



# Development of snow crab *Chionoecetes opilio* (Crustacea: Decapoda: Oregonidae) invasion in the Kara Sea

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## Abstract

With current climate trends, longer ice-free periods and increased human activity are observed in the previously hard to access Arctic Siberian seas. This provides for a rare opportunity to observe the progress of species invasion in pristine areas. The snow crab, *Chionoecetes opilio*, is a unique example of an alien Brachyura crab in the Arctic. Its distribution, population size structure, as well as biotic and abiotic conditions affecting its survival in the Kara Sea are discussed. Crabs were collected using trawl sampling in 2014. It has been estimated that the invasion took place in the late 2000s through the northern and eastern borders with the Barents Sea. Presently, snow crabs are found throughout the western part of the sea, from Kara Gates to St. Anna Trough; the entire area between Yamal Peninsula and Novaya Zemlya; and the northeastern shelf of the sea. Benthic abiotic conditions of the Kara Sea are unlikely to limit survival and further progress of snow crab population. However, the length of the ice-free period could limit its reproduction potential. The collected data do not allow us to presume the existence of a reproducing population, yet the presence of a settler-size group in the central part of the western Kara shelf could indicate local recruitment. Food availability in the Kara Sea is unlikely to limit growth of early benthic stages of snow crabs such as those collected in 2014. However, the question remains open whether benthic productivity is sufficient to allow these crabs to reach commercial sizes.

**Keywords** Alien decapods · Population size structure · Non-indigenous species distribution · Arctic

## Introduction

The opilio snow crab (*Chionoecetes opilio*, O. Fabricius, 1788) belongs to the family Oregonidae. This is one of the very few Brachyura taxa (mostly from the genus *Hyas*) that are present in the Arctic Seas. The snow crabs' natural habitat encompasses the northern region of the Pacific Ocean, from the Bering Strait to the waters of British Columbia, and from the northern part of the Sea of Japan to the Korea Strait (Ogata 1973). It is common in the Chukchi Sea (Bluhm et al. 2009). A few findings have been recorded from the eastern part of the Eastern Siberian Sea and the western region of the Beaufort Sea, and just one finding is known from the border of the Eastern Siberian and Laptev Seas (Sokolov et al. 2009). The north-western Atlantic is also part of the

natural habitat of *C. opilio*, from the northernmost western coast of the USA to the Davis Strait (Squires 1990).

Snow crabs were found for the first time in the Barents Sea in 1996 (Kuzmin et al. 1998). Evidently, this was the result of an introduction, although its origin and the vector can only be hypothesized (Pavlov and Sundet 2011; Sokolov 2014; Strelkova 2016). Based on the estimation of time required for the crab caught in 2004 to reach its size, it can be hypothesized that the introduction took place in the 1980s (Pavlov 2006) or between 1987 and 1993 (Strelkova 2016). The most probable scenario is that the crab was transported to the Barents Sea in the larval stage with ballast water, brought in by ships from the north-western Atlantic (Pavlov 2006; Pavlov and Sundet 2011; Sokolov 2014).

The growth and expansion of the snow crab population in the Barents Sea is well documented due to the commercial fishery research of the NM Knipovich Polar Research Institute of Fishery and Oceanography (PINRO) and the joint standard trawl survey of PINRO and the Institute of Marine Research of Norway. In less than 15 years, this species occupied a substantial part of the central and

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eastern parts of the Barents Sea, becoming most abundant in waters near the Novaya Zemlya archipelago (an area influenced by the cold transformed Barents Sea water mass) (Kuzmin et al. 1998; Pavlov and Sundet 2011; Sokolov 2014; Bakanev 2015; Zimina et al. 2015; Bakanev et al. 2016).

The expansion of the snow crab population in the Barents Sea can be mostly explained by the transportation of larvae by currents (Pavlov 2006; Pavlov and Sundet 2011; Sokolov 2014), although active migrations of adult crabs also play a role. Tagging of crabs has shown that adults are capable of walking long distances, of up to 201 km in 87 days, although the overall advancement and speed are substantially lower. No general tendency of crab movements towards any particular direction has been observed (Goryanina 2015).

By 2007–2008, *C. opilio* had been found near the border between the Barents and Kara Seas, at the northernmost tip of the Novaya Zemlya archipelago, and in the vicinity of the Kara Strait (Sokolov 2014; Bakanev et al. 2016). However, during research expeditions in 2007, these crabs were not observed in the Kara Sea (Anisimova et al. 2007; Spiridonov et al. 2015; Strelkova 2016). During an extensive trawl survey in 2012, adults and larvae of snow crabs were found at several stations in the south-western part of the Kara Sea (Zimina 2014). In 2013, adult crabs were found in approximately 20% of commercial trawl survey stations in the south- and north-eastern parts of the sea (Sokolov 2014). These and other PINRO studies of snow crabs in the Barents and Kara Seas have been summarized by Sokolov et al. (2016). However, the methods of collecting used in these expeditions (i.e., commercial trawls and plankton nets) made it possible to study only relatively large crabs or larvae which may have recently emigrated from the Barents Sea and provided no information on the young classes of the invading population.

Current climate trends, longer ice-free periods and increased human activity are observed in previously hard to access Arctic Siberian seas. Alien decapod species are rare in the Arctic and *C. opilio* is a unique example of an alien Brachyura crab in this region (Spiridonov and Zalota 2017). Prior to the invasion of the snow crab, only one native oregonid spider crab, *Hyas araneus*, was found in the regions of the Kara Sea bordering the Barents Sea (Vassilenko and Petryashov 2009). This allows for a rare opportunity to observe a species invasion in a previously pristine area. Further expansion of snow crabs into the Kara Sea has been observed during the cruise of the research vessel (RV) “Professor Shtokman” to the Kara Sea in 2014 (Spiridonov et al. 2015). The present paper aims to describe the snow crab distribution and population composition (with particular reference to juveniles) during the process of their ongoing invasion into the Kara Sea.

## Materials and methods

### Kara Sea oceanographic conditions in 2007–2014

The oceanographic conditions in the western Kara Sea are strongly influenced by its water exchange with the Barents Sea and by the advection of fresh waters of river runoff origin (Dobrovolsky and Zalogin 1982; Pavlov and Pfirman 1995; Zatsepin et al. 2010a, b, 2015). The major inflow of the Barents Sea water takes place through the strait between the North Island of the Novaya Zemlya and Franz Josef Land Archipelagoes. A less intensive and seasonally variable inflow also exists through the Kara Gate Strait between the South Island of Novaya Zemlya and Vaigach Is. (Dobrovolsky and Zalogin 1982; Ozhigin et al. 2011). In 2014, this flow was negligible in August and increased in September, following the seasonal reduction of river runoff in the Kara Sea (Schuka et al. 2015c).

The freshened surface waters of the Ob and Yenisei rivers runoff spread as a result of both geostrophic and wind-driven circulation over extensive areas in the central or southeastern Kara Sea (Zatsepin et al. 2010b). The direction of currents in the saline subsurface waters may be different and even inverse (Schuka et al. 2015b, c; Zatsepin et al. 2015). The freshened water originating from the river runoff is usually advected mainly to the north and northwest of the extensive Ob–Yenisei estuary. However, in 2012, due to the prevailing winds, it was significantly displaced to the east (Zatsepin et al. 2010b). In the south-western Kara Sea, the waters of the Barents Sea origin mix with the Kara Sea waters and are advected by the Yamal Current along the western coast of the Yamal Peninsula and further north (Pavlov and Pfirman 1995; Zatsepin et al. 2010a). In the summer of 2014, this current was expressed as a system of meanders and eddies with altering flow directions (Schuka et al. 2015b). The current from the Barents Sea which flows along the north-western coast of Novaya Zemlya meets the Kara Sea waters of eastern Novaya Zemlya in the western branch of the St. Anna Trough and there forms a topographically determined frontal zone of high biological significance (Flint et al. 2015; Zatsepin et al. 2015). The direction of the Eastern Novaya Zemlya current along the eastern coast of the archipelago appears to be variable. In different years, it has been reported to be directed south-west (Pavlov and Pfirman 1995) or north-east (Zatsepin et al. 2010a, 2015). According to instrumental measurements performed in the summer and autumn of 2014, this current was generally directed south-west (Schuka et al. 2015c).

Spring sea ice conditions in the years preceding the observed records of snow crabs and in 2011–2014 are distinctly different. In late May 2007–2013, the entire

Kara Sea was still covered by first-year ice of 30–200 cm thickness (except for some polynya areas), except in 2011 when most of the western part was either ice-free or covered with young (less than 30 cm thick) ice. Late May of 2014 was characterized by an extensive development of the Eastern Novaya Zemlya polynya surrounded by dense drifting ice. In most years since 2007, 70–100% ice was still present in most parts of the Kara Sea until mid-June, except for extensive areas north-east and east of Novaya Zemlya. In mid-June 2011 and 2012, there was a significant area of open water in the western Kara Sea. However, there were belts of pack ice of various concentrations along the Yamal Peninsula (in 2011) and between the Yamal Peninsula and the North Island of Novaya Zemlya (in 2012). Since 2011, most of the western Kara Sea was ice-free by mid-July (AARI 2007–2014).

### Material collection

Material was collected during the 128th cruise of RV “Professor Shtokman” to the Kara Sea which took place during August–September 2014. Bottom trawling was performed in the open part of the Kara Sea as well as in the bays of the Novaya Zemlya archipelago (Fig. 1). The coordinates, depth and sediment descriptions of the trawl stations are summarized in Table 2. Records of temperature, salinity, oxygen concentrations and pH at each station were obtained during the expedition and kindly supplied by our colleagues.

Mega- and macrofauna were collected using a Sigsbee trawl with a steel frame of 2 m breadth and 35 cm height. The trawl was equipped with a double net: the outer one

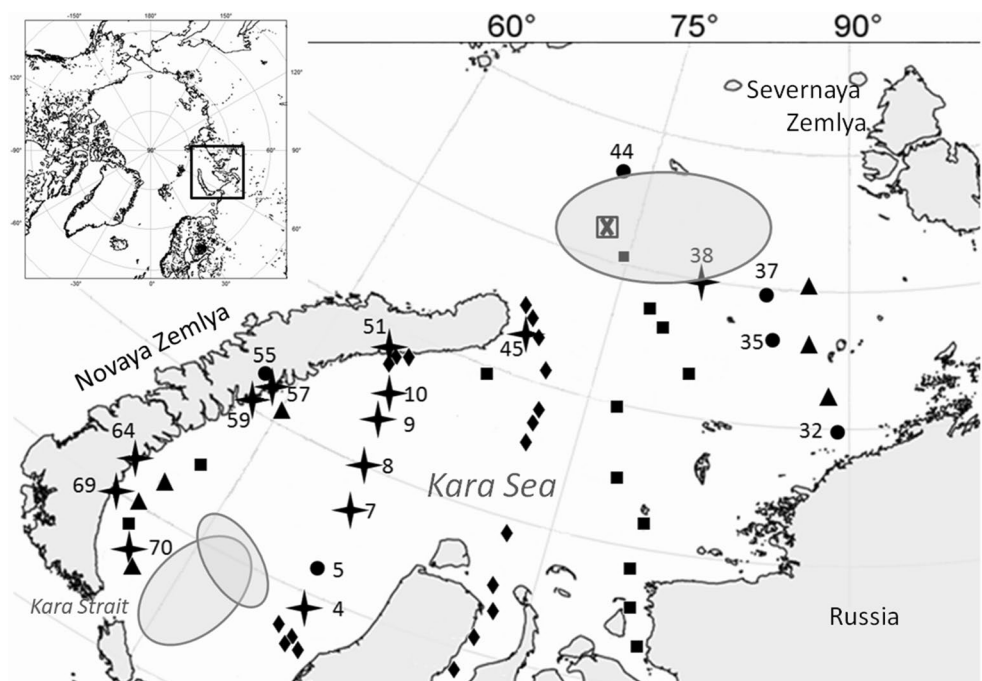
had 45-mm mesh and the inner one a 4-mm mesh. As the catches were normally very large, two or three 5-L buckets of unwashed material were extracted as an aliquot subsample, washed through a 1-mm mesh and separately fixed for subsequent detailed sorting and weighing in the laboratory on land. Primary fixation of organisms was carried out with 6% neutralized formaldehyde and then transferred into a 75% alcohol solution. The rest of the catch was washed through on a system of 10- and 1-mm metal meshes. It was then visually inspected, where crude species composition was described and their relative abundance ranked (“dominant”, “leading”, “common” and “present”) based on visual approximation of their biomass.

Comparative material of juvenile *Hyas araneus* was collected from fouling communities in the expedition on board the RV “Kartesh” to the Baidara Bay (southwestern Kara Sea) in the same year.

All decapods (crabs and shrimps) were extracted from the aliquot subsamples in our Moscow laboratory. The biomass of the overall subsample was measured. Crabs were sexed based on visual characteristics and measured (carapace width; CW) using calipers. Crabs with a CW less than 10.5 mm could not be sexed based on visual characteristics. For the purpose of simplifying the discussion, in this paper crabs with a CW less than 10.5 mm are referred to as juveniles and crabs larger than that are referred to as subadults (no large crabs which had reached sexual maturity were caught).

For subsequent analyses, the data was grouped by transects: along the east coast of the Novaya Zemlya archipelago (ECNZT) (stations 51, 55, 57, 59, 64, 69, 70), the

**Fig. 1** Bottom trawling stations of the Institute of Oceanology RAS expeditions in the Kara Sea marked with/without snow crabs as follows: *diamonds* 54th cruise of Research vessel (RV) “Akademik Mstislav Keldysh” in 2007 (no crabs found); *squares* 59th cruise of RV “Akademik Mstislav Keldysh” in 2011 (*square with a cross* the only finding of snow crabs during that expedition); *triangles* 125th cruise of RV “Professor Shtokman” in 2013 (no known findings of crabs); *stars and circles* 128th cruise of RV “Professor Shtokman” in 2014 (*circle* station where no crabs were found; *star* station where crabs were found); *gray ovals* area where crabs have been previously found based on the literature (Sokolov 2014; Zimina 2014)



Yamal–Novaya Zemlya transect (YMNZT) (stations 4, 5, 7, 8, 9, 10), and the northern shelf transect (NShT) (stations 32, 35, 37, 38) (Table 2). Two stations did not belong to any transect mentioned above: station 45 which was placed in the St. Anna's Trough; and the northernmost station 44.

### Identification of early juveniles of *Chionoecetes opilio*

Adult *Chionoecetes opilio* are readily distinguishable from *Hyas* spp. by a carapace length-to-width ratio. It is distinctly greater than 1 in *Hyas* and equal or less than 1 in *Chionoecetes*. This character is used in the contemporary identification key to the Arctic decapod crustaceans (Vassilenko and Petryashov 2009). However, megalopa larvae of *C. opilio* and *Hyas* spp. are very similar and have carapaces longer than broad (Korn and Kornienko 2010). Juvenile crab instars of both *C. opilio* and *H. araneus* have a carapace length to width ratio greatly exceeding 1 [ $1.41 \pm 0.015$  ( $n = 11$ ) and  $1.56 \pm 0.029$  ( $n = 8$ ) for juveniles with carapace width around 5 mm, respectively]. They may be distinguished by: a relatively longer merus of pereiopod (walking leg) 2, exceeding or equal to the carapace width in *C. opilio* versus being much shorter in *H. araneus*; leaner and less hairy pereio-pods; a roader gap between the rostral spines; and a spine-like versus a relatively broad quasi-triangular exorbital lobe. In addition to those, juvenile snow crabs practically never have fouling organisms (except for occasionally attached foraminiferans), while *Hyas* spp. are normally covered by various sessile invertebrates or algae (Fig. 2).

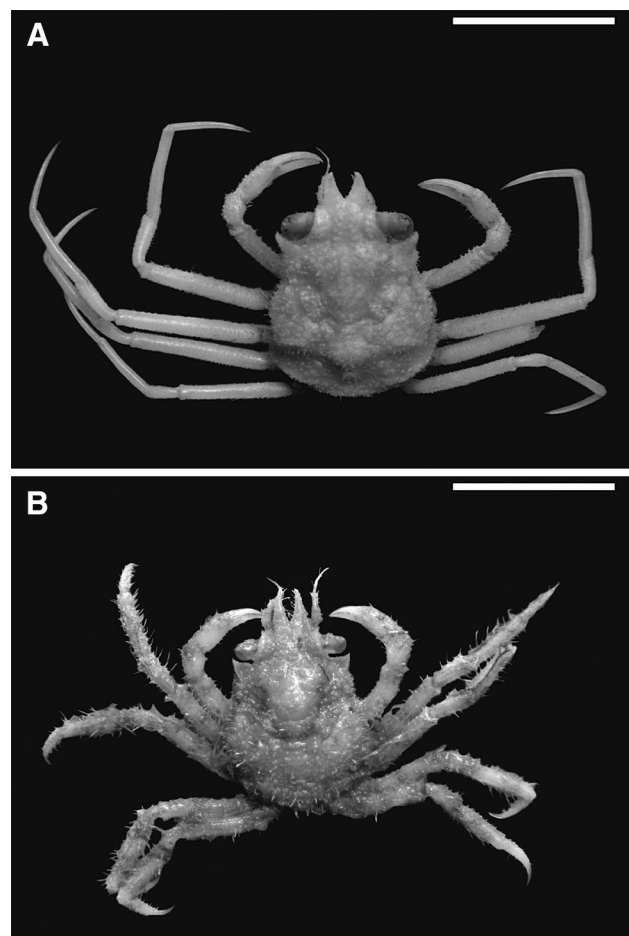
### Processing of data

The size structure of collected crabs was analyzed using mixing model analysis in PAST software (Hammer 2013). The best fit models were selected using the Akaike information criterion (Akaike 1974) and log-likelihood criteria. Due to the absence of quantitative data, we used ANOSIM analysis of Rho based on Spearman's rank correlation coefficient. The ranks were assigned based on a visual assessment of the relative biomass of species in the catches. The Kendall correlation coefficient was calculated using the Microsoft Excel package.

## Results

### Size composition and distribution of snow crabs

The first finding of snow crabs was in the north-west of the Kara Sea in 2011 and consisted of two subadult males (CW: 22.4 and 31.0 mm) (Fig. 2). In late August–September 2014, snow crabs were recorded in the catches from the western



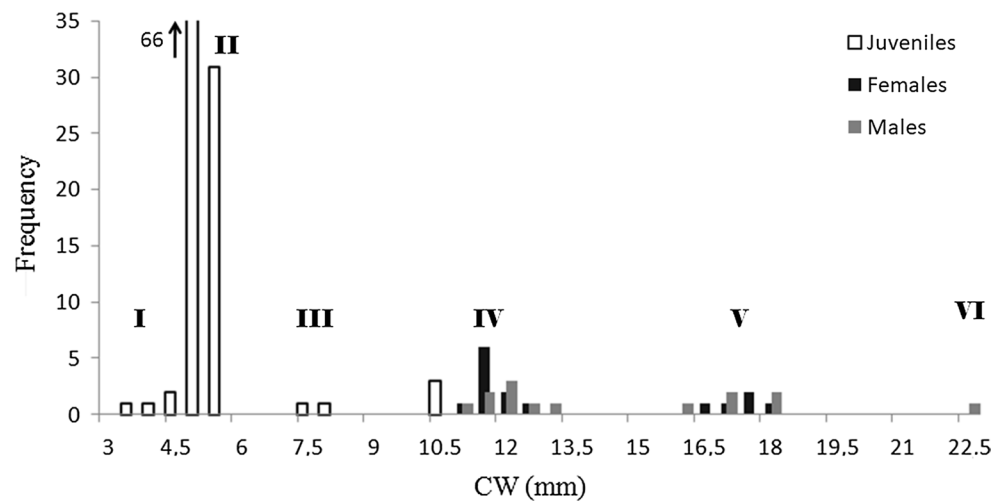
**Fig. 2** Comparison of juvenile oregonid crabs (carapace width 4.5–5.0 mm) from the Kara Sea. **A** *Chionoecetes opilio*, Research vessel “Professor Shtokman”, station 70; **B** *Hyas araneus*, Baidara Bay, August 2016. Scale bar 10 mm

and north-western parts of the Kara Sea, but were not found to the east of station 38. Overall, 137 crabs were collected.

In 2014, most crabs in the aliquot subsamples (Fig. 3) were within the size range of 3–22 mm. The only exception was two large males (CW of about 80 mm) caught at station 38. However, these specimens did not reach the Moscow laboratory. The majority of crabs (106) were very small (juveniles) and could not be sexed based on visual inspection: 2 individuals of CW 3.8 mm; 99 ind. of  $5 \pm 0.2$  mm; 2 ind. of  $7.6 \pm 0.2$  mm; and 2 ind. of about 10 mm. Larger crabs, which could be sexed, were not numerous (only 15 females and 14 males). Mixed model analysis has shown two distinct size groups in females and males (CW about 11 and 17 mm) (Table 1). An additional size group (CW of about 22.2 mm) can be added to males, which was not observed in the mixed model analysis due to the low sample size (single individual) (Table 1).

Examination of visual analysis and aliquot subsamples revealed that crabs were present along the ECNZT at 6

**Fig. 3** Size group frequencies of *Chionoecetes opilio* collected from trawl aliquot subsamples in 2014



**Table 1** Results of mixing model analysis of all *Chionoecetes opilio* collected from trawl aliquot subsamples in the Kara Sea in 2014

	Size groups (carapace width $\pm$ SD (mm))						Log likelihood	Akaike IC	<i>n</i>
	I	II	III	IV	V	VI			
Juveniles	3.8 $\pm$ 0.3	5 $\pm$ 0.2	7.6 $\pm$ 0.2	10 $\pm$ 0.0			92.84	-168.2	106
Females				11.5 $\pm$ 0.4	17.2 $\pm$ 0.5		-4.77	21.53	15
Males				11.7 $\pm$ 0.5	17.8 $\pm$ 2.2	22.2 <sup>a</sup>	-15.96	44.36	14

*n* number of specimens analyzed

<sup>a</sup>An additional size group added manually, single individual

of 7 stations with 86% frequency of occurrence; along the YMNZT, they occurred at 5 of 6 stations (83%); and along the NSHT, only 1 station out of 4 (25%) contained crabs. No crabs were found at station 45 in St. Anna's Trough, although crabs were present at the northernmost station 44 (Fig. 1; Table 2). Size group II was present at practically every station where snow crabs were recorded, except for station 38. Other size groups occurred less frequently. The smallest size group I was recorded only at station 8 in the middle of the western Kara shelf in the YMNZT.

Aliquot subsample data and visual estimates of crab abundance in the entire catch did not always coincide. In 3 of 19 trawls, crabs were found in aliquot subsamples, but were not detected during visual inspection of the entire catch on deck (Stations 4, 8, 57). At these stations, all crabs were small juveniles, except for one male (CW 16.9 mm) at station 8 and one male (CW 15.6 mm) at station 57. In one case (station 38), two large snow crabs were observed in the catch, but none were found in the aliquot subsample (Fig. 1). The absence of crabs in aliquot subsamples might indicate that there were no juveniles at this station. However, there was a weak, but statistically significant, rank correlation (Kendall correlation,  $\tau = 0.47$ ,  $p = 0.005$ ) between the number of crabs in the aliquot subsample and qualitative rank of abundance of crabs in the catch. When considering different size groups assessed in aliquots, Kendall correlation coefficient

was higher for subadult crabs (Kendall correlation,  $\tau = 0.4$ ,  $p = 0.016$ ) and lower for small juveniles (Kendall correlation,  $\tau = 0.36$ ,  $p = 0.027$ ).

The highest proportion of crabs caught per transect were at depths greater than 250 m (34.3%) and at depth ranges of 51–100 m (29.1%). Most of the subadults were also caught at these depths (47.8 and 43.8%, respectively), whereas the juveniles were more evenly distributed between the different depth ranges with the highest frequency of occurrence at 51–100 m (32.4%) and 101–150 (22.9%) (Table 3).

### Abiotic and biotic conditions in the area of occurrence

Snow crabs occurred under negative near-bottom temperatures that ranged from  $-1.5$  to  $-0.30$  °C, salinity 33.9–34.9 psu, oxygen concentrations of 6.1–7.5 ml L<sup>-1</sup> (O<sub>2</sub> saturation 75–90.2%) and pH levels of 7.8–8 (Table 4). Most stations where no crabs were found had abiotic properties within the ranges observed at stations with crabs. The only exceptions were stations 32 and 35 where salinity was slightly lower (33.74 psu), but the oxygen concentration levels were much lower (3.8 and 5, respectively), than in the areas inhabited by crabs (Fig. 2).

At stations with the highest number of observed crabs (stations 7, 8, 9 and 70), sediments mostly consisted of fine

**Table 2** Stations where trawl samples were taken during the 128th cruise of RV “Professor Shtokman” to the Kara Sea in 2014

Station	Transect	Depth (m)	Visual rank of crabs' presence	Aliquot subsamples			Sediments
				<i>n</i> total	<i>n</i> juveniles	<i>n</i> subadults	
12804	YMNZT	156–158	0	2	2	0	Brown mud, small round nodules
12805	YMNZT	107–109	0	0	0	0	Brown mud, lots of foraminifera, small pebbles
12807	YMNZT	61–63	3	20	12	8	Light brown mud with disk nodules
12808	YMNZT	173–174	0	13	12	1	Soft mud without nodules or foraminifera
12809	YMNZT	61–63	1	17	14	3	Brown mud with foraminifera
12810	YMNZT	259	1	15	6	9	Brown mud with foraminifera
12832	NShT	50–51	0	0	0	0	Sandy mud, shell, polychaetes tubes, some foraminifera
12835	NShT	93–111	0	0	0	0	Brown mud, nodules, polychaete tubes and shells
12837	NShT	165–182	0	0	0	0	Brown mud with big stones and nodules with crust and some polychaete tubes
12838	NShT	125–128	1	1	0	1	Brown mud
12844	Northern	471–473	2	3	2	1	Soft brown mud with sand
12845	St. Anna's Trough	269–278	0	0	0	0	Brown sandy mud, lots of stones
12851	ECNZT	126–139	2	22	22	0	gray pelite with non-round shale rock fragments
12855	ECNZT	148–149	0	0	0	0	Very soft gray pelite
12857	ECNZT	108–116	0	18	17	1	Gray pelite with pebbles
12859	ECNZT	101–123	1	9	9	0	Gray clay with stones, wood and detached brown algae
12864	ECNZT	48–50	1	4	4	0	Gray clay with stones and nodules
12869	ECNZT	146–151	2	1	1	0	Brown mud with foraminifera
12870	ECNZT	285–286	2	11	5	6	Brown mud with foraminifera

Visual rank of crab presence is based on visual approximation (by the authors) of *Chionoecetes opilio* biomass in trawl subsamples

0 absent, 1 present, 2 common, 3 leading

*n* number of crabs found in aliquot subsamples, *ECNZT* east coast of Novaya Zemlya archipelago, *YMNZT* the Yamal to Novaya Zemlya transect, *NShT* the northern shelf transect

**Table 3** Frequency (%) of occurrences of *Chionoecetes opilio* at different depth ranges of the sampled stations during the 128th cruise of RV “Professor Shtokman” to the Kara Sea in 2014

Depth range (m)	< 50	51–100	101–150	151–250	> 250
% Juveniles	15.0	32.4	22.9	17.5	12.2
% Subadults	0.0	43.8	4.5	4.0	47.8
% Total	9.4	29.1	15.4	11.8	34.3
Total stations	1	3	8	3	4

brown mud, either with or without ferromanganese nodules, pebbles and foraminiferans *Saccorhyza ramose*. At stations 51 and 57, sediments were gray pelite with some coarse material. The substrate at these stations did not differ much from other stations with or without crabs. The only station (55) with a noticeably different substrate (very liquid pelite) did not contain crabs.

In all cases, large macrozoobenthos was clearly dominated by the brittle stars *Ophiopleura borealis* and *Ophiocten sericeum*. Other dominant species included *Elpidia*

**Table 4** Abiotic parameters at sampled stations (subdivided into group with and without crabs) during the 128th cruise of RV “Professor Shtokman” to the Kara Sea in 2014

	Crab present		Crab absent	
	Mean	Range	Mean	Range
Temperature (°C)	$-0.9 \pm 0.4$	-1.5 to -0.3	$-1.2 \pm 0.2$	-1.4 to -1.1
Salinity (psu)	$34.5 \pm 0.3$	33.9 to 34.9	$34.3 \pm 0.4$	33.7 to 34.7
Oxygen (ml L <sup>-1</sup> )	$6.9 \pm 0.4$	6.1 to 7.5	$5.7 \pm 1.3$	3.8 to 6.7
Oxygen (%)	$83 \pm 4.5$	75 to 90.2	$68.8 \pm 15.5$	45.5 to 80
pH	$7.9 \pm 0.1$	7.8 to 8	$7.9 \pm 0.0$	7.9 to 7.95

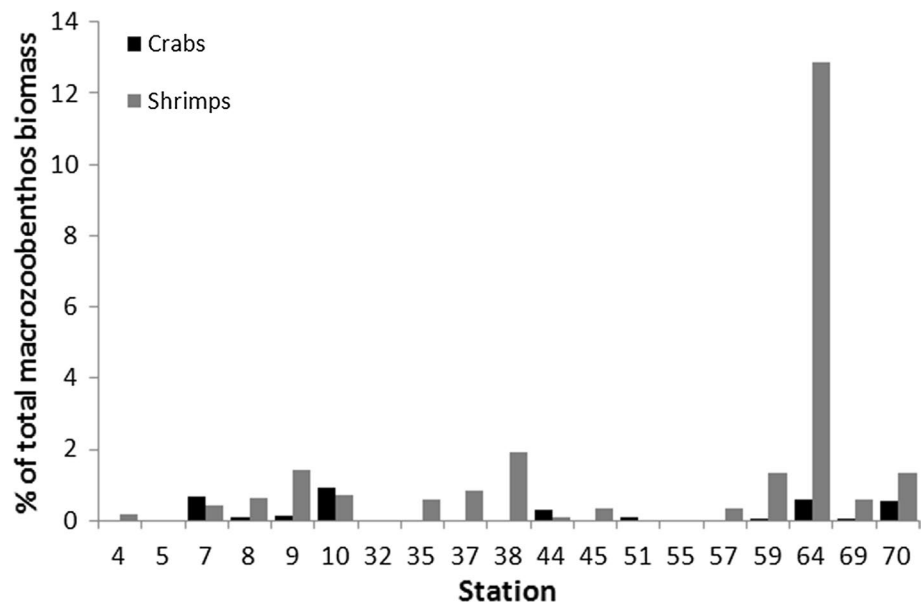
*glacialis*, *Nothria hyperborea*, *Similipecten greenlandicus*, and *Myriotrochus rinkii*. Based on visual ranking of species abundance of trawl catches, ANOSIM analysis of Rho based on Spearman's rank correlation coefficient was performed. No significant differences between species community composition of stations with and without

crabs were found (ANOSIM analysis of Rho,  $R = 0.19$ ;  $p = 0.073$ ).

### Biomass fraction in comparison to other decapods species

In 2014, *H. araneus* was recorded only once in qualitative inspections of the catch near the Kara Gate Straight (the boundary with the Barents Sea). Other decapod species were represented by caridean shrimps, with *Sabinea septemcarinata* and *Sclerocrangon ferox* (Crangonidae) being the most abundant in terms of biomass (Fig. 4). The fractions of snow crab and shrimps to overall biomass along the ECNZT averaged  $0.2 \pm 0.3$  and  $2.4 \pm 4.7\%$ , respectively; along the YMNZT, they averaged  $0.3 \pm 0.4\%$  for crabs and  $0.6 \pm 0.5\%$  for shrimps; and 0.3 and 0.1%, respectively, in St. Anna' Trough. The contribution of young crabs to the megabenthic biomass was lower, but it was comparable to the contribution of all shrimp species. No correlation was found between the percentages of crab and shrimp biomass in all aliquot subsamples (Kendall correlation,  $\tau = 0.22$   $p = 0.20$ ) but a weak positive correlation (Kendall correlation,  $\tau = 0.46$ ;  $p = 0.03$ ) was found for the western part of the survey (excluding Stats 32–38 where no juvenile snow crabs were present).

**Fig. 4** Percentage of the total biomass attributed to *Chionoecetes opilio* and shrimps in the trawl subsamples collected during 128th cruise of RV "Professor Shtokman" in 2014



## Discussion

### Size composition and age structure of the non-indigenous snow crab population in the Kara Sea

Overall mixed model analysis has shown six size groups of collected *Chionoecetes opilio* throughout the Kara Sea (Table 1; Fig. 3). These groups correspond to the instars I–VI described in the literature (Lovrich et al. 1995; Alunno-Bruscia and Sainte-Marie 1998). An additional size group of approximately 80 mm can be added to the results since there were two specimens of this size found at station 38. These two crabs might belong to instar XI, at which stage males could reach sexual maturity and go through terminal molt (Sainte-Marie et al. 1995). Since these crabs were not properly measured in the field (no data on claw morphometry), their maturity status is unknown. In addition, they were found in the northern part of the Kara Sea close to the area of initial findings of snow crabs in earlier years (Institute of Oceanology, RAS finding in 2011, Fig. 1; Sokolov 2014).

The rest of the collected crabs belong to instars prior to sexual maturity (Lovrich et al. 1995; Sainte-Marie et al. 1995; Alunno-Bruscia and Sainte-Marie 1998). For both male and female snow crabs in the North Atlantic, it has been shown that crabs settle and metamorphose into instar I (~3 mm) 3–5 months after hatching. They then molt twice and reach instar III (~7 mm) within 1.5–2 years from hatching, and twice in the third year to reach instar V (~14 mm). Thereafter, they molt approximately once a year (Sainte-Marie et al. 1995; Alunno-Bruscia and Sainte-Marie 1998; Comeau et al. 1998). The majority of the collected crabs

belong to instar II, in their early second year since hatching, i.e., most probably crabs that settled in autumn 2013. Small numbers of crabs found as instar I suggest that the settlement of current recruits has commenced and is either in an early stage or being less successful than in the previous year. Also, the presence of a low frequency of occurrence of crabs of instar III suggest that either molting of instar II to instar III and/or instar III to instar IV is also taking place. Unfortunately, the hardness of the carapace has not been determined with precision, but it is likely that soft-shelled specimens of such small size could have been destroyed during the collection by trawling. Instar IV is comprised of sexed crabs (males and females) and crabs that could not be sexed, based on external visual characteristics. This could be due to authors' errors or due to variation in the development between specimens.

In the literature, the size of instars between different studies and regions did not show strong differences (Ito 1970; Kon 1980; Sainte-Marie et al. 1995; Ernst et al. 2012), although it should be noted that growth and molting frequency can also be affected by temperature and food availability. The bottom water temperature in the Kara Sea, where crabs in early growth stages were collected, is slightly lower than in the Bering Sea (c.  $-1\text{ }^{\circ}\text{C}$ ), but within the range of temperatures where these crabs are found in other areas or at later growth stages (Sainte-Marie et al. 1995; Orensanz et al. 2004; Agnalt et al. 2011). Nevertheless, such a close resemblance of early instar sizes for snow crabs in the Kara Sea with those found in other regions suggests similar growth pattern and possibly timing between these regions. Consequently, we can suppose that the maximum age of crabs found throughout the western part of the Kara Sea is at least 3.5–4 years.

### Distribution and possible existence of a reproductive population of snow crabs in the Kara Sea

The introduction of *C. opilio* to the Kara Sea could have been via larvae transport (the larvae had already been found in 2012; see Zimina 2014) and by active migration of large specimens from the Barents Sea. Through tagging experiments, it has been shown that adult snow crabs are capable of walking long distances (Goryanina 2015). Therefore, they could easily reach the Kara Sea through either the north-western or south-western borders with the Barents Sea, or even from the Matochkin Shar Strait that separates the North and South Islands of Novaya Zemlya. In particular, adult males (CW > 80 mm) discovered on the slope of the Novaya Zemlya Trough in 2012 (Zimina 2014) occurred relatively close to the Kara Sea border of this strait. It cannot be excluded that they walked through to the Kara Sea as adults. However, adult crab migrants would consist primarily

of males, as they are more active, and would have been concentrated closer to the Barents/Kara Seas boundaries.

It is likely that snow crab larvae were transported by the Barents Sea waters that enter the Kara Sea to the north of Novaya Zemlya and through the Kara Gate Strait (Dobrovolsky and Zalogin 1982; Pavlov and Pfirmann 1995; Ozhigin et al. 2011), and then redistributed via the water circulation system inside the sea. In particular, in summer 2014, this current was predominantly directed to the north along the eastern coast of the North Island of Novaya Zemlya (Schuka et al. 2015c). This could have provided a way for snow crab larvae advection from the Barents/Kara Seas boundary into the bays of Novaya Zemlya. In summer 2013, they were recorded throughout most parts of the western Kara Sea, although in much lower abundance than in the Barents Sea at a similar time (Prokopchuk et al. 2016). Since there was a large concentration of breeding *C. opilio* in the north-eastern and south-eastern Barents Sea in the late 2000s (Sokolov 2014; Bakanev et al. 2016; Strelkova 2016), this circulation pattern has probably provided strong propagule pressure since the 2010s. However, based on historic records (Zimina 2014; Strelkova 2016; this study) and instar composition of invaded population reconstructed in the present study, it can be supposed that the initial introduction of *C. opilio* to the Kara Sea from the Barents Sea did not take place until the mid-2000s, and most probably occurred in the late 2000s.

The surface water layer of the Kara Sea is greatly influenced by the winds and by the runoff of two major Siberian rivers, the Ob and the Yenisei, which affects the salinity and direction of water flow (Zatsepin et al. 2010b). Snow crab larvae are sensitive to salinity levels, and thus the top water layer in the Kara Sea is less suitable for their survival than deeper more saline subsurface water layers. However, they may be advected in subsurface layers, which they are known to inhabit in the Barents Sea (Prokopchuk et al. 2016). Furthermore, in 2013, the freshened upper water of river runoff origin was displaced to the east (Zatsepin et al. 2010b) which could also have facilitated the dispersal of the snow crab larvae inside the Kara Sea.

In the North Atlantic and the Bering Sea, larvae hatch from April to June (Incze et al. 1987; Conan et al. 1996; Moriyasu and Lanteigne 1998; Comeau et al. 1999). One of the main cues for larvae hatching appears to be spring plankton blooms (Conan et al. 1996) as the sea ice melts. The development of phyto- and zooplankton populations that follow sea ice decay provides food resources that are critical at early stages of crab larval development (Sulkin 1978; Anger and Nair 1979). Although not much is known about the feeding habits of snow crab larvae in nature, it is likely that they can consume a broad range of zooplankton species. Zoa I larvae of a closely related species *Chionoecetes bairdi* have been shown to ingest phytoplankton (Incze and Paul 1983).



During the last decade, the sea ice melted in March–May in the Barents Sea on the western side of the Novaya Zemlya archipelago and much later (approximately July–August) in the Kara Sea (National Snow and Ice Database Center; AARI 2007–2014). In the Bering Sea, just settled crabs (instar I) occur in late August, and in early September in the Gulf of St. Lawrence (Comeau and Conan 1992; Lovrich et al. 1995; Zheng et al. 2001; Orensanz et al. 2004). The duration of larval stages is highly depend on water temperature, salinity and food availability, and it takes approximately 2–4 months (but also up to 8 months) (Fukataki 1969; Kon 1970; Adams 1979; Kon 1980; Davidson 1983; Conan et al. 1996). Consequently, if larvae hatch in about April in the Barents Sea, they could be transported and survive in the Kara Sea once its plankton community undergoes seasonal development (Hirche et al. 2006; Kosobokova and Hirche 2016). In the Kara Sea, under-ice blooms occur in April (Sazhin et al. 2017). In the central shelf zone, already in April zooplankton communities include significant fractions of copepod nauplii and meroplankton (Kosobokova and Hirche 2016). Thus, sea ice retreat kicks off rapid development of seasonal food resources for crab larvae. Particularly rapid, although spatially variable, spring sea ice decay took place in the Kara Sea in 2011–2014 (see “Kara Sea oceanographic conditions in 2007–2014”). This might have facilitated the successful introduction of snow crab larvae from the Barents Sea to the Kara Sea in 2010–2014.

The area of snow crab distribution in 2014 generally coincided with the area that is under the influence of Barents Sea water (Spiridonov et al. 2015). Therefore, the young instars of *C. opilio* in the Kara Sea may not be from local recruits but from settlers from the Barents Sea.

In summer 2014, the water transport through the Kara Gate Strait was predominately from the Kara Sea to the Barents Sea, and the Yamal Current was expressed more as a series of eddies (Schuka et al. 2015a b, c). This might have restricted the transportation of crab larvae from the Barents Sea far inside the western Kara Sea shelf. Therefore, the presence of the 2014 settlers (size group I) far from the Barents Sea boundaries in the central part of western Kara shelf (station 8) (Fig. 1) allow us to suppose the possibility of local recruitment. The studies conducted by PINRO on the north-western coast of the Yamal Peninsula in 2014 and 2015 have revealed the presence of both juvenile (at depths between 35 and 100 m) and adult males and ovigerous females (deeper than 100 m), which may also indicate the presence of established and reproducing populations (Strelkova 2016). Since this extensive survey reported few adult crabs in other areas, further research is needed to understand whether a breeding population of snow crabs is localized in the south-western Kara Sea and what are the proportions of the Barents Sea emigrants and local recruits.

## The Kara Sea environment and potential for further invasion of snow crabs

The survival and further expansion of snow crab populations in the Kara Sea could be affected by both abiotic and biotic conditions. These include food and suitable substrate availability, temperature, salinity, and the ice cover dynamics of the Kara Sea. It appears that substrate, temperature and salinity of the bottom water are not limiting factors in the current area of the crabs' distribution. There are no substantial differences in these parameters between stations where the crabs were found and those where there were none. The temperature and salinity of the bottom water layer in the studied regions of the Kara Sea are within the limit of the snow crab's tolerance levels of  $-1.8$  to  $7.2$  °C and approximately 34 psu (Powles 1968; Kon 1973; Slizkin 1982; Charmantier and Charmantier-Daures 1995; Perveeva 1999). However, it seems that in the Barents Sea they are limited by the 2 °C isotherm (Agnalt et al. 2011; Jørgensen and Spiridonov 2013). In the Kara Sea, the crabs are found at depths of 50–290 m, predominantly on soft substrate with some ferromanganese nodules, pebbles and foraminiferans. This is similar to the preferred depths (4–690 m) and substrates of *C. opilio* in other areas of its distribution (Kon 1969; Ogata 1973; Slizkin 1982; Sainte-Marie and Hazel 1992; Perveeva 2005; etc.). The exceptions are station 55 with very liquid pelite, and stations 32 and 35 where the oxygen levels seem to be lower than in other areas. The latter two stations have otherwise suitable conditions, but they are under a strong influence of freshwater discharge (Schuka et al. 2015a). This may suppress larval transportation by counteracting the water input from other regions where crabs are present. Henceforth, benthic abiotic conditions of the Kara Sea are unlikely to be limiting factors for the further survival and progress of snow crab populations. However, the ice-free period of the Kara Sea can limit the reproduction potential of local populations, although it seems that in recent years the ice-free period is increasing (National Snow and Ice Database Center; AARI 2007–2017). Model simulation based on current trends towards a warmer and less icy Arctic predicts the continuation of the decrease of summer sea ice cover and a longer open water season following the increased input of warm Atlantic waters to the Arctic Ocean, so that the western Kara Sea may become ice free for about half a year by 2050 (Barnhart et al. 2015). This may further facilitate the spread of snow crab to this basin.

Generally speaking, the Kara Sea is considered to be a low productivity sea compared to the Arctic seas open to input from the Atlantic and Pacific waters (Vinogradov et al. 2000; Romankevich and Vetrov 2001; Demidov and Mosharov 2015; Demidov et al. 2015). However, these productivity estimates may need revision, and general productivity of the Kara Sea may in reality not be as low as previously thought (Hirche et al.

2006). In particular, early bloom at the ice edge, in polynyas or even under the ice in the Kara Sea has similar seasonal timing to the Barents Sea (Sazhin et al. 2017). However, its contribution to the integral production and its flux to the seabed are difficult to assess. Furthermore, the Kara Sea holds abundant benthic diatom communities, which at depths of up to 50 m may contribute significantly to the production available for benthic macroinvertebrates (Sapozhnikov and Kalinina 2015).

The presence of other native predatory decapod species such as crangonid shrimps (i.e. Burukovsky 2009) in higher quantities (Fig. 4) than the snow crabs suggests that small-sized decapod crustaceans may thrive in this area. While most of the fishes in the Kara Sea are benthic feeders, there are no abundant populations of predators such as cod, *Gadus morhua*, or haddock, *Melanogrammus aeglefinus*, as in the Barents Sea (Dolgov et al. 2009, 2014; Dolgov and Benzik 2016) which could potentially compete with snow crabs for food and could consume its juveniles in great quantities. Cod has been shown to affect the growth of invasive crab populations in the Barents Sea (Dolgov and Benzik 2016). There are practically no other species of crabs in extensive areas of the Kara Shelf. The history of crab invasions in other seas of eastern Europe with no or few native crab species provides several examples of a very rapid expansion of invaders over extensive shelf areas (Spiridonov and Zalota 2017). Although further studies to quantify such a statement should be considered, it seems that the benthic community composition does not play a role in the presence or absence of snow crabs at different sample stations. Henceforth, food availability is unlikely to affect the growth of such early benthic stages of snow crabs as those that were collected in 2014 in the Kara Sea. However, the question remains open whether benthic productivity is sufficient to sustain adult snow crab populations of a size comparable to that in the Barents Sea, which is now a significant commercial fishery (Bakanev et al. 2017).

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## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

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