

Commercial fish and shellfish in the Barents Sea: Have introduced crab species affected the population trajectories of commercial fish?

Alexander G. Dvoretzky · Vladimir G. Dvoretzky

Received: 28 May 2014 / Accepted: 4 March 2015 / Published online: 4 April 2015
© Springer International Publishing Switzerland 2015

Abstract The Barents Sea shelf system, particularly the southwestern, western and southern parts, is one of the most productive ocean regions in the world due to the influence of warm Atlantic water. We conducted an analysis of long-term data based on original and published sources focused on the trends in abundance of key commercial species in the Barents Sea. We specifically examined the patterns and characteristics of both invasive species and invasion processes, using the example of two introduced crabs: the red king crab (*Paralithodes camtschaticus*) and the snow crab (*Chionoecetes opilio*), which in polar ecosystems may provide an important case study for improving our ability to predict the impact of new invaders. Warm temperature anomalies were observed in the Barents Sea in the 20th century and in the early twenty-first century, with peaks from 2001 to 2007 and in 2012, associated with a pronounced decrease in total ice cover since 1999. Since their introduction, the stock biomass of red king crabs has varied widely. These fluctuations were associated with high levels of illegal fishing of red king crab. The total biomass of commercial snow crabs increased exponentially in the last decade. Since the late 1990s the stock of northern shrimp has varied with an overall rising trend, although landings in more recent years were relatively

stable. Cod, haddock, and saithe stocks remained at relatively high levels. Capelin stock size is characterized by large fluctuations that are likely to reflect natural processes. Cross-correlation analysis suggests that neither crab species had negative effects on the stocks of important fish. However, a potential negative impact of snow crab on the northern shrimp population could not be rejected due to their overlapping distribution and predator–prey interactions. The high overall productivity of the Barents Sea in recent years, as evidenced by high abundances of major fish stocks, is more likely associated with warming in the Arctic region, and the introduction of both crab species has had no apparent detrimental effects on fish stocks while resulting in positive economic benefits.

Keywords Barents Sea · Oceanographical conditions · Climate · Fisheries · Introduced crabs

Introduction

The Barents Sea represents the largest Arctic continental shelf region. Its northern part borders the Arctic Ocean, while its southern, western, and eastern boundaries are defined by the coasts of Russia and Norway, the shelf break toward the Norwegian Sea and the Novaya Zemlya archipelago, respectively (Loeng and Drinkwater 2007). The total area of the sea is about 1.4 million km² with an average depth of

A. G. Dvoretzky · V. G. Dvoretzky (✉)
Murmansk Marine Biological Institute, 17 Vladimirskaya
Str., Murmansk 183010, Russia
e-mail: vdvoretzkiy@mmbi.info

230 m. The maximum depth (500 m) is in the western part of the Bear Island Trench (Ozhigin et al. 2011). The Barents Sea is also a major passage for Atlantic waters entering from the Norwegian Sea and contributing to the deep waters of the Arctic Ocean (Carmack et al. 2006). In the surface layers, Atlantic water is mainly confined to the southern, western, southwestern and central parts (Wassmann et al. 2006). In the northern part, the upper layer is occupied by less saline and less dense Arctic waters partly originating from the Arctic Ocean. The Polar Front is the boundary between these two main water masses. It is located along the eastern slope of the Svalbard Bank and eastward from Hopen towards Novaya Zemlya (Loeng and Drinkwater 2007). Extensive seasonal variations in ice cover have been recorded in the Barents Sea, where the presence of cold polar water results in an annual average of approximately 40 % of the region being ice covered (Wassmann et al. 2006; Loeng and Drinkwater 2007). Minimum ice coverage occurs in August/September, when the ice edge moves to the north. During maximum ice extent in late winter, approximately 60 % of the sea is ice covered.

Primary production in the Barents Sea is the highest among all Arctic regions, constituting 49 % of the total primary production on the pan-Arctic shelf (Sakshaug 2004; Wassmann et al. 2006). Such high productivity is mainly utilized by zooplankton that are the main food resource for pelagic fish. Subsequently, these pelagic fish, particularly capelin (*Mallotus villosus*), are consumed by cod and haddock (Sakshaug et al. 2009). Therefore, the Barents Sea includes one of the world's largest fishery areas, which is concentrated in permanently ice-free waters in the south and southwest Barents Sea strongly affected by Atlantic water inflow (Wassmann et al. 2006). In general, the state of the Barents Sea food webs is closely linked to the stocks of three economically important species: northeast Atlantic cod (*Gadus morhua*), Barents Sea capelin, and Norwegian spring-spawning herring (*Clupea harengus*). Marine fisheries have always been an extremely important part of the Russian economy, although they did not become a major industry until the twentieth century.

Strong climatic fluctuations have been documented in the Barents Sea during the 20th–21st centuries (Loeng and Drinkwater 2007), as well as correlations between climatic conditions, ocean currents, and fish stocks (see Johannesen et al. 2012). For example, a

regime shift in the Barents Sea in the late 1960s has been connected to the collapse of the Norwegian spring-spawning herring stock (Johannesen et al. 2012). Since the late 1960s, both temperature and the abundance of species at several trophic levels have fluctuated in the Barents Sea. In the past decade, the capelin stock collapsed, but no negative effects were observed in the top predator community (Johannesen et al. 2012). In addition, a warming trend has been recorded in the most recent decade from 2000 to 2012, resulting in the warmest phase observed since regular hydrological observation began in the Barents Sea (Ozhigin et al. 2011).

Introduced species have been identified as major agents of global change and one of the main threats to marine systems because of their direct and indirect impacts on native ecosystems. Their effect on biodiversity, habitat structure, and economically important fisheries is a major source of concern (Dvoretzky and Dvoretzky 2010a; Falk-Petersen et al. 2011). The red king crab (*Paralithodes camtschaticus*) is one of a few large, higher trophic level marine organisms that has become established in a new geographic area. It was introduced to the Barents Sea from the northern Pacific in the 1960s to establish a new commercial fishery. Since then, it has spread from the original area of introduction, Kola Bay, Russia, west along the Norwegian coast and northeast of the Kola Peninsula. King crab is a highly valued delicacy on the international market and currently makes a significant contribution to the income from fisheries in the region (Dvoretzky and Dvoretzky 2014a). Several authors have proposed that the red king crab represents a threat to the other highly productive fisheries through its impact on the ecosystem (Anisimova et al. 2005; Falk-Petersen et al. 2011).

As a large, bottom-feeding, mobile omnivore, red king crab are likely to have a significant impact on the ecosystem through predation and competition. Predation on the eggs of commercial fish (capelin, and lump sucker, *Cyclopteroopsis macalpini*) has been documented in the Barents Sea (Anisimova et al. 2005; Falk-Petersen et al. 2011). Competition for food between crabs and several fish species including long rough dab (*Hippoglossoides platessoides limandoides*), European plaice (*Pleuronectes platessa*), Atlantic wolfish (*Anarhichas lupus*), cod, saithe (*Pollachius virens*), golden redfish (*Sebastes norvegicus*) and shorthorn sculpin (*Myoxocephalus scorpius*)

has been suggested to occur (Pavlova 2008). In the coastal Barents Sea (Russian part), the highest similarity in diets among these species occurred for red king crab and haddock (*Melanogrammus aeglefinus*) (Pavlova 2008).

Another introduced crab species is the snow crab (*Chionoecetes opilio*). In 1996, *C. opilio* was recorded for the first time in the northeast Atlantic (Kuzmin et al. 1999). Some of the fish species noted above may be considered competitors of snow crab because of their overlapping diets (Pavlov 2007). However, information about potential direct and indirect impacts of the alien crabs on the stocks of commercially important species is scarce.

Alien species may impact the populations of native species through hybridization, by facilitating the spread of pathogens, via trophic impacts (grazing, predation, parasitism), and/or competition for resources. Because the red king crab was deliberately introduced to increase the economic potential of the area, it is very important to estimate their impact on the commercially exploited components of the ecosystem. This crab is well acclimated to the new habitat conditions and it presents a good example for studying potential changes in the ecosystem associated with the establishment of an invader. In contrast, snow crab are considered to have been introduced unintentionally to the Barents Sea. There are many other examples of introduced aquatic species worldwide. Therefore, the analysis conducted here may be useful in evaluating potential changes in ecological systems invaded by alien species in terms of effects on other species and the fishery potential of the area.

For these reasons, the main objective of this paper is to provide a brief overview of the oceanographic conditions in the Barents Sea, to describe its fish and shellfish stock fluctuations in the 20th–21st centuries and to examine whether these invasive crabs have affected fish stocks in the Barents Sea.

Materials and methods

Information on the climate dynamics of the Barents Sea ecosystem was gathered using Murmansk Marine Biological Institute's (MMBI's) oceanographic and hydrobiological databases, which have been obtained via MMBI expeditions for more than 75 years and through international data exchanges. The database of

oceanographic transects in the Barents Sea contains more than 200,000 hydrologic stations for the period 1900–2011 (Matishov et al. 2012). An electronic database of Barents Sea ice conditions contains average values for each month from 1960 to 2011. Additionally, we used available published sources to reveal current climatic and ice conditions of the Barents Sea (Wassmann et al. 2006; Ozhigin et al. 2011).

Key life-history conditions of commercially important shellfish and fish species were obtained from published sources (Kuzmin and Gudimova 2002; Gjørseter et al. 2009, 2011; Dvoretzky and Dvoretzky 2010a; Agnalt et al. 2011; Mehl et al. 2011; Pavlov and Sundet 2011; Hvingel and Berenboim 2011; Russkikh and Dingsør 2011; Yaragina et al. 2011). Landing data were obtained for northeast Arctic cod, haddock, saithe, Norwegian spring-spawning herring, capelin (ICES 2013) and northern shrimp (Hvingel and Thangstad 2010). The population dynamics for both crab species and landing data for red king crab were analyzed with the authors' own data and using published materials and reports of the Polar Research Institute of Marine Fisheries and Oceanography (PINRO, Murmansk) and Russian Research Institute for Fisheries and Oceanography (VNIRO, Moscow) (Goryanina et al. 2013; Dvoretzky and Dvoretzky 2014a; <http://www.pinro.ru/>).

We used cross-correlation analysis to determine the relationship between red king crab and commercial fish abundance time series to test for significant correlations at multiple time lags. Such correlations may suggest possible impacts of red king crab on the stock dynamics of these fish. Similar cross-correlations were calculated for snow crab and fish abundance time series. The cross-correlation function is based on the commonly used Pearson correlation, but computes correlations at multiple lags, such that out-of-phase correlations can be detected and the corresponding time lags estimated. Abundance indices of capelin, cod, and haddock (in millions) were taken from Anon (2011). In all cases, abundance data for fish and shrimps were the leading parameters. Abundance data for red king crabs were obtained from Kuzmin (2001); Pinchukov (2008); Pinchukov et al. (2012) and Bakanev and Pinchukov (2014), and from Goryanina et al. (2013) for snow crabs. Cross-correlation analyses were carried out with the STATISTICA 6.0 and NCSS-SPSS 97 software packages.

To evaluate combined effects of environmental conditions and changes in abundance of introduced crabs a canonical correspondence analysis (CCA) was used to investigate the relationship between fish taxa abundances (capelin, cod, haddock, and saithe) and selected environmental variables (mean annual temperature anomaly in the Kola section, mean annual anomaly of sea ice cover in the Barents Sea, red king crab total stock, snow crab total biomass). Fish abundances were $\log_{10}(x + 1)$ -transformed before analysis. The CCA test was performed using version 4.5 of CANOCO (ter Braak and Smilauer 2002); all canonical axes were used to evaluate the significant variables under analysis by Monte Carlo test (999 permutations).

Results

Climatic and ice conditions

The Barents Sea climate shows pronounced variations on different time scales, ranging from seasonal to multidecadal (Wassmann et al. 2006; Ozhigin et al. 2011). Variations in air and sea temperature as well as ice coverage in the Barents Sea tend to fluctuate in phase, and high air temperature correlates with high sea temperature and larger ice-free areas. The short-term climate variability (3–10 years) is strongly associated with changes in the intensity of the Atlantic water inflow (Loeng 1991; Sakshaug et al. 2009) and with regional heat exchange between the atmosphere and ocean (Wassmann et al., 2006; Sakshaug et al. 2009).

Analysis of multi-decadal climate variations has documented cold periods in the beginning of the 20th century and in the 1960s–1980s, and warm periods in the 1930s–1950s and since the 1980s (Ozhigin et al. 2011). Therefore, the period 1900–2007 included two long-lasting warm periods and two long-lasting cold periods. Comparisons of these periods indicate that the amplitude of the air and ocean fluctuations were somewhat different; e.g., while the ocean temperature and ice cover reached extreme values in 2004–2007 compared to those observed earlier, air temperatures did not (Ozhigin et al. 2011).

High ice coverage and low air and sea temperatures were observed during the two first decades of the 20th century (Wassmann et al. 2006; Ozhigin et al. 2011).

The period from 1929 to 1964 was characterized by above-average air temperatures, sea temperatures and ice-free area relative to the corresponding long-term means. This period has been referred to as the early warming of the Arctic (Matishov et al. 2012). In those phases temperature anomalies were up to $+1.0$ °C. From the mid-1960s until the end of the 1980s there was another cold phase in the Barents Sea, which was less pronounced than the 1900–1920s cold phase. After 1988 there was a new warm period, with a temperature maximum in 2006 (Matishov et al. 2012; Dvoretzky and Dvoretzky 2013c). The current warming of the Barents Sea began in the late 1980s and continued until 2006–2007. In 2008 and 2009, sea temperatures decreased while ice cover increased, indicating a cooling tendency in the Barents Sea. As evidenced by salinity data, this increase in temperature in 1990–2012 was mainly caused by strong advection of Atlantic water Ozhigin et al. 2011; Matishov et al. 2012).

Temperature anomalies were registered in the Barents Sea at 0–200 m depths at the Kola Transect in the 20th century and in the early 21st century, with peaks between 2001 and 2007 and in 2012 (Dvoretzky and Dvoretzky 2013c). The Kola Transect along $33^{\circ}30'E$ is unique because of its long observation period, which began in 1900, was interrupted in 1907–1920 and 1942–1944, and has been maintained as a continuous time series since 1945. The water temperature anomaly in the early twenty-first century increased from $+0.23$ °C in 2003 to $+1.44$ °C in 2012, but was interrupted by a moderate cooling trend in 2008–2010 (Fig. 1a).

Variations in air temperature on Arctic sea coasts in the beginning of the 21st century demonstrate the same patterns as the surface waters, although inter-annual fluctuations of mean annual air temperature is much higher (anomalies of opposite sign alternate at 1–2 year intervals). Identified trends depend on the time interval examined: in 1950–1960 the trend was close to zero, in 1980–2005 it was increasing at a rate of about 0.5 °C per 10 years (Matishov et al. 2012). The anomalies in monthly air temperature values in Murmansk since 1919 have been minimal, including over the last two decades when a pronounced warming trend was indicated in many other parts of the world. A prevalence of positive anomalies was found in 2003–2008 (Matishov et al. 2012).

Ice conditions in the Barents Sea demonstrate large seasonal and interannual variability (Wassmann et al.

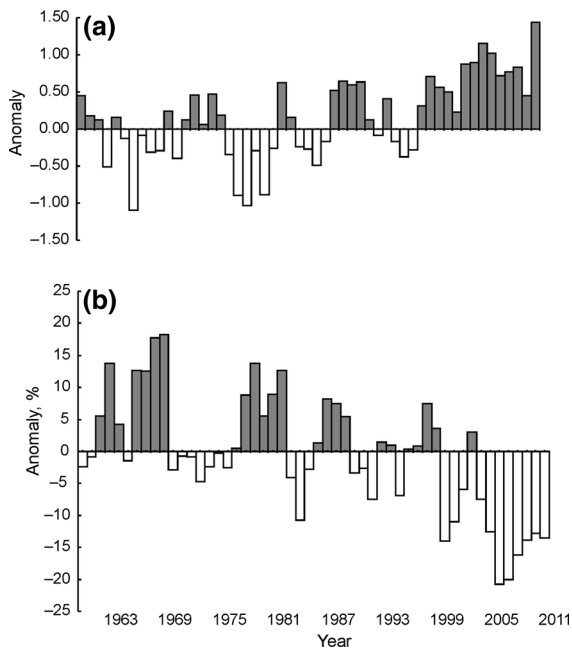


Fig. 1 Mean annual temperature anomalies in the Kola Sect. (0–200 m) (70°30′–72°30′N, 33°30′E) in 1960–2012 (a) according to PINRO data (pinro.ru), and mean annual anomalies (%) of sea ice cover in the Barents Sea from 1960–2011 (b) (Matishov et al. 2012)

2006). A cold period with high positive anomalies in the ice-covered area was observed from 1960 to the early 1990s. Since the 1990s a warm phase with a prevalence of high negative anomalies was recorded. Ice cover was closely associated with sea water temperature. In the Barents Sea, there was a significant correlation between ice coverage in August and water temperature at the Kola Transect in the same month for the period 1960–1998 ($r = -0.83 \pm 0.03$). Since the beginning of the 1990s sea ice conditions in the Barents have been favorable for living marine resources (Matishov et al. 2012). A gradual decrease in ice area to the minimum values in 2006–2007 was observed within this period. However, in 2008–2010 the ice area tended to increase (Fig. 1b). The largest negative anomaly (low ice extent) was observed in 2006 (–21 %). Compared to water temperatures, ice cover anomalies have high inertia and periods of increased ice cover lasting longer than 1 year were observed (Matishov et al. 2012). In the beginning of the 20th century, the years 2006, 2007, and 2008 had the least ice cover: 22, 18, and 17 %, respectively. Complete ice extinction in the Barents Sea for

1 month or longer was observed 10 times in 1960–1998, with all cases in August–October. In 1972, 1984, and 2000 the ice-free period lasted up to 3 months, whereas in 2004 and subsequent years with abnormally light ice conditions, its duration did not exceed 2 months (Matishov et al. 2012).

In summary, total ice cover in the Barents Sea has clearly decreased since 1999, accompanied by positive temperature anomalies in the surface layer.

Shellfish

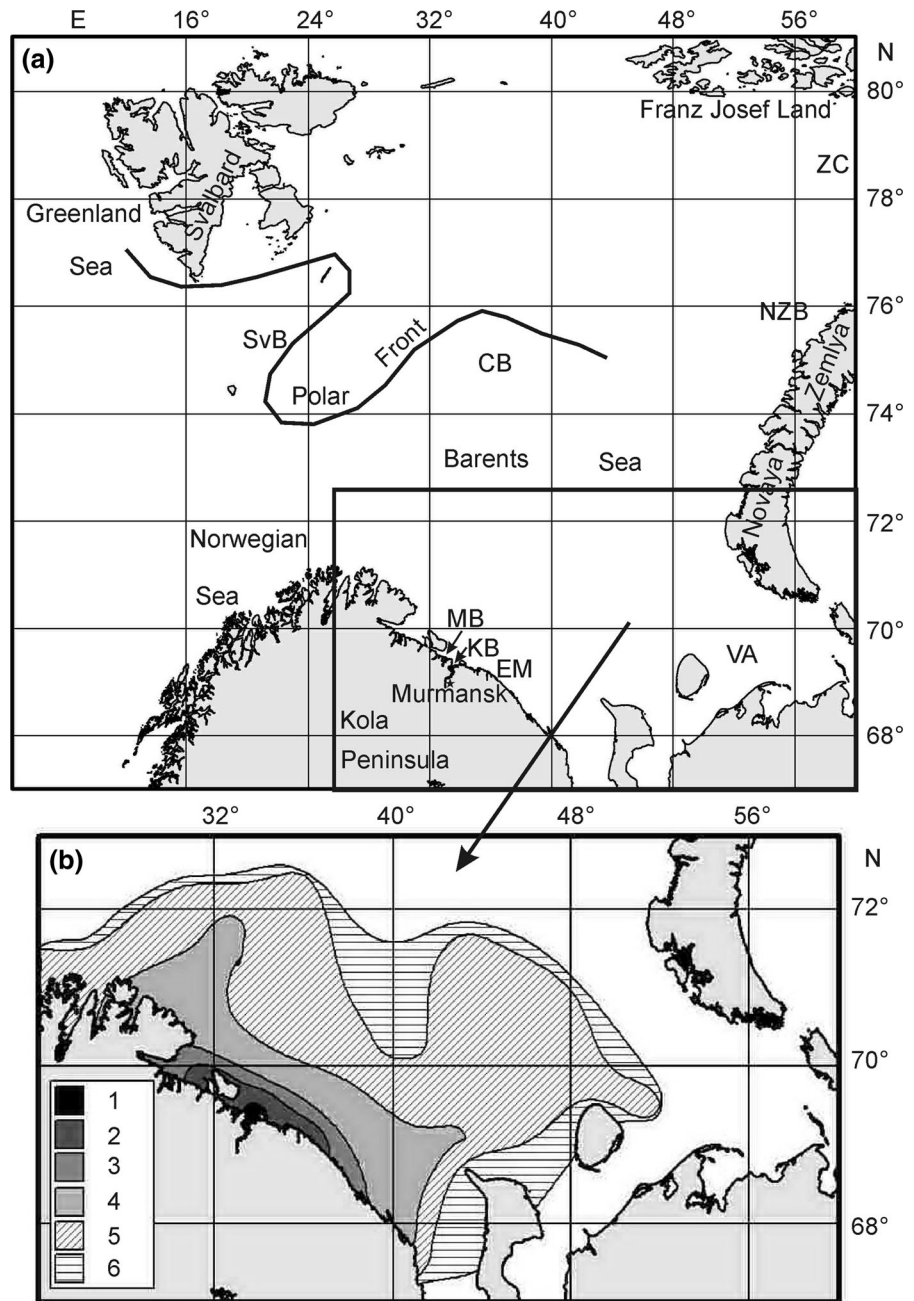
Red king crab

The red king crab is considered to be a shallow water species and occurs in the north Pacific from the Sea of Japan and the Sea of Okhotsk to the western and eastern Bering Sea as far north as Norton Sound, and to the Aleutian Islands and the Gulf of Alaska as far south as British Columbia, Canada (Donaldson and Byersdorfer 2005).

The red king crab is an alien species in the Barents Sea ecosystem. Prior to introduction of the crab, no commercial crab species were found in the Barents Sea. The northern stone crab *Lithodes maja*, a relatively large native king crab species, does not form aggregations suitable for a commercial fishery (Dvoretzky and Dvoretzky 2008). First attempts to introduce the crab into the Barents Sea were undertaken in 1931–1932, but those experiments were not successful because of the inadequate long-distance transportation facilities for live crabs at that time. The second stage of red king crab introduction was undertaken in 1960–1970s. During this period about 3000 adult crabs (6–15 years old), 10,000 juveniles, and 1,600,000 red king crab larvae were released into the waters of the southern Barents Sea, mainly in Kola Bay (Fig. 2a) and adjacent areas of Western Murman. Newly mature crabs and juveniles as well as crab larvae transported from the Far East were also released in the waters of Eastern Murman (Dalnezelenetskaya Bay). These transferred red king crabs were originally caught in Peter the Great Bay (the Sea of Japan) and off the southwestern coast of Kamchatka, the Sea of Okhotsk (Kuzmin and Gudimova 2002).

The first documented report of red king crabs caught in the Barents Sea occurred on August 3, 1974. It was a large (180 mm carapace width, CW) egg-bearing female captured by an amateur fisherman at

Fig. 2 Barents Sea and adjacent waters (a) SvB Svalbard Bank, CB Central Bank, NZB Novaya Zemlya Bank, ZC Zhelaniya Cape, VA Vaygach area, EM Eastern Murman, KB Kola Bay, MB Motovsky Bay. Range expansion of red king crab from the introduction in the 1960s and to present day (b) 1 1961–1969, 2 1970–1977, 3 1978–1990, 4 1991–1994, 5 1995–2002; 6 2005–2008 (Karsakov and Pinchukov 2009)



25–40 m depth in Kola Bay. Subsequently, king crab bycatches in Russian coastal waters have been reported almost annually, and since early 1990 reports of one or more specimens have become more frequent. The crabs were mainly caught in the trawl fisheries for cod and in offshore scallop dredging. King crab observations were also made by sport divers and amateur

fishermen. Accordingly, the matter was brought to the attention of the Mixed Russian-Norwegian Fisheries Commission, which at its meeting in November 1992 requested both countries to intensify and coordinate their research efforts on red king crab with the aim of providing advice to the Fisheries Commission on the state and harvest potentials of the Barents Sea red king

crab stock, and on the possible ecological impact of this new element in the marine fauna. Those coordinated studies on red king crab conducted in 1990–2000s have shown that the red king crab has formed a self-sustaining population in the Barents Sea (Kuzmin and Gudimova 2002).

During the establishment of the population, red king crabs spread both to the west and east of the release sites in 1960–1970 (Fig. 2b). Recently, the first findings of red king crab have been reported in the White Sea, confirming continued range expansion (Dvoretzky and Dvoretzky 2014a).

The red king crab is among the world's largest arthropods, attaining weights of over 10 kg and sizes of 220 mm in carapace length (CL) in the North Pacific and up to 12 kg and 270 mm in the Barents Sea (Dvoretzky and Dvoretzky 2014a). Sizes at maturity for female red king crabs from the coastal Barents Sea range from 104.0 to 110.6 mm CL (Dvoretzky and Dvoretzky 2015).

Red king crabs are high-level predators feeding on the most abundant benthic organisms, i.e. mollusks (bivalvia and gastropods), polychaetes, and echinoderms. In areas with intensive multispecies fishing, they predominantly feed on fish offal. The main predators of red king crabs in the Barents Sea are cod, wolffish, and skates. In Russian waters of the Barents Sea, red king crabs occur from shallow waters to greater than 335 m depth, at temperatures ranging from -0.8 to $+8.5$ °C. In spring (April–May) they form mating aggregations at temperatures of 0 – 2 °C. In autumn (August–September), red king crabs segregate by sex, with males and females forming aggregations at temperatures of 4 – 6 and 5 – 7 °C, respectively (Dvoretzky and Dvoretzky 2014a).

The most common epibionts of red king crabs are *Mytilus edulis* (Bivalvia), *Obelia* spp. (Hydrozoa), and *Circeis armoricana* (Polychaeta). Symbiotic species include *Ischyrocerus commensalis* and *I. anguipes* (Amphipoda), *Tisbe furcata* (Copepoda), *Harmothoe imbricata* (Polychaeta), and *Johanssonia arctica* (Hirudinea) (Dvoretzky and Dvoretzky 2009a, 2010a, 2013a). All species found on the crabs appear to be native to the Barents Sea (Dvoretzky and Dvoretzky 2009b, c). However, *I. commensalis* amphipods were not found at the site examined before the introduction of the red king crab (Dvoretzky and Dvoretzky 2011), indicating that their distribution may have changed in association with this host species

(Dvoretzky and Dvoretzky 2010a). In contrast to the Pacific Ocean the amphipods do not affect egg mortality of red king crabs in the Barents Sea (Dvoretzky and Dvoretzky 2010b).

The population dynamics and aquaculture approaches to red king crab in the Barents Sea have been extensively studied and developed due to the species' high commercial value and introduced status (Dvoretzky and Dvoretzky 2010c, 2012, 2013b, 2014a, b, 2015). Dynamics of the total and commercial stock of red king crabs have been assessed based on trawl survey data (Fig. 3a). From 1994 to 2003 its commercial stock; i.e., the number of legal male red king crabs (>150 mm carapace width) grew from an estimated 23,000 to 13,300,000 individuals. Recent levels are sufficient to support catch rates required for commercial fishing. The red king crab commercial fishery in Russian waters of the Barents Sea started in 2004, and from 2005 to 2013 the landings of red king crabs (Fig. 3b) were lower than the recommended catch rates (total allowable catches). Nevertheless, the commercial stock of the Barents Sea red king crab has decreased from 9,514,000 crabs in 2004, to 6,639,000 crabs in 2006, and to 4,305,000 crabs in 2008. In 2009 and 2010, the total numbers of legal males were estimated to be 1,504,000 and 1,583,000 crabs, respectively, and in 2011 this value increased to a level of 2,965,000 crabs (Dvoretzky and Dvoretzky 2014a updated). While these values were determined from trawl survey data, levels in 2012 and 2013 were calculated using a catch survey analysis model (CSA), resulting in estimates of 11,900,000 and 25,000,000 crabs, respectively. The mean weight of a legal male decreased from 4.2 kg in 1998 to 3.2 kg in 2003 and increased again to 4-kg in 2004–2007, with 3 kg observed in recent years (Fig. 3c).

Trawling is known to have some limitations including the lack of sampling in shallow water (trawls are usually used deeper than 70 m), dependence of catch rates on the bottom sediment, and sex selectivity due to the patchy distribution of red king crabs. For this reason, coastal waters of the Barents Sea, in particular the main reproductive areas for Barents Sea red king crab west of Dalnezelenetskaya Bay (Dvoretzky and Dvoretzky 2014a), were surveyed in June–September 2003–2007 using SCUBA diving. Based on these surveys, the abundance of immature red king crab in waters <40 m increased over this time, while the stock of commercial males decreased

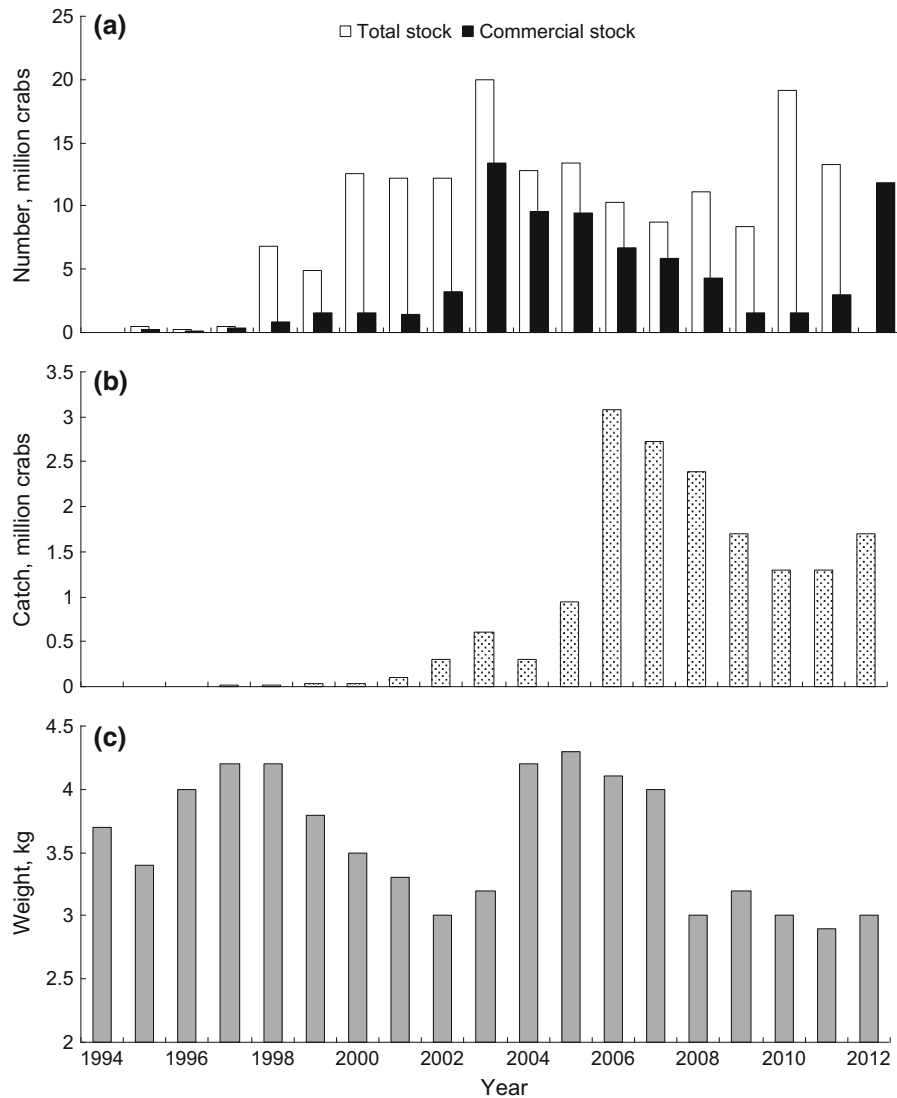


Fig. 3 Dynamics of total (*all crabs*) and commercial (crabs with >150 mm carapace width) stock (a), catch rates (b) and mean weight of a legal male (c) of the red king crab in Russian

waters of the Barents Sea in 1995–2012 (from Dvoretzky and Dvoretzky 2014a, updated with Shamray 2013; Bakanev and Pinchukov 2014)

(Table 1). This agrees with a decreasing trend in the total commercial stock of red king crab based on the trawl data (Fig. 3a).

Snow crab

The snow crab is a true crab belonging to the family Oregoniidae. It is a subarctic species found in the north Pacific in the Sea of Japan, the Sea of Okhotsk, and the Bering Sea north of the Alaska Peninsula. In the northwestern Atlantic Ocean the snow crab is found

from southern Greenland and Canada south to Casco Bay in Maine, USA. Snow crab also inhabit the Arctic Ocean, the Beaufort Sea to Cape Perry and the shelf of the Laptev Sea, and the East Siberian Sea (Jadamec et al. 1999). Adult snow crab are usually found at depths from 0 to 450 m, and temperatures from 0 to 5 °C. The species is most often found on mud and sand bottoms where it buries itself during the daytime (Agnalt et al. 2011; Pavlov and Sundet 2011).

In 1996, snow crab was recorded for the first time in the northeast Atlantic when five individuals were

Table 1 Stock of immature, mature, and commercial red king crabs, *Paralithodes camtschaticus*, in the coastal waters of the Barents Sea (depth <40 m) based on diving surveys, 2003–2007 (cited from Dvoretzky and Dvoretzky 2014a)

Group	Carapace width (mm)	2003	2004*	2005**	2007***
Mature males	>100	4,410,000	4,990,000	4,090,000	No data
Legal males	>150	3,090,000	3,490,000	3,280,000	1,730,000
Mature females	>100	11,100,000	17,720,000	3,380,000	6,080,000
Immature crabs	<100	55,110,000	42,800,000	27,990,000	162,900,000

* Excluding Motovsky Bay

** The areas to the east of the Maliy Oleniy Island only

*** Excluding the Seven Islands area

captured by Russian commercial fishing vessels in the Barents Sea (Kuzmin et al. 1999). Two more individuals were reported in 1998, and eight in 1999. Their sizes ranged from 41 to 123 mm carapace width (CW). Ballast water was suggested as a possible vector. More crabs have since been reported, mainly collected as by-catch in bottom-trawls (Agnalt et al. 2011; Pavlov and Sundet 2011).

Before 2005, most Russian data on captured snow crabs came from bottom trawl surveys and fishing vessels with one or two scientists on board. Since 2003, joint Russian-Norwegian ecosystem surveys have been carried out in the Barents Sea in August–September. These surveys permitted closer evaluation of snow crab distributions. Snow crabs occur mainly in the eastern Barents Sea, but single animals have also been recorded in the western and northern parts of the Sea (Agnalt et al. 2011; Pavlov and Sundet 2011).

Russian fishermen captured the first two crabs in the Norwegian part of the Barents Sea in 2001 during trawling at 71°37′–72°01′N and 19°16′–20°44′E. The first record of capture by local fishermen in Norwegian waters is from 2003, when two specimens were caught off the coast of Finnmark. Since then, this crab has been caught as bycatch both in the coastal gillnet fishery and during scientific and commercial trawling in the central and northern Barents Sea (Pavlov and Sundet 2011).

Since 2006, the quantity of crab bycatch in the northeastern and southeastern Barents Sea has increased. At the same time, the incidence of small crabs within aggregations has increased. These areas therefore seem to be favorable nursery grounds for snow crabs. A significant number were also captured in the central Barents Sea. The known range of the

introduced snow crab is between 79 and 69°N, 56–27°E. When comparing the known distribution patterns in 2009 and 2006, an increase in the overall abundance of crabs, especially in the eastern part of the Barents Sea is noted. In 2007 the main area of crab distribution was in the northeastern regions, whereas in the following year the crabs were found over a much larger area, including south of Novaya Zemlya. In 2008, three male crabs were captured in southern St. Ann Trough; i.e., north of Novaya Zemlya Island at the entrance to the Kara Sea (Agnalt et al. 2011). In 2009, a single male crab was caught in the northeastern Barents Sea (79°03′N 51°10′E) by a Russian research vessel during an ecosystem survey (Pavlov and Sundet 2011). The main food items of snow crabs in the southeastern Barents Sea are polychaetes, mollusks, crustaceans and echinoderms. Snow crabs were found in the diet of bottom fish, primarily cod, and more rarely in haddock, wolffish, and thorny skate (Pavlov 2007).

The results of Joint Russian-Norwegian ecosystem surveys conducted recently have shown a tendency for an increase in the total number of snow crabs. The main part of the population was observed in the Russian Economical zone of the Barents Sea. Lower concentrations of snow crabs were found in international waters of the Barents Sea. Recent trap surveys (June–July 2013) have shown that the largest proportion of legal males (CW > 100 mm) occupies the areas adjacent to Goose Bank and the southern extremity of Novaya Zemlya. The commercial stock of the Barents Sea snow crab was estimated to be 370,000,000 individuals (Goryanina et al. 2013). No Russian snow crab fishery has been implemented, but from December 2012 to mid-2013, a Norwegian

vessel caught ~100 t of snow crabs in international waters of the Barents Sea. In May 2013, one Spanish vessel had joined this fishery and its catch of snow crabs exceeded 100 t by July 2013 (Goryanina et al. 2013).

According to PINRO and VNIRO survey data, male snow crabs predominated (>99 %) both in the open part of the Barents Sea and in the Russian Economical zone of the Barents Sea. Size frequency distributions of the crabs were similar in both regions. Large legal males predominated (84 %) in the catches and the greatest density of crabs (145–320 individuals per km²) was recorded to the south of Goose Bank. The majority of crabs collected had old or very old shells (70–90 %). Crabs with new shells accounted for <1 % by number (Goryanina et al. 2013).

Spatio-temporal patterns of the total abundance of snow crabs suggest an expansion of the area inhabited over the last 7 years (Fig. 4). The distribution has continuously spread to new areas, including waters off Novaya Zemlya and the coastal sites adjacent to the archipelago. In 2012, maximum catches of snow crab were as high as 5000 individuals per 15 min of trawling in the coastal waters near Zhelaniya Cape. This level was 10 times higher than in 2011. A high abundance of crabs was also registered in the Vaygach area (Goryanina et al. 2013).

A trap survey conducted in June–July 2013 estimated the number of legal males in an area of 18,000 square nautical miles to be 102,585,000 individuals. The main part of the total stock, however, was dispersed over a larger area. The total area with relatively low snow crab abundance (<9,000 individuals per 1 square mile) was estimated to be 15,200 square nautical miles (~84 % of the total area of survey). This finding suggests that only relatively small areas of the snow crab distribution (<3000 square nautical miles) with high snow crab density are profitable for the commercial fishery (Goryanina et al. 2013).

The total biomass of commercial snow crabs (median, thousand t) gradually increased from 60 t in 1996 to 188,260 t in 2013 (Table 2) (Goryanina et al. 2013). Based on the management rules applied for the Russian Far East, a total allowable catch (TAC) for snow crabs (experimental fishery) has been set at a level of 2000 t. But owing to the introduced status of snow crab, it was recommended to decrease the TAC to 1000 t (5 % of the estimated commercial stock).

Northern shrimp

The northern shrimp (pink, deep-water or deep-sea shrimp) is a discontinuous circumboreal species. It occurs on the continental shelves from Georges Bank (about 41°N) in the western north Atlantic, north to the Davis Strait (about 72°N), through East Greenland and Iceland to the northeast Atlantic, including the Norwegian Sea, the Barents Sea, and the North Sea. The species has also been reported from the Pacific in areas off British Columbia, the Gulf of Alaska and the Bering Sea, Japan and eastern Russia (Berenboim 1992; Hvingel and Berenboim 2011 and references therein).

Northern shrimp are usually associated with soft, muddy substrates, temperatures between 1 and 8 °C and salinities between 25.9 and 35.7 psu. Shrimp are found in near-bottom waters throughout most of the Barents Sea at all temperatures observed, but mostly at 200–400 m. The highest concentrations are found around Svalbard and in the central parts of the Barents Sea, which are also the most important fishing grounds (Hvingel and Thangstad 2010; Hvingel and Berenboim 2011).

The depths and temperatures where the highest concentrations of northern shrimp are found in the Barents Sea tend to vary (Hvingel and Berenboim 2011). In the east, they form concentrations at lesser depths and much lower temperatures than in the central, southern, and Svalbard areas of the Barents Sea. However, in the Barents Sea northern shrimp prefer habitats with similar bottom topography in most of the area: the slopes of bottom depressions, basins, and the foot of slopes of shallow banks. Aggregations of northern shrimp occur, as a rule, in frontal zone areas. Frontal zones form where waters of warm currents of Atlantic or coastal origin interact with cold Arctic or transformed Atlantic waters on the slopes of basins and shallow banks (Hvingel and Berenboim 2011). A frontal zone is characterized by sharp gradients in temperature in the near-bottom layers, powerful vertical water circulation, muddy bottom, and high rates of plankton and benthos production. The biotic and abiotic factors governing the formation of concentrations of northern shrimp thus include both the bottom topography and the interaction of water masses of different origins. In addition, a correlation between the distributions of northern shrimp and *Sedentaria* polychaetes in the Barents Sea has also

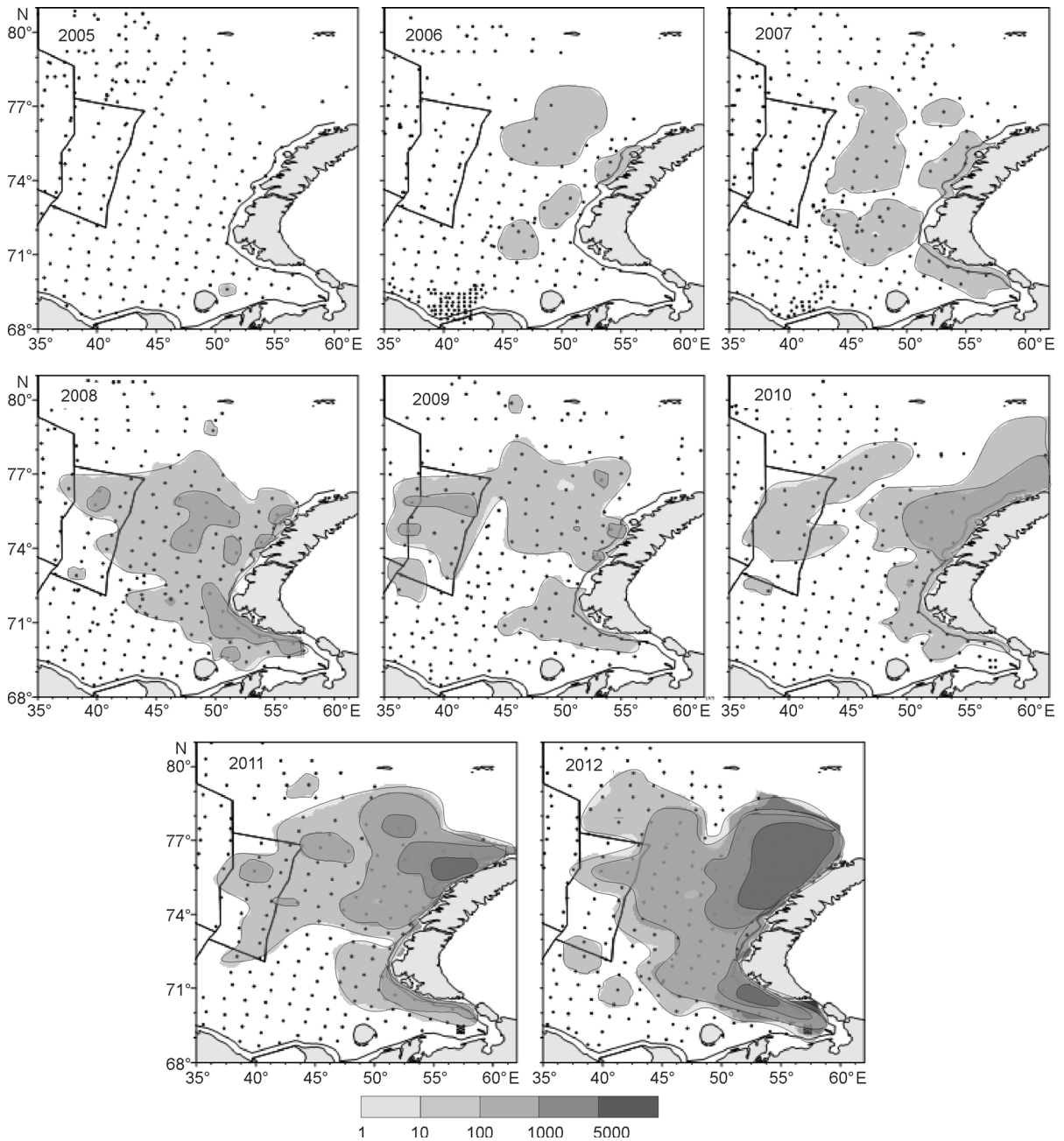


Fig. 4 Distribution of the total catch of snow crab (individuals per 15 min of trawling) in the Barents Sea from 2005 to 2012 (Goryanina et al. 2013)

been observed. Concentrations of northern shrimp in the Barents Sea coincide with areas where polychaete biomass amounts to more than 50 % of the total benthic biomass (Hvingel and Berenboim 2011). The distribution of northern shrimp in the northwestern part of the Barents Sea, off Franz Josef Land and in the

Kara Sea, is primarily due to the transport of larvae by Atlantic waters to these areas (Hvingel and Berenboim 2011).

Shrimp biomass and demography have been recorded annually by means of bottom trawl surveys since 1982. Until 2004, Russia and Norway ran

Table 2 Biomass of commercial snow crabs (median) in the Barents Sea from 1996 to 2013 (Goryanina et al. 2013)

Year	Biomass (t)	Year	Biomass (t)
1996	60	2005	7000
1997	20	2006	7150
1998	30	2007	8220
1999	120	2008	15,550
2000	200	2009	31,780
2001	170	2010	57,830
2002	620	2011	96,950
2003	2760	2012	144,020
2004	3650	2013	188,260

separate targeted shrimp surveys in their respective Exclusive Economical Zones. Russian/Soviet surveys were carried out in April–June from 1984 to 2005. The research area comprised central and eastern parts of the Barents Sea and the Svalbard area. About 100–150 hauls were conducted annually. The Norwegian shrimp survey took place in spring from 1982 to 2004. It covered the central and western parts of the Barents Sea, with about 200–250 hauls annually. In 2004 the joint Norwegian-Russian “Ecosystem survey of the Barents Sea” was initiated (Hvingel and Berenboim 2011). Since 2006, the ecosystem survey data, together with information from the fishery, have been incorporated into a mathematical model of stock dynamics (Hvingel and Kingsley 2006). This model provides an integrated estimate of past, present and future stock dynamics. It is also used to evaluate various future catch scenarios and thus provide the basis for advice to fisheries management authorities.

Since the 1970s, the estimated shrimp stock biomass has been above its maximum sustainable yield level. A steep decline in stock biomass was observed in the mid 1980s following some years with high catches, and the biomass estimate came close to the maximum sustainable yield level. The estimate of mean biomass has varied considerably since the early 1980s. Since the late 1990s the stock has varied with an overall rising trend. From 2004 to 2006 biomass increased by about 66 % and then decreased again back to the 2004 level in 2008. The 2010–2012 values were back up close to that of 2006 (Hvingel and Thangstad 2012). Overall size distributions of northern shrimp indicate a relatively large amount of

smaller shrimp in 2004, which was the likely basis for the observed increase in stock biomass until 2006. The recruitment index—estimated abundance of shrimp at 13–16 mm CL supposed to enter the fishery in the following 1–2 years—decreased since 2004.

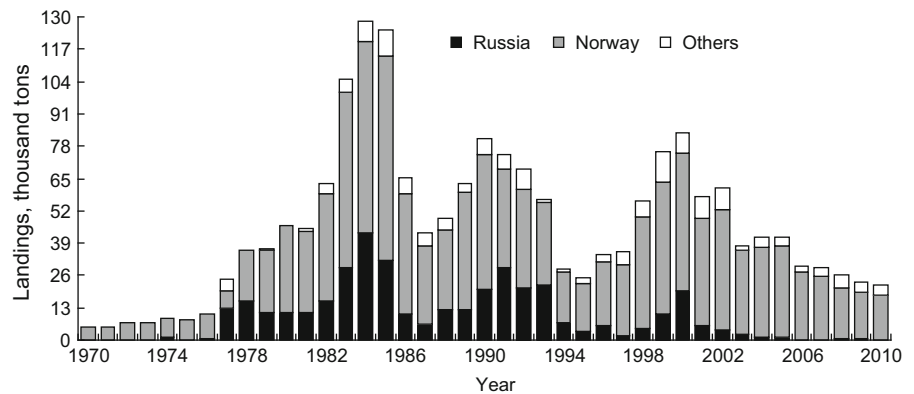
Since the early 1980s annual landings have fluctuated, with local minima and maxima separated by periods of 8–9 years. Overall catches have ranged from 22,000 to 128,000 t. The most recent peak was seen in 2000 at approximately 83,000 t. Catches thereafter declined to 23,000 t in 2009. Based on data until August (logbooks and information from the industry) the total catch in 2010 is estimated at 22,000 t (Hvingel and Thangstad 2010) (Fig. 5).

The spatial distribution of northern shrimp biomass changed from 2004 to 2012 with areas of high shrimp density gradually shifting further east in the Barents Sea (Hvingel and Thangstad 2012; Zakharov and Lyubin 2012). A noticeable shift is seen from 2007 to 2009 when biomass in the central part of the Barents Sea declined while biomass in the Novaya Zemlya area increased. In recent years, shrimp are generally found in shallower water in recent years. A general decline in the 500–600 m range—depths typically found around Svalbard—was observed until 2010, after which the biomass increased again (Hvingel and Thangstad 2012). According to PINRO data, shrimp catches varied from several grams to 115 kg per 15 min of trawling. The largest catches of northern shrimp were found in the eastern and northern parts of the Barents Sea (Central Bank, Novaya Zemlya Bank, Franz-Victoria Trough) and to the north of the Svalbard Archipelago. In the southeastern part of the Barents Sea and the Svalbard Bank no northern shrimps were observed (Zakharov and Lyubin 2012).

Fish

The Barents Sea and adjacent waters encompassing the Lofoten-Vesterålen area play a vital role in the life history of the major fish stocks in the northeast Atlantic: northeast Arctic cod, northeast Arctic haddock, northeast Arctic saithe, Norwegian spring-spawning herring, and capelin (Olsen et al. 2010). Cod, haddock and capelin stocks form the basis for large fisheries in the Russian part of the Barents Sea as well as being vitally important as prey and predators in the ecosystems of the Barents and Norwegian Seas.

Fig. 5 Nominal landings of northern shrimp by nation in 1970–2010 (Hvingel and Thangstad 2010)



Northeast Arctic cod

Northeast Arctic cod dominate the ecosystem due to their great abundance, wide distribution, long migrations and omnivorous feeding habits. Northeast Arctic cod are widely distributed along the Norwegian coast and in the Barents Sea as far north as 80°N (Svalbard) and 78°N (Great Bank) and up to the western coast of Novaya Zemlya and the southwestern part of the Kara Sea in the east (Yaragina et al. 2011, and references therein). The southernmost distribution is observed during spawning, which usually takes place in Norwegian coastal areas (mainly between 67°30'N and 70°N). Less intensive spawning has been observed as far south as 60°N (off the island of Sotra) and as far northeast as Motovsky Bay (Yaragina et al. 2011). The 0-group cod drift from spawning grounds northwards and eastwards and in autumn they can be found over most of the Barents Sea.

The main distribution area of cod is located between the continental slope and the Polar Front. The life cycle of the cod is closely linked to warm and saline Atlantic waters. The species distribution is bounded in the north by the Polar Front zone, an area where Atlantic waters mix with colder Arctic and transformed Barents Sea waters. In certain periods of the year, cod are concentrated close to the frontal zone areas where large quantities of prey are available (Olsen et al. 2010; Yaragina et al. 2011).

Cod is an extremely flexible and generalist northern-boreal species. In the course of its evolution it has adapted well to the variable and harsh conditions of the Barents Sea. Cod occur at depths down to 600 m, but mainly at 100–300 m. They are mostly found at temperatures of 0–7 °C. In winter mature cod avoid

temperatures below 1–2 °C, but they are found at 0 °C and even lower during feeding migrations in summer and autumn when their distribution depends on food availability rather than temperature (Yaragina et al. 2011). Fish are believed to have disordered osmoregulation and endocrine gland function in low-temperature waters (Yaragina et al. 2011). A temperature of 2 °C has been considered to be the most favorable for the physiological processes and maintenance of an optimal energy balance for cod. Young cod occur in the Barents Sea at wider ranges of temperature and salinity than adults, including bottom temperatures from –1.8 °C (Hopen and Novaya Zemlya Bank areas) to 14.8 °C (Murman coast bays) and salinities from 7 to 35 psu.

Cod in the Barents Sea are long-lived fish, characterized by a fair growth potential, high individual fecundity and great fluctuations in year class strength. Recruitment to the commercial stock begins at the age of three. The theoretical maximum age of cod is approximately 30 years (Tretyak 2000), but fish older than 15 years are rarely found in commercial catches nowadays (Yaragina et al. 2011). In stock assessments, the instantaneous natural mortality rate is assumed to be 0.2 for cod aged 3 years and older, with estimates of mortality caused by cannibalism added for the younger age groups (ICES 2008). Cod natural mortality is age-dependent and can be expressed as a function of age, approaching infinity toward maximum age, which is equal to the maximum theoretical life span in the absence of a fishery (Tretyak 1984). According to these calculations, cod had the lowest mortality at the age of 8–9 years, and the mean natural mortality coefficient for ages 3–16 was equal to 0.12, which is 60 % of the estimate adopted by the Arctic Fisheries Working Group (ICES 2008).

Northeast Arctic cod play a dominant role in the Barents Sea ecosystem as important predators, influencing practically all trophic links. Cod consume a very wide range of food items and can switch relatively easily to prey that are more abundant in a given season and area (Yaragina et al. 2011). Cod juveniles and adults belong to different trophic groups. Cod juveniles are mainly plankton predators while older fish feed on larger crustaceans (shrimp) and fish (Dalpadado and Bogstad 2004). In the diet of the oldest cod, larger fish species predominate. A few marine mammals and polar bears are the only known predators of adult cod in the Barents Sea (Bogstad et al. 2000). However, young cod (larvae, juveniles and fry) may serve as prey for larger marine organisms such as herring, Greenland halibut, long rough dab, skates, and even jellyfish, whose prey-predator size ratios and behavior enable them to catch small cod. The most important predators of young cod are likely to be their older conspecifics (Yaragina et al. 2011). Cod larvae start exogenous feeding 5–7 days after hatching, while they still have a yolk sac. The first food of cod larvae includes nauplii of Copepoda, mainly *Calanus finmarchicus*, crustacean eggs, Rotatoria, and larvae of Bivalvia. The main prey of Barents Sea cod are capelin, herring, polar cod (*Boreogadus saida*), sandeel (*Ammodytes* spp.), snake blennies (*Lumpenus lampretaeformis*), young cod and haddock, long rough dab (*Hippoglossoides platessoides limandoides*), and redfish. The second important group in the diet of cod is crustaceans, primarily small pelagic crustaceans of the families Euphausiidae and Hyperiididae, nekto-benthic shrimp *Pandalus borealis*, and bottom-living crustaceans (Amphipoda, Cumacea, hermit crabs *Pagurus* spp., spider crabs *Hyas* spp., etc.) (Yaragina et al. 2011).

Northeast Arctic cod is currently, and possibly also historically, the largest cod stock in the world. Between 1913 and 2013, the total stock size has varied between 700,000 and 4,200,000 t (in 1946), while the spawning stock has ranged between 100,000 and 2,220,000 t. In the last decade, these levels were 1,360,000–3,470,000 and 290,000–2,220,000 million t, respectively (Table 3). Recruitment at age three has ranged between 100,000,000 and 1,600,000,000 t. The variation in recruitment seems to have been larger before about 1990 (Yaragina et al. 2011).

Catches of Northeast Arctic cod ranged from 190,000 to 1,200,000 t, averaging 583,000 t (Fig. 6a).

Table 3 Cod total stock biomass and spawning stock biomass over 2001–2013 (ICES 2013; Shamray 2013)

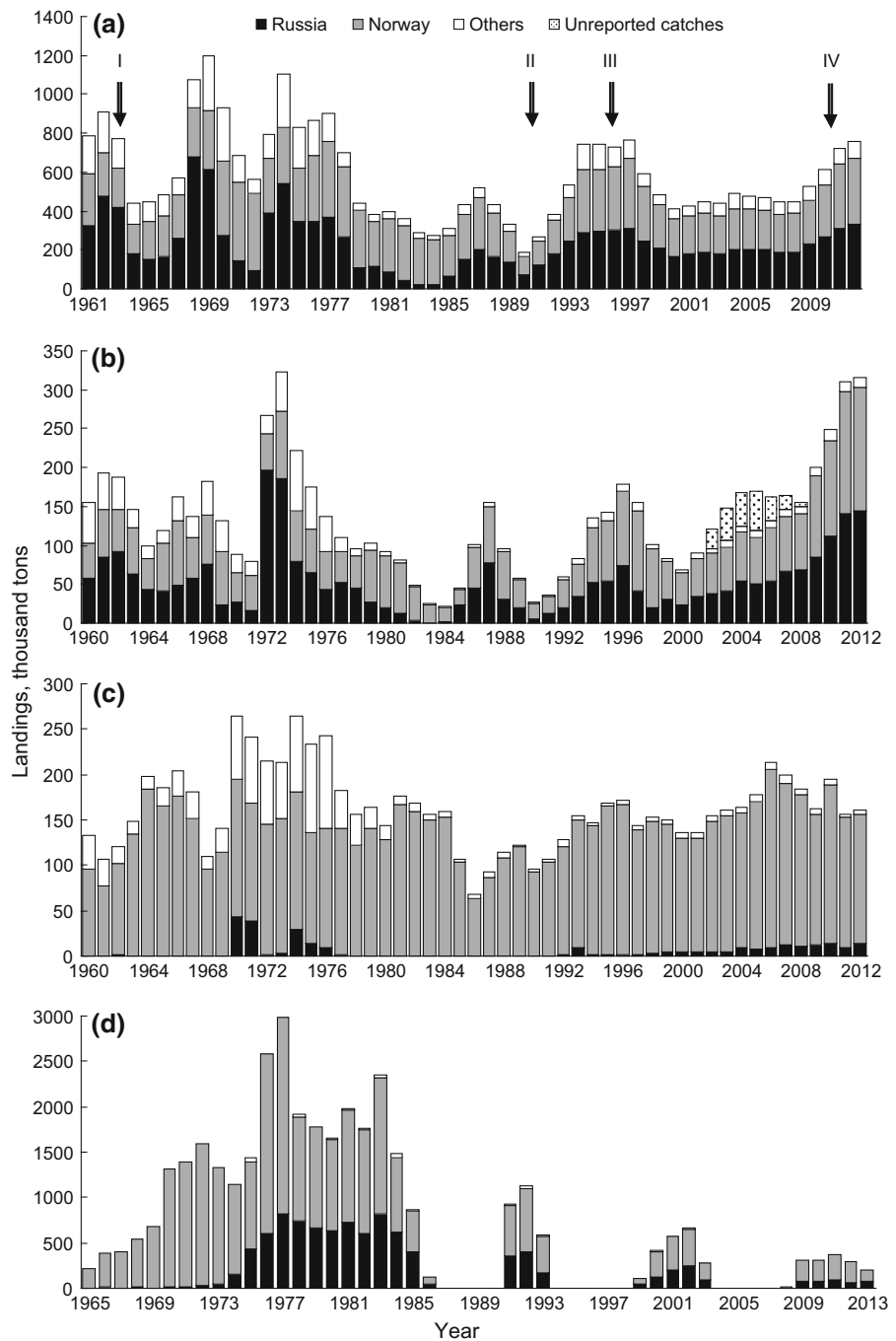
Year	Total stock biomass	Spawning stock biomass
2001	1,360,000	290,000
2002	1,280,000	330,000
2003	1,410,000	490,000
2004	1,830,000	650,000
2005	1,700,000	800,000
2006	1,500,000	660,000
2007	1,200,000	440,000
2008	1,600,000	590,000
2009	2,300,000	840,000
2010	2,880,000	1,350,000
2011	2,838,000	1,488,000
2012	2,611,000	1,551,000
2013	3,470,000	2,220,000

From a level of about 900,000 t in the mid-1970s, total catch declined steadily to around 300,000 t in 1983–1985. Catches increased again in 1987 before dropping to 212,000 t in 1990, the lowest level recorded in the post-war period. From 2000 to 2009, the reported catches were between 400,000 and 520,000 t, but there were additional unreported catches. Catches increased again in the last 3 years, reaching 754,000 t in 2012 (Fig. 6a). The fishery is conducted both with an international trawler fleet and with coastal vessels using traditional fishing gears. The quota established by the Joint Norwegian-Russian Fisheries Commission for 2013 was equal to 1,000,000 t. In addition, the TAC for Norwegian Coastal Cod was set to the same value for 2013 as for 2012: 21,000 t (ICES 2013).

Haddock

Haddock are boreal gadids that live at depths to 600 m or more in water with normal oceanic salinity and temperatures ranging from 2 to 10 °C. Haddock are widely distributed in the North Atlantic Ocean. Large populations are found in the Barents Sea, the North Sea to the west of Scotland and around Iceland and the Faroe Islands, and off Newfoundland, Nova Scotia, and New England. The largest population is the Arcto-Norwegian or northeast Arctic haddock, which inhabits the Barents Sea and the eastern part of the

Fig. 6 Catch history of Barents Sea cod (a), haddock (b), saithe (c) and capelin (d) (ICES 2013). *I* Introduction of red king crab, *II* establishment of the Barents Sea red king crab population, *III* introduction of snow crab, *IV* exponential growth of snow crab abundance



Norwegian Sea. There are also several small local haddock stocks along the Norwegian coast. Although the northeast Arctic haddock can reach a length of 110 cm and a weight of 14 kg, the most common commercial catches range from 40 to 65 cm in length and from 1 to 3 kg in weight. Haddock become

sexually mature at a length of about 40–60 cm. Depending on growth and sex, haddock mature at 4–7 years of age (Russkikh and Dingsør 2011).

Haddock feed primarily on small invertebrates, although larger individuals of the species may occasionally consume fish. Benthic animals (echinoderms,

mollusks, polychaetes, and crustaceans) are their main prey (Bergstad et al. 1987). Depending on age and season, haddock vary their diet, switching between fish, plankton, and benthos. During the spawning migration of capelin, haddock prey on capelin and their eggs on the spawning grounds. When capelin abundance is low or when their areas do not overlap, haddock can compensate for the lack of capelin with other fish species; e.g., young herring, or euphausiids and benthos (Russkikh and Dingsør 2011). The commercial (fishable) stock consists of fish more than 3 years old. The highest recorded age is more than 20 years, but most commercial catches are dominated by fish between three and 6 years old (Russkikh and Dingsør 2011).

Haddock is one of the most important commercial fish species in the Barents Sea and the fishery has long traditions both in Russia and Norway. Haddock is mainly fished by trawl as by-catch in the fishery for cod, while a directed trawl fishery for haddock catches a variable proportion of total catches. On average approximately 33 % (30 % in 2012) of the catch is taken with conventional gears, mostly longline, which in the past was used almost exclusively by Norway. Some of the longline catch is from a directed fishery, which is restricted by national quotas (Russkikh and Dingsør 2011).

The exploitation rate of haddock has been variable. The highest fishing mortalities for haddock have occurred at low to intermediate stock levels and historically show little relationship with the exploitation rate of cod, in spite of haddock being primarily caught as by-catch in the cod fishery. However, the more restrictive quota regulations introduced around 1990 have resulted in a more stable pattern in the exploitation rate. The exceptionally strong year classes 2004–2006 have contributed to the strong increase in stock size and spawning stock biomass that have been seen in recent years. These year classes are estimated to be 97, 88, and 75 % mature in 2013. The following year-classes were much weaker, therefore stock size and spawning stock biomass are expected to decrease, which again will result in lower recommended catch limits. However, the ICES Arctic Fisheries Working Group predicts relatively high stock levels within acceptable fishing mortalities in the coming years (ICES 2013).

A regular Russian trawl fishery began in 1920, and has continued year round since 1925. In 1930–1970,

except for the war years, there was a dramatic increase in the international trawl fishery in the Barents Sea and a dramatic rise in haddock landings. In the 1920s, average annual landings were about 30,000 t and by the 1970s, the average was about 160,000 t. This early trawl fishery was mainly directed at young and immature haddock and had a huge impact on stock numbers (Russkikh and Dingsør 2011).

Since 1960, the total annual catch of haddock has ranged from 21,000 to 322,000 t. In recent years Norway and Russia have been responsible for more than 90 % of the landings (Fig. 6b). The official landings (those reported to ICES and contained in the Statlant statistics) (ICES 2013) for 2011 amount to 306,900 t, and the provisional official landings for 2012 are 315,033 t. These are the highest landings of haddock since 1973. In recent years, estimates of illegal, unreported and unregulated (IUU) catches of haddock have been added to reported landings for the years 2002 and onwards. In 2007 to 2009 two estimates of IUU catches were available, one Norwegian and one Russian. At the benchmark assessment it was decided to base the final assessment on the Norwegian IUU estimates. From 2009 and onwards, a joint Norwegian-Russian Analysis Group under the Mixed Norwegian-Russian Fisheries Commission has provided joint estimates of IUU catches (Fig. 6b). Based on these, the Arctic Fisheries Working Group decided to set the IUU estimate for haddock in 2009–2012 to 0 (ICES 2013). For 2013, the mixed Norwegian-Russian Fisheries Commission agreed on a TAC of 200,000 t, which was below the advice of 238,000 t based on last year's assessment (ICES 2013).

Saithe

Saithe, an active gregarious fish, is only found in the north Atlantic. In the northwestern part there is only one small stock, which straddles the border between Canada and the USA. In the northeastern Atlantic saithe have been separated into six stocks however, the boundaries are not always well defined. The main areas occupied by these stocks are west of Ireland, west of Scotland, off Iceland and the Faroes, in the North Sea and along the coast of Norway. Northeast Arctic saithe are found along the Norwegian coast from 62°N to Cape Kanin, the Goose Bank, and Kolguev Island in the southeastern Barents Sea. They

also occur in the Svalbard area, but normally only in low numbers.

In April–June, the 2–3 cm long saithe fingerlings begin to migrate from the open ocean to the coastal zone. In summer and autumn large numbers of juvenile (0-group) saithe occupy the coastal zone, in some years as far east as the inlets of the Motovsky and Kola Bays and the eastern Murman coast. Saithe yearlings may also occur in this region. Juvenile saithe are found regularly at certain localities where the depth is 60 m or less. These fish are usually schooling and are often observed in dense concentrations where currents concentrate prey items (Mehl et al. 2011). By the age of two, saithe have usually left the near-shore areas and aggregate in the coastal region at depths of less than 100 m. Such aggregations, which may consist of 2–5 year old fish, are the basis for the purse seine fishery. Further offshore, saithe may be both pelagic and demersal, and are mainly found at depths between 0 and 300 m. At less than 200 m they are normally close to the bottom or in the lower half of the water column, but as water depth increases they spread relatively further up into the water column (Stensholt et al. 2002), and at depths greater than 300 m a large proportion may occupy the pelagic part of the water column.

The main prey items for young saithe are copepods (*Calanus*), krill, and other crustaceans (Mironova 1961; Nedreaas 1985), while older fish gradually prey more on fish such as herring, sprat, young haddock, Norway pout and blue whiting (Mehl 2005). Along the coast of Finnmark, saithe feed intensively on capelin during the spawning season of the latter (Rist 2005). In the smallest size group (20–39 cm), krill was the dominant prey item, while fish dominated as prey in the larger fish, most prominently in the north. In the northernmost region, herring was the most important item of fish prey, followed by haddock, Norway pout and blue whiting. (Mehl et al. 2011).

Landings of northeast Arctic saithe were high in 1970–1976 with a maximum of 274,000 t in 1974 (Fig. 6c). Catches declined sharply after 1976. This was partly caused by the introduction of national economic zones in 1977. The stock was accepted as being exclusively Norwegian, and quota restrictions were imposed on fishing by other countries, while the Norwegian fishery remained unrestricted for several years. Another decline followed, and in 1986 landings amounted to no more than 70,000 t. Subsequently

landings increased and reached 212,000 t in 2006, followed by a decline to 161,000 t in 2012 (Fig. 6c). Since 1960 average annual catch has been 163,000 t (Norway 137,000 t). The Norwegian fishery, which currently accounts for more than 90 % of total landings, employs various types of gear, while other nations mainly use bottom trawls. During the past 10 years about 40 % of the Norwegian catch has been taken by bottom trawl, 25 % by purse seine, 20 % by gillnet, and 15 % by other conventional gear (longline, Danish seine, and handline). The gillnet fishery, which primarily targets spawning fish, is most intense during the winter, while purse seining targets immature saithe in the summer months, and the trawling takes place fairly evenly throughout the year. In the Russian trawl fishery in the Barents Sea, saithe have mostly been a bycatch species (Mehl et al. 2011).

Discarding, although illegal, occurs in the saithe fishery, but is not considered a major problem in the assessment. Due to its near-shore distribution saithe is virtually inaccessible for commercial gears during the first couple of years of life and there are no reports indicating overall high discard rates in the Norwegian fisheries (ICES 2013). There are reported incidents of IUU in the purse seine fishery, mainly related to minimum landing size. Observations from non-Norwegian commercial trawlers indicate that discarding may occur when vessels targeting other species catch saithe, for which they may not have a quota or have filled it. However, there are no quantitative estimates of the level of discarding available. Following the agreed management plan implies a TAC of 164,000 t in 2012. The spawning stock biomass is expected to decrease by 11 % in 2012 and to remain above B_{pa} (spawning stock biomass in relation to the precautionary approach) at the beginning of 2013. The advice from ICES for 2013 was to follow the agreed management plan, which implies a TAC of 164,000 t in 2013 (ICES 2013).

Capelin

Capelin are small, pelagic, schooling, planktivorous forage fish that attain a maximum length of 22 cm at a maximum age of 7 years. The species is semelparous; i.e., they spawn only once in their lifetime, although certain studies suggest that some individuals may survive after spawning. Capelin have a circumpolar distribution, with major stocks located on both sides of

the Bering Sea, in the Newfoundland–Labrador area, on both sides of Greenland, at Iceland, and in the Barents Sea. There is one large oceanic stock of capelin in the Barents Sea and additional local stocks in at least one fjord in northern Norway (Gjøsæter et al. 2009, 2011).

Copepods, krill and amphipods are major prey of capelin. The relative importance of these prey varies with season, year and capelin size. The importance of copepods decreases with increasing capelin length, while euphausiids and amphipods are most important for adult capelin (Dalpadado et al. 2002). Barents Sea capelin serve as food for several predators. The capelin main predators are cod. It has been estimated that between 1984 and 2007, cod consumed from 0.2 to 3.0 million t of capelin annually, depending on the sizes of cod and capelin stocks. Other capelin predators include haddock, Greenland shark (*Somniosus microcephalus*), Greenland halibut (*Reinhardtius hippoglossoides*), Esmark's eelpout (*Lycodes esmarkii*), thorny skate (*Amblyraja radiata*), long rough dab, beaked redfish (*Sebastes mentella*) and many others (Gjøsæter et al. 2011). Marine mammals such as seals (mainly harp seals *Pagophilus groenlandicus*) and whales (mainly minke whales *Balaenoptera acutorostrata* and humpback whales *Megaptera novaeangliae*) are also significant predators (Gjøsæter et al. 2011). Harp seals alone consume from 23,000 to 812,000 t of capelin per year, depending on stock size. Seabirds also consume capelin; the main avian predators are common guillemots and puffins. The quantity of capelin consumed annually by predators other than cod probably does not exceed one million t (Olsen et al. 2010; Gjøsæter et al. 2011).

Capelin are specialized plankton feeders and are the most important planktivorous fish in the Barents Sea. Other fish at the same trophic level are herring and polar cod, but because herring in the Barents Sea are limited to the southern parts of the area, there is not much distributional overlap with capelin. The polar cod primarily utilizes larger zooplankton forms. Due to their semipelagic behaviour, adult polar cod mostly feed near the bottom, while capelin feed throughout the water column. Polar cod are found in Arctic and mixed water masses, while capelin feed in both Atlantic and Arctic waters (Gjøsæter et al. 2011).

Capelin have a short life cycle, and they display significant fluctuations in abundance due to highly varying levels of recruitment and natural mortality. In

periods of repeated weak recruitment, the stock undergoes a serious decline and may remain for several years in a depressed state that results in a complete ban on fishing. On the other hand, when the stock is in a good state it provides the basis for a substantial fishery that can be sustained for many years (Olsen et al. 2010; Gjøsæter et al. 2011).

The monitored history of capelin stock size is characterized by three stock collapses: 1985–1989, 1993–1997, and 2003–2006 (Fig. 6d). During these collapses, the stock was below 1,000,000 t as measured in autumn. Apart from these periods, the stock has mostly been at a level of 2,000,000–6,000,000 t, with peaks in 1975 and 1991, when capelin biomass was estimated acoustically to exceed 7,000,000 t. Landings increased sharply in the 1950s, but declined to almost zero in 1962–1964. From 1973 onwards, the catch continued to rise until the mid-1980s (Fig. 6d).

When exploitation became intensive, the fishery was continued throughout the year. At first there were no restrictions on the fishery and the catch reached a peak of 3,000,000 t in 1977, when the Norwegian catch was 2,163,000 t and the Russian catch was 821,000 t. Management of the fishery started in 1979, and in 1981–1984 the Joint Fisheries Commission established levels of spring and autumn total allowable catches according to, and even above, the scientifically recommended maximum level defined during the joint Russian-Norwegian investigations. After the peak in 1977, total catches were stable until 1985. In this period the autumn catch was as much as the spring yield, and in 1982–1984 it was even larger. At the same time, the proportion of immature fish aged 1–2 years in the autumn fishery often exceeded 20 %, some years comprising half of the total catch. During the next 5 years the population of capelin was depressed, leading to a complete closure of the fishery from autumn 1986 to 1990, inclusive. The catches taken from the recovered stock in 1991–1993 were relatively small compared to the period 1970–1985. The fishery was closed again in spring 1994, when a new stock collapse was evident, but was opened on a recovered stock in 1999–2003. The fishery was thus closed from autumn 1986 until 1990, from autumn 1994 until 1998 and again from 2004 until 2008. In recent years, the fishery has been restricted to a winter fishery only, and about 500,000 t are taken annually (Gjøsæter et al. 2011; ICES 2013). The total catches that were taken during spring 2013 amounted to

121,000 t by Norway and 60,400 t by Russia, 18,700 t below the agreed TAC (ICES 2013).

Relationships between stocks of alien crabs and fish species

Capelin abundance was not significantly cross-correlated with abundance of red king crabs, whereas cod abundance and haddock were positively correlated with king crab abundance 8 years earlier (time lag -8) ($r = 0.59$) and 2 years earlier (time lag -2) ($r = 0.57$), respectively (Fig. 7). Similarly to capelin, there were no significant cross-correlations between abundance time series of saithe and red king crab. Cross-correlation analysis also indicated that abundance of snow crab had a significant but weak positive correlation with the abundance of red king crab at 8 years earlier ($r = 0.51$) (Fig. 7).

Capelin abundance was positively cross-correlated with abundance of snow crabs at lags of $+2$ and $+3$ years ($r = 0.71$ and $r = 0.77$, respectively) (Fig. 7). The cross-correlation analysis of cod abundance and snow crab biomass indicated that a strong positive correlation occurred at a lag 0 (current year) ($r = 0.90$) (Fig. 7). Similarly, cross-correlations of both cod landings and cod total stock biomass (TSB) with snow crab biomass were significant at 1 year earlier, current year, and 1 year later in the case of landings ($r = 0.60$, $r = 0.90$, $r = 0.64$, respectively) and current year, 1, and 2 year later in the case of TSB ($r = 0.82$, $r = 0.82$, $r = 0.60$, respectively).

Positive but large time lags of $+5$ to 6 years and $+4$ to 6 years were found for cross-correlations between abundances of haddock and snow crabs (Fig. 7) and between saithe and snow crabs, respectively. The snow crab and northern shrimp abundance time series were cross-correlated with each other: lags of 0, $+1$, and $+2$ years were significant and negative ($r = -0.60$, $r = -0.57$, $r = -0.52$, respectively), whereas a lag of $+10$ years was significant and positive ($r = 0.64$) (Fig. 7). Additional cross-correlation analysis on shrimp biomass and cod abundance indicates that weak negative correlations occur at lag 0 and $+1$ ($r = -0.51$ and $r = -0.56$, respectively). Negative time lags of 0 and $+1$ year were also found for cross-correlations between shrimp biomass and cod TSB ($r = -0.57$ and $r = -0.54$, respectively).

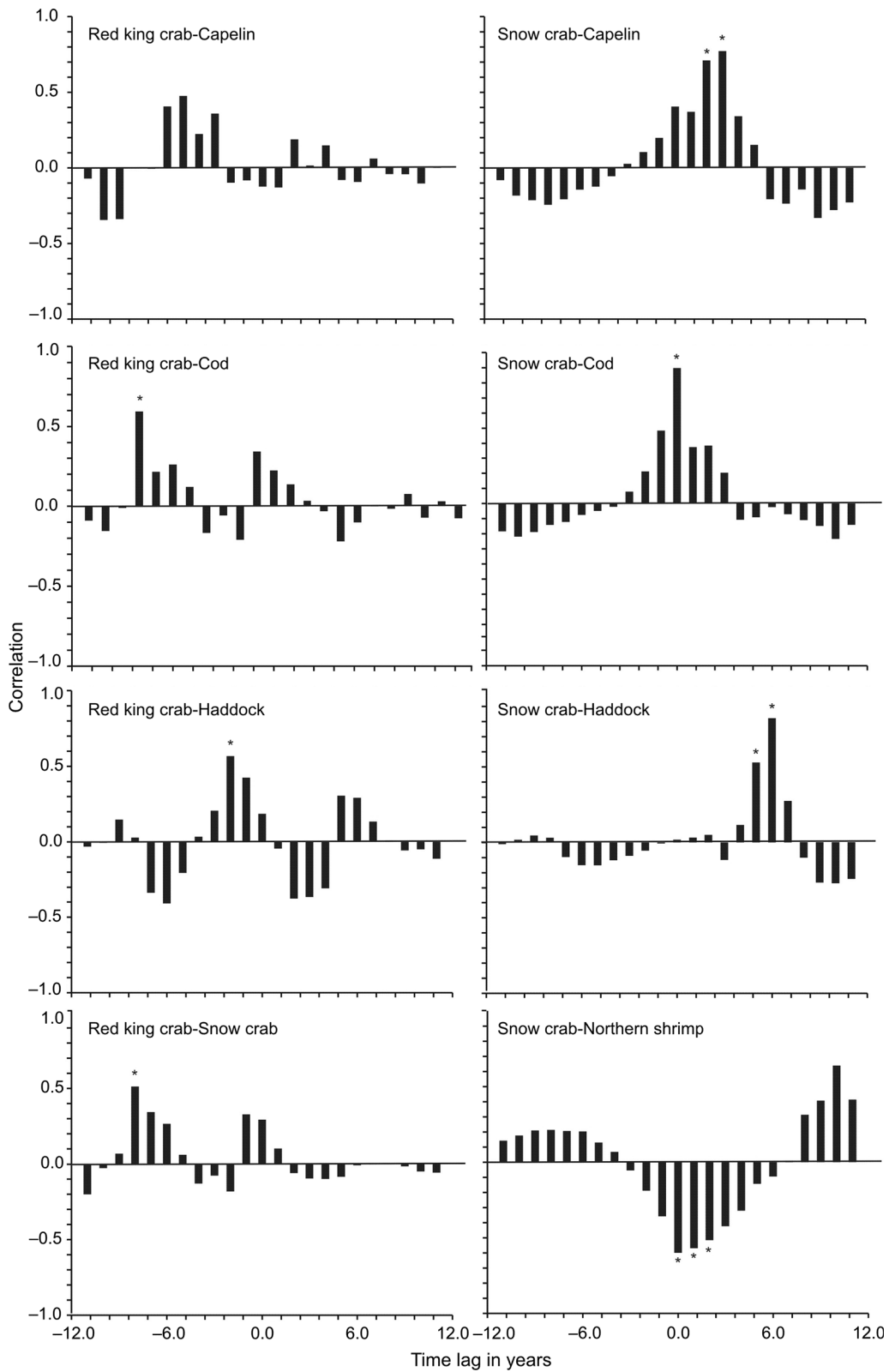
Canonical correlation analysis was undertaken to assess the association of environmental conditions

together with abundance time series of introduced crabs on the abundance characteristics of commercial fish species and showed no associations between the crab and fish abundances. The species–environment correlation for the CCA first axis was 0.72 and the cumulative explained variance for the species–environmental relationship was 89.9 %; when adding the second axis this improved to 99.6 % (Fig. 8). Only one environmental variable (mean annual temperature anomaly in the Kola section) from the four characteristics included in the analysis was significant (Table 4).

Discussion

Our analysis of the available data on dynamics of water temperature, temperature anomalies, and ice conditions in the Barents Sea has shown some oscillations. The most recent warming of the Barents Sea began in the late 1980s and continued until mid-2000. In subsequent years, sea temperatures have been decreasing while the ice cover has increased, indicating a cooling tendency in the Barents Sea. Temperature conditions are known to be key features affecting the productivity of the area and the fishery potential of marine ecosystems (Matishov et al. 2012). The last decade appears to be a favorable period for both native and introduced species.

The size of the total red king crab stock varied significantly with a peak in 2003, followed by a gradual decrease of both total and commercial stocks over the next 7 years. Several reasons could be proposed to explain the observed oscillations. First, the Barents Sea red king crab, as an invader, could dramatically reduce its own food resources, which could lead to a decrease in the number of crabs. Some authors have shown that red king crabs, especially in high density aggregations, are able to reduce the abundance of benthic organisms (Pavlova 2008). Second, changes in oceanographic conditions could lead to a shift in red king crab distribution and its abundance as well. For example, in 2005–2008, an increase in water temperature due to a high advection of heat with warm currents of Atlantic origin led to crab migration and changes in their distribution. Third, illegal fishing could lead to a strong decline in the red king crab stock (Dvoretzky and Dvoretzky 2009d). The number of illegally caught red king crabs is



◀ **Fig. 7** Cross-correlation between the abundances of red king crabs and snow crabs and the abundances of commercially important species in the Barents Sea. Asterisks show significant correlations ($p < 0.05$)

considered to be higher than the TAC (Dvoretzky and Dvoretzky 2014a). A long-term study conducted by MMBI scientists in Dalnezelenetskaya Bay (Dvoretzky and Dvoretzky 2013b) supports the patterns mentioned above especially illegal fishing. The total number of red king crabs at this coastal site was relatively stable over the period 2002–2007, with some fluctuations caused by mass recruitment in 2006 that was preceded by the large proportion of females in 2005. Recruitment was also high in 2002 and 2007. In 2008, we observed a decline of the total stock of red king crabs (Dvoretzky and Dvoretzky 2013b). This decline corresponds to a decrease in the stock of red king crabs in coastal waters of the Barents Sea. Furthermore, in 2009 we observed a higher crab stock

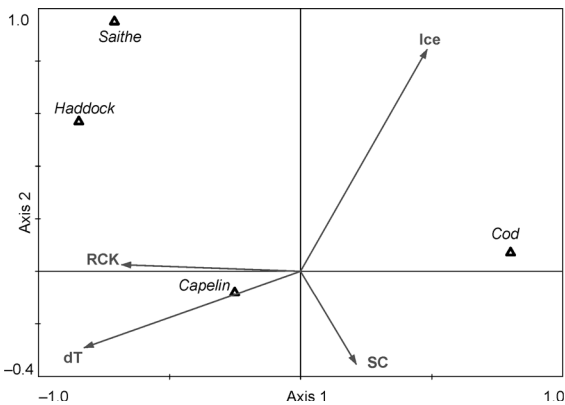


Fig. 8 CCA biplot for fish taxa abundance and environmental variables. Scores of overall environmental characteristics (dT—mean annual temperature anomaly in the Kola section, Ice—mean annual anomaly of sea ice cover in the Barents Sea, RCK—red king crab total abundance and SC—snow crab total abundance) and species in the plane of the first two axes of the CCA ordination are shown

Table 4 Ranking of environmental characteristics (dT—mean annual temperature anomaly in the Kola section, Ice—mean annual anomaly of sea ice cover in the Barents Sea, RCK—red

Environmental variable	F	p value	Explained variation %
dT	3.75	0.016	8
RCK	1.23	0.310	2
Ice	0.81	0.484	1
SC	0.27	0.808	0

than in 2008, although its value was lower than in the previous period 2002–2007. This increase could be a result of a ban on red king fishing from January until September 2009. Therefore, in general, the decline in red king crab abundance could be associated with illegal fishing that led to a decrease of the total number of crabs in coastal waters of the Barents Sea in 2008. The suggested high level of illegal fishing is supported by observations of red king crabs with fragments of forbidden gears (Dvoretzky and Dvoretzky 2013b). Similar trends were also observed for the Norwegian red king crab: a clear decline of commercial males was associated with illegal fishing and high exploitation rates (Hjelset 2014a).

In the Russian part of the Barents Sea, the near coastal zone has been closed to crab fishing since 2008. Fishing pressure on the crab population has been reduced. As a result an increase in the size of the commercial stock has been recorded over the last 3 years in the Russian Economic Zone under the conditions of relatively low levels of exploitation. The recovery of the population is confirmed by relatively high numbers of pre-recruits in 2010–2012 (Bakanev and Pinchukov 2014).

A new population of snow crabs in the Barents Sea has been recently established. In the first phase, only a few observations of this crab were recorded, but the total biomass of commercial snow crabs has exponentially increased. The impact of this introduced species both on the bottom communities and on ecosystem functions is poorly understood (Hjelset 2014b).

Both visual (Table 5) and cross-correlation data analyses did not reveal any negative associations between red king crab and shrimp fluctuations. The negative correlations between biomass of snow crabs and shrimp may also be explained by predator–prey interactions. The weight fraction of *P. borealis* in the stomachs of Barents Sea snow crabs was 6.9 %; i.e.,

king crab total abundance and SC—snow crab total abundance) that significantly (999 Monte Carlo permutations in CCA, $p < 0.05$) influenced distribution of fish taxa in the Barents Sea

Table 5 Biological features for commercial species and their overlaps with red king crab (RKC) and snow crab (SC) in the Barents Sea (adapted from Berenboim 1992, Rose 2005 and Olsen et al. 2010)

Species	Environmental limits					
	Depth range (m)	Feeding temperature range (°C)	Spawning period (months)	Spawning depth range (m)	Spawning temperatures (°C)	Spawning salinity (psu)
Northern shrimp	200–400	-1...+6	7–9	200–300	+0.7...+3.3	35+
Cod	10–500	-1...+10	3–7	40–350	-0.5...+6	33–35
Haddock	80–300	+4...+8	1–7	80–150	+6...+7	35–35.2
Saithe	150–200	+3...+10	11–2	100–200	+7...+8	35.2+
Capelin	10–250	-1...+2	3–4	10–100	+1.5...+6.5	32–34.6

Species	Overlap with introduced crabs					
	Spawning area		Larvae distribution		Juvenile and adult distribution	
	RKC	SC	RKC	SC	RKC	SC
Northern shrimp	–	+	–	+	–	+
Cod	+	–	+	–	+	+
Haddock	–	–	+	–	+	–
Saithe	–	–	–	–	+	–
Capelin	+	–	+	–	+	+

the shrimp is not a dominant food item of snow crabs (Pavlov 2007). In comparison to fish species, the alien snow crab has a negligible effect on shrimp. In addition, shrimp were only caught in areas where bottom temperatures were above 0 °C. Highest shrimp densities were observed between zero and 4 °C, while the limit of their upper temperature preference appears to lie at about 6–8 °C. The warming of the western Barents Sea coincides with the shift in shrimp distribution eastward, thus temperature is probably a factor in explaining this change in spatial distribution and biomass (Hvingel and Thangstad 2012).

In the last decade the total stock size of cod was high. The dynamics in stock numbers by age are driven by changes in recruitment and mortality, and the historical variation in total stock numbers is linked to these two factors. When fishing mortality is high, few fish survive until old age and the stock is dominated by young fish. High mortality may reduce the spawning stock to a level where recruitment is impaired and thus causes a stock collapse. The low recruitment in most of the 1980s may have been caused by the low spawning stock in that period (Yaragina et al. 2011). While reduced recruitment tends to be associated with low stock size, reduced growth and increased natural mortality may reduce production when stocks are very high. These effects

have not been well quantified for the Northeast Arctic cod, since there are no data for extremely low and extremely high stock size (Yaragina et al. 2011). In the last decade, reported catches have been increasing. Similar positive tendencies were reported for other commercially important fish species, while saithe catches have been relatively stable.

A literature survey analysis showed that the youngest stages of haddock have no overlap with either crab species in terms of diet (Pavlova 2008). Older specimens could compete for food with red king crab and the largest dietary overlap was found between red king crab and haddock. However, small recently molted crabs with soft shells could be a main food item for the cod at the coastal sites. Cross-correlation analyses found no negative associations between time series of the red king crab and fish abundance. These findings suggest that red king crab did not negatively affect the stocks of important fish species. Positive correlations found between abundances of red king crabs and cod and haddock had large time lags and more likely had low importance. In addition, these correlations were positive and do not support the prediction that red king crab could significantly affect stocks of commercially important fish due to competition for food, as has been hypothesized by some authors (Pavlova 2008; Falk-Petersen et al. 2011).

The results of cross-correlation analyses suggest that the introduction of snow crab had no negative impact on fish populations because all significant correlations were positive. Snow crab, as an Arctic species, have limited overlap with the fish species examined in the analysis and top-down effects have low significance, however, the possibility of some negative effects on snow crabs could not be rejected. Snow crabs in the size range of 3–30 mm CW are particularly vulnerable to predation, as are soft-shelled crabs in the molting season (Orensanz et al. 2004). During the 1980s–1990s, at the start of a warm climatic phase (Drinkwater 2009; Matishov et al. 2012), principal cod migration routes began to change. During the abnormally warm period of 2004–2006, migrations were directed both east and north and their distribution overlapped with snow crab area. Despite this, the lack of spatial overlap (Table 5) and the limited opportunity for trophic interactions with most of the fish species, except at the edges of the snow crab range, explains the absence of negative correlations between the snow crab abundance and fish stocks.

Though capelin is a relatively small species, it is considered a key forage species in the Barents Sea ecosystem. Both the spatial distribution and abundance indices of the stock show great variations. During the last decade there has been a general expansion of its distribution area and a northward shift of the high-concentration areas, which some authors relate to the high temperatures and low ice cover observed in the northern Barents Sea during the period (Gjøsæter 1998). The monitored history of capelin stock size is characterized by three stock collapses, in 1985–1989, 1993–1997, and 2003–2006 (Gjøsæter et al. 2011). Some authors have attributed the latest collapse to the increased stock of the red king crab. Falk-Petersen et al. (2011) proposed that crab predation on capelin eggs could negatively impact the fish population. In years of small capelin populations, the impact of egg predation could have population-level consequences if capelin spawn in areas with high densities of red king crab. However, Anisimova et al. (2005) estimated that in 2001, a year of heavy predation by crabs on capelin eggs, the crab consumed just 0.03 % of the eggs and concluded that egg predation did not represent a threat to the capelin population. The results of our cross-correlation analysis support this finding. Moreover, based on indirect knowledge of stock dynamics in the Barents

Sea, there are many reasons to believe that capelin stock size fluctuations are functions of the ecological processes in the area, and should be regarded more as natural perturbations (climate impacts) than as anthropogenic instability in the ecosystem or the impact of red king crabs. The same conclusion holds for snow crab as well.

Recent studies have shown that ocean temperature and ice cover set the large-scale limits on capelin distribution (Gjøsæter et al. 2011; Ingvaldsen and Gjøsæter 2013). There is strong evidence that the intensive exploitation of capelin has extended the severity and length of periods when the capelin stock has been at low levels (Gjøsæter et al. 2011). In general, there is little evidence that either introduced crab species affected the abundances of major fish species in the Barents Sea. This conclusion is supported by the results of the CCA test. We found that only temperature conditions contributed significantly to the year-to-year variation in abundance of four main fish taxa explaining 8 % of the variation. According to the CCA other environmental characteristics including total abundance of commercial crabs did not affect interannual fluctuations of fish abundances suggesting that the two invasive species had no discernable impact on the total stock of capelin, cod, haddock, and saithe. In general, the effects of changes in temperature conditions on fish stocks are well known. Climate-driven changes in fish populations may result from several often interlinked mechanisms: (a) a physiological response to changes in environmental parameters, such as temperature, (b) a behavioural response, such as avoiding unfavourable conditions and moving into new suitable areas, (c) population dynamics, through changes in the balance between rates of mortality, growth, and reproduction in combination with dispersal, which could result in the establishment of new populations in new areas, or abandonment of traditional sites, (d) ecosystem level changes in productivity and/or trophic interactions (Rijnsdorp et al. 2009). Similarly to many other fisheries, the cod, haddock, saithe and capelin fisheries in the Barents Sea area also closely linked to seasonal and interannual variations in temperature conditions affecting their spawning, abundance and migrations (Roderfeld et al. 2008; Matishov et al. 2012).

Therefore, we conclude that on balance the successful establishment of red king crab in the Barents

Sea has not adversely affected major fish stocks while resulting in positive economic benefits. According to Eurostat (<http://appsso.eurostat.ec.europa.eu>) the total income from the sale of red king crabs landed in Norway were €18.55 million and €15.65 million in 2011 and 2012, respectively. Official data for the crabs landed in Russian waters of the Barents Sea are not available. Using the catch data for 2012 and 2013 (5209 and 5531 t, respectively) and prices of crabs (leg sections) in the Russian market (€30.1 and €31.8 per kg), we estimate that the minimal economic benefit of red king crab could be as high as €100.2 million and €125.2 million or \$128.7 million and \$166.4 million in 2012 and 2013, respectively. Similarly, using the prices for snow crabs from the Far East, we calculated that the processed 1000 t of *C. opilio* (TAC for 2014 season) could lead an income of approximately €2.6 million. Our results, however, do not rule out negative effects on other parts of the ecosystem and, in the particular case of snow crab, the ecosystem may not yet have adjusted to the introduction of a new species that is still increasing exponentially.

Acknowledgments The English text of paper and its readability was greatly improved thanks to careful editing and valuable remarks of Jeffrey Muehlbauer. Franz Mueter, Gretta Pecl and an anonymous referee provided valuable suggestions to improve the manuscript. This study was supported by the projects of the Russian Academy of Sciences: “Development of theoretical basis of the rational use of red king crab stock and its aquaculture in the Barents Sea” (No 01.20.0405070), “Red king crab in the Barents Sea ecosystem: a role of the invader in the bottom communities and in the coastal biological production” (No 01.2010.57396), and “Monitoring the status and population dynamics of red king crab in the coastal Barents Sea”. Financial support was also received from the Russian President Grant “The biology of Arctic crustaceans in relation to climatic fluctuations” (MK–52.2014.4).

References

- Agnalt A-L, Pavlov V, Jørstad KE, Farestveit E, Sundet J (2011) The snow crab, *Chionoecetes opilio* (Decapoda, Majoidea, Oregoniidae) in the Barents Sea. In: Galil BS, Clark PF, Carlton JT (eds) In the wrong place—alien marine crustaceans: distribution, biology and impacts. Springer, Heidelberg, pp 283–300
- Anisimova N, Berenboim B, Gerasimova O, Manushin I, Pinchukov M (2005) On the effect of red king crab on some components of the Barents Sea ecosystem. Ecosystem dynamics and optimal long-term harvest in the Barents Sea fisheries. In: Proceedings of the 11th Russian—Norwegian Symposium, Murmansk, Russia. IMR/PINRO Joint Report Series, 2005/2:298–306
- Anon (2011) Survey report from the joint Norwegian/Russian ecosystem survey in the Barents Sea August–October 2011. IMR/PINRO Joint Report Series, No. 3/2011. Institute of Marine Research, Bergen
- Bakanev SV, Pinchukov MA (2014) Red king crab. In: Shampray EM (ed) Current state of marine biological resources of the Barents Sea and North Atlantic in 2014. PINRO Press, Murmansk, pp 40–42 (in Russian)
- Berenboim BL (1992) Northern shrimp *Pandalus borealis* Krøyer in the Barents Sea (biology and fishery). Preprint. PINRO Press, Murmansk (in Russian)
- Bergstad O, Jørgensen T, Dragesund O (1987) Life history and ecology of the gadoid resources of the Barents Sea. Fish Res 5(2–3):119–161
- Bogstad B, Haug T, Mehl S (2000) Who eats whom in the Barents Sea. NAMMCO Sci Publ 2:98–119
- Carmack E, Barber D, Christensen J, Macdonald R, Rudels B, Sakshaug E (2006) Climate variability and physical forcing of the food webs and the carbon budget on panarctic shelves. Progr Oceanogr 71:145–181
- Dalpadado P, Bogstad B (2004) Diet of juvenile cod (age 0–2) in the Barents Sea in relation to food availability and cod growth. Polar Biol 27:140–154
- Dalpadado P, Bogstad B, Gjøsæter H, Mehl S, Skjoldal HR (2002) Zooplankton–fish interactions in the Barents Sea. In: Sherman K, Skjoldal HR (eds) Large marine ecosystems of the North Atlantic. Changing states and sustainability. Elsevier Science B.V., Amsterdam, pp 269–291
- Donaldson WE, Byersdorfer SE (2005) Biological Field techniques for Lithodid crabs. Alaska Sea Grant College Program, University of Alaska, Fairbanks
- Drinkwater K (2009) Comparison of the response of Atlantic cod (*Gadus morhua*) in the high-latitude regions of the North Atlantic during the warm periods of the 1920s–1960s and the 1990s–2000s. Deep Sea Res II 56:2087–2096
- Dvoretzky AG, Dvoretzky VG (2008) Epifauna associated with the northern stone crab *Lithodes maia* in the Barents Sea. Polar Biol 31:1149–1152
- Dvoretzky AG, Dvoretzky VG (2009a) Some aspects of the biology of the amphipods *Ischyrocerus anguipes* associated with the red king crab, *Paralithodes camtschaticus*, in the Barents Sea. Polar Biol 32:463–469
- Dvoretzky AG, Dvoretzky VG (2009b) Distribution of amphipods *Ischyrocerus* on the red king crab, *Paralithodes camtschaticus*: possible interactions with the host in the Barents Sea. Estuar Coast Shelf Sci 82:390–396
- Dvoretzky AG, Dvoretzky VG (2009c) Fouling community of the red king crab, *Paralithodes camtschaticus* (Tilesius 1815), in a subarctic fjord of the Barents Sea. Polar Biol 32:1047–1054
- Dvoretzky AG, Dvoretzky VG (2009d) Limb autotomy patterns in *Paralithodes camtschaticus* (Tilesius, 1815), an invasive crab, in the coastal Barents Sea. J Exp Mar Biol Ecol 377:20–27
- Dvoretzky AG, Dvoretzky VG (2010a) Epifauna associated with an introduced crab in the Barents Sea: a 5-year study. ICES J Mar Sci 67:204–214
- Dvoretzky AG, Dvoretzky VG (2010b) The amphipod *Ischyrocerus commensalis* on the eggs of the red king crab *Paralithodes camtschaticus*: egg predator or scavenger? Aquaculture 298:185–189

- Dvoretzky AG, Dvoretzky VG (2010c) Hemolymph molting hormone concentrations in red king crabs from the Barents Sea. *Polar Biol* 33:1293–1298
- Dvoretzky AG, Dvoretzky VG (2011) Population biology of *Ischyrocerus commensalis*, a crab-associated amphipod, in the southern Barents Sea: a multi-annual summer study. *Mar Ecol* 32:498–508
- Dvoretzky AG, Dvoretzky VG (2012) Does spine removal affect molting process in the king red crab (*Paralithodes camtschaticus*) in the Barents Sea? *Aquaculture* 326–329:173–177
- Dvoretzky AG, Dvoretzky VG (2013a) Copepods associated with the red king crab *Paralithodes camtschaticus* (Tilesius, 1815) in the Barents Sea. *Zool Stud* 52:17
- Dvoretzky AG, Dvoretzky VG (2013b) Population dynamics of the invasive lithodid crab, *Paralithodes camtschaticus*, in a typical bay of the Barents Sea. *ICES J Mar Sci* 70:1255–1262
- Dvoretzky VG, Dvoretzky AG (2013c) Epiplankton in the Barents sea: summer variations of mesozooplankton biomass, community structure and diversity. *Conti Shelf Res* 52:1–11
- Dvoretzky AG, Dvoretzky VG (2014a) Red king crab in Russia: populations, fisheries, and symbionts. In: Stevens BG (ed) *King crabs of the World: biology and fisheries management*. CRC Press (Taylor & Francis Group), Boca Raton, pp 501–518
- Dvoretzky AG, Dvoretzky VG (2014b) Size-at-age of juvenile red king crab (*Paralithodes camtschaticus*) in the coastal Barents Sea. *Cah Biol Mar* 55:43–48
- Dvoretzky AG, Dvoretzky VG (2015) Size at maturity of female red king crab, *Paralithodes camtschaticus*, from the coastal zone of Kola Peninsula (southern Barents Sea). *Cah Biol Mar* 56:49–54
- Falk-Petersen J, Renaud P, Anisimova N (2011) Establishment and ecosystem effects of the alien invasive red king crab (*Paralithodes camtschaticus*) in the Barents Sea—a review. *ICES J Mar Sci* 68:479–488
- Gjørøseter H (1998) The population biology and exploitation of capelin (*Mallotus villosus*) in the Barents Sea. *Sarsia* 83:453–497
- Gjørøseter H, Bogstad B, Tjelmeland S (2009) Ecosystem effects of the three capelin stock collapses in the Barents Sea. *Mar Biol Res* 5:40–53
- Gjørøseter H, Ushakov NG, Prozorkevich DV (2011) Capelin. In: Jakobsen T, Ozhigin VK (eds) *The Barents Sea ecosystem, resources, management*. Tapir Academic Press, Trondheim, pp 201–214
- Goryanina SV, Bakanev SV, Pavlov VA (2013) PINRO data explained a TAC of the snow crab for correcting its landing in 2014. Additional data for total allowable catch of water biological resources in fishing areas in inland seas of the Russian Federation, on the continental shelf of the Russian Federation, in Exclusive economical zone of the Russian Federation, in the Azov and Caspian Seas. http://www.vniro.ru/pages/odu_correct/dop_2014_strigun_opilio_bar.pdf. Accessed 12 May 2014 (in Russian)
- Hjelset AM (2014a) Fishery-induced changes in Norwegian red king crab (*Paralithodes camtschaticus*) reproductive potential. *ICES J Mar Sci* 71:365–373
- Hjelset AM (2014b) Report from the workshop: Workshop on king- and snow crabs in the Barents Sea, Tromsø, 11–12 March 2014. https://www.imr.no/filarkiv/2014/05/hirapp_18-2014_king_and_snow_til_web.pdf/nb-no
- Hvingel C, Berenboim BL (2011) Northern shrimp. In: Jakobsen T, Ozhigin VK (eds) *The Barents Sea ecosystem, resources, management*. Tapir Academic Press, Trondheim, pp 172–185
- Hvingel C, Kingsley MCS (2006) A framework to model shrimp (*Pandalus borealis*) stock dynamics and quantify risk associated with alternative management options, using Bayesian methods. *ICES J Mar Sci* 63:68–82
- Hvingel C, Thangstad T (2010) Catch, effort and derived biomass and mortality indices from the Norwegian fishery for northern shrimp (*Pandalus borealis*) in the Barents Sea and round Svalbard. NAFO SCR Doc 10/55. Serial no. N5846:1–14
- Hvingel C, Thangstad T (2012). Research survey information regarding northern shrimp (*Pandalus borealis*) in the Barents Sea and Svalbard area 2004–2012. NAFO SCR Doc 12/50. Serial no. N6112:1–13
- ICES (2008) Report of the Arctic Fisheries Working Group. ICES Document CM/ACOM:1
- ICES (2013) Report of the Arctic Fisheries Working Group (AFWG), 18–24 April 2013, ICES Headquarters, Copenhagen. ICES CM 2013/ACOM:05
- Ingvaldsen RB, Gjørøseter H (2013) Responses in spatial distribution of Barents Sea capelin to changes in stock size, ocean temperature and ice cover. *Mar Biol Res* 9:867–877
- Jadamec LS, Donaldson WE, Cullenberg P (1999) Biological field techniques for *Chionoecetes* crabs. Alaska Sea Grant College Program, Fairbanks
- Johannesen E, Ingvaldsen RB, Bogstad B, Dalpadado P, Eriksen E, Gjørøseter H, Knutsen T, Skern-Mauritzen M, Stiansen JE (2012) Changes in Barents Sea ecosystem state, 1970–2009: climate fluctuations, human impact, and trophic interactions. *ICES J Mar Sci* 69:880–889
- Karsakov AL, Pinchukov MA (2009) Distribution and habitat conditions of red king crab in Russian waters of the Barents Sea. *Probl Fish Oceanogr* 6(1):150–163 (in Russian)
- Kuzmin SA (2001) Red king crab. In: Shibanov VN (ed) *Current state of marine biological resources of the Barents Sea and North Atlantic in 2001*. PINRO Press, Murmansk, pp 34–35 (in Russian)
- Kuzmin SA, Gudimova EN (2002) Introduction of the Kamchatka (red king) crab in the Barents Sea. Peculiarities of biology, perspectives of fishery. KSC RAS, Apatity (in Russian)
- Kuzmin SA, Akhtarina SM, Menis DT (1999) The first findings of the snow crab *Chionoecetes opilio* (Decapoda, Majiidae) in the Barents Sea. *Can Transl Fish Aquat Sci* 5667:1–5
- Loeng H (1991) Features of the physical oceanography of the Barents Sea. *Polar Res* 10:5–18
- Loeng H, Drinkwater K (2007) An overview of the ecosystems of the Barents and Norwegian Seas and their response to climate variability. *Deep Sea Res II* 54:2478–2500
- Matishov GG, Dzhenyuk SL, Denisov VV, Zhichkin AP, Moiseev DV (2012) Climate and oceanographic processes in the Barents Sea. *Ber Polarforsch* 640:63–73
- Mehl S (2005) Stomach analyses of Northeast Arctic saithe sampled during the saithe survey Varanger-More 1998–2003. Preliminary results. Working document no. 7 to the Arctic Fisheries Working Group, 19–28 April 2005

- Mehl S, Zuykova NV, Drevetnyak KV (2011) Saithe. In: Jakobsen T, Ozhigin VK (eds) The Barents Sea ecosystem, resources, management. Tapir Academic Press, Trondheim, pp 281–291
- Mironova NV (1961) Migrations, concentration composition and feeding of saithe (*Pollachius virens* L.) in the Barents Sea. In: Anon (ed) Hydrological and biological features of murman coastal waters. USSR Academy of Sciences, Murmansk, pp 59–90 (in Russian)
- Nedreaas K (1985) Food and feeding of young saithe, *Pollachius virens* (L.), on the coast of Western Norway. ICES Document CM 1985/G:22
- Olsen E, Aanes S, Mehl S, Holst JC, Aglen A, Gjørseter H (2010) Cod, haddock, saithe, herring, and capelin in the Barents Sea and adjacent waters: a review of the biological value of the area. ICES J Mar Sci 67:87–101
- Orensanz J, Ernst B, Armstrong DA, Stabeno P, Livingston P (2004) Contraction of the geographic range of distribution of snow crab (*Chionoecetes opilio*) in the eastern Bering Sea: and environmental ratchet? CalCOFI Rep 45:65–79
- Ozhigin VK, Ingvaldsen RB, Loeng H, Boitsov VD, Karsakov AL (2011) Introduction to the Barents Sea. In: Jakobsen T, Ozhigin VK (eds) The Barents Sea ecosystem, resources, management. Tapir Academic Press, Trondheim, pp 39–76
- Pavlov VA (2007) Feeding of the snow crab *Chionoecetes opilio* (Fabricius, 1788) in the Barents Sea. VNIRO Proc 147:226–229 (in Russian with English abstract)
- Pavlov VA, Sundet JH (2011) Snow crab. In: Jakobsen T, Ozhigin VK (eds) The Barents Sea ecosystem, resources, management. Tapir Academic Press, Trondheim, pp 168–171
- Pavlova LV (2008) Red king crab trophic relations and its influence on bottom biocenoses. In: Matishov GG (ed) Biology and physiology of the red king crab from the coastal zone of the Barents Sea. KSC RAS Press, Apatity, pp 77–104 (in Russian)
- Pinchukov MA (2008) Red king crab. In: Lepesevich YM (ed) Current state of marine biological resources of the Barents Sea and North Atlantic in 2008. PINRO Press, Murmansk, pp 46–50 (in Russian)
- Pinchukov MA, Bakanev SV, Pavlov VA (2012) In: Lepesevich YM (ed) Current state of marine biological resources of the Barents Sea and North Atlantic in 2012. PINRO Press, Murmansk, pp. 47–50 (in Russian)
- Rijnsdorp AD, Peck MA, Engelhard GH, Möllmann C, Pinnegar JK (2009) Resolving the effect of climate change on fish populations. ICES J Mar Sci 66:1570–1583
- Rist FT (2005) Diet of cod, haddock and saithe related to the capelin spawning migration. Cand. Scient. Thesis, Department of Fisheries and Marine Biology, University of Bergen, Norway, December 2005
- Roderfeld H, Blyth E, Dankers R, Huse G, Slagstad D, Ellingsen I, Wolf A, Lange MA (2008) Potential impact of climate change on ecosystems of the Barents Sea Region. Clim Change 87:283–303
- Rose GA (2005) On distributional responses of North Atlantic fish to climate change. ICES J Mar Sci 62:1360–1374
- Russkikh AA, Dingsør GE (2011) Haddock. In: Jakobsen T, Ozhigin VK (eds) The Barents Sea ecosystem, resources, management. Tapir Academic Press, Trondheim, pp 271–280
- Sakshaug E (2004) Primary and secondary production in the Arctic Seas. In: Stein R, Macdonald RW (eds) The organic carbon cycle in the Arctic Ocean. Springer, Berlin, pp 57–81
- Sakshaug E, Johnsen G, Kovacs K (eds) (2009) Ecosystem Barents Sea. Tapir Academic Press, Trondheim
- Shamray EA (ed) (2013) Current state of biological resources of the Barents Sea and North Atlantic in 2013. PINRO Press, Murmansk (in Russian)
- Stensholt BK, Aglen A, Mehl S, Stensholt E (2002) Vertical density distributions of fish, a balance between environmental and physiological limitation. ICES J Mar Sci 59:679–710
- ter Braak CJF, Smilauer P (2002) CANOCO reference manual and CanoDraw for Windows user's guide: software for Canonical Community Ordination (version 4.5). Microcomputer Power, Ithaca, NY, USA
- Tretyak VL (1984) A method of estimating the natural mortality rates offish at different ages (exemplified by the Arcto-Norwegian cod stock). In: Godø OR, Tilseth S (eds) Reproduction and Recruitment of Arctic cod. In: The Proceedings of the Soviet-Norwegian Symposium, Leningrad, 26–30 September 1983. Institute of Marine Research, Bergen, pp 241–274
- Tretyak VL (2000) Modeling of age-dependent instantaneous coefficients of natural mortality for Northeast Arctic cod. ICES Document CM 2000/V:09
- Wassmann P, Reigstad M, Haug T, Rudels B, Carroll ML, Hop H, Gabrielsen GW, Falk-Petersen S, Denisenko SG, Arashkevich E, Slagstad D, Pavlova O (2006) Food webs and carbon flux in the Barents Sea. Progr Oceanogr 71:232–287
- Yaragina NA, Aglen A, Sokolov KM (2011) Cod. In: Jakobsen T, Ozhigin VK (eds) The Barents Sea ecosystem, resources, management. Tapir Academic Press, Trondheim, pp 225–270
- Zakharov DV, Lyubin PA (2012) Results of Russian investigations of the northern shrimp in the Barents Sea in 2004–2012. NAFO SCR Doc. 12/60. Serial no. N6112:1–5