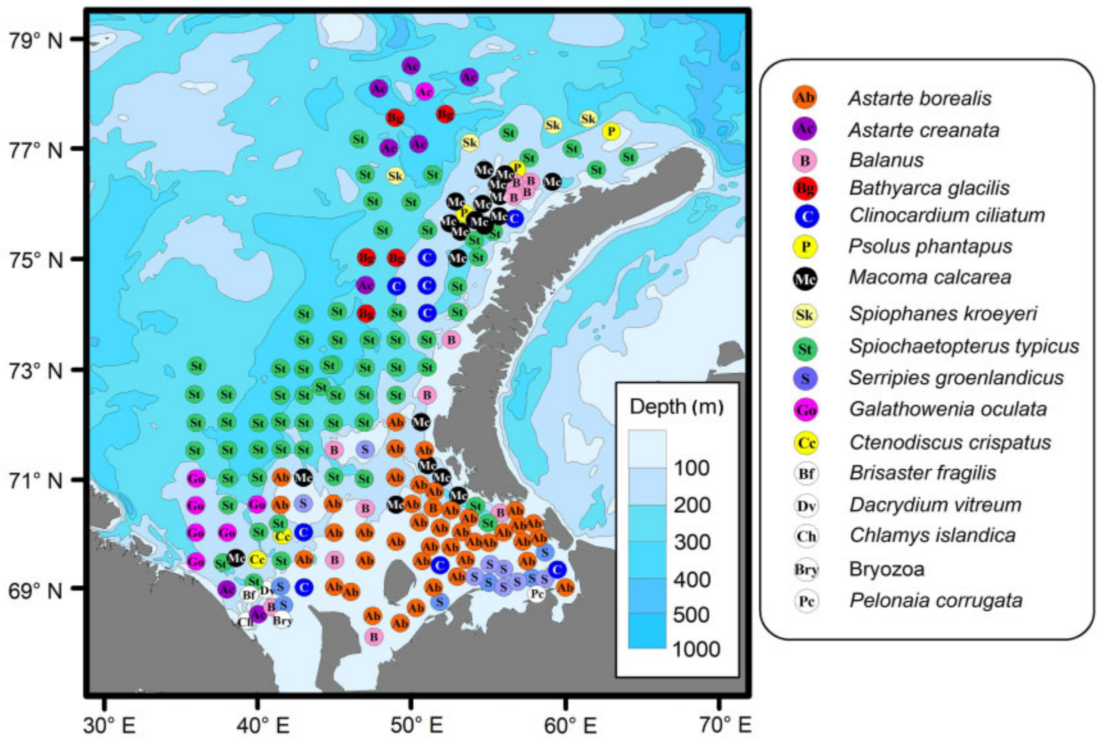

Figure 4. Distribution of the macrozoobenthic communities in the eastern part of the Barents Sea in 2003–2006.

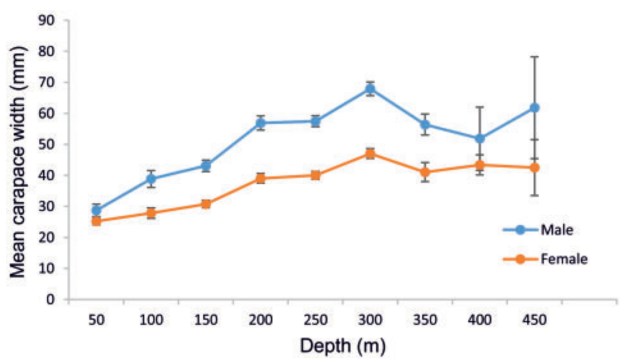

Figure 5. Vertical stratification of snow crab by carapace width in the Barents Sea from 2004 to 2019.

massive populations of the brittle star *O. robusta* and the holothurian sestonophage *P. phantapus*. The abundance of *O. robusta* at some stations reached 1500 no. m^{-2}.

Communities with a dominance of sedimentary polychaete *S. typicus* are widespread in the Barents Sea and, within the studied area, occur in almost all the deep-sea bottom regions. It occupies the southern, western, and northern slopes of the Novaya Zemlya Bank and is observed on the slopes of the Novozemelsky Trench and the Admiralty Peninsula. As in the central part of the Barents Sea, the community of *S. typicus* is formed at medium depths (200–250 m), predominately on soft-silt and silty-sandy substrates.

In the southeastern part of the Barents Sea, the most widespread community is the bivalve mollusc *A. borealis*. It occupies almost the entire central part of the Pechora Sea at depths of 50–130 m with silty-sandy and mixed substrates. The biomass and density of benthic settlements here may exceed 1 kg m^{-2} and almost 10 000 no. m^{-2}, averaging ~400 g m^{-2} and 4000 no. m^{-2}, respectively. Species of polychaetes such as *S. typicus*, *Maldane sarsi*, and *G. oculata* can serve as secondary or tertiary dominant players in this community.

Stations located in the southern part of the Novozemelsky Trench are characterized by massive settlements of the large bivalve mollusc *C. ciliatum*. Despite the fact that this mollusc is widespread throughout the studied area, only in this area is it the dominant species of the benthic community.

At depths of <100 m, a community of fouling organisms is formed consistently, typically associated with fine to coarse-stony material, among which barnacles of the genus *Balanus* dominate.

On the Novaya Zemlya Bank, on mixed sediments, and at depths of ~100–200 m, a significant amount of biomass can be formed by a relatively large holothurian—the sestonophage *P. phantapus*. At some individual stations, it acts as a leading species among the bottom-dwelling organisms.

The stock of macrozoobenthos in the eastern part of the Barents Sea (an area of ~612 000 km^2), estimated by the method, amounted to 92.1 million tonnes of matter, of which 76.7 million tonnes (83%) is comprised of items found in the diet of snow crab. The benthic biomass of the snow crab prey within the studied water area varied from 1.1 to 2281.1 g m^{-2} and, on average across the region, amounted to 164.1 ± 17.3 g m^{-2}. The proportion of suitable benthos at different stations varied from 7.1 to 100%, mean 84.7 ± 1.3% (median 91.5).

The presented data indicate that both the abundance and composition of the Barents Sea benthos are favourable for the successful development and long-term sustainability of the snow crab population.

Table 2. List of taxa of free-living invertebrates found in the stomachs of snow crab in the Barents Sea from 2000 to 2019.

Taxon	Taxon	Taxon
Foraminifera g. sp.	Copepoda g. sp.	*Hiatella arctica* (Linnaeus, 1767)
Hauerinidae g. sp.	Amphipoda g. sp.	*Hiatella* sp.
Porifera	*Ampelisca macrocephala* Liljeborg, 1852	*Bathyarca glacialis* (Gray, 1824)
Porifera g. sp.	*Haploops* sp.	*Bathyarca* sp.
Cnidaria	*Haploops laevis* (Hoek, 1882)	*Ciliatocardium ciliatum* (Fabricius, 1780)
Anthozoa g. sp.	*Ampelisca* sp. *Byblis* sp.	*Serripes groenlandicus* (Mohr, 1786)
Actiniaria g. sp.	Gammaridae g. sp.	Cardiidae g. sp.
Hydrozoa g. sp.	Lysianassidae g. sp.	*Chlamys islandica* (O. F. Muller, 1776)
Nemertea	Stegocephalus sp.	*Macoma calcarea* (Gmelin, 1791)
Nemertea g. sp.	Cumacea g. sp.	*Macoma* sp.
Nematoda	*Diastylis goodsiri* (Bell, 1855)	*Astarte borealis* (Schumacher, 1817)
Nematoda g. sp.	*Diastylis* sp.	*Astarte crenata* (Gray, 1824)
Cephalorhyncha	*Eudorella* sp.	*Astarte* sp.
Priapulus caudatus Lamarck, 1816	Decapoda g. sp.	*Crenella decussata* (Montagu, 1808)
Priapulidae g. sp.	*Sabinea septemcarinata* (Sabine, 1824)	*Mya* sp.
Annelida	*Sclerocrangon ferox* (Sars G.O., 1877)	*Nuculana pernula* (O. F. Müller, 1779)
Polychaeta g. sp.	*Sabinea* sp.	*Nuculana* sp.
Spiochaetopterus typicus M Sars, 1856	*Sclerocrangon* sp.	*Musculus sp.*
Maldanidae g. sp.	*Chionoecetes opilio* (O. Fabricius, 1788)	*Thyasira flexuosa* (Montagu, 1803)
Maldane sarsi (Malmgren, 1865)	*Hyas araneus* (Linnaeus, 1758)	*Yoldia hyperborea* (Gould, 1841)
Nicomache lumbricalis (Fabricius, 1780)	*Hyas* sp.	*Yoldiella intermedia* (Sars, 1865)
Praxillella sp.	*Pagurus pubescens* Krøyer, 1838	*Yoldiella lenticula* (Møller, 1842)
Orbiniidae g. sp.	*Pagurus* sp.	*Portlandia* sp.
Lumbrineridae g. sp.	*Macrura g. sp.*	*Portlandia arctica* (Gray, 1824)
Lumbrineris sp.	*Pandalus borealis* Krøyer, 1838	*Yoldiella* sp.
Lumbrineris tetraura (Shmarda, 1861)	*Pandalus* sp.	*Ennucula tenuis* (Montagu, 1808)
Aglaophamus sp.	*Meganyctiphanes norvegica* (M. Sars, 1857)	*Ennucula* sp.
Nephtyidae g. sp.	Euphausiidae g. sp.	Pectinidae g. sp.
Nephtys sp.	Isopoda g. sp.	*Similipecten greenlandicus* (G. B. Sowerby II, 1842)
Nereis zonata (Malmgren, 1867)	*Saduria sabini* (Krøyer, 1849)	Scaphopoda g. sp.
Harmothoe sp.	*Saduria* sp.	*Antalis entalis* (Linnaeus, 1758)
Gattyana sp	Mysidacea g. sp.	*Antalis* sp.
Polynoidae g. sp.	Ostracoda g. sp.	*Siphonodentalium lobatum* (G. B. Sowerby II, 1860)
Galathowenia oculata (Zachs, 1923)	Mollusca	Brachiopoda
Myriochele heeri (Malmgren, 1867)	Mollusca g. sp.	Brachiopoda g. sp.
Owenia fusiformis (Delle Chiaje, 1844)	Caudofoveata g. sp.	*Hemithyris psittacea* (Gmelin, 1791)
Myriochele sp.	Solenogastres g. sp.	Bryozoa
Owenia sp.	Gastropoda g. sp.	Bryozoa g. sp.
Oweniidae g. sp.	*Moelleria costulata* (Møller, 1842)	Echinodermata
Chone sp.	*Margarites* sp.	Echinodermata g. sp.
Ampharete borealis (M. Sars, 1856)	*Margarites groenlandicus* (Gmelin , 1791)	*Eupyrgus scaber* Lütken, 1857
Ampharete sp.	Trochidae g. sp.	Echinoidea g. sp.
Ampharetidae g. sp.	*Scaphander punctostriatus* (Mighels and Adams, 1842)	*Strongylocentrotus* sp.
Melinna sp.	*Cryptonatica affinis* (Gmelin, 1791)	*Strongylocentrotus pallidus* (Sars G. O., 1872)
Cirratulidae g. sp.	*Euspira pallida* (Broderip and Sowerby, 1829)	Asteroidea g. sp.
Brada sp.	Naticidae g. sp.	Ophiuroidea g. sp.
Flabelligeridae g. sp.	*Frigidoalvania janmayeni* (Friele, 1878)	*Ophiocten sericeum* (Forbes, 1852)
Cistenides hyperborea Malmgren, 1866	*Frigidoalvania* sp.	*Ophiocanta bidentata* (Bruzelius, 1805)
Pectinaria sp.	*Marsenina glabra* (Couthouy, 1838)	*Ophiura sarsii* (Lütken, 1855)
Terebellidae g. sp.	Mangeliidae g. sp.	Ophiuridae g. sp.
Spionidae g. sp.	Buccinidae g. sp.	*Heliometra glacialis* (Owen, 1833)
Sabellides borealis (M. Sars, 1856)	*Colus* sp.	Chordata
Sipuncula	*Buccinum* sp.	Tunicata g. sp.
Sipunculidea g. sp.	*Neptunea* sp.	Ascidiacea g. sp.
Golfingia vulgaris vulgaris (de Blainville, 1827)	*Admete viridula* (Fabricius, 1780)	*Cnemidocarpa rhizopus* (Redikorzev, 1907)
Golfingia sp.	Bivalvia g. sp.	
Nephasoma sp.	*Montacuta spitzbergensis* (Knipowitsch, 1901)	
Arthropoda		
Crustacea g. sp.		
Calanus finmarchicus (Gunnerus, 1770)		
Calanus sp.		

Snow crab diet composition

The obtained data on the snow crab diet in the Barents Sea as a whole allow us to conclude that its diet shows no fundamental differences from the diet of this species in the Far Eastern seas. As in the native part of its habitat, crabs feed mainly on the most widespread and accessible benthic groups in the Barents Sea. A similar phenomenon was noted in the Far Eastern seas (Nadtochij *et al.*, 2001; Tarverdieva, 2001; Chuchukalo *et al.*, 2011a, b).

The mean total SFI of the Barents Sea snow crabs is also similar to that of Far Eastern populations. For example, Tarverdieva (1981, 2001) gives the SFI values from the Bering Sea for juveniles—28.0 and 25.7%, for adult crabs—7.5%, and for commercial males (>100 mm CW)—6.9%.

Interestingly, the crab diet in the Barents Sea has one notable difference from that of snow crab in the Far Eastern seas. The feeding intensity of female Barents Sea snow crab is significantly higher (approximately twofold) than that of males. So far, a logical explanation for this fact has not been found. Whether this is an anatomical and physiological feature of the Barents Sea females or has been caused by the new living conditions remains to be seen.

During comparisons of the dietary data for invasive/introduced crab species in the Barents Sea—snow crab and red king crab—similar mean values of the SFI were noted—>10% for individuals with a carapace width of up to 100 mm (Manushin, 2003). A significant difference for snow crab is that its individuals can have an index of 100% or more, which has never been recorded for the red king crab. The qualitative composition of food in the digestive systems of both species is somewhat different—for the red king crab, bivalve molluscs, brittle stars, starfish, and crustaceans are more prevalent, while for snow crab, it is bivalve molluscs, polychaetes, crustaceans, and brittle stars.

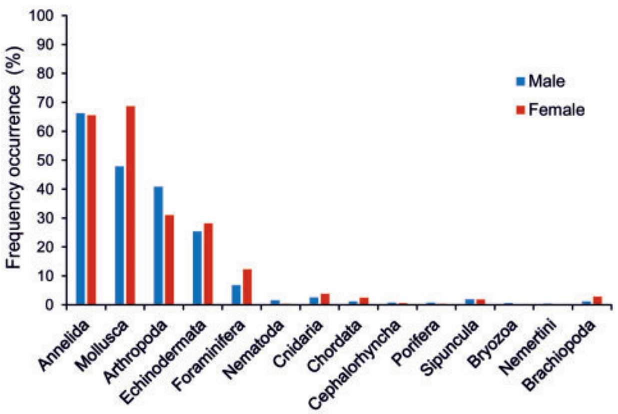

Figure 6. Frequency occurrence of different types of invertebrate in the diet of both male and female snow crabs in the Barents Sea from 2000 to 2019.

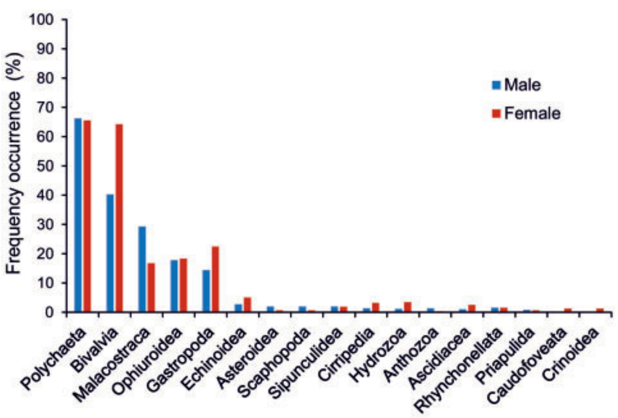

Figure 7. Frequency occurrence of different types of invertebrate in the diet of both male and female snow crabs in the Barents Sea from 2000 to 2019.

Impacts of consumption by snow crab

Typically, a quantitative assessment of food consumption by commercial crabs is estimated either from the results of processing data from daily trawling stations, or from experimental feeding, or by compiling mass balance equations of energy metabolism (Sushchenya, 1975). However, diurnal station monitoring has not been carried out for snow crab in the Barents Sea. The literature on the diet of this type of crab is scarce and relates mainly to prey diversity (Tarverdieva, 1981; Squires and Dawe, 2003).

Attempts to estimate the daily ration of Far Eastern snow crab individuals (Nadtochij *et al.*, 2001; Chuchukalo *et al.*, 2011a, b, 2012) showed consumption values of 1.4–5.5% of body weight. These data, however, are very approximate because, in the first two studies, the material was collected at different places from a wide range of depths, so they do not reflect the dynamics over time, rather the changes in prey consistency in different areas. Chuchukalo *et al.* (2012) do not provide direct data on daily consumption but highlight a daily intake of 2.4% of body weight. Meanwhile, it is well known that the level of food intake in ectothermic animals depends on both body weight and ambient temperature. However, the authors of these studies themselves

Table 3. Mean SFI and reliability of its difference between male and female snow crabs based on ANOVA in the Barents Sea from 2000 to 2019.

Food group	Male SFI (%)	Female SFI (%)	$F_{fact.}$	F_{crit}	*p*-Value
All food	8.57 ± 0.62	14.02 ± 1.36	17.41	3.85	0.00003
Fish	1.27 ± 0.40	0.25 ± 0.09	4.02	3.85	0.045
All benthos	9.12 ± 0.64	14.76 ± 1.46	16.19	3.85	0.00006
Annelida	3.07 ± 0.39	4.55 ± 0.60	4.72	3.85	0.030
Arthropoda	2.41 ± 0.32	2.83 ± 0.50	0.55	3.85	0.46
Echinodermata	1.22 ± 0.25	2.12 ± 0.64	2.29	3.85	0.13
Mollusca	1.28 ± 0.16	4.16 ± 0.61	30.15	3.85	0.00000005

Table 4. SFI in relation to carapace width of both male and female snow crabs in the Barents Sea from 2000 to 2019.

Food group	Male SFI (%)	Female SFI (%)	F_{fact}	F_{crit}	*p*-Value
All food	8.57 ± 0.62	14.02 ± 1.36	17.41	3.85	0.00003
Fish	1.27 ± 0.40	0.25 ± 0.09	4.02	3.85	0.045
All benthos	9.12 ± 0.64	14.76 ± 1.46	16.19	3.85	0.00006
Annelida	3.07 ± 0.39	4.55 ± 0.60	4.72	3.85	0.030
Arthropoda	2.41 ± 0.32	2.83 ± 0.50	0.55	3.85	0.46
Echinodermata	1.22 ± 0.25	2.12 ± 0.64	2.29	3.85	0.13
Mollusca	1.28 ± 0.16	4.16 ± 0.61	30.15	3.85	0.00000005

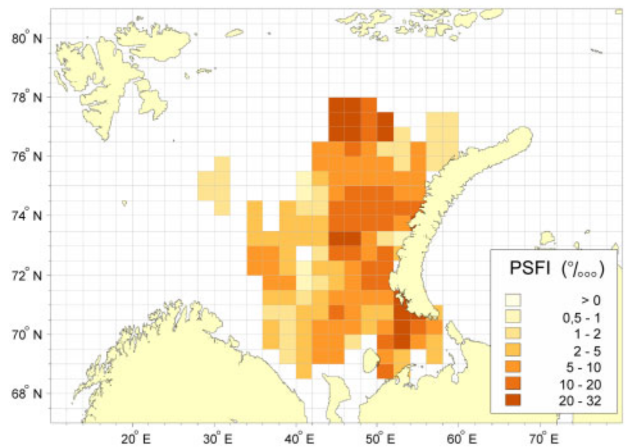

Figure 8. Long-term distribution of mean PSFI of benthic snow crab prey in the Barents Sea.

Table 5. Parameters of the snow crab population in the Barents Sea and estimates of its minimum exemption level of benthic organisms in 2005–2017.

Year	Population (no. in millions)	Mean crab weight (g)	Mass of consumed food [g (no. × year)]	Biomass of consumed food (t year^{-1})	Benthos exemption (t year^{-1})	Crab density (no. m^{-2})	Benthos exemption [g (year×m^2)]$^{-1}$
2005	2.5	255	60	153	278	0.00006	0.0060
2006	6.5	147	38	247	450	0.00013	0.0088
2007	8.6	139	36	312	567	0.00013	0.0083
2008	45.3	104	28	1 284	2 338	0.00049	0.0245
2009	36.9	132	35	1 278	2 326	0.00026	0.0152
2010	104.3	50	15	1 597	2 907	0.00031	0.0098
2011	307.1	25	9	2 627	4 782	0.00420	0.0566
2012	436.5	32	11	4 596	8 364	0.01295	0.2574
2013	826.1	59	18	14 539	26 462	0.00865	0.2709
2014	727.7	51	16	11 331	20 623	0.00236	0.0914
2015	704.6	89	25	17 515	31 877	0.00228	0.0762
2016	240.7	63	19	4 477	8 149	0.00110	0.0411
2017	680.2	55	17	11 315	20 594	0.00688	0.2310

recognize that the results they have obtained are mostly theoretical.

Due to the complex size and gender structure, large differences in the age of coming to maturity, growth rates, and the number of moults over a lifetime, along with the extremely scarce information on the biological parameters of the Barents Sea population of snow crab, there is currently no way to arrive at the correct balance equations of energy metabolism. At the same time, in this situation, based on the importance of assessing at least the minimum food intake by snow crab, it is possible to use a similar species for which the level of daily food intake is known in relation to body weight and, in turn, extrapolate its characteristics to estimate the daily intake of snow crab (Sushchenya, 1975).

In this research, to obtain the needed numbers regarding the daily diet of snow crab, the equation parameters for the Barents Sea red king crab were used, taking into account the fact that this

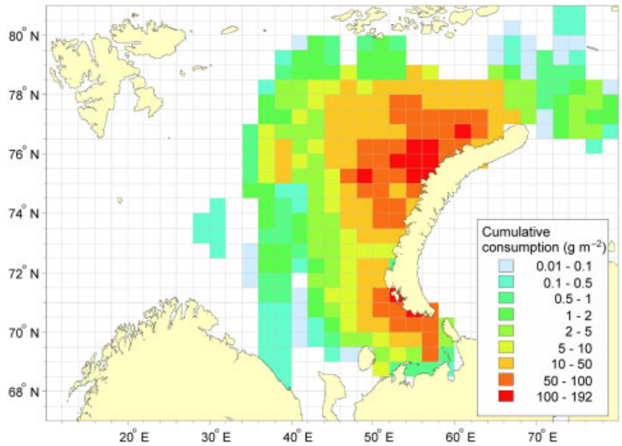

Figure 9. Cumulative consumption of benthos (g m^{-2}) by snow crab, 2005–2017.

species has been more thoroughly researched in relation to trophic activity (Manushin, 2003). Assuming that the nutritional needs of individuals of the same weight from these two species are approximately equal, we can use the equation for the red king crab dependence on daily ration demand based on the mass of the individual and ambient temperature (Sushchenya, 1975). The only modification of this power equation is to correct the temperature scale to the living conditions of snow crab—a temperature of −2°C was taken as zero. The resulting equation is as follows:

$$P = 0.05 \times W^{-0.16} \times T^{1.65}, \quad (3)$$

where P = daily diet (% of body weight), W = weight of crab (g), and T = modified surrounding temperature ($t+2$; °C).

The snow crab population index is calculated annually based on ecosystem survey data. The mean weight of an individual is the ratio of the total mass of crabs caught to their total number for each year. The mean temperature at which crabs of this species live in the Barents Sea was taken as 0°C, based on the fact that most of the population throughout the entire time lives in the temperature range of about −2°C to +2°C. The long-term mean proportion of benthos in the food lump was calculated to be 0.91 ± 0.01%. The values of the approximate minimum food intake by snow crab, obtained on the basis of the listed initial data, are shown in Table 5.

As with the red king crab, it is generally accepted for snow crab that during feeding on benthos, almost half of the captured food mass is lost and does not enter the stomach. Thus, the actual exemption of benthos is twofold higher than the biomass eaten by the crab to meet its needs.

Lately, the estimated minimum biomass of benthos destroyed by the Barents Sea population of snow crab has been ∼30 000 tonnes annually. Actual losses of benthic biomass through consumption by the entire snow crab population in the Barents Sea are, of course, greater. One of the reasons for this is that small crabs, due to their low catchability by fishing gear, are not taken into account in the calculations. Another reason for the underestimation of the biomass of consumed benthos is the high uncertainty in the estimates of snow crab abundance. In addition, the assessment of food consumption based on the mean weight of an individual (calculated over the entire population, excluding the actual size structure) also introduces a significant error into the results.

In recent years, there has been an increase in the consumption of benthos by snow crab, which has significantly increased the pressure of this predator in certain areas of the Barents Sea. This increase is directly dependent on the increase in the density of *C. opilio*. According to the roughest estimate, the perturbation of benthos by snow crab in the Barents Sea has now increased by at least 70-fold in comparison with 2005 (see Table 5). Even with likely gross underestimation of indices, we find that snow crab exerts the most severe impact on the bottom communities in the northeast of the Barents Sea and at the southern tip of the Novaya Zemlya archipelago (Figure 9).

Conclusions

The areas of mass inhabitation of snow crab in the Barents Sea coincide with those of the most abundant and diverse benthic fauna, which provide a rich forage base for both juveniles and adults. Areas most densely populated by juvenile crab coincide chiefly with the area predominantly populated by the bivalves *M. calcarea* and *A. borealis*; the deeper habitats of mainly adult crabs coincide with the widespread population of the polychaete *S. typicus*.

The amount of macrozoobenthos in the eastern part of the Barents Sea is estimated to be 92.1 million tonnes, of which 76.7 million tonnes are a potential food supply for snow crab. According to a rough estimate and likely low estimate, the crab currently consumes at least 30 000 tonnes of benthos annually, which is 0.1–0.2% of the total macrozoobenthic biomass in the studied area. Even taking into account some underestimation of the level of benthos consumption by the population as a whole, this value can be considered to be very insignificant.

At the same time, taking into account the extremely uneven distribution of the density of the crab population and the level of their consumption of benthos within the current habitats, in the places of their densest clusters in the Novaya Zemlya Bank water and at the southwestern tip of the Novaya Zemlya archipelago, a stronger top-down press effect of snow crab on local bottom-dwelling populations is expected.

The obtained results indicate a fairly wide range of snow crab diet in the Barents Sea. The range of forage objects includes representatives of almost all the main groups of the Barents Sea benthos. As in the native part of the range, crabs in the Barents Sea feed mainly on the most abundant and accessible bottom-dwelling organisms.

The differences in the diet of females, males, juveniles, and adult individuals were shown. Commercial males and females differ in their main forage items and between commercial-sized and non-commercial-sized males in secondary items. This fact is directly related to the differentiated habitats of these groups. Juveniles and females prefer shallow areas, such as the Novaya Zemlya Bank, with the local communities dominated by bivalves (*M. calcarea, A. borealis, Astarte crenata*, and *C. ciliatum*), while males live deeper on slopes and in depressions, where, on muddy sediments, the most accessible food items are polychaetes and crustaceans.

An increase in the proportion of fish in the diet of snow crab is observed only in males with a carapace width of >90 mm. The consumption of fish by the crab is sporadic, and the high percentage of consumption by large males is explained by the higher mobility of adult specimens.

Acknowledgements

We acknowledge the joint Norwegian-Russian Ecosystem surveys of IMR and PINRO and all colleagues and staff on the ships, in the laboratories, and in the offices. We thank the anonymous reviewers of the manuscript for their useful comments.

References

Anisimova, N. A., Jørgensen, L. L., Lyubin, P. A., and Manushin, I. E. 2011. Benthos. *In* The Barents Sea—Ecosystem, Resources, Management. Half a Century of Russian-Norwegian Cooperation, pp. 121–159. Ed. by T. Jakobsen and V. Ozhigin. Tapir Academic Press, Trondheim. 825 pp.

Bakanev, S. V. 2015. Dispersion and assessment of possible distribution of snow crab opilio (*Chionoecetes opilio*) in the Barents Sea. Printsipy ehkologii, 15: 27–39. (In Russian)

Bakanev, S. V. 2017. Prospects snow crab *Chionoecetes opilio* fishery in the Barents Sea. Voprosy rybolovstva, T18, 3: 286–303. (In Russian)

Borutsky, E. V., Verigina, I. A., Zhetenkova, M. V., Karpevich, A. F., Fortunatova, K. R., and Chayanova, L. A. 1974. Methodical Manual on the Study of Nutrition and Food Relations of Fish In Vivo. Nauka. Moscow. 254 pp. (In Russian)

Brêthes, J.-C. F., Desrosiers, G., and Coulombe, F. 1982. Food of the Snow Crab (Chionoecetes opilio) from the Southwestern Part of the Gulf of St. Lawrence (*Chaleur Bay area*). Alaska Sea Grant Report, 82-10: 319–335.

Chuchukalo, V. I., Nadtochij, V. A., Borilko O. Yu., Kornejchuk, I. A., Nuzhdenko, S. A., and Dolganova, A. S. 2012. Daily ration and some biological features of snow crab *Chionoecetes opilio* in the Japan Sea in spring. Izvestiya TINRO, T171: 226–232. (In Russian)

Chuchukalo, V. I., Nadtochij, V. A., Fedotov, P. A., and Bezrukov, R. G. 2011a. Feeding and some biological features of snow crab *Chionoecetes opilio* in the Chukchi Sea. Izvestiya TINRO, T167: 197–206. (In Russian)

Chuchukalo, V. I., Nadtochij, V. A., Koblikov, V. N., and Borilko, O. Y. 2011b. Feeding and some ecological features of mass commercial crab species from the northwestern Japan Sea in early spring. Izvestiya TINRO, T166: 123–137. (In Russian)

Czeckanovski, J. 1909. Zur differencial Diagnose der neandertalgruppe. Korrespondenz-Blatt der Deutschen Gesellschaft für Anthropologie l, 40: 44–47.

Divine, L. M., Bluhm, B. A., Mueter, F. J., and Iken, K. 2017. Diet analysis of Alaska Arctic snow crabs (*Chionoecetes opilio*) using stomach contents and δ^{13}C and δ^{15}N stable isotopes. Deep Sea Research Part II: Topical Studies in Oceanography, 135: 124–136.

Kolts, J. M., Lovvorn, J. R., North, C. A., Grebmeier, J. M., and Cooper, L. W. 2013. Effects of body size, gender, and prey availability on diets of snow crabs in the northern Bering Sea. Marine Ecology Progress Series, 483: 209–220.

Kun, M. S., and Mikulich, L. V. 1954. Food composition of Far Eastern commercial crabs at summer. Izvestiya TINRO, T41: 21–42.

Lepland, A., Rybalko, A., and Lepland, A. 2014. Seabed Sediments of the Barents Sea. Scale 1:3 000 000. Geological Survey of Norway (Trondheim) and SEVMORGEO (St. Petersburg). https://www.ngu.no/en/news/new-seabed-sediment-map-barents-sea (last accessed 10 February 2020).

Lovrich, G. A., and Sainte-Marie, B. 1997. Cannibalism in the snow crab, *Chionoecetes opilio* (O. Fabricius) (Brachyura, Majidae), and its potential importance to recruitment. Journal of Experimental Marine Biology and Ecology, 211: 225–245.

Manushin, I. E. 2003. Characteristics of food consumption by red king crab in the Barents Sea. In Kamchatskij krab v Barentsevom more, pp. 189–202. Ed. by B. I. Berenboim. Izd-vo PINRO. Murmansk. 383 pp. (In Russian)

Manushin, I. E. 2008. Srednyaya massa osobi kak pokazatel' skorosti oborota veshchestva v populyatsiyakh vodnykh ehktotermnykh zhivotnykh. The mean mass of an individual as an indicator of the rate of matter turnover in populations of aquatic ectothermic animals. Mat. X nauch. seminara, pp. 29–34. "Chteniya pamyati K.M. Deryugina". (In Russian)

Mullowney, D., Morris, C., Dawe, E., Zagorsky, I., and Goryanina, S. 2018. Dynamics of snow crab (*Chionoecetes opilio*) movement and migration along the Newfoundland and Labrador and Eastern Barents Sea continental shelves. Reviews in Fish Biology and Fisheries, 28: 435–459.

Nadtochij, V. A., Chuchukalo, V. I., and Koblikov, V. N. 2001. On the feeding of snow crab (*Chionoecetes opilio*) in the Anadyr Bay in the Bering sea. Izvestiya TINRO, T128: 432–435. (In Russian)

Nizyaev, S. A., Bukin, S. D., Klitin, A. K., Perveeva, E. R., Abramova, E. V., and Krutchenko, A. A. 2006. The Manual for the Study of Commercial Crustaceans of the Far Eastern seas of Russia. SakhNIRO, Yuzhno-Sakhalinsk. 114 pp. (In Russian)

Nosova, T. B. 2016. Feeding of snow crab *Chionoecetes opilio* in the Kara Sea at summer 2014. Morskie Biologicheskie Issledovaniya: dostizheniya i Perspektivy, T1: 227–230. (In Russian)

Pavlov, V. A. 2007. Feeding of snow crab *Chionoecetes opilio* (Fabricius, 1788) in the Barents Sea. Proceedings of VNIRO, T147: 99–107. (In Russian)

Shannon, C. E. 1948. A mathematical theory of communication. Bell System Technical Journal, 27: 379–423.

Squires, H. J., and Dawe, E. G. 2003. Stomach contents of Snow Crab (*Chionoecetes opilio*, Decapoda, Brachyura) from the Northeast Newfoundland Shelf. Journal of Northwest Atlantic Fishery Science, 32: 27–38.

Stevens, B. G. (Ed.). 2014. King Crabs of the World: Biology and Fisheries Management. CRC Press, Boca Raton, FL, USA. 624 pp.

Sushchenya, L. M. 1975. Quantitative Patterns and Nutrition of Crustaceans. Nauka i tekhnika, Minsk. 208 pp. (In Russian)

Tankovskaya (Nosova), T. B., and Pavlov, V. A. 2014. Feeding of snow crab *Chionoecetes opilio* in the Eastern Barents Sea. *In* Problemy i perspektivy razvitiya rybokhozyaj-stvennogo kompleksa na sovremennom ehtape, pp. 144–146. PINRO, Murmansk. (In Russian)

Tarverdieva, M. I. 1981. About feeding of snow crabs *Chionoecetes opilio* and *Chionoecetes bairdi* in the Bering Sea. Zoologicheskij Zhurnal, T60: 991–997. (In Russian)

Tarverdieva, M. I. 2001. Feeding of crab commercial species inhabiting the Far Eastern seas shelfs. *In* Issledovaniya biologii promyslovykh rakoobraznykh i vodoroslej morej Rossii, pp. 148–156. VNIRO. Moscow. (In Russian)

World Register of Marine Species (WoRMS). 2020. http://www.marinespecies.org/index.php (last accessed 10 February 2020).

Zakharov, D. V., Strelkova, N. A., Luybin, P. A., and Manushin, I. E. 2016. Macrozoobenthos communities in the areas of the snow crab distribution in the Barents and Kara seas. *In* Snow crab Chionoecetes opilio in the Barents and Kara seas Murmansk, pp. 59–74. Ed. by K. M. Sokolov. Izd-vo PINRO. Murmansk. 242 pp. (In Russian)

Zinchenko, A. G. 2001. Geomorfologicheskaya osnova kompleksnykh landshaftno-geoekologicheskikh issledovaniy Barentseva morya. *In* Opyt sistemnykh okeanologicheskikh issledovaniy v Arktike, pp. 476–481. Izd-vo Nauchnyy Mir. Moscow. (In Russian)

Handling editor: Emory Anderson